The Biology of Decapod Crustacean Larvae

Book · January 2001

CITATIONS
332

READS
3,903

1 author:

Klaus Anger
Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research
217 PUBLICATIONS **7,498** CITATIONS

SEE PROFILE

The Biology of Decapod Crustacean Larvae

Klaus Anger
Biologische Anstalt Helgoland, Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung, 27498 Helgoland, Germany

ABSTRACT: About 90% of the extant species of the Decapoda live in oceans and adjacent coastal and estuarine regions, and most of them pass through a complex life history comprising a benthic (juvenile-adult) and a planktonic (larval) phase. The larvae show a wide array of adaptations to the pelagic environment, including modifications in functional morphology, anatomy, the molting cycle, nutrition, growth, chemical composition, metabolism, energy partitioning, ecology, and behavior. Due to these adaptive traits, which are the principal subject of this volume, decapod larvae are more like unrelated holoplanktonic organisms rather than resembling the conspecific benthic juveniles and adults. Emphasis is here on the lesser known anatomical, bioenergetic, and ecophysiological aspects of larval life, because morphology has already extensively been documented in the literature. Changes in biological parameters (e.g. rates of feeding, growth, metabolism) are shown in successive developmental stages, within individual stages, and as repsonses to environmental factors. Particular attention is paid to interrelationships between intrinsic phenomena (molting cycle, organogenesis, growth) and the overlaying effects of extrinsic factors (e.g. food, temperature, salinity, pollution). Concluding from the available data, we may identify major bias and gaps in our present knowledge of larval biology. For instance, biochemical, physiological, and anatomical aspects have been investigated much less than larval morphology, ecology, and behavior, and bioenergetic parameters have largely been studied as isolated physiological traits rather than attempting to quantify the overall partitioning of chemical energy. Little is known also about intraspecific variability within or between separate populations. This remains a major challenge for larval biologist, because knowledge of phenotypic plasticity and genetical divergence, e.g. in larval morphology or stress tolerance, is of utmost importance for the understanding of evolutionary adaptation and speciation. In particular, early ontogenetic adaptations to extreme or unpredictable ecological conditions are important in the evolutionary transitions from marine to limnic or terrestrial environments. We also need more comparisons between field and laboratory observations in order to "calibrate" data from the field with those obtained under controlled conditions; inversely, those comparisons should help to identify "domestication effects" and other artifacts that are potentially pertinent to laboratory data. Furthermore, future research should increasingly consider effects which persist through successive life-history phases, e.g. those of embryonic acclimatization on larval stress tolerance, or the significance of larval condition for later settlement and recruitment success.

TABLE OF CONTENTS

PREFACE AND ACKNOWLEDGEMENTS

They have just started to live a life of their own, apparently incomplete and fragile – yet they are perfectly adapted to their environment. Larvae are fascinating animals! This is what I wish to demonstrate with this book, first of all, to researchers, students, and visitors of the multidisciplinary, rapidly growing field of larval biology, especially to those who are interested in the Decapoda as one of the major crustacean taxa. Among the potential "visitors" to this publication, there are thousands of biologist world-wide who study adult crustaceans and may wish to find an introduction, or some specific information, on the ontogeny of the particular traits they are investigating. Also among the biologists working on larval Decapoda, our rapidly increasing specialization renders it more and more difficult to overlook the various aspects of larval life such as morphology, anatomy, physiology, biochemistry, ecology, behavior, etc. It is thus another principal purpose of this synopsis to help broaden our views towards other disciplines, for instance by means of reviewing morphology for physiologists, biochemistry for ecologists, and so on. Many aspects of larval bology, in particular the ecological and behavioral features that are associated with feeding, predator avoidance, or mechanisms of dispersal and recruitment, are similar between larval decapods and other plankton, including fish larvae. Hence, some of the information collated here may be useful also for non-crustacean "larvologists" and for other planktologists, especially for those looking for universal patterns that may have been selected for in the pelagic environment, in general. Some of these common patterns are considered as adaptive traits that may be associated with life-history strategies, for instance larval export from estuaries, or bet-hedging strategies in habitats with unpredictable conditions. These aspects of larval life may thus provide comparative information for theoretical considerations of life-history evolution. In summary, the approach of this book is essentially multidisciplinary, attempting to promote an integrated view of the biology of larval Decapoda and other taxa.

I am greatly indebted to various persons who have encouraged and supported this work. First of all, I would like to thank the series editors, Professors R. Vonk and F.R. Schram from the University of Amsterdam, as well as the publishers, who took the risk of a novel "experiment" with uncertain outcome: the production of the first single-authored volume of the Crustacean Issues – with an author who had never written a book before. Thank you all for your confidence and continuous encouragement and help!

Likewise, I thank all colleagues who helped me as reviewers, reading previous versions of one or more chapters and providing highly valuable comments, constructive criticism, and suggestions for improvements; in alphabetical order: G. Charmantier and M. Charmantier-Daures (Montpellier, France), P. Clark (London, UK), J.A. Cuesta (Sevilla, Spain), D.L. Felder (Lafayette, LA, USA), J.A. Freeman (Mobile, AL, USA), S. Harzsch (Ulm, Germany), R.G. Hartnoll (Port Erin, UK), T. Ikeda (Hakodate, Japan), D.A. Jones (Bangor, UK), R. Lemaitre (Washington, DC, USA), D. Lemos (São Paulo, Brazil), S.G. Morgan (Bodega Bay, CA, USA), P. Ouellet (Mont Joli, Canada), J. Paula (Lisboa, Portugal), A. Rodríguez (Cádiz, Spain), C. Rosas (Ciudad del Carmen, Mexico), F.R. Schram (Amsterdam, The Netherlands), M.R.J. Sheehy (Leicester, UK), D. Walossek (Ulm, Germany).

This book is based upon more than two decades of research on decapod crustacean larvae, including numerous contributions from graduate students and technicians. C. Püschel and U. Süsens contributed, as technicians, particularly much to our extensive data base on larval growth and chemical composition, and U. Alexander, as a librarian, as well as several students helped to collect and catalogue the fast growing literature. Thanks are also due to B. Höcker and S. Harzsch for kindly placing at my disposal several original histological and electron microscopical photographs. Throughout this extended period of investigations, many colleagues from various institutes and countries have cooperated with me in joint projects, contributing valuable data and novel ideas, and many of these have, in numerous stimulating discussions, broadened my view. In this context, I should especially mention my former PhD students, R.R. Dawirs, M. Sprung, M.M. Criales, J. Harms, J. Selzer, D. Ismael, K. Schultze, T. Luppi, K. Paschke, and L. Giménez, my "scientific grandson" S. Harzsch, and my principal South American cooperation partners of many years, M. Montú, E.D. Spivak, and G.S. Moreira, as well as their respective students. Much of the recent bibliographic information that I am reviewing here has been discovered during our work for "ZOEA". This "larval development newsletter for carcinologists" (see http://usuarios.tripod.es/Megalopa) has served since seven years as a rich source of literature and other information, and it has always been enjoyable aiding to its production, together with J.A. Cuesta, P.A. López-González, and J.I. González-Gordillo. Recently, I have learned particularly much from G. Charmantier and M. Charmantier-Daures, who have drawn my attention to another fascinating aspect of larval biology, namely the ontogeny of osmoregulation and its implications in larval ecology and life-history evolution. – I consider all these persons not only as highly esteemed colleagues but also as personal friends and, in diverse ways, as contributors to this volume.

Last but not least, I wish to cordially thank my little family for their valuable personal support which made this project feasible, namely my mother, Else Charlotte Anger, and my late father, Hans Anger, who have always encouraged and supported me on my way towards marine biology, and to Michelina and Tanja, who have patiently accompanied and helped me in many ways during the making of this book. Crustacean Issues 14 is especially dedicated to little Tanja, who loves animals – including crustaceans and their larvae – and has often missed her father while he was busy writing this volume.

1 INTRODUCTION

1.1 *The study of decapod crustacean larvae*

Outnumbered only by insects and gastropods, the 42,000 described species of the Crustacea represent one of the largest extant taxa in the animal kingdom, and hence, a major contribution to the earth's biodiversity (Bowman & Abele 1982). According to Tudge (2000), their actual species number may exceede 50,000, and *"several times more might remain to be discovered"*. The same author also says: *"As a group they are extremely ancient, dating well back into the Cambrian at least 500 million years ago, and so they have had plenty of time to evolve and radiate."* This is most conspicuous in the ca. 10,000 known species of the Decapoda. Their earliest record is the shrimp *Palaeopalaemon newberryi* from the Late Devonian (Schram et al. 1978). Since then, this taxon has evolved an impressing variety of life styles, body shapes, colours, and sizes. It comprises pelagic oceanic prawns, freshwater crabs and crayfish, tiny pea crabs living hidden inside the mantle cavity of marine clams or in polychaete tubes, lobsters with up to 60 cm body length, and giant spider crabs spanning more than 3 m between the outstretched claws. Although most of these varieties are known only by specialists, numerous others are quite familiar also to gourmets and fishermen, and thus, have a high economic value (Provenzano 1985).

The vast majority of the Decapoda is found in aquatic environments, with almost 90% living in the sea or in adjacent brackish waters (Kaestner 1980). In the course of their evolution, about 1000 species were able to invade freshwater habitats but less than 100 managed to conquer firm land (Hartnoll 1988a). Most decapods are benthic, i.e. they live on the floors of oceans, rivers and lakes, or in semiterrestrial habitats such as mangrove swamps or salt marshes. Numerous species are commercially exploited by coastal and offshore fisheries, in particular the clawed lobsters (Nephropidae), spiny lobsters (Palinuridae), slipper lobsters (Scyllaridae), large brachyuran crabs such as *Cancer, Callinectes, Chionoecetes*, *Pseudocarcinus* or *Maia*, the anomuran family of the king crabs (Lithodidae), and many species of shrimps and prawns (mostly Penaeidae, Pandalidae, Crangonidae, and Palaemonidae). An incomplete fisheries statistic for the USA (not including king crabs; Williams 1993) may serve as an example of the economic importance of decapods. The official landings comprised a total of 370,000 metric tons of crabs, shrimps and lobsters valued at almost one billion US-$ in one year. These figures are considerably enhanced when the Alaskan king crab fisheries and yields from the commercial aquaculture of prawn and crayfish species are added, and they certainly show an increasing trend in times of declining finfish industries.

The great majority of the marine and most of the terrestrial decapod species have a complex life history: instead of developing directly from the egg to an adult-like benthic juvenile, they produce pelagic larvae that may differ entirely in their morphology and habits from juvenile and adult conspecifics. Such biphasic life cycles are considered as an evolutionary old trait of most metazoans, including the Crustacea (Rieger 1994). Unlike the adults, larvae float in estuarine, coastal or oceanic currents, feeding upon coexisting plankton organisms in the water column. Such pelagic stages of bottom-dwelling species, collectively referred to as *meroplankton*, do not only link successive generations but also provide a major benthic input into the biodiversity and productivity of the world's largest and oldest biotope, the pelagic. Since planktonic larvae are, in general, exposed to quite different selective forces than their benthic parents, they show their own evolutionary adaptations, principally in locomotion and feeding. Their special behavioral traits ensure ei-

ther the retention in the parental habitat or, in other species, the transport between ontogenetically changing environments and, eventually, the return, settlement, and recruitment to the adult populations.

Both a lasting management of natural stocks and the development of commercial cultivation enterprises require thus a profound understanding not only of juvenile and adult life-history stages, but equally well of the small planktonic larvae. In spite of their obviously important role in developmental biology, recruitment and population dynamics, ecology, biogeography, genetics, and in other fields of the basic and applied sciences, our general knowledge of the larval development of crustaceans is rather poor compared with what has been published about benthic juveniles and adults. After 200 years of steadily intensifying research, much of what we presently know about decapod crustacean larvae is still restricted to their external morphology and the number of pelagic stages. In the past fourty years, however, a rapidly increasing number of studies has been produced also on larval ecology, physiology, and biochemistry, so that the ontogeny of various basic biological functions in the Decapoda is increasingly understood, and new fields of scientific research have been propagating recently.

1.2 *Brief history of a research subject*

In the following historical sketch, I cannot possibly review the vast amount of existing literature on decapod larvae. In a statistical analysis of "larval papers" published until 1989, as many as 1194 entries were recorded only for the brachyuran crabs (Rice 1993), and perhaps three times more papers may have been published further to date, when all larval decapods are considered. Hence, some of the exemplary bibliographic references in the following section may remember of milestones that have encouraged the development of new lines of research, whereas others have arbitraily been chosen as examples of various types or directions of investigation. Yet, this broad and necessarily superficial overview of past and current studies on decapod crustacean larvae should allow for embedding the following, more specific chapters of this book in a wider context. More comprehensive historical reviews have been given in several recent overviews (Williamson 1982, Ingle 1992, 1998) and, in particular, in Volume 8 (*"History of Carcinology"*) of the *"Crustacean Issues"* (Rice 1993, Williams 1993).

1.2.1 *The early era of cataloguing larval biodiversity: from "hunting and collecting" to cultivation*

In the scientific literature, one can find a variety of names of decapod crustacean larvae such as nauplius, zoea, mysis, megalopa, glaucothoe, phyllosoma, and others. Their classification is primarily based upon criteria of functional morphology, but their use is often ambiguos and illogical, or it appears to overlap (Williamson 1969, 1982). This confusing abundance of terms has historical reasons. In the late 18th and throughout the 19th century, an increasing number of both professional and amateur naturalists attempted to describe and classify plants and animals. Since these early investigators were unaware of the existence of planktonic larvae in crustaceans and other benthic invertebrates, they described and named numerous larval forms as new "genera" and "species" (Williamson 1915, Gurney 1939, 1942). Later, when science became aware of the larval nature of many of the described species, several of the originally generic names had already been established in the literature and were subsequently maintained to designate particular lar-

val forms. In the meantime, however, only a few of the originally ca. 70 names of crustacean larvae have in the scientific literature survived to modern times (Gore 1985).

The earliest known morphological account of a decapod larva is that by Leeuwenhoek (1699; published 1807); it probably shows the prezoea of the North Sea shrimp, *Crangon crangon* (Ingle 1998). Seven decades later, Linné described a crab larva as a new species, *Cancer germanus* (Linné 1767). Slabber (1778) was probably the first to correctly recognize and describe a decapod larva as such, but his observation was ignored by the developing scientific community, as was Cavolini's description of a late crab embryo that he isolated from the egg case (Cavolini 1787; translation published 1792). Thompson (1828) presented the first evidence from laboratory observations that the previously described "genera" *Zoea* (Bosc 1802) and *Megalopa* (Leach 1815) were not adult crustaceans but pelagic developmental stages of already known bottom-living crab species. In later studies, this author described further larval decapods (see e.g. Fig. 1.1), and larval morphology was soon incorporated in broader taxonomic considerations. H. Milne-Edwards (1834, 1836, 1840), for instance, placed in his three-volume encyclopedia of natural history a dromiid crab with a brachyuran-like adult morphology in the Anomura, based primarily on the anomuran-like appearance of the larvae. Similarly, Fritz Müller (1864) used in his book *"Für Darwin"* larval forms to unravel relationships and evolutionary trends in the Crustacea.

Figure 1.1. Early description of a decapod larva, *Porcellana* spec. (from Thompson 1836).

Initially, however, there was much scepticism against an existence of "metamorphosis" in crustaceans (see e.g. Westwood 1836). Doubts were primarily based on contradicting observations of a direct development in crayfish and freshwater crabs (for further references, see Ingle 1992, 1998). This controversy stimulated an increasing number of biologists to study complex life histories, and more and more pelagic larvae of decapod crustaceans and of other marine invertebrates were scientifically described. The complete course of development, however, in particular the degree of morphological change from a zoea to a megalopa, remained a matter of controverse discussion throughout the 19th century.

Until the first half of the 20th century, most researchers obtained early crustacean larvae from plankton samples or from ovigerous females kept in aquaria; later stages were normally isolated from the plankton, as laboratory-hatched and field-captured larvae could only occasionally be reared through one or a few more molts (Gurney 1939, 1942). Detailed historical reviews of the early morphological investigations on decapod larvae from

the North Atlantic Ocean and the Mediterranean Sea have recently been published by Ingle (1992, 1998). I will therefore mention here only some prominent names that are associated with the early descriptions of crustacean larvae. In an approximate order of their times, we may remember of J.V. Thompson, R.Q. Couch, H. Milne-Edwards, C.S. Bate, F. Müller, C. Claus, A. Dohrn, G.O. Sars, W. Faxon, W.K. Brooks, G. Cano, F.H. Herrick, W.T. Calman, H. Coutière, E.L. Bouvier, E. Sollaud, W.T. Calman, H.C. Williamson, K. Stephensen, H.J. Hansen, R. Santucci, R. Gurney, H. Aikawa, O.W. Hyman, and M.V. Lebour.

These early morphological descriptions were historically important, because they stimulated not only further research on larval crustaceans, but also on the plankton in general. However, most of them have in the meantime lost much of their scientific value. This is not only because they often lacked sufficient detail (Rice 1979, Clark et al. 1998). More critically, the identity of described larvae remained in many cases uncertain, as their assignment to a particular species or genus was often based on mere intuition. As recognized already by early naturalists such as, for instance, Slabber, Thompson, Couch, and Du Cane, the only solution of this problem is to obtain larvae from safely identified females and then to rear them under controlled conditions to metamorphosis. This aim, however, proved technically difficult and remained widely unsuccessful for more than one century and a half.

Although numerous rearing attempts date back to the 19th century (for references see Ingle 1998), only a few researchers succeeded before the 1950s (namely Lebour 1927, Hart 1935, Templeman 1936). One of these, M.V. Lebour, was also one of the first authors who began to surpass the purely descriptive approach. Besides morphology, she addressed questions of larval nutrition, ecology, as well as regional and seasonal distribution patterns in the plankton (Lebour 1922, 1947). Since only natural plankton organisms were at that time available as food, the early rearing experiments were hampered by variable, commonly irreproducible quality of the diet. Thus, significant progress in the laboratory cultivation of decapods had to wait until a new food source for pelagic larvae was discovered.

The most important break-through in the study of crustacean larvae became possible only when the nauplii of the brine shrimp, *Artemia*, were recognized as a suitable laboratory food source (Broad 1957a, b, Chamberlain 1957, Coffin 1958, Knudsen 1958, Forss & Coffin 1960). These are easily available, as they can be obtained after a short incubation of dry, durable cysts in seawater, they show a rather stable food quality, and are readily accepted by most decapod larvae. With the successful introduction of reproducible rearing experiments, the era of mere "hunting and collecting" materials from the field had come to an end, at least in descriptive morphological research. Systematically reliable materials had now routinely become available for most decapod taxa, allowing for descriptions of complete developmental sequences from hatching through metamorphosis. As a consequence, the number of papers on decapod larvae published each year increased dramatically since the 1950s, with a concomitantly increasing proportion of laboratory studies (see Fig. 1.2a).

In some taxa, however, technical problems related to laboratory cultivation have persisted, mostly because their larvae require either smaller or larger food than *Artemia* (e.g. in pea crabs and spiny lobsters, respectively). As a consequence, these groups have in general been studied less extensively than others, still requiring extended tests of different rearing methods. The cultivation of palinurid lobsters, for instance, became only recently

successful enough to allow for a similar progress as in the study of most other decapod taxa (for review, see Kittaka 1994, 1997).

1.2.2 *Half a century of diversification in research*

The powerful tool of reproducible laboratory cultivation caused not only a steep increase in both the quantity and quality of morphological descriptions, but it allowed also for terminating the long-lasting monopoly of the morphological line of research. While papers not dealing with morphology were rare until the 1950s, their proportion increased dramatically thereafter. All major biological disciplines have meanwhile discovered the larvae of decapods as an interesting subject, using them often as a model for larval crustaceans, arthropods, or invertebrates in more general terms. Half a century later, studies of ecological, physiological, behavioral, and related aspects are now increasingly outnumbering the morphological investigations (see Fig. 1.2b).

This recent diversification in the lines of research on decapod crustacean larvae may be exemplified with the "crab lab" of the Duke University Marine Laboratory in Beaufort, USA. In this institute, J.D. Costlow and C.G. Bookhout were among the first who systematically tested new laboratory rearing techniques and routinely used *Artemia* nauplii as a sole or additional food source for decapod larvae. In 1959, they published the first complete morphological description of the larval stages of the blue crab, *Callinectes sapidus* (Costlow & Bookhout 1959), a commercially exploited species, which has meanwhile become one of the best studied crustaceans worldwide. This successful study stimulated numerous further investigations on the larval development of decapods, not only at the "crab lab" but also in several other working groups.

Although most studies through the 1960s and 70s continued to deal with morphology, other aspects of larval biology were now increasingly addressed too. For instance, single or combined effects of ecological key factors such as temperature and salinity, the endocrine regulation of chromatophore activity, regeneration, and the molting cycle were for the first time studied in decapod larvae (Costlow ***et. al.*** 1960, Costlow 1961, 1963a, b, c, Costlow & Sandeen 1961, Pautsch 1961, 1965, Hubschman 1963), and a first brief review of the ecology of larval decapods was published (Costlow & Bookhout 1964). More detailed studies of larval physiology and biochemistry followed soon (Costlow & Sastry 1966, Vernberg & Costlow 1966), and the growing awareness of environmental pollution was increasingly mirrored, especially in the early 1970s, in toxicological studies with decapod larvae as test organisms (Epifanio 1971, 1972, Bookhout et al. 1972, DeCoursey & Vernberg 1972, Vernberg & Vernberg 1974).

As a secondary effect of this upswing in laboratory studies, also field investigations of larval development in their natural environment received a significant impetus. This was a consequence not only of the stimulation that is usually exerted by novel insights and new questions, but also of a steeply increasing availability of reliable morphological descriptions, which allowed for a safer identification of larvae in plankton catches. Beginning in the 1970s, a rapidly increasing number of field studies addressed seasonal, annual and regional variations in larval abundance, horizontal transport and vertical migrations, behavioral and distributional patterns, settlement and recruitment intensities, and other ecological aspects (Sandifer 1973, Epifanio & Dittel 1982, Epifanio et al. 1984). At the beginning of the 21st century, these issues are now among the most extensively studied aspects of larval biology.

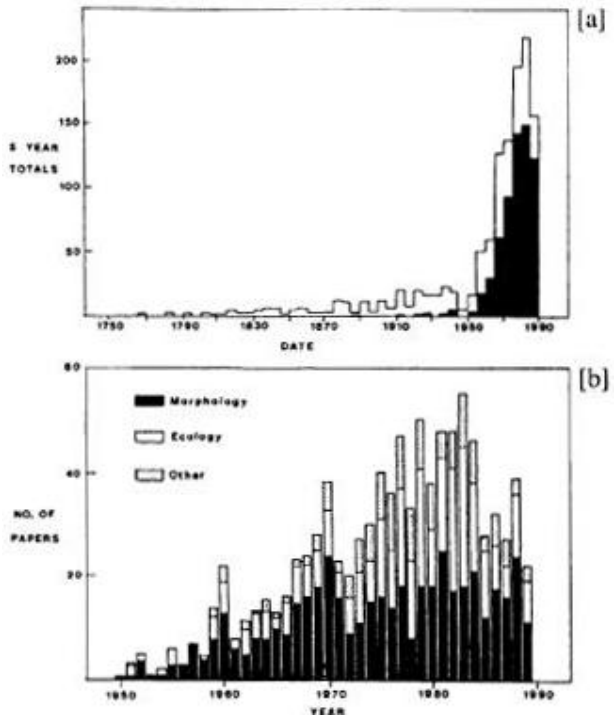


Figure 1.2. [a] Total number of larval crab papers published during each 5-year period between 1750 and 1989. The blacked-in areas represent papers based on laboratory rearing. [b] Yearly production of larval crab papers between 1950 and 1989 according to the broad area of their main subject (from Rice 1993).

In a positive feedback, the interpretation of new field data required and thus stimulated new laboratory studies of larval behavior. In numerous experimental investigations, novel techniques such as infrared video cameras and continuous computer recording were used to analyse patterns of larval swimming and vertical migration unter controlled conditions of temperature, salinity, light, pressure etc. (Sulkin 1973, Forward 1974, Forward & Costlow 1974). Several key mechanisms in the control of larval migration behavior were identified, modelled, and eventually applied to predict patterns of larval distribution and recruitment in the field (Sulkin 1984, 1990, Forward 1989a, b). By the end of the 1980s, the pelagic larvae of benthic marine invertebrates were no longer a *"neglected link"* (Costlow & Bookhout 1970) between the communities of the benthos and the plankton.

Since Lindeman's classical paper (Lindeman 1942), the bioenergetic point of view had increasingly invaded the concepts of ecology. However, it took more than two decades until the first quantitative investigations of feeding and growth in decapod larvae appeared (Reeve 1969). The first complete energy budget of a larval crustacean was published by Mootz & Epifanio (1974). This was in the 1980s followed by a number of increasingly detailed and comprehensive laboratory studies of larval bioenergetics in relation to individ-

ual molting cycles (for review see Anger 1991, 1998). Data of energy partitioning under controlled conditions have become relevant not only in basic scientific disciplines such as comparative larval physiology and ecology, but also in applied investigations in the context of aquaculture and fisheries (Kurmaly et al. 1989a). Recently, J.A. Lindley presented in his field-ecological studies the first attempts to quantify the role of decapod larvae in the productivity of marine planktonic communities (Lindley 1988, Lindley et al. 1994). These estimates are largely based upon laboratory data of larval biomass in combination with both laboratory and field-based data of larval migration and distribution.

1.2.3 *Where are we now?*

Thanks to improved techniques of rearing and experiments, the pelagic larval stages of the decapod crustaceans are now available for almost any kind of investigation which has already been carried out with juvenile or adult life-history stages. Both a steady increase in the number and an improvement of the quality of available morphological descriptions facilitate the taxonomical identification of larvae in plankton samples, and thus, allow for more comprehensive investigations of larval ecology in the field. Moreover, larval morphology is increasingly included in phylogenetic considerations of modern taxonomy (see e.g. Pohle & Marques 2000, and earlier papers cited therein). The development of advanced microtechniques has also greatly enhanced our possibilities of measuring physiological and biochemical parameters in extremely small samples, using for instance elemental (CHN) analysers, gas chromatography (GC) and high-performance liquid chromatography (HPLC) for measurements of chemical composition; selected compounds can be identified and localized applying radioimmunoassays (RIA), immunocytochemical, or radiotracer methods; micro-respirometers and nano-osmometers have become available for measurements of larval oxygen consumption and hemolymph osmolality, respectively; computerized video techniques allow for continuous recordings of larval swimming behavior in the water column.

However, in spite of this considerable increase in the precision of techniques and, consequently, an enormous extension of the research on decapod crustacean larvae, the overwhelming majority of recent publications is still dealing with morphological and ecological themes in approximately equal proportions. Studies of larval physiology, biochemistry, endocrinology, ultrastructure, and some other subjects have remained relatively insignificant, and thus, appear in Rice's recent statistics of larval crab papers collectively as a minor category, summarized as "other" (Fig. 1.2b).

Naturally, larval morphology and ecology will also be considered in this book, but perhaps slightly less than should be expected from their predominance in the literature and in most existing review articles and books. Attempting to aid readjusting this bias, I will emphasize here some lesser known subjects such as larval anatomy, patterns of molting, growth, and metabolism, or physiological and developmental adaptations to specific environments. As another prime goal of this book, I will try to show interrelationships between findings from different disciplines. While I surely acknowledge the necessity of an increasing specialization, showing here numerous examples of those invaluable contributions of specialists from various fields, I will generally advocate a multidisciplinary approach. In summary, when I describe here aspects of the biology of decapod crustacean larvae, I will primarily attempt to open a bit wider the black box labelled in Rice's statistics as "other".

1.3 *Laboratory and field studies: some methodological aspects and constraints*

In spite of significant progress in the development of techniques for both laboratory rearing and field investigations, we must remain aware of specific methodological difficulties and constraints existing in both approaches. Experimental investigators are, in principle, restricted to studies conducted under more or less artificial conditions. For instance, naturally variable factors must be maintained unnaturally constant in order to recognize effects of one or a few isolated factors that are manipulated during an experiment. In the laboratory, decapod larvae are normally fed with brine shrimp nauplii, rotifers, cultivated phytoplankton, or other food sources which they never would encounter in nature. Moreover, the densities of both the reared larvae and their food organisms are in general unnaturally high. Hence, the applicability of experimental results to the natural environments is difficult to test and may thus remain doubtful, in particular for field ecologists (for recent discussion, see Suthers 2000, Elliott & Leggett 2000).

Field ecologists, on the other hand, know only incompletely the temporal and spacial variations in the environmental conditions prevailing during a restricted period of study. In particular, the preceding history of development and growth is normally unknown in plankton organisms (for instance the previous feeding conditions), and even if it were known, each particular study would remain unique, i.e. basically irreproducible. In the case of larval crustaceans, frequently even the taxonomical identity of studied materials cannot always be ascertained. This is often caused by lacking availability, insufficient quality, or poor practical serviceability of morphological descriptions. In addition, specific differences are frequently restricted to small morphological details such as the setation of mouthparts. A safe identification would thus require destructive techniques such as dissection and microscopical examination of appendages, precluding most physiological and biochemical measurements. In summary, generalizations of data and conclusions from either single laboratory or field studies remain doubtful. An interdisciplinary approach, i.e. a combination or critical comparison of results from both sides should thus be particularly fruitful in future research.

This book is primarily based upon experimental laboratory investigations, which reflects not only my own and my students' line of research, but also the present limitations in the state of the art. The overwhelming majority of investigations on ecophysiological, but also on most other aspects of larval life in decapod crustaceans has been conducted in the laboratory, while comparative data from the field have become available only more recently (e.g. Lindley 1988, 1998, Lindley et al. 1994, Harms et al. 1994, Harding & Fraser 1999).

1.4 *Principal processes in the postembryonic ontogeny of the Decapoda: development, molting cycle, and growth*

Before we review, in successive chapters, all major aspects of the larval biology of decapod crustaceans, we should briefly consider a few general traits and processes of their postembryonic ontogeny, clarify some of the most frequently used concepts, and outline implications for the structure of this book.

Larvae of decapods and other benthic invertebrates change during their development in all principal characters, for instance in body size, morphology, anatomy, behavior, nutrition, ecology, physiology, and biochemical composition. Within this array of ontogenetic

changes, it appears useful to differentiate the following levels: (1) The term *development* will be used here to denote qualitative changes (e.g. in morphology or anatomy); (2) the *growth* concept shall primarily refer to quantitative changes (e.g. in body size or weight), although this is associated also with qualitative changes, namely in the chemical composition of living matter. In crustaceans, these major ontogenetic processes are linked through another phenomenon, (3) the *molting cycle*. In this book, I attempt to collate these different aspects of larval biology and to show interrelationships between intrinsic processes (organogenesis, molting cycle) and effects of extrinsic factors such as food, temperature, or salinity.

As in all arthropods, development and growth appear in decapod larvae as discontinuous processes. Changes in morphology and size become visible only in successive stages, and these are clearly separated by events of molting. These discontinuous patterns are enforced by the rigid arthropod exoskeleton, the size and shape of which remain practically constant between two molts. The old cuticle must be shed as an exuvia to allow for a brief soft-skinned period, during which morphological progress and increases in size seem to take place exclusively. However, this impression of discontinuity changes, when we examine anatomical details more closely and more frequently, and when we measure growth in terms of weight rather than size. An increased temporal resolution shows then that each larval stage is a period rather than a point in development and growth, and the formation of new morphological structures and organs as well as the accumulation of living matter occur continually during each molting cycle rather than stepwise.

Within the category of developmental changes, it is practical to distinguish between the levels of external and internal morphology. In the literature, the terms *morphology* and *anatomy* are often used as synonyms, so that both may refer to either external or internal structures (see for instance the preface to the treatise *"Microscopical Anatomy of Invertebrates"*; Harrison 1992). While I acknowledge that the more general term "morphology" (from Greek: form, shape) may refer to any structure (external or internal), I will use it here in its narrower sense, referring to external body structures; this is consistent with the predominant use in the literature. In contrast, the more specific term "anatomy" (from Greek: to cut open) will denote exclusively internal structures. This allows for using the conceptual combination "internal morphology" as a synonym of anatomy (see Harrison 1992), but not "external anatomy" as a synonym of morphology. However, in order to avoid possible confusion, I will evade both of these combinations. External and internal developmental changes will be reviewed separately in this book, in chapters 2 and 3, respectively.

The molting cycle comprises recurrent changes in the structure of the integument and other principal organ systems, which are controlled by hormonal systems. It may thus be understood as a special case of organogenesis which could be included in chapter 3. Consistent with this view, I describe the characteristic structural features of the integument and of the endocrine control system in the context with anatomy (chapter 3), where also the principal functions of other individual organ systems are reviewed. On the other hand, the molting cycle is very complex, bridging morphology with anatomy and development with growth, and it is one of the fundamental biological processes in the Arthopoda. I thus treat it here in some detail separately from the other morphological and anatomical changes (chapter 4). In summary, chapters 2-4 cover most of the qualitative, i.e. developmental aspects of the postembryonic ontogeny of the Decapoda.

In the subsequent chapters (5-9), the quantitative changes of body size and biomass, i.e. ultimately growth, will be embedded within a bioenergetic context. Hence, the quality and quantity of larval feeding, i.e. the basis of all growth processes, will be reviewed first (chapter 5), before we turn to patterns of growth (6), chemical composition (7), and metabolism (8). Reviewing ontogenetic and environmentally induced changes in the overall partitioning of biochemical energy that is taken from food and channelled into growth and metabolism, I will eventually assemble an exemplary energy budget (9). Larval responses and adaptations to their environment will be the subject of chapter 10, where I review general aspects of larval ecology and behavior in the context of previously shown developmental traits and changes. An overall summary of our present knowledge, major remaining gaps therein, and new developments in the scientific fields of larval biology will conclude this volume (chapter 11).

The bibliography cited in this volume may appear extensive, but it actually represents only a minor part of the existing literature on the larval biology of the Decapoda. Where general statements are made, I refer - as far as possible - to books or reviews rather than original research articles. The latter are preferably cited as sources when examples of specific results or contentions are given. In general, preference is given to recent publications, where older papers are cited; some older reviews or key papers are included here as well to facilitate the ingress of "newcomers" to specific fields of research.

In order to facilitate both the reading of the text and the finding of important concepts in the index, terms appear in the text highlighted in *italics* when they are introduced or defined (unless they appear in the heading of a section); otherwise this style is restricted to (1) headings, (2) genus and species names, (3) book titles and journal names, (4) lesser known acronyms and symbols (e.g. *PNR*, *PRS*, *ETSA*; but not for commonly used abbreviations such as HPLC, DNA, ATP, or chemical elements), (5) literal quotations, (6) terms adopted from other languages (e.g. *vice versa*, *in vitro*, *medulla terminalis*, *anlagen*).

2 MORPHOLOGY

The larval development of crustaceans is usually described as a sequence of morphologically distinct stages. Their external characters are meaningful not only for the description of the ontogeny of individual species, but may reflect also phylogenetical relationships between higher taxa (Williamson 1974, Rice 1980, 1983, Martin 1988, McWilliam 1995, Pohle & Marques 2000). Hence, larval forms have been included, since more than a century, in general considerations of taxonomy (see e.g. Milne-Edwards 1834-1840, Müller 1864). In his so-called *"biogenetic law"*, Ernst Haeckel (1866) speculated that larval traits should tend to recapulate phylogenetic changes in the adult body plan. However, it must be cautioned that *"many larval features are secondary adaptations to larval life"* and thus, one should rather say that *"ontogeny creates and does not recapitulate phylogeny"* (Hall & Wake 1999).

Among the principal criteria for the classification of larval forms and developmental patterns, the functional morphology of feeding appendages is of utmost importance. Since several exhaustive reviews of these topics have recently been published by outstanding experts in larval morphology (Rice 1980, 1983, Williamson 1982, Gore 1985, Rabalais & Gore 1985, Felder et al. 1985, Martin 1988, Ingle 1992, Williamson & Rice 1996, Clark et

al. 1998), I will not document here the existing diversity in larval morphology of the Decapoda, nor will I refer in detail to biophysical aspects of their functional morphology (for the latter, see the review by Strathmann 1987).

In this chapter, I will thus only give a brief introduction to larval morphology, define some of the most broadly used morphological concepts, and categorize the principal larval types and developmental patterns in the Decapoda. For practical convenience, I will here widely follow the commonly accepted terminology given in the comprehensive treatise *"The Biology of Crustacea"* (Williamson 1982, Bowman & Abele 1982) and in textbooks (Kaestner 1980). It must be kept in mind, however, that the traditional classification does not always reflect phylogenetic relationships. In recent studies of "phylogenetic systematics", the hierarchy of classes, orders, etc. has widely been abandoned, placing species and higher taxa in "monophyletic groups" (monophyla) which can be compared with closely related taxa of identical origin ("sister groups") and with relatively unrelated "outgroups" (Griffith 1973, 1976, Ax 1987, Scholtz & Richter 1995). I will refer to those units of modern taxonomy where necessary, especially when larval morphology plays a role in the classification of decapod crustacean taxa.

2.1 *Basic concepts of morphological development*

The following concepts are particularly important and thus, should be defined here before we recur to the principal patterns of development:

- *Phase*. This term denotes a sequence of morphologically equivalent developmental stages (for definition of "stages", see below), e.g. all naupliar, zoeal, or juvenile stages combined (Williamson 1982). In the literature, this broad concept refers sometimes to other major sections of the life cycle, for instance embryogenesis or the entire course of larval development, regardless of the stages comprised in it ("embryonic phase", "larval phase").
- *Instar* (or *molting cycle*, *numerical stage*). The terms *instar* and *stage* are in the literature often used as synonyms. In the terminology used in this book, "instar" has a broader meaning than "stage": I use "instar" here as a "molting cycle" or "numerical stage" (Gore 1985). Hence, this concept is neutral in relation to developmental categories, i.e. the appearance of a new instar may or may not be associated with morphological changes. For instance, two successive juvenile instars differ in size but not normally in morphology; thus, they are not referred to as different stages, because these should imply characteristic morphological changes. As another synonym of instar, sometimes *intermolt* can be found in the literature (Williamson 1982). This term, however, should better be avoided in the context of external morphology, because it can be confounded with a particular, anatomically defined molt-stage within an instar, namely molt-stage C in Drach's classification system (see chapter 4). Successive instars within a given phase are denoted with Roman numerals (e.g. zoea I, zoea II; crab I, crab II; etc.). In larvae, different instars represent normally also different stages.
- *Stage* (or *morphological stage*). Morphologically distinguishable instars are, in general, considered and named as different developmental "stages". Roman numerals are added to denote successive stages within a given phase, e.g. zoea I, zoea II, or nauplius I, nauplius II, etc. (Williamson 1982).

While this terminology seems to be clearly defined, in practice it is difficult to find a universally acceptable "stage" concept. Developmental variability, which is particularly

widespread in penaeid and caridean shrimps, complicates its use or may render it meaningless. Molting is sometimes accompanied by little or no morphological change, so that a larva *"…may then be said to repeat a stage (or morphological stage)"* (Williamson 1982). In this case, the "morphological stage" is no longer identical with the "numerical stage" (the instar). It thus becomes an artificial category, describing a certain level of morphological development regardless of the number of preceding molts and developmental pathways leading to it.

For larvae which are on a similar developmental level (i.e. belonging to the same "morphological stage", yet morphologically not identical, and independent of their instar number), Williamson proposed the term *"substages"*. These are denoted with small letters added to the Roman numerals of the "morphological stage" (e.g. zoea Va, zoea Vb, etc.). However, this terminology leads to ambiguity. A particular "morphological stage", for example a "zoea V", may sometimes already be reached in an earlier or later instar, varying among conspecific hatches, populations, or different rearing conditions. The assignment of a "stage" number (the Roman numeral) is then largely arbitrary, depending on intuition and the materials studied. Moreover, the morphological differences between "substages" may be considered negligible by one author but significant by others. In consequence, the same larva may be referred to as a zoea IVa in one paper, but as a zoea Vc, VI or VII in others. As an additional complication, the term "substage" has in the literature been used also with other meanings. In the treatise *"The biology of the Penaeidae"* (Dall et al. 1990), for example, it is a synonym of our "stage" concept, while Dall's "stage" corresponds with our term "phase". Hence, I suggest to redefine or abandon the term "substage".

In laboratory studies, the number of molts passed within a given developmental phase (i.e. the instar number) can usually be determined precisely. I thus propose that, whenever possible, the instar should be given as a part of the name of a larval stage, regardless of the presence or absence of preceding morphological changes. In the example discussed above, I would therefore prefer to say that a developmentally retarded larva, which is in instar VII but corresponds with an arbitrarily defined "morphological stage zoea V", should be called a zoea VII rather than zoea Va. In such a case, however, the information should be added that the zoeal instars V, VI and VII were found to be morphologically similar or largely identical.

In material collected from the field, the number of preceding molts is unknown, unless a taxon shows a relatively short and constant developmental sequence (e.g. most brachyurans). Larvae of species that are known or suspected to show a significant developmental variability (e.g. most shrimps and prawns) can only be classified properly when a comparison with laboratory descriptions is possible. Yet, their "natural" sequence of development remains uncertain, because the occurrence of unknown additional stages or developmental pathways in the field cannot be excluded. In shrimp larvae isolated from the plankton, we can thus only describe the level of morphological development, and then estimate from it the approximate number of preceding molts (in our example above, we could say: about four to six). In field studies, Williamson's "morphological stage" concept has thus a great practical value as a classification unit within an artificial scale of developmental progress.

- *Form*: Variability in the developmental pathway is, as we have seen, caused by molts that are associated with a variable degree of morphological change. In consequence, morphologically different larvae may occur after a fixed number of molts, or practically

identical larvae may be produced after different numbers of molts. Both is common in shrimps, but occurs also in most other decapod groups, although less frequently. An analysis of developental pathways is, on principle, possible only in the laboratory, most precisely in individual rearing experiments.

I propose to name morphologically distinguishable larvae being in the same instar as *"forms"* (comparable with molecular isoforms in chemistry). *"Morphs"* could be another appropriate term, but this may be in conflict with the genetical term, suggesting genetically distinct subpopulations. Different forms within a given instar can be denominated with small letters added to the Roman numerals, which identify the instar (e.g. zoea IVa, zoea IVb). As it is relatively easy to characterize the morphologically most advanced form occurring within a given instar, it should be convenient to assign the letter "a" to this form and the following letters to successively retarded larvae (Criales & Anger 1986).

Compared with Williamson's "substages", this term has the disadvantage that it does not offer an absolute (although arbitrary) scale for the level of morphological development. In consequence, an advanced form within a given instar (e.g. the form "zoea Va") can be morphologically identical with a retarded form of a later instar (e.g. "zoea VIb" or "VIIc"). The developmental stage of a larva is compared within a relative scale, which must be experimentally determined for each instar. This has the advantage that the relation between the morphological "form" and the instar number allows for assessing the viability of different hatches or comparing the quality of different environmental conditions. While viable larvae developing under optimal conditions should develop through the shortest possible sequence of stages (normally showing "form a" in each instar), weak or stressed larvae should pass through a higher number of instars and show morphologically retarded forms. I will recur to this at the end of this chapter (section 2.5).

- *Molt-stage*. The term "stage" has often been used also to classify integumental changes taking place within a molting cycle (Drach 1939). One should thus consistently add explaining attributes such as "larval stage" or "stage of the molting cycle" in order to avoid ambiguity. Trying to evade complicated phrasing, I will use the term "*molt-stage"* to denote developmental steps within the molting cycle (chapter 4).
- *Metamorphosis*: Sudden and dramatic changes in the morphology of two subsequent stages, usually accompanied by changes in behavior, feeding, ecology and physiology, are typical of transitions between different phases of development. As in insects, such major transitions within a life cycle may be termed *"metamorphosis"* (Snodgrass 1956, Passano 1961, Costlow 1968). Unlike some authors who apply this term more widely (Anderson 1973, Williamson 1982), I will not consider gradual morphological changes as a metamorphosis (see below, section on the Caridea type of larval development). On the other hand, I am not entirely excluding it from the Crustacea like Kaestner (1980), nor will I restrict its use to the transition from the last larval to the first juvenile stage. Hence, I apply it to all dramatic transitions within larval development, for instance that from a nauplius to a zoea, from a zoea to a decapodid, or from a decapodid to the first juvenile. This implies that one species can pass during its development through more than one metamorphosis.

2.2 *Principal types of larvae*

In spite of a great variety of larval forms and names, we may distinguish at most three principal types, after which we can term the phases of larval development in the extant Decapoda: nauplius, zoea and decapodid. They are defined primarily by criteria of func-

tional morphology, namely by presence or absence of locomotory appendages (Williamson 1982). In the earliest stages, swimming appendages appear only in the anterior parts of the larval body. In later stages they become functional in successively posterior regions, while the anterior appendages assume new functions, normally as mouthparts. In each phase occur different larval stages, some of which are restricted to certain taxa. The principle types of decapod larvae are briefly explained in this section.

When referring to the tagmata of the body plan, the current terms used in the crustacean literature distinguish usually between a cephalic, thoracic, and abdominal region. In the Malacostraca, the term *"abdomen"* has generally been abandoned and replaced by *pleon*, because it is not considered as homologous with the abdomen of the other Crustacea (Kaestner 1980). In the following sections, the body divisions within each region (head, thorax, pleon) are referred to as *somites*, whereas the divisions of appendages are termed *segments*.

2.2.1 *Nauplius*

The nauplius (Fig. 2.1) is generally considered as the most ancestral type of larva in the Crustacea (e.g. Cisne 1982; for recent review of phylogenetic implications, see Dahms 2000; however, see also controversial discussion by Scholtz 2000). Fossil evidence from the famous Orsten marl deposits in Sweden (see Müller 1983) shows that it existed already in the Upper Cambrian (see Walossek 1999 and earlier papers cited therein). Among the extant Decapoda, the nauplius occurs as a free-living (planktonic) larval form only in the Dendrobranchiata, while all higher decapods (the Pleocyemata) pass through this phase during their embryonic development, encapsulated by the egg membrane. Its principal characteristic is an absence of thoracic somites, and hence, an exclusive locomotion with the anterior cephalic appendages, namely with the antennules, antennae and mandibles (see Fig. 2.1, nauplius I). Also the posterior cephalic appendages (maxillulae, maxillae) are absent or rudimentary. In non-decapod crustaceans with a nauplius stage, the functional appendages are not only natatory, but fulfill also feeding functions; the mandibular protopod bears special setae for the transport of food particles to the mouth. In the Dendrobranchiata, however, the nauplius stages are nonfeeding larvae. As another morphological character of the nauplius, this larval type bears exclusively a small median eye, the "nauplius eye" (see section 3.3).

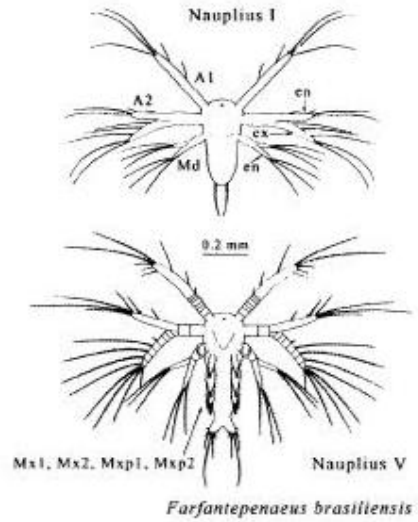


Figure 2.1. First and last stage of the naupliar phase of a dendrobranchiate shrimp, *Farfantepenaeus brasiliensis* (= *Penaeus duorarum*). A1, A2, Md: antennule, antenna, mandible; Mx1, Mx2, Mxp1, Mxp2: non-functional buds of maxillule, maxilla, first and second maxillipeds; en, ex: endopod, exopod (from Dobkin 1961, with permission from NOAA, Seattle, USA; taxonomy after Pérez Farfante & Kensley 1997).

Like a nauplius, the *metanauplius* has a median eye and natatory head appendages, but there are more than three somites, and rudimentary thoracic appendages may be present (see Fig. 2.1, nauplius V). Since the latter are non-functional, the metanauplius belongs to the naupliar phase of development. For convenience and in agreement with the current terminology, I will refer here collectively to all naupliar and metanaupliar stages as "nauplius", denoting successive instars with Roman numerals (abbreviated as N I, N II, etc.).

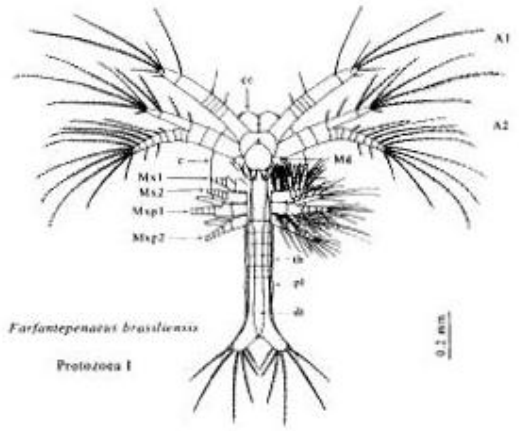


Figure 2.2. First protozoea (PZ I) of a dendrobranchiate shrimp, *Farfantepenaeus brasiliensis* (= *Penaeus duorarum*).) A1, A2, Md: antennule, antenna, mandible; Mx1, Mx2, Mxp1, Mxp2: first, second maxilla, first, second maxilliped; c: carapace; ce: compound eyes; dt: digestive tract; pl: pleon; th: thorax (from Dobkin 1961, with permission from NOAA, Seattle, USA; taxonomy after Pérez Farfante & Kensley 1997).

2.2.2 *Zoea*

This type of larva differs from a nauplius in the presence of functional thoracopods and usually in the presence of paired compound eyes (see Figs. 2.2 - 2.10); the latter may be rudimentary in early protozoea larvae of the Dendrobranchiata (Fig. 2.2). Except for protozoeal stages, the anterior cephalic appendages lose in the zoea phase their natatory function. The antennules and antennae assume functions associated with the mechanical and chemical perception of prey, and the mandibles are especially designed for biting food. The maxillules and maxillae become functional, also being involved in the feeding process; the former bear particularly stout setae for grasping prey, as well as numerous sense organs (chemo- and mechanoreceptors) aiding the selection of food. In the thoracic appendages (at least two pairs of maxillipeds are functional in zoea larvae), the exopods fulfill in general natatory functions, while the endopods hold prey. Pleonal appendages are consistently absent or rudimentary, appearing only as non-functional buds. Several special forms and synonyms may be found in the literature, e.g. *protozoea*, *metazoea*, *mysis*, *phyllosoma*.

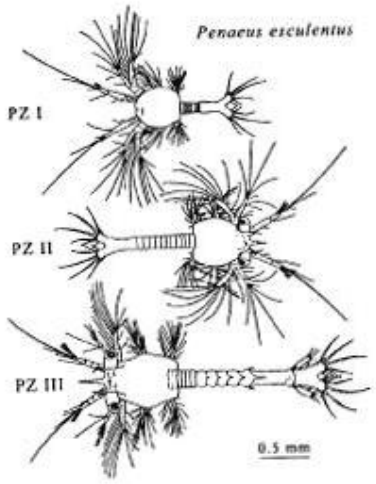


Figure 2.3. Protozoeal stages (PZ I-III) of a dendrobranchiate shrimp, *Penaeus esculentus* (from Fielder et al. 1975, with permission from CSIRO, Collingwood, Australia; taxonomy after Pérez Farfante & Kensley 1997).

Depending on the subsequent larval stage to which a zoea develops at the next ecdysis, we may distinguish between anamorphic and metamorphic zoeae. The former type is defined by molting to another, morphologically similar zoeal stage, whereas the latter (always the last zoeal stage within a developmental sequence) is ordained to undergo a metamorphic molt to a morphologically and behaviorally quite different decapodid stage (for definition see below, section 2.2.3). These two types of zoeae differ morphologically only in the state of development of their non-functional buds of pleonal appendages; major differences, however, exist in their anatomy, molting cycle and physiological traits.

- *Prezoea*: All Decapoda, except for the Dendrobranchiata, hatch from the egg as a zoea or as a prezoea. Although a prezoea has been observed in several decapod taxa (Gore 1985, Konishi & Quintana 1987, Hong 1988a, Dupré & Guisado 1996). Williamson (1982) argues convincingly that it should better be considered as the last embryonic rather than the first larval stage. It has no functional appendages or other larval organs, does not eat, swims exclusively (if at all) by means of abrupt abdominal movements, and it lasts normally only a few minutes before it molts to a zoea or an equivalent. This molting process is incomplete, resembling embryonic ecdyses taking place within the egg membrane (Helluy & Beltz 1990, 1991). In spite of not considering it a zoea, not even a larva, I mention this developmental stage here, because it has often been described in the literature as a zoeal stage.
- *Protozoea* (Figs 2.2, 2.3): In early penaeoid and sergestoid zoeae, all five pairs of head appendages are functional: antennules, antennae, mandibles, maxillules, maxillae. The antennules and the antennae maintain their ancestral natatory function as a remnant of

the naupliar phase, while the mandibles become feeding appendages. Compound eyes are developed but remain rudimentary in the first stage (Elofsson 1969). The functional morphology of the protozoeal feeding appendages is, in general, designed for filter-feeding, although some larger prey can be captured as well by late protozoeal stages (Omori 1979, Emmerson 1980). In spite of showing several transitional characters between a nauplius and a zoea, the protozoeal stages are assigned to the zoeal phase, because they possess functional thoracopods, usually the first and second maxillipeds (Williamson 1982). These particular larval stages of the Dendrobranchiata are followed by typical zoeae, which are similar to those of the Caridea (mostly referred to as *mysis* stages; Fig. 2.4). These are primarily raptorial feeders, retaining only a limited capability for concentrating small food particulates (Strathmann 1987).

- *Metazoea*: This larval form (occurring only in anomuran and some brachyuran crabs) is considered as a special (morphologically advanced) case of a zoea (Williamson 1982). It is characterized by rudimentary appendages posterior to the maxillipeds or having more than two pairs of functional thoracic exopods (Gurney 1942, Kaestner 1980).
- *Mysis*: Gurney proposed this term for stages IV and subsequent of penaeoid and sergestoid shrimps (Gurney 1942; see Fig. 2.4). Later, it has been applied also to larvae of clawed lobsters and some other decapod taxa (Kaestner 1980, Factor 1995a; see Fig. 2.6). Morphologcally it belongs to the zoeal type of larvae (Williamson 1982). In the specific cases of dendrobranchiate shrimps and nephropid lobsters, we may use it in Gurney's definition.

2.2.3 *Decapodid*

In order to replace Gurney's unfortunate, inconsistently used term *"postlarva"* (Gurney 1942), Kaestner (1980) proposed the general name "decapodid" (in the literature sometimes spelled "decapodit") to denote the final larval phase preceding metamorphosis to the first juvenile instar. This concept has been used also in a review of *"postlarval development"* in decapod crustaceans (Felder et al. 1985), although in an ambiguous manner. Gurney's terminology implies a contrasting use of "larva" *vs.* "decapodid", which has caused much confusion and largely unnecessary controversy. I thus advocate here generally the use of Kaestner's decapodid concept and propose to restrict the use of "postlarva" to truely transitional forms, where a safe distinction between late larvae and early juveniles is impossible.

The decapodid phase is characterized by the existence of functional pleonal swimming appendages, the pleopods, while all cephalic and the anterior thoracic appendages (the maxillipeds) assume new functions as mouthparts. The biramous pleopods are often pairwise coupled together by specialized hook structures on the endopods, the *appendix interna*, so that they beat in a coordinated way during swimming. The posterior thoracopods (pereiopods or peraeopods) become walking legs, with or without persisting natatory exopods (Fig. 2.5). Their endopods show already the typical segmentation that is known from the adult decapod leg. Beginning proximally, their segments are termed: coxa, basis, ischium, merus, carpus, propodus, and dactylus. In caridean shrimps, the carpus is often subdivided in several or many smaller segments. Propodus and dactylus can form a chela, especially in the first pereiopod, which is then termed cheliped. In spite of its similarity with a juvenile, a decapodid can be identified by the presence of larval organs, which are absent in juveniles (e.g. the natatory pleopods in brachyurans and anomurans, natatory exopods on the pereiopods of shrimps).

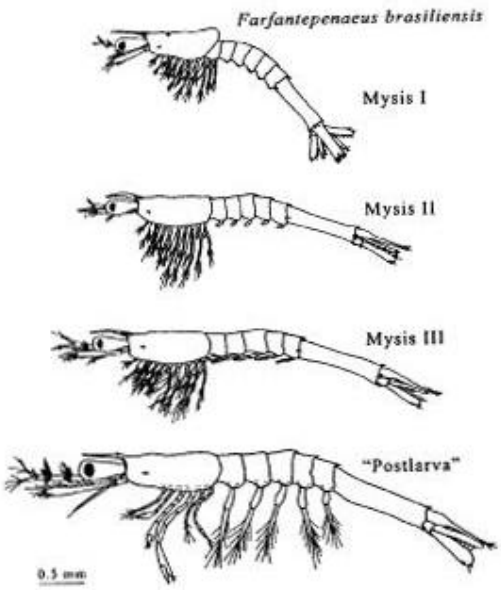


Figure 2.4. Mysis stages (M I-III) and early "postlarva" (juvenile) of a dendrobranchiate shrimp, *Farfantepenaeus brasiliensis* (= *Penaeus duorarum*) (from Dobkin 1961, with permission from NOAA, Seattle, USA; taxonomy after Pérez Farfante & Kensley 1997).

In the taxa Homoloidea (systematic position as ancestral brachyurans or outside the Brachyura under dispute) and Raninoidea as well as in all non-brachyuran Decapoda, somite 6 of the pleon fuses with the telson to form a pleotelson. The pleopods of the pleotelson are in these groups modified as uropods, forming a tail fan. In decapodids of caridean shrimps, natatory thoracopodal exopods persist as zoeal features; often they disappear only gradually during the early juvenile phase. Thalassinid, anomuran and brachyuran decapodids have a juvenile-like appearance with well-developed walking legs and chelae. In the Anomura, the last pair of pereiopods is reduced and morphologically specialized for cleaning the branchial chamber and, in adults, the egg masses.

- *Megalopa* (Figs 2.8-2.10): As an alternative to the term "decapodid", Williamson proposed "megalopa" to replace Gurney's "postlarva", extending an originally brachyuran name to all other crustaceans (Williamson 1969, 1982). However, this has not generally been accepted by researchers working with non-brachyurans. In agreement with major parts of the literature, I will thus use "megalopa" in a more restricted meaning, referring to the decapodid of brachyuran, thalassinid, or anomuran crabs. The equivalent stage in the Palinurida is termed *puerulus* or *nisto* (see section 2.3.4).
- *"Postlarva"*: This concept is *"illogical as a noun"* (Williamson 1969, 1982), because it implies a non-larval nature but is applied to both larval and early juvenile stages.

Its use in the literature is thus highly ambiguous. In particular in papers dealing with applied aspects of the aquaculture and fisheries of shrimps, it remains often obscure whether the authors refer to late larvae, early juveniles, or transitional forms. In morphological descriptions, the reader of a paper may be able to identify the particular meaning of "postlarva", while this is often impossible in studies of laval growth, nutrition, etc. Entirely in agreement with Kaestner's (1980) and Williamson's (1969, 1982) criticisms, I thus urge to avoid as much as possible this ambiguous term.

As a possible exception, the original application of "postlarva" to the Euphausiacea and, among the Decapoda, to the Dendrobranchiata and Caridea may remain to some degree justified, because these groups show a gradual transition between the late larval and the early juvenile phases. I thus propose to restrict the use of the term "postlarva", for practical purposes, to these taxa and to this particular transitional phase, during which larval organs disappear gradually while functional juvenile characters appear simultaneously over several molts. Strictly, however, such stages are still decapodids as long as they show functional larval organs such as natatory exopodids an the pereiopods. Hence, this transitional phase should be considered as a part of larval development, although it shows also traits of the juvenile phase.

2.3 *Patterns of larval development in the major decapod taxa*

In the Decapoda, a few principal developmental patterns may be discerned, based on the type and number of larval stages and on the presence or absence of metamorphic transitions. This rough classification is not necessarily congruent with units of phylogenetic systematics. Its major purpose is a simplification of the variety of developmental modes and sequences that are found among more than one hundred decapod families, attempting to facilitate comparative considerations in larval biology.

2.3.1 *Dendrobranchiata*

Among the Decapoda, the Penaeoidea and the Sergestoidea are considered as phylogenetically ancestral (plesiomorphic) groups; together, they constitute the taxon Dendrobranchiata (Bowman & Abele 1982). Fossil dendrobranchiate decapods have been recognized from several Mesozoic beds, but their origin is believed to date back in the Paleozoic, with major radiation occurring during the Mesozoic (Schram 1982, 1983). The Dendrobranchiata are the only decapods which develop through three larval phases, including several free-living naupliar stages (Fig. 2.1). The uniqueness of this ancestral developmental type is one of the principal arguments for the monophyly and the isolated status of this taxon among the Decapoda. The remaining decapods form together, as a sister group, the Pleocyemata or "higher Decapoda" (Scholtz & Richter 1995).

Among the Dendrobranchiata, the penaeid prawns are commercially fished and cultivated and, in consequence of their high economic importance, are quite well known also outside the scientific community. Comprehensive reviews of their taxonomy and life history were published recently (Burkenroad 1983, Dall et al. 1990, Pérez Farfante & Kensley 1997). The number of naupliar stages varies from five to eight (Omori 1974, Williamson 1982, Dall et al. 1990, Hashizume 1999). The zoeal phase includes three protozoea and two to five mysis stages (Figs. 2.2 - 2.4). Ancestral characters can still be seen in the protozoea stages, where natatory antennae persist from the nauplius phase (Figs. 2.1, 2.2). In the Sergestoidea, special names have been given for the protozoea and mysis

stages, respectively: *elaphocaris* and *acanthosoma* (Gurney 1942). During the subsequent decapodid or "postlarval" phase (in the Sergestoidea named *mastigopus*), juvenile characters are attained gradually over a variable number of molts. Thus, neither the transition between the naupliar and the zoeal phase nor that between late larval (decapodid) and early juvenile stages is truly metamorphic. The penaeid type of development is thus rather gradual or, in Kaestner's terminology, *"regular anamorphic"* (Kaestner 1980).

2.3.2 *Stenopodidea and Caridea*

The Caridea and the Stenopodidea were originally placed (together with the Dendrobranchiata) in the suborder "Natantia". In contrast to the Reptantia, however, this group is no longer considered as monophyletic and thus, is not a valid taxon (Burkenroad 1981, Felgenhauer & Abele 1983b, Abele 1991, Chace 1992). According to the fossil record, the caridean and stenopodidean shrimps are younger than the Dendrobranchiata, dating back to at least the Jurassic period (Glaessner 1969). Among the higher Decapoda (the Pleocyemata), the Stenopodidea are suspected to be the sister group of the Reptantia (Scholtz & Richter 1995). Their oldest fossil record was recently found in layers from the Late Cretaceous of northern China (Schram et al. 2000).

In the adult phase, the caridean and stenopodid shrimps differ from each other primarily in their pereiopods, gills, and pleonal pleura (Kaestner 1980, Schram 1986). Most morphological traits of their larvae appear to be similar (see e.g. Gurney & Lebour 1941, Williamson 1960, 1976, 1982, Seridji 1990); however, relatively little is known about the development of the Stenopodidea. Thus, these two taxa are considered here together.

Caridean and stenopodid larvae hatch as a shrimp-like zoea, normally with sessile compound eyes and natatory exopods on the thoracapodal appendages (Fig. 2.5). The second stage has always stalked eyes. The number and morphology of the zoeal stages shows in general great inter- and intraspecifical variability. When the larvae develop functional natatory pleopods but still retain natatory thoracopodal exopods as larval characters, they comply with the definition of decapodids. According to the available description of laboratory-reared larvae of a species from India, *Microprosthema semilaeve*, it appears that stenopodid shrimps do not generally pass through this developmental phase (Raje & Ranade 1975). Carideans, in contrast, may show several decapodid stages.

The transition between the zoeal and the decapodid phase is gradual in most caridean larvae. Close microscopical examination of live shrimp larvae (e.g. *Palaemonetes argentinus*; pers. obs.), showed that late zoeae have sometimes already sparsely setose and slowly moving pleopods, but these do not participate effectively in larval locomotion, because their setation, musculature and nervous coordination are not yet sufficiently developed. In such cases, it remains a subjective decision whether a researcher classifies a transitional larval form as a morphologically advanced zoea or a retarded decapodid. In addition to the pleopods, also the natatory exopods of the pereiopods and maxillipeds remain functional throughout the decapodid phase, representing a persisting zoeal character. They lose their functionality in the first juvenile stage, but rudiments of thoracic exopods may persist over several juvenile molt cycles, degenerating only gradually. Hence, both transitions between the zoeal and decapodid, and that between the decapodid and the juvenile phases are in the Caridea gradual rather than metamorphic (Fig. 2.5).

As in the zoeal phase of the Caridea, the number of decapodid stages varies inter- and intraspecifically. In the brown shrimp, *Crangon crangon*, for instance, a late zoea (IV, V or VI) may molt directly to a juvenile (skipping the decapodid phase), or it may pass

through one ore a few decapodid stages (Criales 1985, Linck 1995; see section 2.5). In the hippolytid shrimp *Nauticaris magellanica*, five decapodid stages have recently been observed, following a minimum of nine zoeal stages (Wehrtmann & Albornoz 1998). It appears to be a typical trait of the decapodids of caridean shrimps that their molts are often associated with little or no change in size, morphology, and biomass (Knowlton 1974, Criales & Anger 1986, Wehrtmann & Albornoz 1998, Agard 1999).

Except for the progressing development of pleonal appendages, the decapodids of caridean and stenopodid shrimps remain morphologically similar to the preceding zoeae (Fig. 2.5), although their behavior changes. They become increasingly benthic as their pereiopod endopods develop to functional walking legs, and their swimming mechanism differs from that of the fully pelagic zoeae. Decapodids use predominantly pleonal appendages for propulsion (together with the thoracopodal exopods), whereas zoeae swim exclusively with the natatory exopods on the maxillipeds and pereiopods (Felder et al. 1985).

The two most typical traits of the Caridea type of development may thus be summarized as follows: (1) morphological changes are gradual; (2) both the number of instars within a larval phase and the morphological characters of an instar vary intraspecifically. The body form of the larvae is similar to that of adult shrimps and hence, changes only slightly from hatching through larval and juvenile development (Fig. 2.5). No true metamorphoses can be observed between the different phases. Kaestner (1980) classified this hemimetabolic type of larval development *anamorphic*. As a consequence of great developmental variability, quite different larval forms may be found in identical instars of the same species; on the other hand, the same morphological stage may be reached in different instars. As another typical trait resulting from this variability, caridean shrimps pass through an intraspecifically variable, in some cases extremely high total number of larval stages. In a tropical palaemonid shrimp, *Macrobrachium rosenbergii*, for instance, 11 stages were distinguished in one study (Uno & Kwon 1969) but up to 17 in others (Díaz & Kasahara 1987, Agard 1999).

2.3.3 *Nephropoidea (Homarida)*

Bowman & Abele (1982) placed in their systematics of the Decapoda the clawed lobsters (Nephropoidea) and the two superfamilies of crayfish (Astacoidea, Parastacoidea) together in the infraorder Astacidea. The fossil record of this group comprises the period from the Late Permian-Recent, with several radiations during the Mesozoic (Schram 1982, 1983). In a recent taxonomic revision, Scholtz & Richter (1995) separated these apparently paraphyletic taxa. The new system is supported by developmental evidence: while the freshwater crayfish (now jointly referred to as taxon Astacida) have completely eliminated the pelagic larval phase, hatching from the egg as an adult-like benthic juvenile (Hobbs 1991, Huner 1990), the marine lobsters pass through three planktonic larval stages and a semibenthic “postlarva” (Phillips & Sastry 1980, Factor 1995a).

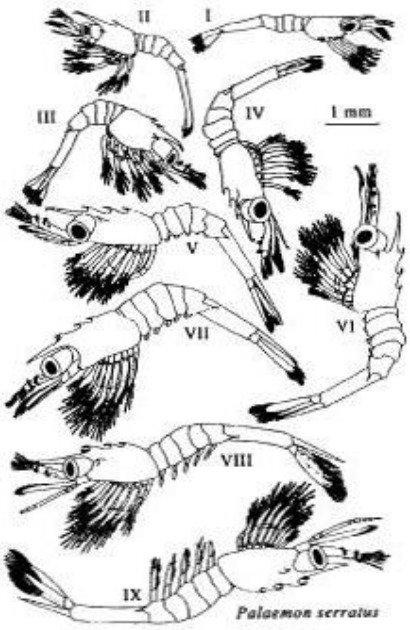


Figure 2.5. Zoeal stages (I-VIII) and early decapodid (instar IX) of a caridean shrimp, *Palaemon serratus* (from Fincham 1983, with permission from The Natural History Museum, London, UK).

Lobster larvae hatch from the egg as a large zoea (in the literature mostly referred to as a mysis), which has functional pereiopods with fully segmented endopods and natatory exopods (Fig. 2.6). Since a similar stage of development is normally reached only in later stages, this type of abbreviated larval development may be classified as *"advanced"* (Gore 1985). As another morphological trait that appears to be typical of this taxon, lobster larvae show a crecent-shaped telson with a large median spine (Scholtz & Richter 1995). The second stage shows pleopod buds. These become biramous and segmented but not yet functional in the mysis III; the uropods also appear in this stage. The swimming appendages of the pleon become functional in stage IV, which is thus no longer a zoea. Settlement also begins in this stage, but this behavioral change becomes more pronounced in the following instars, particularly in V (Templeman 1936, Ennis 1995, Lawton & Lavalli 1995).

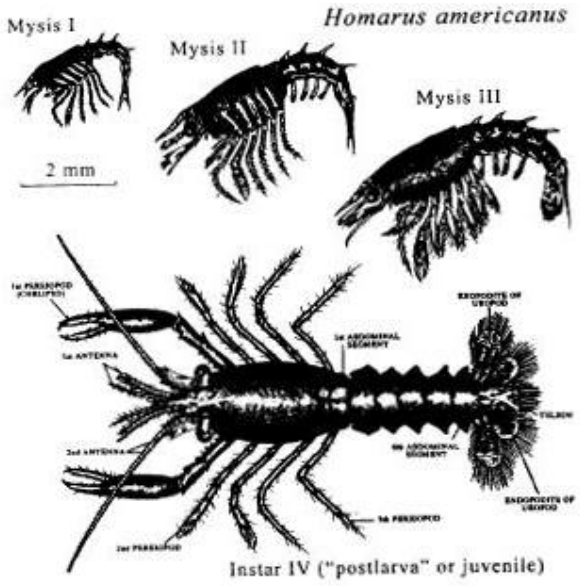


Figure 2.6. Mysis (or zoea) stages I-III and "postlarva" of a clawed lobster, *Homarus americanus*; instar IV is morphologically a juvenile, but shows some transitional (i.e. decapodid) traits in behavior and physiology (after Factor 1995a; original drawings by Hadley 1906).

Ontogenetic changes in the functional morphology of swimming and feeding appendages of clawed lobsters were described in much detail in several original papers, review articles, and books (Laverack et al. 1976, MacMillan et al. 1976, Neil et al. 1976, Factor 1981b, 1989). However, there is still some terminological controversy about the nature of stage IV. This is in the literature usually referred to as a "postlarva" (Phillips & Sastry 1980, Charmantier et al. 1991, Factor 1995a, Lawton & Lavalli 1995) or as a decapodid (Williamson 1982), i.e. basically as a larval stage. This interpretation is based on the presence of natatory pleopods and the persisting swimming behavior in stage IV. However, these arguments are not quite convincing, because active swimming has frequently been observed also in later instars of the lobster as well as in juvenile and even in adult decapod crustaceans that are considered as benthic species (Hartnoll 1971a). Based on this gradual behavioral change in juvenile *Homarus* spp., Hudon (1987) considers all instars from stage IV to those with about 25 mm carapace length (i.e. fairly large juveniles) as "postlarvae". On the other hand, all special larval organs such as the natatory thoracopodal exopods are lost in stage IV, and all morphological, anatomical, physiological and biochemical traits studied so far are practically identical with those in later juvenile instars, although some characteristics (especially in physiology and behavior) appear to be transitional. A clear metamorphosis occurs thus only between the postembryonic stages III and IV (see Charmantier & Aiken 1987, Charmantier et al. 1991, Ennis 1995).

In spite of this evidence for a non-larval nature of stage IV, the view of four larval stages has been maintained by most authors, including the recent treatise *"The Biology of the Lobster Homarus americanus"* (Factor 1995b). I disagree here, because I feel that swimming behavior should not suffice to define stage IV or later instars as truly transitional, i.e. "postlarval" stages equivalent to those in euphausiids and shrimps. Since these instars lack special larval organs and the swimming mechanism is the same as in later juveniles (using the pleopods for propulsion), I prefer to consider instar IV as the first juvenile, which implies that the larval development of the clawed lobsters typically comprises three advanced zoeal (or mysis) stages but no true decapodid or "postlarva" (Fig. 2.6).

2.3.4 *Palinura and Eryonoidea*

The taxon Palinura (in the classical taxonomy an infraorder; Bowman & Abele 1982) was recently renamed Achelata (Scholtz & Richter 1995). It comprises the Palinuridae (spiny lobsters or rock lobsters) and the Scyllaridae (slipper lobsters). These phylogenetically old reptantians (recorded from the Jurassic and Cretaceous, respectively; see Schram 1983, 1986) show a quite different type of larval development compared with the clawed lobsters and all other Decapoda. They hatch as a characterstic zoeal form with a leaf-shaped carapace, called *phyllosoma* (Fig. 2.7). In the fossil record, this larval type has been well documented from the Jurassic Solnhofen Limestone of Germany (Fig. 2.8; Polz 1996).

The zoeal phase of the Palinura comprises a variable number of phyllosoma stages (Ito & Lucas 1990, Booth & Phillips 1994, McWilliam et al. 1995, Mikami & Greenwood 1997a), followed by one decapodid stage (Williamson 1982). In the spiny lobsters, the decapodid is called *puerulus*, while its equivalent in the slipper lobsters is usually termed *nisto* (Fig. 2.7). Since this type of development deviates from those in all other decapods, Williamson (1988) discussed the possibility of a convergent evolution of the Palinura and the rest of the Decapoda. Although this hypothesis has not been followed by other taxonomists, the aberrant phyllosoma larva supports the quite isolated phylogenetic position of the Palinura or Achelata among the Reptantia (i.e. among all Decapoda except the Dendrobranchiata, Caridea, and Stenopodida; Scholtz & Richter 1995).

During the extended phyllosoma phase, which may take from three months to about two years, spiny lobster larvae pass through numerous molting cycles (for review see Booth & Phillips 1994). In *Panulirus japonicus*, for instance, up to 29 instars with 12 morphologically distinct stages have been identified (Inoue 1978). The developmental progress in such a series of instars is anamorphic (Kaestner 1980). Phyllosoma larvae are, as most zoeal forms, raptorial feeders. In contrast to other zoeae, however, they are able to capture also large prey such as young fishes, which they can hold with their thoracic endopods (Lebour 1925; cf. section 5.2.2.7).

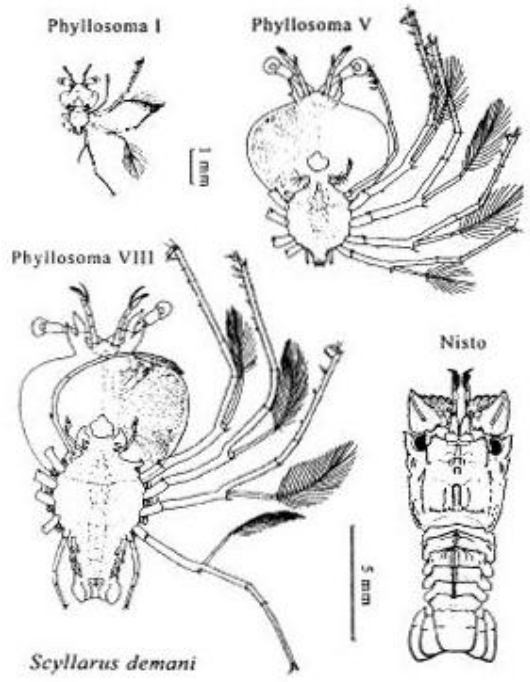


Figure 2.7. Early, intermediate, and late phyllosoma stages (I, V, VIII), and nisto (decapodid) of a scyllarid lobster, *Scyllarus demani* (from Ito & Lucas 1990; with permission from Brill, Leiden).

The subsequent puerulus can still remain pelagic for up to another two months, before settlement and metamorphosis to a benthic juvenile takes place (Booth & Phillips 1994). In some species, the puerulus is a nonfeeding stage (Lemmens 1994). The extremely long pelagic development makes palinurid lobster larvae a good example of *"teleplanic"* or *"long-distance larvae"* (Scheltema 1971), which may be transported over wide oceanic distances (see chapter 10).

In the classification system of Bowman & Abele (1982), also the Eryonoidea with their only family Polychelidae were included as a superfamily in the Palinura. Scholtz & Richter (1995), however, proposed that these deep sea decapods represent an ancestral sister group (renamed Polychelida) of all remaining Reptantia. This separation is supported by evidence from larval morphology: The polychelids do not have phyllosomas but develop through another characteristic type of larva, the *eryoneicus***.** It shows a characteristically inflated carapace (Bernard 1953); morphologically it is a zoea (Williamson 1982). After a variable number of eryoneicus stages, the Eryonoidea or Polychelida pass through several decapodid stages to metamorphosis (Williamson 1982).

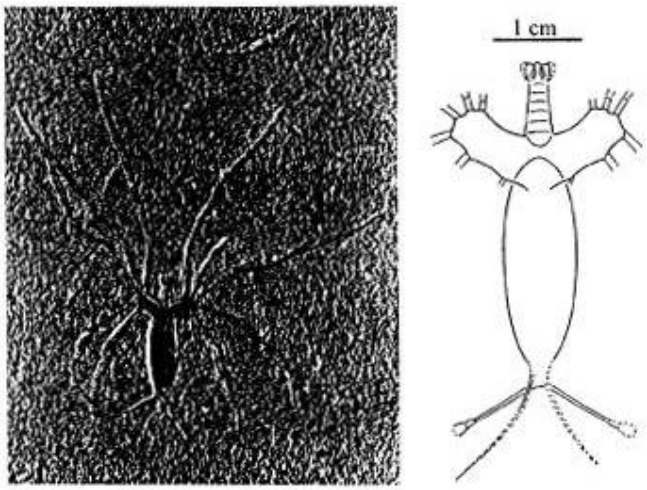


Figure 2.8. Fossil record of a palinuroid phyllosoma larva from the Jurassic Solnhofen Plattenkalks (Germany); right: reconstruction of thorax and carapace (from Polz 1996, with permission from Verlag Pfeil, München, Germany).

2.3.5 *Thalassinidea and Anomura*

The Talassinidea and Anomura have so much in common that taxonomists have repeatedly fused these two decapod groups. Since also major traits of their larval development are similar, I consider these independent taxa here jointly to simplify our classification of the principal developmental patterns. Although Scholtz & Richter (1995) redefined the Anomura as Anomala, I follow here McLaughlin & Holthuis (1985) who proposed to maintain the more commonly used term Anomura. The history of these taxa dates back from the Jurassic (Schram 1982, 1983).

In both groups, hatching from the egg takes place in a shrimp-like zoea. These larvae pass normally through four or five stages (Fig. 2.9); as an exception, the Porcellanidae have consistently only two zoeal stages. In the late zoeal stages of the Anomura, the fifth pereiopods are slender and reduced in size, and they are inserted medially between the coxae of the third and fourth pereiopods; this character appears to be typical of this taxon and in contrast to all other reptant decapods, where the pereiopods are are arranged in a row, showing approximately equal size (for references, see Scholtz & Richter 1995).

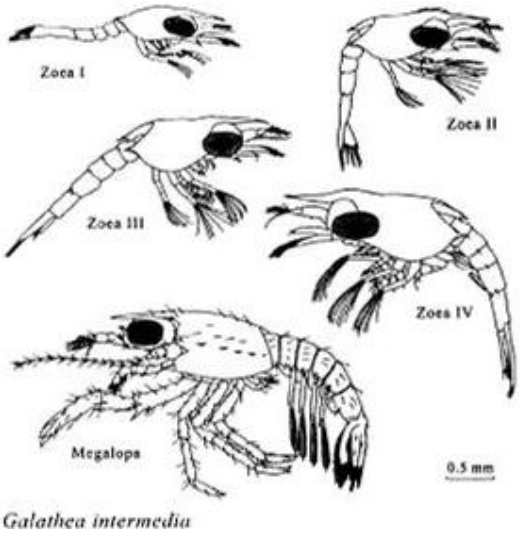


Figure 2.9. Zoeal stages (I-IV) and megalopa of an anomuran crab (or squat lobster), *Galathea intermedia* (from Christiansen & Anger 1990, with permission from The Crustacea Society, Seminole, FL, USA).

While anomuran and thalassinid zoeae are externally similar to caridean shrimp larvae, the total number and the morphology of the individual larval stages vary much less in the thalassinids and anomurans. Some intraspecific variability, however, was noted in a number of individual taxa (Gore 1979, 1985, Christiansen & Anger 1990, Strasser & Felder 2000). Anomuran zoeae swim exclusively with natatory exopods of the maxillipeds. The thalassinids show a tendency toward an abbreviation of the zoeal phase, accompanied by an earlier appearance of advanced morphological characters. Their zoeae use a variable number of posterior thoracic (pereiopod) exopods and show early developed uropods.

The decapodid (consistently one stage only) is in these groups usually named *megalopa* or *glaucothoe*. It is both behaviorally and morphologically similar to the benthic juvenile, with functional walking legs and chelae, lacking thoracopodal exopods, and with the maxillipeds becoming mouthparts (Fig. 2.9). Its locomotory capabilities thus comprise both walking on the ground (with the pereiopods) and swimming in the water column (with the pleopods). The natatory pleopods identify the decapodid as a larva; this character is not present any longer after metamorphosis to the first juvenile stage.

In summary, the anomuran type of larval development (including here that of the thalassinids) is characterized by shrimp-like zoeae and a juvenile-like (benthic or semibenthic) decapodid. It shows little inter- and intraspecific variability in the morphology and number of stages, and it passes through two metamorphoses, one from the last zoeal stage to a morphologically different decapodid, and another from the decapodid to the first juvenile. The first metamorphosis is more pronounced than the second.

2.3.6 *Brachyura*

The Brachyura appeared to the Jurassic, but with major radiation only since the Cretaceous (Schram 1982, 1983). These crabs show, in principle, a similar pattern of development as the anomuran-type larvae (Fig. 2.10). This is particularly conspicuous in the two most ancestral groups, the Dromiacea and Archaeobrachyura, whose larvae are morphologically so similar to those of the Anomura and Thalassinidea, that their systematic position has remained in question for a long time.

Brachyuran larvae hatch as a zoea with natatory exopods exclusively on maxillipeds 1 and 2. With the exception of the ancestral taxa (if these really belong to the Brachyura), maxilliped 3 and the pereiopods never become functional during the zoeal phase. In the Dromiacea and Archaeobrachyura, the zoeae have a shrimp-like (elongated) body form, similar to those of the anomurans and thalassinids. According to Scholtz & Richter (1995), this is the phylogenetically ancestral form, which has been *"inherited from the last common ancestor"* of the Brachyura and Anomura. As a quite unusual and, so far, little accepted alternative hypothesis, Williamson (1998 and earlier papers cited therein) and Williamson & Rice (1996) suggest that the anomuran-like morphology of the dromiid larvae is the result of hybridization (horizontal gene transfer) between anomuran and brachyuran species. In contrast to those presumably plesiomorphic larvae, the zoeae of the higher (or true?) Brachyura have a characteristic spherical carapace shape. In many eubrachyuran taxa, they show long dorsal, rostral, and/or lateral crapace spines.

There is little intraspecific variability in the morphology and number of zoeal stages of the Brachyura, being conspicuous only in taxa which pass through a relatively high number of zoeal stages (Montú et al. 1990). The decapodid represents the typical megalopa, which is similar to the benthic juvenile crab. It has well-developed walking legs and chelae, but it can also swim with natatory pleopods (Fig. 2.10). These larval swimming appendages are reduced in the juveniles. As exceptions of these general developmental patterns, no decapodid stage occurs in the Hymenosomatidae (Williamson 1982, Wear & Fielder 1985, Tirmizi & Kazmi 1987, Horn & Harms 1988, Salman & Ali 1996), or two were occasionally found in other brachyurans (Wear 1967, Montú et al. 1996).

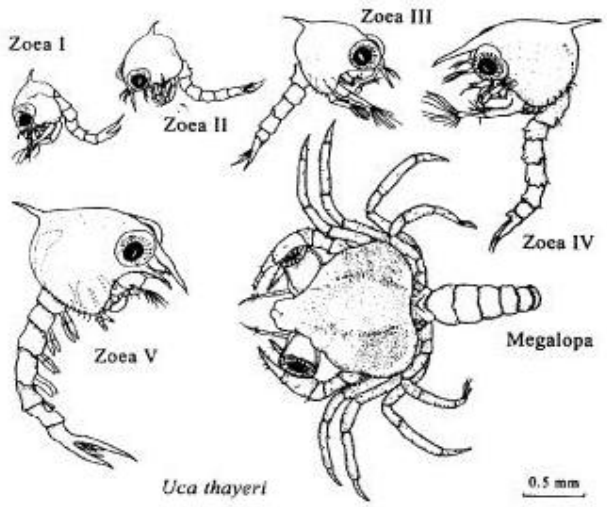


Figure 2.10. Zoeal stages (I-V) and megalopa of a brachyuran crab, *Uca thayeri* (from Anger *et al.* 1990a, with permission from Spektrum, Heidelberg, Germany).

2.4 *Abbreviated development*

For taxa which have, at least sometimes in their evolution, developed a pelagic mode of larval development, it is widely accepted that a complex life history with many larval stages represents a phylogenetically ancestral state, while an abbreviation of this phase is considered as a derived character (Makarov 1968a, b, Jägersten 1972, Strathmann 1978). Although this hypothesis has been challenged with alternative theories (Nielsen 1995), there are well-documented examples among the terrestrial and freshwater decapods, where abbreviated modes of development appeared only recently in evolution (see section 10.4.2).

Species with a reduced pelagic larval phase have been observed in most major taxa of the Crustacea. With the exception of the Dendrobranchiata, this occurs frequently also in the Decapoda, where several types of abbreviated development have been classified (Gore 1985, Rabalais & Gore 1985). The most extreme form of abbreviation is a *direct development*, where no free-swimming larvae exist, and hatching from the egg takes place in a benthic juvenile stage. While this developmental mode is normal in crayfish, crabs and many shrimps living in freshwater, it occurs only exceptionally in marine decapod taxa (for review, see Anger 1995a). Among the latter, the shrimp family Spongicolidae appears to have completely reduced the free-living larval phase, perhaps as an adaptation to a commensal life-style associated with deep-sea sponges (Saito & Konishi 1999). Also the Sclerocrangonidae, which live in high latitudes, show a direct type of development (Makarov 1968a, b).

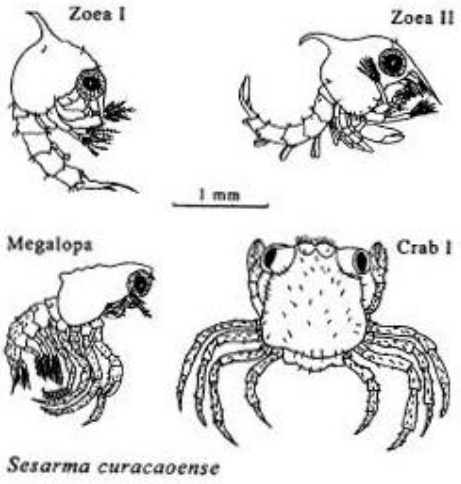


Figure 2.11. Abbreviated larval development in a brachyuran crab, *Sesarma curacaoense*: zoeal stages I, II, megalopa, first juvenile crab. Note negligible growth from hatching through metamorphosis, presumably asssociated with facultatively lecithotrophy (from Anger *et al.* 1995; with permission from Sociedade Brasileira de Carcinologia, São Paulo, Brazil).

In species with an *advanced development*, the larval sequence has a *"shorter duration than that normally occurring in a preponderance of related species in a taxon"* (Gore 1985). Hatching takes place in a morphologically advanced stage of development, in extreme cases as a decapodid, or alternatively, unusually great steps of morphological development may occur in later larval molts. As a general consequence, less larval stages are necessary to proceed to the juvenile phase. The duration of these instars is often shorter than in regular planktonic larvae, so that also the time of total larval development is shortened. As an example among the brachyuran crabs, Figure 2.11 shows the developmental sequence in a tropical grapsid species, *Sesarma curacaoense*, which passes through only two brief zoeal stages (ca. 1-3 days each) and a megalopa. By comparison, most other neotropical *Sesarma* species develop through three zoeal stages, and other grapsid crabs have at least four (lasting 2-5 days each). In *S. curacaoense*, the zoea I is morphologically only slightly advanced as compared with that of other grapsids, but the developmental step to the zoea II is unusually great (Fig. 2.11).

A reduction or complete lack of the larval phase is particularly common among inhabitants of freshwater, high latitudes, and deep sea environments (Thorson 1950, 1961, Ghiselin 1987, Komai & Mizushima 1993; for review see Sastry 1983a). This indicates that the mode of development is, within the limits of phylogenetic constraints (Strathmann 1977), subject to selection by environmental factors. An abbreviated or lacking larval development has often been associated with an insufficient, unpredictable, or seasonally short

production of planktonic food. A key role of nutritional factors in the selection of developmental modes has been inferred primarily from another trait that is commonly associated with an abbreviated larval development: compared with species that pass through a regular pelagic development, those with an abbreviated mode show frequently an enlarged egg size. The hatching stage is thus unusually large, and is commonly also morphologically advanced. Since enhanced amounts of organic reserves may persist from the embryo through one or more larval stages, this allows for a partially or entirely lecithotrophic (i.e. food-independent; see chapter 5) mode of development. A few examples of hatching stages with enhanced initial energy reserves are shown in Figure 2.12. Further examples will be discussed in context with food uptake (section 5.1) and ecology (sections 10.2.1, 10.4).

In several palaemonid freshwater shrimp species living in the Amazon and adjacent river systems, the development from hatching to the first juvenile stage comprises only one or a few nonfeeding, benthic decapodid-like stages with functional pereiopods and segmented pleopods (e.g. Magalhães & Medeiros 1998 and several earlier studies cited therein; Melo & Brossi-Garcia 1999). Similar life histories have been described from numerous other caridean shrimps living in freshwater streams and subterranean caves (e.g. Strenth 1991; see also recent papers by Villalobos & Álvarez 1999, Román et al. 2000; extensive reviews in Dobkin 1969, Pereira & García 1995). In Figure 2.12, the first postembryonic stage of *Pseudopalaemon chryseus* from the Amazon is shown as an example (Magalhães 1987). Since the pereiopods have, in these species, commonly no exopods, even early larvae are morphologically closer to juveniles than to a regular caridean decapodid. The most conspicuous difference from the adult-like juveniles is the initial lack of uropodes; these appear only in the third postembryonic stage. Compared with the degree of abbreviation in *Sesarma curacaoense* (Fig. 2.11), the development in these shrimp species is much more advanced, coming close to a direct mode of development. Among the brachyuran crabs, an abbreviated development through two lecithotrophic zoeal stages and a feeding megalopa was described in a fiddler crab, *Uca subcylindrica* (Fig. 2.12; see Rabalais & Cameron 1983, 1985).

This crab species releases its larvae in ephemeral rainfall puddles in semi-arid regions, where water persists only a short time and food is not normally available. The zoea I hatches in a morphologically advanced state, with developed pleopod buds corresponding to those of the zoea V stage in all other known *Uca* species (cf. *U. thayeri*, Fig. 2.10). *Sesarma curacaoense* (Fig. 2.11) shows a similar type of development as *U. subcylindrica*, although its larvae are only facultatively lecithotrophic, i.e. they eat food when it is available but are capable of endotrophic development when it is absent (see section 5.1). In those species, a partial or exclusive utilization of internal energy reserves is reflected by little or no larval body growth (cf. the carapace size of successive stages in Figs. 2.10, 2.11).

The king crab *Lithodes maja*, a subarctic deep-water species, may serve as an example from the marine anomurans. It produces extremely large larvae (Fig. 2.12), which develop through three zoeal stages and a megalopa to metamorphosis; all larval stages of this species are lecithotrophic (Anger 1996b). By comparison, most other marine anomurans have at least four feeding zoeal stages.

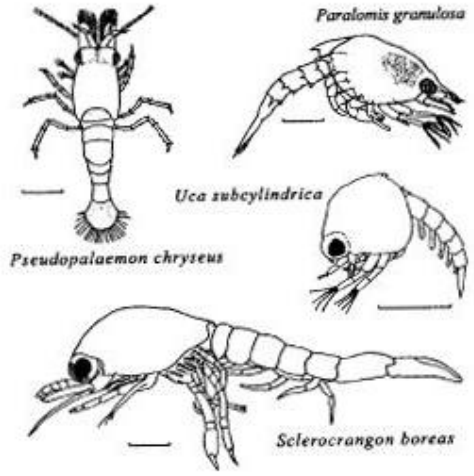


Figure 2.12. Lecithotrophic first-stage zoeae of decapod species with an abbreviated type of larval development; examples of caridean shrimps (*Pseudopalaemon chryseus*, *Sclerocrangon boreas*), anomurans (*Paralomis granulosa*), brachyuran crabs (*Uca subcyclindrica*; cf. regular development in *U. thayeri*, Fig. 2.10); scale bars: 1 mm (from: Magalhães 1987, with permission from INPA, Manaus, Brazil; Makarov 1968a, with permission from Brill, Leiden; Rabalais & Cameron 1983, with permission from The Crustacea Society, Seminole, FL, USA; Campodónico & Guzmán 1981, with permission from Brill, Leiden).

While the relationship between abbreviated development and food limitation appears plausible in most cases, others cannot be explained with limited or extremely seasonal food supply. At least one tropical marine spider crab, *Mithrax spinosissimus*, has a lecithotrophic development, without showing a recognizable selective advantage (Provenzano & Brownell 1977, Tunberg & Creswell 1988). Further exceptional cases of abbreviated or lecithotrophic larval development in tropical or moderate climates are known among the marine Brachyura (Hale 1925, 1931, Wear 1967), Anomura (Dechancé 1963, Provenzano 1968, Gore 1979, G.J. Morgan 1987a), Thalassinidea (Nates et al. 1997, Thessalou-Legaki et al. 1999), and Caridea (Dobkin 1968).

Lecithotrophy is frequently but not necessarily associated with an abbreviated mode of development. In several palaemonid shrimp species which live as adults in brackish or freshwater habitats, the larvae are rapidly exported to adjacent estuaries or coastal zones. In many of these species, only the zoea I is lecithotrophic, and this may be followed by numerous feeding stages (see section 10.3.1).

2.5 *Variability in morphological development*

The course of larval development in the Decapoda is, in general, considered as constant and species-specific in terms of the number and morphology of successive stages. How-

ever, intraspecific variability in the morphology of individual stages and in developmental pathways has been observed in numerous decapod taxa, both in the laboratory and field (e.g. Ewald 1969, Haynes 1979a, b, Criales 1985, Fincham 1985 and earlier papers, Charmantier & Aiken 1987, Díaz & Bevilacqua 1987, Wehrtmann 1989, Christiansen & Anger 1990, Minagawa 1990a, Montú et al. 1990, 1996, Linck 1995, Pestana & Ostrensky 1995, Mikami & Greenwood 1997a, Strasser & Felder 2000, Thatje & Bacardit 2000). This phenomenon appears frequently in taxa with a high number of larval instars (≥5) but less in those with a lower number of stages. Hence, variability of developmental pathways is common among the penaeid and caridean shrimps as well as in spiny lobsters, while it has never been observed in majid crabs, which almost invariably pass through two zoeal stages and a megalopa (only known exception: direct development in *Paranaxia serpulifera*; see Rathbun 1914, G.J. Morgan 1987b). In the terminology of the arachnological and insect literature, the majid pattern of development would be termed *canalized* (i.e. genetically fixed), while instable pathways are termed *plastic* (environmentally modified; Higgins & Rankin 1996). Naturally, some interpopulational variability (presumably associated with differences in average climatic conditions) may generally occur in larval body size, spine length, and morphometric details, even in taxa with a strongly canalized development such as the Majidae (Pohle 1991).

In arthropod taxa with a variable type of development, the possible range of variability within a species or population is bounded by genetic factors. Within these genetically set constraints, environmental factors may induce development through different pathways (Higgins & Rankin 1996). More immediately, both the number of larval molts and the morphological change between subsequent stages are controlled by intrinsic factors, namely the titer of neurohormones produced in the eyestalk ganglia and, probably, by juvenile-hormone-like factors such as methyl farnesoate, *MF*, produced in the mandibular organs (Knowlton 1994, Charmantier & Charmantier-Daures 1998, Abdu et al. 1998a, b; see chapters 3 and 4). The activity of those hormonal factors, on the other hand, is influenced by both intrinsic (genetically determined) developmental programmes and extrinsic (e.g. seasonal) parameters.

While the early investigators tended to consider developmental variability in decapod larvae as a laboratory artifact, there is at present no more doubt that the pathway of larval development can vary intraspecifically. In taxa where the genetically confined range of plasticity is wide, for example in caridean shrimps, the environmentally induced diversity of trajectories should be even greater in the natural pelagic environment than in the laboratory, where physical and nutritional conditions are kept more uniform (Knowlton 1965). This has been demonstrated also in krill and other euphausids (see e.g. Makarov 1974, Silas & Mathew 1977, Makarov & Maslennikov 1981), suggesting that developmental variability is a common trait in the ancestral taxa of the Eucarida.

Variable trajectories have been observed not only among conspecific hatches from different females, but also among sibling larvae reared together under identical conditions, reflecting primarily genetic variability (e.g. Christiansen & Anger 1990, Montú et al. 1990); as an additional, non-genetic cause of variability, maternal factors such as individual variability in egg size might play a role. In larval brown shrimp, *Crangon crangon*, for instance, intraspecific developmental variability has been documented starting from the second zoeal stage (Linck 1995). Three forms may be distinguished in the zoea II, differing slightly in total body size and, more conspicuously, in the development of the first pereiopod (P1; Fig. 2.13). In the morphologically most advanced larvae (form IIa), the P1

has a segmented endopod and an incipient terminal setation, while this ramus is unsegmented in the less advanced form IIb; in both forms, the exopod bears natatory setae. In the most retarded larvae (zoea IIc), both the endopod and the exopod are rudimentary, without segmentation and setae.

The degree of morphological variability increases in the later larval stages. In the zoea VI of *Crangon crangon*, four forms were described, differing again in body size and in the development of the appendages (Fig. 2.14). In the retarded form zoea VId, the P1 is similar to that in the zoea IIIa, the zoea IVb, or the zoea Vc. In the first decapodid stage, at least two forms can be distinguished, differing primarily in the developmental state of the antennae, the maxillipedes, the pereiopods, and the pleopods. Depending on its developmental state, this stage may molt to another decapodid instar or directly to the juvenile. As an additional pathway, a morphologically advanced zoeal stage (zoea IVa, Va or VIa) can skip the decapodid and develop directly to a benthic juvenile (Linck 1995).

In addition to intraspecific genetic and maternally caused variability, plastic responses to various environmental factors have been demonstrated in many species of decapod larvae (e.g. Knowlton 1974, Minagawa 1990a). In the larvae of both *Crangon crangon* and *C. allmanni*, for example, unfavourable rearing conditions such as unsuitable food supply, low salinities, or extreme temperatures tended to increase the number of stages, and hence, to decrease the rate of morphological development between successive molts (Criales 1985, Criales & Anger 1986, Linck 1995). This indicates that a prolonged developmental sequence with additional larval stages may occur also as an unspecific effect of stress. Hence, it is not surprising that an enhanced number of larval instars was observed in shrimp (*Palaemonetes pugio*) larvae reared under exposure to sublethal mercury concentrations; as an additional enhancement of morphological variability, the pollutant caused also deformities, in particular in telson morphology (Shealy & Sandifer 1975). Other toxic substances that are released into the aquatic environments should cause similar effects and thus, enhance the variability in developmental pathways of shrimps and other taxa with a plastic type of larval development.

In *Crangon crangon*, the principal developmental pathways vary also with season and geographical origin. As a consequence of seasonally varying egg size, larvae hatching in late winter or early spring are typically larger and have a shorter developmental sequence than summer larvae (Linck 1995, Paschke 1998; see section 10.2.3 of this volume). While this kind of variability reflects the generally high degree of plasticity in *C. crangon*, geographic variation might indicate that there are also genetic differences between regionally separated populations. According to preliminary observations, larvae originating from the western Baltic Sea tend to develop, under identical conditions, faster than those from the North Sea (Linck 1995). In seawater, larvae from the Baltic Sea population reached the first juvenile instar usually after only 4 or 5 stages (including normally one decapodid), while North Sea larvae needed 5 or 6 instars. However, this possible difference is veiled by high intrapopulational variability, with numerous developmental pathways and up to 8 larval stages in both populations (Criales 1985, Linck 1995).

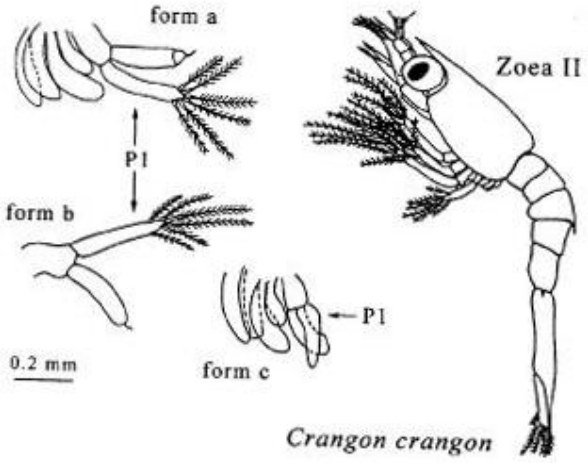


Figure 2.13. Intra-stage morphological variability in early caridean shrimp larvae; example: pereiopod 1 (P1) in three forms (a, b, c) of the zoea II stage of *Crangon crangon*; in forms a and c also buds of P2-5 shown, similar in form b (from Linck 1995, with permission from the author).

Plasticity in developmental pathways has been observed in virtually all higher decapod taxa, although not usually as pronounced as in the Caridea. Among the Brachyura, it is commonly found in portunid and grapsid crabs, especially in species that have relatively many zoeal instars (Montú et al. 1990). However, plasticity is not necessarily associated with a variable number of instars in a given developmental phase. In less conspicuous cases, it may be restricted to variability in morphological details or proportions of particular larval stages. On this level, at least some degree of variability may occur universally, even in taxa which show a constant number of larval instars. However, only few data on morphological plasticity are available for decapods other than shrimps and prawns. Among the exceptions, climatically induced regional variability in body size and spine length was observed in Dungeness crab (*Cancer magister*) zoeae from Alaskan and Californian waters (Shirley et al. 1987). In laboratory experiments where ovigerous females were held at various temperature conditions (1-15°C), significant effects were observed in posthatching size and morphometric traits, with larger larvae produced at lower temperatures.

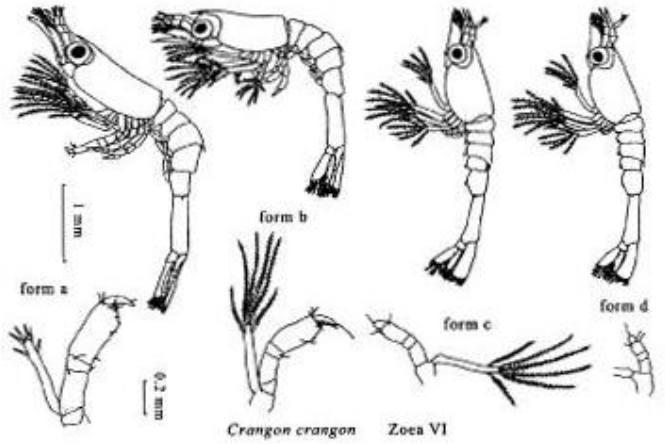


Figure 2.14. Intra-stage morphological variability in late caridean shrimp larvae; example: larval body size and pereiopod 1 in four larval forms (a-d) of the zoea VI stage of *Crangon crangon* (from Linck 1995, with permission from the author).

As another example of morphological plasticity in brachyuran crab larvae, we observed environmentally induced variability in the zoeae of *Eriocheir sinensis*, the Chinese mitten crab (Furigo & Anger, unpubl. data). After hatching (at 20 ‰), the larvae were reared at salinities of 15, 25, and 32 ‰, and growth in successive zoeal stages was measured as increase in total length (*TL*; defined as the distance from the tip of the rostral spine to the tip of the dorsal spine) and carapace length (*CL*). Interestingly, *TL* was observed to grow generally faster than *CL*, and this allometry was consistently stronger at reduced salinities. In consequence, the *TL/CL* ratio increased not only ontogenetically, but also with decreasing salinity (Fig. 2.15). Since this quotient is an indicator of spine length in relation to actual larval body size, these patterns may be interpreted as a morphological response to a decreasing boyancy both in lower salinities and in successively heavier larval stages. Proportinally longer carapace spines may thus help the larvae to maintain their vertical position in the water column, reducing their energetic costs for swimming against negative boyancy.

The developmental plasticity of *Eriocheir sinensis* larvae is not restricted to presumable morphometric responses to changes in boyancy. Under unfavourable combinations of low temperatures with low salinities, an additional zoeal stage (VI) and occasionally an additional megalopa was observed (Anger 1991b, Montú et al. 1996). The same phenomenon has been documented also in other grapsid crab species, including *Chasmagnathus granulata* (Pestana & Ostrensky 1995, Giménez 2000), *Armases (= Metasesarma) rubripes*, and several others (see Montú et al. 1990). Since plasticity in larval morphology and developmental pathways is closely linked with morphogenesis, the molting cycle, and growth, we will revisit this phenomenon of larval biology in the following sections.

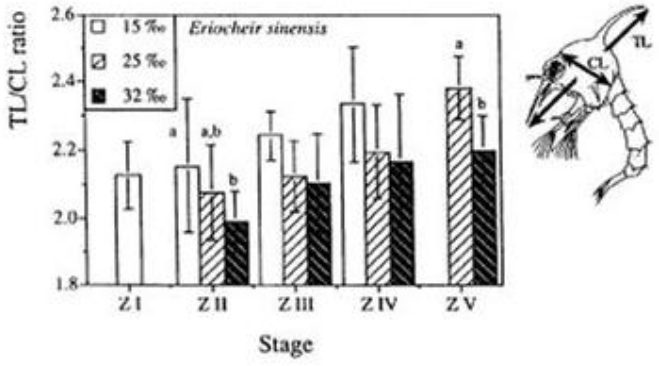


Figure 2.15. Morphometric relation (quotient, mean ±SD) between carapace length (CL) and total length (TL) from the tip of the rostral spine to the tip of the dorsal spine in the zoeal stages (ZI-V) of the Chinese mitten crab, *Eriocheir sinensis*, reared at different salinities (15, 25, 32 ‰; incubation of embryos and hatching at 20‰ (after Furigo & Anger, unpubl. data).

3 ANATOMY AND ORGANOGENESIS

Anatomical structures of adult decapod crustaceans are well documented in several textbooks and review articles (see Johnson 1980, Kaestner 1980, McLaughlin 1983, Bell & Lightner 1988, Felgenhauer 1992a, b, Harrison & Humes 1992, Forest 1994). However, the ontogeny of the general body plan and of the individual organs (organogenesis) have been studied much less until about two decades ago. Only recently has an increasing number of investigations addressed the anatomical features of decapod larvae. These studies suggest that most internal structures which are known from adult decapods appear early during embryonic or larval development, and they change only little in the later life-history phases. After a thorough investigation of the anatomy of crab larvae, Trask (1974) concluded that *"the major difference between the first, intermediate and last larval forms is basically one of size of the various systems involved, rather than absolute complexity."* However, there are also several conspicuous ontogenetic changes, which are generally associated with changes in life style, ecology, nutrition, or behavior.

In the internal organization of the larval body, nervous and alimentary systems occupy proportionally more space than in adult crustaceans (Figs. 3.1, 3.2); in the latter, muscle and gonad tissues are relatively larger. The ontogenetically early appearance of an advanced central nervous system is probably necessary for an adequate coordination of complex larval orientation and swimming behavior (see chapter 10), while an early developed alimentary system reflects the great nutritional requirements for sustenance of larval development and growth (see chapter 5). On the other hand, changing food sources exploited by larval and adult decapods, respectively, require significant ontogenetic changes in the functional morphology of the digestive tract and other organs involved in the acquisition and processing of prey (Factor 1989). In many decapods, particularly in estuarine species, the successive life-history stages also experience changes in the physico-chemical conditions of their particular environments, e.g. in salinity. Hence, conspicuous changes occur also in the anatomy and functionality of osmoregulatory organs and tissues (Bouaricha et al. 1994).

In this chapter, I review the general anatomy and principal organ systems of larval decapods, paying special attention to those structures which change ontogenetically, as these are most relevant for various aspects of larval biology. Where no major differences between larval and adult anatomy are known or suspected, I will sometimes infer details from well-documented adult features. This includes the use of some illustrations which were not available with similar clarity or completeness from published studies of larval decapods.

3.1 *Integument*

Comprehensive reviews of the *"Dynamics of the Integument"* of the Crustacea (Stevenson 1985), the *"External Anatomy and Integumentary structures"* of the Decapoda (Felgenhauer 1992a), and even an entire book on *"The Crustacean Integument - Morphology and Biochemistry"* (Horst & Freeman 1993) have recently been published, including historical accounts of important studies from the past two centuries. In general, the crustacean cuticle is similar to that in insects and other arthropods, for which further books and reviews

are available (see Neville 1975). It will thus suffice to summarize in this section the principal cuticular structures. Characteristic changes during individual molting cycles will be reviewed below (chapter 4).

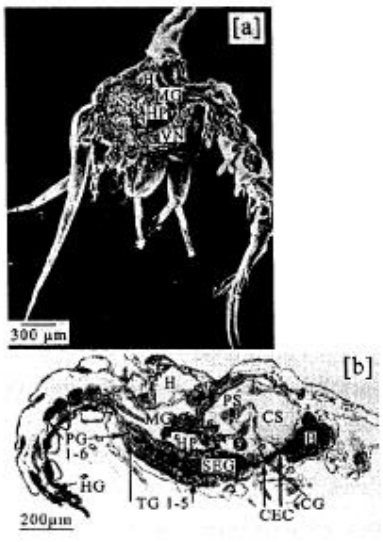


Figure 3.1. General anatomy of decapod larvae, whole mount parasagittal sections: [a] *Hyas araneus*, zoea II; paraffin-carved section (from Höcker 1988, with permission from the author; for description of paraffin-carving see Oshel 1985, Felgenhauer 1987); [b] *Carcinus maenas*, megalopa (from Harzsch & Dawirs 1993, with permission from BAH, Helgoland, Germany). B: brain; CEC: circumesophageal connective; CG: commissural ganglion; CS: cardiac stomach; H: heart; HG: hindgut; HP: hepatopancreas; MG: midgut; PG 1-6: pleon ganglia 1-6; PS: pyloric stomach; S: stomach; SEG: subesophageal ganglia; TG 1-5: thoracic ganglia 1-5; VNC: ventral nerve cord.

In larvae, the integument is generally thinner than in juvenile and adult crustaceans, but it has basically the same structure (Christiansen & Costlow 1982, Freeman 1993). It is comprised of a basement membrane, a single layer of low columnar to cuboidal epidermis cells which is covered by a thin membranous layer of proteins and chitin (the latter only in benthic forms), and the three-layered cuticle. A hypodermis with dermal glands is found beneath the epidermis (see sections 3.5, 3.7). Ducts of these glands as well as fine pore canals with extensions of epidermal and nerve cells pass through the adult cuticle; however, pore canals appear to be absent in crustacean larvae (Freeman 1993).

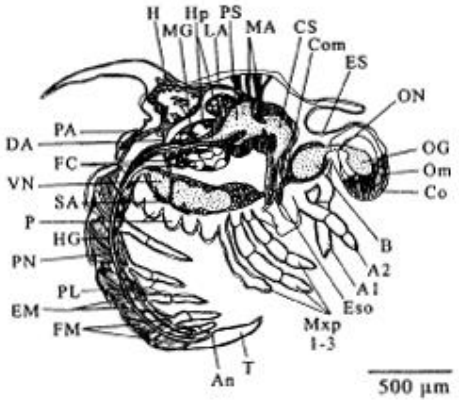


Figure 3.2. Anatomy of a decapod larva (megalopa of the yellow rock crab, *Cancer anthonyi*; reconstruction from parasagittal sections). A1: antennule; A2: antenna; An: anus; B: brain; Co: cornea of compound eye; Com: commissure; CS: cardiac stomach; DA: descending arteria; EM: extensor muscles; Eso: esophagus; ES: eye stalk; FC: ferment cells of digestive gland (hepatopancreas); FM: flexor muscles; H: heart; HG: hindgut; Hp: hepatopancreas; LA: lateral arteria; MA: mandibular adductor muscles; MG: midgut; Mxp 1-3: maxillipeds 1-3; OG: optic ganglia; Om: ommatidium of compound eye; ON: optic nerve; P: pereiopod stumps; PA: posterior aorta; PN: pleon nerve; PS: pyloric stomach; PL: pleopods; SA: sternal arteria; T: telson; VN: ventral nerve mass (after Trask 1974; with permission from Springer, Heidelberg, Germany).

Based on mitotic activity and morphogenetic specialization, we may distinguish six different cell types in the epidermis of larval crustaceans (Freeman 1993): (1) *Larval epidermal cells* show rapid replication in the cell cycle that accompanies the molting cycle. As a consequence of their high mitotic activity, they have a low cytoplasm to nuclear volume ratio and remain unspecialized. They may differentiate to one of the following cell types. (2) *General epidermal cells* show a slower replication rate and a proportionally larger cytoplasm volume. They are involved in the formation of cuticle structures. (3) *Arthrodial membrane cells* are found beneath the specially thin cuticle that is characteristic of the regions between segments or somites, in particular at sites of epidermal invagination (see section 4.1.3). (4) *Seta and spine cells* form so-called *"setal organs"*, which control the complicated mechanism of setagenesis during the molting cycle. At least in *Artemia*, they may become polyploid. (5) *Tendinal cells* (also termed *tendon* or *tendonal* cells) are characterized by microtubules and microfilaments, and by a pronounced peripheral location of the nucleus. Their function is the attachment of muscles to the cuticle. (6) *Gill cells* are specialized epidermal cells in regions where gills or related structures develop. They show greatly folded membranes in the apicolateral cell region and in general little attachment to the cuticle.

Within the cuticle, the innermost, relatively thick layer is termed *endocuticle*. It is followed by the *exocuticle* and, on the surface, by a thin *epicuticle*. At the electron-

microscopical level, each of these principal layers appears multilayered, revealing a highly complex structure. The epicuticle is comprised of tanned lipoproteins and is, at least in adult crustaceans, free of chitin (Johnson 1980, Stevenson 1985). The other two layers contain densely packed lamellae of chitin-protein microfibrils, usually in a characteristic helical appearance. While the exocuticle is chinone-tanned, this appears not to be the case in the endocuticle. In benthic stages, both the endocuticle and exocuticle may be further strengthened by calcium salts, the deposition of which is controlled by cytoplasmatic extensions of the underlaying epidermal cells. These reach through the pore canals to the basis of the epicuticle. The exocuticle may be impregnated with melanin pigments.

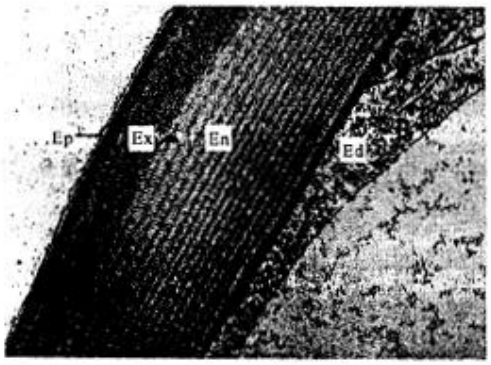


Figure 3.3. Ultrastructure of the larval integument (TEM): *Pagurus bernhardus* (Anomura), zoea II; Ed: epidermis; En: endocuticle; Ep: epicuticle; Ex: exocuticle (from Jarminowski 1990, with permission from the author).

The endocuticle of planktonic decapod larvae is generally unmineralized and much thinner than in benthic juveniles and adults, especially in relation to the exocuticle; the membranous layer is still lacking (Christiansen & Costlow 1982, Freeman 1993). This structure (Fig. 3.3) is typical of pelagic crustaceans in general (Pütz & Buchholz 1991), probably because increasing energetic costs for swimming would not allow for the development of a heavier cuticle. Since a pelagic or semipelagic life style is considered as ancestral in the Decapoda, the thin larval cuticle may represent the phylogenetically original condition (Scholtz & Richter 1995).

After the metamorphic molt from the last pelagic zoeal stage to the semibenthic megalopa (especially in brachyuran and anomuran crabs), the endocuticle becomes proportionally thicker and shows an incipient mineralization, at least in the carapace region (Höcker 1988). This fortified integumentary structure may provide a mechanical protection against

parasites and small benthic predators. The pelagic stages, in contrast, may escape from predation by rapid jumping (or "flying"; Verity & Smetacek 1996). This behavioral response is possible due to the light cuticle and a relatively high investment in the formation of pleonal and/or thoracal musculature. As an additional (morphological) adaptation, zoeae show frequently long carapace spines which may serve against both small pelagic predators (e.g. fish fry) and passive sinking (see sections 2.5, 10.1.6).

Conspicuous developmental changes in the integument should be expected also in cases where the benthic adults show a special life style. One of the most peculiar adaptations was described in hermit crabs (*Pagurus bernhardus*), where the pleonal cuticle is unusually thick and uncalcified, showing deep wrinkles, grooves and funnel-shaped gland ducts (Erri Babu & Anger 1987). These structural modifications function as an adhesive organ which, together with proteinaceous secretions from underlying gland cells, attach the surface of the pleon to the inner walls of the snail shell. These structures begin to develop in the megalopa stage (Jarminowski 1990), which is known to settle and to accept early a shell (Dawirs 1981).

3.2 *Gills and associated structures*

Besides fulfilling a protective function, the integumentary system is also a route for the transport of gases and ions between the external medium and the body fluid (respiration, excretion, osmoregulation, ion regulation). In adult decapods, these transport processes take place in the gills and other specialized, permeable regions of the body surface, namely in the inner walls of the lateral carapace folds, the *branchiostegites* and adjacent tissues of the branchial chamber. Comprehensive reviews of morphological, histological, ultrastructural, biochemical and biophysical properties of transport tissues and cells were given by Mantel & Farmer (1983), McMahon & Wilkens (1983), Felgenhauer (1992b), Taylor & Taylor (1992), Schoffeniels & Dandrifosse (1994), Péqueux (1995), and Charmantier (1998). Regardless whether their main function is in the transport of gases or in that of ions, these organs have some features in common: a thin and uncalcified cuticle (increased permeability), an amplification of the surface area, an external ventilation of the medium (not in early larval stages), and an internal perfusion with hemolymph. Exchange processes depend on both diffusion and membrane transporters.

Gills arise in the Decapoda near the dorsal junction of the coxae of thoracic appendages with the body wall and extend into a branchial chamber, which is formed by the ventrolateral extensions of the carapace. While blood vessels perfuse the gills and branchiostegites internally, external ventilative currents are created by the scaphognathites (fused exopods and epipods of the maxillae); these are also referred to as "gill bailers" (Felgenhauer 1992b). Water enters the branchial chamber through ventral and posterior openings (in adult crabs only through an inhalant opening above the second maxilliped) and usually leaves it near the mouth. Van Dover et al. (1982) compared and classified the ontogeny of the scaphognathites in 340 species of anomurans and brachyurans, obtaining eight types of larval morphology. These features are considered also as valuable criteria in the taxonomical classification of higher decapod taxa.

In adult Decapoda, we distinguish up to four principal gills in each thoracic segment, depending on their position of attachment (Fig. 3.4): (1) a *pleurobranch* inserted in the body wall above the base of the appendage, (2) an anterior and (3) a posterior *arthrobranch* attached to the arthrodial membrane between the coxa and the body wall; (4) a *po-*

dobranch inserting in the coxa of the thoracopod. In addition, sometimes an *epipod* (also termed *flabellum* or *mastigobranch*) and small *setobranchs* are present on the coxa. While the number and arrangement of gills (the gill formula) are considered as a phylogenetic criteria and thus, are used in the taxonomic classification of the Decapoda, the gill surface area changes with habitat conditions and individual growth.

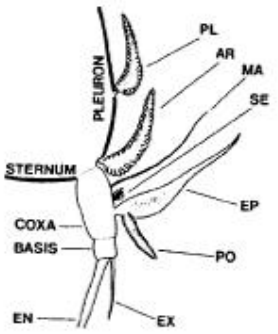


Figure 3.4. Terminology of gills and associated structures in adult decapods (schematic presentation; note: not all of these structures are necessarily present on a single appendage); AR: arthrobranch; EN: endopod; EP: epipodite; EX: exopod; MA: mastigobranch; PL: pleurobranch; PO: podobranch; SE: setobranch (from Hong 1988b, with permission from Taylor & Francis, London; see www.tandf.co.uk).

In different taxonomical groups of the Decapoda, three principal morphological types of gill are distinguished: (1) *dendrobranchiate* (only in the Penaeioidea and Sergestoidea), (2) *trichobranchiate* (in crayfish, lobsters, some dromiacean crabs), and (3) *phyllobranchiate* (in Caridea, Anomura, and most Brachyura); also intermediate forms have been found. The dendrobranchiate type has a central axis, from which paired lateral branches arise, each showing numerous secondary rami. The latter are consistently absent in trichobranchiate gills, where tubular rami arise in a serial order from the central axis. The structure of phyllobranchiate gills is similar, but their rami are leaflike in shape. Despite differences in the vascularization and gross morphology of these gill types, their functional anatomy is basically the same. As a result of specialization of the branchial epidermis, some distinctive types of tissues and cells occur in all gills and associated structures (for comprehensive review of histological and ultrastructural details, see Taylor & Taylor 1992).

In brachyuran crabs (but not in lobsters and crayfish), there are striking morphological and functional differences between the anterior and posterior portions of each gill. The former have predominantly a respiratory function (although also showing responses to osmotic changes), while the latter serve primarily in osmoregulation and ion regulation. Particularly thin epithelial structures are found in the anterior parts, where gas transport takes place. In the posterior areas, the presence of numerous mitochondria and extensive infoldings in the basal and lateral membranes are considered as characteristic features of cells that are involved in ion transport (*ionocytes*). In this region, at least six different cell

types occur in the Decapoda (Felgenhauer 1992b, Taylor & Taylor 1992). Similar anatomical structures were observed in the branchiostegites.

Although functional gills are generally absent in the early larval stages (at least in crabs; this is probably different in lobsters), a capacity of hyper-osmoregulation in dilute media occurs in several decapod taxa from the time of hatching (Charmantier 1998; cf. section 10.1.2 of this volume). However, there is little information about the ontogeny of the underlaying mechanisms. In nauplius larvae, the entire body surface may participate in respiration, excretion and other processes of transport and regulation. The zoea, in contrast, has a more rigid exoskeleton and a lower relation of body surface:volume and thus requires specialized integumentary structures. In histological and electron microscopical investigations, ion transporting tissues could be detected in the larval branchiostegites and adjacent structures associated with the branchial chamber (Talbot et al. 1972a, b, Felder et al. 1986, Furigo 1993, Bouaricha et al. 1994). As typical traits, they feature an attenuated cuticle, stain with silver techniques, and show structural modifications that are known from adult gills (see Mantel & Farmer 1983, Péqueux 1995). These comprise enlarged epidermal cells with deep basal infoldings of the cytoplasmic membrane, an apical microvilli border, and numerous elongated, cristate mitochondria (Fig. 3.5).

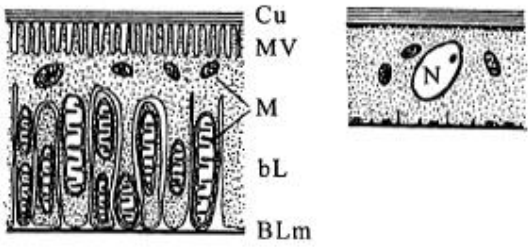


Figure 3.5. Ultrastructure of a putative ion-transporting cell (ionocyte) from the gill region of a larval mitten crab, *Eriocheir sinensis* (left); comparison with a non-transporting epidermal cell (right); schematic views (reconstructed from TEM); bL: basal labyrinth; BLm: basal lamina; Cu: cuticle; M: mitochondia; MV: microvilli; N: nucleus (from Furigo 1993, with permission from the author).

Gill buds have been observed from the late zoea phase, initially inserting in the basicoxal part of the developing thoracopods, before they migrate to their final positions. Lamellate, functional gills are typically found only in decapodids and juveniles (Hong 1988b, Furigo 1993, Bouaricha et al. 1994). The Chinese mitten crab, *Eriocheir sinensis*, may be an exception. It lives in freshwater during the juvenile and adult life-history phases, but its larvae hatch and develop under brackish or marine conditions. The gills are highly developed and show an early lamellisation, suggesting that they may become partially functional in the last zoeal stage (Fig. 3.6). Thus, the ontogenetic return of mitten crab larvae from the lower to the upper estuarine zones (i.e. from saltwater toward limnic

conditions) may begin already during the metamorphic transition from the pelagic zoea V to the semibenthic megalopa.

Due to the application of electron-microscopical and new vascular casting techniques, the understanding of the structures and functions of gills and associated tissues has greatly increased in the past two decades. For instance, recent studies have shown a particularly great importance of the brachial septum or analogous structures for the separation of unoxygenated and oxygenated hemolymph, and the return of the latter to the pericardial sinus (Taylor & Taylor 1992). However, details of the ontogeny of respiratory structures in gills and lungs have remained widely unknown. The same applies to the ontogeny of ion transporting cells and tissues (Charmantier 1998).

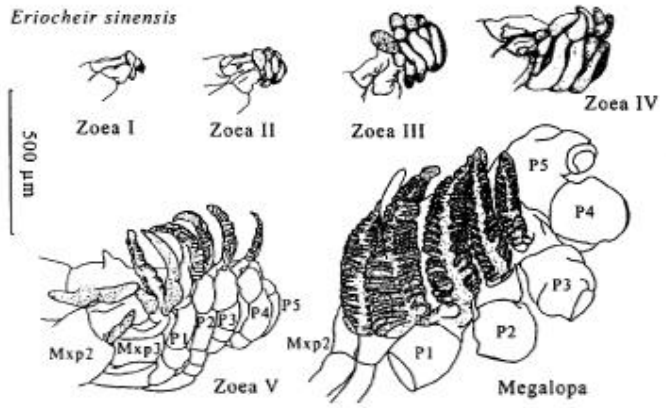


Figure 3.6. Ontogeny of gills in the larval stages (zoea I-V, megalopa) of the Chinese mitten crab, *Eriocheir sinensis*. MXP2, 3: maxillipeds 2, 3; P1-5: pereiopods 1-5 (from Furigo 1993, with permission from the author).

3.3 *Sensory organs*

Integumentary sensory structures are quite common and frequent on the entire body surface, where physical and chemical signals from the surrounding environment must be detected. Besides some specific sensors that perceive only one kind of information (*mechanoreceptors, chemoreceptors*), most are bimodal (mechanochemoreceptors), combining the anatomical features and functions of the two types. Other sensors monitor the movements and positions of own joints (*proprioreceptors*). The highest concentrations of integumentary sensors are found in the antennules, antennae, mouthparts, and walking legs, where the encounters with food and substrates are most frequent. Extensive reviews of morphology, ultrastructure, electrophysiology and functions of integumentary and proprioreceptive sensors were given by Derby (1989), Wiese et al. (1990), Felgenhauer (1992a), Fingerman (1992), Govind (1992), and Chaigneau (1994b). A brief summary of the most

common types and their occurrence in larvae should thus suffice in this section. Besides mechano- and chemoreceptive sensors, crustacean larvae possess dorsal organs with practically unknown functions, as well as nauplius eyes and two major types of compound eyes, which will be reviewed below.

In larval decapods, the maxillipeds are in general the most important feeding appendages, and hence, show the highest density of mechano- and chemoreceptive sensors (for general review of larval sense organs see Laverack 1988a, b). Their number on larval limbs is low in early stages but increases gradually during development. The same should apply to muscle receptor organs and other proprioreceptors, but practically nothing is known about their ontogeny. Each sensor is innervated by at least one neuron, usually by more. In aesthetascs, up to about 350 primary afferents were counted. As a consequence of the increasing number of receptors and new axons, the central nervous system develops an increasing number of appropriate new junctions.

3.3.1 *Mechanoreceptors*

Structure, functional mechanisms, anatomical classification, and numerous other aspects of mechanoreceptive organs have been extensively reviewed in the treatise *"The Biology of Crustacea"* (Bush & Laverack 1982). Among these sensors, some are proprioreceptive, others perceive water currents and mechanical contacts with food or predatory organisms. While various types of muscle receptor organs and further proprioreceptive sensor types are located within the body, primarily monitoring movements and posture of muscles and skeletal elements, cuticular and supracuticular mechanoreceptors are found on the body surface (Govind 1992). Most of the existing knowledge has been obtained from adult rather than larval crustaceans, but the available evidence suggests that most organs are already present and structurally similar in the free-living larval stages.

Mechanoreceptive setae (*sensillae*; Fig. 3.7) belong to the most frequent integumentary organs. They have usually a movable socket at the base and various other cuticular components that are produced by enveloping cells. Information of mechanical deformations is conveyed by bipolar hypodermal neurons. Several types of sensillae have been identified (Felgenhauer 1992b), for instance *"cuticular articulated peg"* organs that occur in clusters on walking legs and mouthparts of lobsters (but not on brachyuran crabs). When they are located around joints, they may also function as proprioreceptors. On the flexible joints of walking legs, also *"funnel canal organs"* have been observed, presumably with similar functions. Low-frequency vibrations may be detected by *"hair-fan organs"*, functionally comparable with the lateral line systems of fishes. Furthermore, *"scale organs"* and *"tuft organs"* were described as putative mechanoreceptors. Also the *statocyst*, which is normally located in the base of the antenna, may be considered as a mechanoreceptor.

Nishida & Kittaka (1992) described the morphology and location of seven different types of integumental mechanoreceptors in final-stage phyllosoma larvae of a spiny lobster, *Jasus edwardsii*. Comparison with the structure of adult receptors suggests that the sensory organs on the dorsal surface of the larval cephalosome function as current sensors. While the number of sensillae increases in general during the course of larval development, some may be specific larval organs and thus, disappear or change their form after metamorphosis (Laverack 1988b).

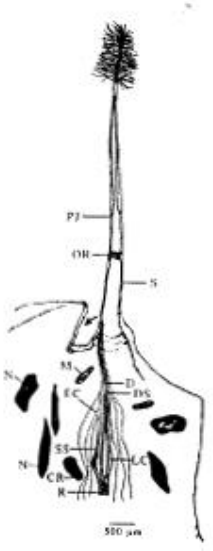


Figure 3.7. Mechanoreceptive sensilla (schematic drawing) of a shrimp, *Atya innocous*. CR: ciliary region; D: dendrites; DS: dendritic sheath; EC: enveloping cells; LC: liquor cavity; M: mitochondrium; N: nucleus; OR: occluded region; PJ: pseudojoint; R: rootlet; S: seta; SS: support structure (from Felgenhauer & Abele 1983a, with permission from The Crustacea Society, Seminole, FL, USA).

3.3.2 *Chemoreceptors*

Chemical signals convey information about the quality of water or benthic substrata, the presence and adequacy of food (odor, taste), presence and sexual state of conspecifics (*pheromones*), or the presence of predators (*kairomones*) (Derby & Atema 1988, Laverack 1988a, Rittschof 1992, Hallberg et al. 1997). In late larval stages, waterborne cues from the adult habitat, e.g. from estuaries or salt marshes, play a crucial role in the metamorphosis of decapod species (see section 10.5.1 of this volume). All those environmental signals are perceived with specialized sensory organs on the body surface, referred to as chemoreceptors (for review see Ache 1982, Govind 1992) In addition, there are also internal chemoreceptors which stimulate the mechanical and chemical digestion in the foregut, midgut and hepatopancreas; putative chemosensory cells have been detected in the developing stomach of lobster embryos (Meier & Reichert 1990). The innervation of the various chemoreceptors was reviewed in detail by Govind (1992).

Two major types of chemoreceptive setae may be distinguished, with and without apical pores. Communication between the environment and microtubules in the receptor may thus be provided either by means of open pores (Fig. 3.8) or through a very thin cuticle. The pore type is typically found in the aesthetascs (sensory hairs of the antennules), which are widespread among larval decapods (Laverack 1988a, Nishida & Kittaka 1992, Hallberg et al. 1992). Other chemoreceptors are commonly found on the maxillipeds and other mouthparts and on the dactyls of the pereiopods, some of these responding to changes in salinity. In the gills of a clawed lobster, a putative receptor for oxygen concentration was detected and described morphologically and ultrastructurally (Laverack & Saier 1993).

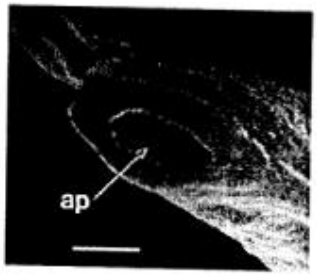


Figure 3.8. Chemoreceptive sensilla (tip) of a shrimp, *Atya innocous*. ap: apical pore; SEM, x30.000 (from Felgenhauer & Abele 1983a, with permission from The Crustacea Society, Seminole, FL, USA).

3.3.3 *Dorsal organs*

This organ complex occurs in a wide range of crustaceans. In decapod larvae, it is located in the frontal carapace region between the eyes. While it was originally considered as peculiar of the zoeal and decapodid phases of larval development (Laverack 1988b), a more recent paper describes it also from adult shrimps (Laverack et al. 1996). It is not identical with the embryonic "dorsal organ" of many arthropods (Kaestner 1980), but it appears similar to the *glabella* of trilobites (Barrientos & Laverack 1986). At present, however, it remains uncertain if these organs are homologous.

The morphology, histology and ultrastructure of dorsal organs have been extensively studied by M.S. Laverack and collaborators (see Laverack 1988b, 1990, Laverack et al. 1996). They consist in general of one central glandular portion and four peripheric sensory grooves, each with a diameter of a few micrometers. According to histological and ultrastructural studies, the dorsal organs fall into two major categories. One shows a great morphological diversity and probably various, widely unknown functions, the other is the *"sensory dorsal organ"* of Laverack. Its innervation originates at the tritocerebrum region of the brain, reaching the dorsal organ indirectly through the tegumentary nerve (Laverack & Sinclair 1994). The body of available evidence suggests that the sensory dorsal organ may be a pressure detector (*baroreceptor*; Laverack et al. 1996).

3.3.4 *Nauplius eye and frontal organs*

The ancestral nauplius eye is typical of the naupliar phase, but it persists in most decapods (except for most Brachyura) throughout the adult phase. Together with ventral and dorsal frontal organs, it forms a *median eye complex* (Elofsson 1963, 1966). The term "frontal organ", however, has sometimes also been applied to the organ of Bellonci, which is treated in section 3.9.3.

In early penaeid larvae, the unpaired nauplius eye is the only functional eye. It consists of three or four *pigment-cup eyes* with variable numbers of photoreceptor cells. The globose pigment-cup eyes are enclosed in a cup-shaped layer of pigment cells. Photoreceptor cells are located in the proximal-central region, forming a dense border of microvilli, the

rhabdomeres. Dense layers of endoplasmatic reticulum, the *phaosomes*, function as a primitive lense. From each photoreceptor cell, a nerve axon passes towards the protocerebrum. Since the pigment-cup eyes have a partial pigment screen for the retina, some directional vision and a perception of different light intensities is possible during the nauplius phase. This allows for an initiation of the "shadow response" (see section 10.1.3.3), but not for forming an image (Cronin 1988).

The ontogeny of the median eye complex was studied in much detail in the larvae of several decapod species, mostly in those of penaeid and caridean shrimps (Elofsson 1963, 1966). A gradual development throughout the naupliar phase was observed in larval Dendrobranchiata, while the higher Decapoda hatch from the egg with well developed and functional nauplius eyes and dorsal organs (see Fig. 3.13). In penaeids, the nauplius eye is present from hatching, but becomes functional only from the fourth or fifth nauplius stage. Both the dorsal and ventral frontal organs are in this taxonomic group reduced, both in the adults and larvae.

3.3.5 *Compound eyes*

The compound eyes of the Decapoda and other crustaceans have been subject of intensive research throughout the past two centuries (for review of their anatomy and physiology see Cronin 1986, 1990, Fordyce & Cronin 1989, Hallberg & Elofsson 1989, Nilsson 1989, Dall et al. 1990). Some authors suggested that the structure of compound eyes may be a conservative character within broad taxonomical limits and thus, should represent a useful criterion in phylogenetic considerations (Shaw & Stowe 1982, Cronin 1986, Fincham 1980, 1984, 1988, Land 1980, Gaten 1998, Harzsch et al. 1999a). Others, however, argued against taxonomical relationships between optical design and phylogenetic position. Since the optic design of compound eyes varies not only among different taxa but also during ecologically and behaviorally different phases of the life cycle (e.g. planktonic larvae *vs.* benthic adults), it may represent an adaptation to differential needs rather than a phylogenetically conservative trait (Nilsson 1983, Nilsson et al. 1986, Douglass & Forward 1989).

Compound eyes consist, in general, of numerous stereotyped subunits, the *ommatidia*, and each of these has a fixed number (usually eight) of concentrically arranged light-sensitive *retinular cells.* The inner face of these cells is characterized by closely packed microvilli that are concentrated in the light path. This photosensitive membrane structure is termed *rhabdom*. Between the photoreceptor cells there are optically isolating *pigment cells*, while groups of *cone cells* form the *crystalline cone* above them. These are covered by transparent sections of the cuticle, the outer *cornea*. This array of optical elements in each ommatidium shields the rhabdom against scattered light and thus enhances the directionality of vision. At the proximal end, bundled axons pass from the retinula cells through holes in the basement membrane to the optic ganglia of the central nervous system.

As an inevitable consequence of this optical design, there is a trade-off between light sensitivity and resolving power. This can be shown in the two main types of compound eyes, which can be distinguished according to the distance between the crystalline cone and the rhabdomeres of the retinula cells. In the *apposition eye*, the retinular cells touch apically the base of the cone cells. In the *superposition eye*, the retinular and cone cells are separated by a wide space of crystalline threads. Since each of their rhabdomeres receives light also from neighbouring ommatidia, this eye type has, in general, a lower optical

resolution than the apposition type; however, this disadvantage is mitigated by special optical modifications (Gaten 1998). On the other hand, this eye type is more light-sensitive and thus, advantageous for species that live under dim light conditions (most aquatic crustacea). Within each of these two principal eye types, several specific designs may be distinguished in the Decapoda (Nilsson 1989).

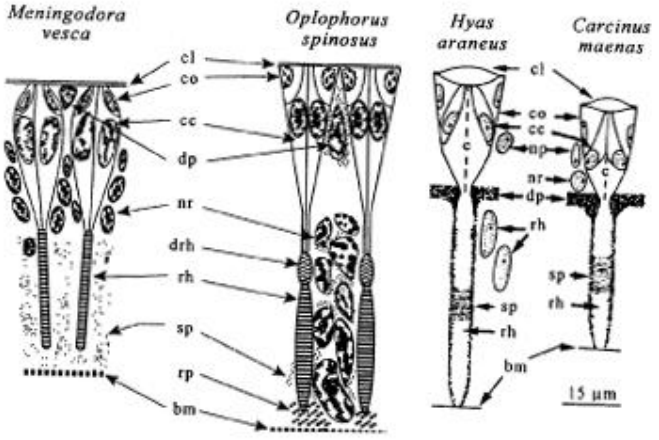


Figure 3.9. Ommatidia (schematic drawing) of the zoea I of oplophorid shrimps (*Meningodora vesca*, *Oplophorus spinosus*) and brachyuran crabs (*Hyas araneus*, *Carcinus maenas*). bm: basement membrane; c: crystalline cone; cc: crystalline cone cell; cl: corneal lens; co: corneagenous cell; dp: distal pigment; drh: distal rhabdom; np: nucleus of pigment cell; nr: nucleus of retinula cell; rh: rhabdom; rp: reflecting pigment; sp: shielding pigment (from Gaten & Herring 1995, with permission from Wiley, New York, USA; from Harzsch & Dawirs 1995a, with permission from Spektrum, Heidelberg, Germany).

In a recent review, Gaten (1998) suggests that the reflecting superposition eye is a symplesiomorphic trait, i.e. it was probably present already in the ancestor of the Decapoda. It was evolved only once (probably during the Devonian) from the ancestral type, the apposition eye. According to this hypothesis, it was later lost in some taxa, either as an adaptation to particular new habitats (e.g. in the families Aristeidae and Aeglidae) or by *progenetic paedomorphosis* (in the paguroid hermit crabs and the higher brachyurans). The latter phenomenon is a particular type of heterochronic development, where *"sexually mature adults possess features characteristically found in early developmental stages of related forms (e.g. juvenile or larval features)"* (Brusca & Brusca 1990). Comparing the ontogeny of compound eyes and neurogenesis in various decapod crustaceans and in hemimetabolous insects, Harzsch et al. (1999a, p. 294) found *"considerable similarities in the mechanisms by which accretion of compound eyes and growth of the optic lobes is achieved, suggesting an evolutionary conservation of these mechanisms"*.

Among the Decapoda, the ontogeny of complex eyes was studied in penaeid and caridean shrimps (Elofsson 1969, Fincham 1984, Douglass & Forward 1989, Gaten & Herring 1995), anomurans (Fincham 1988), crayfish (Hafner et al. 1982), clawed and spiny lobsters (Parker 1890, Meyer-Rochow 1975), and in brachyuran crabs (Harzsch & Dawirs 1995a). In general, decapod larvae hatch with apposition eyes (Fig. 3.9). These are retained throughout all life stages in some Brachyura. In most other decapods, the apposition eyes are gradually transformed to the superposition type during the late larval and/or the juvenile phase. As exceptions, some pelagic and hydrothermal vent shrimps (Oplophoridae, Bresiliidae) with an abbreviated (advanced) type of development hatch with superposition eyes (Gaten & Herring 1995, Gaten 1998, Gaten et al. 1998a, b).

In penaeid shrimps, the freshly hatched nauplius has not only a functional nauplius eye, but also clearly developed *anlagen* of compound eyes. These consist of two flat optical discs that are located between the bases of the antennules (Elofsson 1969). Their cells have large nuclei and show frequently mitotic activity. In consequence, the *anlagen* increase in size and differentiate gradually throughout naupliar development, together with neuronal, vascular and muscular structures of the future eyestalk. Remarkably, fully formed compound eyes with ommatidia and optic centra appear only in the second protozoea stage. Hence, the protozoea I is, in this respect, transitional between a nauplius and a zoea larva, although it has been assigned to the zoeal phase of development according to its external functional morphology (see section 2.2). The gradual development of the compound eyes proceeds in penaeid shrimps throughout the subsequent protozoea, mysis, and "postlarval" stages, showing an increase in the number and packing of ommatidia. The adult structure is approximated in the final ("postlarval") phase of larval development. There is still a considerable discrepancy in the state of development in early "postlarval" and adult eyes, indicating that the gradual perfection of their structures continues in the juvenile phase (Elofsson 1969).

Compared with the Dendrobranchiata, the Pleocyemata have a more condensed type of development, passing through the naupliar phase within the egg membrane. In consequence, the larvae hatch from the egg in a more advanced state of development, with fully functional compound eyes. These show hexagonally packed, roughly circular lenses with apposition optics. In later stages of larval and juvenile development, they are gradually squared and eventually, acquire the superposition optics (Fincham 1984, 1988).

In shrimp and anomuran larvae, the eyes appear to be more developed in the dorsal and posterior parts, with larger and more densely packed lenses, while the ommatidial units in the ventral and anterior parts are set further apart. The former, which show a particularly high resolution, face upwards in the normal swimming position. This arrangement allows for scanning the water column above, which is probably an adaptation for planktonic larvae to regulate their depth position according to light levels and to avoid approaching predators. The anterior and ventral parts of the eyes, in contrast, have a lower resolution but an enhanced sensitivity. At least some species appear to use superposition optics in these eye parts and can thus perceive weaker light signals from the water column below (Fincham 1988, Gaten & Herring 1995).

The larvae of brachyuran crabs hatch with apposition eyes which are similar to those of the adults. Besides the optical design, the visual pigments (rhodopsins) also show an early appearance of the species-specific adult type (Cronin et al. 1995). In a comparative study of two species, the spider crab *Hyas araneus* and the portunid *Carcinus maenas*, differences in the size of the eyes as well as in the numbers and lengths of ommatidia were ob-

served, corresponding with differences in larval body size (Harzsch & Dawirs 1995a). The relative length of the rhabdom appears to be species-specific, remaining rather constant during larval development (ca. 57 to 60% of total ommatidium length in *C. maenas*, 64 to 68% in *H. araneus*). The diameter of the hexagonal facets, in contrast, varies only little (between 14 and 17 µm), independent of the species and developmental stage. During the course of development, in both species, more ommatidia are added and packed at an increasing density. Consequently, the interommatidial angle tends to decrease, which enhances the power of optic resolution. Consistently smaller angles and higher numbers of ommatidia in *H. araneus* suggest that the spider crab larvae have a better vision than larval shore crabs, but otherwise, only minor histological differences were found between these species. During later development, changes of proportions take place within the eyes of both species. In particular a lengthening occurs in the crystalline cone in relation to the corneagenous cells. The pigment shield becomes more elaborate with pigment cells appearing between the crystalline cones. In caridean shrimp larvae, the late development of the adult eye pigment pattern has been interpreted as an adaptation to larval life in the plankton, where a transparent appearance may serve as a camouflage and thus reduce predation (Nilsson 1983, 1989, Douglass & Forward 1989).

3.4 *Circulatory System*

Among the Crustacea, the circulatory system of the Decapoda and other Malacostraca is relatively well developed (for review see Kaestner 1980, McLaughlin 1983, Felgenhauer 1992b, Martin & Hose 1992, Gribble 1994, McMahon 2001). However, as a consequence of the general coelom reduction in the Arthropoda, it is also here partially reduced and open, so that the blood and coelomatic fluids are mixed (therefore named *hemolymph*). The circulatory system of larval decapods is very similar to that of the adults (see Fig. 3.2). Veins are almost absent and functionally replaced by open *sinuses*, from where the venous hemolymph returns to the pericardium, and eventually, through paired ostia (in the Decapoda most commonly three) into the heart. The direction of the hemolymph flow is controlled by valves in the ostia and aortae. The heart lies in the pericardial sac, directly beneath the dorsal integument of the posterior ("cardiac") carapace region. As main vessels, an anterior (or ophthalmic) and a posterior aorta (*AA*, *PA*), a descending artery (*DA*), and two paired lateral arteries (*LA*) have been identified in both adult and larval decapods. The *AA* and *PA* may be considered as extensions of the heart although they do not have muscles (Kaestner 1980). The *AA* branches into several progressively smaller arterioles and provides the brain and the eyestalks with hemolymph; in many adult decapods it is functionally supported by an "auxiliary heart", the *cor frontale*. The *PA* serves the pleonal musculature, and the *LA*s the alimentary system, the antennal glands, mouthparts, and swimming appendages. The *LA*s branch off from the anterior part of the heart. The *DA* (originally paired) leaves the heart from the posterior portion, passing ventrally through the nerve cord and then continuing both anteriorly and posteriorly as a sternal or subneural artery (Fig. 3.2). It transports hemolymph to the thoracopods, mouthparts, and the ventral nerve cord. All arteries open sooner or later into the large ventral sinus or other open spaces, from where the hemolymph passes through body cavities and respiratory organs (gills or branchiostegites) before it eventually returns to the heart.

The hemolymph consists of the serum fluid and several types of blood cells (*hemocytes*) suspended therein. The former has its principal functions in the transport of respira-

tory gases and excretory, nutritional and hormonal compounds. The latter are primarily involved in coagulation (wound repair) and immunological and pathological functions such as phagocytosis of foreign particles and dead cells. The unpigmented hemocytes are produced in hematopoietic tissues, which are located near the rostrum (in shrimps), or attached to the cardiac stomach (in lobsters and crabs). They vary in morphological, physiological and biochemical characters (Williams & Lutz 1975, Martin & Hose 1992, Clare & Lumb 1994). Small hyaline cells are believed to develop to larger granulocytes (filled with mucopolysaccaride granula), cyanoblasts (probably specialized in hemocyanin production), and presumably also to much larger amoeboid reserve cells (carrying lipoprotein stores). The latter are involved in the production of new cuticle layers before and after each ecdysis. However, the genealogy, classification and cytochemical separation of blood cells has remained a matter of controversy and thus needs further investigation (Martin & Hose 1992). While this applies even to adult decapods, the ontogeny of the hemocytes is yet less known.

Developmental and environmentally induced changes have been described in the molecular structure of the major blood pigment, hemocyanin (Markl 1986, Terwilliger & Terwilliger 1983, Wache et al. 1988, Terwilliger 1991, Brown & Terwilliger 1998, Terwilliger & Dumler 2001). Hemocyanin is characterized by a central copper atom (in contrast to hemoglobin, where it is iron), and several protein subunits. Some of these subunits are lacking in embryos and larvae but expressed in the juvenile phase. Hemocyanin is produced in the hepatopancreas. It is blue when it is oxidized, but otherwise colourless. It occurs in several forms with molecular weights between 450,000 and 1,000,000, binding up to six times more oxygen than hemoglobin (24 *vs.* 4 atoms per molecule).

3.5 *Tegumental glands*

In the hypodermis (beneath the epidermis; see section 3.1) there are frequently exocrine dermal glands which are connected to the cuticle surface by ducts passing through the layers of the epidermis and cuticle (Fig. 3.10). These tegumental glands are predominantly involved in lubrication and tanning of the cuticle, probably they have also bacteriostatic and antifouling functions, and they show structural changes related to the molting cycle.

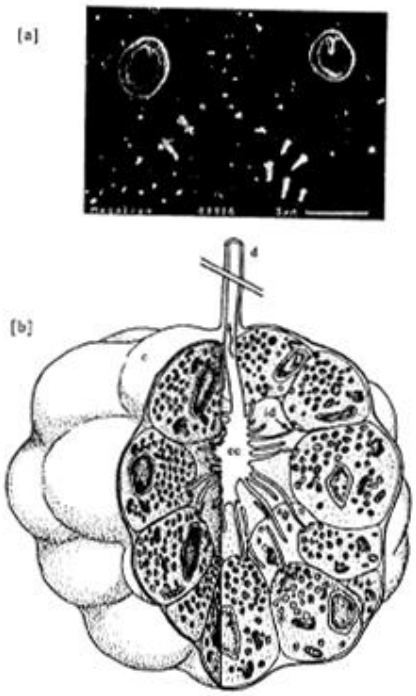


Figure 3.10. Tegumental glands. [a] duct openings at the cuticular surface of the mouth region (labrum) of a spider crab (*Hyas araneus*) megalopa; SEM; [b] rosette tegumental gland (schematic drawing, reconstructed after TEM); c: individual secretory cell; cc: central collecting canal; d: collecting duct; id: intercellular duct ([a] from Höcker 1988; [b] from Felder & Felgenhauer 1993, with permission from Blackwell, Oxford, UK).

The morphology, location, and physiological functions of the various types of tegumental glands have been reviewed for adult Decapoda (Felgenhauer 1992a, Fingerman 1992, Talbot & Demers 1993). They occur ubiquitously in most regions of the external body surface and have been reported from most decapod taxa. While they are usually scattered all over the body, higher concentrations have been observed on mouthparts, walking legs, pleonal appendages, setal sockets, and eyestalks. They occur frequently also on internal integumentary surfaces, for instance in the foregut and hindgut, gills and statocysts. In the alimentary canal, they probably lubricate the passage of food with mucus secretions. The pleopodal tegumental glands of adult female lobsters were observed to show secretory activity patterns that are associated with both the ovarian and the molting cycle (Talbot & Zao 1991).

Tegumental glands may consist of one, a few, or a larger group of hypodermic gland cells (in the latter case termed *rosette gland*; Fig. 3.10), a duct, and a funnel-shaped pore at the cuticle surface. The duct is lined by a thin epicuticle layer. In multicellular glands,

secretory products leave the cells through a system of small intercellular ducts and pass to a larger central collecting canal. Rosette glands are particularly common in gills, pleopods, and in the hindgut. The ultrastructure of the gland cells is characterized by a nucleus, numerous mitochondria, rough endoplasmatic reticulum, and stacked Golgi profiles. Membrane-bound secretory products are frequent during periods of high activity, which is regulated by molting, digestive, or other cycles, depending on the site and function of a particular gland.

In an anatomical study of spider crab (*Hyas araneus*) larvae, tegumental glands were found in late embryos (prezoea) and freshly hached zoeae (Höcker 1988). Typical rosette glands were found particularly concentrated on the mouthparts and the labrum of the larvae. Within the gland cells, numerous droplets of secretory products could be demonstrated with histological staining techniques.

The nuclei were generally located near the periphery of each cell group, opposite to the central collection duct. In an electron-microscopical image, the secretory function of the tegumental glands was reflected in numerous vacuoles and a well-developed Golgi apparatus. As in the adults, typical ducts and funnel-shaped pores could be detected. These observations suggest that the tegumental glands of the brachyuran crabs develop their final structures and functions early in ontogeny, attaining full functionality at hatching. The same appears to apply to caridean shrimps, wherein typical tegumental glands were histologically described for larvae (Hubschman 1971).

3.6 *Excretory organs*

The decapod excretory glands (or "kidneys") are located near the base of each antenna. They are evident at the onset of larval development in shrimps (*Palaemonetes*; Hubschman 1971) and crabs (*Cancer anthonyi*; Trask 1974). However, it has remained unclear if the excretory organs are fully functional in larval stages. Compared to adults, a low level of magnesium excretion was measured in larval crabs (*Cancer magister*; Brown & Terwilliger 1992) and lobsters (*Homarus americanus*; Newton & Potts 1993), suggesting that the antennal glands may not have reached their full functional capacity.

Comprehensive reviews of the anatomy and function of antennal glands and other exocrine organs in adult decapod crustaceans have recently been given within the treatise *"Microscopic Anatomy of Invertebrates"*. The predominant traits of the antennal glands can be summarized as follows: hemolymph filtrate is delivered by an arteriole to a terminal saccule of the antennal gland, the *coelomosac*, which is interpreted as a remnant of the coelom (Fig. 3.11). It is composed of mesodermally derived podocytes, which perform an ultrafiltration function comparable to the glomerular nephron of the vertebrates. From the coelomosac, the urine passes to a spongy *labyrinth*, where selective reabsorption of proteins takes place. It is then transported through a tubule of variable length, the *nephridial canal*, into a *bladder*. Eventually, the urine is released through an excretory pore at the antennal base, the *nephropore.* It appears that, beyond the mere existence in larvae, nothing is known about the ontogeny of this organ. Inferring from its role in adult estuarine crabs, it might be involved in the regulation of magnesium ion concentrations in the blood (Dehnel 1967).

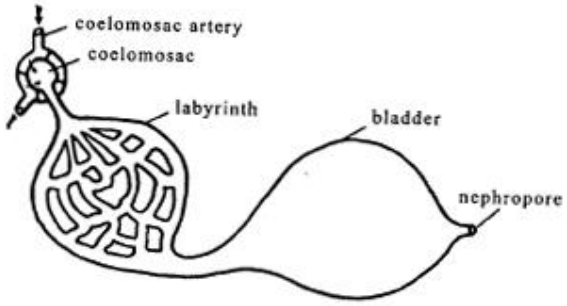


Figure 3.11. Antennal gland (schematic drawing; from Holliday & Miller 1984; with permission from The American Zoologist).

3.7 *Musculature and connective tissues*

Details of the ultrastructure, histochemistry and function of connective and muscle tissues as well as muscular stretch receptors have been reviewed for adult decapods (Mellon 1992). The musculature of the Crustacea shows in general three principal groups of muscles: (1) paired dorsal and ventral longitudinal muscles, which pass through almost the entire body, inserting on intraskeletal elements in each segment; (2) three pairs of dorsoventral and one pair of horizontal muscles in the thoracic somites; (3) two groups of lateral appendage muscles. The muscles are attached to the cuticle via specialized epidermal cells, the tendinal cells (Freeman 1993; see section 3.1).

First anatomical descriptions of the musculature in decapod larvae were given more than half a century ago (Daniel 1930, 1931; for a more recent account see Trask 1974). According to these studies, it appears to be simpler but, in principle, similar to that of adult decapods. In the lobster (*Homarus americanus*), for instance, it could be shown that the lateral pleonal muscles which later become involved in larval locomotion are very early developed, with a functional innervation appearing during embryogenesis, long before the external swimming appendages are formed (Kirk & Govind 1992; see also literature on the ontogeny of neuromuscular systems in crustaceans cited therein). A more complex sequence of ontogenetic changes can be seen in the pleonal musculature of brachyuran crabs. It shows its highest stage of development in the megalopa stage, including longitudinal extensor and flexor muscles that control the overall position of the pleon as well as segmental locomotory pleopod muscles. In benthic juveniles, in contrast, these muscles are no longer needed for swimming, and thus, are greatly reduced after metamorphosis.

The connective tissues consist of cells and extracellular fibers, with fibrils of collagen or other, chemically similar fibrous components (Mellon 1992). As a typical component of connective tissues in the Crustacea, there is an amorphous extracellular matrix. They form protective coats on the inner surface of other internal organ systems, in particular in

association with the nervous system, arteries, and muscular stretch receptors. Major concentrations are found also near the intestine and its caeca, predominantly serving as storage sites for proteins, fats and other reserve substances. Hardly anything is known about the ontogeny of connective tissues.

3.8 *Chromatophores*

Morphological colour change and its neuroendocrine control in decapod crustaceans has been studied for at least a century (Rao 1985). It is based on mesodermally derived pigment cells, the chromatophores. Four major types may be distinguished in adult Crustacea: *melanophores* (black), *erythrophores* (red), *leucophores* (white), and *xanthophores* (yellow). Colour change is achieved by hormonally controlled movements (contraction or dilation) of pigments within the cytoplasm, while the shape and size of the chromatophore cells remain constant.

In larval decapods, chromatophores are generally believed to serve as a camouflage against visually oriented predators (however, see controversial results by Morgan & Christy 1997), and they are important as a sunscreen that protects the larvae against damage caused by ultraviolet light in the surface layer of the water column (see section 10.1.6.1). Studies of the regulation of chromatophore activity in decapod crustacean larvae were carried out with several species of caridean shrimps and brachyuran crabs (Broch 1960, Costlow 1961, 1968, Hubschman 1963, Rao 1967). Chromatophorotropic effects exerted by eyestalk removal or exposure to extracts of nervous tissues indicated consistently that larval chromatophores are under neuroendocrine control, similar to those of adult crustaceans (for recent review, see Charmantier & Charmantier-Daures 1998; cf. also following section).

3.9 *Nervous and neuroendocrine systems*

Comprehensive reviews of the neuroanatomy and neurophysiology of adult decapod crustaceans were given by Sandeman (1982), Wiese et al. *(*1990), Govind (1992), Sandeman et al. (1992, 1993), and Chaigneau (1994a). In adult and larval decapods, the central nervous system comprises the dorsal *brain* (or *supraesophageal ganglion*), which is composed of a *proto-*, *deuto-*, and *tritocerebrum*, and the ladderlike *ventral nerve cord*. The optic nerves, which are extensions of the protocerebrum, pass to the *eyestalk ganglia* and the *sinus gland* (Fig. 3.12). In some deep sea shrimps living associated with hydrothermal vents, the eyestalks are reduced, and associated organs such as the organ of Bellonci and the sinus gland are found near the cerebral ganglia (Charmantier-Daures & Segonzac 1998). The ontogeny of the unusual thoracic eyes in these species is not completely known, and their evolution from stalked compound eyes of an ancestral deep sea shrimp is under discussion (Gaten et al. 1998a, b).

3.9.1 *General anatomy of the nervous system*

A pair of circumesophageal commissures connects the brain with the subesophageal ganglion in the ventral nerve cord, where the ganglia of the mouthparts and maxillipeds are fused. The ventral cord reaches from the head to the anal region, consisting of a chain of large paired ganglia (mostly 17 in the Malacostraca), corresponding with the three postantennal cephalic, the eight thoracic, and the six pleonal appendage pairs (Kaestner 1980).

The segmental structure of the ventral nerve mass is well recognizable in larval decapods (Figs. 3.1, 3.2, 3.12). In the adults, in particular in the Brachyura, there is a fusion of ganglia, resulting in a partial compression of the central nervous system.

Although the size and complexity of the neural structures increases during early development, most of these structures are already present in embryonic and larval stages, at least in the Pleocyemata (Trask 1974, Frydel 1979, Laverack 1988c, Helluy & Beltz 1990, Harzsch & Dawirs 1993, Helluy et al. 1993, 1995). In freshly hatched penaeid shrimp nauplii, the nervous system comprises only a neuropile including a ring around the stomodaeum and nerves that pass to the cephalic appendages (Elofsson 1969). The differentiation begins with a local concentrations of nerve cells, representing an incipient formation of ganglia. In later naupliar stages, the size and differentiation of the neuropile increases gradually, commissures develop, and ganglionic swellings become visible near the buds of the anterior thoracic appendages (maxillipeds 1 and 2). The development of the nervous system proceeds gradually also throughout the subsequent protozoeal, mysis, "postlarval", and juvenile stages. The stomatogastric nervous system appears in the second protozoeal stage.

Complementing neuroanatomical studies, the ontogeny of neurotransmitter systems has recently been studied in decapod crustaceans. In the lobster (*Homarus americanus*) the production of serotonin, proctolin, and others could be demonstrated in early embryonic stages (Helluy & Beltz 1990, Beltz et al. 1992, Kilman et al. 1999). Incipient immunoreactivity in the protocerebrum indicated that the development of the brain starts, in this taxon, at about 11% of the time of embryogenesis; almost the entire central nervous system is already fully developed at ca. 50% (except for the accessory lobes of the deutocerebrum). Also dopamine immunoreactivity has been detected in this embryonic stage (Cournil et al. 1995). Further details of the ontogeny of the nervous system (*neurogenesis*), in particular of the brain, have been elucidated in recent studies on lobster and crab embryos (Harzsch et al. 1998, 1999b).

While the innervation of motoric organs appears to be widely complete at hatching, that of the sensory system develops more gradually in successive larval stages. The number of sensory neurons grows enormously during development and exceeds considerably that of the motor and inhibitory neurons (Laverack 1988c). In addition, however, there are developmental changes in the functional morphology of appendages (particularly in metamorphic transitions; e.g. from a natatory to a mouthpart function), and new locomotory organs such as the pereiopods or pleopods must be rapidly activated in the posterior body regions. This requires major neuronal reorganizations, which have been studied recently (Kirk & Govind 1992, Harzsch & Dawirs 1993, 1994, 1995b, 1996a, 1996b). As a consequence of dramatically increasing needs for nervous coordination in both sensory and locomotory organs, the central nervous system, in particular the brain, inceases during postembryonic development significantly in size. In spider crab (*Hyas araneus*) larvae, from hatching to the first juvenile stage more than a ten-fold increase was recorded in the olfactory lobe, and a more than 100-fold growth occurred in the neuropile volume of the thoracic ganglia (Harzsch & Dawirs 1994, 1996a). In the American lobster, the olfactory lobe grows from hatching to adulthood more than 600-fold, representing a conspicuous centre of neurogenesis (Helluy et al. 1995).

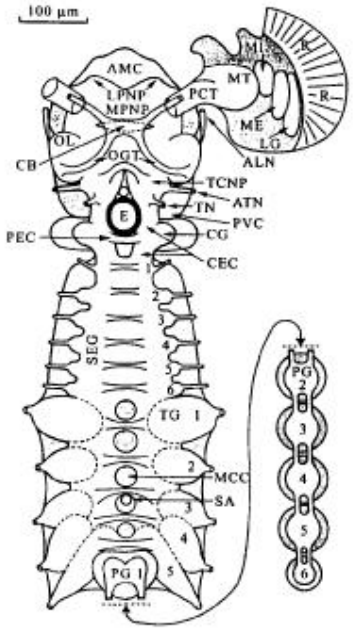


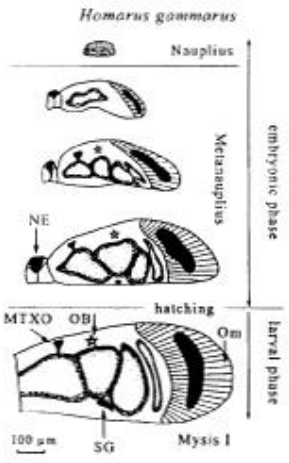
Figure 3.12. Central nervous system of a late brachyuran crab larva (megalopa of *Carcinus maenas*; schematic model). ALN: antennulary nerve; AMC: anterior medial cells; ATN: antennary nerve; CB: central body; CEC: circumesophageal connective; CG: commissural ganglia; E: esophagus; LG: *lamina ganglionaris*; LPNP: lateral protocerebral neuropile; MCC: medial cell column; ME: *medulla externa*; MI: *medulla interna*; MPNP: medial protocerebral neuropile; MT: *medulla terminalis*; PEC: postesophageal commissure; PG 1-6: pleon ganglia 1-6; OGT: olfactory globular tract; OL: olfactory lobe; PCT: protocerebral tract; PVC: posterior ventral cells; R: retina; SA: sternal artery; SEG 1-6: neuromeres 1-6 of the subesophageal ganglion with segmental commissures and nerve roots; TCNP: tritocerebral neuropile; TG 1-5: thoracic ganglia 1-5 with segmental commissures and nerve roots; TN: tegumentary nerve (from Harzsch & Dawirs 1993, with permission from BAH, Helgoland, Germany).

The postembryonic organogenesis of the nervous system has been studied in particular detail in crab larvae (Harzsch & Dawirs 1994, 1995b, 1996a, b). It includes a continuous proliferation of neuroblasts in the brain and the ventral nerve cord throughout zoeal development. During the megalopal molt cycle, the mitotic activity of neuroblasts decreases dramatically, while previously produced neurons are continually differentiated, i.e. integrated in already existing neuronal networks. Only in the olfactory lobe of the brain does some proliferative action appear to persist through both metamorphoses (zoea-megalopa, megalopa-juvenile), as certain clusters of ganglion mother cells delay their final mitosis. New immunohistochemical methods allow for an identification of specific neuron classes and thus, for more detailed studies of their maturation during the course of larval development.

3.9.2 *The X-organ-sinus-gland complex and other neuroendocrine systems*

Neurosecretory and neurohemal sites have been identified in the brain, the eyestalks, the post-commissural organs, and the pericardial organs of adult crustaceans (Cooke & Sullivan 1982, Fingerman 1992). Among these organs, the *eyestalk system* has been studied most extensively, including numerous species of decapod larvae (for recent review, see Charmantier & Charmantier-Daures 1998). It comprises typically the following ganglia (in an order from the proximal to the distal end of the eyestalk; Fig. 3.13): *medulla terminalis*, *medulla interna*, *medulla externa*, *lamina ganglionaris*.

While the two former ganglia develop from cells of brain *anlagen*, the two latter appear to derive from optic discs (*anlagen* of compound eyes; Elofsson 1969). These ganglia bear endocrine cell groups, the X-organs, which transmit their secretions through nerv tracts to an adjacent neurohemal organ, the *sinus gland* (for extensive discussion of the various types of terminals and release mechanisms: see Fingerman 1992). From this collection vesicle, which is normally located between the *medulla interna* and *medulla externa*, neurohormones are released into the circulatory system. In spite of a predominant neurohemal nature of the sinus gland, the historical name "gland" (Hanström 1937) may be justified to some extent, as a minor part of the hormones appears to be produced by intrinsic cells (May & Golding 1983). However, probably more than 90% of the axonal terminals in the sinus gland belong to the major neurosecretory site, the *medulla terminalis* X-organ (Cooke & Sullivan 1982); additionally, *medulla externa* and *medulla ganglionaris* X-organs occur, as well as giant neurons which are considered as presumptive neurosecretory cells (Hubschman 1963, Rotllant et al. 1994). This system is found also in unstalked compound eyes (e.g. in embryos and first-stage zoea larvae of the Pleocyemata), but apparently not in the naupliar eye. In penaeid nauplii, however, Elofsson (1969) observed structures that he interpreted as non-functional primordia of compound eyes. In eyestalkless crustaceans such as isopods, these ganglia remain parts of the brain. In several anomurans and some shrimps, an emergence of ganglia from the eyestalk back to the protocerebrum may have occurred secondarily in evolution (Fingerman 1992).



ı-sinus-gland complex was discovered several decades ag(jor neuroendocrine centre in the Crustacea (review of old sle 1956). Numerous studies of its structures and functio nd a great variety of eyestalk neurohormones, biogenic am rs has been identified, chemically characterized and/or loc try (Cooke & Sullivan 1982, Kleinholz 1985, Skinner 19(erman 1992, Govind 1992, Keller 1992, Charmantier et al. ang et al. 1999). These include the molt-inhibiting, the ma gonad-inhibiting, the hyperglycemic, the red pigment-co sing, and the distal retinal pigment light-adapting hormo tebrate hormones, biologically active substances could be s, which were originally known from vertebrates, e.g. opi ine-enkephalin, secretin, and "substance P" (Mancillas et a Jaros 1986, 1990, Fingerman 1992).

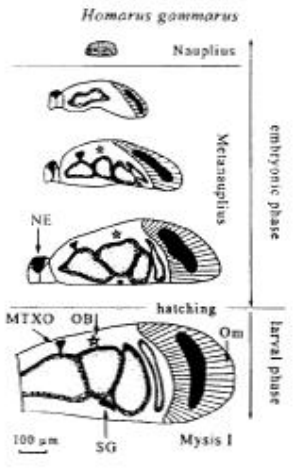


Figure 3.13. Ontogeny of the neuroendocrine centres in the eyestalk of the European lobster, *Homarus gammarus* (schematic drawing). LG: *lamina ganglionaris*; ME: *medulla externa*; MI: *medulla interna*; MT: *medulla terminalis*; MTXO: *medulla terminalis* X-organ; NE: nauplius eye; OB: organ of Bellonci; Om: ommatidia; PSSG: presumptive site of the sinus gland; SG: sinus gland (from Rotllant et al. 1995, with permission from Balaban, Rehovot, Israel).

Although the eyestalk system is known mostly from studies of adult crustaceans, several observations center on embryos and larvae (Christiansen 1988, Rotllant et al. 1994, 1995, Chan et al. 1998, Charmantier 1998, Charmantier & Charmantier-Daures 1998). Orlamünder (1942) observed in embryos of a terrestrial anomuran, the coconut crab *Birgus latro*, cells corresponding to the X-organ of adult crustaceans. Pyle (1943), studying embryos and larvae of lobsters (*Homarus americanus*) and pea crabs (*Pinnotheres maculatus*), described for the first time the ontogeny of the X-organ-sinus-gland complex. Another early account of the embryogenesis of the X-organ was given by Dahl (1957), who studied the marine shrimp *Crangon allmanni*. Subsequently, detailed studies were carried out on the development of neurosecretory and sensory structures in the eyestalks of larval shrimps (both penaeid and caridean), anomuran and brachyuran crabs, and clawed lobsters (recent review: Charmantier & Charmantier-Daures 1998).

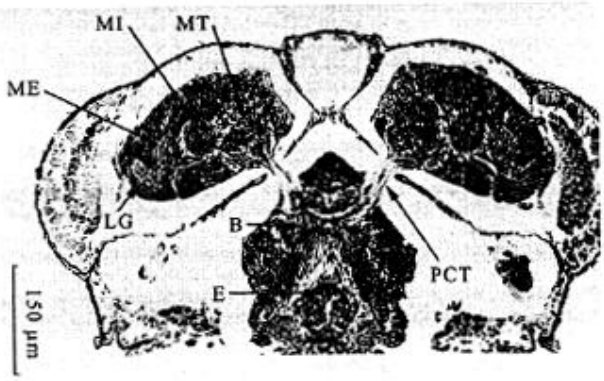


Figure 3.14. Eyestalk ganglia in an early larva with unstalked eyes, the zoea I of the spider crab, *Hyas araneus*. B: brain; E: esophagus; LG: *lamina ganglionaris*; ME: *medulla externa*; MI: *medulla interna*; MT: *medulla terminalis*; PCT: protocerebral tract (from Höcker 1988, with permission from the author).

While the eyestalk system of the Dendrobranchiata develops gradually through the naupliar and zoeal stages (Elofsson 1969), most of its structures are in the Pleocyemata present at hatching (Figs. 3.13, 3.14). In some larval carideans, however, the sinus gland and associated neuroendocrine structures (e.g. the giant neurons) were found only in later larval stages (Hubschman 1963, Bellon-Humbert et al. 1978). In taxa with an abbreviated or lacking larval development (e.g. in crayfish and potamid freshwater crabs), the sinus gland and X-organs are always present at hatching (Matsumoto 1958, Gorgels-Kallen & Meij 1985). Their early functionality was demonstrated in European lobster (*Homarus gammarus*) larvae applying immunocytochemical and *in situ* hybridization techniques (Webster & Dircksen 1991, Rotllant et al. 1993, 1994, 1995). In the brain of late embryos and freshly hatched larvae of a swimming crab (*Charybdis feriatus*) Chan et al. (1998) detected with a PCR technique the expression of genes coding for neuropeptides that are typically released from the eyestalk system.

Even where the eyestalk system is well developed at hatching, its neuropiles increase significantly in size throughout larval development. In spider crab larvae, for instance, this increase in volume is about ten-fold from hatching to the first juvenile stage. In the development of the retina and optic neuropils of the brachyuran eyestalk system, probably three separate proliferation zones are involved (Harzsch & Dawirs 1995a, Harzsch et al. 1999b). These regions of cell multiplication can be localized with a relatively new technique: a synthetic thymidine analogue (5-bromo-2'-deoxyuridine; BrdU) is incorporated into the DNA of mitotic cells and then detected with a monoclonal antibody (Harzsch & Dawirs 1994). In future research, this and other immunohistological methods will allow for achieving deeper insights in the course and mechanisms of neurogenesis and, in general, in organogenesis.

In summary, the available evidence suggests that decapod neurohormones are produced in larval eyestalks, fulfilling largely the same regulatory functions as in juvenile and adult life-history stages (Charmantier & Charmantier-Daures 1998). Among others, these functions comprise control of the molting cycle, morphogenesis, regeneration, carbohydrate and calcium turnover and other metabolic functions, chromatophore and retinal activity, osmo- and ionic regulation, growth, and sexual maturation.

Among the neuroendocrine factors of the eyestalk system, the molt inhibiting hormone (*MIH*) may be one of the most important in the context of larval development and growth. Its presence was recently demonstrated in late embryos and early larvae of a crab (Chan et al. 1998). Besides *MIH*, also the crustacean hyperglycemic hormone (*CHH*) and the gonad-inhibiting hormone (*GIH*) have been immunocytochemically detected in the eyestalks of larval decapods (Rotllant et al. 1993, Giulianini et al. 2000). In addition to the X-organ-sinus-gland complex, several other neuroendocrine sites have been identified (Fingerman 1992). Among these, the postcommissural organs of the Decapoda emerge from the tritocerebral commissure behind the esophagus, controlling several chromatophorotropic ac-

tivities such as black, white, and red pigment concentrations. The pericardial organs release neurohormones that were shown to influence the rate of heart beat. The anterior ramifications, which were detected close to the pericardial organs of brachyurans, represent probably neurohemal organs. To my knowledge, none of these neuroendocrine structures has been studied in larval decapods.

3.9.3 *The organ of Bellonci*

There has been much confusion of the organ of Bellonci with the X-organs, and even its functional classification as part of the nervous system (Chaigneau 1994b) or as a non-neural endocrine gland (Felgenhauer 1992b) is controversial. After several name changes, it was eventually named after its discoverer who observed it first in an isopod, more than one century ago (Bellonci 1881). Since very little is known about its presence and anatomical features in larvae, the following description is based on observations from adult decapods.

The organ of Bellonci is normally located in the eyestalks, usually near or attached to the *medulla-terminalis* X-organ, and closely associated with a sensory pore (Chaigneau 1978). The latter, however, is poorly developed or absent in most brachyuran crabs, and it may be absent also in some deep sea shrimps (*Segonacia mesatlantica*; Charmantier-Daures & Segonzac 1998). In other deep sea species (*Rimicaris exoculata, Charocaris chacei*), no eyestalks are developed, and the organ of Bellonci is located in front of the cerebral ganglia (Charmantier-Daures & Segonzac 1998). When the organ of Bellonci appears separated from the *medulla terminalis*, these structures stay in connection by a nerve (Chaigneau 1994b).

While the ultrastructure of its cells appears rather uniform, their overall shape and arrangement, their position, and even their presence appears to vary among decapod taxa (Fingerman 1992). One of its most typical traits is the presence of laminar and tubular structures, the so-called *onion bodies*. The ultrastructure of Bellonci organs was described in detail for caridean shrimps, e.g. *Paratya tasmaniensis* (Lake & Ong 1970), *Palaemon serratus* (Bellon-Humbert & Chaigneau 1982), *Macrobrachium rosenbergii* (Hallberg & Kauri 1992), and the shore crab, *Carcinus maenas* (Smith 1974). Dense layers of rough endoplasmatic reticulum ("phaosomes") in the Bellonci organ of an atyid shrimp resemble the anatomy of the nauplius eye and may thus represent sensory structes (Juberthie-Jupeau & Chaigneau 1975). However, it has remained under dispute, whether this organ has a sensory or a secretory function. According to its ultrastructure in crabs and shrimps, it may have both (Smith 1974, Bellon-Humbert & Chaigneau 1982). It was speculated that sensory inputs may stimulate the release of endocrine factors, similar as in the pineal organ of ectotherms.

In penaeid shrimp larvae, the organ of Bellonci appears near the developing *medulla terminalis* of the last naupliar stage, the nauplius V (Elofsson 1969). In larvae of caridean shrimps (*Alpheus leptodactylus*, *Crangon allmanni*, *Palaemonetes* spp., *Palaemon* spp.), anomuran crabs (*Pisidia longicornis*) and nephropid lobsters (*Homarus gammarus*), the organ of Bellonci is present at hatching (Dahl 1957, Hubschman 1963, Little 1969, Bellon-Humbert et al. 1978, Iman 1982, Le Roux 1989, Rotllant et al. 1994). In shrimp larvae, it appears initially enclosed in the *medulla terminalis*, showing the typical onion bodies. It grows during subsequent larval development to almost six-fold size, differentiates, and migrates within the eyestalk system (Bellon-Humbert et al. 1978). Vacuolization, however, which is considered as an indicator of beginning secretory activity, starts from

an intermediate zoeal stage (IV). Also the giant neuron appears at this time and grows until metamorphosis to three-fold size. There seems to be no or only a loose association between the organ of Bellonci and a minute *"larval sensory pore"*; the main sensory pore develops in the last decapodid or in the first juvenile stage. Several typical adult traits of the organ of Bellonci were first observed in the decapodid-juvenile transition, namely: the final (rostroventral) position within the eyestalk, partial extrusion out of the *medulla terminalis*, formation of a connecting nerve tract between this ganglion and the organ of Bellonci, the appearance of contact zones with the main sensory pore complex and the neurosecretory cells of the *medulla terminalis* X-organ. In lobster larvae, in contrast, both the vesicular and an onion-body type of cells were observed from hatching in the organ of Bellonci, which is located near the perikarya of the *medulla interna* and *medulla terminalis* and distally associated with the sensory pore complex (Rotllant et al. 1994).

3.10 *Non-neural (epithelial) endocrine glands*

3.10.1 *Y-organs*

Gabe (1953) discovered in the cephalothorax of 25 decapod and numerous other malacostracan crustacean species a paired organ, which he tentatively named *"Y-organ"*. Its structure resembled that of the molting glands of insects, and its cells showed cyclic vatiations throughout the molting cycle, suggesting that this newly discovered organ was involved in the regulation of molting. This hypothesis was soon confirmed experimentally (Echalier 1954, 1955). In a treatise on the *"Endocrine Control in Crustaceans"* (Carlisle & Knowles 1959), the Y-organs were homologized with the prothoracic glands of insects. However, it took another decade to show in crustaceans the presence of the already known insect molting hormone, *ecdysone* (Butenandt & Karlson 1954), although in a slightly modified form, 20-hydroxyecdysone (usually referred to as 20-OH-ecdysone, in the older literature also as *"crustecdysone"*; Hampshire & Horn 1966). Activity variations in this and chemically similar steroid hormones were detected within the molting cycle (Carlisle & Connick 1973, Willig & Keller 1973), and after the appearance of new techniques (chromatography, radioimmunoassay), the Y-organs could be identified as the site of synthesis (Chang et al. 1976, Keller & Willig 1976). Some authors suspected that the nervous system might be involved in the formation of the Y-organs (Echalier 1954, Chaudonneret 1978), however, this speculation could not be corroborated by later histological and ultrastructural studies. Most of the available evidence suggests an ectodermal origin (Charmantier et al. 1996).

In both adult and larval decapods (except for naupliar stages, where a documentation is lacking so far), the Y-organs are associated with the epidermis, usually located in the maxillary or maxillular somite, where they are attached to the inner walls of the branchiostegites (Fig. 3.15a). In larval crabs, the Y-organs are integrated in the epidermis, showing an insertion zone, i.e. a direct contact of Y-organ cells with the inner carapace cuticle (Höcker 1988). This is otherwise typical of the Astacidea, which are considered phylogenetically more ancestral than the Bachyura (Lachaise et al. 1993). In juvenile and adult crabs, in contrast to their larvae, the Y-organ has separated from the cuticle and can clearly be distinguished from the underlaying epidermal tissues. It may thus be speculated that this ontogenetic change in the position of the Y-organs reflects an evolutionary tendency, in agreement with Haeckel's so-called "biogenetic law" (Haeckel 1866). Compara-

tive observations of early ontogenetic changes may be worth-while to elucidate this possible developmental tendency.

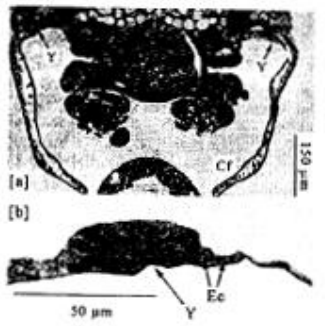


Figure 3.15. Y organ (Y) in the zoea I of a spider crab, *Hyas araneus*; [a] position on the proximal inner surface of the branchiostegites; [b] histological structure; mb: maxillar base; Cf: carapace fold; vnc: ventral nerve cord (from Höcker 1988, with permission from the author).

The Y-organs show a uniform structure characterized by a basement membrane, fold dria, but a poorly developed Golgi apparatus and a lack of obvious secretory granules. In the higher Crustacea, they appear to become functional during embryogenesis (Le Roux 1983a, Christiansen 1988, Lachaise et al. 1993, Charmantier & Charmantier-Daures 1998, Subramoniam 2000). This generalization is consistent with an early appearance of ecdysteroids and a conspicuous increase in their titer as soon as embryonic Y-organ structures are differentiated (Spindler et al. 1987, Goudeau et al. 1990, Lachaise et al. 1993).

Recent anatomical studies of the embryonic development in lobsters have shown that there are molt-cycle-like processes already within the egg membrane, which may be controlled by the same hormonal system as in later life-history phases (Goudeau et al. 1990, Helluy & Beltz 1991). In embryonic and larval decapods, including various species of crabs, shrimps and lobsters, the Y-organs have been identified and histologically described (McConaugha 1980, Le Roux 1982a, Buchholz 1984, Höcker 1988). According to these investigations, there is a gradual increase in size and lobulation, but no other conspicuous ontogenetic changes were found during the course of larval development in their histology or ultrastructure. There are, however, structural changes that are related to activity changes during individual molting cycles (see below, section 4.3).

3.10.2 *Mandibular organs*

Located near the base of the mandibles, the Crustacea bear another pair of ductless endocrine glands, the mandibuar organs (*MO*). Le Roux (1968) discovered and described them briefly from 20 decapod species. However, since their exact location and shape remained unclear from the early descriptions, the *MO* were initially often confused with Y-organs (clarified by Sochansky et al. 1972, Le Roux 1974; for recent review of anatomical and functional features of the *MO*, see Hinsch 1990, Fingerman 1992, Charmantier et al. 1996). While these organs vary among species in size, shape and histological details, their

ultrastructure has some traits in common, e.g. a central location of the nucleus, highly folded cell membranes, a well-developed smooth endoplasmatic reticulum (*SER*), numerous ring-shaped mitochondria, a Golgi apparatus of variable appearance, and usually a poorly represented rough endoplasmatic reticulum (*RER*). In the lobster (*Homarus americanus*), three different cell types were described (Borst et al. 1994), which may be separated in two histologically distinct regions (Le Roux 1968, 1969). At least in some species, the *SER* appears to change through the molting cycle (Aoto et al. 1974, Byard et al. 1975).

The function of the *MO* has remained widely unclear and is under current investigation. At least one highly interesting function could be established: in the *MO* of a spider crab (*Libinia emarginata*), Laufer and collaborators discovered methyl farnesoate (*MF*), a compound that is structurally similar to a *juvenile hormone* (*JH III*) of the insects (Laufer et al. 1986, Borst et al. 1987; for recent review see Charmantier et al. 1996, Charmantier & Charmantier-Daures 1998). The production and release of *MF* and its precursor, farnesoic acid, was shown also in vitro in the *MO* of several crab and shrimp species. In adult decapods, these substances stimulate ovarian development and vitellogenesis, comparable with the *corpora allata* of the insects (Charmantier et al. 1996). The hemolymph titer of *MF* in crabs is correlated with reproductive readiness (Ahl et al. 1996, Wainwright et al. 1996a). The *MO* and its secretory product, *MF*, appear thus to be involved in the development of the reproductive system. Moreover, there is recent evidence suggesting that *MF* may be involved in osmoregulation (Lovett et al. 2001).

So far, only few indications of the classical *JH* functions have been found in larval development and metamorphosis. In contrast to insect *JH III*, exogenous *MF* caused in larval lobsters (*Homarus americanus*) only a small delay in metamorphosis and no morphological effects (Borst et al. 1987). In late palaemonid prawn (*Macrobrachium rosenbergii*) larvae, juvenoid-like effects such as retarded larval development and an occurrence of intermediate morphological forms were recently observed (Abdu et al. 1998a). The opposite effect, however, i.e. stimulated metamorphosis, was observed in barnacle larvae (Yamamoto et al. 1997). Effects of experimental eyestalk ablation and *MO* implantation in adult decapods indicated consistently that both organs are involved in the control of the molting cycle, probably stimulating the production of ecdysteroids (Charmantier et al. 1996).

The presence of the *MO* has been demonstrated in larvae of various decapod species, located near the limit between the mandibles and the maxillules (Le Roux 1974, 1991). According to histological observations after eyestalk ablation, their synthetic activity is controlled by factors of the X-organ-sinus-gland complex (Le Roux 1983b, Charmantier et al. 1996). The mechanisms of the neuroendocrine regulation of *MF* biosynthesis are currently under intense investigation using adult *Cancer* crabs as a model (Wainwright et al. 1996a, 1998, Tang et al. 1999). *In vitro* experiments with *MO* cell cultures have shown that a neuropeptide produced in the eyestalks, the mandibular organ-inhibiting hormone (*MO-IH*), inhibits a key enzyme in the biosynthesis of *MF*, the farnesoic acid-O-methyltransferase. Also recent experiments with eye stalk removal and sinus gland injections in crayfish confirmed that the production of *MF* is under neuroendocrine control by the eye stalk system (Chaves 2001).

While exogenous insect *JH* or synthetic mimics thereof have repeatedly been shown to affect larval development and metamorphosis (Charmantier et al. 1988), very little information is available on the presence and role of endogenous *MF* or related substances in larval decapods. In lobster and prawn larvae, *MF* was detected only in low concentrations

(Borst et al. 1987, Abdu et al. 1998b). Several observations of reduced morphogenesis and delayed metamorphosis in the presence of exogenous insect *JH* suggest that the mode of action of the chemically related putative "crustacean juvenile hormone", *MF*, may be similar as in insects (see Charmantier & Charmantier-Daures 1998, Abdu et al. 1998a).

3.10.3 *Androgenic gland*

As another epithelial endocrine organ of the Malacostraca, the androgenic gland is involved in the development of the male sexual structures of crustaceans. Although it was anatomically discovered in a crab (*Callinectes sapidus*; Cronin 1947), its function was first demonstrated in amphipods (Charniaux-Cotton 1954). In decapods, it is always located near the subterminal ejaculatory part of the *vas deferens*. Its anatomy, however, varies greatly among species, and several chemical compound classes have been discussed as possible *androgenic hormones* produced therein; among the candidates, again *JH*-like substances such as farnesylacetone have been detected (Kleinholz 1985, Fingerman 1992).

The expression of the androgenic gland is under the control of sex-determining genes (Ginsburger-Vogel & Charniaux-Cotton 1982). During larval development, it occurs in both sexes, but later it is reduced in females (Le Roux 1991). As in the mandibular organ, its activity is under neuroendocrine control of the eyestalks. After eyestalk ablation in several larval decapods, the androgenic gland cells became hypertrophic and the development of male sexual organs was accelerated, causing spermatogenesis to begin as early as in the megalopa stage (Payen et al. 1971, Le Roux 1982b, 1984).

3.11 *Alimentary system*

Comprehensive accounts of the anatomy and function of the digestive system in adult Decapoda were recently given in the treatise *"Microscopical Anatomy of Invertebrates"* (Felgenhauer 1992b, Icely & Nott 1992), in the book series *"The Biology of Crustacea"* (Dall & Moriarty 1983) and *"Crustacean Issues"* (Felgenhauer & Abele 1989), and in textbooks such as Grassé's *"Traité de Zoologie"* (Ceccaldi 1994). Except for the lecithotrophic nauplius stages of the Dendrobranchiata, which have only an incompletely developed, non-functional gut without lumen (Dall et al. 1990), the alimentary system of larval decapods is less complex but otherwise already similar to that of the adults (for extensive bibliography and review, see Icely & Nott 1992). Hence, much of the existing evidence from studies of adult decapods can be extrapolated to decapod larvae.

3.11.1 *General organization of the digestive tract*

In both adult and larval decapods, the alimentary canal is typically divided into three distinct parts: *foregut*, *midgut* and *hindgut* (Trask 1974, Factor 1989). In contrast to the ectodermally derived foregut and hindgut regions, the midgut (including its blindly ending *caeca* and the *midgut gland* or *hepatopancreas*) is of endodermal origin and thus, the only portion that is not lined by a cuticle layer. Anatomy and principal functions of this system will be briefly described here, following the direction of the passage of food. Numerous further details and specific modifications in individual decapod taxa can be found in the books and review articles cited above.

3.11.2 *External feeding structures and esophagus*

Larvae grasp food particles with their mouthparts, in particular with the maxillulae, maxillae and maxillipeds. In brachyuran zoeae, the pleon is bent anteriorly to press large prey items against the mouth region (Herrnkind 1968). Advanced forms such as the mysis stages of clawed lobsters (see Factor 1995a) or the decapodids of most other groups use also functional pereiopods. Food is then masticated by the mandibles, before it passes through the mouth into the anterior part of the foregut, the *esophagus*. Its lumen can be adjusted to prey size by means of longitudinal folds in the walls, and food passage is further facilitated by lubricating mucus secretions from surrounding tegumental glands (see section 3.5). After passing an esophageal sphincter (in many higher Decapoda also an elaborate esophageal vent), the food passes further into the *cardiac stomach chamber* (in the terminology of Dall & Moriarty 1983 and Dall et al. 1990 named *anterior proventriculus*). Sphincter and valve prevent a reflux from to the esophagus.

3.11.3 *Cardiac stomach and gastric mill*

During the zoeal phase, some mechanical maceration of food may be achieved by peristaltic movements of the cardiac stomach, where longitudinal cuticle folds are found on the inner surface (Höcker 1988). This process of extracellular digestion, however, becomes more efficient when the decapodid or juvenile phase of development is reached. In the higher Decapoda, additional longitudinal cuticle ridges, ossicles and teeth appear as robust skeletal elements in the cardiac chamber. They are connected to one another by ligaments and moved by the extrinsic foregut musculature. This complex (and in later developmental stages increasingly calcified) apparatus is termed *"gastric mill"*. Its principal components are a median tooth, a pair of lateral teeth, and often accessory lateral teeth (Fig. 3.16). Various forms of ossicles have been described and classified for adult Decapoda; they can be assigned to three basic types (Felgenhauer & Abele 1989). In some decapod groups, the complexity and robustness of the gastric mill appear to be related to the predominant food source of a given species, but numerous exceptions suggest that also its phylogenetic history may have a strong influence on the structure of the foregut (Icely & Nott 1992). A gastric mill is lacking or vestigial in penaeid and caridean shrimp larvae, where the cardiac portion of the foregut remains structurally simple compared with that in all other decapod groups (Le Roux 1971, Regnault 1972, Lovett & Felder 1989, Abubakar & Jones 1992).

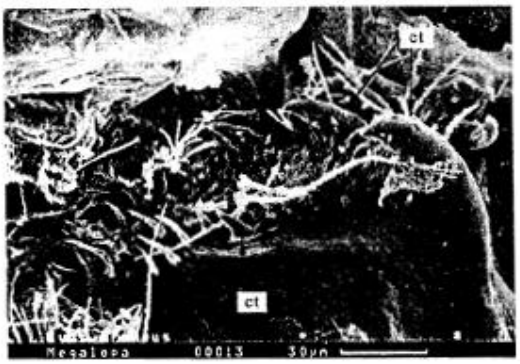


Figure 3.16. Cardiac stomach of the megalopa of a spider crab, *Hyas araneus*. ct: cuticular teeth. SEM (from Höcker 1988, with permission from the author).

Factor (1989) suggested adaptive ontogenetic changes in the structure of the feeding system of decapod larvae. Zoeae show consistently a complex morphology in their external mastication organs, the mandibles, but only simple cuticular structures in the cardiac stomach chamber. In the decapodid and juvenile phase, the mandible structure becomes less complex, while the cardiac stomach develops a gastric mill. These metamorphic, inversely directed changes in the complexity of external and internal feeding structures reflect an abrupt ontogenetic change in feeding ecology and habit, namely from a suspension-feeding planktonic zoea to a demersal stage that predominantly feeds on solid benthic prey (e.g. juvenile molluscs, small crustaceans). The latter type of food is apparently macerated more efficiently in the gastric mill than by the mandibles. In addition to structural changes (formation of the filter apparatus), the zoea-decapodid transition appears to be associated with a steep increasing in the hepatopancreas volume and activity of digestive enzymes produced therein (Kumlu & Jones 1995a).

In clawed lobsters, these changes occur between postembryonic stages III and IV. Similar patterns were found in studies of the functional morphology of crab (Minagawa & Takashima 1994, Li & Li 1995) and palinurid lobster larvae (Nishida et al. 1990). In the latter, however, these changes in feeding structures occurred not at the settling stage (the puerulus) but in the subsequent juvenile. A gastric mill is here absent during the phyllosoma phase and in the puerulus, but appears in the first juvenile. As in other decapods, the external mouthparts lose their morphological complexity during this metamorphosis (Lemmens & Knott 1994). This delay of metamorphic changes in the feeding structures of palinurids may be explained by absense of food uptake in the puerulus and a recommencement of feeding activity in the first juvenile, as there is evidence from several species of palinurid lobsters that the puerulus is a secondarily nonfeeding stage (see section 5.2.1).

A different pattern was observed in a scyllarid (shovel-nosed) lobster, *Ibacus ciliatus* (Mikami & Takashima 1993a, Mikami et al. 1994). The nisto stage (equivalent to the pu-

erulus of the palinurids) shows a proventriculus structure which is similar to that of the adults (for literature on adult stomach anatomy in scyllarids, see Factor 1989). However, cuticular spines, grooves, teeth, and a filter press, which are already present in the phyllosoma phase, become secondarily reduced in the nisto. In this case, this is not consistent with the authors' interpretation of a change from soft planktonic to solid benthic food. It might rather suggest that the nisto stage shows, similarly as the puerulus of spiny lobsters, a reduced or even lacking food uptake. Since larval feeding was not checked in this or other cultivation experiments with scyllarid lobsters (review: Marinovic et al. 1994), further data are necessary for a better understanding of the functional morphology of the alimentary system in the Scyllaridae. Similar observations have been reported from anomuran king crabs (*Paralithodes* spp.), where transitorily reduced structures in the alimentary tract suggest that the decapodid is a nonfeeding stage (Abrunhosa & Kittaka 1997a, b; see section 5.1.2).

3.11.4 *Pyloric stomach*

After internal mastication in the cardiac stomach, small and medium-sized food particles pass over the cardiopyloric valve into the dorsal part of the pyloric stomach chamber (or *posterior proventriculus*). Food is compressed here by a complex system of filtering setae, the *filter press*, which allows only small particles to pass to the ventral part of the pyloric chamber (Fig. 3.17). This filter system is lacking in the protozoeal stages of the Dendrobrachiata (Lovett & Felder 1989), but exists in all other zoeae, although usually less complex. After being screened by one or two layers of setae, the filtrate of the gastric juice passes through the fine *gland filter* (or *ampulla*), into the ampullary chambers. From there, the liquid passes through the ampullary channels into the midgut gland (hepatopancreas), where intracellular digestion takes place. Larger residual particles (in general those above ca. 1 μm size) pass from the dorsal part of the pyloric chamber through a pylorointestinal valve directly into the midgut, and from there to the hindgut and anus.

3.11.5 *Hepatopancreas*

The larval hepatopancreas is, in most decapod crustaceans, anatomically similar to that of the adults. During the course of development, it grows considerably in size, in general without significant structural changes (Hinton & Corey 1979, Storch & Anger 1983, Anger et al. 1985, Sasaki et al. 1986, Factor 1989, Abubakar & Jones 1992, Biesiot & McDowell 1995, Li & Li 1998). Conspicuous reconstruction processes may occur, however, in species where the early larval stages are nonfeeding, followed by planktotrophic stages (see section 5.1.1).

The hepatopancreas is a bilobed system of blind ending tubuli which occupies most of the space within the cephalothorax; in hermit crabs, it extends into the pleon. The tubuli open into paired collection canals that pass ventrolaterally to the pyloric portion of the stomach (sometimes to the midgut or to the transition between midgut and pyloric stomach). While digestive fluid is delivered here, the filtered gastric fluid is transported in the opposite direction into the hepatopancreas (for detailed discussion of the circulation of fluids, see Icely & Nott 1992). The glandular tubuli of the hepatopancreas are surrounded by a basal lamina, which is underlain by striated muscle cells and extensions of pigment cells. The intertubular space is occupied by hemolymph sinuses.

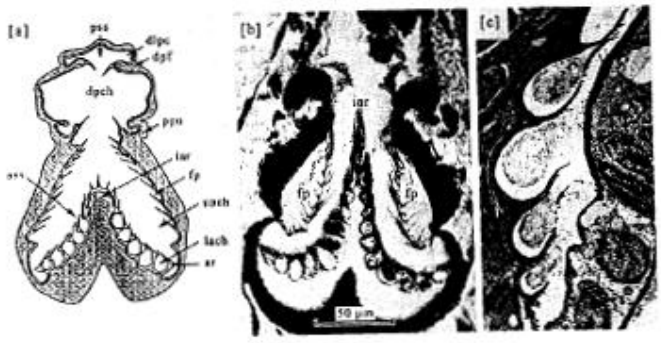


Figure 3.17. Pyloric stomach (not to scale); [a] *Litopenaeus setiferus*, "postlarva" (schematic drawing); [b] *Hyas araneus*, megalopa (transversal section); [c] *Pagurus bernhardus*, zoea II (TEM, x3100; note presence of food particles in lower ampullary chambers). ar: ampullary ridge; ass: ampullary setal screen of the gland filter; dlpc: dorsolateral pyloric channel; dpch: compaction structures in the dorsal region of the pyloric chamber; dpf: dorsal pyloric fold; fp: filter press of the gland filter iar: interampullary ridge; lach: lower ampullary chamber; ppo: prepyloric ossicle; pss: pyloric setal screen for dorsolateral pyloric channel; uach: upper ampullary chamber ([a] from Lovett & Felder 1989, with permission from Wiley, New York, USA; [b] from Höcker 1988, with permission from the author; [c] from Jarminowski 1990, with permission from the author).

As suggested by its name, the hepatopancreas fulfills hepatic, pancreatic as well as intestinal functions. Besides numerous digestive enzymes, the respiratory blood pigment hemocyanin also is produced in the midgut gland (Gelissen et al. 1991), as well as proteins that are involved in the detoxification of alien substances (xenobiotics; James & Boyle 1998). Its cells show an activity rhythm that follows the cyclic uptake of food and appears to be hormonally regulated by the eyestalk complex. In both adult and larval decapods, the hepatopancreas epithelium consists of four principal cell types (Fig. 3.18): *"embryonic"*, *"fibrillar"*, *"resorptive"*, and *"blisterlike"* cells (*E*-, *F*-, *R*- and *B-cells*; for comprehensive review of the ultrastructure, nomenclature and genealogy of these cell types, see Gibson & Barker 1979, Hopkin & Nott 1980, Icely & Nott 1992, Vogt 1993, Biesiot & McDowell 1995). An additional type, the *"midget"* or *M-cells*, was first described from adult penaeid prawns (Al-Mohanna et al. 1985), but found also in caridean shrimps and other higher Decapoda (Icely & Nott 1992). Their occurrence in larval decapods, however, has not been documented. Probably, the M-cells store organic reserves.

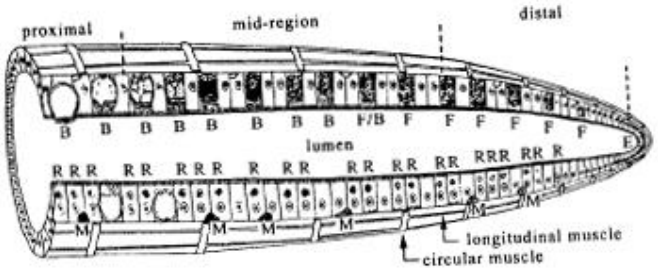


Figure 3.18. Anatomy of a hepatopancreas tubule (schematic drawing) in a penaeid shrimp, *Penaeus semisulcatus*; location of cell types (B, E, F, M, R) during intermolt. E cells are located at the blind end in the distal region, from where they devide, differentiate, and replace lost cells in the other regions; F cells are confined to the mid-distal region; B cells extend from the mid- to proximal region; R cells are most frequent along the tubule epithelium, M cells are relatively rare (from Al-Mohanna & Nott 1989; with permission from Springer, Heidelberg, Germany).

The E-cells are located at the blind ends of the hepatopancreatic tubules (Fig. 3.18). They are undifferentiated and mitotically active. Arising from these "embryonic" cells, the other cell types fulfill specialized physiological functions. These have been elucidated with electron-microscopical, immunocytochemical, radiotracer, and energy dispersive X-ray analysis. The available evidence suggests that the larval hepatopancreas is morphologically and functionally similar to that of the adults (Storch & Anger 1983, Abubakar & Jones 1992, Biesiot & McDowell 1995).

The F-cells are characterized by a basally located nucleus, a well developed rough endoplasmatic reticulum (*RER*), abundant golgi profiles and mitochondria, and a conspicuous brush border. Their major functions are the uptake of nutrients by means of pinocytosis or contact digestion and subsequent molecular absorption on the microvilli, and the secretion of digestive enzymes. Using immunocytochemical techniques, individual digestive enzymes could be identified, and it could be shown that they are synthesized in the highly basophilic F-cells, transported to the pyloric stomach, and eventually stored in their active molecular form in the cardiac chamber (Vogt et al. 1989). When nutrients are sequestered into the supranuclear vacuoles, these may expand to large vacuoles, and the F-cell may transform into a B-cell.

The B-cells have primarily secretory functions, producing most of the digestive enzymes, and they can absorb nutrients by pinocytosis (Gibson & Barker 1979). Their blisterlike appearance is caused by large vacuoles, which squeeze the cytoplasm with the nucleus, the *RER*, and other organelles to the periphery. In the apical cell portion, there are numerous membrane invaginations which form channels extending into the interior of the cell.

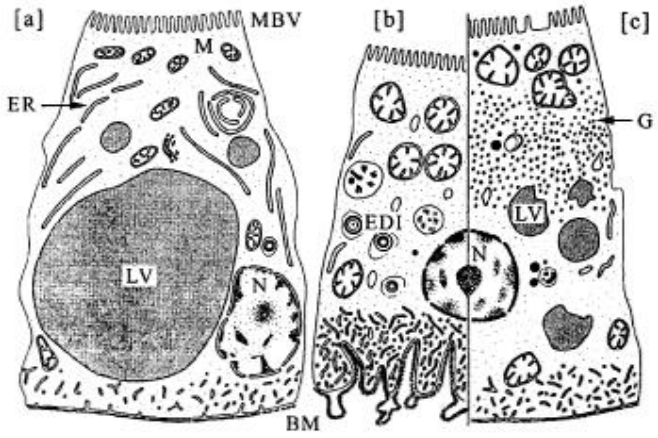


Figure 3.19. Ultrastructure (schematic drawing) of an R-cell in the hepatopancreas of an early larval spider crab, *Hyas araneus*, zoea I; [a] continually fed larva; [b] after 16 days of starvation; [c] 12 days of starvation and subsequent feeding (4 days). BM: basal membrane; EDI: electron-dense inclusions; ER: rough endoplasmatic reticulum; G: glycogen granules; LV: lipid vacuole; M: mitochondria; MVB: apical microvilli border; N: nucleus. Note: swollen mitochondria, only partially repleted lipid vacuoles, and atypical glycogen storage after starvation (from Storch & Anger 1983, with permission from BAH, Helgoland, Germany).

The R-cells have a columnar shape, bear a prominent brush border, the nucleus is located at a central position, and their cytoplasm contains numerous storage vesicles (Fig. 3.19). They are the most numerous cell type in the hepatopancreas, fulfilling predominantly functions of intracellular absorption and storage of nutrients and minerals. The final products of digestion are stored in vacuoles or transferred to the hemolymph system.

In freshly hatched crab and lobster zoeae, large lipid vacuoles with stored yolk materials from the egg are the most prominent feature (Storch & Anger 1983, Anger et al. 1985). They persist under favourable feeding conditions, but are conspicuously reduced when food is absent or not accepted (Storch & Anger 1983, Anger et al. 1985, Mikami et al. 1994, Nishida et al. 1990, Takahashi et al. 1994). Also other cell organelles such as the mitochondria, the endoplasmatic reticulum and the basal membrane may show effects of nutritional stress (Fig. 3.19). Some of these ultrastructural alterations can become irreversible after prolonged starvation, in particular swollen mitochondria and reduced lipid vacuoles, indicating a severe damage to the enzymatic system of lipid conversion and storage (Storch & Anger 1983, Anger et al. 1985).

Characteristic structural changes in the R-cells and F-cells were observed not only during starvation, but also in response to other stress factors such as pollutants (Storch et al. 1982, Vogt 1990) or bacterial and viral diseases (Vogt 1992a, b). Hence, the hepatopancreas as a whole has been referred to as a *"mirror of the environment"* (Storch 1985) or a *"monitor organ"* (Vogt et al. 1985) indicating the physiological condition of crustaceans.

3.11.6 *Midgut and hindgut*

The anatomy of the midgut (or intestine) is relatively simple, although its basement membranes may develop an unusually complex, three-layered structure (Factor 1981a). In most decapod larvae, it shows blindly ending tubules, the anterior and posterior *caeca* (or *diverticulae*). These are particularly well developed in the herbivorous early stages (protozoeae) of penaeid shripmps, but they are absent in the larvae of caridean shrimps, or reduced in nephropid lobster and brachyuran crab larvae (Jones et al. 1997a).

Since this portion of the alimentary canal has an endodermal origin, it is not lined by a cuticle. It is dominated by only one type of cells, whose ultrastructure suggests mainly absorptive and osmoregulatory functions. Moreover, the intestine plays an immunological role, is involved in the excretion of waste metabolites from the hemolymph, and produces the chitinous peritrophic membrane, in which fecal matter of most decapods is wrapped. Putative neuroendocrine cells have been described beneath and within the intestinal epithelia (Mykles 1979, Factor 1981a). Furthermore, bacteria are commonly found in the midgut lumen and may supply nutrients and vitamins (Dall & Moriarty 1983).

The ontogeny of the midgut was extensively investigated in larvae of penaeid prawns (Talbot et al. 1972c, Lovett & Felder 1989, Abubakr & Jones 1992). In the lecithotrophic nauplius stages, the midgut has no lumen and cannot be identified easily. In the subsequent protozoeal stages, the intestine consists of a simple tube and well-developed anterior caeca. According to their large size and complex ultrastructure, which resembles that of the midgut gland, the caeca fulfill hepatopancreatic functions. Since both the external feeding appendages and the gastric mill show a simple structure, this intestinal anatomy suggests, corroborated by enzymatic data, that the breakdown of larval food is primarily enzymatic (Galgani & Benyamin 1985, Lovett & Felder 1990a). Stomach contractions act here primarily to mix ingested food particles with enzymes, playing an insignificant role in the mechanical breakdown of food (Jones et al. 1997a, b). The retainment of both digestive and absorptive functions in the anterior midgut caeca throughout the zoeal phase appears to be a unique feature of the penaeids (Lovett & Felder 1990b). The activity of digestive enzymes decreases to a minimum in the transition between the late mysis and the early "postlarval" phase, when the midgut caeca decline while the hepatopancreas is not yet fully developed (Lovett & Felder 1990a). In clawed lobsters (*Homarus americanus*), in contrast, the larval midgut has a similar morphology as that of the juveniles, including reduced caeca and a well-developed hepatopancreas (Hinton & Corey 1979, Factor 1981b, Biesiot & McDowell 1995).

The posterior portion of the alimentary canal, the hindgut, is lined with a cuticle and shows in many decapods cuticular spines and scales. These appear to direct fecal pallets towards the anus, which is located in the telson. As in the esophagus, there are tegumental glands that probably lubricate the passage of fecal pellets. The epithelium is involved in ion transport (Mykles 1979). As in the midgut, ontogenetic changes of the hindgut were studied in penaeid larvae and juveniles (Lovett & Felder 1989). It appears in the first protozoeal stage as a simple tube, and during the mysis phase it developes gradually increasing cuticular ridges that are covered with setae.

3.12 *Reproductive system*

As in the other principal organ systems of decapod crustaceans, a review of the structure of reproductive organs has been given in the treatise "*Microscopic Anatomy of Inverte-*

brates" (Krol et al. 1992). Again, most of the available evidence originates from studies of adult decapods, while ontogenetic changes are known only little. Decapods become sexually mature only after passing through a more or less extended juvenile phase including numerous molting cycles; however, the gonads may begin to develop much earlier (Charniaux-Cotton & Payen 1985). Their ontogeny is particularly interesting in those species which show a sex reversal, for instance several pandalid and other caridean shrimps (Shumway et al. 1985).

Primordial gonad tissues have been identified in the second thoracic somite of embryonic and larval stages of several carideans, anomurans, and brachyurans (Payen et al. 1971, Payen 1974, Le Roux 1976, 1992, Schultze 1993). From eyestalk ablation experiments can be inferred that sexual differentiation is not under direct neuroendocrine control. There is, however, an indirect control via the androgenic gland, at least in male individuals (see section 3.10.3). In a protandric hermaphrodite, the shrimp *Pandalus montagui*, the freshly hatched zoea I stage bears five to seven gonad cells near the ventral proximal part of the pericardial sac (Schultze 1993). During the course of larval development, these cells show continuous mitotic activity, eventually forming an H-shaped gonad in the first juvenile stage. In the European lobster, *Homarus gammarus*, a similar structure is visible at the end of the embryonic period, and the first zoeal stage shows a pair of gonoducts (Le Roux 1992). In the anomuran crab *Pisidia longicornis*, sexual differentiation is in the megalopa stage far enough advanced to allow, at least in some individuals, distinguishing between male and female larvae; the genital orifices become visible in the second juvenile instar (Le Roux 1976). In the Norway lobster, *Nephrops norvegicus*, the genital openings appear in the first juvenile (Farmer 1974), while this is later in another clawed lobster, *H. gammarus*, where the genital openings allow for an identification of sex only in later juveniles with about 8 mm carapace length, and pleopod and thelycum morphology differentiate still later (Le Roux 1992). In some brachyuran crab species (*Callinectes sapidus*, *Rhithropanopeus harrisii, Menippe mercenaria*), differential morphology of pleopods was observed in second-instar juveniles (Payen 1974).

In summary, the primary reproductive organs develop usually very early, i.e. in the late embryonic or early larval phase, although they become functional much later, in sexually mature adults. Secondary sexual characters such as modified pleopods, in contrast, are absent in larvae and appear only during juvenile growth. From numerous studies it appears that malacostracan crustaceans are primarily hermaphroditic, possessing the genetic programmes for the expression of both sexes. The decision as to which is eventually utilized may depend on the concentration of androgenic hormone that is produced in the androgenic gland and, possibly, in the *anlagen* of secondary sexual characters (Charniaux-Cotton & Payen 1985).

4 THE MOLTING CYCLE

When, more than half a century ago, the French zoologist P. Drach studied the anatomy of the integument in adult edible crabs (*Cancer pagurus*), he noted that the structures of the cuticle and the underlying epidermis are subject to conspicuous changes between subsequent molts (Drach 1939). He named these recurrent periods *"cycle d'intermue"* ("intermolt cycle") and described them primarily as an integumentary cycle. Drach's classification system for the molting cycle was later further elaborated and generalized for the crustacea (Skinner 1962, Tchernigovtzeff 1965, Drach & Tchernigovtzeff 1967), and has been applied, in a simplified form, to decapod larvae (Broad & Hubschman 1963, Freeman & Costlow 1980, Anger 1983, Hatfield 1983), and even embryos (Helluy & Beltz 1990, 1991). It comprises five principal molt-stages, each of which can be further divided into several hierarchically lower orders of substages. In Drach's terminology, successive molt-stages are denoted by capital letters from *A* to *E*, substages by subscript Arabic numerals (e.g. D_1, D_2). Since the term "intermolt" has been widely accepted to denote a particular stage within the molting cycle (see below), I will not use it here as a synonym of "molting cycle", as Drach and several other authors did.

In this chapter, I will first describe the principal anatomical events of the molting cycle, with special reference to changes in the integument of crab larvae. In this context, changes associated with the development of external morphological characters of successive larval stages (for instance, changes in body shape, formation of new spines or appendages; see chapter 2) are referred to as *morphogenesis*. Subsequently, I will briefly consider cyclic changes that have been observed in other organs (hepatopancreas, blood), and account for the intrinsic regulation of the molting cycle.

Like most cyclic phenomena in biology (e.g. reproductive cycles, seasonal migration patterns), the molting cycle is principally under endocrine control. I will thus briefly recur later to the major hormone-producing organs, i.e. the Y-organs, the X-organ-sinus-gland complex, and the mandibular organs, the principal anatomical and functional traits of which are described in chapter 3. Several effects of intrinsic and extrinsic factors, or interactions thereof, are limited to certain periods within the molting cycle. Hence, *"critical points"* in development, which determine the appearance or strength of controlling and modulating effects, will be another subject of this chapter. Among the extrinsic factors affecting the molting cycle, temperature and nutrition are of utmost importance (see sections 6.2.1, 6.3). The light rhythm is another potentially significant environmental parameter influencing larval growth, molting, and development (Aiken 1969, Aiken & Waddy 1976, Mikami & Greenwood 1997b, Charmantier & Charmantier-Daures 1998).

The anatomical and physiological changes related to the molting cycle have important implications for most other aspects of larval biology. Hence, the molting cycle and its control will be considered as determining factors also in the following chapters of this book, explaining variations in larval feeding, growth, chemical composition, metabolism, energy partitioning, behavior, and ecology.

4.1 *The stages of the integumentary cycle*

In large adult crustaceans, a thick multilayered integument (see section 3.1) and long molt cycle intervals allow for recognizing small histological and histochemical changes and hence, for establishing a fine system of molt-stages and substages. These dynamics were reviewed in Volume 9 of the treatise *"The Biology of Crustacea"* (Skinner 1985b, Stevenson 1985) and in the book *"The Crustacean Integument - Morphology and Biochemistry"* (Horst & Freeman 1993).

Compared with adult decapods, planktonic larvae have a thinner integument with a less complex structure and shorter instar durations. The subdivision of the molting cycle remains thus less elaborated, with broader categories than in adults. As a technical advantage, however, larvae have generally a transparent integument, which allows for a microscopical routine examination of entire individuals without using time-consuming histological techniques. Similarly, only transparent body parts such as epipodites or pleopods are used in microscopic routine checks of the principal stages in adults, although this implies a loss of information on substages.

Since integumental changes occur not entirely synchronously and cannot be equally well recognized in all body regions of a larva, a well-defined reference region must be selected. The larval telson is particularly suitable, because it is transparent and can easily be mounted in an horizontal plane (Fig. 4.1). In decapodid stages, pleopods can additionally be used to check for integumentary changes (Anger 1983). Also antennae and carapace spines have been used to study the molting cycle in larvae (Freeman & Costlow 1980) and, in non-brachyuran Decapoda, the uropods represent another suitable reference structure (Smith & Dall 1985, Dall et al. 1990).

Complete or partial descriptions of larval molting cycles have become available for brachyuran crabs (Freeman & Costlow 1980, McConaugha 1980, Anger 1983), caridean shrimps (Broad & Hubschman 1963, McNamara et al. 1980), and American lobsters (Rao et al. 1973, Sasaki 1984). Detailed descriptions were given also for the molting cycle in early juvenile crayfish (referred to as "larvae"; van Herp & Bellon-Humbert 1978) and "postlarval" penaeid shrimps (Huner & Colvin 1979). In addition, histological, histochemical and ultrastructural details were studied in the integument of larval crabs and palaemonid shrimps (Christiansen & Costlow 1982, Christiansen et al. 1984, Christiansen 1986, Freeman 1990, 1991).

In a description of the successive molting cycles in spider crab (*Hyas araneus*) larvae, I distinguished only the principal molt-stages (Anger 1983): *A-B* (early and late *postmolt* combined); *C* (*intermolt*), which may be combined with *A-B,* as the transitions between these molt-stages are gradual and not always clear in light-microscopical observations of whole-body mounts); *D* (premolt) with substages D_0, D_1, and $D_{2\text{-}4}$ (early, intermediate and late premolt); *E* (the short process of *ecdysis*).

In the following account of the integumentary cycle in developing decapod larvae, I will widely use *Hyas araneus* as a model to demonstrate gross structural changes in the larval integument (Fig. 4.1). Information on the epidermal cell cycle and other ultrastructurural details is based upon several investigations by J.A. Freeman and coworkers, who used predominantly brine shrimp (*Artemia*), but also brachyuran crab and caridean shrimp larvae as models (for review, see Freeman 1993, 1995). However, the general applicability of Freeman's classification system of the epidermal cell cycle and the various cell types remains to be ascertained in further decapod larvae.

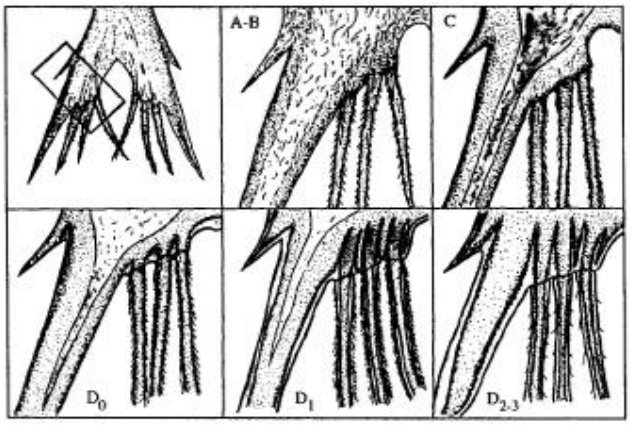


Figure 4.1. Schematic presentation of integumentary changes in a crab zoea during the molting cycle; upper left: reference region in the telson; *A-B*, *C*, D_0, D_1, $D_{2\text{-}3}$: principal stages and substages of the integumentary cycle (from Anger 1992, with permission from Spektrum, Heidelberg, Germany).

4.1.1 *Postmolt (A-B)*

During and shortly after ecdysis, in molt-stage *A* or *early postmolt*, aquatic crustaceans take up considerable amounts of water. Consequently, they increase rapidly in body size, evaginate spines, setae and appendages, and stretch their thin and limp cuticle. The extent of this stretching process depends mainly on the increase in epidermal cell number achieved prior to ecdysis (Cheng & Chang 1993). The attainment of final size and morphology of the new instar is a rapid process. In larvae, the early postmolt period lasts only a few minutes; it takes longer in juveniles, but usually less than one hour. During this brief stage, aquatic crustaceans perform pumping movements and drink water; otherwise they remain behaviorally inactive. In consequence, pelagic larvae tend to sink in the water column during ecdysis and in early postmolt.

During molt-stage *A*, the epidermis has a spongy structure with numerous large lacunae (Fig. 4.2a). The new cuticle consists initially of only two principal layers: the exocuticle and epicuticule. Synthesis of the endocuticle begins immediately and continues throughout postmolt and intermolt (cf. section 3.1). Since the animals do not eat while they are soft-skinned, postmolt cuticle formation is initially based on stored materials (see section 4.2.1). A short nonfeeding period is enforced not only by the softness of the external feeding appendages. Also, the cuticular structures in the foregut and the gastric mill (where present) are too limp for an effective mechanical maceration of food particles.

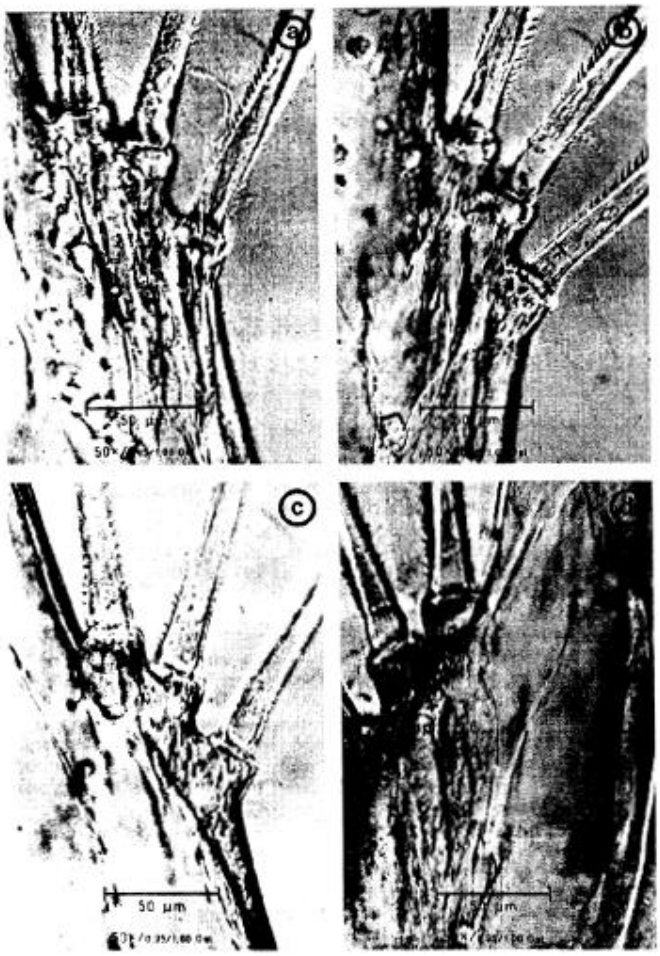


Figure 4.2. Integumentary changes in a crab larva during the molting cycle (*Hyas araneus*, zoea I, telson); early and intermediate molt-stages (after Anger 1983a, with permission from BAH, Helgoland, Germany). [a] early postmolt (molt-stage *A*; immediately after hatching): spongy epidermis with spacious lacunae, thin cuticle; [b] late postmolt (molt-stage *B*; <10% of instar duration, ID): condensing epidermis, shrinking lacunae; [c] intermolt (molt-stage C; 20% ID): condensed epidermis, thickened cuticle; [d] early premolt (molt-stage D_0; 35% ID); principal characteristic: beginning epidermal retraction from the cuticle (apolysis, ap), first visible at setal bases; maximum thickness of cuticle and epidermis.

As soon as the body has reached its final dimensions (molt-stage *B*, *late postmolt*), the epidermal tissues begin to attain a denser appearance (Fig. 4.2b), and the cuticle is strengthened. These processes continue throughout the postmolt and most of the intermolt

stages. Cuticle synthesis is apparently independent of external food materials. In zoea I spider crab (*Hyas araneus*) larvae, the chitin content increased after hatching more than four-fold, regardless whether the larvae were fed or starved (Anger & Nair 1979). Planktonic zoeae show, in general, an uncalcified cuticle (see section 3.1), implying that their growth is restricted to the addition of organic layers, especially in the endocuticle. In megalopae and benthic juveniles, in contrast, the cuticle is more rigid and partially calcified. Calcium deposition begins here soon after molting and continues through intermolt. In marine decapods, Ca^{2+} is taken up from the surrounding water, while terrestrial and freshwater forms mobilize previously deposited carbonates from the hepatopancreas.

On the ultrastructural level, a pronounced cell cycle accompanies the molting cycle (Freeman 1993). Many epidermal cells (in particular the *"larval epidermal cells"*; see section 3.1) have undergone mitosis shortly before ecdysis and thus, show a small average cell size and a low cytoplasm to nuclear volume ratio. Their average cell size increases gradually during postmolt, so that the epidermal structure shows an increasing tissue density and decreasing lacunar spaces. Endocuticle secretion does not appear to depend much on microvilli, as probably the entire apical cell surface or at least specific sites thereof are involved in the completion of the postmolt cuticle.

During postmolt and early intermolt, resting epidermal cells may enter the cycling (replicating) population, while previously cycling cells may differentiate and become permanently nonreplicating (Freeman 1993). In crab larvae, the postmolt-stages *A* and *B* combined take usually less than about 10% of total instar duration (Anger 1987a).

4.1.2 *Intermolt (C)*

In adult crustaceans, the beginning of the intermolt period (molt-stage C_1) is defined by the termination of chemical changes in the preecdysial cuticle (Drach 1939, Stevenson 1985). Although this criterion is difficult to ascertain in larvae without using histological or ultrastructural techniques, molt-stage *C* appears also here as a period of developmental arrest. The endocuticle is fully developed, and total cuticle thickness has reached its maximum. The epidermis, however, continues to grow throughout intermolt. This is microscopically visible as a continually increasing density and extension of epidermal tissues and a decrease of lacunar spaces (Fig. 4.2c). This phase of epidermal growth is not primarily based on cell proliferation but on an increase in average cell volume (Freeman 1993).

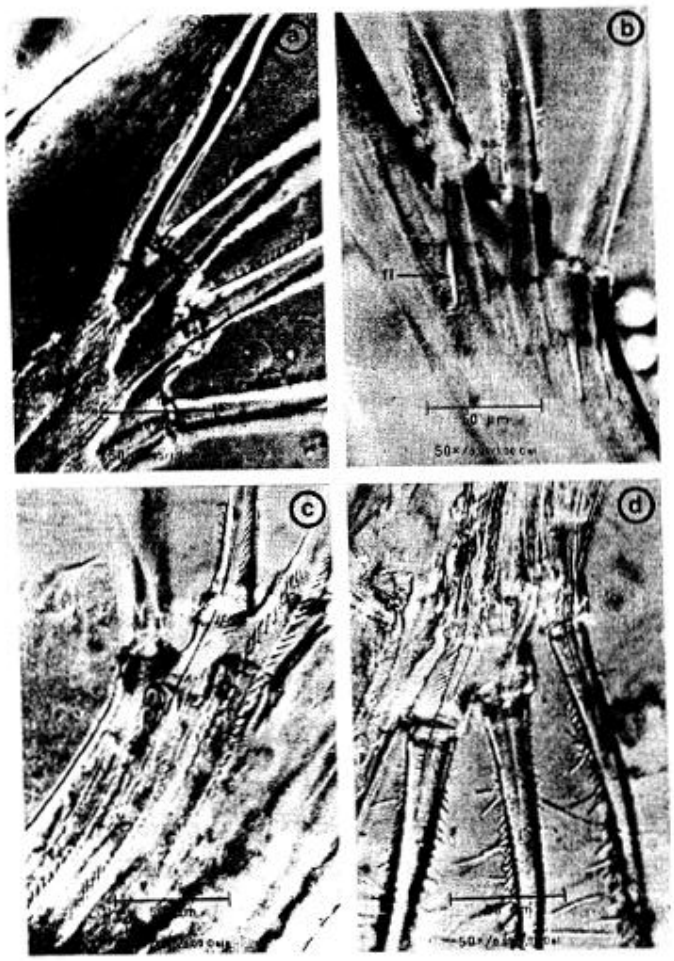


Figure 4.3. Integumentary changes in a crab larva during the molting cycle (*Hyas araneus*, zoea I, telson); intermediate and late molt-stages (after Anger 1983a, with permission from BAH, Helgoland, Germany). [a] early premolt (molt-stage D_0; 55% of instar duration, ID): as in Fig. 4.2e but with advanced apolysis (ap); [b] intermediate premolt (molt-stage D_1; 65% ID): principal characteristic: morphogenesis, with folds of epidermal invagination (fi) at setal bases, appearance of secondary spinules (ss) on the surface of retracted setal epidermis; [c] late premolt (molt-stage$D_{2\text{-}3}$; 90% ID): characteristic: new cuticle clearly visible on the surface of the retracted epidermis, morphogenesis terminated, maximum infoldings; [d] late premolt (molt-stage D_4; immediately prior to ecdysis, molt-stage *E*); withdrawal of epidermis from old cuticle.

The co-occurrence of maximal growth with minimal development may be the most typical trait of molt-stage *C*. In adult crustaceans, the exoskeleton continues to harden, reaching the final state of rigidity in substage C_3; when the formation of the membranous layer is completed, the final substage, C_4, begins. However, planktonic crustaceans have

generally a poorly hardened and uncalcified cuticle which lacks also a membranous layer (Pütz & Buchholz 1991). Hence, these criteria cannot be applied to decapod larvae, making a subdivision of their intermolt phase impractical.

During the intermolt period of anamorphic zoeae (i.e. in those developing to another, morphologically similar, zoeal stage; see section 2.2.2), there are no dramatic structural changes in the integument. In metamorphic zoeae which develop to a decapodid or juvenile, by contrast, some morphogenesis begins already during molt-stage *C*. This may be observed in the buds of pereiopods and pleopods, which become functional in the subsequent megalopa (Anger 1983a). It seems to be a typical trait that this morphogenesis begins first near the arthrodial membranes, probably indicating an early differentiation of the arthrodial membrane cells (Freeman 1993).

On the ultrastructural level, the apical membrane of the epidermal cells shows during molt-stage *C* a planar conformation, being fully attatched to the cuticle, while the Golgi apparatus is poorly developed, reflecting a minimal secretory activity. In late intermolt, however, an incorporation of radiolabelled bases was shown experimentally (Wittig & Stevenson 1975, Freeman 1993), indicating that DNA replication begins during this molt-stage. It continues throughout the intermediate or late premolt stages as a preparation for epidermal mitoses. It is at present not known whether or how ecdysteroids stimulate DNA synthesis in larval crustaceans (Freeman 1993, Chang 1995).

In first-stage larvae of several decapod species, the total duration of molt-stages *A* to *C* combined was about one third to one half of the total instar duration, with about 20 to 40% in intermolt alone (Anger 1983a, 1987a). In successively later larval stages of *Hyas araneus*, there was an increasing trend in both the absolute and relative length of molt-stage *C*, from ca. 22% in the zoea I to 37% in the megalopa. In juvenile and adult crustaceans, intermolt is the longest molt-stage; it becomes the final state in adults that have reached terminal anecdysis (Hartnoll 1985, Skinner 1985a, b).

4.1.3 *Premolt (D)*

***D_0* (early premolt).** This substage was introduced later into Drach's classification system (Charniaux-Legrand 1952, Skinner 1962, Drach & Tchernigovtzeff 1967). Soon after the integument has attained what appears to be its final thickness and structure, a characteristic event occurs: the beginning withdrawal of the epidermis from the cuticle (Fig. 4.2d). This process, termed *apolysis* (Jenkin & Hinton 1966), is facilitated by proteolytic and chitinolytic enzymes (Spindler-Barth et al. 1990, Peters et al. 1999). It initiates morphogenesis in all regions of the body, representing the most typical event of substage D_0. Apolysis begins first in those structures which are programmed to undergo marked morphogenetic changes, in particular at the base of newly formed setae, spines and appendages, before it proceeds through other body regions. On the surface of major setae, an incipient formation of secondary spinules is apparent soon after apolysis. The epidermis appears highly condensed and attains an increasingly fibrous structure, particularly in setae that are withdrawing from the old cuticle sheath (Fig. 4.3a). Ultrastructurally, the apical region of the epidermal cells demonstrates a change from a planar conformation to one with numerous microvilli (Freeman 1993). These surface structures continue to grow in height during premolt, while the epicuticle is secreted at the tips of the microvilli.

In metamorphic zoeae, morphogenesis of the posterior thoracic and pleonal appendages may begin earlier, proceeding throughout premolt. These processes begin with myomere formation and advance rapidly with the differentiation of limb buds and associated struc-

tures. In the zoea II of *Hyas araneus*, for instance, this can be observed particularly well in the pereiopods (Fig. 4.4). These thoracic appendages develop from initially undifferentiated buds to walking legs and chelae, becoming functional immediately after the molt to the megalopa. While the duration of the intermolt period (*C*) increased in successive larval stages of *Hyas araneus*, D_0 tended to become shorter, from 26 to 15% of total instar duration. In the zoea I of several other decapod species, average D_0 durations between 18 and 28% were observed.

***D*$_1$ (intermediate premolt).** Whilst apolysis continues in some regions of the larval body, the reference structure (in our example the telson) undergoes another conspicuous change: the beginning *invagination* of epidermal tissues. As in apolysis, this morphogenetic event becomes first visible near the base of setae and spines (Fig. 4.3b). Compared with the relative durations of molt-stages *C* and D_0, the intermediate premolt period (D_1) remained fairly constant (about 15-18%) in the successive larval stages of *Hyas araneus*.

During the second half of this substage of the molting cycle, the setae become fully separated from the old cuticle, and only thin epidermal filaments connect the tips of the retracted setae with the inner distal end of the old cuticle sheath (Fig. 4.5). Morphogenesis is now conspicuous, with new setae and spines being formed, and well-developed secondary spinules appearing on their surfaces. In some body regions, the epidermis attains a pleated appearance, indicating continued tissue growth and increasing surface area.

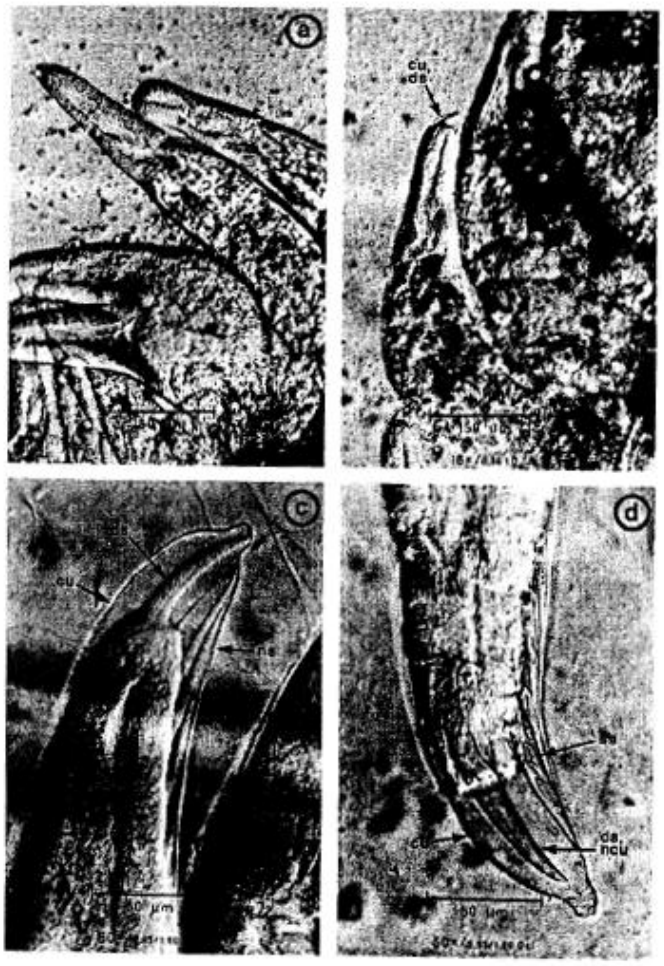


Figure 4.4. Morphogenesis during the molting cycle of a metamorphic zoeal stage of a crab (*Hyas araneus*, zoea II): formation of dactyl spines (ds), new setae (ns), and secondary spinules (ss) under the cuticular sheaths (cu) of the developing pereiopods (after Anger 1983a, with permission from BAH, Helgoland, Germany). [a] early intermolt (molt-stage *C*; 25% of instar duration, ID): pereiopods undifferentiated; [b] late intermolt (molt-stage *C*; 40% ID): epidermal retraction from the cuticle, cu, and incipient morphogenesis: beginning of segmentation and dactyl spine formation; [c] early premolt (molt-stage D_0; 60% ID): advanced formation of dactyl spines and new setae on dactylar segment; [d] late premolt (molt-stage $D_{2\text{-}3}$; >90% ID): formation of dactyl spine and new setae terminated, new cuticle (ncu) conspicuous on epidermal surface.

At the end of D_1, the folds of invagination reach their maximal depth in the telson setae. In contrast to *C*, molt-stage D_1 is characterized by a maximum rate of morphogenesis and decreasing epidermal tissue growth. Besides the formation of new structures, there is a considerable enhancement of the surface area in already existing body parts. These invaginations and other internal folding processes are major prerequisites for later postmolt growth. They are achieved by an enlargement of epidermal cells, which may in some body regions double in height (Freeman 1993).

In adult crustaceans, substages D_1' to D_1''' may be distinguished based on the depth of invagination (Stevenson 1985). The mechanisms of setal development (*setagenesis*) have been under considerable dispute, in particular the question of invagination *vs.* splitting of epidermal tissues (Aiken 1973, Tchernigovtzeff 1976, Dexter 1981, Graf 1986, Freeman et al. 1992).

Reconstruction processes such as setagenesis, including a lengthening of previously existing setae and spines, and the formation of new structures are typical morphogenetic events. In metamorphic zoeae, significant degeneration processes occur too. In the zoea II of *Hyas araneus*, for instance, the furca of the telson is reduced, so that the outer rami and the inner setae disappear gradually (Fig. 4.5). Deep epidermal retraction and subsequent resorption belong here to the most typical events of substage D_1, resulting in the morphogenesis of the typical megalopa telson (lacking a furca; Fig. 4.5c). Likewise, the dosal carapace spine is greatly reduced at the transition from the last zoeal stage to the megalopa (in many species it disappears completely; see Freeman & Costlow 1983). Such processes may be associated to some degree with *programmed cell death* or *apoptosis* of differentiated cells, which typically occurs in remodelled regions of the integument (Wyllie et al. 1980).

***$D_{2\text{-}4}$* (late premolt).** The onset of the late premolt period (substage D_2) is indicated by the first appearance of a new cuticle on the epidermal surface of setae and spines. It is microscopically visible as a thin yellowish layer, chiefly representing exocuticle material. The results of the preceding morphogenesis become thus more conspicuous in late premolt, when the new structures are fixed and optically pronounced by the new cuticle on their surfaces (Figs. 4.3c, d). Since the development of the new cuticle is a gradual process, a further subdivision of the late premolt period into substages is difficult in small larval decapods, although it may be possible in larger forms such as lobster larvae (Sasaki et al. 1986).

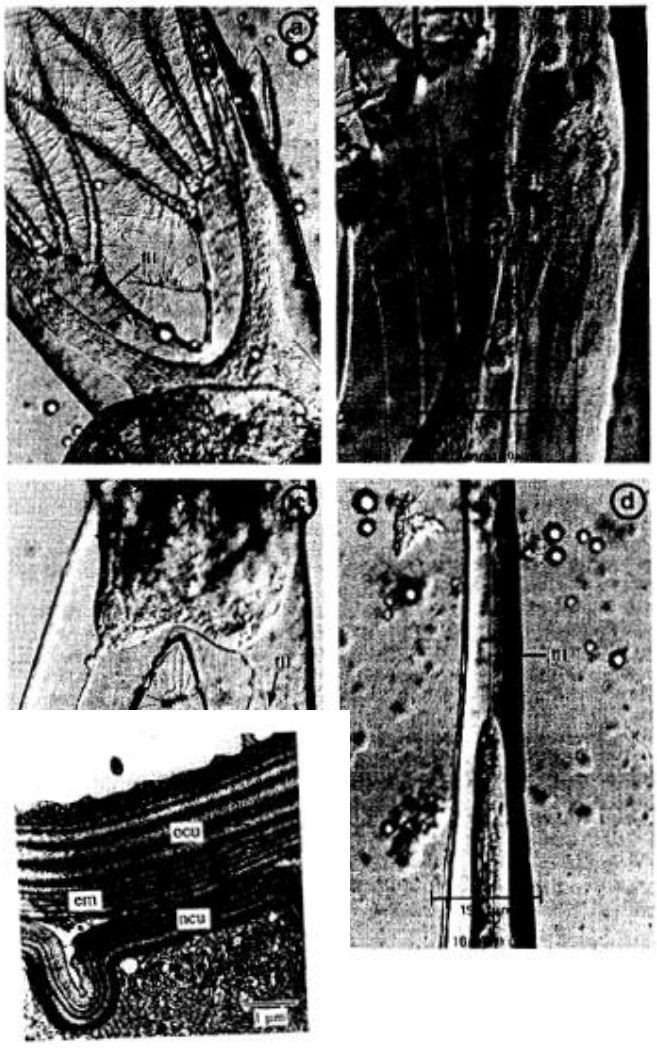


Figure 4.5. Morphogenesis during the molting cycle of a crab (*Hyas araneus*) megalopa (after Anger 1983a, with permission from BAH, Helgoland, Germany). [a] intermediate premolt (molt-stage D_1; 75% of instar duration, ID): retraction and degeneration of epidermal tissues in the zoeal furca; epidermis of inner telson spines reduced to thin filaments (fil), incipient reduction of outer rami; [b] as in [a], close-up; [c] late premolt (molt-stage $D_{2–3}$; >90% ID): advanced resorption of epidermal tissues, outer rami reduced to thin filaments, formation of the bilobed megalopa telson; (d) retraction and resorption of epidermal tissues in the dorsal carapace spine, with distal parts reduced to a thin epidermal filament.

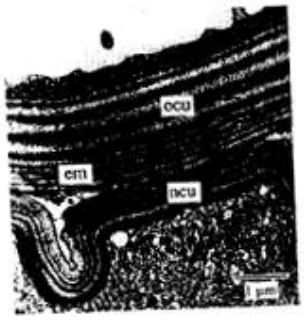


Figure 4.6. Cuticle of a crab larva (*Hyas araneus*, zoea II) in late premolt (D_3); TEM. em: ecdysial membrane; ncu: new cuticle; ocu: old cuticle (from Höcker (1988, with permission from the author).

A closer examination with transmission electron dysial membrane and an increasing gap of apolysis e (Fig. 4.6). The thickness of the new cuticle may eventually reach about one third of that in the old one. Its surface area is substantially enlarged by deep wrinkles and invaginations. This allows, during and immediately after ecdysis, for a rapid inflation of tissues with water taken up from the environment, and hence, for postmolt increase in larval body size (see section 6.2.2). In contrast to adult crustaceans with a thick and calcified cuticle, at least the pelagic zoeal stages do not show signs of a significant resorption of old cuticle material. This process might play a certain role, however, in benthic or semibenthic decapodid stages with a more rigid exoskeleton.

For the cycling population of epidermal cells, late premolt is typically the period of replication (Freeman 1993). After mitosis, there are no signs of an immediate increase in cell volume. The epidermal cells remain small with closely packed nuclei. The mechanism of surface enlargement at ecdysis remains little understood. It is probably associated with changes in cell shape and distribution in the early postmolt epidermis. The duration of the late premolt period appears to be highly variable among decapod species, ranging from less than 10 to almost 30% of total instar duration (Anger 1987a).

4.1.4 *Ecdysis (E)*

In larval decapods, the molting process is a very brief process of usually less than a minute. It is preceded by a conspicuous, sometimes macroscopically visible uptake of water at the end of the late premolt period (substage D_4). As in adult decapods, the old cuticle ruptures between the carapace and the pleon, where the larva begins to draw itself out of the old exoskeleton. The exuvia is eventually stripped off with the aid of the posteriorly bent pleon.

4.2 *Other cyclic changes*

In addition to the cyclic dynamics of integumentary structures in crustaceans, molt-cycle related changes occur also in the anatomy, biochemistry, and physiology of other organ systems (Yamaoka & Scheer 1970, Skinner 1985a, b, Chang 1995). Most cyclic processes, however, are known from adults rather than larvae. I will treat here only some con-

spicuous changes in the hepatopancreas and the hemolymph, while cyclic patterns in feeding, growth, chemical composition, respiration, and excretion will be reviewed in the following chapters.

4.2.1 *Hepatopancreas*

Several structural, physiological and biochemical traits of the hepatopancreas undergo cyclic changes associated with nutrition and molting (Icely & Nott 1992, Chang 1995). However, this has received little attention in larval decapods, and it is sometimes difficult to conclude whether such changes are controlled directly by the molting cycle and its hormonal regulation system, or indirectly, as a consequence of cyclically varying feeding activity. Since the available evidence suggests that the typical structures and functions of the hepatopancreas appear early in the ontogeny of the Decapoda (see section 3.11.5), I will review here some typical patterns that have been observed in adults, assuming that they are similar in larval stages. In a particularly detailed investigation, Al-Mohanna & Nott (1989) found the following molt-cycle related changes in the various hepatopancreas cell populations of adult penaeid shrimps, *Penaeus semisulcatus*.

During the nonfeeding postmolt stages (*A*-*B*), the F-cells (fibrillar cells) dominate in the tubular epithelia of the hepatopancreas, together with the R-cells (resorptive cells). The F-cells cells produce and secrete zymogen for extracellular digestion and take up material for intracellular ingestion. From the beginning of molt-stage *C*, i.e. soon after the first ingestion of food, the frequency of F-cells begins to decrease, as they differentiate into B-cells (blister-like cells). This takes place particularly in the mid and proximal regions of the hepatopancreas tubules. The F-cells reach their minimal concentration in early or intermediate premolt (D_0-D_1), but increase again in late premolt ($D_{2\text{-}4}$).

The B-cells, which originate from F-cells, pinocytose materials from the tubular lumen for intracellular ingestion, beginning in early molt-stage *C*. The digested materials are stored in vacuoles, until the whole cells are eventually extruded into the lumen. Secretory granules that are discharged from the F-cells may aid in the extracellular digestion of broken-down B-cells. During the premolt phase, the abundance of B-cells decreases with decreasing feeding activity.

As another event that is initiated by food uptake in early intermolt (*C*), a burst of mitotic activity occurs in the population of E-cells (embryonic cells). These differentiate into other cell types that are extruded into the lumen. E-cell proliferation, which takes place at the distal ends of the tubules, decreases gradually from the intermolt throughout the premolt stages, while feeding activity declines concomitantly. Both the uptake of food and the mitotic activity of the E-cells cease before ecdysis (molt-stage D_4).

The abundance of R-cells remains comparatively constant during the molting cycle, usually dominating within the hepatopancreas epithelia. However, cyclic changes were observed in their typical lipid and glycogen inclusions. R-cells absorb soluble nutrients from the lumen and store them, predominantly as lipids, in conspicuous vacuoles and particles (Fig. 3.19). These reserves increase through the intermolt stages and reach their greatest extension in early premolt, D_0. During the subsequent premolt stages, they diminish again, concommitantly with the decrease in feeding. During the later premolt stages, R-cells are partly discharged into the tubular lumen, in particular in vicinity to B-cells. Broken-down R-cells are replaced by newly divided and subsequently differentiating E-cells.

Since there is no uptake of food during the period from late premolt to early postmolt, B-cells take up nutrients that originate from discharged R-cells to sustain the animal during temporary fasting. During molt-stages *A-B*, large vacuoles in the B-cells, concurring with a lack of enzyme vacuoles in the R-cells, reflect the absence of exogenous nutrients. In the R-cells, an extensive smooth endoplasmatic reticulum, large vacuoles, and various residual materials are conspicuous during this period of the molting cycle. As another consequence of the nonfeeding period, total weight of the hepatopancreas decreases to a minimum. These losses of both organic and inorganic reserves are replenished during the subsequent molting cycle.

4.2.2 *Hemolymph*

The molting cycle is associated with major changes in the balance of water and ions, and consequently, there are cyclical changes in the chemistry of the hemolymph. Also in this respect, very little is known about larval stages, but again, extrapolations from adults seem to be justified. This includes cyclic changes in the permeability of transport tissues (gills, branchiostegites) and variations in the activity of nephridial organs (antennal glands), which are probably under neuroendocrine control.

Due to a significant uptake of water during and shortly after ecdysis, the overall concentration of ions and organic molecules, i.e. the osmolality of hemolymph, is generally minimum in early postmolt (Mantel 1985). As a consequence of a transitorily increasing permeability of their integument, the osmoregulatory capacity of decapod larvae was observed to decrease immediately after ecdysis (Charmantier et al. 1994, 1998). It increased again during the subsequent intermolt stages, as the water and ion permeability of the integument decreased. During premolt, water losses may be reduced by lowering the rates of urination and ammonia excretion (Regnault 1979, Mantel & Farmer 1983).

The composition of crustacean blood changes also due to cyclic variations in the production of hemocytes (***hematopoiesis***; see section 3.4). During early postmolt, only very few hemocytes were found in the hematopoietic tissues of penaeid shrimps (Martin & Hose 1992). This was followed by an increasing mitotic activity through molt-stage D_0. During the subsequent stages of the premolt period, the newly produced hemocytes were released into the lumen of hemolymph sinuses, while the rate of hematopoietic mitoses declined. A similar cycle was observed in the shore crab, *Carcinus maenas*, but with high mitotic rates through late premolt, D_3 (Marrec 1944). Since hemocytes occur already in larval stages, we may expect similar cycles in hematopoietic tissues and hemolymph.

Numerous cyclical changes in the biochemical and mineral composition of crustacean blood have been described in the literature, but it remains unclear which of those patterns apply also to larvae. For example, the blood serum protein may typically increase throughout the premolt stages, as a consequence of partial resorption of cuticular protein (Yamaoka & Scheer 1970). However, cuticular resorption should not play a significant role in planktonic zoeae, and the protein content of their hemolymph may thus remain constant. On the other hand, minimum protein concentrations during the period of endocuticle synthesis should occur in both adult and larval decapods. Improved microanalytical techniques applied in future studies will show the extend to which we can infer, in this respect, larval traits from observations in adults.

4.3 *The hormonal control of the molting cycle*

The molting cycle is primarily controlled by steroid hormones that are produced in paired epithelial glands in the cephalothorax, the Y-organs or molting glands. The secretory activity of these endocrine organs, on the other hand, is regulated by neuropeptides that are produced in the X-organs of the eyestalk ganglia, namely by molt-inhibiting hormones (*MIH*). Additionally, also a stimulating factor from the mandibular organs (*MO*) may be involved in the control of the Y-organs. General anatomical and functional aspects of these hormone-producing organs were treated in the preceding chapter (sections 3.9.2, 3.10.1, 3.10.2), while the following sections focus on their significance for the control of the molting cycle.

4.3.1 *Y-organs and molting hormones (ecdysteroids)*

In both adult and larval decapod crustaceans, molt-cycle controlling ecdysteroid hormones are produced in the Y-organs. All available evidence suggests that in principle no ontogenetic changes take place after hatching, so that observations from adult decapods should apply also to their larval stages (Charmantier et al. 1996, Charmantier & Charmantier-Daures 1998). As in other steroid-secreting glands, the secretory products are not stored in conspicuous amounts in the cytoplasma, and thus, no granules can be used as cytological indicators of the secretory activity in Y-organs. However, consistent with their role in the regulation of the molting cycle, characteristic variations in organ size and in histological and ultrastructural traits occur during the course of the molting cycle (Fingerman 1992, Charmantier et al. 1996). In several species of brachyuran crabs (Matsumoto 1962, Simione & Hoffman 1975, Bressac 1976b) and crayfish (Burghause 1975), the size of the Y-organs was observed to increase after eyestalk removal or near the intermolt-premolt transition, i.e. when an increasing secretion of ecdysteroids should be expected.

Signs of a gland hypertrophy were observed also in the Y-organs of larval crabs (*Cancer anthonyi*), where an increasing number and size of cytoplasmatic vacuoles suggested an increase in the synthetic activity at early premolt (McConaugha 1980). This change was more pronounced in cells located near the hemocoelic sinus, indicating that secretory products should be released soon into the hemolymph. Also cell divisions in the Y-organs were seen exclusively during premolt. This observation is consistent with an increasing mitotic activity in the Y-organs of adult crabs both after eyestalk ablation (Bressac 1976a) and during premolt (Bressac 1978, 1988).

In adult freshwater shrimps (*Palaemon paucidens*), cyclic changes were primarily observed in the average cell size of Y-organs (Aoto et al. 1974). It was minimum in molt-stage *C*. In early premolt (D_0), the cells began to grow substantially, and until late premolt ($D_{3\text{-}4}$) they reached approximately twice their average intermolt size. After ecdysis, the Y-organ cells decreased again in size. Also the morphology and size of the mitochondria and the smooth endoplasmatic reticulum showed distinct changes during the molting cycle, the most conspicuous being a 15-fold increase in mitochondrial size during late intermolt and early premolt. At the transition of intermolt and early premolt, an increase in number as well as changes in morphology were seen also in the mitochondria of Y-organ cells of two brachyuran crab species, *Cancer antennarius* and *Portunus trituberculatus* (Hinsch et al. 1980, Taketomi & Hyodo 1986).

Similar observations were made in larval spider crabs (*Hyas araneus*), where cyclic activity patterns in the mitochondria of the Y-organs suggested an increasing synthetic rate

during the second half of the molting cycle (Höcker 1988). These changes were accompanied by changes in nucleus size. It was largest during the early molt-stages, before the nuclei passed through mitoses; they became smaller in premolt, sometimes showing signs of degeneration. The latter phenomenon was observed also in adult crabs and shrimps after eyestalk ablation, and interpreted as a possible indication of a holoendocrine mode of secretion (Simione & Hoffman 1975, Bressac 1978, Le Roux 1974, 1977). In the Y-organs of adult crabs, changes were observed also in the number of infoldings in the cell membrane, showing an increase during premolt (Hinsch et al. 1980, Taketomi & Hyodo 1986). Consistently, these morphological and ultrastructural changes indicate a peak production of ecdysteroids near the epidermal event of apolysis (transition between molt-stages *C* and D_0) and throughout premolt.

The chemical nature of the endocrine products of the Y-organs, the ecdysteroids, was first demonstrated by D.H.S. Horn's working group, who analysed great amounts of waste from spiny lobster (*Jasus lalandii*) fisheries (Horn et al. 1966, Hampshire & Horn 1966). Many details of the structure and function of the molting glands as well as molecular mechanisms of hormonal regulation have been elucidated since. Endocrinological aspects were exhaustively reviewed, for instance, in the book *"Ecdysone, from Chemistry to Mode of Action"* (Koolman 1989) and in several recent articles (Birkenbeil 1990, Spaziani 1990, Fingerman 1992, Charmantier-Daures & Charmantier 1994, Charmantier & Charmantier-Daures 1998, Chang 1995, Charmantier et al. 1996).

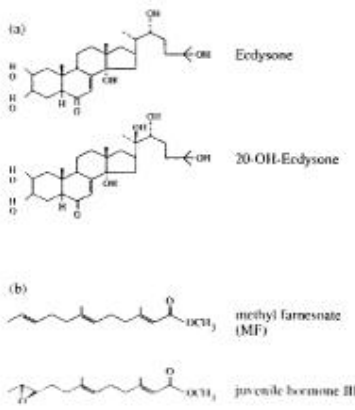


Figure 4.7. Structure of some crustacean hormones: [a] two species of ecdysteroids or molting hormones (ecdysone and 20-hydroxyecdysone; arrow indicates the additional hydroxyl group at the C-20 atom), with their precursor, cholesterol; [b] comparison of the putative crustacean juvenile hormone (methyl farnesoate, MF) with the insect juvenile hormone III.

Ecdysone, which is chemically identical with the i
higher Crustacea produced in the Y-organs, from whe
In the hepatopancreas, the epidermis, and in several
to 20-OH-ecdysone (Fig. 4.7). Besides these two
steroids, some further metabolites such as 3-dehyc
have been described (Chang 1995). The epidermis, where specific receptors have been found (Londershausen et al. 1982), is considered as the primary target tissue of ecdysteroids.

In order to study the ontogeny of the hormonal regulation of the molting cycle, effects of exogenous ecdysteroids were tested in fourth-stage American lobsters (*Homarus americanus*; see Rao et al. 1973) and in zoeae of brachyuran crabs (*Cancer anthonyi*, *Rhithropanopeus harrisii*; see McConaugha 1979, Freeman & Costlow 1983, 1984, McConaugha & Costlow 1981). These experiments showed that ecdysteroids, which were already known from insect endocrinology, exert great influence on the molting cycle and morphogenesis in larval and early juvenile decapods, including crucial integumental processes such as apolysis and, in metamorphic zoeae of crabs, dorsal spine resorption. For instance, exogenous 20-OH-ecdysone was shown *in vitro* to initiate the typical premolt changes in isolated integumentary tissues of crabs (*R. harrisii*), while crude extracts from the eyestalks of larval shrimps (*Palaemonetes vulgaris*) inhibited these effects (Freeman & Costlow 1984).

These experiments show not only the interaction of two hormonal factors but also suggest that major molecular structures and functional mechanisms may be universal among the Decapoda. Moreover, the available evidence suggests that the hormonal control system of the molting cycle is widely developed at hatching, i.e. it is similar in larval and adult decapods. This is corroborated by studies of the early ontogeny of ecdysteroid production in eggs of crayfish, caridean shrimps, and brachyuran crabs (for references, see Spindler et al. 1987, Charmantier & Charmantier-Daures 1998). It could be shown by radioimmunoassay (RIA) that ecdysteroid production begins already during embryogenesis. As in insects, rising titers were in general observed at the beginning of metamerization, and again when the larval Y-organ appeared microscopically. With a combined technique of high performance liquid chromatography (HPLC) and RIA, ecdysone and 20-OH-ecdysone could be identified as prominent ecdysteroids, showing in their ratio conspicuous developmental changes as well as specific differences among crab and shrimp species.

Direct evidence of cyclic changes in the titer of molting hormones in larval decapods was shown by RIA in two decapod species, the lobster *Homarus americanus* (Chang & Bruce 1981) and the spider crab *Hyas araneus* (Spindler & Anger 1986, Anger & Spindler 1987). These studies suggest that the course of the molting cycle and its regulation do not differ significantly between larval and adult decapods. In crab larvae, 20-OH-ecdysone was identified as the predominant molecular form, followed by ecdysone. As in most adult crustaceans, for which measurements are available (see Skinner 1985a, b), the concentration of molting hormones is in decapod larvae minimum during postmolt and maximum in premolt. In lobster larvae, the maximum ecdysteroid titer was reached approximately in the middle of each larval instar (however, the molting cycle was in these experiments not precisely checked), while this occurred later within the premout period in spider crab larvae. If the role of ecdysteroids were restricted to the initiation of apolysis, then their titer should be maximum in late intermolt and decrease subsequently. However, the patterns found in spider crab larvae may indicate that ecdysteroids have to fulfill further functions during premolt. Since no other comparative studies are available, it remains uncertain which of these patterns in the hormone titer is typical of an undisturbed larval molting cycle.

Molting hormones control the integumentary cycle, the production of cuticle layers and, in particular, chitin synthesis. In experiments with cultured insect cell lines, ecdysteroids were observed to inhibit cell proliferation and chitin synthesis, while they stimulate the expression and secretion of chitinolytic enzymes and regulate genes that are involved in morphogenesis (Spindler-Barth et al. 1995, Spindler-Barth & Spindler 1998).

Although the rate of hormone secretion is largely under intrinsic control, it may be modulated by extrinsic factors such as food availability. After initial starvation and subsequent feeding, the peak is delayed and the molting cycle becomes longer (Anger & Spindler 1987; see below, section 4.5). Also exogenous chemicals such as synthetic insect growth regulators may interfere with the hormonal sytems. Dimilin, for instance, was shown to inhibit the incorporation of N-acetylglucosamine in the cuticle of crab larvae, independent of the stage of the molting cycle (Christiansen & Costlow 1982, Christiansen et al. 1984).

4.3.2 *X-organs and molt-inhibiting hormones (MIH)*

The presence of a molt-inhibiting hormone (*MIH*) in the eyestalks has been postulated since Zeleny (1905) described a molt-accelarating effect of bilateral eyestalk ablation in fiddler crabs. In numerous experimental investigations, further indirect evidence of a multi-functional endocrine system in the eyestalk ganglia and associated structures has been gathered. As principal neuroendocrine production sites and neurohemal organs, respectively, the X-organs and sinus glands were anatomically localized and described (section 3.9.2). In adult crustaceans, the removal of these structures caused, among numerous other effects, generally an increase in the titers of molting hormones, a shortening of subsequent molting cycles, and enhanced growth. On the other hand, an experimental application of sinus gland extracts, either injected *in vivo* into the hemolymph or added *in vitro* to Y-organ tissue cultures, reduced the production of ecdysteroids (for review, see Cooke & Sullivan 1982, Skinner 1985a, b, Chang 1995, Charmantier & Charmantier-Daures 1998).

An enhancement of molting frequency and growth was observed also in eyestalk ablated decapod larvae (e.g. Freeman & Costlow 1980, Snyder & Chang 1986a, Gross & Knowlton 1997, 1999). In larval lobsters (*Homarus americanus*), this effect was accompanied by earlier and higher peaks in the ecdysteroid titer (Snyder & Chang 1986a). An injection of sinus gland extract from juveniles into larvae, on the other hand, oppressed the production of ecdysteroids and prolonged the molting cycle (Snyder & Chang 1986b). Consistent with anatomical studies of the X-organs and other endocrine sites, these experiments indicated that the hormonal regulation system of the molting cycle develops early in the ontogeny of the Decapoda, becoming generally functional from hatching. As an exception, penaeid and caridean shrimp larvae may reach a full functionalilty of their eyestalk systems only in later stages (see Gross & Knowlton 1997).

In the past decade, more direct evidence of the hormonal regulation of the molting cycle could be gathered with the availability of novel techniques. In adult shore crabs (*Carcinus maenas*) and lobsters (*Homarus americanus*), respectively, Webster & Keller (1986) and (Chang et al. 1987) confirmed the neuropeptide nature of the molt-inhibiting hormones, and soon were also their amino acid sequences described (Chang et al. 1990, Webster 1991). The presence of *MIH* in larval eyestalks could subsequently be demonstrated with immunocytochemical methods, namely in the perikarya connected with the *medulla terminalis* X-organ, the sinus tract, and the sinus gland of *C. maenas* (Webster & Dircksen 1991). In late embryos and early zoea I larvae of a crab, *Charybdis feriatus*, the expression of *MIH* genes was recently shown with PCR techniques (Chan et al. 1998).

Arguing that the quantities of *MIH* produced by crab zoeae are probably much lower than in megalopae and juveniles, Freeman et al. (1983) suggested that this ontogenetic difference could explain why the early planktonic larvae pass much more rapidly through their molting cycles than the later stages. With regard to the selective forces in their dif-

ferential environments, this would help the zoeae to avoid pelagic predation, whereas the semibenthic decapodids have more time to adjust to benthic life and find a suitable habitat. While this speculation is interesting in the context of larval ecology and life-history evolution, it remains to be tested in future endocrinological studies of the balance between neuropeptides and ecdysteroids in decapod larvae.

The chemical structure of *MIH* is similar to that of the other eyestalk neuropeptides. For instance, it is 90% identical with that of the crustacean hyperglycemic hormone, *CHH* (Chang et al. 1990), and it is very similar also to the newly discovered mandibular-organ inhibiting hormone (Wainwright et al. 1996b) and the gonad-inhibiting hormone. It is thus not surprising that *MIH* shows also significant *CHH* activity, which suggests that this neurohormone may be involved in osmoregulation as well (Charmantier-Daures et al. 1994; Charmantier 1998). However, as Chang (1995) said in his review, *"the actual role of the individual members of this family of multi-functional peptides in vivo remains to be determined"*. If this statement is true for adult crustaceans, it certainly applies even more to their larvae.

4.3.3 *Juvenile hormones (JH)*

While molting hormones are clearly regulated by an inhibitory factor, *MIH*, there may be additionally a stimulating factor comparable to the juvenile hormone (*JH*) of insects. Experimental exposure of crab and lobster larvae to insect *JH* or chemically related substances (terpenoids) has been shown to affect their development and survival. Endogenous crustacean factors that are chemically related to the *JH-III* of insects, namely methyl farnesoate (*MF*) and related compounds, have recently been identified in mandibular organs (*MO*) of adult Decapoda (Fig. 4.7, cf. section 3.10.2). However, the function of *MF* as putative crustacean *JH* in the regulation of morphogenesis and molting in larvae has remained largely unclear (Christiansen 1988, Abdu et al. 1998a, Charmantier & Charmantier-Daures 1998). Based upon its absence in several situations and species, Freeman (1993) suggested that *JH* is in the Crustacea not generally involved in these processes and may thus have other functions. On the other hand, *MF* was observed to stimulate the production of ecdysteroids in the Y-organs of adult shrimps, crabs and lobsters, and consequently, has an enhancing effect on molting frequency (Yudin et al. 1980, Tamone & Chang 1993). Likewise, enhanced ecdysteroid titers were observed in lobster larvae reared in water containing exogenous *MF* (Chang et al. 1993). These experimental observations suggest that the *MO* and their major product, *MF*, are involved in the regulation of the molting cycle of both adult and larval decapods.

This hypothesis is corroborated by anatomical investigations. As in the Y-organs, molt-cycle related morphological and ultrastructural changes were observed in the *MO*. In *Carcinus maenas*, the size of this organ was observed to be smallest shortly before, during and after ecdysis (late premolt to early postmolt), and the cytoplasm appears structurally different from the other molt-stages (Démeusy 1975). Vacuoles disappear at molt-stage D_0, are transitorily lacking through ecdysis, and increase to a maximum during late postmolt through intermolt. In crayfish (*Procambarus clarkii*), the development of the smooth endoplasmatic reticulum was found to be maximum in intermolt (Miyawaki & Taketomi 1971), and in the *MO* of caridean shrimps (*Palaemon paucidens*), mitochondrial enlargements were seen during the premolt stages D_0-D_1 (Aoto et al. 1974).

While these changes in the *MO* do not allow for drawing safe conclusions on changes in *MF* secretion, in particular in larval stages, an association of the *MO* with the molting

cycle may be postulated. Although the relationship between its control system and *MF* remains unclear, it may be speculated that *MIH* or another eyestalk factor could regulate the activities of both the Y-organs and the *MO*, and when the strength of the inhibition by neuropeptides declines, *MF* may stimulate the ecdysteroid secretion in the Y-organs.

4.4 *Autotomy and regeneration*

Autotomy and regeneration have intensively been studied as molt-cycle related processes in adult crustaceans, but only little in larvae. This includes, however, a detailed account of the histological mechanisms of wound repair and regeneration in crab larvae (Freeman 1983).

The first investigations of the relationships between larval molting cycles, metamorphosis, and regeneration were published by Costlow (1961, 1963a, b). He observed that the megalopa of the blue crab, *Callinectes sapidus*, is able to autotomize its chelae when these are stimulated mechanically. The separation of the appendage occurred at the same point as in adults, within the basi-ischiopodite. An immediate regeneration, i.e. a new limb formation during the same molting cycle, occurred only when the limbs had been lost during the first half of the time within an instar, while later injury was repaired during the subsequent molting cycle. This response pattern was later observed also in the megalopa of another crab, *Rhithropanopeus harrisii* (McConaugha & Costlow 1980), where the process of chela regeneration was later studied also on the histological and ultrastructural levels (Lumb et al. 1991).

The first half of the megalopa molting cycle corresponds roughly with molt-stages A-C combined (see above). Hence, the threshold event for the initiation or delay of regeneration appears to be the onset of premolt (D_0). When autotomy occurs before this point (during postmolt or intermolt), the formation of a new appendage is incorporated within the reconstruction programme of the premolt phase. When limb loss occurs later (in premolt), the regeneration must be postponed into the next molting cycle. This response pattern in larval regeneration is similar to that of adult crustaceans (Skinner 1985a, b), suggesting an early development of the control mechanisms in molting and regeneration.

Interestingly, a "D_0 threshold" has been identified also in relation to nutritional effects on the molting cycle (see following section). This suggests that the same intrinsic control factors may be involved, namely endocrine changes associated with epidermal apolysis. Thus, an increase in the ecdysteroid titer may set the signal for an autonomous course of subsequent morphogenesis and ecdysis. The final (premolt) phase of the molting cycle seems thus to follow a fixed developmental programme which is not interrupted by extrinsic factors such as injury or lack of food.

4.5 *Critical points in the molting cycle*

While the molting cycle is largely under intrinsic control, effects of numerous extrinsic factors such as temperature, salinity, nutrition, or water chemistry superimpose the hormonal regulation. Some of these environmental factors (e.g. temperature) affect primarily the frequency of molting, whereas others (e.g. nutrition) appear to have more influence on the size increment at ecdysis. As both the average duration of successive instars and the size increase per molt are also measures of growth, we will later recur in some detail to such effects (section 6.3.3). Here, I will primarily review interactions between the intrinsic

control of the larval molting cycle and environmental key factors, especially food availability.

Complete inhibition of molting by continuous lack of food has been well documented in both adult and larval crustaceans (e.g. Kurata 1962, Passano 1960, Roberts 1974, Kon 1979, McConaugha 1985). However, in a patchy environment such as the pelagial, transitory periods of poor food availability are much more likely to occur than long-lasting starvation. This does not imply that temporary lack of food has little importance as an ecological factor. As we have seen in the preceding section on regeneration, the response of the larval molting cycle to an extrinsic factor may depend not only on the kind and strength of a factor, but also on the timing of its impact.

In spite of potentially important interactions between molting, growth and development, the effects of temporary starvation were ignored for a long time in investigations on larval crustaceans. This is in contrast to the research on fish larvae, where the availability of food at a critical developmental stage has long been recognized as a crucial determinant of later chances of survival (Blaxter & Hempel 1963). Similarly, distinct developmental periods with differential sensitivity against nutritional stress have been detected also in larvae of insects (Nijhout 1975, Sehnal 1985), cirripedes (Harms 1982, West & Costlow 1988, Qiu et al. 1997), copepods (Lopez 1996), and molluscs (His & Seaman 1992). In brine shrimp (*Artemia* spec.) metanauplii, processes of epidermal cell enlargement and proliferation, and hence, of growth and morphogenesis, were shown to depend only during particular developmental periods on nutritional factors (Freeman 1995, Freeman & Porterfield 1996).

In our first experimental investigation of this aspect of the larval biology of decapod crustaceans (Anger & Dawirs 1981), we found two different critical points: (1) the *"point of no return"* (*PNR*), (2) the *"point of reserve saturation"* (*PRS*). These critical points, which will be explained in the sections below, were later found in the larvae of various species of crabs, shrimps, clawed lobsters, and spiny lobsters, suggesting that they represent general traits in the development of decapod crustaceans (Anger et al. 1981a, Dawirs 1984a, Gore 1985, Staton & Sulkin 1991, Wehrtmann 1991, Mikami & Takashima 1993b, Mikami et al. 1995, Anger 1995b, d, Abrunhosa & Kittaka 1997c). Hence, the degree of nutritional vulnerability in different species or developmental stages can be quantitatively compared using the *PNR* and the *PRS* as measures of the dependence on food.

4.5.1 *The point of no return (PNR)*

When decapod crustacean larvae hatch from the egg, they have already lost, during embryogenesis, significant parts of the original biochemical reserves that a female invests into its offspring. In spider crab (*Hyas araneus*) larvae, for instance, about two thirds of the initially available lipids and one third of the initial protein pool are catabolized by the embryos and lost with the egg membrane (Petersen & Anger 1997). In several palaemonid shrimp and brachyuran crab species, the remaining organic reserves suffice for an initial period of lecithotrophic development through one or a few larval stages (see section 5.1.1). Most decapod larvae, however, require food from hatching.

When food is transitorily lacking from the beginning of the molting cycle, the initial starvation period will cause a significant developmental delay (Anger & Nair 1979, Anger & Dawirs 1981, Anger et al. 1981a, Dawirs 1984a, McConaugha 1985, Staton & Sulkin 1991, Mikami & Takashima 1993b, Mikami et al. 1994, Abrunhosa & Kittaka 1997c). This increase in the duration of development (*D*) through a given larval instar after a tem-

porary time of initial starvation (t) is illustrated in a conceptual model (Fig. 4.8). D increases proportionally with the time of food deprivation, indicating that the molting cycle is suspended during the period of initial starvation. An additional delay (t') reflects a period for recovery after subsequent feeding. Since also t' increases proportionally with the duration of food deprivation, the total time of developmental arrest is normally longer than the starvation period, t. Interestingly, however, D remains unaffected by very short starvation periods in the earliest phase of the molting cycle, which reflects the short non-feeding period in early postmolt (see above, section 4.2.1).

When the time of starvation exceeds a certain limit, a larva loses its capability to recover from nutritional stress. This critical point was termed the *"Point of no Return", PNR* (Anger & Dawirs 1981). After passing the *PNR*, starved and subsequently fed larvae may remain able to survive for extended periods, but they have lost their capability of normal development and are deemed to die without molting to the next stage. Microscopical examination of such individuals showed that, in most larvae, the development did not proceed beyond the transition between molt-stages C and D_0 (Anger 1984a). However, when feeding was resumed near the time of the *PNR*, some larvae developed further through the premolt stages and reached another critical point, the *"exuviation threshold"* (see below, section 4.5.3), i.e. they died in the transition between late premolt and ecdysis, unsuccessfully attempting to molt (Anger 1987a).

Developmental arrest and detrimental late effects of starvation have been documented in numerous species of planktotrophic decapod larvae, but the nature of the irreversible damage has been studied only little. In king crab (*Paralithodes camtschaticus*) larvae, a reduced capability of food capture was observed after starvation periods (Paul & Paul 1980). However, in various other larval decapods there was a significant influence of later food supply on subsequent development and survival, indicating that the larvae were still able to consume and convert food (Anger 1987a); hence, this effect may not generally be crucial, although it can contribute to the *PNR* phenomenon.

As another potentially causal mechanism, electron-microscopical examination showed significant changes in the ultrastructure of the digestive system, in particular in the R-cells of the hepatopancreas (Storch & Anger 1983, Anger et al. 1985). In starved spider crab (*Hyas araneus*) and lobster (*Homarus americanus*) larvae, these cells shrank in size, lost lipid vacuoles, and showed deeply folded basal membranes and pathologically inflated mitochondria (see section 3.11.5; Fig. 3.19). These effects of starvation remained reversible as long as the *PNR* had not been surpassed. After longer lasting periods of food deprivation, however, the lipid droplets could not be fully restored, and the mitochondria remained swollen and reduced in number. In *H. araneus* larvae, also unusual depositions of glycogen occurred after subsequent feeding, indicating a pathological shift in the storage metabolism of the R-cells. It is thus likely that ultrastructural and physiological damage is principally responsible for the loss of developmental capabilities after the *PNR*.

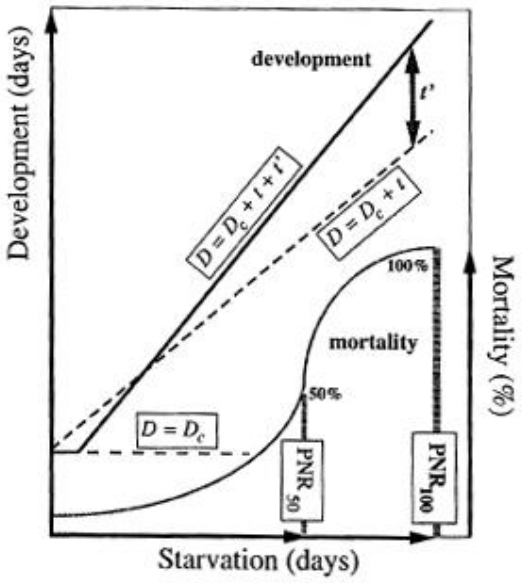


Figure 4.8. Conceptual model of the Point of no Return (*PNR*): larval development and mortality in relation to differential periods of initial starvation. PNR_{50}, PNR_{100}: time of initial starvation (in days) after which 50% or 100% of the larvae, respectively, lose their ability to develop after refeeding successfully to the subsequent larval stage. *D*: duration of development through a given larval instar; D_c: *D* in a continuously fed control group; *t*: time of starvation (in days); *t'*: additional time of recovery (negative in postmolt, increasing with *t*); possible relationships between *D* and *t* are described as linear regression equations.

Cytological effects of starvation have been observed also in several other organs of starved crustaceans, namely in the midgut epithelia, antennal glands, and gills; ultrastructural changes in the hepatopancreas, however, represented the most characteristic effects (Vogt et al. 1985, Storch 1985). In general terms, it is interesting to note that the effects in the various organelles vary among cell types, depending on the function of a given tissue or organ to which these belong. Those structures, which are most important for the function of a given cell type, are generally conserved as long as possible, while others, less crucial, are sacrificed first. For instance, the microvilli in the hepatopancreas and midgut, the basal labyrinth in the antennal glands, or the membranes in muscle cells are preferentially conserved. When significant structural damage has occurred, mortality is also in later larval stages enhanced, even if these are reared under optimal feeding conditions (Anger & Dawirs 1981, Anger et al. 1981a). In the survivors of initial starvation periods, the repair of damage requires an additional time of development (*t'* in Fig. 4.8).

As a quantitative index for comparative studies of the *"nutritional vulnerability"* (Sulkin 1978) or *"nutritional flexibility"* (Sulkin & van Heukelem 1980) in different species or developmental stages, the PNR_{50} has been proposed (Anger & Dawirs 1981). It is

defined as the time of initial starvation at which 50% of the larvae lose their capability to recover after subsequent feeding (see mortality curve in Fig. 4.8). This theoretical value (the median) can be estimated graphically (Anger 1987a) or from a sigmoidal equation describing the percentage of successfully recovering larvae as a function of the duration of initial starvation. This index is statistically better defined than the starvation time causing irreversible damage to all larvae (PNR_{100}). As the maximum time of survival under continued starvation, the PNR_{100} may vary considerably among sibling larvae, reflecting individual variability in organic reserves. High PNR_{50} values indicate large initial energy stores and thus, a high degree of independence from food. Lecithotrophic larvae have enough reserves to develop independently from food through at least one entire molting cycle, i.e. their *PNR* value exceeds the duration of a molting cycle.

When the PNR_{50} of stage-I spider crab (*Hyas araneus*) and shore crab (*Carcinus maenas*) larvae was compared with concurrent losses of biomass, apparently critical values of about 25-30% energy loss were found (Anger & Dawirs 1982, Dawirs 1987). However, no sufficient quantitative data from other decapod species are available to allow for generalization of the relationships between starvation-induced biomass loss and the *PNR*. Moreover, our present knowledge of the *PNR* in different decapod species is widely restricted to first-stage larvae, and usually to only one experimental condition of temperature and salinity (normally close to the presumable optimum of a given species). Preliminary studies suggest that the nutritional vulnerability varies with rearing conditions, especially when effects of various stress factors interact (Anger et al. 1981b). Future investigations should thus analyse interactions of environmental factors with critical points in the molting cycle, and later larval stages should be investigated increasingly.

4.5.2 *The point of reserve saturation (PRS)*

The existence of irreversible damage, and consequently, a *"Point of no Return"* after long periods of starvation may not be very surprising. Another critical point, however, could not necessarily be expected: after relatively short initial periods of feeding, a larva reaches its *Point of Reserve Saturation* (*PRS*) and becomes independent from food for the rest of the molting cycle. Initial feeding periods that are shorter than the *PRS* do not allow for subsequent autonomous development. The *PRS* is thus defined as the point in a molting cycle, where well-fed larvae have gained sufficient organic matter or energy (they have "saturated" their reserves) to develop successfully through premolt and ecdysis, independent of presence or absence of food. As in the *PNR*, this phenomenon is graphically illustrated in a conceptual model (Fig. 4.9).

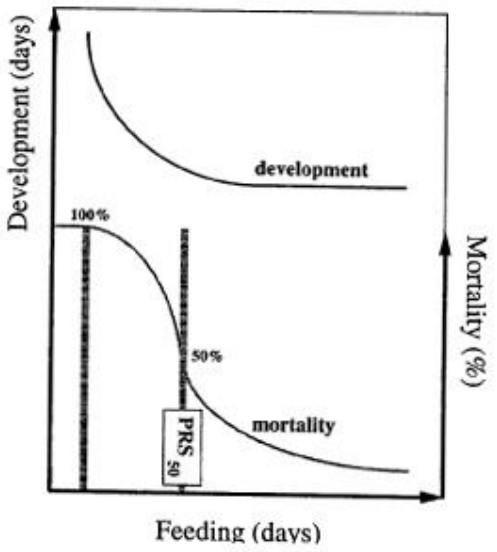


Figure 4.9. Conceptual model of the Point of Reserve Saturation (*PRS*): larval development and mortality in relation to differential periods of initial feeding and subsequent starvation. PRS_{50}: time of initial feeding (in days) after which 50% of the larvae have acquired the ability to develop successfully to the subsequent larval stage, independent of further food availability.

In zoea-I larvae of several decapod species, the *PRS* was reached after feeding periods corresponding with about one fifth to maximally one half of total instar duration. In other words, the final 50-80% of development through an instar are potentially (facultatively) lecithotrophic, provided that sufficient food has been available before. In a comparative microscopical study with several species, this critical point was identified as a particular molt-stage, namely the transition between intermolt and early premolt (C-D_0); based on this finding, the *PRS* was named also *"D_0 threshold"* (Anger 1987a). It appears that an autonomous developmental programme is initiated at the onset of molt-stage D_0, which cannot be interrupted by later lack of food.

As the *PNR*, the *PRS* may be used as a comparative index of nutritional vulnerability in different species or developmental stages (see e.g. Staton & Sulkin 1991, Anger 1995b, d). Since there is always considerable individual variability among equally treated and genetically similar sibling larvae, it is again useful to determine the median time within the molting cycle, when 50% of a given larval population have reached nutritional independence for the rest of the instar (PRS_{50}). The quantification of this index is possible with the same graphical or statistical methods as in the *PNR*. When the time of initial feeding is shorter than the PRS_{50}, some indiviuduals (<50%) develop successfully through premolt and ecdysis also in later absence of food, but usually with a lengthened instar duration

(see Fig. 4.9). However, this developmental delay due to late starvation is normally much weaker than the delay after an earlier timing of food deprivation, and this effect may not even occur consistently (Anger 1987a).

The interaction between nutrition and the endocrine control of the larval molting cycle was studied only in spider crab (*Hyas araneus*) larvae (Anger & Spindler 1987). In one experimental group, zoea I larvae were starved from the D_0 threshold until they reached the zoea II stage, i.e. exclusively during the premolt period, then re-fed. In the subsequent zoea II molting cycle, the ecdysteroid titer changed with a cyclic pattern, but the peak in the ecdysteroids concentration and the time of the subsequent molt to the megalopa occurred three to four days later than in the continuously fed control group. This significant developmental delay was primarily caused by a lengthening of the intermolt stage in the zoea II. This implies a delay in the onset of molting-hormone production and in the occurrence of integumental apolysis (molt-stage D_0). During the extended intermolt period, the larvae tripled their organic biomass, partially catching up with the continually fed control larvae. The ecdysteroid concentrations per unit of biomass measured at the transition between molt-stages C-D_0 and at the time of the hormone peak (early D_1), respectively, were similar in the previously starved and the control group. This suggests that the hormone titer must reach a certain level in relation to biomass (or particular constituents thereof) to initiate apolysis and autonomous development through premolt and ecdysis. However, generalisations from this single study are certainly premature; comparative studies with further species should be worth-while to elucidate the interrelationships between nutrition, growth, development, and the hormonal regulation of the larval molting cycle.

In summary, the experiments which led to the discovery of the *PNR* and the *PRS* showed that the timing of starvation is at least as crucial as its duration. Equally long periods of food deprivation cause severe effects in survival and development if they begin soon after hatching or molting, weak effects if they occur in the middle of the molting cycle, or no significant effects if starvation begins only in premolt. In the latter case, however, a significant developmental delay occurs within the subsequent instar (Anger & Dawirs 1981). Hence, the nutritional vulnerability of decapod larvae decreases during the course of a molting cycle, from 100% in postmolt and intermolt (complete dependence on food), to 0% in premolt (secondarily reached facultative lecithotrophy). This decrease in the nutritional dependence is not gradual but occurs abruptly at the D_0 threshold or *PRS*.

The transition between intermolt and premolt may be critical also in relation to environmental effects other than starvation. For example, there is generally a species-specific lower limit of temperature, below which the molting cycle is suspended. In rearing experiments with the subtropical-boreal crab *Eriocheir sinensis*, for instance, larval development did not proceed beyond the first zoeal stage when the temperatures were below 12°C (Anger 1991b). Microscopical examination of larvae which were kept at lower temperatures revealed that their molting cycle was invariably (at 6°C), or in most individuals (at 9°C), arrested in molt-stage *C*. Those individuals which passed the transition from intermolt to premolt (occurring only at 9°C) died when they were approaching ecdysis (*"exuviation threshold"*, see following section).

In larval shore crab, *Carcinus maenas*, it was recently shown that the D_0 threshold may apply also to effects of transitorily occurring unsuitable salinities (Anger et al. 1998). Under hyposaline conditions, mortality was enhanced at the intermolt-premolt transition and again near ecdysis. Also, significant reduction of growth due to osmotic stress occurred during the postmolt and intermolt stages, but not any longer in premolt. In contrast, even

short periods of initial exposure to low salinity caused later a significantly enhanced mortality and development duration, and a reduction in larval growth.

In summary, the "D_0 threshold" may be critical in a much more general sense, i.e. not only in relation to effects of lacking food, but also to those of unsuitable temperature, salinity, and possibly, other environmental stress factors. This may in part be associated with a depression of growth, which primarily takes place during the postmolt and intermolt period of the molting cycle. The subsequent burst of ecdysteroid production may thus be prevented either indirectly by insufficient biomass accumulation, or directly, due to effects of stress on the hormonal regulation system.

4.5.3 *The exuviation threshold*

Ecdysis has long been known as a critical point in the development of in decapod larvae and other arthropods. In individuals which are naturally weak or exposed to unfavourable conditions of temperature, salinity or water quality, mortality may increase dramatically as soon as molting is approached. As a typical but unspecific syndrome of stress, many larvae do not succeed in stripping off the complete exuvia; such "crippled" individuals are usually deemed to die later, as they cannot eat, swim and grow normally. This critical point within the molting cycle was termed *"exuviation threshold"* (Anger 1987a).

After short initial feeding periods and subsequent starvation, larval mortality was usually enhanced at the exuviation threshold. Surprisingly, this occurred often earlier than the death of continually starved individuals. This seeming paradox may be explained when we look at the course of the molting cycle in these two experimental treatments. In continually starved larvae (or in those fed for extremely short initial periods), the molting cycle is arrested in intermolt. This phase is characterized by maximum rates of growth but minimal developmental change, and its duration is particularly flexible. Stress factors, in general, tend to lengthen primarily this molt-stage, while others may remain largely unaffected. Thus, the larvae are able to survive over extended periods with development arrested in intermolt.

The situation is different in larvae that have passed the D_0 threshold. Their development through premolt is autonomous, and they approach ecdysis without a significant delay. It appears that, once a larva has started the molting process, it has entered a particularly instable state that requires an immediate "decision": either successful development to the subsequent larval stage or, in weak larvae, death in an unsuccessful attempt to molt. An arrest in this molt-stage is not possible. This instability of the transition from late premolt through ecdysis seems to make ecdysis especially vulnerable to any kind of stress or weakness.

5 NUTRITION

Quality and quantity of food are key determinants for the survival and development of heterotrophic organisms. In order to describe their trophic role in an ecosystem, we thus require detailed information on the feeding characteristics of individual taxa, including the mode, selectivity, and overall quantity of food uptake. In aquatic environments, especially in coastal marine regions, decapod crustaceans belong to the most typical and most frequent inhabitants. Hence, their freely swimming larvae should play a significant role not only as prey for carnivorous zooplankton and fishes, but also as consumers of smaller plankton.

In addition to the ecological context of energy transfer within food webs, nutritional information has considerable practical implications both in the commercial production of economically valuable species (Provenzano 1985) and in scientific research cultivation (Kinne 1977). In rearing experiments, in general, the conditions of feeding are artificially controlled and optimized in order to achieve an efficient production of edible crustaceans or to obtain a maximum number of survivors as material for subsequent morphological, ecological, or physiological investigations. In the natural pelagic environment, on the other hand, the availability of suitable food organisms varies greatly due to temporal and spatial patchiness of plankton distribution (Dubois 1975, Omori & Hamner 1982, de Wolf 1989, Davis et al. 1991, Lennert-Cody & Franks 1999). Thus, planktonic food may at least sometimes become a limiting factor for survival and growth of consumers, in particular for predators (Olson & Olson 1989, Verity & Smetacek 1996, Hansen 1999). Thorson, one of the pioneers of larval ecology, expected that severe food limitation, i.e. starvation, should be one of the most important causes of larval mortality in the plankton (Thorson 1950). Even if this far-reaching generalization is considered as an exaggeration (see Parsons et al. 1977), the differential capabilities of decapod larvae to capture, ingest and convert the various types of available plankton remain critical for their survival and recruitment in different geographic regions, depths zones, or seasons.

In consequence of its biological key role, the nutrition factor has received special attention in the crustaceological literature. Numerous original research articles and various reviews have been published, especially in the past two decades. A general review of *"Feeding and nutrition"* in crustaceans was given already in volume I of the treatise *"The Physiology of Crustacea"* (Marshall & Orr 1960). Twenty years later, a bibliography of papers dealing with the nutritional requirements of shrimps and prawns (i.e. not including lobsters, crayfish, and crabs) listed about 500 articles (New 1980); since then, the number of publications must have grown exponentially. In the same year appeared, within the treatise *"The Biology and Management of Lobsters"*, a review of lobster nutrition (Conklin 1980). Soon after this, a *"Handbook of Mariculture"* was published (McVey 1983), aspects of *"Nutrition and larval growth"* were reviewed in Volume 2 of the *"Crustacean Issues"* (McConaugha 1985), and an article on the *"Role of nutrition in lobster recruitment"* appeared (Castell & Kean 1986). Newsletters such as *"The Crustacean Nutrition Newsletter*, *"The Lobster Newsletter"*, *"The Crab Newsletter"*, and several specialized scientific journals such as *Aquaculture*, *Aquaculture Research,* the *Journal of the World Aquaculture Society* (formerly *Mariculture Society*), and *Aquaculture Nutrition* have re-

ported in regular intervals on numerous aspects of the artificial cultivation and nutrition of crustaceans.

Further updates appeared in the 1990s, reviewing penaeid shrimp nutrition (Dall et al. 1990), nutritional effects on maturation and reproduction in commercially cultivated crustaceans (Harrison 1990), and nutritional needs of larval shrimps (New 1990, Teshima et al. 1993), spiny lobsters (Kanazawa & Koshio 1994), and nephropid lobsters (Aiken & Waddy 1995). Covering a broader taxonomic range, chapters on *"Larval Feeding"* or *"Larval Nutrition"* were included in the books *"Reproduction of Marine Invertebrates"* and *"Ecology of Marine Invertebrate Larvae"*, respectively (Strathmann 1987, Boidron-Métairon 1995). More specifically, a chapter of the recent volume *"Crustacean Nutrition"* (D'Abramo et al. 1997) is exclusively dedicated to *"Larval Nutrition"* (Jones et al. 1997a).

In this extensive literature, however, there is a conspicuous bias. Most studies are related to the cultivation of commercially exploitable species such as penaeid and palaemonid shrimps, homarid lobsters, crayfish, and large crabs. Moreover, many nutritional studies have been directed towards the development of artificial feeds for rearing and masting rather than aiming at a better understanding of the trophic role of decapod crustacean larvae in pelagic food webs.

Attempting to compensate in part this bias towards applied research, focus here is on fundamental rather than aquaculture-related aspects of nutrition, and will show preferentially examples from lesser known species. The present chapter deals with the quality and quantity of larval feeding in general terms, while specific nutritional effects on molting, growth, chemical composition, or metabolism are compiled in chapters 4, and 6-8, respectively. Most of the available information is based upon controlled cultivation experiments in the laboratory, but I will address also the question of natural food sources in the pelagial. Before I review the larval requirements of external materials and energy, cases of partial or full independence from food are discussed.

5.1 *Feeding vs. nonfeeding larvae: the planktotrophy-lecithotrophy continuum*

Although most larval decapods require planktonic food (***planktotrophy***), there are also various examples of nonfeeding larvae. This mode of development, which is based upon the degradation of internal reserves, is commonly referred to as *endotrophy* or *lecithotrophy*. It is generally considered as an adaptation to low or unpredictable food production in the environment where larval development takes place. Most frequently, lecithotrophy has been observed in high latitudes (Thorson 1950), freshwater environments (e.g. Magalhães & Medeiros 1998 and earlier papers cited therein), and the deep sea (Thorson 1961, 1964, Pond et al. 1997). However, even in areas that are highly productive on average, temporal or spatial variablity in the plankton may lead to a transitory or local occurrence of food limitation. This factor is considered as one of the key determinants for survival, development and growth of larvae and other zooplankton (Thorson 1950, DeFreese & Clark 1983, Huntley & Boyd 1984). Effects of food limitation have been demonstrated also in the field, for instance in copepods (Heinle 1981, Lopez 1996), mysids (Mohammadian et al. 1997), larval polychaetes (Hansen 1999), as well as in fish (May 1974) and decapod larvae (Strathmann 1987, Olson & Olson 1989, Anger 1995c).

5.1.1 *Primary lecithotrophy*

As an adaptation to recurrent food limitation, heterotrophic organisms can accumulate chemically bound energy while food is available in sufficient quantities, and store it in specialized tissues such as the hepatopancreas or the ovaries. In decapods, this occurs especially during oogenesis, i.e. during the benthic adult phase of the life-cycle. Thus, the fuel for partially or entirely food-independent larval development originates in general from remaining parts of the egg yolk, implying that the degree of lecithotrophy or planktotrophy depends primarily on the extent of energy investment into female reproduction. This phenomenon thus may be termed yolk-based or *primary lecithotrophy*.

Planktotrophy and lecithotrophy have usually been considered as alternative strategies in a dichotomous life history evolution (for recent discussion see Poulin et al. 2001). However, we know now that these developmental patterns are only extremes in a continuum (for references see Anger 1995a). Transitional patterns have been found within individual larval stages, in sequences thereof, or in both. In some species, strongly enhanced yolk stores allow for an entirely nonfeeding development from hatching through metamorphosis (*full lecithotrophy*), but in others only for development through one or a few early larval stages.

Table 5.1. Comparison of the endotrophic potential in larvae of western Atlantic Sesarminae (Grapsidae) species, in order of decreasing egg size: relationships between size, carbon (C) content, and carbon:nitrogen weight ratio (C:N) of eggs in a late embryonic stage; total number (#) of zoeal stages; developmental stage that is maximally reached in the absence of food (starvation from hatching). The zoeal stages of *M. depressus* (and probably *S. fossarum)* are nonfeeding (obligatory lecithotrophy); those of *A. ricordi*, *A. rubripes*, and *A. cinereum* require food for molting to the zoea II (fully planktotrophic development); all others are transitional, showing various degrees of facultative lecithotrophy.

Species	Egg size (mm)	C ($\mu g \cdot ind^{-1}$)	C:N ratio	# zoeal stages	Stage reached w/o food	Reference
Metopaulias depressus	1.50	250	6-6.6	2	crab I	(1)
Sesarma fossarum	1.40	300	7-7.5	2 (?)	crab I (?)	(2)
Sesarma curacaoense	0.60	25	5-6	2	megalopa	(3)
Armases miersii	0.59	20	5-6	3	zoea III	(4)
Sesarma rectum	0.55	14	5-6	3	zoea III	(2)
Sesarma reticulatum	0.45			3	zoea II	(5)
Armases angustipes	0.40	6.5	5	4	zoea II	(2)
Armases roberti	0.40	6	4.4	4	zoea II	(2), (6)
Armases ricordi	0.35			4	zoea I	(6)
Armases rubripes	0.35	2.7	4.5	4-5	zoea I	(2), (7)
Armases cinereum	0.32			4	zoea I	(5)

References: (1) Anger & Schuh 1992, (2) Anger (unpubl. data), (3) Anger 1995d, (4) Anger 1995b, (5) Staton & Sulkin 1991, (6) Diesel & Schuh 1998, (7) Montú et al. 1990; (?) = presumably; blank spaces = no C or N data available.

Transitional modes between planktotrophy and lecithotrophy have been observed, for instance, in several grapsid crab species from the western Atlantic region (Table 5.1). A comparison of their reproductive and developmental traits shows that the phenomenon of

yolk-based lecithotrophy is commonly associated with an enhancement of egg size and a curtailed meroplanktonic phase (cf. section 2.4; Figs. 2.11, 2.12). While fully marine grapsids have normally 5 or more zoeal stages, estuarine and semiterrestrial species have 3 or 4, and fully limnic or terrestrial relatives have only 2 (Rabalais & Gore 1985). Egg size, carbon content, the carbon:nitrogen ratio (an index of available energy stores; see section 7.2.3), as well as the nutritional flexibility of the early larval stages tend to increase with developmental abbreviation (Anger 1995a).

As a first step in the evolution of lecithotrophy, slightly enhanced yolk reserves may reduce the *"nutritional vulnerability"* of newly hatched larvae (or increase their *"nutritional flexibility"*; for terminology see Sulkin 1978, Sulkin & van Heukelem 1980). Those nutritionally more flexible (or less vulnerable) larvae can develop at low levels of food quality or quantity, but not in complete absence of food, i.e. they remain planktotrophic. Among the examples in Table 5.1, this applies to *Armases ricordi*, *A. cinereum*, and *Armases* (= *Metasesarma*) *rubripes*. Without food supply, the first-stage larvae of these species are not able to develop successfully through a complete molting cycle, to the zoea II.

In species where the yolk stores are moderately enhanced, the first larval stage may gain a limited capability of food-independent development, so that the zoea I can develop successfully, also in complete absence of food, from hatching to the zoea II stage. However, such nutritionally little vulnerable larvae may conserve also their ability to capture and ingest prey when it becomes available. This transitional, highly flexible mode of development is termed *facultative lecithotrophy* (Anger 1995b, d, Thessalou-Legaki et al. 1999). Among the species listed in Table 5.1, this has been observed in *Armases roberti*, *A. angustipes*, and *Sesarma reticulatum*.

In the next step of increasing endotrophic potential, the internal energy stores may suffice for facultative lecithotrophy through more than one initial larval stage. The semiterrestrial crab species *Sesarma curacaoense*, *S. rectum*, and *Armases miersii*, are typical examples, reaching their final zoeal stage or even the megalopa, when necessary, without food.

A further increasing storage of yolk may allow for full (obligatory) lecithotrophy in one or more early larval stages, usually followed by a reduced endotrophic potential, i.e. facultative lecithotrophy or full planktotrophy in later instars. This pattern was found in the larvae of a terrestrial crab, *Metopaulias depressus* (for its ecology, see section 10.4). This species produces extremely large eggs, and its two zoeal stages are entirely nonfeeding. Subsequent to the fully lecithotrophic phase of development, the remaining yolk still allows for facultative lecithotrophy in the megalopa stage. With even larger egg mass (see C in Table 5.1), closely related limnic species such as *Sesarma fossarum* or *S. windsor* appear to follow the same transitional pattern, approaching or reaching full lecithotrophy (Anger 1995a). Further examples of lecithotrophy-planktotrophy transitions within sequences of larval stages can be found in numerous palaemonid freshwater shrimps, where the first zoeal stage is lecithotrophic, at least facultatively, but the subsequent stages are planktivorous (for species and references of literature, see section 10.4).

5.1.2 *Secondary lecithotrophy*

In all aforementioned examples of endotrophy, the fuel for food-independent larval development originates from an enhanced reproductive energy investment of the adult females, i.e. ultimately from benthic sources. In some species, however, the crucial energy reserves

are stored during another phase of the life cycle, and they originate from a different source. The females of such species produce small eggs, from which feeding larvae hatch. The early larval stages accumulate plankton-derived organic matter, which then allows a later stage (usually a benthic decapodid) to develop without food through metamorphosis. Immediately after this event, the first juvenile stage usually resumes the feeding activity. This special case of endotrophic development was termed *"secondary lecithotrophy"* (Anger 1989).

This developmental mode has been known from barnacles, where the cypris larva depends on the nutrition of the preceding naupliar stages. It does not eat, even when its energy stores are poor and food is available (Crisp 1974, West & Costlow 1988). Likewise, the megalopa stage of several hermit crab (*Pagurus*) species is secondarily nonfeeding (Anger 1989, Harvey & Colasurdo 1993, Harvey 1996). According to recent studies of the functional morphology of mouthpart and foregut structures in other anomurans, the same appears to apply to the megalopae of the king crab species *Paralithodes camtschaticus*, *P. brevipes*, and *P. platypus* (Abrunhosa & Kittaka 1997a, b). The same pattern was observed also in several rock lobster species, where the puerulus stage utilizes exclusively the energy accumulated by the preceding phyllosoma larvae (e.g. Nishida et al. 1990, Booth & Phillips 1994, Kittaka 1994, Lemmens 1994, Lemmens & Knott 1994, Takahashi et al. 1994, Abrunhosa & Kittaka 1997a, McWilliam & Phillips 1997, Jeffs et al. 1999, in press).

Independence from food in the last (premetamorphic) larval stage cannot be explained as an adaptation to food limitation, because the settling decapodid has usually access to deposited benthic food sources, and thus, does not depend on the plankton alone. This suggests that additional environmental factors can select for lecithotrophy. Anger (1989) hypothesized that secondarily nonfeeding development in decapodid stages may increase the chance to find a suitable substrate for settlement and metamorphosis. This mode of development could thus be an adaptation to a particularly high degree of habitat specialization such as, for example, the unconditional need for a hard substratum in barnacles, or that for an empty snail shell in hermit crabs. On the other hand, there are also many examples of hermit crab species with a feeding megalopa (Harvey 1996). Hence, a general explanation of secondary lecithotrophy has to await further comparative studies of this phenomenon. In the puerulus stage of rock lobsters, the selective force may not be found in an extreme habitat specialization but in a very long duration of the onshore transport across the continental shelf of tropical or subtropical regions. In these waters, the production of large plankton or small nekton with suitable size and accessibility may be insufficient for the nutrition of the large, nektonic pueruli.

5.2 Qualitative aspects of feeding

Based upon primary food sources, the trophic role of decapod crustacean larvae in the plankton may be described as detritivores, herbivores, carnivores, or omnivores (Jones et al. 1997a, b). This ecological classification, including knowledge of possible ontogenetic changes in nutrition, is crucial also in commercial aquaculture projects. The predominent food source of planktonic crustaceans is usually reflected by differential mouthpart morphology, in particular of the mandibles. Although this relationship has little been studied in decapod crustacean larvae, the available evidence suggests similar patterns in their functional morphology, namely the occurrence of blunt grinding mandibles in herbivores,

sharp pointed teeth in carnivores, and intermediate forms in omnivores (for recent review and illustrations, see Jones et al. 1997a).

Before considering quantitative requirements for food in decapod larvae, basic information on qualitative needs is given here, including the chemical composition and size of prey, as well as behavioral aspects of selective feeding.

5.2.1 *Nutritional requirements*

Although a major part of the available literature deals primarily with adult rather than larval decapods, most of what is known about the chemical aspects of nutrition should apply also to larval stages. The available evidence suggests that those food components which can not be synthesized by the adults are essential also for larvae. On the other hand, one should expect that larvae require additional food components which can be synthesized *de novo* only in later life-history stages when more complex organ systems have developed. Moreover, the sensitivity of larvae to food shortage or lack of essential dietary substances is generally enhanced due to higher metabolic intensity and more rapid biochemical turnover than in adults.

There are several technical difficulties in the study of nutritional requirements in aquatic crustaceans including, in particular, larval stages (for recent review of experimental prerequisites and constraints, see Jones et al. 1997a). In consequence, we know only little about the ontogeny of biosynthetic capabilities in the Crustacea and thus, depend to a great extent on available data from juveniles and adults. As all heterotrophic organisms, decapod crustacean larvae require dietary proteins, lipids, carbohydrates, minerals, and vitamins for successful growth and development. The rate or efficiency of conversion, however, varies among the major compound classes, depending on the overall composition of food. Abundant materials may be catabolized to produce energy, while limited compounds should preferentially be saved in storage tissues. In lobster (*Homarus americanus*) larvae, for instance, the efficiency of protein conversion was observed to increase, when the average dietary protein content was low, indicating an increasing digestion and storage or a decreasing utilization of proteins as a substrate for metabolic energy production (Capuzzo & Lancaster 1979a, Kanazawa 1990).

5.2.1.1 Proteins and other nitrogenous compounds

Dietary protein requirements are, in general, particularly high in rapidly growing early life-history stages, to provide for rapid tissue synthesis. In penaeid shrimp larvae, for example, the requirements for total proteins may range from ca. 30-56% (for references see Jones et al. 1997a). Using techniques of microencapsulation (see Jones et al. 1979, Levine et al. 1983, Teshima & Kanazawa 1983a, Kanazawa 1990) and radiotracers (e.g. Villamar & Langdon 1993), ten amino acids have been identified as essential dietary componenents for both adult and larval crustaceans (Dadd 1977, Claybrook 1983, Sick & Millikin 1983, Teshima et al. 1986a, 1993). They are the same as in finfish and higher animals, namely: arginine, valine, threonine, methionine, leucine, isoleucine, phenylalanine, lysine, histidine, and tryptophan. Since these important precursors of protein synthesis can not be synthesized *de novo*, their concentrations within larval biomass vary with quality and quantity of food. Non-essential amino acids, in contrast, depend also on the developmentally and environmentally controlled regulation of their formation. In this category, we may list asparagine, serine, glutamic acid, proline, glycine, alanine, cystine, and tyrosine.

Digestibility and nutritional value of dietary proteins depend highly on their amino acid composition and on accompanying food components. Additionaly, the protein requirements may vary ontogenetically. In the protozoea II stage of grass shrimp (*Penaeus monodon*), for instance, the *in vitro* protein digestibility of three differently formulated diets was the same, while it varied significantly in the mysis II stage (Sheen & Huang 1998). The diets with higher protein digestibility allowed consistently for higher survival through the "postlarval" and juvenile phase. However, in the larvae of another prawn, the palaemonid species *Macrobrachium rosenbergii*, no significant ontogenetic changes in the composition of larval biomass or in the nutritional requirements were observed, as long as a suitable protein source was available which resembled the amino acid profile of the larvae (Roustaian et al. 2000).

5.2.1.2 Carbohydrates

In commercial aquaculture, polysaccharides such as starch and dextrin are usually included in artificial feeds as a bulk energy component to spare expensive proteins (Capuzzo & Lancaster 1979a, Capuzzo 1982, Harrison 1990). In penaeid shrimp larvae, carbohydrate requirements ranged from 7.5-33% (Kurmaly et al. 1989a, Kanazawa 1990). As a complementary food source, carbohydrate polymers may play a similar role also in the plankton, where diatoms and other microalgae are much more abundant than high-protein zooplankton (see section 5.2.2). Although dietary carbohydrates are not essential for crustaceans, they are stored in the musculature and hepatopancreas, primarily as glycogen. These deposits can be mobilized when required to serve as precursors of metabolic intermediates in energy production, or for the synthesis of non-essential amino acids, nucleic acids, and cuticular chitin.

5.2.1.3 Lipids

In penaeid shrimp (*Marsupenaeus japonicus*) larvae, Kanazawa (1990) observed a demand of about 5.5% total lipids. However, the heterogeneous nature of this chemical fraction of food renders it difficult to generalize such figures, because the dietary requirements vary among the different lipid classes (Jones et al. 1997a; for brief chemical characterization and terminology of lipid classes, see section 7.5.2 of this volume). Neutral lipids, in particular *triacylglycerides* (*TAG*), are a major energy source and, in most decapod larvae, the predominant form of storage. During periods of famine, internally accumulated lipid reserves are crucial for survival. The hepatopancreas is the principal site of both storage and processing (Chang & O'Connor 1983; cf. sections 3.11.5, 7.5.2). Several other lipids, including *phospholipids* (e.g. lecithin; Briggs et al. 1988, Coutteau et al. 1997), *sterols* (Whitney 1969, Teshima 1972, Teshima & Kanazawa 1986), and long-chain *highly unsaturated fatty acids* (*HUFA*) with ≥20 C atoms can not, or can only insufficiently, be synthesized *de novo* by crustaceans and thus, must be absorbed from food (Jones et al. 1979, Levine & Sulkin 1984, Kanazawa et al. 1985, Mourente & Rodríguez 1997, D'Souza & Loneragan 1999). Such essential fatty acids are believed to play a crucial role in food webs of aquatic ecosystems, even on an evolutionary level (for recent review, see Arts et al. 2001).

Phospholipids are important components of all cell membranes and, hence, play a crucial role in processes of osmoregulation, namely in the activation of the sodium pump (see section 10.1.2). In addition, they represent the predominant transport form of lipids in the hemolymph, normally in combination with proteins (as high-density lipoproteins). The

formation of these complex molecules is based on a conversion of glycerides and fatty acids that are absorbed from food or mobilized from internal stores. Dietary phospholipids may aid also the transport of cholesterol, especially from the hepatopancreas to the hemolymph (Kanazawa & Koshio 1994).

Since fatty acids are relatively inert, their metabolism requires an esterification to thioesters and the action of other molecules. Among these, carnitin (a product of the protein metabolism) plays a special role in the turnover of lipids, particularly for the transport of fatty acids through membranes into the mitochondria. In penaeid shrimps, growth was enhanced when additions of L-carnitin were included in their diet (Jayaprakas & Sambhu 1996). Hence, carnitin might play an important role in the nutrition of decapod larvae, where processes of growth are particularly intense and demanding.

Also dietary sterols play a major role in growth, metabolic maintenance, and in the regulation of regeneration and the molting cycle. Larval decapods, together with other crustaceans, are incapable of *de novo* sterol synthesis (Whitney 1969, Teshima 1972; Teshima et al. 1986b). Among these compounds, cholesterol is an essential precursor for the biosynthesis of the molting hormones (ecdysteroids; see section 4.3, Fig. 4.7). Other dietary sterols (e.g. phytosterols) can be utilized as well, but these have been shown to be inferior to cholesterol in promoting growth (for references, see Harrison 1990).

Within the *HUFA* family, eicasopentaenoic (20:5n-3) and docosahexaenoic acid (22:6n-3) appear to be particularly important for larval growth (for references, see Jones et al. 1997a, Sulkin & McKeen 1999). Enhanced concentrations of these fatty acids have been observed within the ovarian lipid fraction (Teshima & Kanazawa 1983b, Jeckel et al. 1989a, b). Essential *HUFA* persisting from egg yolk may thus reduce the nutritional vulnerability of freshly hatched larvae. A limited ability has been shown, at least in some shrimp larvae, to convert 18:3n-3 (linolenic acid) to higher n-3 *HUFA* such as 22:5n-3 (docosapentaenoic acid), 20:5n-3, and 22:6n-3 (Jones et al. 1979, Kanazawa et al. 1979a, b, Teshima et al. 1992, Roustain et al. 1999). However, the capability for desaturation and prolongation of carbon chains is generally not sufficient to sustain growth and development. In consequence, *HUFA* with ≥20 C atoms must be taken up with food. When decapod larvae cannot ingest sufficient amounts, they show reduced growth and survival, lower resistance against osmotic stress and disease, delayed development, and sometimes supernumerary stages (see e.g. Kanazawa et al. 1985, McConaugha 1985, Mourente & Rodríguez 1997, Takeuchi et al. 1999a-c, D'Souza & Kelly 2000). Also the precursors to the essential long-chain fatty acids (in the marine Crustacea principally 18:3n-3) must be taken up from food, as animals are, in contrast to plants, generally not capable of a *de novo* synthesis of n-3 and n-6 fatty acids (Moreno et al. 1979). As an adaptation to these dietary requirements, essential *HUFA* are not normally utilized as an energy source unless available in excess.

A low level of essential *HUFA* in the diet has been shown to affect the reproductive performance of adult females and to reduce the viability of the resulting embryos (Cahu et al. 1995). As a consequence, this effect should decrease also the physiological condition of freshly hatched larvae and thus, the chances of subsequent larval development, survival, and growth in the plankton. Similarly, reproductive exhaustion during the course of a spawning period may lead to a decline in the initial fat content, growth, and overall condition of successively produced larvae (Palacios et al. 1998, 1999); in general, such maternal effects are probably associated with variation in the *HUFA* concentration in eggs and early larvae (Cavalli et al. 1999). Also in sea urchins and bivalves, maternal malnutri-

tion has been demonstrated to affect not only fecundity, but also egg size and larval growth (Bertram & Strathman 1998). Such late effects of adult nutrition on larval fitness represent a potentially important but little studied aspect of nutritional and developmental physiology. In the larval biology of the Crustacea, future research must show the general significance of these and other non-genetic maternal effects.

Another compound class within the lipid family, carotenoids, can not be synthesized by animals, in general, and must thus be taken up from food. In crustaceans, carotenoids occur as free pigments, esterified to fatty acids, and associated with macromolecules such as chitin, proteins, or carbohydrates. They play important roles as precursors of vitamin A synthesis, as antioxidants or light shields, and in hemolymph transport (Harrison 1990). The significance of carotenoids as protectors against high-energy light is conspicuous in the larvae of some tropical grapsid crab species, namely *Armases miersii* and *Sesarma curacaoense* (for details of their ecology, see section 10.4). They develop in supratidal rock pools or other extremely shallow temporary water bodies occurring in mangrove swamps, where they may be exposed to intense solar radiation. In contrast to the larvae of closely related marine species, their integument shows an unusually dark pigmentation, presumably concentrated carotenoid pigments, shielding them against oxydative photodamage.

5.2.1.4 Vitamins and minerals

Compared with the available data on requirements for essential amino acids and lipids, little is known about other nutritional needs of larval crustaceans. Vitamins are an important category of essential dietary substances, at least in artificial cultures where larvae develop under monotonous nutritional conditions (Fisher 1960, Sedgwick 1980, Shigueno & Itoh 1988, Shiau & Lung 1993, Dall 1995; for vitamin requirements of juvenile penaeid shrimps, see recent papers by Reddy et al. 1999a, b, Shiau & Chen 2000). Ascorbic acid (vitamin C), for instance, is known as an antioxidant and as an enzyme cofactor in collagen formation, which should be particularly important in the embryonic and larval stages of crustaceans (Harrison 1990, Merchie et al. 1997). In a commercially cultivated prawn, *Marsupenaeus japonicus*, Kanazawa (1990) demonstrated the larval requirements for thiamine, riboflavin, pyridoxine, nicotinic acid, folic acid, cyanocobalamin, choline, inositol, and Vitamis A, C, D, and E. As shown in *Litopenaeus vannamei*, the physiological condition of larvae may be influenced also indirectly, through the vitamin content in the diet of egg-producing females (Wouters et al. 1999).

Micronutrients (trace elements) and minerals are required as enzyme cofactors in numerous metabolic functions. Frequent minerals such as calcium, magnesium, sodium, potassium, and chloride, but also trace elements can be taken up directly from the surrounding water, especially across the thin epithelia of the gill chamber and the intestine. Thus, they are normally not limiting for aquatic decapods, at least not for those living in marine or brackish environments. In freshwater habitats, on the other hand, where the larvae of several species of palaemonid, atyid and hippolytid shrimps as well as some grapsid crabs develop, minerals may be scarce and thus, growth-limiting. Knowledge of these needs are particularly important in the aquaculture of freshwater prawns (*Macrobrachium rosenbergii*), where Zang et al. (1995) identified and quantified six essential micronutrients that must be added to the water as a prerequisite for successful cultivation. In another study on the same species, Mallasen & Valenti (1998) found that calcium and potassium were the most important ions for larval developement. Arun & Subramanian (1998) showed in another freshwater prawn, *M. malcolmsonii*, that selenium plays a significant role, especially

for the activities of antioxidant enzymes in the hepatopancreas of the embryonic and larval stages.

Indirect evidence of Ca^{2+} requirements was shown in the larvae of a terrestrial crab, *Metopaulias depressus*, which develop in rainwater (see section 10.4). The females of this species exhibit brood care behavior including the introduction of empty snail shells into the breeding habitat, where they serve as a calcium source (Diesel 1997). Besides in numerous physiological processes, calcium is important as a structural component of the cuticle, at least in the decapodid stage. In *M. depressus*, this critical role is reflected in a steeply increasing ash content as soon as the megalopa stage is reached (Anger & Schuh 1992). On the other hand, dietary calcium was observed to reduce the growth-promoting effect of phosphorus in juvenile penaeid shrimps, *Penaeus monodon* (Peñaflorida 1999). In summary, one may say that the needs for macroelements and micronutrients still represent open fields for future studies on the physiology of decapod crustacean larvae.

5.2.2 *Principal food sources, prey size, feeding behavior*

In the natural plankton, larvae have access to a wide variety of potential food sources, including organic solutes, detrital matter, bacteria, unicellular and chain-forming algae, protozoans, and an enormous diversity of metazoan zooplankton. These items differ greatly both in qualitative and quantitative aspects, offering the various larval forms and stages an opportunity for optimal food selection. In the following sections, major types of potential food, specific nutritional characteristics of different taxa and larval stages, and mechanisms of selectivity are reviewed.

5.2.2.1 Dissolved organic matter (*DOM*)

Among the potentially available energy sources in the ocean, the amounts of dissolved organic matter (*DOM*) probably exceed the quantity of all particulate food (for literature, see Boidron-Métairon 1995). Plankton grazers, including decapod crustacean larvae, belong to the most important sources of leached organic materials (Strom et al. 1997). However, an uptake and conversion of *DOM* has not been demonstrated in higher crustaceans, in contrast to several other marine invertebrate taxa, e.g. soft-bodied echinoderm and mollusc larvae (e.g. Manahan et al. 1989, Manahan 1990, Jaeckle 1994). This apparent lack of resource exploitation by decapod larvae is a consequence of the relatively impermeable cuticle, which inhibits a transepidermal transport of large organic molecules. Thus, all non-lecithotrophic decapod crustacean larvae are considered as obligatory particle feeders. As an exception among the Crustacea, the metanauplii of *Artemia* spec. were shown to take up *DOM* through the gut wall, when drinking was stimulated by the presence of small particles (Provasoli & Shiraishi 1959). It would be interesting to test decapod crustacean larvae for the possible occurrence of this mechanism.

5.2.2.2 Microorganisms

Bacteria and small protozoans represent abundant, and thus, potentially important particulate food sources. In the planktological nomenclature, these organisms belong to the categories of *nanoplankton* (defined as size class 2-20 µm) and picoplankton (<2 µm). As in *DOM*, however, those small organisms appear poorly accessible to most decapod crustacean larvae, at least as long as they are available only in suspension. As an exception, the protozoeal stages of the Dendrobranchiata are capable of efficient suspension feeding, retaining particles as small as about 10 µm. The larvae of the shrimp *Farfantepenaeus*

paulensis, for instance, were shown to ingest bacteria, flagellates, and ciliates (Thompson et al. 1999). In most pleocymate decapod larvae, in contrast, constraints of functional mouthpart morphology prevent an efficient retainment of such small particles, so that protozoans as a sole food source are not sufficient to sustain development. On the other hand, uptake and conversion of unicellular organisms was shown to lengthen the time of survival in comparison with completely starved larvae, allowing occasional, although usually incomplete, development through one or more stages (Anger & Nair 1979, Sulkin et al. 1998a, Lehto et al. 1998). This suggests that microorganisms may be a significant complementary energy source, especially when larger food is scarce.

5.2.2.3 Detritus and fecal pellets

Bacteria and protozoans should be more accessible and become more important as food items, when they are associated with larger detrital aggregates ("marine snow"; Biddanda 1986, Kiørboe et al. 1990, Lampitt et al. 1993, Shanks & Walters 1997, Dilling et al. 1998, Kiørboe 2000). This is corroborated by observations on the larvae of a small crab, *Ebalia tuberosa*, where preferential feeding on detritus was described (Schembri 1982). Also the early larvae of a prawn, *Penaeus monodon*, and of a crab, *Portunus trituberculatus*, were successfully reared with bacteria, protozoa and other microorganisms forming "microbial food assemblages" (Maeda & Liao 1994). In the zoea I stage of another crab, *Hemigrapsus oregonensis*, microbially enriched seagrass detritus was insufficient to allow for development to the following instar, but delayed larval mortality in comparison to a starved control indicated its utilization (Lehto et al. 1998). Also, when detritus was added to suboptimal concentrations of *Artemia*, early crab larvae showed an increased survival. Thus, microbially colonized detrital aggregates are likely to play a role as a supplementary food source for decapod larvae in natural plankton assemblages.

Similarly, fecal pallets with attached microorganisms are abundant in the plankton and might thus play a major role in the nutrition of planktonic crustaceans (Suh et al. 1991). The zoeae of a penaeoid shrimp, *Solenocera atlantidis*, were observed retaining their own feces as an attached mass that is apparently incubated for microbial colonization and later ingested by the larvae (Youngbluth 1982). Unfortunately, quantitative data on these potentially significant nutritional aspects are practically absent for larval decapods. The same is true for the possibly important role of symbiontic gut bacteria, which have been studied quite extensively in adult but not larval crustaceans (see Colorni 1985, Harris 1993). The gut flora may contribute essential micronutrients that are lacking in particulate food, or aid the digestion by breaking down polysaccharides or proteins and liberate otherwise unavailable nutrients.

Indirect evidence of some uptake of detrital matter by decapod crustacean larvae has recently been shown using stable isotope techniques. In particular, the ratios $^{13}C:^{12}C$ and $^{15}N:^{14}N$ are used as indicators of the origin of particulate organic matter. The physical basis, methodological aspects, and numerous examples of their application have been compiled in the book *"Carbon Isotope Techniques"* (Coleman & Fry 1991). In tropical estuaries and coastal mangrove areas, where numerous decapod species are found, one would expect that detritus from decaying mangrove leaves and other terrestrial plants might play a significant role as a carbon source for the larval stages. In juvenile penaeid prawns living in Malaysian mangrove swamps, for instance, a recent study showed with stable isotope techniques that the contribution of mangrove carbon to tissue biomass may be as high as 84% (Chong et al. 2001). Other studies from Brazil, Costa Rica, and Australia, how-

ever, have shown that this does not generally apply to larval decapods, except for the earliest developmental stages in a very restricted nearshore zone (Schwamborn 1997, Dittel et al. 1997, Loneragan et al. 1997). Later larval stages are normally transported offshore, where other (apparently preferred) food sources become available. Yet, it is possible that the larvae of some crustacean species depend more than others on plant detritus, or this energy source may be especially important in particular regions. For instance, a significant uptake of detrital matter by the zoeae of the mangrove-climbing tree crab, *Aratus pisonii*, was observed (Schwamborn 1997). Since only very few investigators have applied stable isotope techniques to decapod larvae, future studies might change our present view of the trophic significance of detritus and its attached microflora and microfauna.

5.2.2.4 Phytoplankton

Planktonic algae (Fig. 5.1A), at least those in the microplankton category (20-200 µm size), appear to be the primary if not sole food source of small larval forms, especially in the filter-feeding protozoeal stages of the Dendrobranchiata (e.g. Omori 1979, Emmerson 1984, Dall et al. 1990, Leong et al. 1991, Preston et al. 1992, Ronquillo et al. 1997). This changes usually in the last protozoeal stage, where filter-feeding on small algae and raptorial feeding on larger prey may occur together (Emmerson 1980, 1984, Yúfera et al. 1984, Rodríguez et al. 1994). Later (mysis) stages become increasingly carnivorous.

Zoeae and decapodids of the higher Decapoda, in general, are primarily raptorial feeders, retaining only a limited capability for filter-feeding of small particles (Strathmann 1987). In spite of mechanical constraints (small particle size in relation to the functional morphology of the larval mouthparts), successful uptake and conversion of planktonic microalgae has frequently been shown, also in relatively large larvae such as caridean, anomuran, and brachyuran zoeae (e.g. Regnault 1969a, Paul et al. 1979, Criales & Anger 1986, Nakanishi 1987, Villamar & Brusca 1987, Harms & Seeger 1989, Harms & Anger 1990, Harms et al. 1991, Lehto et al. 1998). Among the latter, pinnotherid crab larvae appear to utilize phytoplankton with particularly great success (Strathmann 1987). In the snow crab (*Chionoecetes opilio*), the significance of planktonic algae as a regular food source may be reflected in the seasonal timing of reproduction, which appears to be coordinated with pulsed phytoplankton production (Starr et al. 1994). This should guarantee that freshly hatched larvae can optimally exploit the short spring bloom in high latitudes (see section 10.2).

Phytoplankton appears thus to be one of the principal food sources for decapod crustacean larvae, in general. This was suggested already by Lebour (1922), who analysed larval gut contents with simple microscopical techniques. The presence of remaining hard parts of phytoplankton in guts and feces was more recently demonstrated also with light- and electron-microscopy; moreover, algal pigments were chemically detected in field-caught larvae using high-performance liquid chromatography, HPLC (Youngbluth 1982, Preston et al. 1992, Meyer-Harms & Harms 1993, Harms et al. 1994).

The general significance of phytoplankton as a natural food source for larval decapods is in contrast, however, to the results of numerous experimental comparisons of the nutritional value of monospecific diets. Zooplankton species allow in most cases better larval survival, growth and development than an exclusive feeding on planktonic algae (see e.g. Broad 1957a, Roberts 1974, Sulkin 1975, Bigford 1978, Harms & Seeger 1989, Harms et al. 1991, Ostrensky et al. 1997, Zhang et al. 1998a). When the zoeae of the tanner crab, *Chionoecetes bairdi*, were fed with phytoplankton, they ingested only about 14% of the

amount of carbon necessary to compensate for their respiratory losses (Incze & Paul 1983). As in the case of microorganisms, this energetic deficit may partly be explained by mechanical inefficiency of feeding on algae. Differences in mechanical accessibility may explain also why chain-forming diatoms generally sustain larval development better than small flagellates or other unicellular algae (Regnault 1969a, Stickney & Perkins 1979, Criales & Anger 1986, Harms et al. 1991). In Figure 5.1, *Biddulphia* is shown as a typical example of a relatively large, chain-forming diatom that has been tested successfully as a food for crab and shrimp larvae (Harms & Seeger 1989, Harms et al. 1991).

Besides mechanical constraints in the functional morphology of feeding, inferior chemical quality or digestibility may reduce the food value of some algae. In the larvae of a hermit crab, *Pagurus longicarpus*, for instance, egestion of intact diatom cells was observed (Roberts 1974). This indicates that the gastric mill and/or the digestive enzymes of these larvae are not appropriate for mechanical or chemical breakdown of this armored type of phytoplankton.

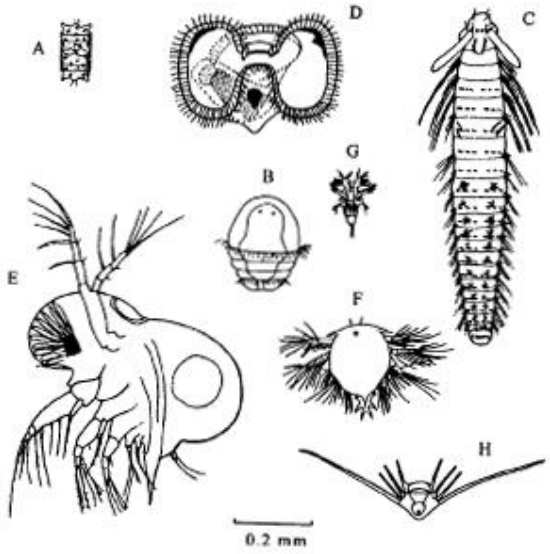


Figure 5.1. Potential food organisms of decapod crustacean larvae. A. phytoplankton (diatom, *Biddulphia* spec.); B. early, C. late polychaete larva; D. mollusc larva (gastropod veliger); E. cladoceran (*Podon* spec.); F. cirripede larva (balanoid nauplius); G. copepod (calanoid metanauplius); H. echinoderm larva (ophiuroid pluteus) (from Newell & Newell 1977, redrawn to uniform scale to allow for approximate comparison of size; with permission from the authors).

When very small, normally inaccessible phytoplankton cells are eaten and concentrated by filter-feeding zooplankton, their nutrients become available also for larger predatory zooplankton including most decapod larvae. This mechanism of indirect uptake plays cer-

tainly an important role in the natural environment, and it allows for experimental studies of microalgal food quality, excluding the confounding effects of prey size. This was recently demonstrated in experiments with larvae of crabs (*Portunus trituberculatus*, *Cancer* spp.) which were fed with rotifers (*Brachionus plicatilis*) that had previously been incubated with microflagellates (Hamasaki et al. 1998, Hartman & Sulkin 1999, Sulkin & McKeen 1999, Takeuchi et al. 1999a). In *Cancer* larvae, similar rates of larval survival and development as in an *Artemia*-fed control group were observed, when the rotifers contained *Isochrysis*, while the rearing success was lower with *Dunaliella*-fed rotifers. The inferior dietary quality of the latter species was presumably caused by a lack of certain long-chain n-3 *HUFA* (see section 5.2.1.3). Likewise, *Portunus* larvae showed higher survival with an increasing n-3 *HUFA* level in the rotifers (Takeuchi et al. 1999a). The content of these essential fatty acids varies not only among phytoplankton species but also with environmental conditions, in particular with nitrate availability; nitrogen-limited unicellular algae were shown to have a lower n-3 *HUFA* content and a lower protein:energy ratio, causing delayed development in penaeid shrimp (*Penaeus semisulcatus*) protozoeae (D'Souza & Kelly 2000).

It may be summarised that planktonic algae represent, in spite of their relatively poor mechanical or chemical accessibility, a regular component of the natural food spectrum of most decapod crustacean larvae, including those of the higher Decapoda which are generally considered as canvivores. In the early feeding stages (protozoeae) of the Dendrobranchiata, special adaptations such as the presence of midgut caeca, high enzyme levels, and short gut evacuation times allow an efficient utilization of this abundant food source. Phytoplankton should thus play a significant role not only directly, but also indirectly as "background plankton", which has recently been shown to influence the rate of carnivorous feeding (Johnson & Shanks 1997).

5.2.2.5 Microzooplankton

As we have seen, small zooplankton (commonly in the size range 20-200 μm; Fig. 5.1B, F, G) appears to be generally superior to phytoplankton both in terms of mechanical accessibility and chemical quality (i.e. calorific value). In the field, it is usually available in abundance and should thus play a predominant role as a natural food source, especially for small larval forms. In the guts of early shrimp (*Pandalus borealis*) larvae, for instance, remains of cirripede and copepod nauplii, small larval polychaetes and echinoderms, and phytoplankton were found together (Stickney & Perkins 1981). In laboratory experiments with very small larvae, for instance the zoea I and II of the crab *Chasmagnathus granulata*, a diet of small rotifers allowed for better survival than larger *Artemia* nauplii, which apparently can not be caught or ingested as efficiently by the early zoeae (Ostrensky et al. 1997). This changed in the later stages, where the ability to catch larger prey increased. These larger larvae were reared more successfully with brine shrimp nauplii as a sole food. Similar observations were made in blue crab (*Callinectes sapidus*) larvae (Sulkin 1978), where the zoea I grew well with small echinoid embryos, rotifers, or polychaete larvae, but later stages required larger prey. However, also large zoeae, for example those of the majid crab *Hyas araneus*, are able to ingest ciliates, rotifers, and early polychaete trochophores (Anger & Nair 1979). Similarly, the relatively large larvae of king crab (*Paralithodes camtschaticus*), tanner crab (*Chionoecetes bairdi*), and pink shrimp (*Pandalus borealis*) can successfully be reared with small copepods as food (Paul et al. 1979). A limited capability for suspension feeding appears to persist through later developmental

stages, including the early benthic juveniles of lobsters and other large decapod species (for review see Loo et al. 1993).

5.2.2.6 Mesozooplankton

Larger zooplankton (0.2-2 mm; Fig. 5.1C-E) appears to be the preferred diet of the late developmental stages and other large larvae. In the guts of larval lobsters, *Homarus americanus*, for instance, remains of larval and adult copepods, cladocerans, gastropod larvae, fish eggs, crab larvae, and insect pieces have been identified (Harding et al. 1983). The particle diameters of these food items showed an increasing tendency in the successive larval stages. In crab magalopae, remains of other decapod larvae were detected, suggesting predatory or cannibalistic behavior (Lebour 1922, 1927).

It is generally believed that decapod larvae depend on chance close encounters allowing for mechanical prey perception (Broad 1957a, Rice & Williamson 1970, Gonor & Gonor 1973). In contrast to juveniles, they are appearently not capable to respond with directed swimming after chemical or optical perception of prey at a distance (Moller 1978). On the other hand, available data of zoeal clearance rates (i.e. the volume swept clear per unit time) in relation to food size shows that the mechanism of capturing larger prey must be more efficient than that of filter-feeding (Omori 1979). Thus, it remains doubtful if zoea larvae have really such limited capabilities of searching and hunting prey (see discussion by Strathmann 1987). More recent experimental observations on lobster (*Homarus gammarus*) larvae showed that food capture results from chance encounter, but the discrimination of edible and inedible particles may depend on the presence of low molecular-weight chemoattractants (Kurmaly et el. 1990).

In carnivorous decapod larvae, the upper threshold prey size approximates or may even exceed the body size of the predator. This is most conspicuous in, but not restricted to, cases of larval cannibalism, which have been observed both in laboratory cultures and in nature (Lebour 1927, Anger 1995c, Gardner & Maguire 1998). In zoeal forms, the thoracic endopods play a predominent role in prey capture, while the exopods function in swimming. This has been described, for instance, in larvae of caridean shrimps (Broad 1957a, Moller 1978), porcellanid crabs (Gonor & Gonor 1973), and brachyuran crabs (Knudsen 1960).

In small brachyuran zoeae, the telson typically supports the thoracic endopods in capturing and retaining prey. This predation behavior was described in detail for the zoeae of a fiddler crab, *Uca pugilator*. A physical contact with large particles stimulates a particular tail lashing behavior, so that potential prey organisms are held fast between the carapace and the bent pleon, i.e. they are *"pinned between the spines of the telson and the anteroventral spine"* of the carapace, before they are processed with the cephalic appendages (Herrnkind 1968; Fig. 5.2). It appears that small larvae "suck out" or bite off primarily the soft body parts of their prey while they discard the hard parts. Larger larvae, in contrast, e.g. late stages of caridean shrimps, have been observed to swallow entire brine shrimp nauplii (Kumlu & Jones 1995a).

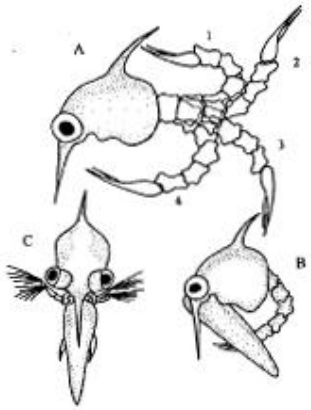


Figure 5.2. Diagrammatic illustration of prey capture by pleon lashing in a brachyuran crab zoea (*Uca pugilator*). A: sequence of pleonal positions (1-4) during the lash; B: *Artemia* nauplius pinned between the telson and anteroventral spine of the zoeal carapace; C: before ingestion, the position of the nauplius is adjusted until its anterior is in contact with the mandibles of the zoea (from Hernkind 1968; with permission from Brill, Leiden).

5.2.2.7 Macrozooplankton and other large prey

Larger prey items (>2 mm) should be accessible only to larval lobsters and other large forms such as the decapodid stages of shrimps and crabs. Brachyuran crab megalopae, for instance, have in laboratory cultures successfully been reared with large benthic food such as live worms or pieces of mussel, fish, or crab meat. Similarly, the mysis larvae of the Norway lobster, *Nephrops norvegicus*, grew well in cultures with live juvenile and adult *Artemia* of approximately their own body size provided as food (Anger & Püschel 1986). On the other hand, Rotllant et al. (2001) showed that the relatively large larvae of this species are also capable of an efficient utilization of *Artemia* nauplii. Their study showed that the quality of food may be more important than its size: small but nutrient-enriched brine shrimp nauplii (previously incubated with lipids and vitamis) allowed for significantly better larval growth and survival than large but nutritionally poor frozen adult *Artemia* and other large food items that were experimentally tested.

Large food items appear to be important for the phyllosoma larvae of spiny and slipper lobsters (Palinurida). Lebour (1925) observed a phyllosoma capturing and holding young fishes with the thoracic endopods, while it swam with exopod movements. Mitchell (1971; unpublished M.Sc. thesis cited by Phillips & Sastry 1980; not seen) observed that the early phyllosoma larvae of *Panulirus interruptus* preferred chaetognaths, fish larvae, hydromedusae, and ctenophores. It is thus not surprising that the early rearing attempts with spiny lobster larvae often failed, when small *Artemia* nauplii were given exclusively as food. Their cultivation has become increasingly successful since fish fry or pieces of polychaetes, mussels, or clams were offered (Batham 1967, Inoue 1978, Takahashi & Saisho 1978, Kittaka 1994, 1997, Mikami & Greenwood 1997a, b).

In a rock lobster species from Australia, *Jasus edwardsii*, the first-stage phyllosoma was recently observed to attach and feed on the large larvae of the Tasmanian trumpeter fish, *Latris lineata* (MacMillan et al. 1997). Scanning electron-microscopical examination showed that the mouthparts of the phyllosoma are well adapted to scrape and cut off pieces from large soft surfaces such as fish skin or gelatinous makrozooplankton (e.g. large scyphozoans). The presence of skin-pigment particles inside their digestive tract provided evidence of actually ingested fish integument.

This unusual mode of larval feeding might be common among the Palinurida. There are several observations of scyllarid phyllosoma larvae "riding" on scyphomedusae, suggesting that jelleyfish and other large makrozooplankton serve as a means of transport (Shojima 1963, Thomas 1963, Herrnkind et al. 1976; see also photo in Phillips & Sastry 1980, p. 40). This behavior, called "piggyback riding", has been reported also from larvae of a caridean shrimp, *Pandalus danae* (Marliave & Mills 1993). In large phyllosomas, however, scyphomedusae might be utilized also as a food source. In an unidentified, extremely large phyllosoma larva (7 cm body length) which was caught from a depth of about 200 m off Bermuda, the occurrence of nematocysts in the fecal matter indicated an uptake of cnidarian tissues (Sims & Brown 1968).

These results suggest that the larvae of at least some slipper lobsters may have evolved from predators towards ectoparasites, attacking prey that is much larger than themselves. However, the feeding ecology of phyllosomas is generally little known, leaving the test of this hypothesis as an interesting new field for behavioral research. Possibly, similar modes of feeding may occur also in other decapod taxa. Zoeae of a xanthid crab (*Carpilius corallinus*), for instance, were observed eating pieces of fish and snail meat (Laughlin et al. 1983). Although this behavior seems to be exceptional among the brachyuran zoeae, future comparative studies of larval feeding might reveal further surprising exceptions.

5.2.3 *Selectivity*

The great variability in size and quality of naturally available potential food sources has favoured the evolution of selective feeding mechanisms and, in consequence, selectivity is a general phenomenon in particle feeders (Grahame 1983, Strathmann 1987). In decapod larvae, the relevant sensory system involved in the selection of prey is non-visual, primarily based on mechano- and chemoreceptive sensillae that are concentrated on the antennules, maxillipeds and other mouthparts of larval decapods (see chapter 2).

In zooplankton, in general, selection by size is chiefly determined by constraints in the functional morphology of feeding organs (Marshall & Orr 1960, Frost 1977, Grahame 1983). In decapod larvae, this is primarily associated with the morphology of the cephalic and the anterior thoracic appendages which serve as mouthparts. The development of internal feeding structures such as the gastric mill may play an additional role in food selection (see section 3.11). Since the mouthparts grow during the course of larval development, the size of preferred prey increases generally with the body size of the larva. In penaeid and other dendrobranchiate shrimps, this change is usually associated with a shift from herbivorous to carnivorous feeding (e.g. Kurmaly et al. 1989b, Dall et al. 1990). In early blue crab (*Callinectes sapidus*) zoeae fed with a mixed diet, a preferential feeding on small prey items (rotifers, *Brachionus plicatilis*) was observed, while a switch towards larger prey (brine shrimp nauplii, *Artemia*) occurred after the zoea III stage (McConaugha et al. 1991). However, also later stages continued to ingest rotifers as an additional food source. The same trend was recently shown in the larvae of another crab species, *Pano-*

peus herbstii (Harvey & Epifanio 1997). The zoea I ate about twice as many *Brachionus* than *Artemia*, even when the concentration of brine shrimp nauplii in the food mixture exceeded that of rotifers in a ratio 4:1. The zoea IV, in contrast, ingested consistently more *Artemia* than *Brachionus*, regardless of the mixture. Interestingly, brine shrimp nauplii accounted in both stages for the majority of the energetic intake, due to a 5.5-fold higher energy content per individual ingested. Similar ontogenetic changes in particle size selection were observed in penaeid shrimp larvae (Yúfera et al. 1984, Hirata et al. 1985). From these results we may conclude that (1) there is a selectivity for small prey in early larval stages, but a preference for larger prey in late stages; (2) this selectivity is not exclusive, i.e. also early larvae can eat relatively large prey, and late larvae continue to accept small prey; (3) ingestion of large prey is energetically advantageous, also in small (early) larvae.

There are mechanical constraints to feeding other than by prey size alone. Penaeid shrimp larvae, for instance, are capable of selecting between rounded and irregular particles, accumulating rejected items in a bolus below the mouth (Kurmaly et al. 1989b). Crab (*Cancer magister*) and hermit crab (*Pagurus longicarpus*) larvae were shown to discard mussel and oyster larvae, probably because larval mollusc shells can withstand the action of their mouthparts and thus, inhibit ingestion (Reed 1969, Roberts 1974). Other decapod larvae, however, were shown to break and ingest such type of prey (Lebour 1922, 1927, Harding et al. 1983). Similarly, long spines are effective means of defense against predation by decapod larvae and other small pelagic predators (Morgan 1987, 1989, 1990, 1992).

In addition to mechanical constraints in the predator-prey relationship, chemically induced selectivity has been demonstrated in numerous planktonic crustaceans (Poulet & Marsot 1978, Cowles et al. 1988). In early shrimp (*Macrobrachium rosenbergii*) larvae, chemical cues from potential food were shown to stimulate a feeding response: when juice from crushed and filtered *Artemia* was added to the water, the zoeae accepted eagerly also artifical food particles which they otherwise rejected or ate only incompletely (Kumlu & Jones 1995a). Also lobster (*Homarus gammarus*) larvae were observed to select potential food particles according to specific flavours (Kurmaly et al. 1990). Several compounds in this study were chemically identified as stimulating cues, e.g. L-glutamic acid, inosine-5-monophosphoric acid, and trimethylamine. Interestingly, however, a monotonous feeding regime caused a conditioning effect, i.e. an increasing frequency of rejection of previously accepted food items; eventually, the same particles were only accepted again after changing their flavour. The authors suggest that this was an effect of low energetic value of the food particles; when the prey was adequate energetically (e.g. when lobster larvae were offered as prey), it was always taken without rejection. The degree of selectivity may change also during the course of development. In lobster and caridean shrimp larvae, later stages were shown to accept an increasing range of food particles (Jones et al. 1997a).

Zooplankton may show not only a chemical attraction by potential prey organisms, but also a negative feeding response to predator odor. When planktonic copepods were exposed to exudates from planktivorous fish, they reduced their the feeding activity (Cieri & Stearns 1999). This “hiding” response has not been experimentally demonstrated in decapod larvae, but it may occur there as well. Also potential planktonic prey organisms have frequently been shown to release or to contain chemical substances that serve as a defense against pelagic predation (for recent review, especially of the occurrence of secondary metabolites as chemical defense in marine invertebrate larvae, see Cowart et al. 2000).

Besides mechanical and chemical factors, also behavioral features of the potential food organisms limit the feeding success of predatory zooplankton. In a recent study of food uptake in mysids (Viitasalo & Rautio 1998), the authors concluded that selectivity frequently may not really exist but reflect only the differential escape capabilities and morphological defenses of the available prey species. In crab zoeae, it was observed that passively drifting echinoderm eggs and embryos were readily taken up, whereas actively swimming pluteus larvae escaped more easily from predation (Rumrill et al. 1985, Pennington et al. 1986). Similarly, crab larvae may discriminate between brine shrimp nauplii and rotifers, possibly not only based upon differential size but also on swimming behavior of the prey (Harvey & Epifanio 1997).

The degree of selectivity depends also on the state of a predator's hunger (Nakamura 1974) and on total prey concentration, including the so-called background plankton (Johnson & Shanks 1997). In most experiments where various concentrations of mixed diets were tested, planktonic crustaceans became increasingly selective with increasing food density, i.e. more indiscriminate when food was less abundant (Paffenhöfer & Knowles 1978, Yúfera et al. 1984). Thus, we may expect that decapod larvae are, under natural conditions, poorly selective, because the average concentrations of potential food are generally lower in the pelagial than in laboratory cultures. As a consequence of this opportunistic feeding behavior, the composition of their natural diet should widely depend on the concentrations of available prey organisms.

In summary, decapod crustacean larvae are capable of particle selection by size or chemical quality, but they are generally omnivorous when food is scarce. Their trophic role in the plankton may thus be described as both suspension feeders and predators. When given a choice, they tend to carnivory, with a preference for relatively large prey. In the natural environment, their diet should thus consist of variable mixtures of phyto- and zooplankton. In laboratory experiments, such mixed diets have frequently been shown to promote growth and survival better than monospecific food, as qualitative deficiencies of single components are compensated by others (Broad 1957a, Williams 1968, Sandifer 1972, Bigford 1978, Ebert et al. 1983, Villamar & Brusca 1987, Fernández de Puelles 1985, McTigue & Zommerman 1991).

5.3 *The quantity of food uptake*

Besides knowledge of qualitative aspects of larval feeding, quantitative information is necessary to understand the trophic relationships in a pelagic community or to optimize the nutritional conditions in scientific or aquaculture-related rearing experiments. As in most other aspects of larval biology, this raises the old principal question of whether laboratory or field data provide better insights and to what extent the former can be extrapolated to natural conditions (cf. section 1.3; see also discussion in MacKenzie et al. 1990, Suthers 2000, Elliott & Leggett 2000). In the following section, I will recur to this problem, addressing specific technical difficulties in the measurement of ingestion rates and implications for the extrapolation to natural conditions.

Laboratory feeding rates have been determined using mostly *Artemia* nauplii or monospecific phytoplankton cultures as a food source, while little quantitative information exists on the uptake of natural prey species, and even less on selective larval feeding behavior in mixed assemblages of food organisms. Hence, the available data must be treated with caution, in particular when extrapolations to field conditions are attempted. Strath-

mann (1987) argued convincingly that much of the literature on larval feeding rates may significantly underestimate the actual rates of food uptake under natural conditions, because the prey offered or other experimental factors may often have been inappropriate. Thus, in situ experiments with natural mixtures of prey should generally yield a more reliable picture of larval growth and feeding. However, the disadvantage of this type of experiments is in its poor reproducibility. When information is needed on developmental variation in food uptake, for instance between the stages of the molting cycle or in successive larval instars, there is normally no alternative to measurements under controlled conditions in the laboratory. Likewise, this applies to the study of effects of environmental factors such as temperature, salinity, or the food factor itself (e.g. the species or density of prey).

When we attempt to find general patterns in the quantity of food uptake in relation to environmental factors, taxonomic position, or the developmental stage, we often need to compare ingestion rates in larvae with unequal size and biomass, and frequently also the type of food varies. Especially when the stage-specific demands for size, behavior, or quality of prey change during the course of development, an interpretation of differential feeding rates is impossible in terms of numbers of prey ingested. Hence, feeding rates should be converted to units of biomass ingested (dry mass, carbon, or energy; Omori 1979, Hirata et al. 1985, Anger 1991a). Since ingestion rates depend also strongly on the size of the consumer, it may further be necessary to convert the absolute values (rates of uptake per individual) to biomass-specific ingestion rates, i.e. weight, carbon, or energy of ingested food expressed as a fraction of the consumer's biomass.

In the following section, technical problems associated with the quantitative measurement of feeding rates are reviewed, before developmental patterns and extrinsic effects are discussed.

5.3.1 *Measurements of ingestion rate: technical constraints to accuracy*

In grazing experiments, the uptake of particulate food is usually quantified with conventional particle counts carried out at the beginning and the end of defined intervals of time; as an alternative, radiotracer techniques have been employed in planktology (Rigler 1971, Schiller et al. 1977, Lynch et al. 1986). Extrapolations to field conditions may be unrealistic, because (1) it is impossible to simulate the quality, quantity, diversity, and spatial distribution of natural food sources in the plankton; (2) with particle-counting techniques, measurable feeding rates can be obtained only at unrealistically high experimental densities of both the predator and the prey organisms; (3) larvae do not always swallow entire, well-defined particles, but lose or discard major fractions of their food. Most of these losses occur as a *"leakage"* (Pechenik 1979) or *"leaching"* (Dagg 1974) of liquid and fine particulate matter. The failure to ingest all killed prey is in the literature also referred to as *"overhunting"* (Ikeda 1977) or *"wasteful killing"* (Johnson *et. al.* 1975).

As a further complication, the rate of food uptake varies not only among larval stages, between the molt-stages within an instar, with changes in environmental factors, and with the density and quality of food, but also with the preceding feeding history. The same incertainties apply to the quantities of leached materials and fecal losses. Direct measurements of lost materials are rendered difficult by rapid colonization, conversion, and degradation by bacteria and protozoans. Hence, only few quantitative data of larval ingestion, leaching, and defecation are available in the literature. Leaching has widely been ignored,

treating it as a technically uncontrollable factor (for general discussion and references see Kurmaly et al. 1989a, Anger 1991a).

As an attempt to control, at least partially, losses occurring during the feeding process, a combination of regular microscopical techniques with computer-aided quantitative image analysis may be imployed (Anger & Dietrich 1984, Dietrich & Uhlig 1984, Dawirs & Dietrich 1986). With this technology, the projection area of remaining food particles, including pieces of partially eaten prey, can be measured quite accurately and converted to biomass data. However, size-biomass calibrations with intact prey organisms are required, and losses with leached liquids and small particles remain as an unresolved problem. Additionally, there may be differences in the chemical composition of eaten and uneaten pieces of food, even if the size and weight of the latter can be quantified correctly. This problem should be particularly great in small larvae that suck out rather than swallow their prey (see above). These and other technical problems may explain the great individual variability that usually occurs in parallel measurements of ingestion rates, even among sibling larvae that are treated identically.

In spite of all those technical problems, quantitative estimates of food uptake are necessary for interspecific comparisons or to identify developmental and environmental changes in feeding activity. This is possible to some extent as long as the methodical error is kept constant. In the following sections, I will show examples of relative changes, which are often more important than the absolute values of food uptake. Among the factors that are known to affect the rate of ingestion, the concentration of food, the state of hunger, temperature, salinity, and developmental changes may be the most important.

5.3.2 *Variation in food availability: response patterns in feeding activity*

In a widely accepted model of filter-feeding, ingestion rate increases as a linear function of particle concentration until a plateau is reached (Strathmann 1987). Above the saturation concentration, the ingestion rate remains constantly high, while the clearance rate decreases with further increasing food density. These theoretical relationships should in principle apply also to raptorial particle feeding, because the rate of capture depends on the chance of encounters with prey organisms, and thus, on food density (Gerritsen & Strickler 1978). This has been experimentally quantified in larvae of various decapod species, including several species of sergestid, penaeid and caridean shrimps, clawed and spiny lobsters, and brachyuran and anomuran crabs (Carlberg & van Olst 1976, Anger & Nair 1979, Omori 1979, Paul et al. 1979, Emmerson 1980, Yúfera et al. 1984, Yúfera & Rodríguez 1985a, b, Chu & Shing 1986, Wong et al. 1989, Minagawa & Murano 1993a, Harvey & Epifanio 1997, Zhang et al. 1998b, Moss et al. 1999, Tong et al. 2000).

Both the overall level of feeding and the concentration where the plateau is reached depend on prey characteristics and the larval stage. As an example, the relationship between the ingestion rate per larva and density of prey is shown here for several zoeal stages of a raninid crab, *Ranina ranina* (Fig. 5.3; for developmental changes in feeding activity, see section 5.3.4). Figure 5.4 shows the increase in the weight-specific rate of ingestion with increasing food concentration in caridean shrimp larvae.

At low food concentrations, the feeding rate may become so low that larval development is delayed, and growth and survival are reduced (for review see McConaugha 1985). At plateau concentrations, on the other hand, growth is at a maximum (Emmerson 1980, Yúfera & Rodríguez 1985b). However, the available data indicate that only unnaturally high densities of monospecific prey allow for satiated feeding and maximal growth. When

early zoeae of a spider crab, *Hyas araneus*, were fed with natural prey items (larval spionid polychaetes, *Polydora ciliata*), maximum ingestion was reached only when the food concentration exceeded about 1000 prey individuals per litre; this is well above the highest densities ever recorded for *Polydora* larvae in the plankton (Anger & Nair 1979).

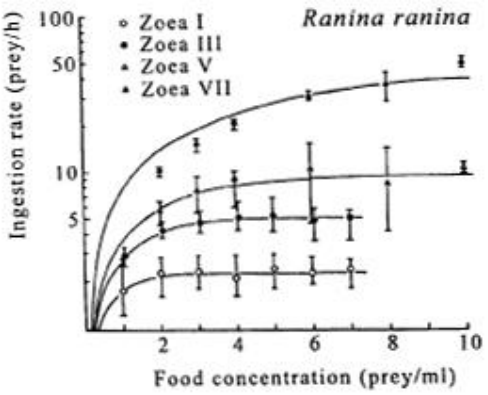


Figure 5.3. Ingestion rate (numer of prey eaten per hour per individual) in relation to the density of prey (*Artemia* spec. nauplii) in four larval stages of a raninid crab, *Ranina ranina* (from Minagawa & Murano 1993a, with permission from Elsevier, Oxford, UK).

In most experimental studies, the ingestion rate increased over a wide range with food concentrations, often without reaching a plateau (see Fig. 5.4). Hence, the available evidence suggests that larval feeding in the natural environment is typically limited by suboptimal food densities (Strathmann 1987, 1996). On the other hand, quantitative deficits may be compensated by higher quality of mixed natural plankton as compared with monospecific laboratory food. Moreover, the generally patchy distribution of particles in the water column, which may sometimes lead to transitory periods of famine, can cause also temporary abundance of food. The inhomogeneous particle distribution is caused by physical processes, namely small-scale turbulence, which was recently shown to enhance also feeding activity and growth in planktonic copepods (Saiz et al. 1993, Alcaraz 1997; for recent controversial discussion see also Irigoien et al. 2000, Peters & Marrasé 2000). As another possible adaptation to patchiness, larvae may respond to chemical cues, swimmming actively towards dense food patches. This response has recently been shown, for the first time in larval invertebrates, in echinoid larvae (Metaxas & Young 1998). As an opposite pattern, active avoidance of small-scale scarcity of food has been observed in copepods (Dagg 1977). In future research, similar behavioral response patterns may be found also in larval decapods.

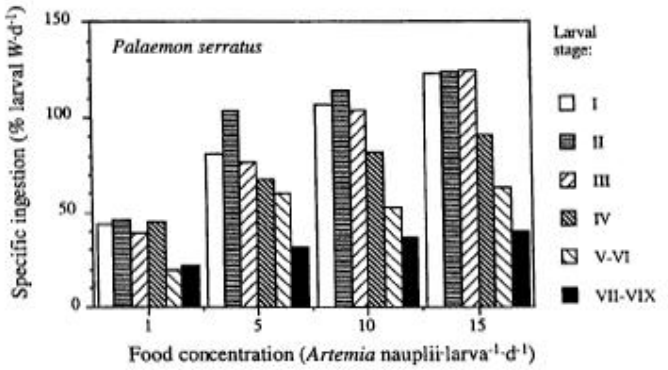


Figure 5.4. Weight-specific rates of ingestion (in % of larval dry mass, *W*, eaten per day) in caridean shrimp, *Palaemon serratus*, larvae at four different levels of food density (expressed in numbers of *Artemia* spec. nauplii given per larva per day; redrawn after data from Yúfera & Rodríguez 1985b).

A simulation model of larval survival in an environment with patchy distribution of food particles suggests that differential selection pressures are exerted on small *vs.* large types of larvae (Winemiller & Rose 1993). In fish larvae, the simulation predicts that larger larvae have an advantage when prey is locally strongly clumped, especially when the average level of food density is low. Small larvae, on the other hand, should survive better under conditions of high average food concentration and a low level of small-scale patchiness. Also in freshwater cladocerans, large species were shown to have a selective advantage under conditions of low average resource density (Gliwicz & Lampert 1993). Hence, resource patchiness occurring on a large spatial scale should select for the production of a high number of small offspring (as in most fish and decapod species), while a strong small-scale (or short-term) variability in food availability should select for a production of less but larger larvae. These interesting theoretical relationships, which may explain the evolution of differential life history strategies, remain to be tested in experimental and field studies of larval feeding and survival.

Under conditions of irregular availability or permanently low concentrations of food, hunger should generally enhance the feeding activity ("maximal feeding strategy"). This was observed in some although not all larval stages of a penaeid shrimp, *Metapenaeus ensis* (Chu & Shing 1986). In mud crab (*Rhithropanopeus harrisii*) larvae, starvation caused changes in phototactic behavior, suggesting that hunger stimulates the larvae to ascend to the water surface, where phytoplankton production is higher (Cronin & Forward 1980). However, the feeding response to variability in food concentration might actually be yet more complicated. In a recent experimental study with freshwater zooplankton (Plath 1998), it was shown that the enhancement of feeding activity after starvation depends not only on the duration of the period of food deprivation but also on the overall nutritional condition of the consumer, i.e. on the long-term feeding history. As another complication

in the functional response to famine, the same study suggests that the feeding activity at low food levels may be reduced to save energy rather than enhanced to maximize ingestion. This finding contradicts the hypothesis of a "maximal feeding strategy" and supports the "optimal foraging strategy" in zooplankton; it remains to be ascertained whether this applies also to decapod crustacean larvae.

Short periods of food deprivation may thus enhance the appetite and subsequent ingestion rates, while longer periods of poor food availability induce energy saving mechanisms, including a reduction of feeding activity. Under conditions of severe food limitation, extended periods of starvation will eventually cause a serious impairment in the capability to catch and process prey. In king crab (*Paralithodes camtschaticus*) larvae, such detrimental effects were observed already after 60 to 84 h (Paul & Paul 1980). In several other species, however, no such effects were observed, even after prolonged periods of famine (Kon 1979, Anger & Dawirs 1981, Anger et al. 1981a, b, Anger 1987a). This suggests a great deal of interspecific variability.

In summary, most decapod larvae appear to be well adapted to temporary lack of food. Among the adaptations that maximize the overall rate of feeding, there are behavioral responses to hunger, water turbulence, gradients in particle concentration, or food odor. Moreover, the degree of selectivity tends to decrease at low food levels, i.e. larval feeding becomes increasingly opportunistic when food is scarce. As a consequence, hungry larvae take particular advantage of the superior chemical quality of mixed food, which compensates for a reduced quantity. Larval survival and development in the plankton may be favoured by additional unknown feeding mechanisms, e.g. those allowing for clearing a larger volume of water (or to process water at lower particle concentrations) when the available food particles are on average larger than those commonly concentrated by filter-feeders (Strathmann 1987). Together, such mechanisms explain the successful development of decapod larvae in the field in spite of low average zooplankton concentrations.

5.3.3 *Diurnal feeding rhythms*

Diurnal activity rhythms appear to be another source of variation in the feeding rate of decapod larvae, although the available evidence is incongruous. In zoeae of a raninid crab, *Ranina ranina*, for instance, 2.6 to 2.8 times higher ingestion was measured during daylight than in darkness (Minagawa & Murano 1993b). Similarly, the larvae of a caridean shrimp, *Hippolyte inermis*, ate more by day than by night (Regnault 1969a). Also enhanced larval growth under conditions of long photoperiod and bright light observed in the Australian giant crab, *Pseudocarcinus gigas*, suggested a maximum feeding activity during daylight (Gardner & Maguire 1998). In the latter case, this corresponded with an increasing intensity of cannibalism at longer photoperiods. A tendency of higher rates of food uptake during periods of light was observed also in larval mud crab, *Rhithropanopeus harrisii*, although this effect was only weak in this species (Cronin & Forward 1980).

In contrast to these consistent observations, no variation in relation to light conditions was found in the feeding rates of larval king crabs, *Paralithodes camtschaticus* (Kurata 1960). Also in mud crab (*Panopeus herbstii*) zoeae, neither feeding rate nor selectivity for prey was influenced by light conditions (Harvey & Epifanio 1997). Moreover, the larvae of several other decapod species have been reared with equal success in light and darkness, suggesting that the light factor was not important for their feeding (e.g. Costlow & Bookhout 1962, Dawirs 1982, Sulkin et al. 1998b). Further indirect evidence from larval

growth data suggests that the feeding response to variation in light varies considerably among taxa and may not show a general pattern (see section 6.4.3).

As Strathmann (1987) pointed out, there is no experimental evidence for visual search for prey in decapod larvae. Yet, light may act as a trigger for enhanced swimming actvity and thus, affect larval ingestion rates indirectly. Strathmann proposed the hypothesis that zoeae show undirected swimming, scanning a certain area normal to their path. This implies that the volume swept clear is proportional to the larval swimming speed. If this is enhanced by environmental cues such as changes in light or turbulence, the feeding rate will increase as well. Such an indirect stimulation would not be associated with visual hunting, but could be an adaptive response to daily vertical migrations of potential prey organisms in the natural environment. This may explain also, at least in some species, observations of enhanced feeding and growth under light conditions.

5.3.4 *Developmental variation among stages*

Since planktotrophic larvae grow during their development in size and biomass, successive stages require increasing amounts of energy per individual and unit of time. In consequence, not only the overall level of feeding, but also the minimal concentration where ingestion reaches its maximum (the plateau concentration) increases in successive stages (Fig. 5.3). In the zoeae of *Ranina ranina*, for instance, the minimum food density for satiated ingestion increased from about 2 *Artemia* nauplii/ml in the zoea I to 8/ml in the zoea VII (Minagawa & Murano 1993a).

When the total quantity of food ingested during the course of a molting cycle is compared among successive larval instars, in some species a gradual increase found (Logan & Epifanio 1978, Wienberg 1982, Yúfera & Rodríguez 1985a, Zhang et al. 1998b). More commonly, however, it increased exponentially with the number of stages (e.g. Kurata 1960, Mootz & Epifanio 1974, Carlberg & van Olst 1976, Levine & Sulkin 1979, Omori 1979, Johns & Pechenik 1980, Johns 1982, Dawirs & Dietrich 1986, Minagawa 1994). These pattern may not hold any longer in premetamorphic stages such as decapodids. The megalopa of the spider crab *Hyas araneus*, for instance, consumed considerably less food than should be expected from the previous increase between the zoeal instars (Anger & Dietrich 1984, Harms et al. 1991). In another brachyuran crab, *Rhithropanopeus harrisii*, larval feeding rate decreased during the last zoeal stage (Levine & Sulkin 1979). Particularly low ingestion rates in premetamorphic stages may be associated with the advent of dramatic changes in morphology, ecology, and behavior. In species where the early benthic life-history stages show highly specilized habitat requirements, those needs should select for a strongly reduced feeding activity at settlement and, eventually, may lead to secondary lecithotrophy (section 5.1.2).

When biomass-specific rather than absolute ingestion rates are compared among successive larval stages, there is usually a decreasing trend throughout development (Anger 1991a, Jones et al. 1997a). However, there is great interspecific variation in the average level, and maybe, in the patterns of ontogenetic change. In spider crab (*Hyas araneus*) larvae, the maximum rates reached in the zoeal stages an equivalent of about 40% of larval energy content consumed per day, but only about 15% in the megalopa (Anger & Harms 1989). Similar values (on a dry-weight basis) were found in lobster (*Homarus americanus*) larvae, with average daily consumption rates decreasing from initially 40% to about 30% (Logan & Epifanio 1978).

Far higher biomass-specific feeding rates have been observed in the larvae of caridean and penaeid shrimps (Yúfera & Rodríguez 1985a, b, Yúfera et al. 1984). In *Palaemon serratus*, the early larval stages (zoea I-III) consumed an equivalent of up to 125% of their own biomass per day, depending primarily on food concentration, while later stages consumed successively lower amounts of prey in relation to larval biomass (Fig. 5.4). Interestingly, the average daily feeding rates of the zoea I did not fit well in this general pattern, showing relatively low values. This is consistent with the observation that the zoea I of palaemonid shrimps frequently reveal an endotrophic tendency, reaching in several species full lecithotrophy (see section 5.1.1). The zoea I stage of a closely related species, *Palaemonetes varians*, ingested at the highest tested food concentration an equivalent of 231% of larval weight per day (Yúfera & Rodríguez 1985a). The weight-specific feeding rate decreased subsequently throughout larval development, reaching 69%·d^{-1} in the "postlarva" (in this case unclear whether referring to a decapodid or a juvenile stage).

Yet higher ingestion rates are reached by early larval stages that feed exclusively or primarily on phytoplankton. The fully herbivorous protozoea I of *Melicertus kerathurus*, for instance, consumed up to 10 times its own body weight (i.e. 1000%!) per day (Yúfera et al. 1984). Although the specific feeding rate decreased considerably during later development, even the mysis and "postlarval" stages ate still about 200%·d^{-1} as long as their food was suitable in size and concentration. However, when exclusively rotifers were offered as prey (apparently too small for the late developmental stages), there was a much stronger ontogenetic decrease in the specific feeding rates. In protozoeae of *Fenneropenaeus indicus*, the daily ingestion of diatoms averaged about 860% of larval dry mass, while mysis larvae still ate 520% (Emmerson 1980). Comparable values were reported by Kurmaly et al. (1989a) for *Penaeus monodon*, with 390, 200, and 90% measured in the protozoeal, mysis, and "postlarval" phase, respectively. From these consistent patterns we may conclude that high biomass-specific daily ingestion rates measured in late developmental stages should indicate omnivorous feeding behavior; this is known, for instance, for *F. indicus* (Jones et al. 1997a).

Deviating results were obtained in the protozoeal stages of another dendrobranchiate shrimp, *Sergestes similis*, with maximum biomass-specific (carbon-based) ingestion rates reaching only about 70-100%·d^{-1}, and decreasing values in later larval and juvenile stages (about 30%·d^{-1}; Omori 1979). Similarly, the maximum feeding rates measured in the larvae of *Metapenaeus ensis* ranged between ca. 30-100%·d^{-1} (Chu & Shing 1986). As a rare exception, an ontogenetically increasing specific ingestion rate was reported in this study.

The discrepancy between the low average biomass-specific feeding rates in *Hyas araneus* as compared with most other decapod species is possibly associated with differences in their latitudinal origin, and thus, differential temperature adaptation. The spider crab shows a boreal-subarctic distribution, whereas all shrimp species mentioned above are tropical or subtropical. The latter are adapted to high temperatures, where they show a rapid larval development and hence, high daily energy requirements. Additionally, spider crabs like *H. araneus* show a tendency towards an abbreviation of larval development (only two zoeal stages) which may be associated with an enhanced endotrophic potential, and thus, some complementary utilization of internal reserves.

5.3.5 *Variation during the molting cycle*

When the rate of ingestion is measured in small intervals during the development through a larval instar, molt-cycle related variation in feeding activity may be detected (Fig. 5.5;

cf. section 4.2.1). As a general pattern, the feeding rate increased after ecdysis, reached a maximum in the postmolt or intermolt phase, and decreased throughout the premolt stages (Kurata 1960, Regnault 1969a, Anger & Dietrich 1984, Dawirs & Dietrich 1986, Anger et al. 1989a, Minagawa & Murano 1993a). Similar changes in daily food uptake, i.e. particularly low feeding activity at the beginning and near the end of the molting cycle, were observed also in adult penaeid shrimps (Hill & Wassenberg 1992), suggesting that this may be a common pattern in decapods.

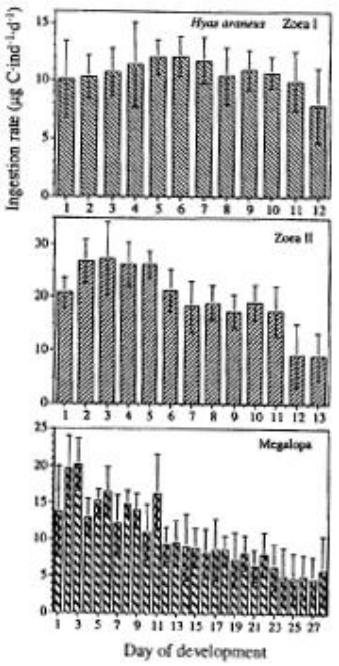


Figure 5.5. Molt-cycle related variation in the ingestion rate (expressed in µg carbon, C, per day per individual) of the successive larval stages of a spider crab, *Hyas araneus*, reared under constant conditions; food: *Artemia* spec. nauplii (after data from Anger et al. 1989a).

This pattern is plausible, as the new exoskeleton is soft during early postmolt, so that the feeding appendages and (where present) the gastric mill are temporarily nonfunctional. The same applies to late premolt, when there are again cuticular reconstruction processes requiring, at least shortly before ecdysis, that the uptake of food is interrupted. Since these periods, especially early postmolt, are associated with rapid physiological and behavioral changes, a low temporal resolution of ingestion measurements will cause great errors and high variability in estimates of feeding rate. As an additional source of variability among parallel measurements, the molting cycle is not strictly coordinated among sibling larvae, especially in late larval stages.

Molt-cycle related patterns in the rate of larval food uptake may be veiled also by overlaying diurnal rhythms related to the light cycle (section 5.3.3), or by variations in the quantity or quality of available prey (section 5.3.2). When large chain-forming diatoms (*Biddulphia sinensis*) were given as food to spider crab (*Hyas araneus*) larvae, their inges-

tion rates were on average lower, yet following the same arched pattern as when fed with *Artemia* nauplii (Harms et al. 1991). However, when smaller or qualitatively inferior phytoplankton species were offered (*Thalassiosira rotula*, *Skeletonema costatum*), the average feeding rates decreased further, and the typical pattern in relation to the molting cycle was lost. In addition, the shape of the feeding curves may vary among successive larval stages. In *H. araneus*, for instance, the time of maximal daily ingestion showed a shift from intermediate towards progressively earlier stages of the molting cycle (see Fig. 5.5).

The biomass-specific (energy-based) ingestion rates of larval *Hyas araneus* were consistently maximal in postmolt, decreasing throughout the molting cycle (Anger 1991a). In zoeae, maximum rates of ca. 40% per day were measured during postmolt, but <20% in premolt. In the megalopa, the feeding activity decreased during the molting cycle from maximally ca. 15% to <5% per day. Clearly not enough comparative data are available to allow for generalizations of these molt-cycle related patterns in larval feeding rate.

5.3.6 *Physico-chemical effects: temperature, salinity, pollutants*

While a reduced feeding activity can have intrinsic causes associated with development or the molting cycle, it occurs frequently also as an unspecific effect of stress, e.g. under unfavourable conditions of temperature, salinity, poor food quality, or exposure to toxic substances. Moreover, the feeding activity decreases generally with decreasing metabolic requirements at lower temperatures (Wienberg 1982, Paul & Nunes 1983, Yúfera & Rodríguez 1985a, b, Dawirs & Dietrich 1986, Zhang et al. 1998b, Tong et al. 2000).

The enhancement of daily feeding by high temperatures is, at least in some stages or species, weaker than the concurrent acceleration of development. Due to this difference in the temperature-dependence of two processes, the cumulative amounts of food that are ingested during the time of a larval instar may decrease with increasing temperature, as experimentally demonstrated in larve shore crab, *Carcinus maenas* (Dawirs & Dietrich 1986). When the temperature exceeds the optimum of a species or larval stage, also the daily (instantaneous) rates of ingestion will decrease, while the metabolic losses may be further enhanced (Johns 1982, Minagawa 1990b). As a consequence of such energetically adverse conditions, the larvae show reduced growth and survival. At unfavourably low temperatures, on the other hand, the decline of the feeding activity can be stronger than reduction of the metabolic demand, and in consequence, larval growth and survival will also decrease (see Dawirs & Dietrich 1986). Similarly, effects of famine are enhanced by temperatures below the optimum, in spite of reduced metabolic losses (Paul & Paul 1980, Anger et al. 1981b).

As another stress factor, unsuitable salinities are known to affect most biological processes in aquatic invertebrates, including their feeding activity. In larvae of marine decapod species such as the shrimp *Pandalus borealis* or the crab *Cancer irroratus*, the rate of ingestion was shown to decrease at reduced salinities (Wienberg 1982, Johns 1982). In the larvae of another marine crab, *Ranina ranina*, feeding activity was depressed in both diluted and hypersaline media (Minagawa 1992). A reduction of larval food uptake was observed also during exposure to pollutants such as water-soluble hydrocarbons from crude oil (Johns & Pechenik 1980), toxic metals (Cr, Cu, Ni; Wong et al. 1993), or after contamination of food particles with hydrocarbons (Gharrett et al. 1985).

5.4 *Activities of digestive enzymes*

Our review of the nutrition of decapod crustacean larvae has shown that there is ample evidence for a generally omnivorous, widely opportunistic mode of feeding (except for the herbivorous penaeid protozoeae), with characteristic developmental shifts in the preferred size and type of prey. We know that most larval decapods eat both phyto- and zooplankton in variable quantities, which largely depend on developmental stage, composition and concentration of food, and physical factors. A broad food spectrum, however, does not necessarily mean that the larvae are physiologically adapted to utilize all types of food equally well. In general terms, the efficiency of conversion depends primarily on the available mechanisms for mechanical and chemical maceration of food (e.g. feeding appendages, gastric mill, filter apparatus, digestive enzymes), and on gut evacuation time (*GET*, the span between ingestion of food and egestion of feces). The available data suggest that digestive enzyme activities show a negative relationship with *GET*, especially in penaeid shrimp larvae, but a positive correlation with ingestion rates (Jones et al. 1997a). Hence, larvae that feed on different trophic levels or at different food concentrations can tune their feeding rate, *GET*, and digestive enzyme activities to control the overall assimilation of food.

During the *GET*, the degradation of dietary macromolecules depends on the presence and activation of specific digestive enzymes, which are synthesized and stored primarily in the hepatopancreas (or, in early penaeid shrimp larvae, in the midgut caeca; see section 3.11.6). Since the hepatopancreas grows conspicuously in size during the course of larval development, it should generally produce increasing quantities of digestive enzymes. In spite of this simple and plausible relationship between digestive gland development and secretion of digestive enzymes, however, there has been considerable discussion whether the efficiency of food conversion depends primarily on the ontogeny of the digestive organ system or rather on a regulation of the activities of existing enzymes in response to variations in food quantity or quality (see e.g. Lovett & Felder 1990a, b, c, Jones et al. 1993, Kamarudin et al. 1994, Rodríguez et al. 1994, Kumlu & Jones 1995a, b, 1997).

In the following section, a brief account of the principal mechanisms of enzyme regulation is given, problems related to the comparability of literature data are discussed, and major ontogenetic and nutritional variations in digestive enzyme activities of decapod crustacean larvae are reviewed. Eventually, a simple conceptual model of putative interactions between feeding level, secretion or activation of digestive enzymes, and growth shall serve as a brief summary of the available data on the digestive physiology of larval decapods.

5.4.1 *Principal mechanism of regulation*

Quality and quantity of available food sources vary throughout ontogeny and with environmental conditions. Thus, an organism needs the capability to readjust its physiological mechanisms of food utilization according to the present feeding level and nutritional requirements. Besides a response in the rate of food uptake or *GET*, the most effective control mechanism should be in a regulation of digestive enzyme activities. This is possible on either a genetic or a physiological level.

Since enzyme synthesis, in general, is under direct genetic control, regulation can occur as an activation or repression of genes, acting in three different ways (see Hochachka & Somero 1984; for recent review of environmentally mediated enzyme induction see also

Henry 2001): (1) *quantitative regulation*, adjusting enzyme concentrations; (2) *qualitative regulation*, in the species of produced enzymes; (3) a *combined regulation*, in the relative proportions of different enzyme variants (*isoenzymes*), which catalyse the same reaction but may show different catalytic characteristics. These types of regulation are very specific but generally slow processes, requiring at least several hours to become effective. Since the environmental conditions may change much faster, the genetic level of enzyme regulation plays a significant role in ontogenetic changes (namely between successive larval instars; see Jones et al. 1997b) rather than in short-term responses to variations in the quality or concentration of food.

When a faster response is required, the available enzymes can most efficiently be activated or repressed by changes in the concentration of their chemical substrate or by interactions with specific metabolites of the catalysed reaction (*"positive and negative modulators"*). Modulatory enzyme regulation occurs typically at the initial step of the catalytic reaction, i.e. at the formation of the enzyme-substrate complex. The speed of this process depends highly on the specific affinity between an enzyme and its substrate. At variable substrate concentrations, the affinity can be enhanced or depressed by modulators, allowing for an optimal speed of the catalytic reaction (Hochachka & Somero 1984). These rapid mechanisms of enzyme regulation should play an important role in decapod crustacean larvae in the field, where they are exposed to rapidly varying food sources.

5.4.2 *Individual* vs. *specific activity*

Since the activities of digestive enzymes are measured as rates of substrate degradation, we do not know whether different results reflect variations in enzyme quantities, isoenzyme composition, substrate-induced activation or repression of pre-existing enzymes, or a combination of these regulation mechanisms. This makes it sometimes difficult to distinguish between ontogenetic changes in enzyme secretion and those induced by differential feeding levels or changing nutritional requirements. As a consequence of an ontogenetic increase in body size, also the size of the digestive gland and the overall quantity of digestive enzymes secreted will increase. Thus, the *absolute activity* (expressed in *International Units*, IU, per individual) are generally correlated with total biomass in successive larval stages. Short-term substrate-induced activation or repression of already existing enzymes, by contrast, may cause independent or inversely related variations in the individual enzymatic activities and biomass.

In order to make enzyme activities directly comparable among differently sized stages or species, *biomass-specific activities* (expressed in IU per unit biomass) are commonly given in the literature. In merely ontogenetic, genetically controlled changes of total enzyme secretion, these values should theoretically change only little, whereas great variations may be expected as a result of fast adaptive responses to variable feeding conditions. Thus, it is generally assumed that different mass-specific digestive enzyme activities reflect differences in feeding habits, namely among carnivorous, herbivorous, and omnivorous larvae (section 5.4.4).

In most publications, specific enzyme activities are given in relation to the total protein content, in others as fresh or dry mass-specific values. When dry mass (W) is used as a reference base, problems may arise due to differential ash contents of larval biomass. Since the inorganic fraction varies greatly among species, larval instars, and even within individual molting cycles (cf. section 7.1.2), different mass-specific activity values may reflect taxonomic or ontogenetic differences in biomass composition rather than those in

the digestive intensity of the responsible organs and tissues. In the semibenthic, heavily sclerotisized instar IV of the European lobster (*Homarus gammarus*), for instance, extremely low *W*-specific trypsin activities were measured, although the individual enzyme activity had increased (Kumlu & Jones 1997). Most probably, this was primarily a consequence of a dramatically increasing mineral content rather than a change in digestive physiology.

Such problems, in addition to those in the statistical evaluation of relative data in general, have recently evoked a far-reaching criticism of normalization techniques such as the use of size-specific values (see Packard et al. 1999). Some of these problems can be amended using the ash-free dry mass, *AFW*, rather than total *W*, excluding variation in the inorganic fraction as a potential source of error. Since *AFW* contains variable amounts of enzymatically inert materials such as fat deposits, protein should be a better reference base for enzyme activities. Within this biomass fraction, however, the proportions of enzymes, muscles, nervous tissues, and structural proteins may vary significantly among stages or species, so that similar artifacts can still occur. As an example of this effect, we may compare changes recorded in the individual and protein-specific trypsin activities of zoea I spider crab (*Hyas araneus*) larvae fed carnivorously or herbivorously, respectively (Harms et al. 1991). When exclusively diatoms (*Biddulphia sinensis*) were given as food, the proteolytic activity per individual decreased by about one half in comparison to *Artemia*-fed zoeae; the protein-specific activity, by contrast, was about 30% higher in diatom-fed larvae. The cause of this discrepancy was in differential growth rates; total body protein (the reference base) increased in herbivorously fed larvae by only 22%, but by 178% in the *Artemia*-fed group.

In contrast to total body protein, the protein content of the major digestive organ (in crustaceans usually the hepatopancreas) should thus be a suitable reference base for specific activity values. Unfortunately, however, this is impractical in larval stages. In conclusion, it seems to be impossible to find fully comparable units of enzyme activity measured in whole-body samples of decapod crustacean larvae.

5.4.3 *The major digestive enzymes of larval decapods*

Numerous hydrolytic digestive enzymes (proteases, lipases, carbohydrases, chitinases) have been identified and characterized in adult crustaceans (Vonk 1960), while much less is known about their occurrence in larval stages. The first paper dealing with the digestive enzymes of larval decapods was, to my knowledge, published only in 1973, describing ontogenetic changes in the activities of amylase and an unspecified protease in the caridean shrimp *Palaemon serratus* (van Wormhoud 1973). Later, comparative data have become available for larvae of various species of caridean and penaeid shrimps, brachyuran crabs, and clawed lobsters (for recent review, see Jones et al. 1997a, b; Sheen & Huang 1998, Lemos et al. 1999, 2000).

These studies have consistently shown that larval decapods have, compared with adult crustaceans, simple digestive systems, generally reliant on a high activity level of relatively few digestive enzymes (Lovett & Felder 1990a, b, c, Jones et al. 1997a, b). Some of these hydrolytic enzymes appear already during embryonic development, i.e. before first food uptake (Li et al. 1995, Shaojing et al. 1995). As a possible complementary mechanism of food digestion in decapod larvae, a participation of exogenous enzymes (originating from prey organisms) has been proposed (Lovett & Felder 1990a, b). However, this was later found to be insignificant (Jones et al. 1993, Kamarudin et al. 1994). Possibly,

also enzymes produced by endosymbiontic microorganisms may assist in digestion (see Harris 1993), but this has not been investigated in larval stages.

Among the digestive enzymes studied in larval decapods, trypsin-like proteases have received particularly great attention. Consistent with most of the literature, these enzymes will in the following sections briefly be referred to as "trypsin", although they are not identical with vertebrate proteases. This type of enzymes is responsible for up to about 60% of total proteolysis in the hepatopancreas of adult penaeid prawns (Galgani et al. 1984), and it appears to be the dominant digestive enzyme also in larval decapods (MacDonald et al. 1989, Lovett & Felder 1990a, Jones et al. 1997a). Among the various decapod taxa, the highest trypsin levels have been observed in the herbivorous protozoeae of penaeid prawns and in early brachyuran crab zoeae, while nephropid lobster and caridean shrimp larvae revealed far lower protease activities (Jones et al. 1997b).

As in several holoplanktonic crustaceans, the carbohydrase α-amylase has commonly been measured also in studies of the digestive physiology of decapod larvae. Surprisingly high activities were observed, although the substrate of this enzyme (starch) hardly occurs in potential food organisms such as diatoms and most zooplankton (Gaudy & Boucher 1983). It has been speculated that amylase production in decapod larvae might represent a phylogenetic relic from herbivorous ancestor species (Hirche & Anger 1987a). In carnivorously fed zoeae of the spider crab *Hyas araneus*, an almost parallel increase was observed in the activities of amylase and trypsin, suggesting that these enzymes could be activated and repressed by the same factor (Hirche & Anger 1987a). However, an equally increasing activity could also simply reflect a proportionally constant enzyme production in the growing hepatopancreas. Shifts in the trypsin:amylase ratio occurring during the megalopa stage, especially under exposure to nutritional stress, indicate that these enzymes may, in principle, be regulated independently (Harms et al. 1991). Changes in this activity ratio were observed also in the larvae of other species (Fang & Lee 1992, Rodríguez et al. 1994, Jones et al. 1997b), suggesting that amylase has a function in decapod larvae, in spite of the scarcity of its substrate.

A disproportionate increase in the activitiy of amylase was frequently observed during herbivorous feeding. Since planktonic algae contain, in general, less protein but more carbohydrates than zooplankton, this response may be explained as a co-regulation of amylase with another carbohydrase. Among these, laminarinase has been considered as a candidate (Meyer 1992). This enzyme digests chrysolaminarin, the principal storage product of most phytoplankton including diatoms (Haug & Myklestad 1973). In shore crab (*Carcinus maenas*) larvae, its activity showed a significant correlation with that of amylase (Meyer 1992). Also in this crab species, the amylase activity was surprisingly high, independent of substrate availability; on average, it was about four to eight times higher than the laminarinase activity.

In penaeid shrimp larvae, also activities of acid phosphatase, carboxypeptidase, and a non-specified esterase have been demonstrated, besides amylase and trypsin, while pepsin and lipase activities could not be detected (Lovett & Felder 1990a, b, Kamarudin et al. 1994). In stage I lobster larvae, in contrast, lipase was also found and characterized (Biesiot & Capuzzo 1990).

5.4.4 *Trophic position*

The provision of an organism with digestive enzymes is generally believed to be related to its phylogenetic position (Kozlovskaya & Vaskovsaky 1970, Kristensen 1972). However,

quantitative studies in closely related taxonomic groups also suggested differences associated with their feeding habits, i.e. trophic position. In marine invertebrates, high proteolytic activities accompanied by low activities of carbohydrases have often been attributed to a primarily carnivorous mode of feeding, whereas an inverse relation was interpreted as an indication of herbivorous or omnivorous nutrition (e.g. Brun & Wojtowitz 1976). This seems to be corroborated by low protease and relatively high carbohydrase activities in phytoplankton-fed crab larvae (*Hyas araneus*, *Carcinus maenas*; Harms et al. 1991, 1994).

In most recent studies of the digestive physiology of other larval decapods, however, rather the opposite pattern has been observed. In penaeid shrimp larvae, for instance, high proteolytic activities occurred during herbivorous feeding (i.e. especially during the protozoeal stages), while low and intermediate levels were measured with carnivorous and mixed diets, respectively (Jones et al. 1993, Le Vay et al. 1993, Rodríguez et al. 1994, Kumlu & Jones 1995b). High proteolytic activity was observed also in herbivorous copepods (Harris et al. 1986). Likewise, high weight-specific tryptic activities were found in herbivorous copepods and in omnivorous crab larvae as compared to predominantly carnivorous lobster larvae (Kumlu & Jones 1997). In a recent review and interspecific comparison of trypsin activity in planktonic crustaceans (including various developmental stages of penaeid and caridean shrimps, nephropid lobsters, brachyuran crabs, as well as copepods and *Artemia* metanauplii), Jones et al. (1997b) demonstrated a consistent positive relationship between trypsin activity and the degree of herbivory (Fig. 5.6). Additionally, however, the mass specific trypsin activity is controlled also by differential body size, as large larvae tend to show a lower proportion of digestive activity in relation to other tissues (e.g. hepatopancreas *vs.* muscles).

According to Jones et al. (1997b), this pattern indicates that high proteolytic activity occurs as a response to low-protein food sources such as phytoplankton, maximizing the assimilation of scarce nutrients. This would be important in herbivorous larvae such as penaeid protozoeae, because they show a much shorter *GET* than omnivorous and carnivorous larvae. In late developmental stages which are better capable of regulating the activities of digestive enzymes, measurements of tryptic activity should thus provide an assay for diet digestibility (Jones et al. 1997b).

Despite these plausible relationships, interspecific variation is often difficult to interpret, as it may reflect the phylogenetic rather than trophic position, or differential body size. Moreover, the reference base of comparison (enzyme activities per individual or per unit of dry mass, protein, etc.) requires further standardization.

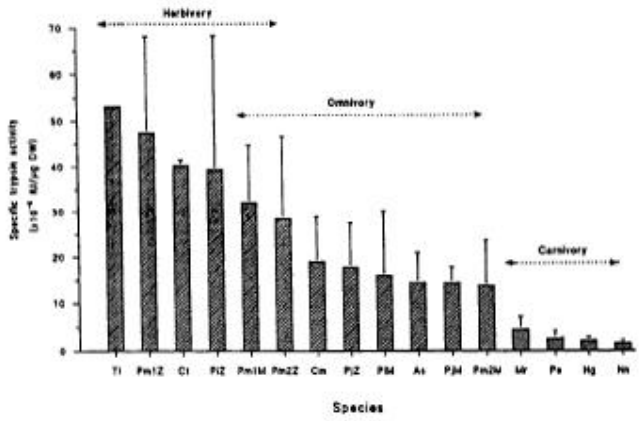


Figure 5.6. Biomass-specific trypsin activities (x10^{-5} IU per µg W; mean ± SD) in different decapod larvae (D), calanoid copepods (C), and brine shrimp (B); species: Tl, *Temora longicornis* (C); Pm1Z, *Penaeus monodon*, protozoea I-mysis I (D); Ct, *Centropages typicus* (C); PiZ, *Fenneropenaeus indicus*, protozoea I-mysis I (D); Pm1M, *Penaeus monodon*, mysis II-"postlarva" I (D); Pm2Z *Penaeus monodon*, protozoea I-III (D); Cm: *Carcinus maenas*, zoea I-megalopa (D); PjZ, *Marsupenaeus japonicus*, protozoea I-mysis I (D); PiM, *Fenneropenaeus indicus*, mysis II-"postlarva" I (D); As: *Artemia salina* (B); PjM, *Marsupenaeus japonicus*, mysis II- "postlarva" I (D); Pm2M, *Penaeus monodon*, mysis I-III (D); Mr, *Macrobrachium rosenbergii*, zoea I-instar XI (D); Pe, *Palaemon elegans*, zoea I-instar IX (D); Hg, *Homarus gammarus*, mysis I-instar IV (D); Nn, *Nephrops norvegicus*, mysis I-III (D) (from Jones et al. 1997b, with permission from Elsevier, Oxford, UK).

5.4.5 *Ontogeny of digestive capacity and nutritional requirements*

Most studies of digestive enzyme activities in decapod crustacean larvae have considered gross ontogenetic changes among successive stages, widely ignoring variations within the individual molting cycles. In general, the average activities per individual (sometimes also biomass-specific values) were found to increase during larval development, reflecting an increasing size and functionality of the hepatopancreas. Abrupt changes were sometimes observed between particular instars, varying among species and enzymes studied.

Particularly high biomass-specific activities of digestive enzymes were observed in the protozoeal stages of penaeid prawns (Rodríguez et al. 1994, Kumlu & Jones 1995b, 1997; Sheen & Huang 1998, Lemos et al. 1999, 2000). These early larvae eat primarily or exclusively phytoplankton (in contrast to the subsequent mysis stages which are omnivorous or predominantly carnivorous), growing generally well with algal diet alone. This suggests a greater capability for conversion of phytoplankton biomass as compared with the mysis stages and most other larval decapods, which are generally more carnivorous. The physiological basis of this capability is a particularly high activity of digestive enzymes, primarily trypsin, probably due to the presence of anterior midgut caeca in these stages. These traits have been interpreted as special adaptations to a low-energy type of food (Kumlu & Jones 1995b, 1997).

In experimental studies of feeding and digestion in the larvae of higher Decapoda (Pleocyemata), the type of food is usually not changed during the course of development. An increase in the activity of digestive enzymes is therefore generally interpreted as an indication of ontogenetic progress in the development of the alimentary system, namely in the hepatopancreas. This should explain why early zoeal stages of caridean shrimps, which have a smaller hepatopancreas and lower digestive enzyme activities than the late stages, were found to be particularly dependent on high-energy food sources like *Artemia* nauplii (Kumlu & Jones 1995a).

In contrast to these observations in shrimps, no increasing capability of phytoplankton utilization could be detected in the late larval stages of brachyuran crabs (*Hyas araneus*, *Carcinus maenas*; Harms et al. 1991, 1994). When these were fed with diatoms (after previous rearing with *Artemia*), they showed a similar reduction in growth, survival, and digestive enzyme activities per larva as the earlier stages. The mass-specific values showed inconsistent trends, depending on the proportional change in absolute enzyme activities and larval biomass, respectively. Thus, these crab larvae were apparently unable to enhance their digestive enzyme activities under poor feeding conditions to maximize the utilization of limited nutrients, which suggests a very limited capability of enzyme regulation.

The following example shows that differential production or activation of enzymes is not the only control mechanism in the conversion of food. In the larvae of two caridean shrimp species, *Palaemon elegans* and *Macrobrachium rosenbergii*, a gradual increase in tryptic activity (both per individual and in relation to biomass) was observed from hatching to an intermediate larval stage, but this was followed by a decrease throughout the later instars (Kumlu & Jones 1995a). The downregulation of enzyme activities in later stages, notwithstanding the continued development and growth of the hepatopancreas, was interpreted as an adaptation to an increasing efficiency in the uptake of large, high-energy prey (*Artemia*). Interestingly, the decrease in enzyme activity was counterbalanced by an increase in gut evacuation time (*GET*). Food conversion and growth could thus remain constantly high in the late larval stages, because food materials were exposed for a longer period to the action of digestive enzymes, compensating for their reduced activity. A maximum activity of digestive enzymes in an intermediate larval instar was observed also in several penaeid species (Galgani & Benyamin 1985, Kumlu et al. 1992, Kamarudin et al. 1994, Rodríguez et al. 1994). It should thus be interesting to ascertain in future comparative studies, if a combination of prolonged *GET* and downregulated enzyme activities represents a general pattern in the regulation of food conversion in late penaeid and caridean shrimp larvae.

Molt-cycle related changes in digestive enzyme activities of larval decapods were first measured in the spider crab *Hyas araneus* (Hirche & Anger 1987a). When *Artemia* nauplii were exclusively given as food, the absolute (per individual) activities of amylase and trypsin increased gradually throughout zoeal development, with consistently higher values in trypsin. Similarly, the activities of amylase and an unspecified protease increased gradually during the mysis I stage of *Homarus americanus*, regardless whether the larvae were fed or not (Biesiot & McDowell Capuzzo 1990). These patterns appear to reflect a gradual increase in the size and enzyme production of the hepatopancreas, independent of variation in the feeding conditions.

In *Hyas araneus*, the digestive enzyme activities increased from hatching and reached a maximum in late postmolt or early intermolt of the megalopa molting cycle, thereafter

they decreased. The pattern of decreasing enzyme activities in a late stage of development resembles that observed in shrimp larvae. However, this was probably not compensated by an increasing *GET*, as the megalopa showed a premolt decrease also in its ingestion rate (see Fig. 5.5) and in biomass (see section 6.2.3). Similar molt-cycle related growth patterns as in the megalopa were observed also in juvenile spider crabs (Anger et al. 1992), suggesting that the megalopa approaches or attains the adult type of regulation in feeding, digestive activity, and growth.

5.4.6 *Putative relationships with feeding level and growth*

In studies of physiological traits in decapod larvae and other zooplankton, varying activities of digestive enzymes have frequently been compared with variations in food concentration and feeding rates, without finding universal relationships. In shrimp and crab larvae exposed to conditions of starvation, a decrease in digestive enzyme activities was generally observed (Harms et al. 1991, 1994, Rodríguez et al. 1994, Kumlu & Jones 1995a). At suboptimal feeding levels, e.g. with phytoplankton given as a sole diet to carnivorous or omnivorous larvae, the digestive enzyme activities were in some cases enhanced (maximizing the conversion of scarce nutrients), but reduced in others.

In spite of inconsistent results, the available data may allow the proposal of a conceptual model of possible interactions among food concentration, ingestion rate, survival, growth, and digestive enzyme activities (Fig. 5.7). The term food "concentration" is not restricted to the density of suspended particles, but may translate also to differential food quality (e.g. the dietary protein level of phytoplankton *vs.* zooplankton). This model attempts to explain why positive correlations between feeding rates and enzyme activities were observed in some studies, but negative or no relationships in others (for references and discussion see Harms et al. 1991). The following nutritional levels may be distinguished in Figure 5.7:

- At extremely low food densities (concentration range [A]), particle feeders may not even begin to capture and ingest food; there seems to be a species-specific lower threshold concentration for the initiation of a feeding response (Strathmann 1987). Survival of planktotrophic larvae is impossible under such conditions (starvation), and digestive enzymes show a minimum activity. At slightly higher concentrations [B], some food will be ingested, but this low feeding level is quantitatively insufficient to allow for growth; some prolonged survival (compared with unfed individuals) may become possible though. Within the concentration range [A]-[B], the activities of digestive enzymes remain low, without a measurable response to small variations in food concentration or ingestion; hence there is no correlation between enzyme activities and either ingestion, growth, or survival.
- Above a hypothetical threshold concentration, the energy of absorbed materials exceeds that of the metabolic losses, and hence, allows for tissue growth. Over a certain range [C], both the amounts ingested and the activities of digestive enzymes should increase with food density (positive correlation). This implyies that both ingestion and growth are food-limited, and digestive enzyme activities are regulated according to the availability of substrate. If this assumption is correct, the conversion of increasing amounts of ingested food is guaranteed by enhanced secretion or activation of enzymes, while malnutrition should, at this level of food density, induce a reduction of enzyme activity. Most data from brachyuran crab larvae reared on different diets fit into this scheme. Under food limitation, gut evacuation time (*GET*) should remain

maximum, and food particles may be recycled from the intestine back into the hepatopancreas and (where present) the anterior midgut caeca (see Lovett & Felder 1990c).

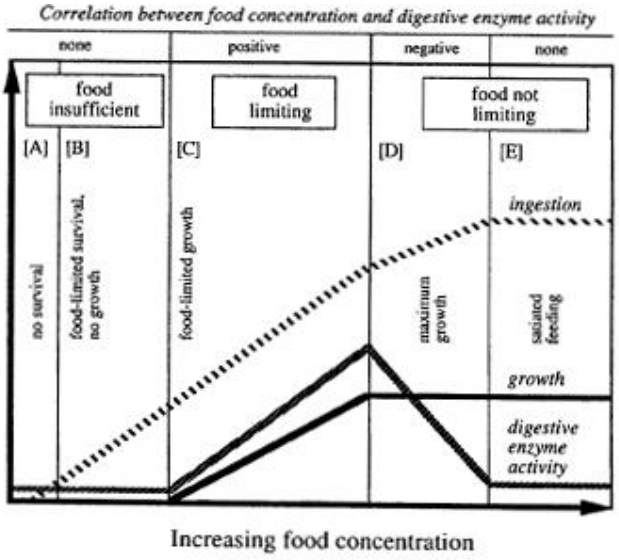


Figure 5.7. Conceptual model of presumable relationships between feeding level (food concentration), ingestion rate, growth, survival, and digestive enzymes activities (for detailed explanation, see text; after data from Harms et al. 1991).

- The rate of ingestion continues to increase when food densities become higher than necessary (range [D]). Under these conditions, excess quantities of available substrate may induce a reduction in the activities of digestive enzymes. In consequence, the absorption efficiency is decreased, and assimilation and growth, which have reached genetically set maxima, remain constant. At such high feeding levels, the actvities of hydrolytic enzymes should thus be negatively correlated with food density. This pattern has frequently been observed in the tryptic activity of penaeid and caridean shrimp larvae (Jones et al. 1997b). As an additional regulation mechanism, *GET* may decrease with further increasing food availability.
- When the food concentration exceeds the level of maximally possible ingestion (range [E]), the rates of food uptake and growth should remain constantly high, while the digestive enzyme activities (and possibly, *GET*) should reach a minimum. When "superfluous feeding" occurs under conditions of high food density, as it has been observed in copepods and other zooplankton (Conover 1966), digestion is poor or prey

may pass alive through the gut. Thus, there should be no correlation between enzyme activities, food density, or ingestion rate at such high feeding levels.

Although this conceptual model remains largely speculative, it can be tested experimentally and may thus stimulate further research on the nutritional physiology of decapod larvae and other zooplankton.

6 GROWTH

Growth can be measured as a change in body size or weight during a defined period, or as the time required to reach a determined size or developmental stage. The characteristics of molting and growth in the Crustacea have been described in detail for juvenile and adult life-cycle stages (e.g. Kurata 1962, Hartnoll 1982, 1985, Botsford 1985, Chang 1995), while much less is known about larval growth patterns (Rice 1968, Gore 1985, Anger 1991a, 1998). As another limitation to our knowledge, most studies of larval development and growth were carried out in the laboratory under constant and, presumably, close-to-optimum conditions of nutrition, temperature and salinity, while quantitative data of larval biomass in the field are relatively scarce (see Nichols & Lawton 1979, Lindley 1988, Paul et al. 1990, Harms et al. 1994, Juinio & Cobb 1994, Lindley et al. 1994, Anger 1995c, Anger & Schultze 1995, Ouellet et al. 1995, Welch & Epifanio 1995). Moreover, most publications deal with economically important decapods such as prawns, lobsters, or large crab species, while other taxa have received less attention. More comparative data from field and laboratory research, and from more species, are thus necessary to enhance the general understanding and predictability of larval growth in decapod crustaceans.

In this chapter, I will first review the most commonly used measures of larval growth and describe typical patterns of change in body size and biomass during development under constant, favourable rearing conditions in the laboratory. One may expect that these patterns represent developmental changes in maximum growth, which is reached only under physically and nutritionally optimized conditions. However, data from field studies show that natural growth rates may sometimes exceed those obtained in the laboratory (e.g. Knight 1968, Nichols & Lawton 1979, Ebert et al. 1983, Harms et al. 1994, James-Pirri & Cobb 1997, González-Gordillo & Rodríguez 2000). This implies that the experimentally defined maximum must occasionally be corrected upwards. The lower end of the relative scale, over which changes in larval biomass are theoretically possible, is defined by losses measured in planktotrophic larvae deprived of food, or in larvae with a fully lecithotrophic (nonfeeeding) type of development. We may thus expect that intermediate levels of growth are most common in nature, where nutritional and other environmental limitations occur. Examples of depressed growth under suboptimal conditions are shown in subsequent sections of this chapter.

Occasionally larger body size in field-caught larvae may be caused by selective mortality of smaller individuals, either directly as a consequence of pysiological weakness, or indirectly due to greater vulnerability to predation. Also, unfavourable conditions may occur in laboratory cultures, e.g. high larval density, poor or variable water quality, wall effects in rearing containers etc., and the monotonous laboratory food may be qualitatively inferior to mixed natural food sources, potentially reducing the otherwise positive effects of *ad libitum* concentrations that are normally provided in cultivation experiments. However, the scarcity of comparative larval growth data from the field does not allow for generalization. If future studies show that higher growth rates in the natural plankton represent the rule rather than an exception, then growth observed in laboratory cultures should be considered as an estimate of an average rather than maximum possible growth.

In spite of doubts related to the comparability of absolute growth data from artificial rearing and field collections, respectively, laboratory experiments remain an essential tool

to observe and quantify basic biological priciples and ecological response patterns. These are the primary subject of this chapter. Finally, I will discuss here possible mechanisms of intrinsic growth control, attempts of point estimates of growth rate in the field, and the production and loss of exuviae

6.1 *Age determination*

Estimates of growth rate require a knowledge of absolute age or time elapsed in relation to a defined life-history event. Hence, most available data originate from laboratory studies where the times of hatching and subsequent molts are known. Two decades ago, it seemed that a simple chemical method would allow for age determination also in the field. In various animals including vertebrates and invertebrates, an accumulation of *"age pigments"* was described, collectively named *"lipofuscin"* (for references of older literature, see Hirche & Anger 1987b). These pigments were identified as peroxidation products of the lipid metabolism which cannot be digested in the lysosomes, and hence, should theoretically be accumulated in a time-dependent manner (Fletcher et al. 1973, Leibovitz & Siegel 1980). Ettershank (1983, 1984) quantified, for the first time in field-caught crustaceans, the putative lipofuscin in Antarctic krill. The first study of solvent-extractable age pigments in laboratory-reared decapod larvae (*Hyas araneus*) was that by Hirche & Anger (1987b). However, the concentrations of the soluble compounds of interest were found to be correlated with larval biomass rather than age.

Subsequently, several comparative investigations of age pigments in crustaceans and other poikilotherms (Sheehy & Ettershank 1988, Sheehy & Roberts 1991, Sheehy 1996) showed that the solvent-extractable autofluorescence measured in previous studies was in fact not identical with lipofuscin age pigment. True lipofuscin accumulates in the central nervous system, where it can be detected cytologically. Extensive investigations on the quantity of morphologically identifyable lipofuscin in the brains and eyestalks of crustaceans such as crayfish (e.g. Sheehy 1990, Belchier et al. 1998), prawns (Sheehy et al. 1995), crabs (Sheehy 2000), as well as clawed and spiny lobsters (Sheehy et al. 1996, 1998, 1999) indicate that the pigment is in general a good measure of the chronological age. So far, however, the applicability of this method has not been tested in larval crustaceans with known age.

6.2 *Maximum growth under constant conditions: measures, patterns and models*

This section describes patterns of growth in planktotrophic larvae reared under constant, physically favourable, and nutritionally unlimited (*ad libitum*) conditions. Since variations in extrinsic factors are experimentally excluded, changes in growth rate should reflect intrinsic processes, i.e. development. These patterns can be described with regression equations linking the number of molts, body size, biomass, and time. With such empirical models, it is possible to predict the size or biomass in successive instars, or time-dependent changes within a molting cycle. Indices of growth derived from these models can be applied in ecology and aquaculture to assess and compare the quality of environmental conditions.

6.2.1 *Molting frequency*

When arthropod growth is measured in terms of size increments, a stepwise pattern is obtained, reflecting the sudden increase in body size immediately after each ecdysis. In a series of instars, growth can thus be described as a molting frequency, f_m. This is defined as average number of instars or stages (S) passed during a given time (t), while the reciprocal value of f_m represents the average duration of development (D) per instar:

$$f_m = \frac{S}{t} \tag{6.1}$$

$$D = \frac{1}{f_m} = \frac{t}{S} \tag{6.2}$$

In most larval and juvenile crustaceans reared under constant conditions, D increases in successive instars with body size (Kurata 1962, Hartnoll 1982). Where D remains constant (*"isochronal development"*; Miller et al. 1977), S is a linear function of the time of development, t:

$$S = a \cdot t + b \tag{6.3}$$

In this and the following equations, the constants a and b are fitted parameters defining the slope of the regression line and the intercept with the Y-axis, respectively.

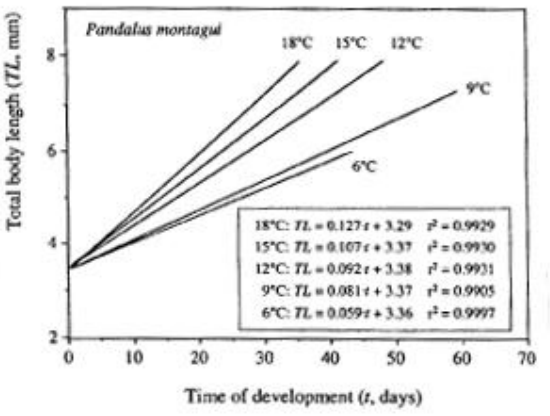


Figure 6.1. Linear relationship (Eq. 6.3) between the number of stages (S) and the time of development (t) in shrimp larvae, *Pandalus montagui*, reared at different constant temperatures; r^2: coefficient of determination for least-square linear regression equations) (redrawn after data from Schultze & Anger 1997).

This simple linear pattern appears to be common in caridean shrimps (e.g. Rothlisberg 1979, Fincham 1985 and earlier papers cited therein, Criales & Anger 1986, Willführ-Nast et al. 1993, Schultze & Anger 1997), but has been observed also in the zoeal stages of some anomuran and brachyuran crabs (Fagetti & Campodónico 1971, Minagawa 1990a). As an example, Figure 6.1 shows the linear increase in the number of larval stages in Aesop shrimp, *Pandalus montagui*. The slope of the regression line increases with temperature, reflecting the increase in f_m (see below, Equations 6.13-6.15). On the other hand, poor nutrition, unfavourable salinity, or other adverse conditions, tend to lengthen the average duration of successive stages. Thus, the regression coefficient (a) in Equation 6.3 may be used as a comparative index of molting frequency.

6.2.2 *Size increment*

In taxa with a gradual type of morphological development, the increase in larval body size (length, L) may be described as a linear function of the number of consecutive stages, S:

$$L = a \cdot S + b \tag{6.4}$$

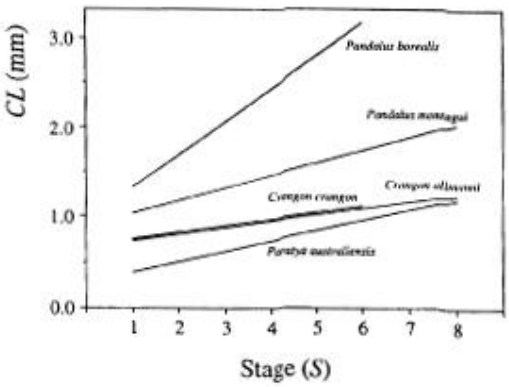


Figure 6.2. Linear relationship (Eq. 6.4) between body size (carapace length, *CL*) and the number of stages (*S*) in caridean shrimp larvae; regression equations, coefficients of determination (r^2); redrawn after data from:

Crangon allmanni: $CL = 0.072 \cdot S + 0.65$ [$r^2 = 0.993$] (Criales & Anger 1986)
Crangon crangon: $CL = 0.073 \cdot S + 0.68$ [$r^2 = 0.986$] (Linck 1995; North Sea population)
Pandalus borealis: $CL = 0.365 \cdot S + 0.97$ [$r^2 = 0.994$] (Shumway *et al.* 1985)
Pandalus montagui: $CL = 0.144 \cdot S + 0.89$ [$r^2 = 0.990$] (Schultze & Anger 1997)
Paratya australiensis: $CL = 0.114 \cdot S + 0.28$ [$r^2 = 0.982$] (Walsh 1993; estuarine population)

Such a relationship implies a constant absolute size increment per molt, but a declining percentage increment. As practical measures of size, total body length (*TL*) or carapace length (*CL*) have been used most commonly. In Figure 6.2, a linear increase in size is exemplified with data from several caridean shrimp species. This simple relationship holds in general throughout the zoeal and early decapodid stages, but sometimes not any longer

in late (not consistently occurring) decapodid instars and in early juveniles. These transitional stages, which are in the literature often collectively referred to as "postlarvae" (see section 2.2), show frequently longer molting cycles, smaller size increments at ecdysis, and the number of instars may vary among species, hatches, individuals within a hatch, or rearing conditions (Rothlisberg 1979, Criales & Anger 1986, Schultze & Anger 1997).

In taxa where both the instar duration and the increment between successive larval stages remain constant (Equations 6.3, 6.4), body size (L) can be described as a linear function of the time of development, t:

$$L = a \cdot t + b \tag{6.5}$$

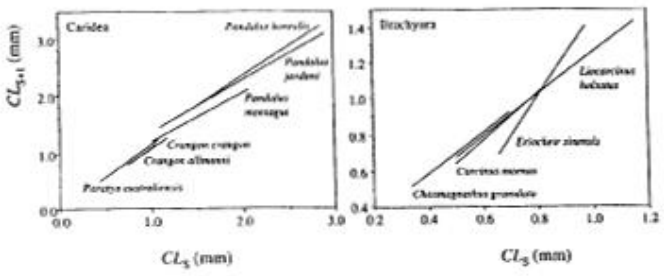


Figure 6.3. Linear relationship (Eq. 6.5) between body size (total length, *TL*) and the time of development (t) in shrimp larvae, *Pandalus montagui*, reared at five different constant temperatures; r^2: coefficients of determination for least-square regression equations (redrawn after data from Schultze & Anger 1997).

This applies, for example, to *Pandalus montagui* (Fig. 6.3). Similar patterns have been found in *P. jordani* (Rothlisberg 1979), *P. borealis* (Shumway et al. 1985), and various *Palaemon* spp. (Fincham 1985 and earlier papers; Yúfera & Rodríguez 1985a). Linear relationships between age, the number of instars, and body size may thus be typical of caridean shrimps. In some species, however, non-linear models gave a better fit of predicted and observed data. In *Macrobrachium vollenhovenii*, for instance, the time-dependent increase in body length was described as an exponential function (Willführ-Nast et al. 1993), and in spiny lobster larvae as a parabola (fitted with a third-order polynomial equation; Mikami & Greenwood 1997a). The time-dependence of larval size may be described with yet another commonly used model of growth, the von Bertalanffy equation (Bertalanffy 1957, Guerao *et. al*. 1994, Wang & Thomas 1995, Rotllant et al. 2001). However, this model contains an asymptotic term of "final" size or biomass, which may not be an appropriate parameter in the description larval growth (see Alford & Jackson 1993, Day & Taylor 1997).

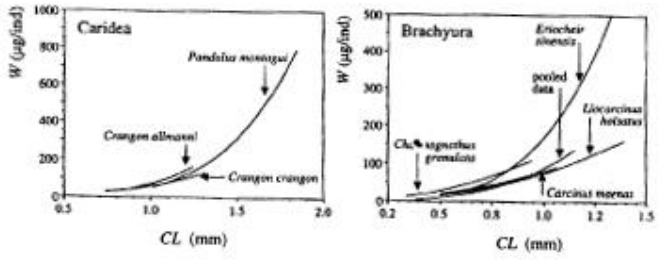


Figure 6.4. Hiatt diagrams of size increments (Eq. 6.6) in successive larval stages of caridean shrimp and brachyuran crab species: carapace length in stage S (CL_S) plotted against CL in subsequent stage (CL_{S+1}); least-square linear regression equations, r^2: coefficients of determination; redrawn after data from:

Crangon allmanni:	$CL_{S+1} = 1.057 \cdot CL_S + 0.02$	[$r^2 = 0.992$]	(Criales & Anger 1986)
Crangon crangon:	$CL_{S+1} = 1.141 \cdot CL_S - 0.05$	[$r^2 = 0.991$]	(Linck 1995)
Pandalus borealis:	$CL_{S+1} = 1.041 \cdot CL_S + 0.26$	[$r^2 = 0.970$]	(Shumway *et al.* 1985)
Pandalus jordani:	$CL_{S+1} = 0.915 \cdot CL_S + 0.44$	[$r^2 = 0.994$]	(Rothlisberg 1979)
Pandalus montagui:	$CL_{S+1} = 0.975 \cdot CL_S + 0.19$	[$r^2 = 0.921$]	(Schultze & Anger 1997)
Paratya australiensis:	$CL_{S+1} = 1.137 \cdot CL_S + 0.02$	[$r^2 = 0.994$]	(Walsh 1993)
Carcinus maenas:	$CL_{S+1} = 1.284 \cdot CL_S + 0.00$	[$r^2 = 0.996$]	(Rice & Ingle 1975a)
Liocarcinus holsatus:	$CL_{S+1} = 1.160 \cdot CL_S + 0.10$	[$r^2 = 0.962$]	(Rice & Ingle 1975b)
Chasmagnathus granulata:	$CL_{S+1} = 1.137 \cdot CL_S + 0.13$	[$r^2 = 0.976$]	(Boschi *et al.* 1967)
Eriocheir sinensis:	$CL_{S+1} = 2.208 \cdot CL_S - 0.75$	[$r^2 = 0.999$]	(Montú *et al*. 1996)

Gradual patterns of growth allow for using another simple model that has frequently been applied to juvenile and adult, but less to larval crustaceans, the Hiatt plot (Hiatt 1948). This is basically a description of average size (or biomass) increments in a series of molts. Size in an instar (L_S) is plotted against that in the subsequent instar (L_{S+1}), so that postmolt size can be predicted from premolt measurements:

$$L_{S+1} = a \cdot L_S + b \tag{6.6}$$

There has been controversial discussion about the most appropriate form of this model (linear *vs.* non-linear; see Mauchline 1976). Although this might vary among species and developmental stages, the linear version appears to describe larval size growth adequately (Kurata 1962, Reeve 1969, Rothlisberg 1979; examples shown in Fig. 6.4). As a rule, Hiatt plots should be used only where larval development consists of a fairly high number of morphologically similar instars, e.g. in species of caridean shrimps, or in raninid, portunid, and grapsid crabs.

Kurata (1962) distinguished three growth patterns based on the slope (a) of the Hiatt plot. In his terminology, all brachyuran crab species that are used in Figure 6.4 as examples of this relationship, as well as the shrimps *Paratya australiensis* and *Crangon* spp., show *"progressive geometric growth"* (arbitrarily defined by a >1.05). In this pattern, successive molt increments increase with increasing premolt size. This growth type was

most strongly pronounced in the successive zoeal stages of the Chinese mitten crab, *Eriocheir sinensis* ($a = 2.2$).

When a is close to a value of 1.0 (defined range: 0.95 to 1.05), the average growth increment remains practically constant and independent of premolt size. This type, by Kurata referred to as *"arithmetic growth"*, was found in the shrimps *Pandalus borealis* and *P. montagui*; also the larvae of *Crangon crangon* came very close to this pattern.

The smallest increments per ecdysis were recorded in the shrimp *Pandalus jordani* ($a = 0.911$ and 0.915 in field-caught and laboratory-reared larvae, respectively; Rothlisberg 1979). Thus, they belong to the third category, *"retrogressive geometric growth"* ($a < 0.95$). Since, in this growth type, the size increment in successive molts decreases with increasing premolt size, the body size of these larvae shows an asymptotic pattern when it is plotted against the stage number.

In general, the Hiatt plot may be used as a rough description of the overall patterns of size or biomass growth, with major changes in the slope (inflection points) indicating transitions between different life-history phases (e.g. larval *vs.* juvenile, or juvenile *vs.* sexually mature). A more detailed analysis of growth patterns should consider both the absolute and percentage size increments in successive developmental stages, including possible changes in the degree of variation within individual instars. In a study of larval and juvenile growth of a shrimp species, *Palaemon elegans*, Hartnoll & Dalley (1981) showed that phase transitions may be reflected by transitorily decreasing variation in instar size. In this case, the two stages immediately preceding and following metamorphosis, respectively, showed a relatively constant size, which appeared to be achieved by a negative feedback between premolt size and the percentage increment at ecdysis.

6.2.3 *Mass increment*

Biomass (*B*) can be expressed as *wet mass* or *"fresh weight"* (*FW*), *dry mass* (*W*), or *ash-free dry mass* (*AFW*); the symbol *W* is derived from "weight", which is in the literature commonly used instead of "mass". Likewise, the energy content (*E*), amounts of organically bound elements (e.g. carbon, C; nitrogen, N; hydrogen, H), proximate biochemical constituents (e.g. protein, lipid), or other quantitative measures of living matter (see chapter 7) can be used as measures of biomass. Again, its increase in a sequence of developmental stages can be described by means of a Hiatt plot. In contrast to size growth, the description of weight increments in successive molts appears to be better when a power function is applied (linearized after logarithmic transformation of both pre- and postmolt biomass data, B_S, B_{S+1}):

$$B_{S+1} = b \cdot B_S^{\,a} \tag{6.7}$$

$$\ln B_{S+1} = a \cdot \ln B_S + \ln b \tag{6.7a}$$

In fitted regressions, the parameter a is frequently close to 1.0, so that this relationship may become almost linear. As in the size increments (Fig. 6.4.), weight growth shows a great deal of interspecific variability. Among the examples shown in Figure 6.5, brachyuran crab larvae show generally larger weight increments than caridean shrimp larvae, again with the steepest increments in the zoeae of *Eriocheir sinensis*. Shrimp larvae, on the other hand, have mostly a higher initial weight, tend to pass through more stages, and reach a larger final size and biomass as compared with larval crabs.

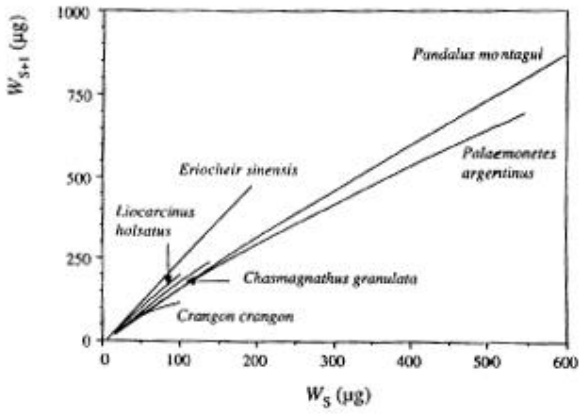


Figure 6.5. Hiatt diagrams of biomass increments (Eq. 6.7) in successive larval stages of caridean shrimp and brachyuran crab species: dry mass in stage *S* (W_S) plotted against *W* in subsequent stages (W_{S+1}); least-square regression equations, r^2: coefficients of determination; s redrawn after data from:

Pandalus montagui:	$W_{S+1} = 2.41 \cdot W_S^{0.923}$	[$r^2 = 0.994$](Schultze & Anger 1997)
Palaemonetes argentinus:	$W_{S+1} = 2.85 \cdot W_S^{0.873}$	[$r^2 = 0.978$](Anger, unpubl. data)
Crangon crangon:	$W_{S+1} = 5.59 \cdot W_S^{0.657}$	[$r^2 = 0.892$](Criales 1985)
Liocarcinus holsatus:	$W_{S+1} = 1.57 \cdot W_S^{1.044}$	[$r^2 = 0.998$](Harms 1990)
Chasmagnathus granulata:	$W_{S+1} = 2.91 \cdot W_S^{0.889}$	[$r^2 = 0.940$](Anger & Ismael 1997)
Eriocheir sinensis:	$W_{S+1} = 1.52 \cdot W_S^{1.088}$	[$r^2 = 0.986$](Mataliotaki 1991, Anger, unpubl.)

The examples compiled in Figure 6.5 show also that the patterns of interspecific variation in the weight increments of successive larval stages does not always reflect those in size increments (cf. Fig. 6.4): in the Hiatt plots of size growth, *Pandalus montagui* shows a weaker slope than *Crangon crangon* (a = 0.98 *vs.* 1.06), while the opposite is true for the comparison of weight increments (a = 0.92 *vs.* 0.66). This indicates that the relation between size and biomass varies among species, superimposed by interspecific variation in morphometric proportions.

Larval biomass, *B*, is an allometric function of body size, *L* (Kurata 1962, Reeve 1969, Hirota & Fukuda 1985, Lindley 1988). This function can be linearized by logarithmic transformation of both variables:

$$B = b \cdot L^a \tag{6.8}$$

$$\ln B = a \cdot \ln L + \ln b \tag{6.8a}$$

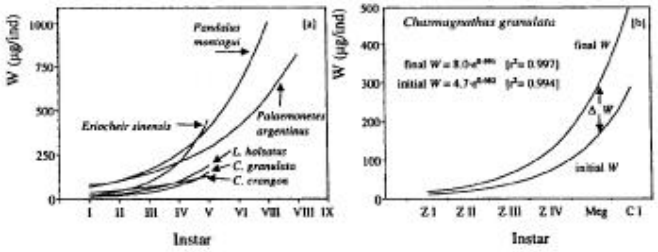


Figure 6.6. Allometric relationships (Eq. 6.8) between biomass (dry mass, *W*) and size (carapace length, *CL*) in successive larval stages of caridean shrimp and brachyuran crab species; least-square regression equations, r^2: coefficients of determination; redrawn after data from:

C. allmanni:	$W = 68.1 \cdot CL^{3.877}$	[$r^2 = 0.989$]	(Criales & Anger 1986)
C. crangon:	$W = 58.0 \cdot CL^{2.834}$	[$r^2 = 0.950$]	(Linck 1995)
P. montagui:	$W = 50.7 \cdot CL^{4.498}$	[$r^2 = 0.982$]	(Schultze & Anger 1997)
C. maenas:	$W = 79.3 \cdot CL^{2.110}$	[$r^2 = 0.999$]	(Rice & Ingle 1975a, Dawirs *et al.* 1986)
L. holsatus:	$W = 74.5 \cdot CL^{2.341}$	[$r^2 = 0.996$]	(Rice & Ingle 1975b, Harms 1990)
C. granulata:	$W = 123 \cdot CL^{2.156}$	[$r^2 = 0.976$]	(Boschi *et al.* 1967, Anger & Ismael 1997)
E. sinensis:	$W = 166 \cdot CL^{3.846}$	[$r^2 = 0.935$]	(Montú *et al.* 1996, Mataliotaki 1991)
pooled data:	$W = 88.1 \cdot CL^{3.239}$	[$r^2 = 0.982$]	(Hirota & Fukuda 1985)

Using this model, Hirota & Fukuda (1985) calculated a pooled regression of dry mass *vs.* carapace length in larvae from various crab families. When this is compared with examples of the size-weight relationship in some other brachyuran taxa, the multispecies-regression curve appears intermediate (Fig. 6.6). This comparison shows, similarly as the Hiatt plots (see above), considerable interspecific variability in the growth patterns of crab larvae. Among our examples, the zoeae of *Eriocheir sinensis* are characterized not only by especially great molting increments in both size and weight (cf. Figs. 6.4, 6.5), but also by particularly steep slopes in the allometric size-weight function. The larvae of two Portunid crab species, on the other hand, show weaker than average slopes.

Since the chemical composition of larval biomass varies relatively little among crab taxa (Anger & Harms 1990), these differences reflect an interspecific variation in the ratio of total body volume (and hence, weight) to carapace length rather than variability in biomass density. The availability of more specific regressions for single families, genera, or species should thus enhance the accuracy of conversions of larval size to biomass data, for instance in estimates of plankton production in the field (see Lindley 1988, 1998b). In caridean shrimp larvae, less variable body proportions may render such conversions more reliable than in brachyurans.

When biomass (B) is compared among successive instars, it shows an exponential increase with the number of stages, S (linearized by logarithmic transformation of B; e is the base of the natural logarithm, ln; if the decadic logarithm ($\log_{10}$) is used for linearization of the equation, e must be replaced by a constant of 10:

$$B = e^{b} \cdot e^{a \cdot S} \tag{6.9}$$

$$\ln B = b + a \cdot S \tag{6.9a}$$

This relationship, in the literature referred to as "Brook's law" (Kurata 1962), has commonly been observed in larval decapods (e.g. Nates & McKenney 2000a; for recent review, see Anger 1998). In Figure 6.7a, it is exemplified with growth data from several species of shrimps and crabs, using the postmolt dry mass (W) as a measure of B in successive larval stages.

This comparison shows that there is considerable interspecific variability in both the slopes (a) and the intercept parameters (b) of the regression lines. The height of a growth curve depends on the initial biomass in a species (with the term b as a fitted approximation of lnB in stage-I larvae) and on the molt-stage in which biomass was measured. Similar as in the Hiatt plot, parameter a may be used as an index of the average biomass increment per instar, allowing for comparisons among taxa or different rearing conditions.

For the time of development through an instar, biomass is in this function treated as if it remained constant. In contrast to size, however, B may actually change dramatically, increasing up to more than threefold during an individual molting cycle (Anger & Dawirs 1982). In Figure 6.7b, this increment is illustrated as the gap (ΔW) between the regression curves calculated separately for time-dependent changes in postmolt and premolt weight, respectively, of crab larvae (*Chasmagnathus granulata*). Hence, when this model of growth is applied to decapod larvae, it should always be specified whether initial, final, or an "average" weight is plotted against the stage number.

When growth is measured with a sufficiently high temporal resolution, the molt-cycle related patterns of change in biomass during the time of an instar can be analysed. The zoea I stage of the spider crab *Hyas araneus*, which has a long molt cycle duration, is taken here as a particularly suitable example. In Figure 6.8, the rates and patterns of change in two commonly used measures of biomass are compared: wet mass (*FW*) and dry mass (*W*).

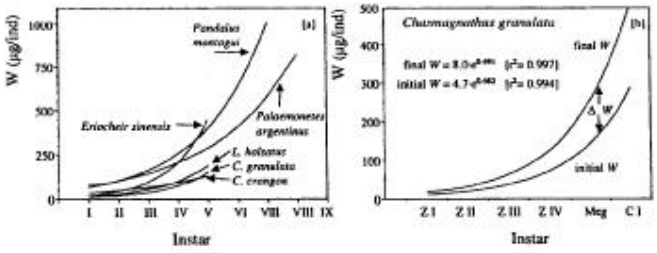


Figure 6.7. Exponential relationship (Eq. 6.9) between biomass (dry mass, *W*) and the number of successive stages (*S*); [a] initial larval *W* plotted against *S* in various caridean shrimp and brachyuran crab species; [b]: separate regressions for initial and final *W* in a crab, *Chasmagnathus granulata*; Δ*W*: mass increment in individual instars; after Anger & Ismael (1997). [a]: regression equations, r^2 (coefficients of determination), redrawn after data from:

Crangon crangon:	$W = 23.5 \cdot e^{0.341 \cdot S}$	$[r^2 = 0.917]$	(Criales & Anger 1986)
Pandalus montagui:	$W = 41.0 \cdot e^{0.458 \cdot S}$	$[r^2 = 0.994]$	(Schultze & Anger 1997)

Palaemonetes argentinus:	$W = 50.3 \cdot e^{0.350 \cdot S}$	[$r^2 = 0.975$]	(Anger unpubl. data)
Liocarcinus holsatus:	$W = 8.5 \cdot e^{0.615 \cdot S}$	[$r^2 = 0.999$]	(Harms 1990)
Chasmagnathus granulata:	$W = 4.6 \cdot e^{0.691 \cdot S}$	[$r^2 = 0.990$]	(Anger & Ismael 1997)
Eriocheir sinensis:	$W = 9.3 \cdot e^{0.776 \cdot S}$	[$r^2 = 0.994$]	(Mataliotaki 1991)

Under constant laboratory conditions of *ad libitum* feeding, zoeal *FW* increased in *Hyas araneus* by about 25% from hatching to the end of the first instar. However, when *W* or the organic carbon content (C) per individual is taken as a measure of biomass, much higher growth increments are obtained. *W* increased to more than double of its initial value, and the C fraction by a factor of about three (i.e. with an increment of ca. 200%). Thus, changes in *W* reflect those in organic biomass far better than *FW*. This difference in the quality of *FW* and *W* as measures of living matter is shown also when we compare changes during conditions of continual feeding or starvation, respectively. While *W* decreased throughout most of the time of food deprivation (Fig. 6.8b), *FW* continued to increase with a similar pattern as in fed larvae, although at a lower rate (Fig. 6.8a). Characteristics of the various measures of biomass will be discussed in more detail in the context with the chemical composition of the larval body (chapter 7).

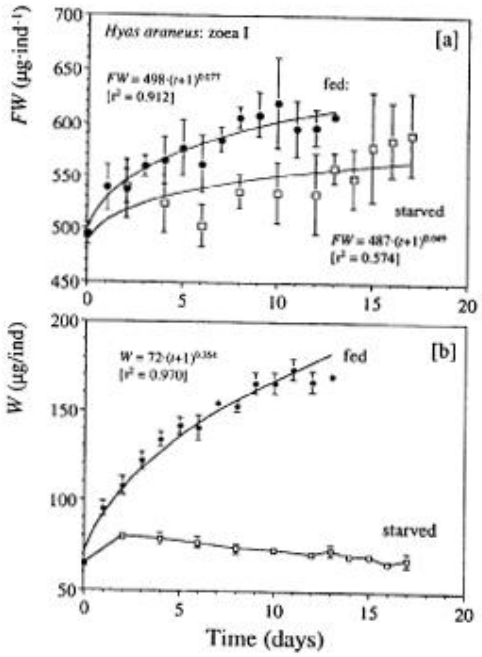


Figure 6.8. Patterns of change in [a] wet mass (*FW*) and [b] dry mass (*W*) of continually fed or starved zoea I larvae of a spider crab, *Hyas araneus*; mean ± SD; regression equations (Eq. 6.10) describing *FW* or *W* (for fed larvae only) as non-linear functions of the time of development, *t*; r^2: coefficient of determination (redrawn after data from Anger 1998).

Regardless whether we quantify biomass in terms of *FW*, *W*, or C, the pattern of growth within a molting cycle appears under constant and favourable feeding conditions normally as a parabola-shaped curve (Fig. 6.8). Most of the increase in *B* occurs during the first half of the molting cycle, i.e. in postmolt and intermolt (molt-stages *A*-*C*), levelling off through premolt. This pattern can be described with a power function linking biomass (*B*) with the time (*t*) of development (after transformation of *t* to (*t*+1) to eliminate zero values; Anger & Dawirs 1982):

$$B = b\cdot(t+1)^a = B_0\cdot(t+1)^a \tag{6.10}$$

In this model, the intercept parameter (*b*) may be re-termed B_0, as it is a fitted estimate of the initial ($t = 0$) value of *B* (usually given in µg or mg per individual). This equation can be linearized by logarithmic transformation of both the dependent and independent variable:

$$\ln B = \ln B_0 + a\cdot\ln (t+1) \tag{6.10a}$$

When molt-cycle related growth is compared among species or stages with different body size, it is convenient to express the increase in *B* as a fraction or a percentage of the initial biomass value, B_0. Hence, Equation 6.10 must be divided by B_0 to obtain relative biomass, B_r (and multiplied with a factor of 100 to obtain percentage values):

$$B_r = (t+1)^a\cdot 100 \tag{6.10b}$$

In Figure 6.9, absolute and relative growth patterns are compared among the three larval stages of the Norway lobster, *Nephrops norvegicus*, with biomass expressed in µg carbon, *C*, per individual and in % of initial (early postmolt) biomass, B_0, respectively. In the absolute values, all larval instars show similar patterns of *C* accumulation (Fig. 6.9a). The growth curves appear to parallel each other, with successively higher B_0 values (196, 372, and 650 µg *C*). However, the slopes of these regression curves show actually the opposite trend, decreasing from 0.334 (mysis I) to 0.187 (mysis III). This can be seen clearly when *C* is given in % of B_0 (Fig. 6.9b). This comparison shows also that the mysis III stage, due to its longer molting cycle duration, may eventually reach similar final B_r values as the preceding stage, in spite of a weaker slope.

Daily (instantaneous) rates of growth within a larval stage are obtained by differentiation of Equation 6.10:

$$dB/dt = a\cdot B_0\cdot(t+1)^{(a-1)} \tag{6.10c}$$

dB/dt is highly dependent on initial biomass, B_0. Large larval forms, for instance the mysis stages of lobsters, may reach far higher daily biomass increments per individual than small ones, e.g. portunid crab zoeae. For comparative purposes, it is therefore convenient to express instantaneous growth rates in weight-specific rather than absolute terms (Omori 1979). With our power function, the weight-specific rate of growth ($dB/B\cdot dt$) can be obtained by dividing Equation 6.10c by Equation 6.10, yielding a simple expression:

$$dB/B \cdot dt = \frac{a}{t+1} \tag{6.10d}$$

W-specific growth rates have the dimension of a fraction of the present larval biomass (*B*) or, when multiplied with a factor of 100, a percentage of *B* per unit of time (usually per day). According to Equation 6.10d, the fitted parameter *a* in Equation 6.10 represents an estimate of the initial (t = 0) weight-specific growth rate in a given larval instar and species.

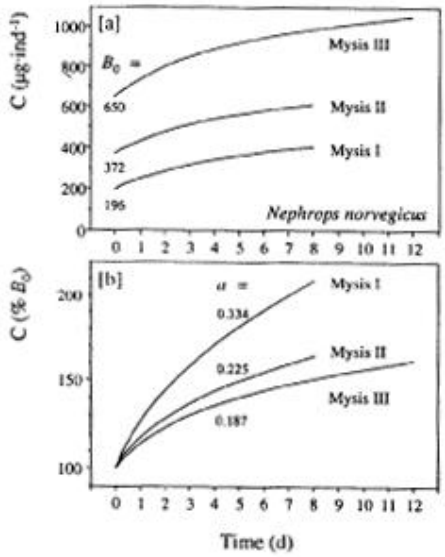


Figure 6.9. Patterns of change in carbon during the time of the molting cycle in successive larval stages (mysis I-III) of a clawed lobster, *Nephrops norvegicus*; [a] absolute C (µg/individual), [b] C as a percentage of the initial biomass value (B_0) in each stage; coefficients: *a*, slope; B_0, intercept of the fitted regression equations (Eq. 6.10) describing C as a function of the time (*t*) within each molting cycle (redrawn after data from Anger & Püschel 1986).

As an alternative to Equation 6.10, a second-order polynomial equation may be used to describe the parabola-pattern of growth during a molting cycle (Anger & Jacobi 1985, Dawirs et al. 1986, Minagawa et al. 1993):

$$B = B_0 + a \cdot t - c \cdot t^2 \tag{6.11}$$

The intercept with the Y-axis is here again a fitted estimate of the initial biomass (B_0) in an instar, while parameters *a* and *c* define the curvature of the relationship between biomass and time. In the polynomial model, the instantaneous rate of larval growth (dB/dt) decreases as a linear function of the time (*t*) of development:

$$dB/dt = a - 2 \cdot c \cdot t \tag{6.11a}$$

This expression indicates that the constant a in Equation 6.11 is a fitted estimate of the initial (t = 0) growth rate per day, while c is the slope parameter, defining the rate of change (i.e. of decrease) in the instantaneous rate of biomass growth.

The weight-specific instantaneous rate of growth, $dB/B \cdot dt$, is given as the quotient of Equations 6.11a and 6.11:

$$dB/B \cdot dt = \frac{a - 2ct}{B_0 + at - ct^2} \tag{6.11b}$$

While a power function (Equation 6.10) describes a continuous gain of biomass throughout the molting cycle, the polynomial model (Equation 6.11) predicts that B increases to a maximum and may decrease during the premolt period. This pattern has been observed especially in late zoeal stages and decapodids. When the time of maximum biomass (t_{max}) is reached, the instantaneous rate of growth (Equation 6.11a) must become zero. Hence, t_{max} can easily be estimated from the regression parameters of Equation 6.11:

$$t_{max} = \frac{a}{2c} \tag{6.11c}$$

When this quotient is higher than the duration, D, of a given molting cycle this model predicts, like the power function (Equation 6.10), a continuous gain but no final decrease in biomass. Thus, the polynomial model may be more universally applicable than Equation 6.10, although it has the disadvantage to be more complex, introducing an additional fitted parameter, c.

Regardless of which of these two models (Equations 6.10 or 6.11) is applied to describe the parabolic pattern of larval growth throughout a molting cycle, the instantaneous rates of biomass accumulation (both in absolute and weight-specific terms) tend to decrease during the time of an instar. This pattern, which was first described for the spider crab *Hyas araneus*, has consistently been observed in the larvae of various decapod taxa, and it may thus be considered as a growth rule in decapod crustacean larvae (for review, see Anger 1991a, 1998). Using again the larval stages of *H. araneus* as a typical and extensively studied example, this recurrent pattern is illustrated in a simplified graphical model (Fig. 6.10), assuming a linear decrease in daily growth rates (i.e. applying a polynomial function, Equation 6.11).

This schematic presentation indicates that the biomass-specific instantaneous growth rate, $dB/B \cdot dt$, is during a short initial phase of the molting cycle (molt-stage *A*) negative, because the soft exoskeleton does not allow for capturing and ingesting prey (see section 5.3.5). Soon after the onset of feeding (molt-stage *B*), $dB/B \cdot dt$ increases rapidly to a maximum. In the zoea I of *Hyas araneus*, biomass increments of up to ca. 40% per day were observed in this early phase of the molting cycle. Later instars, by contrast, did not reach such high maximum growth rates. In the megalopa of *H. araneus*, maximum growth did not exceed about 15% of present larval biomass per day, and a decrease in biomass (negative growth) occurred commonly throughout the second half of the molting cycle. These premolt losses may be explained by decreasing and eventually ceasing food uptake prior to ecdysis, especially before metamorphosis. Since also the exuvial losses tend to increase in successive larval stages (section 6.7), biomass-specific net growth decreases in

general in successive stages of larval development. Almost identical patterns of larval growth as in our "model species" *H. araneus*, were found also in various other decapods (Shin & Chin 1994, 1995, Anger & Ismael 1997, Anger 1998).

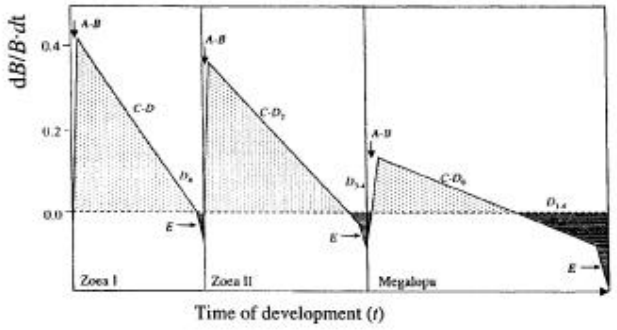


Figure 6.10. Schematic presentation of molt-cycle related changes in the weight-specific instantaneous growth rate (d*B*/*B*·dt; expressed as a fraction of larval biomass gained or lost per day) during the time of larval development in a decapod (typical example: the spider crab *Hyas araneus*; polynomial model, Eq. 6.11); *A*-*E*: stages of the molting cycle.

6.3 *Nutritional constraints: endotrophic development and food-limited growth*

All models that are shown above describe an approximation of the maximum possible biomass growth of planktotrophic larvae developing under constant, close-to optimal feeding conditions. The lower extreme in our theoretical scale is found in planktotrophic larvae living in complete absence of food (starvation) and in nonfeeding larvae (obligatory lecithotrophy). In both cases, biomass will continually decrease as a consequence of catabolic losses (endotrophy). Patterns that are transitional between the extremes of maximal feeding and complete starvation (or full lecithotrophy) occur under conditions of limited food supply and in cases of facultatively lecithotrophic development.

6.3.1 *The extreme cases: planktotrophy, starvation, full lecithotrophy*

During nonfeeding development and, in planktotrophic larvae, under conditions of complete food deprivation, biomass, *B*, has been found to decrease as an exponential function of time, *t* (Anger & Dawirs 1982, Anger 1986):

$$B = B_0 \cdot e^{-a \cdot t} \tag{6.12}$$

This relationship becomes linear when biomass data are logarithmically transformed and plotted against the time:

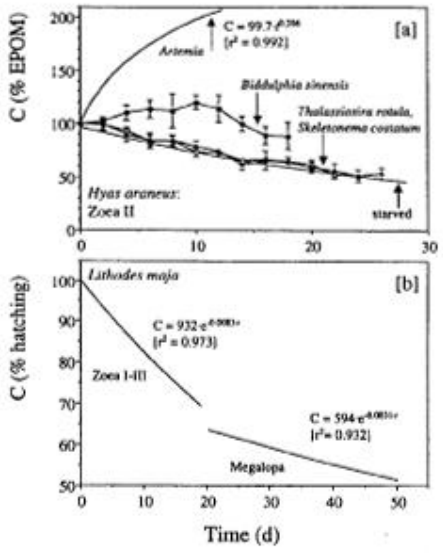


Figure 6.11. Changes in organic biomass (carbon, C) during [a] food limitation or [b] lecithotrophic development; [a] planktotrophic zoea II spider crab (*Hyas araneus*) larvae fed with different diets (*Artemia* nauplii; diatoms: *B. sinensis, T. rotula, S. costatum*) or starved: C given as a percentage of the early postmolt (EPOM) content (in µg, mean ± SD); growth of *Artemia*-fed zoeae described as a power function (Eq. 6.10), biomass loss in starved individuals as an exponential function of time, *t* (Eq. 6.12); regression curves given without data points, for clarity of graph (after Harms et al. 1991); [b] fully lecithotrophic stone crab (*Lithodes maja*) larvae: biomass loss described as an exponential function of time (*t*) of development (Eq. 6.12); fitted parameters given for regressions of absolute C values (µg/individual) plotted against *t* from hatching (zoeae) or from the beginning of the megalopa stage, respectively; r^2: coefficient of determination (redrawn after data from Anger 1996b).

$$\ln B = \ln B_0 - a \cdot t \qquad (6.12a)$$

This pattern has been documented, for example, in starved larvae of the spider crab *Hyas araneus* and, more recently, in the nonfeeding larvae of northern stone crab, *Lithodes maja* (Fig. 6.11). Similar patterns (although described with a different regression model) were observed in larval shore crab, *Carcinus maenas* (Dawirs 1983). In general, the rate of biomass loss per day is maximum during the initial phase of a period of famine, later this rate levels off. This is an effect of a an energy-saving physiological response to starvation, namely a reduction of the metabolic rate (see section 8.3.3). Before continually starved larvae of *H. araneus* or *C. maenas* died, they had usually lost about 50% of their initial carbon and energy contents.

Similar losses of organic matter were observed during the fully lecithotrophic larval development of *Lithodes maja*, which takes about three months from hatching through metamorphosis (Fig. 6.11b). In contrast to planktotrophic larvae exposed to continual starvation, physiological damage due to endotrophic degradation of internal structures is, in this case, prevented by initially enhanced energy stores. *L. maja* produces extremely large (ca. 2 mm) eggs, equipped with great amounts of organic matter.

When average rates of biomass degradation are compared among successive larval instars of *Lithodes maja*, significant ontogenetic changes in behavior and metabolic activity become evident (Fig. 6.11b). While the patterns in the three pelagic zoeal stages remain quite similar and can be described with a single regression equation, dramatic changes were observed in the megalopa. This stage shows an increasingly benthic and sluggish behavior, and thus, metabolizes much less energy than the free-swimming zoeal stages. These bioenergetic and behavioral changes are clearly reflected in a decreasing exponent (parameter *a*, Equation 6.12), being –0.0083 and –0.0031 in the zoeae and megalopae, respectively. Immediately after metamorphosis, the juvenile stone crabs begin to eat and grow rapidly, showing in their biomass the typical parabola pattern that is known from planktotrophic larvae (Equation 6.11).

6.3.2 *Intermediate patterns: partial food limitation and facultative lecithotrophy*

Fully planktotrophic larvae react quite sensitively to food limitation. In larval lobsters (*Homarus americanus*), for instance, growth was depressed, survival reduced, and the resulting juveniles were smaller, when food was given at lower densities (Carlberg & van Olst 1976). Similarly, larval body size of penaeid shrimps (*Litopenaeus stylirostris*), xanthid crabs (*Panopeus herbstii*), and spiny lobsters (*Jasus edwardsii*) increased less at lower prey concentrations (Abreu-Grobois et al. 1991, Welch & Epifanio 1995, Moss et al. 1999).

Effects of food limitation were demonstrated also in spider crab, *Hyas araneus*, larvae fed with monospecific cultures of algae (Fig. 6.11a). With phytoplankton as a sole diet, not only the height but also the shape of the biomass curves was transitional between the typical parabola pattern of maximum growth with *Artemia* (Equation 6.10) and the exponential decrease under complete starvation (Equation 6.12). With large diatoms (*Biddulphia sinensis*), the crab larvae showed a weak biomass increase during postmolt and intermolt, followed by a slight decrease during premolt, i.e. an arc-shaped growth pattern that may be described with a parabolic function (Equation 6.11). Less appropriate diets (*Thalassiosira rotula*, *Skeletonema costatum*) caused a gradual, almost linear decrease in biomass, approximating the typical pattern known from starved larvae (Equation 6.12).

Intermediate patterns of growth should be expected also in larvae with an enhanced but incomplete independence from food (facultative lecithotrophy; see section 5.1.1). This developmental mode occurs in habitats where the larvae encounter, on average, an insufficient or unreliable production of food (see section 10.4). It was described, for example, in the zoeal stages of two semiterrestrial crab species from Jamaica, *Armases miersii* and *Sesarma curacaoense*. Compared with fully planktotrophic larvae, the reduction of growth during starvation was found to be surprisingly weak in the larvae of these species; on the other hand, they showed unusually low growth rates even when food was abundant (Anger & Schultze 1995, Anger 1995c). These traits were interpreted as a consequence of the partially endotrophic mode of development, which probably implies a generally reduced

feeding activity, also when food is available in sufficient density. This is reflected also by very small increments in body size of successive larval stages (see section 2.4, Fig. 2.11).

6.3.3 *Critical points in the molting cycle: is there a critical biomass?*

Effects of food availability and of other environmental factors on larval development and growth do not remain constant throughout the course of a molting cycle. The sensitivity against nutritional or other stress changes at particular "critical points" (section 4.5). This raises the question if these critical points are associated with particular (i.e. critical) levels of biomass.

Point of reserve saturation, *PRS*. The phenomenon of facultatively endotrophic development exists, in principle, also in fully planktotrophic decapod larvae. When they pass the point of reserve saturation (*PRS*, also termed D_0 threshold), the larvae acquire the ability to finish, independent of further food availability, their development through an instar. Under optimal feeding conditions, the *PRS* may be reached after passing through only one fifth to one half of the time of the molting cycle. This is a consequence of substantial biomass accumulation during a short initial period, reflecting the typical growth patterns in well-nourished decapod larvae (see Equations 6.10, 6.11; Figs. 6.8-6.11). In the zoea I of *Hyas araneus*, the *PRS* was observed at about 30% of the molt-cycle duration; at this time, the energy content had increased by about 70% since early postmolt (Anger & Spindler 1987). The zoea-I of *Carcinus maenas* reached this critical point after passing through ca. 20% of its molting cycle, with a concurrent biomass gain of about 60% (Dawirs 1986). These figures suggest that similar critical biomass increments might be necessary to reach the D_0 threshold in different crab species; however, certainly more comparative studies should be made available to allow for generalizations.

Exuviation threshold. As another critical event, the molting process may depend on a certain minimum biomass. During the premolt stages of the molting cycle, the rate of larval growth declines in general, resembling that in facultatively lecithotrophic larvae (Fig. 6.10). This is consistent with a decrease in feeding activity during premolt (section 5.3.5, Fig. 5.5). When food is absent during this phase, under previously favourable feeding conditions, the stored reserves suffice to meet the energetic requirements for metabolism and development through ecdysis.

In the zoea I of *Hyas araneus* starved after the D_0 threshold, even more than the previously accumulated biomass can be catabolized without losing the capability for successful molting (Anger & Spindler 1987). Thus, an early postmolt zoea II may show a lower biomass than a freshly hatched zoea I, and still remain viable. By comparison, continually fed larvae molt with a threefold higher biomass to the zoea II. Similar results were obtained in zoea I *Carcinus maenas* larvae (Dawirs 1986, Harms et al. 1990), where one day of initial feeding provided enough energy to develop in later absence of food through premolt and ecdysis. As in *H. araneus*, the early zoea II contained in this case less carbon and lipid than a zoea I at hatching. This indicates that the exuviation threshold depends very little on a particular critical premolt biomass.

Point of no Return, *PNR*. When planktotrophic larvae are continually starved from postmolt, they reach another critical point, the Point of no Return (*PNR*; cf. section 4.5.1). After this, irreversible damage (chiefly in the R-cells of the hepatopancreas; section 3.11.5, see Fig. 3.19) does not allow any longer for a recovery from famine. In the zoea I of *Hyas araneus*, the PNR_{50} was observed after ca. 8 days of starvation, when about 20-27% of their initial carbon pool was lost (Anger & Dawirs 1982, Anger 1986). Similar

losses were measured also at the PNR_{50} of the zoea I of *Carcinus maenas* (Dawirs 1983). The larvae of both species died when they had lost about one half of their initial biomass. These similarities suggest that critical lower limits of biomass might be associated with the *PNR* and the maximal time of survival under starvation; however, this applies probably only to newly hatched first-stage larvae which rely exclusively on remaining yolk reserves. Later, the previous feeding conditions appear to be crucial for the severity of starvation effects, as one can see in the examples shown in the paragraph above (see Dawirs 1986, Anger & Spindler 1987, Harms et al. 1990). Again, generalizations require more comparative studies of critical points, larval molting cycles, and growth.

6.4 *Effects of physical and chemical factors*

In all preceding sections of this chapter, exclusively developmental (i.e. intrinsic) and nutritional factors have been considered in relation to larval growth. These basic patterns are modulated by effects by numerous environmental variables such as temperature, salinity, or toxic chemicals.

6.4.1 *Temperature*

Besides nutrition, temperature is one of the most important extrinsic factors in the regulation of growth. Its most conspicuous effects are found in the frequency of molting, which is closely associated with the increase in body size and biomass in successive stages (section 6.2). As in all chemical and most biological processes, the duration of development (D) in a given stage decreases with increasing temperature (T). In decapod larvae, this relationship can be described with a hyperbolic function (Equation 6.13), which becomes linear after logarithmic transformation of both variables (Equation 6.13a).

$$D = b \cdot T^{a} \tag{6.13}$$

$$\ln D = \ln b + a \cdot \ln T \tag{6.13a}$$

In the linearized regression, the constants a and b determine the slope and the intercept with the Y-axis, respectively. The fitted parameter a is negative, reflecting the inverse relationship between D and T (Fig. 6.12). This power function has been applied to describe the temperature-dependence of development duration in larvae of several species of caridean shrimps (Criales & Anger 1986, Schultze & Anger 1997), anomurans (Lindley 1990), and brachyuran crabs (Nichols et al. 1982, Anger 1983b, Dawirs 1985, Ismael et. al. 1997).

As an alternative to the commonly used power function (Equation 6.13), also *Belehrádek's equation* (Equation 6.14) can be used to describe the temperature-dependence of developmental rates (Belehrádek 1935, 1957).

$$D = a \cdot (T - \alpha)^{-b} \tag{6.14}$$

In this modified power function, an additional fitted parameter, α, is introduced. It is termed the *"biological zero"*, representing the temperature at which the molting frequency, $1/D$, theoretically becomes zero (i.e. $D = \infty$). This equation has been applied to describe the temperature-dependence of development in copepods (e.g. Escribano et al. 1998) and lobsters (*Homarus americanus*, *Panulirus japonicus*; MacKenzie 1988, Ma-

tsuda & Yamakawa 1997), or larval respiration rate as a function of temperature (section 8.3.5).

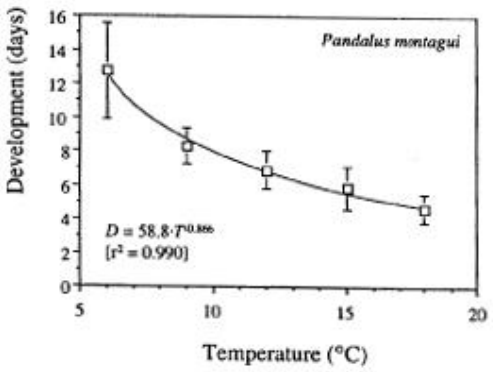


Figure 6.12. Average larval molt-cycle duration (D, mean ± SD) of a shrimp (*Pandalus montagui*) in relation to temperature (power function, Eq. 6.13); r^2: coefficient of determination (redrawn after data from Schultze & Anger 1997).

In some species, an exponential model (Equation 6.15) gave a better fit of predicted and observed data of development at different temperatures (Lindley 1990, Anger 1991b); in this function, a and b are again fitted constants, and e is the base of the natural logarithm:

$$D = e^{b} \cdot e^{a \cdot T} \tag{6.15}$$

$$\ln D = b + a \cdot T \tag{6.15a}$$

The temperature-depencence of biological and chemical processes such as development or metabolism can quantitatively be compared with an index, the temperature coefficient, Q_{10}:

$$Q_{10} = \left(R_2 / R_1\right)^{(10/[T_2 - T_1])} \tag{6.16}$$

The Q_{10} compares two rates (R_1, R_2) measured at two different temperatures (T_1, T_2, with $T_2 > T_1$), based upon van't Hoff's equation of thermodynamics. As an example, Figure 6.13 shows the Q_{10} for molting frequency, f_m, in the larval stages of a crab, *Chasmagnathus granulata*; in this graph, the value for the lowest temperature range is missing in the megalopa because there was no survival to metamorphosis at 12°C (Ismael et. al. 1997). As a common pattern, the Q_{10} depends not only on the developmental stage but

also on the temperature range considered, decreasing in general at higher temperatures. In larval *C. granulata*, this becomes increasingly evident in the late zoeal stages.

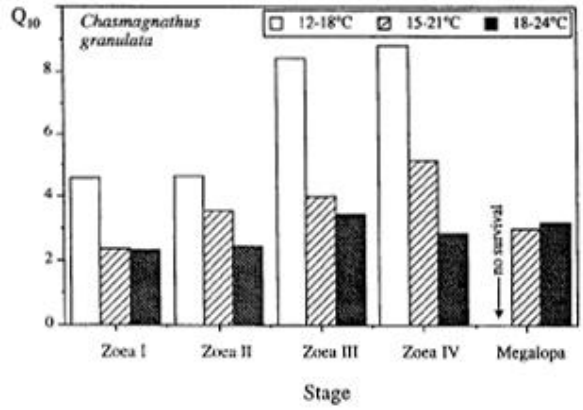


Fig. 6.13. Temperature coefficient (Q_{10}) of the instantaneous rate of development (molting frequency, f_m) in the successive larval stages of a crab, *Chasmagnathus granulata* (redrawn after data from Ismael et al. 1997).

Besides molting frequency, also the final size and biomass of individual larval stages may be affected by temperature. A larger size has frequently been observed in the colder parts of the distribution area of a taxonomic group (*"Bergman's size rule"*; see Kinne 1970). Among the crustacean larvae, this tendency has been found in barnacles (e.g. Harms 1986) and decapods (Hartnoll & Mohamedeen 1987, Shirley et al. 1987, Sulkin & McKeen 1994, Sulkin et al. 1996, Furota 1996, Matsuda & Yamakawa 1997, Lindley 1998a, Robinson & Tully 2000, Thatje & Bacardit 2000). However, exceptions of this rule have also been observed, for instance in a comparison of spider crab (*Hyas* spp.) larvae originating from different geographical regions (Pohle 1991). In caridean shrimps, high temperatures tend to decrease the size increment per instar and to increase the number of stages, which may eventually lead to similar final size (Knowlton 1974, Criales & Anger 1986, Linck 1995).

Most of the experimental evidence suggests that growth is maximum near the temperature where the physiological performance of a given stage or species is optimal; thus, it decreases at both higher and lower temperatures (Regnault 1969b, Rothlisberg 1979, Kunisch & Anger 1984, Dawirs et al. 1986, Anger 1987b, MacKenzie 1988, Laughlin & French 1989a, Minagawa 1990b, Sulkin & McKeen 1994, 1996, Matsuda & Yamakawa 1997). This indicates that the degree of temperature-dependence of two principal developmental processes, namely molting and growth, diverges at extreme temperatures. At the lower end of the tolerated range, it seems that reduction of the instantaneous rate of bio-

mass accumulation is stronger than the deceleration of development, while at unfavourably high temperatures the enhancement of biomass growth appears to be weaker than the concurrent acceleration of the molting frequency. In a recent review of larval growth (Anger 1998), this presumable effect was exemplified with the temperature-dependence of biomass growth in larval shore crab, *Carcinus maenas*. The larvae of the spider crab, *Hyas araneus*, may be used as another example (Fig. 6.14).

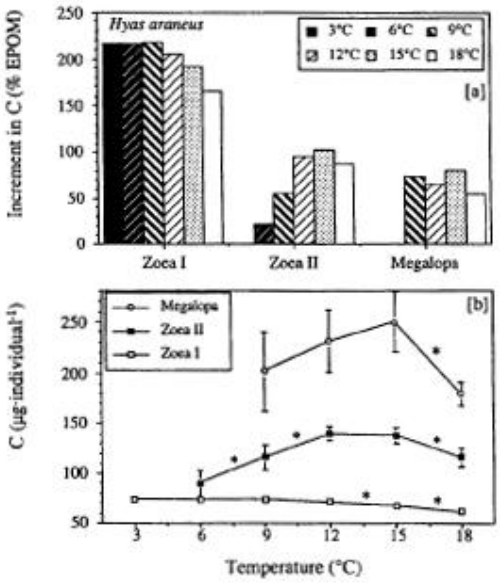


Figure 6.14. Growth of spider crab (*Hyas araneus*) larvae reared at different constant temperatures; [a] increments in carbon (C, in % of initial [early postmolt, EPOM] values); [b] final (late premolt) C per individual in each stage; mean ± SD; * = statistically significant differences ($P<0.05$; Mann-Whitney U-test; Anger, unpublished data).

According to the maximum biomass achieved in successive stages, this species shows an ontogenetic shift in the stage-specific temperature optimum. In the zoea I, maximum biomass increments and highest survival occurred in the range from 3-9°C, while the zoea II and the megalopa grew and survived better at higher temperatures (12-15°C); in these experiments, no survival through metamorphosis occurred at 3-6°C. This apparent shift in the temperature preference observed under constant conditions in the laboratory corresponds with a seasonal increase in water temperature during larval development in the field. Throughout the geographic range of this boreal and subarctic species, the larvae hatch in late winter when temperatures are at their minimum (ca. 3°C in the North Sea), and the subsequent stages develop in spring when water temperature rises gradually (cf.

section 10.2). Thus, the shift in the optimum may be based upon a genetic adaptation to recurrent (i.e. predictable) seasonal changes in the water temperature. This is suggested also by consistently low larval tolerance of 18°C. In the southern North Sea, this is near the average summer maximum, which is reached only after the time of settlement and metamorphosis in *Hyas araneus*, and thus, is not normally experienced by the larvae of this species (Anger 1983b).

6.4.2 *Salinity*

As another environmental key factor, salinity is known to influence the chances of survival and the rate of development in decapod larvae (see e.g. Kinne 1971). Compared with the effects of temperature, however, the influence of salinity on the duration of development through individual stages is relatively weak, and little is known about salinity-induced changes in larval size or biomass.

Salinity effects have recently been demonstrated in the rate of carbon accumulation of larval shore crab, *Carcinus maenas* (Anger et al. 1998). This species, which is a typical inhabitant of coastal and estuarine environments, may release its larvae in brackish water about half the strength of seawater. The zoeae are subsequently transported to more saline coastal or offshore waters, where most of their later development occurs (Queiroga et al. 1994). The successive larval stages may thus encounter varying salinity regimes, with a high probability that brackish conditions prevail after hatching. In laboratory experiments, even short initial periods of exposure to reduced salinities (one day, 20‰) reduced significantly the rate of C accumulation during the first larval stage, and hence, may later decrease the chance of successful recruitment. When the larvae were reared from hatching at different constant salinities (15-32‰), their growth rates decreased, within this ecologically realistic range, with decreasing salinity.

The semiterrestrial crab *Armases miersii* may be used as another example of salinity effects on larval growth. In the Caribbean, this species is known to release its larvae in supratidal rock pools, where salinity can vary between extremely diluted and hypersaline conditions (<5 to >50‰; Anger 1995c, Schuh & Diesel 1995a). Not surprisingly, all larval stages show an extreme degree of euryhalinity (Schuh & Diesel 1995b, Anger 1995c, 1996a, Charmantier et al. 1998). Yet, the rates of biomass accumulation measured during development under different salinities show that extreme (both enhanced and reduced) salt concentrations affect larval growth negatively (Fig. 6.15). The range for maximum growth was wide in the beginning of larval life (15-45‰), but it narrowed throughout the time of zoeal development, shifting gradually towards a higher salinity (45‰). Interestingly, however, the opposite trends were observed thereafter.

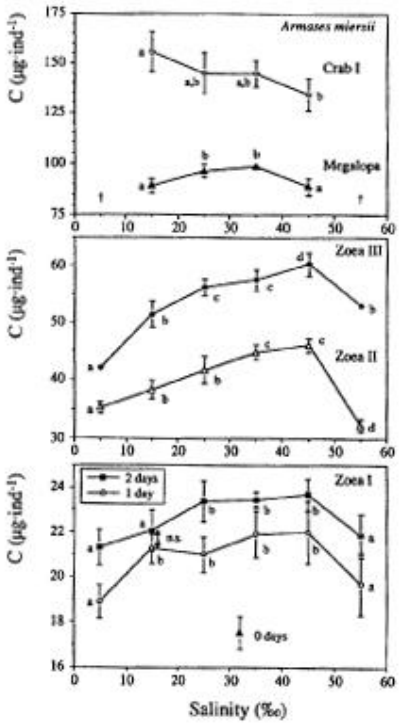


Figure 6.15. Growth of crab (*Armases miersii*) larvae reared at different constant salinities: carbon content (C, mean ± SD) at hatching, after one day, and in late premolt zoea II, zoea III, megalopa, and first juvenile stage; different letters indicate statistically significant differences ($P<0.05$) (redrawn after data from Anger et al. 2000).

These ontogenetic shifts cannot be explained as an adaptation to predictable changes occurring in the natural habitat. Instead, it may reflect a developmental change in the physiology of these crab larvae (Anger et al. 2000). From hatching, they are strong hyperregulators in dilute media, but at salinities >25% they are osmoconformers (Charmantier et al. 1998). The reduction of cumulative zoeal growth in brackish water was thus tentatively interpreted as a consequence of energy expenditure for osmoregulation at low salinities. The megalopa and the juvenile crabs are, in contrast to the zoeae, also capable of hyporegulation in concentrated media, and thus, they should require an extra energy for this process. Concurrently, the hyperregulation in dilute media may become energetically more efficient after the formation of functional gills in the megalopa (cf. section 3.2). Thus, the apparent backward shift in the salinity optimum (Fig. 6.15) could be a consequence of increasing energetic needs for hyporegulation and decreasing costs of hyperregulation. However, this tentative interpretation remains widely speculative (but also

testable), as long as too little is known about the actual energetic costs for osmoregulation and the potential consequences for growth in decapod larvae.

6.4.3 *Other environmental factors*

Besides nutrition, temperature and salinity, a number of further extrinsic factors such as photoperiod, pH, oxygen concentration, and pollutants affect the survival and development of decapod larvae. Relatively little, however, is known about the influence of such variables on larval size and biomass.

6.4.3.1 Light

Inconsistent effects of daylength and/or light intensity on larval growth were demonstrated in various species of crabs (*Ranina ranina*, Minagawa 1994; *Pseudocarcinus gigas*, Gardner & Maguire 1998) and lobsters (*Homarus americanus*, Aiken et al. 1981; *Thenus orientalis*, Mikami & Greenwood 1997b; *Jasus edwardsii*, Moss et al. 1999). *H. americanus* larvae showed their maximum growth under short-day conditions (1:23h light:dark), while those of *R. ranina* grew better at a 12:12h cycle. In *T. orientalis*, larval growth was negatively affected by a regime with continuous light, while the larvae of the Australian giant crab, *P. gigas*, showed minimum size growth and shortest molt cycle duration in continuous darkness. These effects were associated with light-induced changes in larval swimming or feeding activity.

6.4.3.2 Pollutants

Among the numerous stress factors occurring in the environment, also man-made pollutants are known to affect larval growth. This has been demonstrated experimentally in various studies, only a few examples of which shall be mentioned here, in the specific context with size and biomass; further examples of toxic pollution effects are given in section 10.1.5). In the larvae of the crab *Rhithropanopeus harrisii*, for instance, long-term exposure to sublethal concentrations of aromatic hydrocarbons caused a reduced size at metamorphosis (Laughlin et al. 1978a). Similarly, the growth of lobster (*Homarus americanus*) larvae was depressed in the presence of various organic pollutants (Capuzzo 1977, Capuzzo & Lancaster 1981, Capuzzo et al. 1984), and several pesticides were shown to reduce the rates of larval growth, survival, and metamorphosis in an estuarine shrimp, *Palaemonetes pugio* (Laughlin et al. 1978b, McKenney & Celestial 1993, McKenney et al. 1998). Also in a portunid crab (*Portunus pelagicus*), water contamination with toxic metals such as chromium, nickel, or copper reduced the molting frequency in the larval stages and the growth in subsequent juvenile instars (Mortimer & Miller 1994). Furthermore, water quality may be deteriorated also by naturally occurring toxic substances, for instance those originating from decay of organic matter or released by nuisance blooms of dinoflagellates. Ammonia and various other toxic nitrogenous compounds are normally excreted by aquatic animals, and hence, are a common problem also for growth in the intense commercial culture of edible decapods (e.g. Armstrong et al 1978, Chin & Chen 1987, Chen & Nan 1991, Lin et al. 1993, Zhao et al. 1998, Cavalli et al. 2000).

6.5 *Regulation of growth and the hormesis concept: a cybernetic approach*

Cybernetic models for growth regulation postulate that growth is not necessarily maximized but regulated towards a genetically derived “set point” (Calow 1976, Patten &

Odum 1981, Hartnoll & Dalley 1981). This requires the existence of intrinsic sensors which compare the actual with a "required" rate of growth. When these rates deviate from one another, control elements will change growth-regulating metabolic processes which increase or decrease the actual growth rate accordingly (Fig. 6.16a). Extrinsic factors ("disturbance") may affect these processes, and hence, cause changes in the actual rate of growth. As soon as this deviates from the "required" rate (∑), the control elements will again initiate a correction.

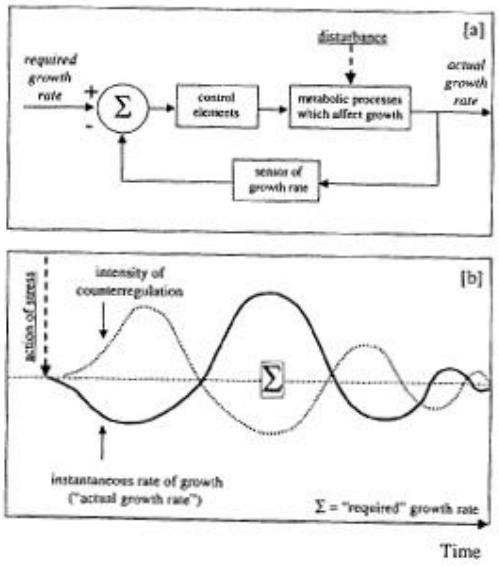


Figure 6.16. [a] Simplified model for growth regulation; [b] expected oscillations of the actual growth rate around a required rate, ∑ (redrawn after Stebbing 1981a, Sanders *et al.* 1985).

Although this conceptual model of growth regulation does not attempt to explain the underlying physiological mechanisms, it postulates predictable reaction patterns which can be tested experimentally. As one of the typical traits of such a hypothetical regulation system, there must be a time lag between the detection of an unrequired change in growth rate and its subsequent correction via the metabolic machinery (Fig. 6.16b). This delayed response causes overcorrections that should be followed by regulations in the opposite direction. In consequence, the actual growth rate oscillates around the "required" rate. Those oscillations appear to be a typical characteristic of self-regulating systems reacting to perturbations (Hubbell 1971). The amplitude of the oscillations should successively dampen over time when the counteraction is effective. However, when the stress effect is greater than the capacity of an organism to compensate for it, the oscillations should theo-

retically increase with time. Furthermore, it has been postulated that the control mechanisms are unspecific, responding similarly to a wide range of environmental effects, for instance pollution, salinity or temperature stress, and they should occur in numerous taxa of microorganisms, plants and animals (Stebbing 1981a, b).

Among the decapod crustacean larvae, such response patterns were reported from mud crab (*Rhithropanopeus harrisii*) zoeae. When these were exposed to sublethal concentrations of triorganotin compounds, they showed enhanced oscillations in their instantaneous growth rate, increasing in number and amplitude with the concentration of the toxicant (Sanders et al. 1985, Laughlin et al. 1985). The increase in amplitude at high organometal levels was interpreted as an indication that the regulation system became increasingly inefficient. At the lowest concentration, in contrast, the amplitude tended to decrease over time, indicating an effective compensation of the perturbation on growth. Similar oscillation patterns were observed also when mud crab larvae were reared at cyclically varying temperature regimes (Sanders & Costlow 1981).

When the upregulation of growth in the presence of a subinhibitory stress signal is stronger than necessary for compensation, the instantaneous growth rate may become higher than in unstressed control individuals. Thus, weak stress signals may transitorily stimulate rather than depress the rates of growth and other biological processes. As a consequence of frequent transitory overcompensations, also the cumulative growth increment may eventually exceed that in an unstressed control (Stebbing 1981b). The phenomenon of enhanced growth after the action of sublethal stress was for the first time observed, more than a century ago, by Schulz (1888) and subsequently confirmed in studies with various types of organisms (for literature, see Stebbing 1981b). It became known as the *"Arndt-Schulz Law"* or *"hormesis"* (Southam & Ehrlich 1943, Collocott 1971).

Hormesis was suggested to occur also in the zoeae of *Rhithropanopeus harrisii* (Sanders & Costlow 1981, Sanders et al. 1985, Laughlin et al. 1981, 1985). When the larvae were exposed to stressful thermal conditions or toxic pollutants, their growth (measured as dry mass) seemed to be enhanced compared with an unstressed control group. Also in a recent study with a grapsid crab species from south-east Asia, *Nanosesarma* (*Beanium*) *batavicum*, a stimulation of larval growth under the exposure to low levels of copper and mercury was reported (Selvakumar & Haridasan 2000).

When we analysed the growth of *Hyas araneus* zoeae for possible indications of the hormesis phenomenon (Pfannschmidt 1995), we realized that there are some principal problems in the detection of this effect in crustacean larvae. Since the regulation of growth is an important issue, not only in larval biology, I will discuss these problems in some detail. The following characteristics of growth and development in crustacean larvae must be considered: (1) as a consequence of developmental (i.e. intrinsic) processes, the instantaneous rate of growth changes greatly among and within individual instars; (2) daily growth rates become very small during the second half of the molting cycle, namely in the premolt phase; (3) stressed larvae tend to lengthen their development through the molting cycle.

Problem (1) requires both a clear separation of successive instars and a high temporal resolution of biomass measurements within a molting cycle. When mass-culture techniques are applied and successive stages are not thoroughly separated in at least daily intervals, the chronological age of the larvae (time from hatching) is generally not a reliable measure of their developmental stage. In mixed samples taken from different molt-stages or even from different instars, the "noise" (i.e. the variability due to inhomogeneity of the

material) is enhanced in relation to the "signal" (the response to disturbance). This problem is particularly severe in fast-growing larvae with short molting cycles, where the number of data points per instar must remain low. In this respect, *Rhithropanopeus harrisii* is certainly much less suitable for this kind of study than *Hyas araneus*.

Problem (2) implies that very small daily biomass increments must be precisely measured and compared between experimentally treated and control larvae; this is technically difficult, especially during the second half of the molting cycle where growth rates are generally low. Consequently, also the possible differences between such small instantaneous growth rates become extremely small, falling sometimes below the detection limits of analytical techniques. On the other hand, insignificant differences may appear tremendous when they are expressed in relative terms, i.e. as a percentage of the instantaneous growth rate in a control group (R%; see Sanders et al. 1985). Relative growth differences may easily reach values of several hundred percent, without being statistically significant or biologically meaningful. In order to reduce these problems of accuracy, we measured the larval carbon content rather than dry mass (which had been used by previous authors as a measure of growth).

Problem (3) is associated with the fact that development will normally proceed at unequal rates in stressed and control larvae. As a consequence, even precisely controlled and equal intervals of sampling cannot guarantee that biomass changes in different experimental groups are compared in identical molt-stages. Due to their delayed development, stressed larvae may remain in an earlier molt-stage, while the unstressed control group has already advanced to a later developmental state. As the instantaneous rate of growth tends to decrease substantially during the course of a molting cycle (see section 6.2.3), control larvae will tend to show a lower rate than stressed individuals with an equal chronological age. This developmental effect may then be misinterpreted as an overregulation of growth after stress, i.e. as "hormesis".

We chose the spider crab *Hyas araneus* for our study, because the larvae of this cold-water species very have long molt-cycle durations, allowing for a high temporal resolution of sampling within an instar. Measuring biomass in daily intervals, we were able to obtain 13 to 16 data points within the zoea I molting cycle. Since *H. araneus* is a stenohaline marine species (Anger 1985), we applied a short-term exposure to reduced salinities as a perturbance on larval growth. After the second day of development, one group of larvae (the control) was left at constant 32‰, whereas two others were exposed for 24 hours to conditions of hypoosmotic stress (20 and 15‰; later referred to as "20‰ group" and "15‰ group", respectively).

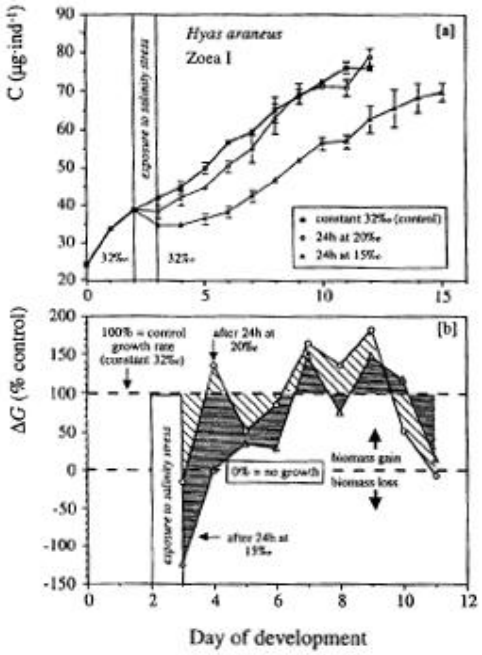


Figure 6.17. Growth of crab larvae (*Hyas araneus*, zoea I) exposed for 24 h to hypo-osmotic stress (15 or 20‰ salinity), compared with an unstressed control group (constant 32 ‰); [a] individual carbon (C) content; [b] relative daily growth rate in experimentally stressed larvae (Δ*G*, in % of concomitant instantaneous growth in the control group) (redrawn after data from Pfannschmidt 1995, with permission from the author).

The results of these experiments are illustrated in Figure 6.17, showing developmental changes in the larval carbon content (in µg per individual) and in the percentage difference (Δ*G*, in %) between the instantaneous growth rates in the control (defined as 100%) and the two experimental treatments. Overshoots and undershoots of growth relative to the control are highlighted as shaded areas (Fig. 6.17b; cf. Fig. 6.16b). No comparisons of growth after day 11 are included in these graphs, because differences in daily C accumulation became insignificant in late premolt, appearing nevertheless as exremely high percentage differences (see problem #2). Moreover, development was shorter in the control, so that no more reference values were available.

Immediately after the experimental disturbance, highly significant differences in larval biomass were measured among all treatments (day 3; Fig. 6.17a). No growth occurred during the 24 hours of exposure to 20‰, and significant amounts of C were lost at 15‰, while a steep increase was measured in the undisturbed control group (32‰). During the following three days, the growth rate in the 20‰-group oscillated around that in the control, with deviations of ca. ±50% (Fig. 6.17b). In consequence, the biomass curves re-

mained almost parallel during this period, and similar final values were eventually measured in the 20‰-group and the control (Fig. 6.17a).

Larvae exposed to 15‰ recovered more slowly from low-salinity stress, reaching a similar growth rate as in the control only more than four days after the disturbance. Transitorily enhanced ΔG values after day 7 of the molting cycle were caused by decreasing instantaneous growth rates in the reference group, which had meanwhile reached the premolt phase (see problem #3). Notwithstanding the delay in development in this group (i.e. despite more time available for growth), the final premolt biomass remained significantly below that in the other two treatments. Thus, no effective compensation of stress-induced growth reduction occurred in this treatment, nor signs of an overcompensation (hormesis).

An indication of compensatory growth was thus found only at a moderate level of stress (20‰-group), but no overcompensation with enhanced cumulative biomass gain. In conclusion, no signs of hormesis could be detected in this treatment. Also transitorily enhanced relative growth (ΔG) values did not indicate an overcompensation (Fig. 6.17b), as this could be also an effect of a slight developmental delay within the molting cycle (problem 3). Likewise, oscillations around the average control growth rate could also be an artifact caused by variable growth in the control group; moreover, these oscillations did not tend to decrease as predicted by the cybernetic model of growth regulation.

Similar response patterns were recently observed also in early zoeae of the shore crab, *Carcinus maenas* (Anger et al. 1998). Immediately after exposure to low-salinity stress, the larvae ceased to grow or lost biomass. During the second half of the molting cycle, in contrast, they recovered and showed slightly higher daily growth rates than larvae reared at more favourable salinities. This transitory enhancement of instantaneous growth after an osmotic shock may resemble hormesis; however, it may again be explained with a developmental delay in the experimentally treated larvae. Their cumulative biomass increments remained consistently below those in the unstressed control group, indicating that the compensation of growth was not fully effective.

In conclusion, there exists no concluding evidence of an occurrence of hormesis in decapod crustacean larvae. In contrast to the predictions of the cybernetic model of growth regulation, all available biomass data with a high temporal resolution suggest that larval growth may be maximized rather than up- and downregulated around a genetically set level, the hypothetically postulated "required rate". The particular growth patterns in crustacean larvae render the detection of possibly existing mechanisms of growth regulation especially difficult. However, the problems discussed and exemplified above may be overcome, when more accurate methods for the measurement of instantaneous growth rates become available. Recent attempts of point measurements of growth will be the subject of the following section.

6.6 *Nucleic acids and growth*

Processes of growth and development are closely associated with the production and metabolism of nucleic acids. Thus, the quantification of DNA and RNA has increasingly been considered as a promising tool for a rapid assessment of the nutritional condition or an analysis of growth rates and mechanisms, namely in fish larvae and other zooplankton (e.g. Clemmesen 1989, 1994, Malloy & Targett 1994). However, only few comparative data of nucleic acids have become available for decapod crustacean larvae. These are reviewed in the following section.

6.6.1 *Point measurements of growth rate*

Since larval growth may vary considerably, even during individual molting cycles, point measurements of instantaneous growth rates would be highly desirable. Such estimates should be useful in studies of comparative physiology (including the analysis of possible mechanism of growth regulation; see above), in the evaluation of larval performance in aquaculture, and in studies of plankton production in the field. Nucleic acids and, in particular, the RNA:DNA ratio have recently been used as indirect measures of instantaneous rates of biomass accumulation.

This method is based on the following theoretical considerations: (1) the amount of RNA carrying information from the nucleus to the ribosomes should be proportional to the rate of protein synthesis (RNA is predominantly ribosomal); (2) the DNA content per cell is constant (most DNA is concentrated in nuclei). Thus, the RNA:DNA ratio should be an index of the average synthetic activity per cell, theoretically allowing for point measurements of biomass growth. A positive relationship between this quotient and growth rate has been observed in a variety of organisms including zooplankton (Båmstedt & Skoldal 1980) and fish (Bulow 1987). Among the decapod crustaceans, this was most convincingly shown in early juvenile lobsters (Juinio & Cobb 1994) and larval penaeid shrimps (Jayaprakas & Sambhu 1996). In lobster (*Homarus americanus*) larvae, a close relationship between the RNA:DNA ratio and growth (expressed as daily increment in protein) was described with a regression model, which considers also temperature effects (Juinio & Cobb 1994). This model has later been used as a routine tool for estimates of *in situ* growth rates of larval lobsters (James-Pirri & Cobb 1997). In penaeid shrimp larvae, a reduced RNA:DNA index was shown to indicate depressed growth during exposure to pollution stress (Galindo et al. 1996).

However, in the literature there are also examples of a poor correlation between growth rate and the RNA:DNA ratio (e.g. Bergeron & Boulhic 1994, Mathers et al. 1994). Controversial results were obtained also in several studies of nucleic acids in decapod larvae (Regnault & Luquet 1974, 1976, Sulkin et al. 1975, Anger & Hirche 1990, Lemmens 1995). This might be partly due to species-specific traits, or it could be a consequence of a more general problem: different organs may show different developmental patterns in growth rates and nucleic acid concentrations. Since the small size of larvae requires measurements of nucleic acids in whole individuals, organ-specific variation cannot be identified. Thus, histochemical and cytochemical rather than conventional biochemical techniques may yield a more detailed image of growth and development. At present, the evidence for a general applicability of the RNA:DNA ratio as a quantitative estimator of instantaneous growth in decapod larvae is still inconclusive.

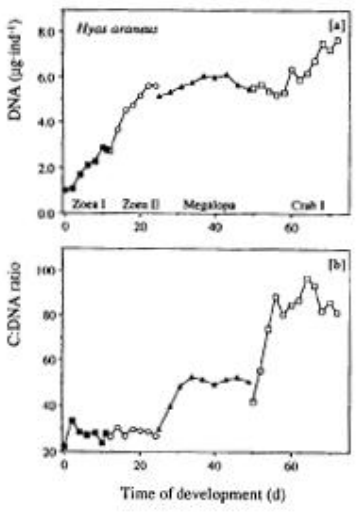


Figure 6.18. Developmental changes in the DNA content of crab (*Hyas araneus*) larvae; [a] content per individual; [b] ratio of carbon:DNA as a measure of average cell biomass (redrawn after Anger & Hirche 1990).

6.6.2 *Hyperplasia, hypertrophy, programmed cell death*

We defined growth as an increase in body size or biomass. On the cellular level, this increase can be theoretically based upon two distinct mechanisms: (1) cell multiplication (*hyperplasia*); (2) cell enlargement (*hypertrophy*). As a third developmental phenomenon, there may be also phases with a reduction in the number of cells (*programmed cell death* or *apoptosis*; see section 4.1.3). In order to distinguish between these processes, we may apply the following considerations. If we assume that the DNA content per nucleus is constant in somatic cells of a given species (Leslie 1955), then an increase in the amount of DNA per individual indicates a proliferation of cells, while a decrease indicates the occurrence of cell death. An increase in the average cell size, on the other hand, should be indicated by an increasing ratio of organic matter to DNA, e.g. in an increasing C:DNA ratio (Anger & Hirche 1990, Lemmens 1995). The inverse quotient (DNA:C) has recently been proposed as an index of the physiological condition of fish larvae (Bergeron et al. 1997). Hence, the parallel quantification of biomass and nucleic acids during the development of larval decapods should allow for an identification of different growth phases based on hyperplasia or hypertrophy, respectively.

As an example of such an analysis, Figure 6.18 shows the DNA content per individual and the C:DNA ratio in the spider crab *Hyas araneus* from hatching to the end of the first juvenile instar. According to gradually increasing amounts of DNA per larva, cell multiplication was the dominating growth mechanism throughout zoeal development from hatching to the beginning of the megalopa stage (Fig. 6.18a). This is consistent with ob-

servations from larval lobsters (*Homarus americanus*) which indicate that the increase in epidermal cell number is crucial for the increase in size at ecdysis (Cheng & Chang 1993).

The C:DNA ratio remained almost constant throughout the zoeal phase of *Hyas araneus* (except for a sudden increase immediately after hatching), indicating that the average cell size did not change much (Fig. 6.18b). Thereafter, a steep incease in this quotient suggests a period of cell enlargement during the postmolt phase of the megalopa, while weakly increasing DNA values indicated a reduced but continued mitotic activity (Fig. 6.18a). During later stages of the megalopa molting cycle (C-D_1), both the number and the average size of cells remained widely constant. Finally decreasing DNA values suggest the occurrence of programmed cell death prior to metamorphosis to the first crab stage. This may reflect major reconstruction processes including cell lysis. In the crab I stage, the average cell size showed another initial increase, which again was followed by relatively constant values, while the DNA content per crab increased gradually throughout the later parts of the molting cycle, without showing signs of cell death.

The similarity of growth patterns in the megalopa and the first crab instar suggests that the last larval stage acquires major characteristics of the juvenile life-history stages. This supports the concept of a two-step metamorphosis in the Brachyura, which is indicated also by similarities in other physiological, anatomical, and morphological traits.

6.7 *Exuvia production*

The formation of the exoskeleton represents an integral part of body growth in the Arthropoda. In budgets of energy or matter, however, it must be considered separately from tissue production, as a loss (see section 9.1). While the synthesis, partial reabsorption, and loss of ecdysial matter have been quantitatively studied in juvenile and adult decapods, little is known about these processes in larval stages. In contrast to the adult exoskeleton, which is heavily calcified in many taxa, the larval cuticle is generally thin and flexible. This difference implies ontogenetic changes in the relative proportions of tissue and cuticle production.

As a general pattern, the percentage of late premolt (*LPM*) biomass cast as exuvial matter shows an increasing trend in successive ontogenetic stages (for references, see Anger 1991a). In the zoeal stages of spider crab and hermit crab species (*Hyas araneus*, *Pagurus bernhardus*), ecdysial losses of ca. 3-6% of total *LPM* energy occurred, whereas significantly higher values (>10%) were measured in the megalopa. An ontogenetic increase in the exuvia production relative to *LPM* biomass was observed also in larvae of caridean shrimps (*Pandalus borealis*) and lobsters (*Homarus gammarus*, *Nephrops norvegicus*). Shrimp zoeae produce generally very thin and fragile exuviae; in *P. borealis*, they contained ca. 4-6% of *LPM* biomass, while the first "postlarva" (in this case probably a juvenile; Shumway et al. 1985) lost about 9% at ecdysis (Ikeda & Aritaki 1991). The same trend was observed in larval lobsters, although on a higher average level (9-30%). However, there are apparently exceptions to the possible rule of ontogenetically increasing exuvial losses. In the zoeae and megalopae of portunid crabs (*Liocarcinus holsatus*, *Carcinus maenas*), they remained generally low (<6% of *LPM* matter), without showing a clear trend.

Exuvial losses may be expressed also as a percentage of total body growth that is achieved during a given instar (Anger 1991a). In *Hyas araneus*, for instance, the three larval stages were found to lose 9, 13, and 35% of their preceding body growth, respectively.

However, comparative data from other larval decapods are too scarce to allow for safe generalizations. In particular, it remains unclear whether those percentage values are normally constant in a given species and developmental stage, or vary with the conditions of feeding or other environmental factors. If the exuvial losses relative to previous growth or *LPM* biomass remain constant, then the absolute values of exuvia production within total growth must be variable. As an alternative, the cuticle thickness may remain widely unaffected by external conditions; in this case, the fraction of *LPM* biomass or of total growth that is lost in exuviation must vary with total body growth.

Indirect evidence from the chemical composition of crab larvae reared at different external salt concentrations suggest that at least the salinity factor affects the thickness and the degree of sklerotisation of the cuticle (see section 7.1). According to changes in the inorganic fraction of larval body mass, a reduced exuvia production per larva should be expected in brackish water as compared with seawater. Variations in cuticle production and resorption should be expected also under different feeding conditions, maybe both in absolute and relative terms. Thus, the absolute exuvia production may generally vary in response to external factors; this does not exclude, on the other hand, that it may vary also relative to previous growth and/or *LPM* biomass. Since such relationships are potentially relevant in aquaculture and production biology, more comparative data of larval growth and exuvia production should be desirable.

7 CHEMICAL COMPOSITION

Changes in body size or biomass, measured in successive stages or within individual molting cycles, may be used to describe the basic developmental patterns of growth, which are further modified by the action of environmental factors (see chapter 6). However, all those patterns may actually vary among the different chemical constitutents of biomass. For instance, significant changes may occur in the relative proportions of water and dry matter, or between organic and inorganic substances, although total wet or dry mass is stable. On the other hand, total body weight may change due to changes in the water or mineral fraction, while the quantity of living matter remains constant. As another example, in postmolt there is regularly a decrease in the relative contents of carbon and nitrogen (C, N; in per cent of dry mass), notwithstanding a concurrent increase in the absolute amounts of these elements (in µg per individual). This pattern is caused by an initially higher rate of increase in the fraction of mineral substances, which temporarily outweighs the increase in organic constituents. Diverging patterns can be observed also within the organic fraction, e.g. in the proportions of C and N.

For a deeper understanding of growth, it is thus essential to quantify not only changes in total biomass, but to consider also changes in its chemical composition. Depending on the question, it may be sufficient to distinguish between gross fractions such as dry matter and water, or ash and organic matter, while more detailed analyses of elemental or biochemical components are required in other cases. Changes in the proportions of various chemical fractions of biomass have frequently been used as indicators of larval "condition" (i.e. health), which is believed to be correlated with the overall chances of survival and recruitment in the field (see reviews by Ferron & Leggett 1994, Suthers 1998; for recent controversial discussion see Suthers 2000, Elliott & Leggett 2000). In this chapter, developmental and environmentally induced changes in the principal chemical fractions of larval biomass are reviewed, quantitative relationships between elemental and biochemical constitutents are shown, which may be used for approximative conversions of one constituent to another, and potential condition indices are discussed.

7.1 *The principal fractions of biomass: water, ash, organic matter*

Biomass, in its widest sense, is the total body mass of an organism, measured as wet mass, *FW* (see section 6.2.3). In a narrower sense, the term biomass is restricted to the fraction of organic matter. This is usually estimated as dry mass (*W*), which excludes the water content of *FW*. However, *W* still consists not only of organic compounds, but contains also a mineral fraction. This can be quantified by complete combustion of dry mass at 500°C and subsequent weighing of the ash residue (Paine 1971, Hirota & Szyper 1975). The difference between total *W* and ash weight, the ash-free dry mass (*AFW*), is considered to represent the fraction of organic matter within biomass.

In the pelagic environment, physical contraints determine to some degree the chemical composition of its freely floating inhabitants, the plankton. It is namely the need for boyancy in the water column which requires a high water content and limits the maximum possible degree of cuticle calcification, i.e. the ash content. The water content of both larval and non-larval planktonic marine crustaceans has been observed to range between ca.

64 and 92% of *FW*, the ash content from about 3 to 25% of *W* (Childress & Nygaard 1974, Morris & Hopkins 1983). Compared with planktonic forms, benthic animals show on average a lower water content and a much larger mineral fraction, regardless of their taxonomic position and developmental stage. This reflects their generally compact, often heavily sklerotisized nature. These differential traits were described also within a single species, the galatheid squat lobster *Munida gregaria*, where two distinct postmetamorphic forms occur, one showing a pelagic, the other a benthic life style (Williams 1980). Hence, the overall chemical composition of meroplanktonic decapod larvae shows more similarity with that of adult holoplanktonic forms (including those belonging to unrelated taxa such as copepods or mysids) than with conspecific benthic life-cycle stages.

7.1.1 *Wet mass and water content*

In chapter 6, we have seen that *FW* changes only little during the course of a molting cycle as compared with the concomitant changes in dry mass (*W*). The same is true for comparisons between fed and starved larvae. Hence, *FW* is generally a poor indicator of age, developmental stage, or nutritional condition of larvae (Anger 1998). This is a consequence of nearly constant body size in a given instar: larval size shows a sudden increase during the brief soft-skinned postmolt period, due to a rapid uptake of water, but it changes only little after the cuticle has become more rigid (see section 4.1). Constraints on the available body volume may thus require a partial mutual replacement of dry matter (including organic constituents) with water in starved larvae, and an inverse exchange in fed individuals. This mutual replacement implies a negative correlation between the percentage of water (as a fraction of total *FW*) and that of the organic constituents (as a fraction of dry mass, *W*). This relationship can be seen in larval growth data obtained from the spider crab *Hyas araneus* (see Anger & Dawirs 1982), where the percent water content correlated negatively with the contents of carbon and nitrogen. More recently, Lemos et al. (1999) demonstrated a significant negative correlation between the percentage of water (%*FW*) and the protein content (%*W*) in the larval biomass of a penaeid shrimp, *Farfantepenaeus paulensis*. Hence, variation in the relative water content should, at least in comparable larval stages or within a given molting cycle, generally indicate opposite variations in organic constituents. In small decapod crustacean larvae, the potential value of the percentage of water as a condition index is reduced by relatively low precision of *FW* determinations; however, it should be a useful additional information.

Some characteristic patterns in the water content of larval biomass are illustrated here with time-dependent changes observed in starved and fed zoea I larvae of the spider crab *Hyas araneus* (Fig. 7.1). Throughout the time of starvation, *W* decreased exponentially (cf. section 6.3.1, Fig. 6.11), while both the absolute (in µg per individual; not shown in Fig. 7.1) and the relative water content (in % of *FW*) increased during the time of food deprivation (r^2 = 0.752 and 0.892, respectively; $P<0.001$). These inverse changes in dry mass and water do not compensate each other, because the increase in the absolute water content is stronger than the concomitant loss in dry matter. In consequence, *FW* increased not only during feeding and growth but also during starvation, showing the same parabola-shaped pattern (see section 6.3.1, Fig. 6.8a). This pattern of time-dependent increase in the water content of starved larvae was found also in later larval stages kept without food (Anger & Dawirs 1982), and it is probably similar in adult crustaceans exposed to nutritional stress (Lemcke & Lampert 1975, Hiller-Adams & Childress 1983, Chu et al. 1994, Gu et al. 1996, Stuck et al.1996).

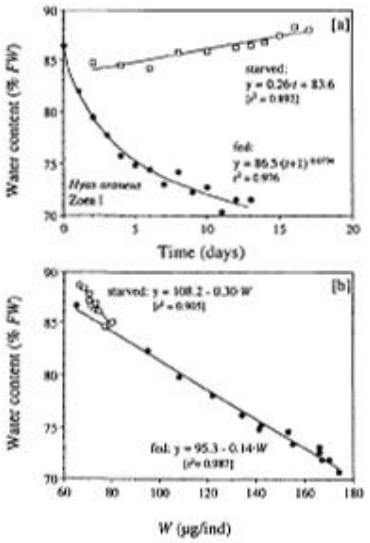


Figure 7.1. Developmental changes in the water content (% of wet mass, *FW*) in fed and starved spider crab (*Hyas araneus*) larvae; water content plotted against [a] the time (*t*) of development; [b] against dry larval weight (*W*); r^2: coefficient of determination for least-square regression equations (redrawn after Anger & Dawirs 1982).

Regardless of feeding or starvation, there is typically a rapid water uptake during and shortly after ecdysis, so that the absolute water content per individual shows consistently a maximum in early postmolt. In fed larvae, this is followed by gradually decreasing values through the later stages of the molting cycle. Hence, the relative water content (in % of *FW*) increases sharply at each ecdysis and during the short postmolt period, but then it decreases exponentially through intermolt and most of premolt (Anger & Dawirs 1982, Sasaki et al. 1986, Anger & Püschel 1986, Minagawa et al. 1993; Fig. 7.1a). In consequence, both fed and starved larvae show, within a given instar, an inverse relationship between dry matter per individual and the percent water content of total wet mass (Fig. 7.1b).

When the water content (in % of *FW*) is compared among the successive zoeal stages of a given species, the average level and the patterns of change within each molting cycle remain similar (Anger & Dawirs 1982, Sasaki et al. 1986, Anger & Püschel 1986, Saotome & Ikeda 1990, Lim & Hirayama 1991, Minagawa et al. 1993, Chu & Ovsianico-Koulikowsky 1994, Savenkoff et al. 1995). Later life-history stages, however, show a decreasing tendency in the average water content. This reflects the ontogenetic change in life style, from fully planktonic zoeae to semibenthic decapodids and, eventually, to fully benthic juveniles.

7.1.2 *Dry mass, organic matter, ash content*

Among the larval Decapoda, the average inorganic mass fraction (as a percentage of *W*) shows little interspecific variation. Most ash measurements from marine decapod larvae fall within a range from ca. 15 to 30% of *W*. Larvae of brachyurans (Anger 1984b, Anger et al. 1989b) and clawed lobsters (Anger & Püschel 1986, Sasaki et al. 1986) appear to show a somewhat higher mineral content than caridean and penaeid shrimp larvae (Saotome & Ikeda 1990, Chu & Ovsianico-Koulikowsky 1994). Extremely low values were found in lecithotrophic larvae. In the zoeal stages of the bromeliad crab, *Metopaulias depressus*, for instance, the ash content was only 7-12% of *W* (Anger & Schuh 1992). It doubled, however, after the metamorphosis to a non-swimming but feeding megalopa stage. This change is typical also insofar, as semibenthic and benthic decapodid stages show generally a higher ash content than pelagic zoeae (see above).

Patterns of change in total biomass are normally dominated by changes in the organic fraction. However, also variations in the mineral content per larva may contribute to those patterns. This is conspicuous in the postmolt increase in both *FW* and *W*, when the integument is particularly thin and permeable, and inorganic constituents can pass it rapidly. Minerals are incorporated and later used for a mechanical reinforcement of the larval cuticle (sklerotisation), and they play a significant role in numerous physiological processes such as osmoregulation and maintenance of the turgor (Foskett 1977).

Using again the spider crab *Hyas araneus* as a model, developmental changes in the inorganic fraction of larval body mass are illustrated in Figure 7.2; in addition, the influence of salinity as a modifying environmental factor is demonstrated in this example. Since *H. araneus* is a stenohaline marine species, its typical developmental patterns can be observed in undiluted seawater (32 ‰ salinity). During the course of larval development, the ash content per individual was found to double from hatching to the middle of the zoea II stage; another threefold increase occurred in the megalopa (Fig. 7.2a). As a percentage of *W*, however, the average ash content tended to decrease from hatching through the end of the zoeal phase (Fig. 7.2b). This indicates that the zoeal stages of *H. araneus* accumulate, on average, proportionally more organic than inorganic compounds. If we assume that most inorganic matter is concentrated in the cuticle, this observation is explained by the fact that the mass of the cuticle increases proportionally to the body surface, while the organic content increases with its volume. The cuticle becomes more calcified in the megalopa, causing in this stage a particularly steep postmolt increase in the ash content both per larva and as a percentage of total *W*. The level of the percentage of ash remained in the megalopa similar as in the zoea II stage, indicating that the increasing calcification in the terminal larval stage was compensated by an equally intense tissue production.

Dramatic changes in the mineral content occur not only between successive stages, but also during individual molting cycles. In *Hyas araneus* larvae reared under constant conditions in seawater, for instance, the ash content varied between 13 and 37% of *W*; greater variation occurred under exposure to reduced salinities (Pfaff 1997). Due to the loss of exuvial materials, there is generally a short transitory decrease in the ash content at ecdysis. Immediately thereafter, minerals are rapidly taken up from the surrounding water, so that the ash content increases steeply. After a maximum in early intermolt, the mineral content tends to decrease gradually throughout the premolt stages (both per individual and in percent of *W*), indicating a partial replacement of minerals with accumulating organic constituents (Fig. 7.2a).

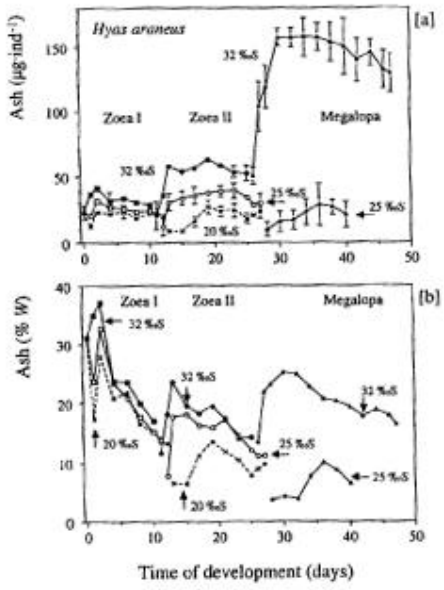


Figure 7.2. Developmental changes in the mineral (ash) content of spider crab (*Hyas araneus*) larvae reared at three different salinities; [a] ash content in µg per individual (mean ± SD, n = 5); [b] in % of dry mass, *W* (redrawn after Pfaff 1997, with permission from the author).

The typical molt-cycle related pattern in the mineral content, with a sudden loss at ecdysis, a steep gain in postmolt, and a gradual loss through premolt, is shown in Fig. 7.2b. The changes in the relative ash content (%*W*) indicate that the uptake of inorganic substances during postmolt is considerably faster than the concomitant accumulation of organic matter. During premolt, in contrast, the proportion of inorganic matter within total dry mass decreases, while the absolute ash content per individual remains stagnant or decreases, while the accumulation of organic matter continues.

All these developmental changes in the mineral content of larval biomass can be eclipsed by effects of environmental variables, in particular by salinity changes in the surrounding water (Lockwood 1976). During development under brackish conditions, the ecdysial mineral losses are more pronounced, whereas the subsequent accumulation in postmolt is weaker or delayed. Thus, the average ash content per individual decreases in reduced salt concentrations (Fig. 7.2a). Higher mineral losses at ecdysis and a reduced storage capacity for inorganic ions are consequences of a poor osmoregulatory capability. In larvae reared continuously at 25 ‰, the body mass of the megalopa contained less minerals per individual than a freshly hatched zoea I; during development in seawater, by comparison, there was a six-fold increase in the inorganic fraction (Fig. 7.2a). Similarly as in the absolute ash values, also the relative mineral content (in % of *W*) decreased on av-

erage at low external salt concentrations (Fig. 7.2b). This indicates that the depression of mineral accumulation at low salinities was proportionally stronger than the reduction of organic tissue growth, in particular after prolonged exposure to dilute media. In spider crab megalopae reared at 25‰ salinity, the ash content decreased to values <10% of *W*, while it was more than twice as high in siblings reared in seawater (32‰; Fig. 7.2b).

In summary, the amounts of inorganic constituents per individual and per unit of *W* vary dramatically both within the molting cycle and in response to salinity. Similar molt-cycle related changes were observed also in the larvae of the Norway lobster (*Nephrops norvegicus*; Anger & Püschel 1986), the American lobster (*Homarus americanus*; Sasaki et al. 1986), and a South American spider crab (*Libinia ferreirae*; Anger et al. 1989b), suggesting that these patterns are typical of larval decapods and, probably, other crustaceans. Unfortunately, however, generalizations are difficult at present, because inorganic constituents have only rarely been measured with sufficient temporal resolution within and among individual larval stages or under various environmental conditions.

Little is known also about the chemical composition of the ash fraction. It his has been studied in benthic, nectonic, and holoplanktonic organisms (see Vinogradov 1953, Nakai 1955) but not in decapod larvae. The literature shows that there is a great deal of variation among taxa. In the planktonic copepod *Calanus finmarchicus*, for instance, K and Na were the predominant elements, followed by Ca and Mg (Mayzaud & Martin 1975). In another pelagic crustacean, the Antarctic krill, Na was present in much higher concentrations than Ca, K and Mg (Nicol et al. 1992). The available data are thus not representative for the inorganic composition of biomass in decapod larvae. In addition, this may change ontogenetically from the larval to the adult phase, and the molting cycle might impose further alterations. Data of inorganic carbon suggest that the process of calcification begins early in the development of crustacean larvae, and thus, it should be interesting to study it with X-ray diffraction techniques (see Medakovic et al. 1997).

7.2 *Elemental composition: carbon, nitrogen, hydrogen*

Within the organic fraction of biomass, carbon (C), nitrogen (N) and hydrogen (H) are the predominant elements, averaging >35, 8-11, and 5-6% of W, respectively (Childress & Nygaard 1974, Hirota & Fukuda 1985, Mashiko 1985, Anger & Harms 1990, Minagawa et al. 1993). Oxygen (O), phosphorus (P), and sulphur (S) are ubiquitous but quantitatively less important. Throughout the scientific literature of the past decades, the contents of C and N have become standard measures of growth and chemical composition in the plankton (e.g. Vinogradov 1953, Beers 1966, Platt et al. 1969, Ikeda 1974, Omori 1978, Gorsky et al. 1988, Hessen & Lyche 1991). The H content is less frequently given, although it may contribute important additional information on the composition of biomass (see Vollenweider 1985). Since only few H data are presently available for comparison, I will concentrate here on the proportions of C and N within biomass (in % of W); changes in their absolute amounts (per individual) are considered as measures of growth rather than composition, and thus, are treated in chapter 6.

The most important organically bound elements can be measured with high precision and accuracy using a CHN analyser as standard equipment. This gas-chromatographic technology has commonly been applied in chemical and geological research and, increasingly, also in planktology and other biological disciplines. In consequence, measurements

of C and N have become standard techniques also in studies of growth and chemical composition of decapod crustacean larvae (Anger 1998).

7.2.1 *Proportions of C, N and H within dry mass*

Developmental changes in the absolute amounts of C, N and H per individual, measured either within or between successive larval molting cycles, are similar to those in total dry mass. Thus, they may be described as functions of the number of stages or of the time of development, applying the same types of regression models as for *W*; these growth patterns are described in detail in section 6.2. However, similar patterns of growth do not necessarily imply that the relative chemical composition of larval biomass remains constant over time. When, for instance, the percentage of C within *W* is measured with a sufficiently high temporal resolution, a typical cyclic pattern is found, which is roughly inverse to that in the percentage of ash (see above). In Figure 7.3, temporal changes in the relative C content (in % of *W*) of the larval stages of a crab (*Chasmagnathus granulata*) are used as an example to demonstrate this developmental pattern.

In all successive instars, the percentage of C drops sharply after ecdysis, consistently followed by an increase throughout the later molt-stages. Exuvial C losses are relatively small and thus, contribute only little to the dramatic initial decrease. This is chiefly caused by the rapid postmolt uptake of inorganic ions, outweighing the concurrent increase in the absolute contents of C and other organic constituents per larva (see preceding section). Later in the molting cycle, the inorganic fraction remains constant or decreases, while the accumulation of C continues; as a consequence, the percentage of C increases substantially during intermolt and premolt. When the average level of C is compared among the successive stages of *Chasmagnathus granulata*, there is an increasing tendency during the zoeal growth phase, leading to a maximum at the end of the zoea IV stage. This is followed by decreasing tendencies in the megalopa and first juvenile instar.

In most decapod species, where developmental changes in the elemental composition were studied with sufficiently high temporal resolution within and between successive larval stages, the same patterns as in *Chasmagnathus granulata* were observed, for instance in *Hyas araneus* (Anger et al. 1989a), *Carcinus maenas* (Dawirs et al. 1986), *Pagurus bernhardus* (Anger 1989), and *Liocarcinus holsatus* (Harms 1990). In a raninid crab from Japan, *Ranina ranina*, the same cyclic patterns within larval molting cycles were found, but the average percent C values in successive stages showed a decreasing tendency (Minagawa et al. 1993).

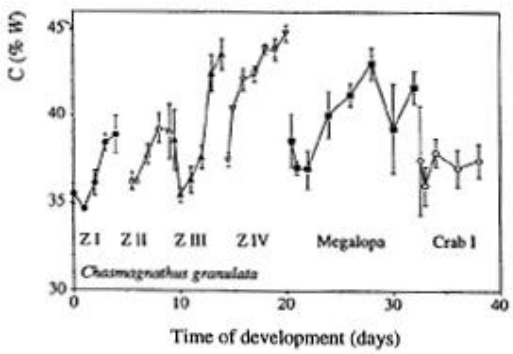


Figure 7.3. Developmental changes in total carbon content (C, in % of dry mass, *W*) in crab (*Chasmagnathus granulata*) larvae reared under constant conditions in the laboratory (redrawn after Anger & Ismael 1997).

In summary, cyclic changes in the relative C content as shown in Figure 7.3 represent a general pattern in decapod crustacean larvae. Changes in the percentages of H and N are generally similar to those in C, but less pronounced in the N fraction. These patterns are primarily dictated by inversely directed changes in the inorganic fraction. In contrast to these molt-cycle related patterns, changes in the average level of C, N and H within total dry mass of successive larval stages may vary among taxa.

7.2.2 *Inorganic C*

The carbon content is certainly one of the most accurate and convenient measurements of organic biomass. However, some C is bound also in carbonates, i.e. within the mineral fraction (Curl 1962, Paine 1971, Hirota & Szyper 1975). Since inorganic C (C_i) is considered to play only a minor role in the biomass of zooplankton (Curl 1962), it has only seldom been quantified. Among the larval Decapoda, the ash residue was only in *Hyas araneus* analysed for the occurrence of inorganic C, N and H (Anger 1984b). Measurable amounts were detected in the C fraction, sometimes accompanied by insignificant traces of N, while H was practically absent. In the three larval stages of this crab species, the ash of the complete body contained on average ca. 7-8.5% C_i.

The C_i values measured in premolt were generally higher than in postmolt, suggesting that the chemical composition of the mineral fraction differs between the cuticle and the rest of the larval body. This was confirmed by direct measurements in exuviae, where the ash residue contained on average ca. 10% C_i. This shows that more carbonates are concentrated in the exoskeleton than in the remaining body parts, indicating an incipient calcification of the cuticle.

When the C_i content of *Hyas araneus* larvae is expressed as a fraction of their total body C, it represents only 1-3%. Inorganic carbon seems thus be negligible within the bioenergetics of decapod larvae. However, the proportion of C_i within total C must become substantially higher in starved individuals, where organic C is metabolized while the

C_i content per individual should remain constant. Hence, energetic losses in the absence of food may be underestimated, when C_i is disregarded as a fraction of total C. A consideration of inorganic C should be important also in benthic juveniles. In the crab I stage of *H. araneus*, the content of C_i amounted to 17% of total C. This reflects clearly the thickness and heavy calcification of the exoskeleton in benthic crustaceans in comparison with planktonic forms.

Compared with the remaining body materials, cast exuviae contain smaller proportions of organic substances (namely chitin and protein) but higher amounts of inorganic matter. The exuvial C_i fraction was in the larval stages of *Hyas araneus* equivalent to about 22-24% of total exuvial C, and it reached as much as 43-50% in juvenile crabs. As a consequence of selective concentration of inorganic matter in the exoskeleton, the mineral fraction shows a much faster molt-cycle related turnover than the organic parts. During the time of one instar, the amounts of ash and C_i per individual increased up to 24-fold; on the other hand, up to 84% of the inorganic matter present in late premolt were lost with the exuvia (Anger 1984b). Studies of exuvial carbon or energy losses should thus consider that significant parts of total C measured in exuviae may actually be bound within the inorganic fraction.

7.2.3 *The C:N ratio*

The nitrogen and hydrogen contents vary during the course of larval development with similar patterns as the C fraction, but with less pronounced variations in N than in C and H (Anger 1998). In order to demonstrate changes in the relative chemical composition of organic biomass, it is thus useful to present mass proportions between single elements. In the literature, the ratios of C:N and C:H have been used as indices. Theoretically, the C:N mass quotient (sometimes given as an atomic ratio) reflects changes in the relative proportions of lipids and proteins; carbohydrates play only a minor role in crustaceans (see section 7.3) and have thus no significant influence on this index (Anger & Harms 1990). However, inorganic C may affect the C:N index when the ash content is high. Total C should in such cases be corrected for C_i (particularly in starved larvae and in juveniles; see above). The C:H ratio is less frequently given in the literature; it may be an indicator of the average degree of saturation in the fatty acid pool and other lipids. Moreover, the H content can be used in stoichiometric conversions of elemental to biochemical constituents (Gnaiger & Bitterlich 1984, Vollenweider 1985).

The C:N ratio shows frequently a steep increase during the postmolt phase, a maximum in intermolt, and a decreasing trend through premolt (Anger 1991a, 1998). This typical pattern is illustrated in Figure 7.4, using again spider crab (*Hyas araneus*) and shore crab (*Carcinus maenas*) larvae as examples. It has been interpreted as a molt-cycle related shift in the relation between the lipid and protein fractions, suggesting that the proportion of lipids increases initially faster than the protein pool. In later molt-cycle stages, the rate of lipid accumulation slows down, while the protein fraction (per individual) continues to increase. This interpretation is corroborated by direct measurements of proximate biochemical composition (see section 7.3).

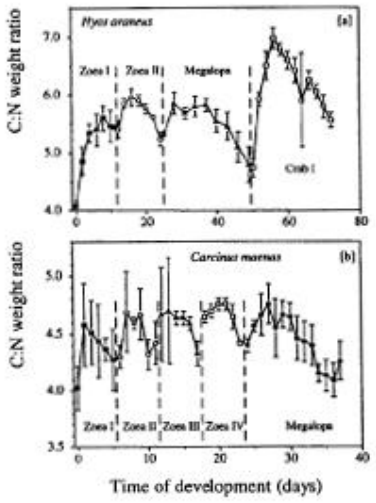


Figure 7.4. Developmental changes in the carbon:nitrogen (C:N) weight ratio of crab larvae reared under constant conditions in the laboratory; [a] *Hyas araneus* (after Anger & Hirche 1990); [b] *Carcinus maenas* (redrawn after Dawirs *et al.* 1986).

Since the percentage of N remains comparatively constant during larval development, changes in the C:N ratio reflect predominantly variation in the C fraction. When the average C:N ratio is compared within a sequence of larval stages, frequently an increasing tendency may be found during the zoeal growth phase, followed by a decrease in the megalopa. As may be seen in our examples in Fig. 7.4, there is not only developmental, but also a great deal of interspecific variability in the average level of the larval C:N ratio. The values measured in *Hyas araneus* were mostly higher than in *Carcinus maenas*. The latter species is, in this respect, closer to the overall average in the Brachyura (Anger & Harms 1990).

Besides significant interspecific variation within a clade, there might be also characteristic differences on higher taxonomical levels. Among the Decapoda, the larvae of brachyuran crabs show on average the highest C:N values, caridean shrimp larvae the lowest, and other groups (Astacidea, Anomura) are intermediate (Anger & Harms 1990). Thus, it appears that the average C:N ratio increases in a sequence of increasingly advanced taxonomical position, i.e. supposedly from ancestral towards derived taxa (cf. chapter 2). If high C:N ratios are considered as indicators of a high lipid:protein ratio and hence, an increased ability to develop independent of food, then this index suggests differences in the average degree of lecithotrophy among these decapod taxa. This corresponds with a presumable evolutionary trend towards an abbreviation of the free-living planktotrophic larval phase (for review see Strathmann 1978, 1985).

The elemental composition of larval biomass varies not only during individual molting cycles and between successive instars, but responds also to the action of environmental

factors. For instance, the C:N ratio tends to decrease under adverse thermal or osmotic conditions (Dawirs et al. 1986, Anger 1987b, Mataliotaki 1991, Seidler 1993, Pfaff 1997). This indicates that a stress-induced depression of growth affects proportionally more the lipid than the protein fraction of biomass, regardless of the kind of stress. Also starvation causes, at least initially, a decline in the C:N ratio, reflecting a preferential utilization of energy-rich lipid components as a substrate for the energy metabolism (Anger 1998). After longer periods of food deprivation, the lipid pool is widely exhausted, so that proteins are increasingly degraded and, in consequence, the C:N ratio will increase (cf. following section).

7.3 *Proximate biochemical composition*

The biomass of decapod larvae is, as in adult crustaceans, predominantly composed of *proteins*, *lipids*, *chitin*, and free *carbohydrates* (with normally >30%, <20%, <15%, and <5% of *W*, respectively; e.g. Holland 1978, Day & McEdward 1984, Sasaki et al. 1986, Anger & Harms 1990, Chu & Ovsianico-Koulikowsky 1994, Anger 1998). Proteins constitute most of the musculature, the epidermal and nervous tissues, and a major fraction of the cuticle (here together with chitin). Proteins predominate also in the hepatoancreas, although this is the only organ where significant amounts of lipid are stored; glycogen may be found as another reserve pool of biochemical energy, but only in minor quantites (Barker & Gibson 1977). Particularly high protein contents were measured in caridean shrimp larvae (on average >40%; Anger & Harms 1990). The lipid content, on the other hand, is enhanced in larvae with a partially or entirely lecithotrophic mode of development (Mashiko 1985, Anger & Schuh 1992, Clarke 1993a, b, Anger 1995a, 1998). Additionally, the nonfeeding larvae of the stone crab (*Lithodes maja*) showed unusually high protein values (48-58% of *W*; Anger 1996b).

The absolute quantities of all proximate biochemical constituents increase substantially during the course of larval growth and development, both within individual molting cycles and in successive stages (see chapter 6). Differential rates of accumulation, however, lead to characteristic shifts in their proportions within biomass. The patterns of developmental variation are further modified by nutritional effects and due to the action of further environmental variables. Such changes may be exemplified again with data from larval *Hyas araneus*, as this species is considered as a typical model of growth patterns in marine decapods (Anger 1998). In an extensive experimental study, feeding, growth, biochemical composition, and activities of digestive enzymes were quantified in all larval stages, each reared under various nutritional conditions (Harms et al. 1991). This included an *Artemia*-fed group (representing the "optimum" control condition), three treatments fed with different phytoplankton species (the diatoms *Biddulphia sinensis*, *Thalassiosira rotula*, and *Skeletonema costatum*), and an unfed group. From this investigation, the first zoeal stage and three experimental conditions (*Artemia*, *Thalassiosira*, starvation) are chosen here to exemplify changes in the two major biochemical fractions, protein and lipid, both in relation to development and in response to differential feeding conditions (Fig. 7.5).

The proportions of both lipid and protein within total dry mass (%*W*) have invariably been observed to decrease during postmolt, regardless of the feeding condition. As in the relative carbon content, this is due to the fast initial increase in the mineral fraction (see section 7.1). The percentages of both biochemical constituents increased thereafter in *Artemia*-fed larvae, but remained low in the other treatments (Figs. 7.5a, b). In optimally fed

larvae, the biomass increase was initially faster in the lipid than in the protein fraction, so that the lipid:protein mass ratio increased throughout postmolt and intermolt, reaching a maximum in early premolt (Fig. 7.5c). During the later premolt stages, this quotient tended to decrease, reflecting a continued increase in protein and a concomitant stagnation or decrease in the lipid pool. Similar patterns were found also in well-fed zoea II and megalopae of *Hyas araneus*.

In starved larvae, three distinct phases of biomass degradation may be recognized. (1) Initially, lipid reserves are preferentially mobilized; this is indicated by decreasing lipid:protein and C:N ratios. (2) When major parts of the accessible lipid pool have been depleted, proteins are increasingly utilized; a significant part of the lipid pool is bound in crucial cell structures such as membranes, and hence, is normally unavailable for the energy metabolism. The phase of predominant protein degradation is indicated by an increase in the lipid:protein and C:N ratios (Fig. 7.5c: days 4-8). (3) In the final phase of starvation, prior to death, also structural lipids may eventually be degraded, so that the lipid:protein ratio decrease again; in this condition, the larvae have passed their point-of-no-return (*PNR*; see sections 4.5.1, 6.3.3) and have thus become unable to recover after re-feeding.

Interestingly, the same pattern of reserve degradation may occur also under other kinds of stress. In experiments where shrimp (*Palaemonetes pugio*) larvae were exposed to high concentrations of fenvalerate, an insecticide, the C:N ratio decreased rapidly during the first week, then it increased and eventually (after 4 weeks), it decreased again, indicating similar changes in the lipid:protein ratio (McKenney et al. 1998). In summary, energy-rich lipid reserves are rapidly mobilized for energy production during short-term absence of food or under other physiological stress (for sites of lipid storage, see section 3.11.5), while the protein pool remains initially stable, reflecting its predominant role in the structures of muscle, integumentary, and nervous tissues. After prolonged periods of stress, proteins and, eventually, structural lipids may be sacrificed for energy production. Similar patterns of biochemical change under starvation conditions had been observed also in adult crayfish (Speck & Urich 1969), suggesting that this sequence of reserve utilization occurs universally in crustaceans.

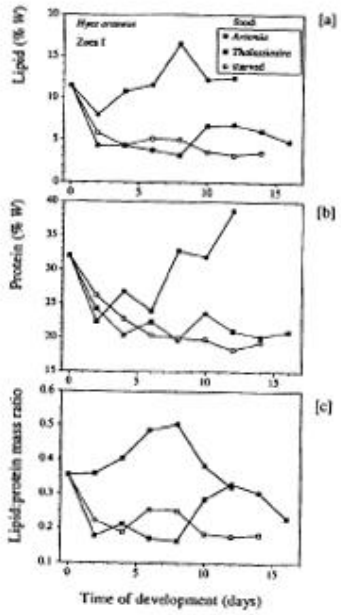


Figure 7.5. Developmental changes in the proximate biochemical composition of early spider crab larvae (*Hyas araneus*, zoea I) reared under three nutritional conditions in the laboratory: fed with *Artemia* nauplii, diatoms (*Thalassiosira*), or starved; concentrations of biochemical fractions in % of dry mass, *W*: [a] lipid, [b] protein; [c] lipid:protein mass ratio (redrawn after Harms *et al.* 1991).

As an intermediate pattern between optimal nutrition and starvation, the consequences of an exclusive feeding with diatoms are shown in Figure 7.5 (*Thalassiosira*). The patterns of change in biochemical composition were in this suboptimal treatment similar to those in the starved group. However, there were also some interesting differences. After the initial phase of predominant lipid catabolization, the phase of increasing protein degradation followed with a delay compared with the starved group, as some (although not sufficient) food was taken up. Likewise, the final phase with another decrease in the percentage of lipid and in the lipid:protein ratio was delayed. Intermediate effects of suboptimal nutrition were observed also in the other two experimental treatments with phytoplankton (*Biddulphia*, *Skeletonema*).

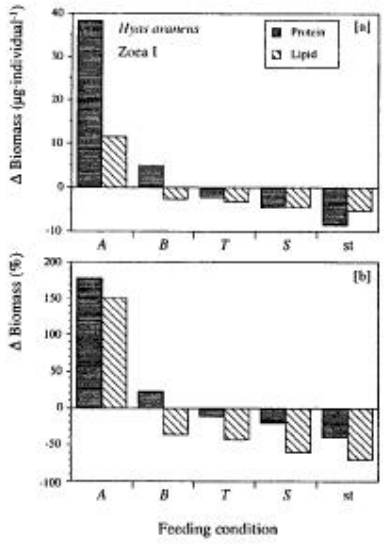


Figure 7.6. Changes in the lipid and protein content (Δ Biomass) of spider crab larvae (*Hyas araneus*, zoea I) fed with brine shrimp nauplii (*Artemia; A*), diatoms (*Biddulphia sinensis*, *Thalassiosira rotula*, *Skeletonema costatum*; *B, T, S*), or starved (st); [a] lipid and protein in µg per individual; [b] in % of the initial (early postmolt) quantities (redrawn after Harms *et al.* 1991).

Typical patterns of accumulation and loss may be found also when cumulative changes in the biochemical composition of biomass are considered after extended periods of development or starvation. During the course of an entire molting cycle, well-fed spider crab zoeae accumulated three times higher overall amounts of protein than lipid per individual (Fig. 7.6a). In relative terms (as a percentage of the initial postmolt quantities; Fig. 7.6b), however, similar accumulation rates were observed. After a long period of starvation, the absolute losses of protein (in µg per individual; Fig. 7.6a) exceeded in *Hyas araneus* eventually those of the lipids, reflecting the larger pool of available protein. By contrast, the relative rate of utilization (as a percentage of the initially available amounts) was higher in the lipid than in the protein fraction (Fig. 7.6b). Thus, the patterns of biochemical change during development or starvation depend on the time scale over which they are observed and on the units in which they are expressed. In general, lipids can rapidly be accumulated or catabolized, while proteins have a slower turnover rate and hence, become important as an energy reserve when starvation lasts for an extended period.

Interestingly, particularly strong shifts in the biochemical composition occurred at an intermediate level of food limitation, including an incease in one constituent but a decrease in another. This effect is llustrated here with the experimental treatment in which exclusively *Biddulphia* was given as food (Fig. 7.6a, b). For *Hyas araneus* larvae, this diatom species is an inferior diet compared with *Artemia*, but (unlike *Thalassiosira* or *Skeletonema*) allows for successful larval development and some, although reduced, growth. An increase occurred here only in the protein fraction, while the lipid content decreased

concommitently both in absolute and relative terms. This indicates that internal lipid reserves (most probably mobilized in the hepatopancreas), together with apparently insufficient materials from ingested food, were invested into epidermal, muscular, and nervous tissue growth, ensuring morphogenesis.

Differential patterns of degradation can be observed also in the biomass fractions of nonfeeding (lecithotrophic) larvae, where development is exclusively based upon the breakdown of internally stored biochemical reserves remaining from the egg (Anger & Schuh 1992, Anger 1996b), or in late larval stages with secondary lecithotrophy (see section 6.3). The latter type of larvae is particularly interesting, as it successively exhibits the patterns of both planktotrophic and lecithotrophic development. In the hermit crab *Pagurus bernhardus*, for instance, the four planktotrophic zoeal stages combined were found to accumulate about 16 times the initially present amounts of protein, and as much as a 40-fold gain was observed in the lipid fraction (Reese 1992). Due to these unequal rates of increase in the absolute amounts, there was also a shift in the proportions of lipid and protein within the dry mass of successive zoeal stages: while the protein fraction remained fairly stable (increasing only slightly from 32 to 36% of *W*), the percentage of lipid increased from 7 to 19%.

These changes were reversed in the megalopa of *Pagurus bernhardus*. During its secondarily lecithotrophic development, this stage catabolized 79% of the initially available lipids, but only 18% of its protein pool. Hence, also the relative composition of dry mass changed, showing only a slight decrease in the proportion of protein (from 36 to 31% of *W*) but a dramatic reduction of the previously accumulated lipid reserves (from 19 to 4%). As a consequence of these ontogenetic changes in biochemical composition, a freshly metamorphosed juvenile contained similar amounts of protein per individual as a late zoea IV, while its lipid content was reduced to the level of a late zoea II.

These discrepancies between initial rates of accumulation and subsequent utilization of different biomass fractions indicate that secondary lecithotrophy in the hermit crab megalopa is almost entirely based on energy that the zoeae take up from food and store as a lipid reserve. By contrast, no substantial amounts of protein are stored or mobilized, so that the protein pool remains available for metamorphosis-related reconstruction processes.

Due to the key role of glucose in the energy metabolism, free carbohydrates have a rapid turnover. In consequence, this fraction remains small in relation to the protein and lipid pools, where significant storage takes place. Within biomass, free carbohydrates constitute generally less than 5% of *W*. In *Pagurus bernhardus* larvae, the absolute amounts per individual increased gradually through zoeal development, from <1 to ca. 3.4 µg (Reese 1992). Interestingly, a continued increase was observed during the endotrophic development of the megalopa. A freshly metamorphosed juvenile hermit crab contained about double the amounts of carbohydrates as a late zoea IV (7.6 µg). This indicates that the degradation of lipids (and to some extent of proteins) leads to an increase in the concentration of free carbohydrates.

Chitin is predominantly associated with cuticle structures and participates very little, if at all, in the accumulation and utilization of energy reserves. When *Hyas araneus* larvae were starved from hatching, they synthesized approximately the same amounts of chitin as well-fed siblings (Anger & Nair 1979). Thus, cuticle secretion appears to have priority over an accumulation of energy reserves, representing fixed costs within the larval energy budget. In consequence, the strength of the mechanical body protection should be widely

independent of the nutritional condition. In starved larvae, this requires a mobilization and reconstruction of internally stored biochemical reserves for chitin synthesis. In aqadult crustaceans, large parts of these energetic costs are regained in late premolt by mobilization and resorption of cuticular matter (Speck & Urich 1971, 1972, Spindler-Barth 1976). The bioenergetic significance of these processes is believed to be small in planktonic larval stages with a comparably thin cuticle, but this assumption remains to be checked with quantitative analyses.

7.4 *Relationships between elemental and proximate biochemical composition*

The elemental composition of biomass, namely the quantities of elements that are almost exclusively bound in organic constituents (C, N, H), can be measured very precisely in small samples (0.2 mg *W*). In contrast, the techniques for direct biochemical measurements are generally less precise than CHN analyses, because they must react to heterogenous classes of organic compounds, each comprised of various species of molecules. In the past few decades, improved micro-analytical methods for proximate biochemical measurements have been elaborated, so that the required sample size has substantially decreased, while the reliability of analytical results has increased (see Holland & Gabbott 1971, Holland 1978, Clarke et al. 1990). In consequence, an increasing amount of data has become available on the chemical composition of larvae and other small marine invertebrates.

Since the quantities of C and N are highly correlated with the amounts of total lipid and protein, respectively, elemental analyses may be used for indirect estimates of the proximate biochemical composition of decapod larvae (Childress & Nygaard 1974, Anger & Harms 1990, Anger 1998). Due to an increasing number of parallel measurements of elemental and proximate biochemical composition, the basis of empirical conversion models has recently improved. However, not enough is presently known about interspecific and developmental variability, or about effects of extrinsic factors that may influence the quantitative relationships between elemental and biochemical constituents. Several examples of variability in these relationships will be shown here.

Conversions of N to protein are quite common in the literature, frequently based on a constant factor of 6.25 (e.g. Le Vay et al. 1993). This is derived from the average N content of proteins (16%), assuming that all measured N is bound in this fraction. However, empirical regression equations calculated from parallel determinations of N and protein (usually applying the Lowry method) have consistently yielded considerably lower conversion factors. In a study of the chemical composition of field-caught planktonic crustaceans, for instance, a linear relationship with a slope parameter of 4.5 was obtained (Childress & Nygaard 1974). This is similar to the N-protein relationship in crab larvae (Anger et al. 1983, Anger & Harms 1990). In other plankton, the fraction of non-protein N was found to be highly variable, reaching in some species as much as 42% of total N (Mayzaud & Martin 1975). Hence, empirical regression models that are based on parallel measurements in aliquot samples and restricted to related taxa should allow for more realistic conversions than a constant factor of 6.25.

As updated versions of earlier empirical regression models (Anger & Harms 1990), the relationships between N and protein and between C and lipid in planktotrophic decapod larvae are shown in Figure 7.7. Data from partially or fully lecithotrophic larvae were excluded from these regressions, because recent studies suggest that the relation between N

and protein in endotrophic larvae may differ significantly from that in strictly planktotrophic forms (Anger 1998). This indicates shifts in the average composition of nitrogenous substances (proteins, free amino acids, nucleic acids, bases, etc.), some of which are not detected with the Lowry method or comparable biochemical techniques. Since the direction and extent of these shifts may vary among taxa, larval stages, and developmental modes, further comparative studies will be necessary to estimate the relative significance of these potential causes of variability. The C:lipid relationship, in contrast to that between N and protein, appears to be widely independent of the stage and developmental mode (Anger 1998).

Not only the developmental mode (planktotrophic *vs.* endotrophic) may affect the quantitative relationships between elemental and biochemical constituents. In feeding larvae, shifts are induced also by adverse nutritional conditions and, probably, by further environmental stress factors. In starved *Hyas araneus* larvae, for instance, the proportions of protein and lipid were reduced not only per individual and as a percentage of dry mass, but also in relation to total N and C, respectively (Harms et al. 1991, Anger 1998).

Differences were found also between field-caught and laboratory-reared shore crab (*Carcinus maenas*) larvae (Harms et al. 1994). In individuals obtained from field samples, the amounts of directly measured proteins were higher in relation to N, while the lipid content in relation to C appeared to be lower than in material produced in the laboratory. These tendencies were tentatively interpreted as a "domestication effect" in artificially reared larvae (Anger 1998). It may be caused by a decrease of structural muscle proteins in relation to other nitrogenous compounds that are not quantitatively detectable with biochemical standard techniques such as Lowry. On the other hand, there seems to be a tendency of fattening, implying that increasing proportions of C are bound in reserve lipids rather than in muscle tissues. This inference is consistent with observations in the American lobster, *Homarus americanus*, where Rooney & Cobb (1991) measured significantly higher swimming speed in field-caught as compared to laboratory-reared larvae. Higher protein contents were observed also in the hemolymph of field-caught as compared to laboratory-cultured penaeid prawns, *Litopenaeus vannamei* (Palacios et al. 2000). Since domestication effects must be considered in extrapolations of laboratory data to field conditions, this phenomenon should be investigated more extensively in future comparative studies with larvae obtained from natural plankton populations and laboratory cultures.

In summary, conversions of elemental to proximate biochemical composition allow for rough estimates that may be useful comparing different larval stages, species, or conditions, but we should caution against possible effects of the developmental mode, feeding conditions, and laboratory artifacts. Since, in small planktonic forms such as decapod larvae, CHN analyses are easier to obtain and more precise than biochemical data, more parallel analyses are desirable to improve the basis for empirical conversion models.

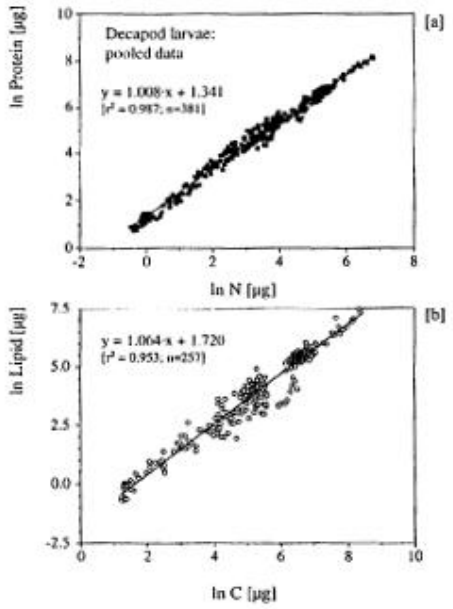


Figure 7.7. Relationships between elemental and proximate biochemical constituents of biomass in planktotrophic marine decapod larvae (pooled data, after logarithmic transformation); [a] protein plotted *vs.* nitrogen, N; [b] lipid *vs.* carbon, C; r^2: coefficients of determination; n: number of parallel analyses (redrawn after Anger 1998).

7.5 *Protein and lipid composition*

When the composition of major biochemical compound classes such as the proteins and lipids is further analysed, a more detailed description of growth and development becomes possible. However, also in this respect contrasts an extensive literature on juvenile and adult crustaceans with scarce information on larval stages. In the following sections, I will review the available data on amino acid and lipid composition of larval biomass.

7.5.1 *Amino acid profiles*

Amino acids are precursors of protein synthesis and hence, their availability is crucial for the manufacture of muscles, connective tissues, respiratory hemolymph pigments, enzymes, and peptide hormones. Moreover, they serve as a nitrogen source for the synthesis of non-protein nitrogenous compounds, including coenzymes, nucleic acids, and nucleotides, and they may be utilized as a metabolic substrate for the production of energy. In embryonic and early (nonfeeding) fish larvae, free amino acids (*FAA*) are suspected to play a key role as an internal energy source (e.g. Claybrook 1983, Finn et al. 1995). However, this could so far not be demonstrated in larval decapods, although a degradation of internal protein stores (implying a subsequent utilization of *FAA*) occurs in planktotrophic larvae during extended periods of starvation (Anger 1986, Dawirs 1987).

The *FAA* pool is comprised of precursors and/or degradation products of the protein metabolism. They occur generally in low concentrations in the hemolymph but at high levels intracellularly (Florkin 1960, Claybrook 1983, Gilles & Péqueux 1983). In the cytosol, they can contribute up to half of the osmotically active molecules and thus, play a significant role for osmoregulation (see section 10.1.2). In crustaceans, a direct uptake of *FAA* from the surrounding water does not occur or is insignificant; this is in contrast to several larval echinoderms, molluscs, bryozoans, and other marine invertebrates, which have access to dissolved organic matter (section 5.2.2.1). Amino acids must thus either be synthesized, mobilized from protein stores, or ingested with particulate food. Variations in *FAA* that can not be synthesized *de novo* (essential amino acids; see section 5.2.1) reflect thus the dietary condition.

Developmental variation in *FAA* concentrations has only little been studied in decapod crustacean larvae. As in other chemical components of biomass, the *FAA* profile may vary within the molting cycle, among developmental stages, taxa, and environmental conditions (Costlow & Sastry 1966, Regnault 1971, Tucker & Costlow 1975, Tucker 1978, Marangos et al. 1990, Burton 1992). Ontogenetic changes were recently observed between early, intermediate, and late larval stages (protozoea II, mysis II, "postlarva" I) of a penaeid shrimp, *Penaeus monodon* (Sheen & Huang 1998). A significant increase occurred in the amino acids arginine and glycine, while a decrease was found in serine, threonine, and valine. In a previous study on larvae, juveniles and adults of the same species (Peñaflorida 1989), the same ontogenetic trends were found in arginine and serine, but no or different patterns of change were detected in the other amino acids. Hence, the available data do not allow for generalization as to ontogenetic trends in *FAA* concentrations of successive larval stages.

In the megalopa of the blue crab, *Callinectes sapidus*, proline, taurine, alanine, glutamic acid, and serine were observed to increase during the premolt stages of the molting cycle (Tucker & Costlow 1975). The increase in *FAA* concentrations prior to ecdysis contributes to a large water intake, and eventually, the rupture of the old cuticle during the molting process. This process is responsible also for the rapid increase in body size during and shortly after ecdysis (see sections 6.2, 7.1). The increase in the rate of *FAA* synthesis during premolt is apparently under hormonal control (Kalber & Costlow 1968). When the eyestalks were removed in the last zoeal stage of the land-crab *Cardisoma guanhumi*, *FAA* concentrations increased significantly earlier, indicating that neuroendocrine factors from the eyestalk ganglia are involved in the control of their metabolism. If this leads also to an enhancement in the final *FAA* concentration, this could explain why eyestalk ablation causes an enhanced increment in body size at ecdysis (see sections3.9.2, 4.3.2).

Major changes in the *FAA* pool were observed in response to salinity variations, usually with dramatically increasing concentrations during conditions of high external osmotic pressure (Claybrook 1983, Gilles & Péqueux 1983; Huong et al. 2001). This compensatory mechanism was observed also *in vitro* in nerve tissues of euryhaline crabs (Schoffeniels & Dandrifosse 1994). According to the scarce data that are available for larvae, particularly great amounts of proline are synthesized to increase the osmotic concentration in the larval tissues (Tucker 1978, Burton 1992). When the megalopa of the blue crab was acclimated to seawater (34‰ salinity), proline comprised 64 % of the total *FAA* pool (Burton 1992). In larvae that were acclimated to a reduced salinity (17‰), in contrast, far lower concentrations were measured, similarly as in adult blue crabs living in brackish water (<25% of total *FAA*). A crucial role of proline in osmoregulation is sug-

gested also by radiotracer experiments with ^{14}C-labelled glutamate as a precursor. The data showed that its *de novo* synthesis is normally very low unless induced by hyperosmotic stress (Burton 1992). Similarly, stone crab (*Menippe mercenaria*) larvae showed at 40‰ salinity ca. eight-fold higher proline concentrations as compared with 20‰ (Tucker 1978).

7.5.2 *Lipid composition*

Lipids play a key role in growth and development of marine invertebrates (see Holland 1978, Heinle 1981, Chang & O'Connor 1983). It should be stressed, however, that the chemical species within this large compound family have only their water-insoluble nature in common; structurally, they are quite heterogenous. They comprise neutral lipids (*NL*) such as fats (triacyglycerides, *TAG*), mono- and diacylglycerides (*MAG*, *DAG*), *free fatty acids* (*FFA*), wax esters (fatty acids esterified with long-chain alcohols), and sterols, but also polar compounds (collectively referred to as polar lipids, *PL*) including the phospholipids (diacylglycerin esters of phosphoric acid), pigments, and sphingomyelin. In addition, lipids are frequently combined in complex molecules with carbohydrates or proteins (glycolipids, lipoproteins). Those various compounds fulfill numerous physiological tasks as constituents of cell organells or energy reserves and, in consequence, the lipid composition reflects changes in developmental state, nutritional condition, and effects of environmental factors. In decapod crustacean larvae, *TAG*, *PL*, and free sterols constitute usually the predominant lipid fractions (Teshima & Kanazawa 1982, Lovrich & Ouellet 1994).

7.5.2.1 The major lipid classes

Most *TAG* is synthesized and stored in the R-cells of the hepatopancreas, where they constitute a major energy reserve (Sasaki et al. 1986, Galois 1987, Chandumpai et al. 1991, Dall et al. 1992). This deposit can be rapidly mobilized to resist nutritional, thermal, or osmotic stress (Sasaki 1984, Pollero et al. 1991, Chen & Lai 1993). In freshly hatched larvae, the *TAG* store represents an energy investment of the female into egg production and thus, may serve an an indicator of the maternal reproductive potential. When, for instance, the spawning period of the shrimp *Litopenaeus vannamei* was artificially prolonged by means of eyestalk ablation, the reproductive potential of the females tended to decline, and this trend was reflected by a decreasing *TAG* content and a deterioration of the physiological condition of consecutively produced nauplii (Palacios et al. 1999). Also toxic pollutants may cause a reduced accumulation of *TAG*, as recently shown in larval and early juvenile mud crabs, *Rhithropanopeus harrisii* (Nates & McKenney 2000b).

It seems that, compared with larval brachyurans, caridean shrimps contain generally less lipids and, in particular, less *TAG*. In *Pandalus* spp. larvae, for example, a total lipid content of only 3-4 % of *W* was found (Schultze 1993, Ouellet et al. 1995); within this small fraction of biomass, *TAG* accounted for only 5 %, while ca. 80 % was identified as *PL*. Also in the shrimp species *Crangon crangon* and *C. allmanni*, *TAG* was found only in traces in the eggs and early zoeal stages; in later stages, it was sometimes not even detectable (Kattner *et. al.* 1994). Very low *TAG* reserves in caridean shrimp larvae correspond with particularly low average C:N ratios (Anger & Harms 1990) and high vulnerability to food limitation (Wehrtmann 1991, Ouellet et al. 1992). However, also some brachyuran species may show very low *TAG* contents. In the larval stages of a xanthoid crab, *Menippe adina*, Nates & McKenney (2000a) measured values of only 1-5% of total lipids, while

phospholipids and steryl esters dominated. Similarly low values (1.6-2.6%) were reported for thalassinid shrimp (*Lepidophthalmus louisianensis*) larvae (Nates & McKenney 2000c). This species shows an abbreviated mode of development and signs of an initial lecithotrophy (Nates et al. 1997), which should thus be based on the utilization of phospholipid stores rather than *TAG* as an internal energy source. In conclusion, generalizations of biochemical traits on higher taxonomic levels would be premature, due to great interspecific variability and a low number of comparative data presently available.

While the *TAG* pool represents the predominant fuel for energetic processes, the protein fraction is primarily bound in tissue structures. As the latter remains comparatively stable, the *TAG*:protein ratio may be used as a bioenergetic condition index. During the larval development of lobsters (*Homarus americanus*), this quotient was shown to increase in successive stages, in particular during the postmolt and intermolt stages of the molting cycle (Sasaki et al. 1986). As a percentage of the lipid fraction, the *TAG* store increased in this species from <3% at hatching (indicating almost complete depletion during embryogenesis) to >50% in stage IV. Similar as the *TAG*:protein quotient, also the *TAG*:DNA ratio, i.e. an estimate of the average *TAG* content per cell, may thus be used as an index of physiological condition in crustacean larvae (see Miron et al. 2000).

As another potentially important lipid class, *wax esters* represent the principal energy reserve in most copepods and several other zooplankton. Although these compounds have rarely been reported in significant quantity from decapod crustacean larvae, they might be important in deep sea species. Large amounts of wax esters (75-82% of the total lipid fraction) were observed in late zoeae and early juveniles of three species of hydrothermal vent shrimps (Pond et al. 1997). Since hydrothermal vents represent short-lived, isolated habitats that are scattered over wide areas of deep sea bottom, their colonization depends on the dispersal of bathypelagic stages which have to bridge large distances, floating for extended periods in nutritionally poor water (Herring & Dixon 1998). Their unusual energy reserve was thus interpreted as an adaptation to a prolonged bathypelagic existence under food-limited conditions. Future biochemical studies will show if a storage of wax esters is more favourable in this particular environment than a deposition of *TAG*.

Phospholipids (with phosphatidyl choline and phosphatidyl ethanolamine as predominant compounds) are polar lipids. Their majority is structurally bound in membranes, where they fulfill crucial physiological functions (Chapelle 1986). Moreover, they are the major transport form of lipids in the hemolymph, accounting for up to 88% of all circulating high-density lipoproteins (Teshima & Kanazawa 1980, Lee & Puppione 1988). Hence, phospholipids remain relatively stable under variable nutritional conditions; their degradation as a bioenergetic substrate begins only after extended periods of starvation and depletion of other energy stores, namely *TAG* (Chandumpai et al. 1991, Pollero et al. 1991).

Also *sterols*, in particular cholesterol, are usually preserved during periods of malnutrition (Chandumpai et al. 1991). Dietary steroids are essential precursors of the molting hormones (ecdysteroids; cf. section 4.3.1) and apparently important also for several other processes of development and growth in decapod larvae (Teshima et al. 1986b). In the lobster *Homarus americanus*, the sterol:protein ratio remained almost constant throughout larval development, ranging between 0.015 and 0.020 (Sasaki 1984). This indicates that these two biochemical compound classes have an approximately equal importance as structual components of larval biomass.

In summary, phospholipids and sterols change relatively little under variable nutritional conditions or in response to other environmental factors, while large variations may occur

in the concentration of *TAG*. This differential response pattern has been used to derive condition indices from lipid composition, for instance the quotients *TAG:FW* (Ouellet et al. 1992, Robertson et al. 2000), *TAG:PL*, or *TAG*:cholesterol (Fraser 1989, Mourente & Rodríguez 1997, Palacios et al. 1998). Those indices, however, appear to respond unspecifically to various kinds of stress, including food limitation, osmotic pressure gradients, or toxic pollutants (see Capuzzo et al. 1984, Fraser 1989, Mourente & Rodríguez 1997).

7.5.2.2 Developmental patterns and nutritional effects

In the preceding sections, we have repeatedly used the larvae of the spider crab *Hyas araneus* as a model to depict changes in the elemental and proximate biochemical composition during development and growth, or in response to nutritional and other environmental factors (see Figs. 7.4-7.6). It is thus convenient to use here the same species for the illustration of effects observed in the major lipid classes, especially as data originating from identical material are available (i.e. analyses of aliquot samples taken from the same set of experiments that was used by Harms et al. 1991; Fig. 7.8).

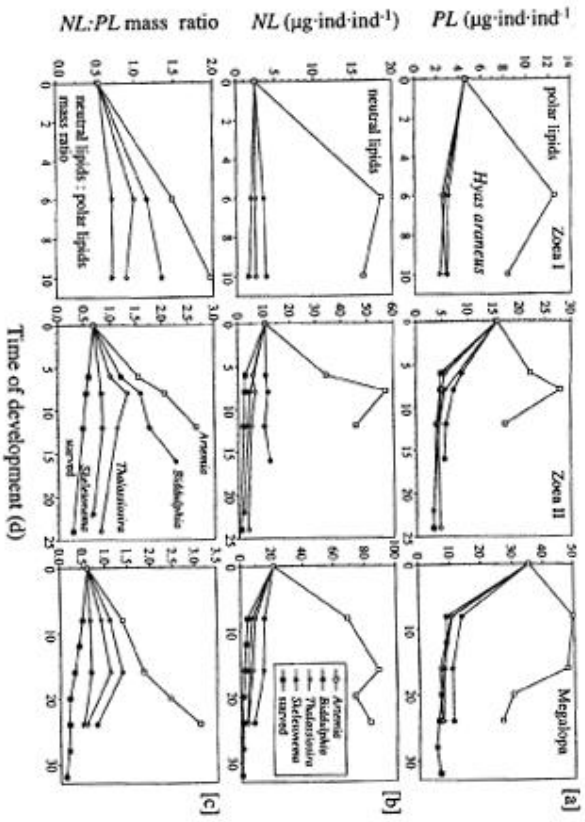


Figure 7.8. Developmental changes in the lipid composition of spider crab (*Hyas araneus*) larvae reared under five nutritional conditions in the laboratory: fed with *Artemia* nauplii, diatoms (*Biddulphia*, *Thalassiosira*, *Skeletonema*), or starved; contents (in µg/individual) of [a] polar lipids (*PL*); [b] neutral lipids (*NL*); [c] *NL*:*PL* mass ratio (redrawn after data from Selzer 1992, Harms & Anger, unpubl. data).

This comparison shows that the patterns of change in the contents of carbon, total lipid, and in the two major lipid classes (*PL*, *NL*) were similar, while that in the protein content was different. In general, carnivorous (*Artemia*-fed) crab larvae accumulated substantial amounts of all these components of food, while herbivorous (diatom-fed) and starved larvae showed stagnant or declining biomass values. According to all criteria used in this experimental series (rates of survival and development, gain or loss of *W*, C, N, H, total lipids, proteins), the tested feeding conditions can be ranked as follows, in a sequence of decreasing nutritional quality: *Artemia* > *Biddulphia* > *Thalassiosira* > *Skeletonema* > starvation. This pattern can be seen also in the average levels of *PL* and *NL* per individual (Figs. 7.8a, b). Among these treatments, a great discrepancy occurred between the *Artemia*-fed and all remaining experimental groups, while phytoplankton-fed and starved larvae were similar.

Well-fed larvae showed a consistent pattern in relation to the larval molting cycle. This was characterized by a steep increase during postmolt and intermolt (more pronounced in *NL*), followed by a decreasing trend during the premolt phase (more pronounced in *PL*). Similar patterns were observed in the contents of *C* and total lipids (cf. Figs. 7.4, 7.5). Thus, the initial phase of C and lipid accumulation is primarily based on a rapid deposition of energy reserves (mostly *NL*), but it includes also a fast synthesis of membranes and other cell materials (reflected in an increasing *PL* content). The protein pool, in contrast, increased gradually throughout the molting cycle or reached a plateau, but it did not decline during premolt.

The storage of *NL* is probably associated with an increase in the average size (or energy density) of cells, in particular of the R-cells of the hepatopancreas (see section 3.11.5). This process should be reflected by an increasing C:DNA ratio (for hypertrophy and hyperplasia as mechanisms of growth, see section 6.6.2). The synthesis of new tissues, in contrast, should be based on rapid cell multiplication, which is generally reflected by increasing DNA concentrations. The premolt decrease in the lipid fraction, particularly in *PL*, may be interpreted as a sign of substantial reconstruction processes prior to ecdysis, obtaining eventually priority over continued growth. This may include programmed cell death (apoptosis), at least when the megalopa stage approaches metamorphosis.

This interpretation is supported by further data from the same study. In the megalopa stage of *Hyas araneus*, where our analyses had a high temporal resolution allowing for an identification of molt-cycle related patterns, mono- and diacyglycerides (*MAG*, *DAG*) showed a maximum in early postmolt and, again, in late premolt. This indicates significant concentrations of *TAG* precursors (at the beginning) or degradation products (near the end of the molting cycle), respectively. *MAG* and *DAG* showed a minimum in early premolt, when total biomass (including *TAG*) approached a maximum.

The amounts of cholesterol increased throughout the first half of the molting cycle and decreased near ecdysis. Like the changes in the *PL* fraction (Fig. 7.8a), this pattern suggests a high rate of synthesis of cell membranes during the initial phase, probably associated with cell multiplication. In premolt, there appears to occur a degradation of membrane materials associated with reconstruction processes. Most probably, these processes of growth and development are under hormonal control, namely by the system of ecdysteroids produced in the Y-organs and by neuroendocrine factors from the eyestalk ganglia (cf. section 4.3).

Dietary effects become more clearly visible when we look at the relative lipid composition rather than at absolute quantities. The *NL:PL* quotient as a measure of proportional changes within the lipid fraction (Fig. 7.8c) indicates differential extents of energy accumulation or loss, respectively, in larvae fed with *Artemia* nauplii, large diatoms (*Biddulphia sinensis*), smaller diatom species (*Thalassiosira rotula*, *Skeletonema costatum*), or kept in complete absence of food. Under conditions of severe malnutrition (starvation, feeding with *T. rotula* or *S. costatum*), the crab larvae lost higher proportions of *NL* than *PL*. Under favourable conditions (feeding with *Artemia*), on the other hand, they gained more *NL* than *PL*. As a consequence, the *NL:PL* ratio showed a consistent and sensitive response to the various feeding levels. Hence, this quotient may represent a convenient indicator of the nutritional condition of decapod crustacean larvae and other zooplankton. However, it must be cautioned that also other kinds of stress can cause a similar (unspecific) response as we have seen in the *TAG:PL* ratio (see above).

In *Artemia*-fed *Hyas araneus* larvae, the *NL* fraction consisted of 55-66 % TAG, 25-37% cholesterol, and maximally 11% *MAG* and *DAG* combined; *FFA* played, with maximally 1.5% of total *NL*, only a minor role. Developmental patterns and dietary effects in total *NL* reflected those in their predominant component, *TAG*. In consequence, the percentage of *TAG* within the lipid fraction showed a clear response to diet, similarly as the *NL:PL* quotient (see Figs. 7.8c, 7.9a), corresponding also with the patterns of survival and development (cf. Harms et al. 1991).

Sterols, in contrast to *TAG*, tend to remain fairly stable at variable feeding conditions. Hence, also the *TAG*:cholesterol ratio has been proposed as a potential index of the physiological condition of fish, bivalve, and crustacean larvae (see Fraser 1989, Mourente & Rodríguez 1997, Harding & Fraser 1999). In larval *Hyas araneus*, however, this quotient appeared to be a less sensitive indicator of food quality than the quotients *NL:PL* and *TAG*:total lipid (Figs. 7.8, 7.9a, b). While the *TAG*:cholesterol ratio of the megalopa stage showed a similar pattern as the *TAG*:lipid relation, less clear patterns were observed in the zoeal stages. As expected, the index decreased under conditions of severe food limitation (feeding with *Skeletonema costatum* or starvation), but remained surprisingly high, at least initially, with diets of intermediate quality (*Biddulphia sinensis*, *Thalassiosira rotula*). This may be explained by the fact that sterols are essential food components and thus, should be preferentially accumulated until a certain amount of reserves has been stored for later use in cellular reconstruction processes. In *Artemia*-fed larvae, an initially rapid storage of sterols (accompanying the storage of *TAG*) may have limited the increase in the *TAG*:cholesterol ratio. Comparably high index values in larvae fed with phytoplankton, on the other hand, may have been caused by a low dietary cholesterol level which does not allow for a significant accumulation of cholesterol, but a deposition (or at least saving) of internally stored *TAG*.

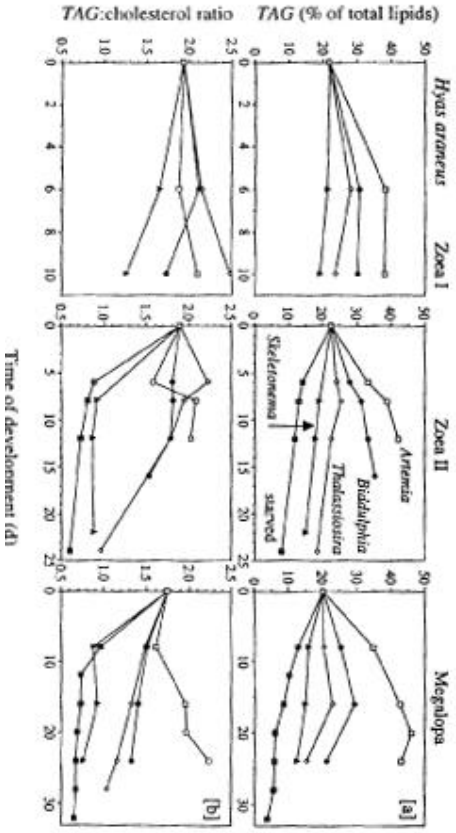


Figure 7.9. Developmental changes in the lipid composition of spider crab (*Hyas araneus*) larvae reared under five nutritional conditions in the laboratory: fed with *Artemia* nauplii, diatoms (*Biddulphia*, *Thalassiosira*, *Skeletonema*), or starved; [a] triacylglicerides (*TAG*, in % of total lipids); [b] *TAG*:cholesterol mass ratio (redrawn after data from Selzer 1992, Harms & Anger, unpubl. data).

In a recent study of growth and biochemical composition of lobster (*Homarus americanus*) larvae developing in their natural pelagic environment, Harding & Fraser (1999) showed a substantial increase in both *TAG* and sterols (Fig. 7.10). This was conspicuous not only in the average values of successive developmental stages, but also during the course of each molting cycle. Since the accumulation of *TAG* in reserve tissues depends on the overall level of food availability, this fraction showed in the field a great deal of variability, with maxima and minima differing by one order of magnitude within individual instars. By contrast, the sterol content varied much less, indicating that only limited quantities of this lipid class are required for the formation of membranes and other body structures, while a deposition of sterols in metabolically accessible energy reserves is insignificant. In the same study, the authors made also an interesting comparison between

field-caught and laboratory-reared lobster larvae, using the latter as a standard for the evaluation of nutritional condition in the plankton. Numerous field-caught lobster larvae had a similarly low *TAG*:cholesterol index as starved larvae in the laboratory (about 0.1), suggesting that food limitation plays a significant role in the pelagial, at least regionally.

The larvae of *Homarus americanus* showed in their *TAG*:sterol ratio a striking variability among developmental stages and feeding conditions. During development from hatching through premolt stage IV, the *TAG* fraction increased by three orders of magnitude, sterols by only one. In consequence, the *TAG*:sterol ratio increased through the course of pelagic development by a factor of several hundreds (total range measured: <0.1 to ca. 40; Fig. 7.10). In the larvae of *Hyas araneus*, by comparison, this index was much higher at hatching (1.9 *vs.* 0.1-0.7 in *H. americanus*), but it changed much less during development to metamorphosis, even under various feeding regimes (total range: 0.6-2.5). After continued starvation, the *TAG*:sterol ratio decreased in *H. araneus* to a minimum value of 0.6 (*vs.* <0.1 in lobster larvae). These findings suggest that an accumulation of energy reserves (primarily *TAG*) obtained from the feeding of plankton should be more crucial for the success of settlement and benthic recruitment in lobster larvae. Spider crab larvae have higher initial energy reserves, and they seem to utilize these more efficiently during development under variable nutritional conditions. In "postlarval" penaeid shrimps (*Melicertus kerathurus*) reared under different feeding regimes, the *TAG*:sterol ratio varied in a yet narrower range than in *H. araneus* (0.8-1.0; Mourente & Rodríguez 1997). In conclusion, interspecific comparisons of biochemical indices must consider also phylogenetic variation in their average level and responsiveness against nutritional and other stress factors.

7.5.2.3 Fatty acid composition

Fatty acids represent another crucial component of the lipid fraction, occurring bound to *NL* or *PL*, and as free molecules (*FFA*). Natural fatty acids show generally an even number of carbon atoms, because their biosynthesis is based upon the successive combination of acetate units. In the generally applied nomenclature, the total number of C atoms is indicated first, followed by the number and position of double C bonds. In the fatty acid 20:5n-3 (eicasopentaenoic acid), for instance, there are 20 C atoms with five double bonds in total, the first of these occurring between C atoms 3 and 4 (counted from the methyl end of the chain). Fatty acids with three or more double bonds are termed *highly unsaturated fatty acids*, *HUFA* (or poly-unsaturated fatty acids, *PUFA*).

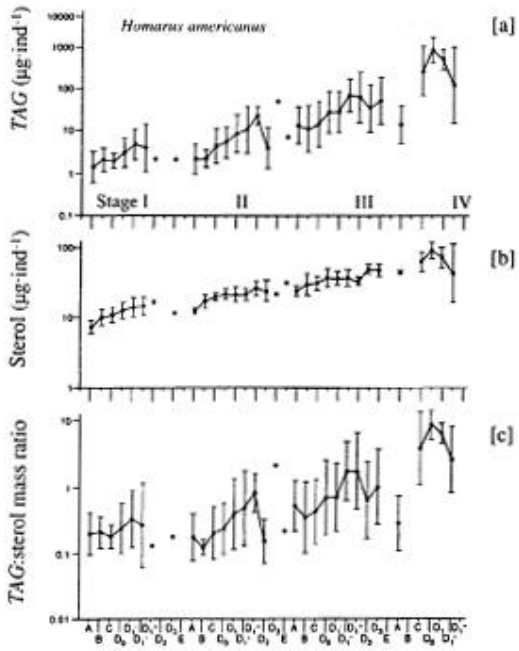


Figure 7.10. Developmental changes in the lipid composition of lobster (*Homarus americanus*) larvae caught from the field (Gulf of Maine, USA); letters A-E (bottom): stages of the molting cycle; [a] triacylglicerides, *TAG*; [b] sterol; [c] *TAG*:sterol mass ratio (redrawn after Harding & Fraser 1999, with permission from Inter-Research, Oldendorf, Germany).

As in most other biochemical aspects of growth, abundant data exist for the fatty acid concentrations in adult benthic Decapoda as well as in holoplanktonic crustaceans such as copepods or krill (see e.g. Floreto et al. 2000, Styrishave & Andersen 2000, Falk-Petersen et al. 2000, Cripps & Atkinson 2000, Virtue et al. 2000, and earlier literature cited therein). By comparison, little has been published on the composition of meroplanktonic decapod larvae. In larval crabs (*Menippe adina*), Nates & McKenney (2000a) observed predominantly the saturated fatty acids palmitic (16:0) and stearic acid (18:0). Within the total fatty acid pool, saturated fatty acids dominated with 49-72% throughout larval development, followed by the fractions of monounsaturates (11-24%), and *HUFA* (16-26%).

HUFA are generally considered as crucial the dietary compounds which have the greatest influence on larval survival, development, and growth (see section 5.2.1.3. Since most *HUFA* are essential food components (i.e. they cannot be synthesized *de novo*), the larvae do not normally utilize these dietary compounds as an energy source but incorporate them preferentially in their body tissues. During periods of starvation, lobster (*Homarus americanus*) larvae utilized monounsaturated fatty acids such as 16:1n-7 and 18:1n-9 to a greater extent than *HUFA*, but also more than their fully saturated analogues 16:0 and 18:0 (Sasaki 1984).

Due to the essentiality of many fatty acids, the *HUFA* profile reflects the composition of diet and, thus, the nutritional condition of larvae (Catacutan 1991; see also section

5.2.1.3). In freshly hatched zoea I larvae, variation in the *HUFA* content may indicate climatic or annual variation in the nutritional condition of females during oogenesis, which also affects the fitness, in particular the nutritional vulnerability of the larvae. In the North Sea shrimp (*Crangon crangon*), for instance, Kattner et al. (1994) observed during a particularly mild winter an additional reproductive period, but the eggs and early zoeae produced during that time showed an extremely low level of *HUFA*. Probably as a consequence of this poor condition, this cohort showed signs of a very high mortality in the plankton.

Relationships between larval nutrition and the *HUFA* content are again exemplified with our data from the spider crab *Hyas araneus* (Selzer, Anger, Harms; unpubl.). In *Artemia*-fed larvae, almost all fatty acids showed a significant increase. This type of food contained predominantly 18:1n-9 cis, 18:1n-9 trans, 18:2n-6, 18:3n-3, and 20:5n-3, while 20:0, 20:1n-9, and 22:6n-3 were particularly scarce. Consistent with these patterns, the concentrations of the most abundant dietary fatty acids increased at the highest rates during larval development, while the accumulation of less abundant molecule species was low or insignificant. Also in herbivorously fed spider crab larvae were the predominant dietary fatty acids accumulated at the highest rates. The diatom species that we tested as to their food value contained particularly high amounts of 22:6n-3, 20:5n-3, and 22:5n-6 (the latter except in *Thalassiosira*). *Biddulphia* had additionally also high levels of the saturated fatty acids 12:0 and 16:0. However, growth and survival of the herbivorously fed larvae remained poor, indicating that the *HUFA* richness of these diatoms did not suffice to compensate other deficiencies in their nutritional value. This was probably due to their low overall level of lipids. The fatty acid concentration per unit of *W* corresponded in *Biddulphia* to about one half, in the other two phytoplankton species to only one fourth of the mass-specific concentrations measured in *Artemia* nauplii.

8 METABOLISM

Development and growth imply conversions of matter and potential chemical energy originating either from ingested food or mobilized from internally stored reserves. These conversion processes are summarized under the term *metabolism*. One part of the assimilated or mobilized compounds can be utilized in synthetic pathways, allowing for an accumulation or reconstruction of tissue materials. Another part is degraded in catabolic pathways, so that chemically bound energy is converted to the universal cellular energy current, ATP. This nucleotide is utilized in numerous processes of life, including the biosynthesis of macromolecules, maintenance of complex structures, locomotion, digestion, etc. (Hochachka 1997).

The intermediary metabolism of the Crustacea does not differ in its principal components and mechanisms from that of most other organisms, i.e. the majority of the metabolic processes depends on the consumption of oxygen (Wolverkamp & Waterman 1960, Hochachka & Somero 1984, Burggren & Roberts 1994). Anaerobic processes play a significant role too, at least in those species or life-history stages that live in stagnant aquatic habitats or other chemically reduced environments (Livingstone 1991). However, the marine pelagial, where most decapod larvae develop, is in general well oxygenated and has thus not selected for special physiological adaptations to anaerobic conditions. In consequence, the rate of larval *oxygen consumption* (commonly referred to as *respiration*) is highly correlated with the overall rate of metabolic processes. As alternative methods for a quantification of the metabolic rate, heat dissipation may be measured with calorimetric techniques (Sprung & Widdows 1986), or the activity of the electron transfer system can be determined biochemically (Owens & King 1975, Båmstedt 1980, Packard 1985).

As another important aspect of the metabolism in animals, nitrogeneous and phosphoric compounds originating from the degradation of macromolecules are excreted (summarized as *excretion*; for review of nitrogen metabolism in crustaceans, see Claybrook 1983, Greenaway 1991, 1999). In this chapter, I will first briefly discuss the potential significance of the adenylate energy charge as a measure of metabolically available energy, the relationships between oxygen consumption and the activity of the electron transfer system, and developmentally and environmentally induced changes in larval respiration and excretion. Eventually, the quantitative relation between these metabolic parameters, the O:N quotient, is discussed as an indicator of the predominant biochemical substrate of energy production.

8.1 *Adenylate nucleotides and energy charge*

The metabolic energy that is potentially available from the adenylate pool to an organism is commonly estimated from measured concentrations of *adenosine-5´–triphosphate* (ATP), *–diphosphate* (ADP), and *–monophosphate* (AMP), using the *adenylate energy charge*, *AEC*, as an index (Atkinson & Walton 1967, Atkinson 1968):

$$AEC = \frac{\mathrm{ATP} + 0.5\,\mathrm{ADP}}{\mathrm{ATP} + \mathrm{ADP} + \mathrm{AMP}} \tag{8.1}$$

While this quotient can theoretically vary between 0 and 1, healthy organisms show normally *AEC* values ranging from 0.8 to 0.9 (Atkinson 1968). Hence, the *AEC* has repeatedly been proposed as a quantitative index of the physiological state of organisms, indicating effects of pollution or other kinds of stress (see e.g. Ivanovici 1980, Romano & Daumas 1981).

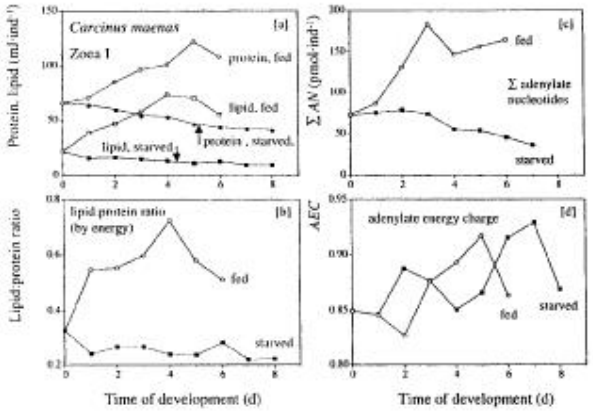


Figure 8.1. Biochemical and physiological changes in shore crab larvae (*Carcinus maenas*, zoea I), fed with *Artemia* nauplii or starved; [a] protein, lipid contents, expressed in units of chemically bound energy (mJoules/individual); [b] lipid:protein ratio (by energy content); [c] total concentration of adenylate nucleotides, $\sum AN$; [d] adenylate energy charge, *AEC* (redrawn after data from Harms et al. 1990).

The *AEC* has been measured in adult crustaceans such as crayfish, crabs, and lobsters (e.g. Dickson & Giesy 1982, Dehn et al. 1985, Schirf et al. 1987, Harris & Santos 2000) but rarely in larvae. Experimental data are available for the nucleotide composition in fed and starved stage I zoeae of the shore crab, *Carcinus maenas* (Harms et al. 1990), and for all larval stages of the spider crab, *Hyas araneus*, fed with different diets (Harms 1992a). Some of the results from the former study are shown in Fig. 8.1 as examples of both molt-cycle related and nutritionally imposed changes in the concentrations of the predominant nucleotides and in the *AEC*.

Under conditions of *ad libitum* feeding and starvation, respectively, the biomass and chemical composition of the zoea I of *Carcinus maenas* showed the typical patterns of biochemical change (Fig. 8.1a; cf. section 7.3, Fig. 7.5). While well-fed larvae rapidly enhanced their lipid stores, the same biochemical fraction was in the absence of food primarily utilized as a substrate for energy production, in this case originating from remaining egg yolk reserves. As a consequence of these changes in the lipid fraction, accompanied by a relatively stable protein content, conspicuous shifts occurred in both experimental

groups also in the lipid:protein ratio (expressed here in energy equivalents; Fig. 8.1b). This change in the biochemical composition was most pronounced during the initial phase of feeding or starvation. During the premolt phase of the molting cycle and after prolonged periods of starvation, by contrast, proportionally more protein than lipid was accumulated or degraded, respectively, causing a reversal of these trends.

These changes in total biomass and proximate biochemical composition during the course of the molting cycle or in response to feeding conditions were clearly reflected in the total content of adenylate nucleotides ($\sum AN$; Fig. 8.1c). Among these, ATP was consistently the predominant compound, generally followed by ADP and AMP. Other nucleotides such as uracil and guanosine triphosphate (UTP, GTP) occurred in lower concentrations. Their quantities increased prior to ecdysis, reaching up to 30% of $\sum AN$. It is interesting to note that $\sum AN$ and ATP increased in fed larvae only until molt-stage D_0, then they remained at a constant level. Another remarkable finding was that an initial increase in ATP occurred also in starved larvae, both per individual and in biomass-specific terms. A decrease in the individual ATP content began only after more than four days of starvation, indicating a gradual depletion of energy reserves.

As a consequence of this variation in ATP, also the *AEC*, i.e. the proportion of ATP in relation to other nucleotides, showed complicated patterns of change. These, however, did not generally reflect the nutritional state of the larvae (Fig. 8.1d). In well-fed larvae, the *AEC* decreased from hatching to the beginning of molt-stage *C* (days 0-2), increased throughout the intermolt and major parts of the premolt phase, and decreased again before ecdysis. In starved larvae, the index showed two peaks, namely about 2 days and again 6-7 days after the onset of starvation. In experiments where the zoeae were initially fed but later starved, the response patterns in $\sum AN$ and *AEC* depended on the timing of food deprivation (Harms et al. 1990): Starvation beginning after the D_0 threshold (see section 4.5.2) allowed for successful development to the zoea II stage, and the nucleotide concentrations changed in a similar fashion as in continually fed larvae. An earlier onset of starvation, in contrast, caused similar changes in larval biomass and nucleotide composition as in the continually starved group.

Similarly as in *Carcinus maenas*, changes in $\sum AN$ but not in *AEC* reflected the feeding level in *Hyas araneus* larvae (Harms 1992a). This suggests that the *AEC* is, at least in some species of crab larvae, not a good indicator of nutritional stress. Presumably, the larvae are able to regulate their energy pool as long as metabolizable reserve stores or some food is available, even if this is insufficient for development. In starved *C. maenas* larvae, the patterns of change in the *AEC* (Fig. 8.1c) may thus be interpreted with two subsequent phases of reserve mobilization: (1) a rapid degradation of the energetically rich but quantitatively minor lipid reserves allows initially for a temporary enhancement of the ATP pool; the *AEC* declines subsequently, when the metabolically available lipids (mostly *TAG*, see section 7.5.2) are depleted; (2) protein is later increasingly utilized as a substrate for energy production, allowing for another increase in the *AEC*; this declines again, when also the metabolizable parts of this biochemical reserve are depleted.

The patterns observed in fed larvae, by contrast, appear to indicate that the initially fast storage of lipid reserves (see Fig. 8.1b) requires major quantities of metabolically available energy, leading to an initial decrease in the *AEC*. These synthetic processes appear to slow down in intermolt, allowing for a gradual increase in the *AEC* throughout major parts of the molting cycle. Another decrease in the *AEC* occurred in late premolt, coinciding with a decrease in total larval biomass and in the lipid:protein ratio (Figs. 8.1a, b). The fi-

nal drop in major biochemical reserves and in the *AEC* reflects most probably the increasing energy demands of the molting process, accompanied by an interruption of feeding. This was suggested also by Lim & Hirayama (1993), who observed cyclic changes, with minima at each ecdysis, in the dry mass-specific ATP content of portunid crab (*Portunus trituberculatus*) larvae.

8.2 *The electron transfer system (ETS)*

The consumption of oxygen (respiration, in the literature usually denoted with the symbol VO_2) is in eukaryotic organisms primarily due to processes of oxidative phosphorylation, which take place in proteinaceous structures embedded in the inner lipoprotein membrane of the mitochondria (Lehninger et al. 1993). These metabolic processes, in which electrons are transferred from organic substrates to O_2, are driven by a complex of at least two classes of enzymes, collectively referred to as respiratory "electron transfer system" (or "electron transport system"), *ETS*. Biochemical measurements of the *ETS* activity (*ETSA*) determine the maximum velocity of electron transfer by NADH-, NADPH-, and succinate dehydrogenases in the respiratory system (for details of assays, see Owens & King 1975, Packard & Williams 1981). Hence, the *ETSA* may be considered as an estimate of the potential (maximally possible) rate of respiration. In contrast to VO_2, the *ETSA* does not appear to vary with the physiological state of the cells (Martinez 1992). Hence, the VO_2*:ETSA* quotient was proposed as an index of *"respiratory efficiency"* of an organism (Savenkoff et al. 1995). Higher than normal values (approaching the theoretical maximum of 1.0) should thus indicate an increasing oxygen consumption in response to higher energy needs, e.g. under exposure to physiological stress. Low index values, on the other hand, should reflect a relaxed state with a high level of remaining reserves for metabolic energy production.

In pink shrimp, *Pandalus borealis*, both VO_2 and *ETSA* per individual increased throughout larval development, while the weight-specific metabolic rates decreased (Savenkoff et al. 1995; Fig. 8.2a). As should be expected theoretically, and in agreement with observations from other plankton (e.g. Del Giorgio 1992), these two independent measurements of metabolic intensity showed a significant positive correlation. However, the developmental increase in successive larval stages was clearly stronger in *ETSA* than in VO_2. In consequence, the VO_2*:ETSA* ratio decreased throughout larval development from about 0.66 after hatching (zoea I) to 0.21 in the decapodid stage (larval instar VI; Fig. 8.2b). This trend in the "respiratory efficiency" index suggests that the earliest larvae are most vulnerable, while older larvae attain an increasing scope for metabolic response to stress (a "leftover capacity"), i.e. a greater ability to manage stress. This conclusion was supported by previous observations in *P. borealis* larvae, where the earliest stages showed the lowest tolerance of nutritional stress (Saotome & Ikeda 1990, Ouellet et al. 1992).

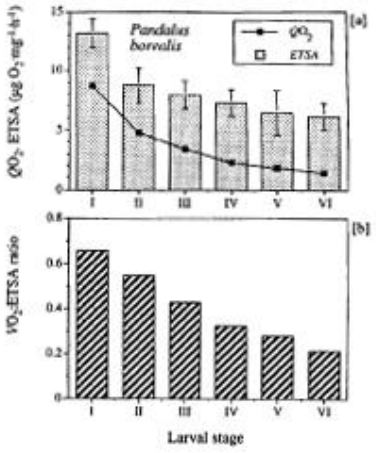


Figure 8.2. Ontogenetic changes in the metabolism of successive larval stages of a shrimp, *Pandalus borealis*; [a] weight-specific rate of oxygen consumption (QO_2) and electron-transport system activity (*ETSA*); [b] quotient of individual oxygen consumption (VO_2) to *ETSA* (redrawn after data from Savenkoff et al. 1995).

Thus, an index based on the relationships between VO_2, *ETSA*, and stress tolerance seems to provide a useful tool for the comparative assessment of the physiological state of an organism. However, this has been tested only little and with controversial results in decapod crustacean larvae. When St-Amand et al. (1999) exposed *Pandalus borealis* larvae to various concentrations of mercury (40-160 ppb), the larvae responded consistently with a decrease in both VO_2 and the VO_2*:ETSA* ratio. This toxic effect on the "respiratory efficiency" was opposite to that predicted by Savenkoff et al. (1995), who expected an increase in VO_2 but a decrease in the presumable "leftover capacity". The metabolic depression observed in these experiments probably reflects an increasing inhibition of the locomotory and respiratory activity of the larvae. On the biochemical level, St-Amand et al. (1999) suggested that it may indicate a disturbance of substrate formation reactions before the respiratory chain, e.g. due to an alteration of glycolysis (for review of the energy metabolism in crustaceans, see Chang & O'Connor 1983).

In conclusion, the VO_2:ETSA ratio can presently not be used as a simple and universal indicator of a physiological response to severe stress. Yet, it might be useful for the detection of weak, sublethal effects draining parts of the assimilated energy away from the synthetic pathways into energy production, i.e. reducing the scope for growth (see section 9.1). In future research, it should thus be worth-while to compare rates of larval respiration, *ETSA*, growth, development, and survival under favourable and moderately stressful conditions. Likewise, the physiological basis and the significance of ontogenetic changes in the VO_2*:ETSA* ratio should deserve attention in future research.

8.3 *Respiration*

Among the intrinsic factors exerting an influence on the rate of respiration (VO_2), there are phylogenetic differences among taxa, behavioral variation in locomotory activity, effects of body size, developmental stage, and hormonal control factors related to growth, regeneration, morphogenesis, and the molting cycle (Christiansen 1988, Chang 1995). These intrinsic patterns are overlayed by effects of environmental variables such as nutrition, the concentrations of respiratory gases (O_2, CO_2), temperature, and osmotic pressure of the medium (for general review, see e.g. Kinne 1967, Vernberg 1983).

Most measurements of respiration rate have been made in an intermediate state of an animal's activity, somewhere between the basal rate and fully active metabolism. Although this condition (commonly referred to as "routine metabolism") is not well defined, it has commonly been accepted as a fairly good approximation of the average oxygen requirements of an organism (Wolvekamp & Waterman 1960, Newell 1979). The experimental error due to variation in activity is probably considerable in large benthic crustaceans such as lobsters and crabs, where inactive, sluggish behavior may alternate with short periods of full activity, e.g. during prey capture, escape from predators, intraspecific aggression, etc. By contrast, this variability should be small in constantly swimming animals including most zooplankton. Since no quantitative information is available on activity-related variation in the respiration rate of larval decapods, I will ignore this aspect, considering it here as negligible.

In the following sections, I will illustrate the dependence of the metabolic rate on major intrinsic and extrinsic factors, namely body size, larval stage, the molting cycle, food availability, concentration of available oxygen, temperature, and salinity. Effects of pollution will be dealt in more detail in the context of bioenergetics (section 9.4.3), because in most experimental studies of larval respiration under the influence of toxic chemicals also aspects of development and growth were considered, sometimes also changes in feeding and in the overall patterns of energy partitioning.

8.3.1 *Body size and developmental stage*

Body size is obviously one of the most crucial intrinsic determinants of the respiration rate per individual, VO_2 (Zeuthen 1953, Bertalanffy 1957). Although the use of weight-specific values implies, in general, various statistical problems (for recent discussion, see Packard & Boardman 1999), we need to eliminate or reduce the influence of size before effects of other factors can be compared. This normalization is commonly achieved with the calculation of weight-specific respiration values (denoted with the symbol QO_2; see below). As a reference base for QO_2, I will use here dry mass (W, in µg or mg) rather than wet mass (FW), because the latter is generally a poor measure of living matter (see sections 6.2.3, 7.1.1). As a dimension of VO_2, I am using µg $O_2 \cdot ind^{-1} \cdot h^{-1}$. Some authors prefer units of gas volume (µl) rather than mass units (µg); these measures can be converted into each other using a factor of 1.4 µg/µl (the specific mass per unit volume of oxygen). However, the exact value of this conversion factor depends on temperature and atmospheric pressure.

The general relationship between individual body dry mass (W) and respiration (VO_2) is commonly expressed with a simple allometric equation (Zeuthen 1953, von Bertalanffy 1957, Wolvekamp & Waterman 1960, Ivleva 1980):

$$VO_2 = a \cdot W^b \tag{8.2}$$

Following the predominant use in the literature, the fitted coefficients *a* and *b* represent here the intercept with the Y-axis and the slope, respectively, in the linearized form of this function (after logarithmic transformation of both the X and Y data; cf. size-weight relationships in section 6.2; Eqs. 7.8, 7.8a).

The mass exponent *b* varies generally between ca. 0.67 and 1.0, indicating that the metabolic rate is proportional to the animal's body surface area (0.67), to it's volume (1.0), or something in between. In most crustaceans (including larvae), the *b* value is intermediate between these theoretical extremes (Wolvekamp & Waterman 1960, Ivleva 1980). A recent analysis of extensive data sets from larval, juvenile, and adult fish showed that this general relationship holds, in principle, over a biomass range of several orders of magnitude, with an ontogenetically decreasing trend in the mass exponent (Bochdansky & Leggett 2001).

Variation in the exponent *b* may be caused by changes in the relation between body shape and volume, in the proportions of living protoplasm and metabolically inert components of biomass (e.g. skeletal materials, fat reserves, etc.), and by overlaying external (ecological) factors. In several studies with decapod crustacean larvae, *b* values above the hypothetical limit of *b*=1 were measured, usually associated with physiological stress. In caridean shrimp (*Palaemon serratus*) larvae, for instance, such high *b* values were observed at the least favourable conditions of temperature and salinity (13°C,13‰S; Yagi et al. 1990). Similarly, *b*>1 was measured in brachyuran crab larvae exposed to unfavourable temperatures (*Cancer irroratus*: 10°C, Johns 1981; *Carcinus maenas*: 25°C, Dawirs 1983). Also in lobster (*Homarus americanus*) larvae, an unusually high value (*b* = 1.24) was found (Capuzzo & Lancaster 1979b). However, a much lower *b* was obtained in another investigation on the same species reared under similar conditions (Logan & Epifanio 1978), suggesting that the former observation might have been associated with some unknown stress related to the culture conditions.

The weight-specific respiration rate (QO_2) is obtained by division of Eq. 8.2 by dry mass (*W*, in mg):

$$QO_2 = \frac{VO_2}{W} = a \cdot W^{(b-1)} \tag{8.3}$$

The dimension of QO_2 is thus $\mu g\ O_2 \cdot mg^{-1} \cdot h^{-1}$. Since the constant *b* is in general below 1.0, the exponent of this function (in Eq. 8.3 in parentheses) becomes negative. This implies a decrease in QO_2 with increasing *W*. The parameter *a* represents the respiration rate of a "unit animal" (i.e. of an individual with 1 mg dry mass) at a given condition.

Both regression parameters, *a* and *b*, vary not only among species and developmental stages, but also with temperature and other environmental factors (for recent discussion of the general comparative ecological and evolutionary significance of mass-specific respiration, see McNab 1999). When parameter *b* in Eq. 8.2 is close to a value of 1.0, the exponent in Eq. 8.3 becomes practically zero. In this case, QO_2 remains constant near a value of *a*, and thus, no correlation exists between QO_2 and *W*. Examples of size-independent variation in the weight-specific respiration rate were observed in larval shrimps and crabs (*Palaemon serratus*, Yagi et al. 1990; *Libinia emarginata*, Schatzlein & Costlow 1978; *Cancer irroratus*, Johns 1981).

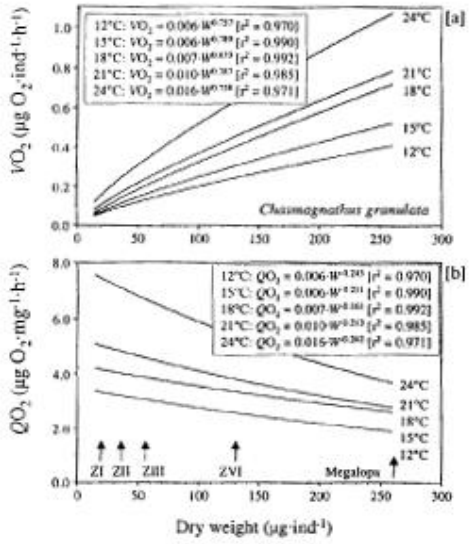


Figure 8.3. Relationships between biomass (dry mass, *W*) and metabolic rate in brachyuran crab (*Chasmagnathus granulata*) larvae reared at various temperatures; fitted regression equations and coefficients of determination, r^2; [a] respiration rate per individual, VO_2; [b] weight-specific rate, QO_2; arrows indicate molts to successive larval stages (redrawn after Ismael et al. 1997).

Since feeding larvae gain weight during the course of development, successive stages show normally a clear increase in VO_2 and a decrease in QO_2. The latter trend is probably associated with a disproportionate increase of metabolically inactive materials such as deposited fat and cuticular matter. The general relationships between VO_2, QO_2, and *W* (Eqs. 8.2, 8.3) are illustrated in Figure 8.3, using the larval stages of a grapsid crab (*Chasmagnathus granulata*) as a typical example. These graphs demonstrate also the influence of temperature on the relation between metabolic rates and *W* (cf. section 8.3.5). Similar relationships were described for larvae of numerous other decapod species (Mootz & Epifanio 1974, Schatzlein & Costlow 1978, Moreira et al. 1981, Vernberg et al. 1981, Dawirs 1983, Anger & Jacobi 1985, Jacobi & Anger 1985a, McNamara et al. 1985, Kurmaly et al. 1989c, Saotome & Ikeda 1990).

An increasing QO_2 with increasing *W* (i.e. a coefficient $b>1$ in Eq. 8.2 and a positive exponent in Eq. 8.3) was observed only exceptionally. In shore crab (*Carcinus maenas*) larvae, for instance, the data presented by Dawirs (1983) indicate an interaction of developmental and thermal effects. Ontogenetically changing response patterns suggest that the late larval stages of this species were particularly sensitive to high temperature stress, enhancing their respiration rate more than the earlier stages. As another exception from the rule, QO_2 was in the shrimp *Palaemon serratus* maximum in an intermediate larval stage, the zoea IV (Yagi et al. 1990). In this case, an enhanced metabolic demand was interpreted as a result of dramatic developmental changes in the mode of feeding, from her-

bivorous (or omnivorous) to carnivorous, probably accompanied by a sudden increase in the number of hepatopancreatic cells and tubules (Richard 1978) and a significant increase in the activity of protease (van Wormhoud 1973). Such changes should be associated with an increasing turnover of dietary matter and energy.

VO_2 and QO_2 values measured in decapodid stages were commonly lower than should be expected from the trends observed throughout the preceding zoeal development. This abrupt decrease in the metabolic activity is associated with profound developmental changes, including a transition from pelagic swimming to benthic crawling and, commonly, decreasing rates of growth and feeding. In species with fully lecithotrophic larvae, there are no interactions between metabolism and feeding, so that effects of the change in life style (from planktonic to benthic) are more conspicuous. This was documented, for instance, as a sudden drop in QO_2 at the transition from the zoea III to the megalopa (both are nonfeeding stages) of the stone crab, *Lithodes maja* (Anger 1996b). This developmental decrease in the metabolic activity is further enhanced in species where the pelagic zoeae are feeding stages but the megalopa becomes not only benthic but also secondarily nonfeeding; this was observed in the megalopa of some hermit crab species and in the puerulus of spiny lobsters (for secondary lecithotrophy, see section 5.1.2).

8.3.2 *Molting cycle*

Effects of the developmental increase in body size and biomass on individual or weight-specific respiration rates have been documented for the successive larval stages of numerous decapod species (for review, see Schatzlein & Costlow 1978, Anger 1991a). However, only few experimental studies showed a sufficiently high temporal resolution to allow for an identification of molt-cycle related changes in larval metabolism. In larvae developing and growing under constant, unlimited feeding conditions, VO_2 increases normally throughout the molting cycle. The increase in VO_2 was gradual in the zoeae of two species of spider crab (*Hyas araneus*, *H. coarctatus*; Anger & Jacobi 1985, Jacobi & Anger 1985a, Anger et al. 1989a), in the early zoeal stages of a hermit crab (*Pagurus bernhardus*; Anger et al. 1990b), and in the larvae of a caridean shrimp (*Macrobrachium nipponense*; Shin & Chin 1994). This correspondence in various stages and taxa suggests that larval respiration may typically change as a linear function of the developmental time within an instar (see Fig. 8.3a). On the other hand, only a weak molt-cycle related increase or inconsistent variation was found in the late zoeal stages of *P. bernhardus* and in the larvae of another spider crab, *Libinia ferreirae* (Anger et al. 1989b, 1990b). In the megalopa stage of the two *Hyas* species and, less clearly, in that of *L. ferreirae*, sigmoidal patterns were found, which may be described with a third-order polynomial regression equation (see Anger & Jacobi 1985, Jacobi & Anger 1985a; see Fig. 8.3b).

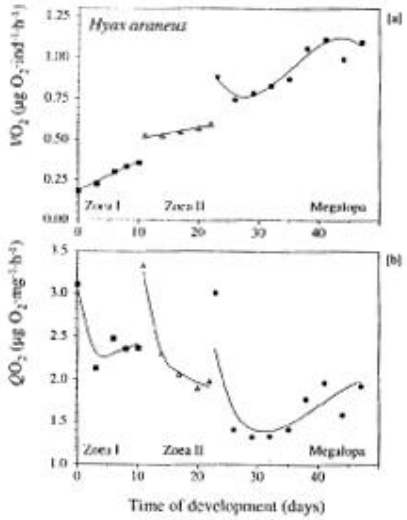


Figure 8.4. Ontogenetic changes in the metabolic rate during development through successive molting cycles of brachyuran crab (*Hyas araneus*) larvae reared at constant temperature (12°C); [a] respiration rate per individual, VO_2; [b] weight-specific rate, QO_2; for regression models see text (redrawn after Anger et al. 1989a).

Due to the scarcity and inconsistency of the available data, it is presently not possible to identify a universal relationship between VO_2 and the time within the molting cycle of decapod crustacean larvae. As a safe generalization, one can only say that larval respiration changes in most cases significantly during the time of each individual instar. This implies that single ("representative") respiration measurements will not yield reliable estimates of the average metabolic rate in successive larval stages. As a minimum requirement, it appears to be necessary to relate physiological measurements to well specified, microscopically checked stages of the molting cycle.

The weight-specific respiration rate (QO_2) of decapod crustacean larvae showed generally a maximum in early postmolt, followed by low and particularly stable values in intermolt (molt-stage *C*), and sometimes a weak increase throughout the premolt stages (Fig. 8.4). This is consistent with observations in adult crustaceans, where metabolic activity was found to be minimum during intermolt, and enhanced shortly before and after ecdysis (see Hagerman 1976, Penkoff & Thurberg 1982). Maximum metabolic activities during postmolt and premolt may be explained by energy-consuming reconstruction processes, while the minimum in molt-stage *C* coincides with a phase of little structural change. As a practical consequence of this recurrent pattern, "representative" measurements of QO_2 in a given larval instar should be taken during the metabolically stable molt-stage *C*, where small errors in the timing of measurements are less critical; the metabolic

rate may be further stabilized by a short fasting period, excluding the specific-dynamic effect of feeding (see following section). It must be considered, however, that the intermolt value may underestimate the average metabolic level in a given instar.

8.3.3 *Feeding and starvation*

Feeding has an immediate enhancing effect on respiration rate, representing the energetic costs of digestion. This effect is commonly referred to as *"specific-dynamic action"*, *SDA* (Lehninger et al. 1993), or *"apparent heat increment"* (e.g. Rosas et al. 1996). It varies more with the quality than with the quantity of food taken up. When the food is rich in protein, the *SDA* may reach 20-30% of the "metabolizable energy" (see section 9.1). On the other hand, it is low (4-8%) when carbohydrates or lipids predominate in the diet (Wieser 1986). When juvenile caridean shrimps were fed with protein-rich animal prey, their respiration rate was enhanced by up to 43%, whereas a consumption of benthic algae caused an increase by only 7% (Nelson et al. 1977, 1985). Also in "postlarvae" of several species of penaeid shrimps (in this case probably referring to decapodid stages), the *SDA* increased with increasing protein content of the diet (Rosas et al. 1996).

Very few quantitative data on this aspect are available for larval decapods. Since larvae differ from the adults in the type and habits of feeding (plankton *vs.* deposit feeders; continuous activity *vs.* interval feeding), it should be interesting to study ontogenetic changes in the level and duration of the *SDA* effect. In lobster (*Homarus americanus*) larvae, values ranging from 17 to 64% were reported, with a duration of up to 48h after feeding (Logan & Epifanio 1978, Capuzzo & Lancaster 1979a). However, some of these estimates appear to be very high and may not generally apply to larval decapods.

Besides showing a short-term response to food uptake, larval respiration may continually be affected by variation in the quality or quantity of available food, ranging from complete absence (starvation) to *"ad libitum"* (i.e. entirely unlimited) feeding conditions; the latter are typical of most laboratory experiments. When planktivorous decapod larvae, which generally have only a low level of internal energy reserves, are exposed to conditions of famine, they respond consistently and almost immediately with a reduction of their metabolic activity (Fig. 8.5). As a consequence of this energy saving effect, the *W*-VO_2 relationship (Eqs. 8.2, 8.3) shows a shift towards a lower level of metabolism in relation to body size (Logan & Epifanio 1978). This response is wide-spread among zooplankton and most other poikilothermal animals (Ikeda 1974, Mayzaud 1976, Calow 1977a). In continuously starved larvae of *Carcinus maenas*, for instance, VO_2 decreased to about 40% of the initial values (Dawirs 1983), in *Hyas araneus* larvae to 12% (Anger 1986).

The pattern of decrease in the individual respiration rate (VO_2) can be described as a logarithmic function of the time of starvation (*t*, in days; cf. Fig. 8.5a):

$$VO_2 = a + b \cdot \ln (t+1) \tag{8.4}$$

The parameters *a* and *b* are again fitted regression constants. The *t* values are transformed to (*t*+1) to avoid zero values; the initial day (0) becomes thus 1, its logarithm 0 (cf. section 6.2; Eq 6.10).

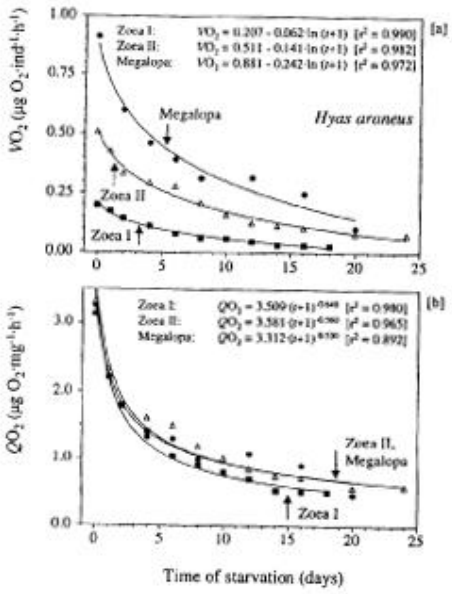


Figure 8.5. Changes in the metabolic rates of successive larval stages of a brachyuran crab (*Hyas araneus*) during starvation; [a] respiration rate per individual, VO_2, [b] weight-specific rate, QO_2, as functions of the time of starvation (t, in days); r^2: coefficients of determination for fitted regression equations (after Anger 1986).

Naturally, starved larvae lose significant amounts of organic biomass, in spite of the energy-saving metabolic response. If the reduction in larval weight (W) were proportionally equal to that in VO_2, then the weight-specific metabolic rate (QO_2) would remain constant (cf. Eq. 8.3). However, not all biomass is available as a substrate for metabolic energy production and thus, W cannot possibly be reduced to a similarly low level as VO_2. In the larval stages of *Hyas araneus*, W decrased maximally by 10-20%, while VO_2 decreased by up to 88%. In consequence, not only VO_2 but also QO_2 will decrease during starvation.

The reduction in QO_2 is very rapid during the initial phase of starvation but weak therafter; this typical hyperbolic pattern is illustrated in Figure 8.5b. In *Hyas araneus*, it was described with best fit as a power function of the time of starvation (regression parameters as in Eq. 8.4; b is a negative value):

$$QO_2 = a \cdot (t+1)^b \qquad \text{(Eq. 8.5)}$$

The particularly rapid initial decrease in QO_2 is actually an effect of our choice of W as a reference base for biomass-specific respiration rate; such a steep decline does not occur in VO_2 (cf. Fig. 8.5a). This discrepancy is due to the rapid, in principle food-independent postmolt increase in the mineral fraction (see section 7.1, Fig. 7.2), and hence, in total W.

The initial decrease in the metabolic rate appears thus more gradual when we use carbon rather than W as a reference base for QO_2.

After extended periods of starvation, the rates of decrease in both VO_2 and W level off, and QO_2 may eventually remain almost constant at a low level (Fig. 8.5b). This indicates that physiological limits are reached, with a condition of largely exhausted energy reserves, where no further reductions of respiration and biomass are possible.

If starvation begins during the postmolt or early intermolt period (i.e. before the *PRS* or D_0-threshold is reached; see section 4.5.2), the metabolic energy saving mechanisms include a suspension of the molting cycle (except for endocuticle secretion; see Anger & Nair 1979, Anger 1984a). According to preliminary observations, the metabolic response to famine changes after the D_0-treshold. When larvae have surpassed this critical point in the molting cycle, they have gathered sufficient internal energy reserves to develop to the next instar in further absence of food. Hence, the metabolism shifts to the developmentally controlled patterns, which are typical of favourable nutritional conditions (see section 8.3.2). Since substantial reconstruction processes take place during premolt, in particular in the epidermal tissues, both VO_2 and QO_2 tend to increase throughout molt-stage D, independent of feeding or starvation. However, this relationship between the metabolic response to starvation and critical points in the molting cycle needs to be scrutinized with further experiments.

Starvation over an extended period represents an extreme scenario that is not likely to occur in the natural environment. Hence, the relationships shown above serve us only to define the lower end of a scale of nutritional conditions that do exist and may be encountered by decapod larvae; the other end is the equally unlikely condition of *ad libitum* food concentrations. Between these extremes, there is a continuum of more or less food-limited conditions, where food is available in suboptimal quantity or quality (see section 5.1), and the pattern of metabolic change during development are intermediate between those described in Figures 8.4 and 8.5.

At intermediate, ecologically realistic feeding levels, stage VIII larvae (probably decapodids) of the prawn *Macrobrachium rosenbergii* showed only a weak respiratory response to differential food qualities, while great changes occurred in the caloric ingestion and growth (Sick 1976). Similarly, when megalopae of the crab *Hyas araneus* were fed exclusively with diatoms (*Biddulphia sinensis*), their respiration (VO_2) was reduced by only 18%, but growth decreased by more than 90% as compared to an *Artemia*-fed control group (Harms & Anger 1990). As a consequence of the unequal deceleration of biomass and respiration per individual, the weight-specific metabolic rate (QO_2) was found to increase rather than decrease under suboptimal feeding conditions.

This effect seems paradoxical, because it is opposed to the energy-saving mechanism that has generally been observed during continued starvation. However, it is consistent with a relatively high oxygen demand for the oxydation of fat (high respiratory quotient, *RQ*; see section 9.1.3). High metabolic rates should allow also for a high level of activity, including constantly high or increasing efforts to search for prey when nutritional stress is incipient. This effect is associated with changes in the chemical composition of larval biomass. Nutritional effects (i.e. changes in the rates of accumulation or degradation) are always particularly strong in the fraction which serves as the predominant energy store; in decapod larvae, such reserves are primarily concentrated in the lipid deposits of the hepatopancreas. These materials are preferentially utilized during undernutrition, while protein stores are generally conserved. Since the maintenance of protein-dominated tissues (e.g.

integuments, nervous and circulatory systems, muscles, etc.) continues to require metabolic energy, VO_2, may remain constant or decreases only insignificantly. On the other hand, the metabolically almost inactive lipid stores are reduced, due to decelerating accumulation or increasing degradation, so that total body mass decreases and, in consequence, the biomass-specific respiration rate increases.

Simliar patterns with constant or increasing weight-specific respiration rates should occur also during endotrophic development. This was observed, for instance, in fully or facultatively lecithotrophic zoeae of shrimps and crabs, where swimming activity is generally high and independent of food, and where metabolically inactive lipid stores are gradually converted into actively respiring tissues (McNamara et al. 1980, Anger & Schuh 1992, Anger 1996b).

On the other hand, extremely low QO_2 values were observed in fully or partially lecithotrophic decapodid stages of several anomuran, brachyuran, and palinurid species (Dawirs 1984b, Anger et al. 1990b, Anger & Schuh 1992, Lemmens 1994, Anger 1996b). During and shortly after molting to these stages, the QO_2 showed in general a steep initial decrease, similar as in feeding larvae. This is mainly caused by a rapid uptake and incorporation of minerals into cuticular structures, causing a sudden increase in total dry mass, and hence, a drop in QO_2. Although respiration normally tends to increase in later molt-cycle stages (in particular prior to metamorphosis), in these cases it remained at a low level, reflecting a benthic and commonly sluggish behavior of the decapodid stage.

8.3.4 *Oxygen concentration*

The primary limiting factor for respiration, in general, is the availability of oxygen in the environment. This is particularly important in aquatic systems, where the abundance of O_2 is only about 3% of that in air. Animals which permanently live in oxygen-limited habitats are capable of metabolic regulation within a wide range of O_2 concentrations. Their respiration rate remains widely independent of variations in O_2 availability (*oxyregulation*). In aquatic organisms, O_2 levels down to about 80% saturation can generally be compensated, while lower concentrations cause a decrease in respiration, mainly as a consequence of reduced activity. The critical limit where animals become *oxyconformers* depends on the species, developmental stage, and environmental factors such as temperature and salinity (Vernberg 1983).

As an additional potentially confounding factor in the oxygen demand of arthropods, the molting cycle must be considered. Just prior to ecdysis, the cuticle has attained a double structure and represents thus an enhanced diffusion barrier for the transport of gases and ions; moreover, the decline in swimming activity which is normally associated with molting should cause a reduced ventilation of the branchial chamber. This may lead to a deterioration of the blood oxygenation status during the late premolt phase, i.e. a transitory hypoxia. This enhances the sensitivity to thermal, osmotic, or other stress, and may cause an enhanced mortality in ecdysis (Clemens et al. 1999). This unspecific response is generally known as *"molt death syndrome"* (*MDS*; see also "exuviation threshold", section 4.5.3).

As a typical response of larvae exposed to critically low oxygen concentrations, the rate of respiration decreases with decreasing partial pressure of O_2. This effect was experimentally shown in king crab (*Paralithodes camtschaticus*; Nakanishi 1987), spiny lobster (*Panulirus interruptus*), and brachyuran crab (*Cancer productus*) larvae (Belman & Childress 1973). As an exceptional case, tolerance of low oxygen concentration was

observed in the larvae of the bromeliad crab, *Metopaulias depressus*, with a critical O_2 level reached only at ca. 14-21% saturation (Diesel & Schuh 1993). This terrestrial species breeds in small volumes of rainwater that is periodically collected in leaf axils of bromeliad plants (see section 10.4.2). Due to decay of fallen leaf litter and other debris, low O_2 concentrations may frequently occur in this quite unique larval habitat, selecting for physiological adaptations to this otherwise uncommon stressor.

8.3.5 *Temperature*

Besides body size, temperature is a key factor in metabolic processes of poikilothermal animals (Kinne 1970, Precht et al. 1973, Vernberg 1983, Prosser 1986). The relationship between individual respiration rate (VO_2) and temperature (T) has in the literature most commonly been described as an exponential function (Eq. 8.6), which implies that the logarithm of VO_2 is a linear function of T:

$$VO_2 = a \cdot e^{b \cdot T} \tag{8.6}$$

$$\ln VO_2 = \ln a \cdot + b \cdot T \tag{8.6a}$$

In this relationship, a and b are again fitted regression parameters, and the constant e is the base of the natural logarithm. The same type of equations can be used also to describe QO_2 as a function of T, multiplying Eq. 8.6 with the reciprocal value of W (cf. Eq. 8.3). These general relationships are illustrated with the same data as for the weight-dependence of respiration (see above, Fig. 8.3), using again the larvae of the crab *Chasmagnathus granulata* as a recently studied example (Fig. 8.6).

As an alternative to this exponential model, Belehrádek's function (Belehrádek 1935, 1957; cf. section 6.4.1) has been used to describe the temperature-dependence of metabolic rates:

$$VO_2 = a \cdot (T - \alpha)^{-b} \tag{8.7}$$

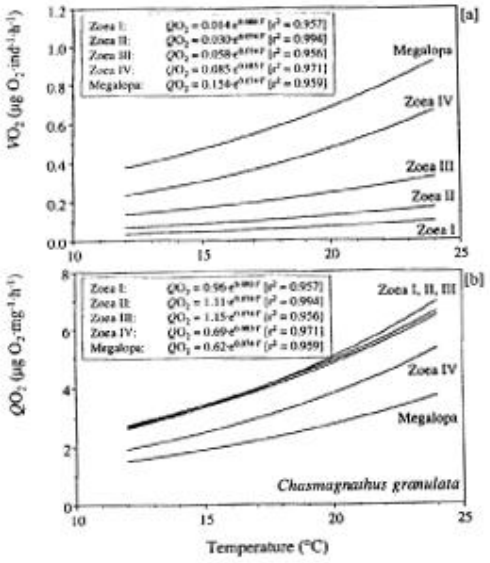


Figure 8.6. Effect of temperature (*T*) on the metabolic rates in successive larval stages of a brachyuran crab (*Chasmagnathus granulata*); fitted regression equations and coefficients of determination, r^2; [a] respiration rate per individual, VO_2; [b] weight-specific rate, QO_2 (redrawn after Ismael et al. 1997).

This function has been introduced in chapter 6 as a description of development duration in relation to temperature (Eq. 6.14). The additional parameter α is termed the *"biological zero"*, i.e. the temperature at which VO_2 theoretically becomes zero. Since α varies with the temperature of acclimation and the geographic distribution of a species, it should be a suitable index in comparative studies of the metabolism-temperature relationship. The Belehrádek equation was applied to respiration data measured in the larval stages of the spider crab *Hyas araneus*, where it gave a better fit than the exponential model; the latter, however, appeared to be more appropriate to describe the temperature-dependence of respiration in a closely related species, *H. coarctatus* (Jacobi & Anger 1985b). Since the shapes of curves fitted with either model differ only little, the exponential function has in the literature been used more frequently, because it is a simpler expression.

As another alternative way of expressing respiration as a function of temperature, the *Arrhenius equation* of biophysics may be used (Bertalanffy 1957, Ivleva 1970, 1980, Precht et al. 1973). Based on this relationship, usually the logarithm of a rate (e.g. ln VO_2) is plotted against the reciprocal of absolute temperature (in Kelvin) to obtain a straight line.

$$VO_2 = a \cdot e^{(-\mu/R \cdot T)} \quad (8.8)$$

In this equation, a and μ are fitted parameters (with μ as the *"temperature characteristic"* of a process), R is the gas constant (1.986 cal·mol^{-1}·degree^{-1}), and T is the absolute temperature (°K). This function is commonly used to describe the temperature-dependence of chemical reactions, but less in studies of metabolic responses on the organismic level. On the other hand, the Arrhenius equation was applied also in a review of relationships between respiration and temperature in oceanic crustaceans (Ivleva 1970). Among the decapod larvae, this model was applied to the protozoeal and "postlarval" stages of a penaeid shrimp, *Penaeus monodon* (see Kurmaly et al. 1989c).

Independent of the model, there is a close positive correlation of metabolism with temperature. However, this applies only within a metabolically viable tolerance range of a species or stage. When an upper critical level is exceeded, the rate of respiration will typically decrease with further increasing temperature, indicating thermal stress. Naturally, this physiological limit is influenced by genetic adaptation to the climatic conditions in a species' geographic range, acclimation (or acclimatization, non-genetic capacity adaptation) to the conditions prior to an experiment, and other environmental factors such as salinity or pollution-induced stress (see Kinne 1964a, 1967, 1970, 1971, Precht et al. 1973, Prosser 1986, Vernberg 1983, Laughlin & French 1989b). In the zoea-I stage of a cold-water shrimp, *Pandalus borealis*, the upper critical level was reached at 9°C (Paul & Nunes 1983; Fig. 8.7), whereas the larvae of the subtropical crab *Chasmagnathus granulata* showed no signs of thermal stress within a range from 12-24°C (Fig. 8.6). In the larvae of several other warm-water species, decreasing QO_2 values were observed only at temperatures exceeding about 25-30°C, depending on species, stages, and the geographic-climatic origin of a population (Vernberg & Costlow 1966, Vernberg 1969, Schatzlein & Costlow 1978, Laughlin & Neff 1981, Moreira et al. 1981, Vernberg et al. 1981, McNamara et al. 1985).

As all physical, chemical and physiological processes, the temperature-dependence of respiration rates can be compared quantitatively among individuals, species or developmental stages, using the temperature coefficient Q_{10}. This index denotes the ratio of two rates measured at two different temperatures (see section 6.2.1; Eq. 6.15). It is mathematically related and can thus be converted to the parameter μ of the Arrhenius equation (Ivleva 1980). Q_{10} values near to or below 2 are considered as a typical sign of *"thermal compensation"* (*eurythermia*), while higher values indicate *"thermal sensitivity"* (Precht et al. 1973). The Q_{10} varies also with the temperature range considered, usually decreasing at higher temperatures. Above a critical limit, Q_{10} may become <1.

In decapods, reproductive traits related to the season of egg hatching may influence the overall level and the critical temperature limit of metabolic rates in the larvae. In a boreal crab, *Cancer irroratus*, maximum respiration rates were measured at about 15-20°C (i.e. a decline occurred above these temperatures; Sastry & McCarthy 1973). By comparison, a closely related and partially sympatric species, *C. borealis*, showed an increase in VO_2 up to 25°C. This interspecific variation in the metabolic temperature response corresponds with the seasonal occurrence of larvae in the plankton. *C. irroratus* zoeae hatch in spring, when the temperature in coastal waters is about 5 to maximally 19°C, whereas *C. borealis* larvae occur exclusively in the summer plankton, at ca. 16 to 23°C.

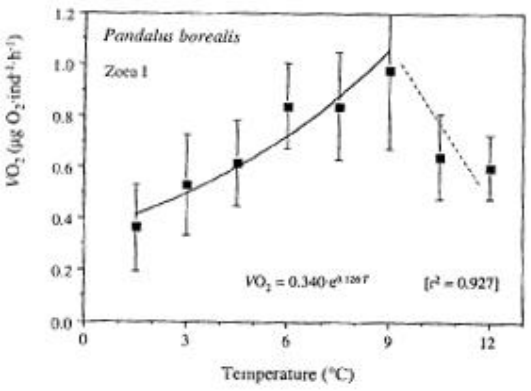


Figure 8.7. Effect of temperature (T) on the respiration rate per individual (VO_2) of the zoea I stage of a caridean shrimp, *Pandalus borealis*. Note: the exponential relationship does not apply any longer when an upper critical temperature has been exceeded (decreasing metabolic rate under thermal stress); r^2: coefficient of determination for fitted regression equation (redrawn after data from Paul & Nunes 1983).

The respiratory response to temperature may vary also among the developmental stages of a species, if these are typically exposed to different conditions. The successive zoeal stages of *Cancer irroratus*, for instance, become increasingly stenothermal (Sastry & McCarthy 1973), which appears to reflect their successive transport to thermally stable offshore waters. In an estuarine crab, *Chasmagnathus granulata*, the zoeal stages (in particular the zoea I) showed a more sensitive metabolic response at higher as compared to lower temperatures (Ismael et al. 1997). Their Q_{10} was about 2.2-3.0 in a temperature range 18-24°C, but only 1.7-2.2 at 12-18°C. The opposite pattern, was observed in the megalopa stage. Also in this species, a changing thermal response in successive stages suggests a genetically controlled adaptation to a sequence of conditions that should typically be encountered during ontogenetic migrations in the field: (1) the zoea I larvae of *C. granulata* hatch during spring and summer in coastal lagoons and salt marshes with, on average, relatively warm and unstable temperatures; (2) from there, the early larvae are rapidly exported to cooler and thermally more stable offshore waters of the southwestern Atlantic Ocean (Anger et al. 1994); (3) after development through four or five zoeal stages, the megalopa reimmigrates into the shallow estuarine environments. It may thus be speculated that a high metabolic sensitivity to temperature variation (with $Q_{10}>2$) could serve, in addition to cues from gradients in salinity and other chemical factors (see section 10.3.1), as a signal that may stimulate differential stage-specific migratory behavior. As a result of this response, the zoeae should tend to leave the warmer parental environment, whereas the megalopa should avoid a retainment in cooler marine waters.

The respiratory response to temperature variation is further influenced by osmotic stress. Overlaying effects of unfavourable salinity conditions were demonstrated, for instance, in the larvae of a caridean shrimp from the Mediterranean Sea, *Palaemon serratus* (Yagi et al. 1990). In this euryhaline, warm-water adapted species, no upper critical limit occurred at temperatures up to 29°C, as long as the salinity was kept within a favourable range (≥19‰S). At 13‰S, in contrast, respiration rate decreased in all larval stages as the temperature exceeded 25°C. This indicates a reduced thermal tolerance under the interfering influence of low-salinity stress. As in other euryhaline shrimp larvae, e.g. *Macrobrachium holthuisi* and *M. amazonicum*, the highest Q_{10} values occurred consistently when *P. serratus* larvae developed under unfavourably low or enhanced salt concentrations (cf. Moreira et al. 1980, Yagi et al. 1990, Zanders & Rodríguez 1992). Again, this indicates a decreasing capability for thermal compensation in the presence of osmotic stress. This interaction is usually most pronounced in the lower temperature range, where the capacity for osmoregulation tends to decrease (Vernberg & Silverthorn 1979).

As an example of interactions with intrinsic factors, it should be mentioned that endotrophic larvae were observed to show a particularly weak response to changes in temperature. In the secondarily lecithotrophic puerulus stage of a spiny lobster, *Palunirus cygnus*, the Q_{10} was significantly lower than in the subsequent feeding juvenile stages (Lemmens 1994). Their unusually low sensitivity to temperature changes, together with a particularly low average QO_2, was interpreted as an energy-saving adaptation related to the endotrophic mode of development. This plausible inference is supported by recent experiments, which showed that the duration of development in facultatively lecithotrophic zoeae of a thalassinid crab, *Callianassa tyrrhena*, is practically independent of temperature (Thessalou-Legaki et al. 1999).

8.3.6 *Salinity*

In aquatic invertebrates, Kinne (1967, 1971) distinguished four major types of metabolic reactions to variation in salinity. Within the tolerable range, the respiration rate may:

(I) increase in subnormal salinities and/or decrease in supranormal salinities;
(II) increase in both sub- and supranormal salinities;
(III) decrease in both sub- and supranormal salinities;
(IV) remain essentially unaffected.

An increase in the metabolic rate under suboptimal salinity conditions is typical of euryhaline species, in particular during exposure to brackish water (types I and II). This metabolic response has commonly been attributed to the energetic requirements associated with osmoregulation (e.g. Remane & Schlieper 1971; but see also Kinne 1971 for arguments against a generalization of this presumable relationship). Most euryhaline species are capable of hyperregulation in dilute media, but not of hyporegulation under hypersaline conditions. In consequence, an exposure to enhanced salt concentrations may cause physiological damage and, as a response to this stress situation, respiration may be depressed in supranormal salinities (type I). Typical marine, stenohaline species belong to type III, where both sub- and supranormal salinities exert stress, which causes a decrease in metabolic activity due to a diminuition of locomotory activity and/or a depression of physiological processes on the cellular and tissue level. This response occurs, in principle, also in euryhaline species when lower or upper critical salinity levels are exceeded, but these limits are reached here only at more or less extreme conditions. Moreover, the critical salinities where regulatory mechanism begin to fail or to break down may shift also

due to preceding acclimatization (Kinne 1971). In extremely euryhaline forms (termed *holoeuryhaline*), the internal compensation for external salinity variation is apparently so efficient that measurements of oxygen consumption in the entire animal do not reflect an enhanced activity in the regulating tissues (type IV).

Among the adult Decapoda, there are numerous examples for each of these four categories (for review of older literature, including examples from non-decapod crustaceans and other invertebrate taxa, see Kinne 1971; for recent references see Aguilar et al. 1998). Euryhaline species which tolerate reduced salinities but suffer under hypersaline conditions (type I) are represented, for instance, by the common shore crab (*Carcinus maenas*) and some semiterrestrial crabs (e.g. *Uca*, *Hemigrapsus* spp.). In type II (supposedly hyper-hyporegulators; cf. section 10.1.2), we find other semiterrestrial crabs (e.g. *Ocypode quadrata*) and several caridean and penaeid shrimps (e.g. *Palaemonetes varians, Macrobrachium tenellum, Metapenaeus monoceros*). Most spider crabs (Majidae) are subtidal marine species, and hence, represent typical examples of type III (e.g. *Hyas araneus*, *Libinia emarginata*). The most typical holo-euryhaline decapod species (type IV) is the Chinese mitten crab, *Eriocheir sinensis*, which can live and grow equally well in freshwater, brackish water, or seawater. Also among the penaeid prawns there are examples of this category (e.g. *Litopenaeus setiferus*, Rosas et al. 1999).

There are various publications in which this classification system has tentatively been applied to larval decapods. These attempts were hampered by complicated interactions with developmental processes and effects of environmental factors other than salinity. For instance, we have seen that unsuitable salinities may change the temperature response or the weight-dependence of metabolic rates; likewise, unfavourable temperatures tend to enhance the metabolic response to salinity variations (Kinne 1971). Depending on the development of the osmoregulatory system, the response pattern and thus, the classification of a particular species may change also ontogenetically. According to the available data, types I-III occur also in larval stages, while holo-euryhalinity (type IV) appears to be restricted to benthic juveniles and adults. The tentative relationships between osmoregulatory and metabolic response patterns under fluctuating salinities (i.e. variable osmotic pressures) are illustrated in a graphical model (Fig. 8.8).

In the larvae of stenohaline marine species, no selection pressure towards an evolution of strong osmoregulatory capabilities exists. Hence, their metabolism reflects osmotic stress when it is measured under conditions of reduced or enhanced salt concentrations. The typical response pattern is a depression of respiration rate at unfavourable salinities (type III). This was demonstrated, for instance, in larval rock crabs (*Cancer irroratus*, Johns 1981), spider crabs (*Hyas araneus*, Ismael 1995), shore crabs (*Carcinus maenas*, Anger et al. 1998), and hermit crabs (*Pagurus bernhardus*, Seidler 1993).

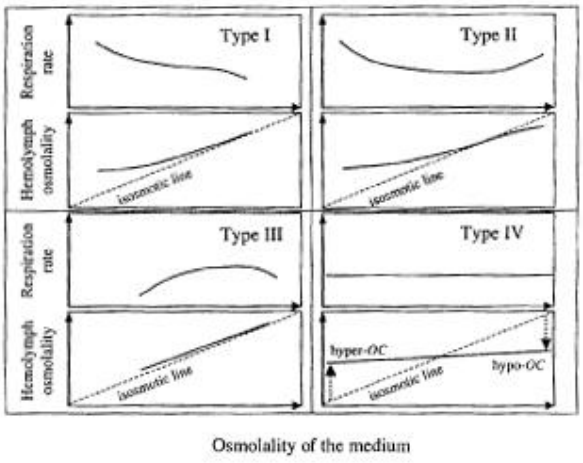


Fig. 8.8. Hypothetical relationships between various patterns of metabolic response to salinity variation (types I-IV; after Kinne 1971; for details see text) and patterns of osmoregulation (after Charmantier 1998); osmoregulatory capacity (*OC*): osmolality difference between the internal (hemolymph) and external medium; isosmotic line: internal and external osmotic pressures are identical.

In species whose larvae show a capability for hyper-osmoregulation, oxygen consumption is generally enhanced when the external salt concentrations are below the internal osmolality, while low metabolic activity occurs at salinities corresponding to the osmolality of the hemolymph (isotonic conditions, usually about 25-28‰), where no extra energy for regulation is needed. At higher salt concentrations, where most decapod larvae are osmoconformers (Charmantier 1998), respiration should remain constantly low or decrease as a result of hyperosmotic stress. This pattern (type I) appears to be typical of the euryhaline larvae of many estuarine species. It was found, for instance, in larval mud crab (*Rhithropanopeus harrisii*, Laughlin & Neff 1981) and in early zoeae of the freshwater shrimps *Macrobrachium amazonicum* (McNamara et al. 1983, Zanders & Rodríguez 1992) and *Palaemon paucidens* (Mashiko 1992).

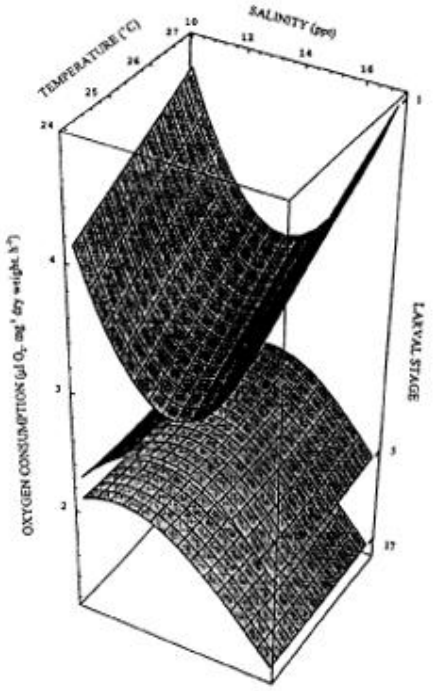


Figure 8.9. 4D-response surface of the mean weight-specific oxygen consumption of caridean shrimp (*Macrobrachium rosenbergii*) larvae as a function of the combined effects of 12 combinations of salinity and temperature during development (three larval instars compared) (from Agard 1999, with permission from Elsevier, Oxford, UK).

In another caridean shrimp living in freshwater, *Macrobrachium petersi*, the adult pattern of hyper-hyporegulation is present already from hatching (Read 1984). Unfortunately, no respiration data are available for the larvae of this species, but we should expect high metabolic rates at both reduced and enhanced salinities. This metabolic response pattern (type II; exemplified in Fig. 8.9) was observed in the zoea I of several other palaemonid species with a similar life-history, namely *M. olfersii* (McNamara et al. 1982, 1986), *M. nipponense* (Mashiko 1992), *M. rosenbergii* (Agard 1999), and *Palaemonetes pugio* (McKenney & Neff 1981, McKenney & Hamaker 1984). In these cases, however, respiration data but no measurements of the osmoregulatory capacity have been published, so that the presumable relationships between larval oxygen consumption and energetic expenditure for osmoregulation remain to be scrutinized experimentally.

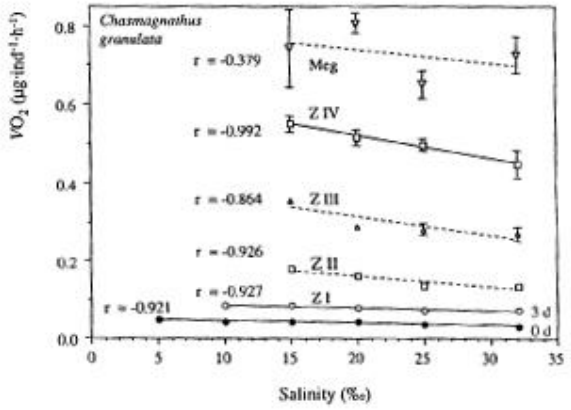


Figure 8.10. Effect of salinity on respiration rate per individual (VO_2) in successive larval stages of a brachyuran crab (*Chasmagnathus granulata*) reared at constant temperature (18°C) and salinity (32‰); all measurements were made during acute exposure to the test salinities for 15h (in zoea I larvae 0 and 3 after hatching; in all other stages only in the middle of the molting cycle); note: all correlations were negative, but only solid regression lines have statistically significant slopes (redrawn after Ismael 1995).

The pattern of metabolic response to salinity variation reflects not only genetic adaptations associated with the general ecology of a species, but may change also ontogenetically. In all four zoeal stages of the euryhaline crab *Chasmagnathus granulata*, respiration showed a weak but consistent increase at reduced salinities (Fig. 8.10); this suggests a weak hyperregulatory capacity. The megalopa of this species, in contrast, showed a minimum respiration near the isosmotic point (at ca. 25‰), and significantly enhanced metabolic rates in both dilute media and full-strength seawater (Ismael 1995). This suggests that the terminal larval stage is, in this species, already capable of both hyper- and hyporegulation. Hence, the zoeal stages of *C. granulata* belong to response type I, whereas the megalopa of the same species should be classified as belonging to type II. A recent study of the ontogeny of osmoregulation in this species (Charmantier et al., in prep.) confirmed that the zoeal stages (in particular the zoea I) are weak hyper-osmoregulators in dilute media, whereas the megalopa attains in principle (only weaker) the adult capability of both hyper- and hyporegulation.

Unlike *Macrobrachium petersi*, several other palaemonid shrimps show ontogenetic changes in their response to salinity variation. In a euryhaline marine shrimp, *Palaemon serratus*, the larval stages showed maximum respiration in seawater and at moderately reduced salinities, but decreasing metabolic rates under both hyper- and hyposaline conditions (Yagi et al. 1990). This pattern (type III) remained widely unaffected by temperature and larval stage, indicating that the larvae of this species are stenohaline, while the adults

are euryhaline; hence, the capability of osmoregulation is in this species attained only in later (presumably juvenile) life-history stages.

While a comparably sensitive response to osmotic stress is common among the larvae of species that are euryhaline as adults, some shrimps show more complicating ontogenetic changes in their physiology. These species have in common that the adults live in freshwater or brackish water, larval development occurs outside the parental habitat, in estuarine or coastal zones, and reimmigration to regions with very low salinities follows in a late larval or early juvenile stage. Several tropical *Macrobrachium* species as well as the North American grass shrimp, *Palaemonetes pugio*, may be considered as typical examples of this life-history pattern. The metabolic response of their zoea I corresponds to type II, which suggests an early appearance of the capability for hyper-hypo-osmoregulation. However, later larval stages of these species showed depressed respiration rates at both reduced salinity and in full-strength seawater (type III). This change indicates a narrowing of their optimum range and a generally declining osmoregulatory capacity (Fig. 8.9). Yet later in ontogeny, the response pattern alters again, as the adult shrimps are extremely euryhaline, showing only a weak respiratory response to changes in the osmotic conditions (type IV).

In estuarine and freshwater species "exporting" their larvae out of the parental habitat and re-immigrating later, this repeated change in the metabolic response of successive life-history stages to salinity variation matches the pattern of ecological change which occur during their ontogenetic migrations (for details of "export strategies" see section 10.3.1). This suggests that these complex life cycles are associated with genetically programmed physiological changes in metabolism and osmoregulation. A transitory decrease in the salinity tolerance and osmoregulatory capacity of intermediate life-history stages may occur not only in freshwater shrimps but also in estuarine crabs whose larval development takes place in coastal marine zones. This ontogenetic pattern was observed in the metabolism of a fiddler crab, *Uca pugilator* (Vernberg et al. 1973). The zoea I of this species showed an enhanced respiration rate in brackish water (20 *vs.* 32‰), which suggests a capability for hyper-osmoregulation in dilute media (type I). The zoea III, by contrast, showed the opposite response, suggesting that the regulatory capability was in this stage greatly reduced (type III). The juvenile and adult crabs become again strong osmoregulators (type II or IV).

If we assume a genetic basis of ecological and physiological changes in successive life-history stages, we may expect that the capability of hyporegulation in concentrated media should first disappear in riverine populations, where no selection pressure for this trait exists. Evidence of this presumable evolutionary change was shown in palaemonid shrimps from Japan, *Macrobrachium nipponense* and *Palaemon paucidens* (Fidhiany et al. 1991, Mashiko 1992). Genetically and ecologically isolated populations of these species inhabit various estuarine and limnic regions. Zoea I larvae originating from estuarine populations showed significantly enhanced respiration rates not only at low but also high salinity (type II); this response was absent in conspecific larvae from limnic populations (type I). Hence, comparative physiological data on the population level suggest, in agreement with genetic evidence, that there is an incipient speciation within these euryhaline shrimp species (Mashiko & Numachi 1993, 2000).

In addition to ontogenetic changes and genetic selection, effects of temperature and other interacting environmental factors can modify the metabolic response of decapod larvae to variation in salinity (e.g. Zanders & Rodríguez 1992). In the zoea I of the palae-

monid shrimp *Macrobrachium holthuisi*, for instance, the type II pattern was found only at an intermediate, apparently favourable temperature (Moreira et al. 1980). Both higher and lower temperatures caused a decreasing respiration in full-strength seawater, but not in brackish water. This change from type II to I suggests that unfavourable temperature conditions may primarily reduce the hyporegulating capacity in concentrated media and thus, cause osmotic damage and a metabolic depression in seawater or hypersaline conditions. The capability for hyperregulation in dilute media, by contrast, appears to be more stable, reflecting its greater importance in the ecology of freshwater and estuarine species.

8.3.7 *Pollutants*

Among the environmental factors that affect the metabolism of decapod crustacean larvae, there are also numerous man-made chemicals. Many of those pollutants are highly toxic and hence, exert stress on organisms, even in very low sublethal concentrations. In the metabolism of larval decapods and other aquatic animals, however, no universal response pattern in relation to pollutants could be identified.

In rock crab, *Cancer irroratus*, larvae exposed to the water-soluble fraction of reffined oil, the metabolic rate increased (Johns & Pechenik 1980). This effect occurred also when larvae of the mud crab, *Rhithropanopeus harrisii*, were exposed to sublethal concentrations of naphthalene in combination with unfavourably low salinity (Laughlin & Neff 1981). At favourable conditions of temperature and salinity, however, this pollutant did not cause significant or consistant effects in larval respiration. Inconsistent results were described also from fiddler crab (*Uca pugilator*) larvae stressed with sublethal concentrations of mercury (DeCoursey & Vernberg 1972, Vernberg et al. 1973).

At a high but sublethal concentration (0.2 $ng \cdot L^{-1}$) of fenvalerate, a pyrethroid pesticide, and under exposure to low salinity (10‰), the respiration rates of the intermediate and late larval stages of the shrimp *Palaemonetes pugio* were significantly enhanced (McKenney & Hamaker 1984). The early juveniles, in contrast, showed depressed metabolism when the exposure coincided with high salinity (30‰). In the same species, respiration was in some larval stages depressed also during exposure to zink, but again, the response to the pollutant depended on the conditions of temperature and salinity (McKenney & Neff 1981). When penaeid shrimp (*Litopenaeus vannamei*) larvae were challenged with sublethal concentrations of several organochlorine pesticides, the response pattern varied among the compounds tested (Galindo et al. 1996). Lindane, chlordane, and DDT caused consistently a depression of the metabolic rate, while enhanced respiration rates were measured during exposure to lorsban. Depressed metabolic rates occurred also in larval lobsters (*Homarus americanus*) during acute exposure to petroleum hydrocarbons, and this effect persisted for several days thereafter (Capuzzo & Lancaster 1981, 1982, Capuzzo et al. 1984). A decline in metabolic activity was observed also when lobster larvae were exposed to toxic drilling fluids (Smith Derby & Capuzzo 1984) or to halogen toxicants (Capuzzo et al. 1976, Capuzzo 1977). In zoea larvae of a shrimp, *Pandalus borealis*, mercury caused a dose- and time-dependend depression in respiration, but not in the activity of the electron transfer system (St-Amand et al. 1999).

In spite of such variable results, a possible rule may be seen in the metabolic response of larvae exposed to toxic pollutants: Respiration rate appears to be enhanced when chemicals are highly diluted or not very toxic, and when the organism disposes of energy-consuming physiological detoxification mechanisms such as the cytochrome P-450 system (for recent review of literature showing in vivo oxydation of xenobiotics in Crustacea,

see James & Boyle 1998). Such mechanisms are most likely found for pollutants that occur also naturally in the environment, for instance organic waste products, many hydrocarbons, and most toxic metals; in those cases, organisms must have evolved strategies for survival in the presence of xenobiotics. The metabolic response to pollutants that can physiologically be counteracted, i.e. an enhanced respiration rate, is comparable with the enhancement of metabolism in euryhaline larvae under the exposure to moderate osmotic stress (see above, response types I and II). The most common, although unspecific response to pollution stress, however, appears to be a depression of the metabolic rate, similar as we have seen in nutritional, thermal, and severe osmotic stress. Observations from adult crustaceans under the influence of chemical stress suggest that this response reflects a depressed locomotory activity (e.g. Papathanassiou 1983, Depledge 1984). In pelagic larvae, this behavioral response should interfere with vertical migrations, feeding, and predator avoidance, and thus, reduce the overall chances of survival and recruitment. Moreover, it must be considered that in nature there is always a mixture of several pollutants and, additionally, interacting environmental factors such as temperature or salinity may be suboptimal. Hence, synergistic stress effects are most likely to occur, and a reduction of metabolism and other vital functions is probably the most common response to toxic substances in the aquatic environment.

8.4 *Nitrogen excretion*

When complex organic molecules are completely catabolized, the two major end products of oxydative degradation are water and carbon dioxide. In materials containing nitrogen or phosphorus (e.g. proteins, nucleic acids), however, the biodegradation in animal tissues does not proceed to the ultimate possible state of oxydation. As nitrogenous end products, ammonia, urea, uric acid, or amino acids may be excreted, all of these representing losses of chemical energy. They are summarized as *excretion*. In decapod larvae and most other aquatic crustaceans, ammonia (NH_3) is the only or major waste product (*ammoniotelism*; Parry 1960, Bidigare 1983, Regnault 1987; for review of the physiological mechanisms and pathways of nitrogen excretion as well as adaptations to environmental conditions in crustaceans, see Greenaway 1991, 1999).

Because of its toxicity, NH_3 cannot be stored but is excreted directly into the surrounding water, predominantly in the ionized form (NH_4^+). The rate of N excretion in ammoniotelic animals is therefore usually measured in terms of ammonia-N released per unit time. In the following section, excretion is given in terms of total ammonia-N, regardless of the actual proportions of NH_4^+ and un-ionized NH_3, which depend on temperature, salinity, and pH of the water (Trussell 1972). Other nitrogenous waste products are disregarded, as they do not appear to play a significant role in aquatic crustaceans. Likewise, the excretion of phosphoric compounds is considered as insignificant and will consequently be ignored as well. This reflects also the literature, where almost no data on phosphate excretion exist for larval decapods, except for a few measurements in unidentified larvae from the plankton (Ikeda et al. 1982, Ikeda 1985); the quantities reported in these papers are about one order of magnitude lower than those of N excretion.

Compared with the quantity of publications dealing with these aspects in adult benthic decapods and, similarly, in holoplanktonic crustaceans such as copepods (Heinle 1981), there are only few and less detailed studies of N-excretion in decapod larvae. This was measured under controlled experimental conditions in larvae of caridean shrimp (*Macro-*

brachium rosenbergii; Sick 1976, Agard 1999), hermit crab (*Pagurus bernhardus*; Tetzlaff 1995), lobster (*Homarus americanus*; Logan & Epifanio 1978, Capuzzo & Lancaster 1979b, c, Capuzzo et al. 1984, Sasaki et al. 1986), and a few brachyuran crab species (*Cancer irroratus*, Johns 1982; *Hyas araneus*, Anger et al. 1989a; *Carcinus maenas*, Harms et al. 1994). Numerous data, in contrast, are available for the "postlarvae" of several penaeid shrimp species reared under various conditions of temperature, salinity, food, or oxygen concentration (e.g. Rosas et al. 1995, 1996, 1999). In addition, field observations have been published for unidentified decapod larvae (Ikeda et al. 1982, Ikeda 1985).

This relative scarcity of excretion data from decapod larvae is associated not only with technical difficulties in the measurement of physiological parameters in small planktonic organisms, but also with the fact that N-excretion has a comparably low significance within the overall bioenergetics of larval crustaceans (section 9.2). In the larvae of a spider crab, *Hyas araneus*, for instance, we measured cumulative excretory energy losses corresponding to only 2-5% of total absorption (Anger et al. 1989a); similar values were measured in other larval decapods (for review, see Anger 1991a). Whithin a nitrogen budget, however, the excretory losses are significant, reaching in *H. araneus* about 44% of total N absorption in all larval stages combined (Anger 1990). Also, the specific-dynamic action of food (*SDA*, see above) is closely related to the energetic costs of the production of nitrogenous excretory compounds (Rosas et al. 1996).

8.4.1 *Body size, developmental stage, molting cycle*

Since successive developmental stages increase normally in biomass, the excretion rate per individual increases, like the respiration rate, as a power function of weight (Eq. 8.2). In contrast, the weight-specific excretion rate decreases with increasing biomass (Eq. 8.3; Logan & Epifanio 1978, Capuzzo & Lancaster 1979a-c, Sasaki et al. 1986, Tetzlaff 1995, Agard 1999). When individual excretion rate is plotted against *W*, the slope of the logarithmic regression is generally similar as in corresponding equations for respiration rate regressed on *W*, usually in the range between 0.6 and 1. In the larval stages of the hermit crab *Pagurus bernhardus*, for instance, the slope parameter of the excretion-dry mass relationship varied at different temperatures between 0.53 and 0.63 (Tetzlaff 1995). When this relationship is compared among temperate-boreal, subtropical, and tropical zooplankton species, the slope parameter tends to increase with typical environmental temperatures (Ikeda 1974); again, this is similar as in oxygen consumption.

In crustaceans, excretion rates are known to vary not only between instars but also within individual molting cycles. Neuroendocrine factors are known to influence the rates of ingestion and digestion of food, and hence, also the excretion of nitrogenous substances. As underlaying intrinsic mechanisms, there are molt-cycle related changes in the nitrogen metabolism of muscles, integuments, the hepatopancreas, and other tissues, as well as changes in the acid-base equilibrium, membrane permeability, and ionic balance (Regnault 1987, Greenaway 1991, 1999). However, so far no consistent pattern of molt-cycle related variation could be described. In adult shrimps, *Crangon crangon*, a maximal excretion was found in early postmolt, while a minimum occurred in late premolt, coinciding with minimal ingestion (Regnault 1979). In the weight-specific excretion rate of larval lobsters (*Homarus americanus*), similar patterns were observed as in adult *C. crangon*, with a minimum in the intermolt phase (Sasaki et al. 1986). However, all three larval stages of the crab *Hyas araneus* showed an opposite pattern, i.e. a maximum in intermolt and minima in the postmolt and premolt stages of the molting cycle (Anger et al. 1989a;

Fig. 8.11). The same pattern was found in caridean shrimp (*Macrobrachium nipponense*) larvae (Shin & Chin 1994). This corresponds, in both species, with a similar pattern in larval feeding rate, suggesting a relationship with the conversion of ingested dietary matter. Although this is plausible and may represent a general pattern, the scarcity of comparative investigations on larval feeding and excretion precludes at present generalizations of this aspect of larval physiology.

8.4.2 *Nutritional and other environmental effects*

In juvenile and adult decapods, numerous studies have shown that both the quality and quantity of food affect not only the amounts of nitrogenous products excreted, but also the major metabolic pathways of their formation (for review see Regnault 1987). Nutritional effects become conspicuous soon after feeding; ammonia excretion may then be enhanced up to four times the initial value (Nelson & Kropp 1985, Rosas et al. 1996). As a universal trend, there appears to be a positive correlation of ammonia excretion with the dietary protein level. Among the larval decapods, this relationhip was demonstrated in the American lobster, *Homarus americanus* (Capuzzo & Lancaster 1979a, b).

In spider crab (*Hyas araneus*) megalopae, we observed lower nitrogen excretion when they were fed exclusively with diatoms (storing predominantly carbohydrates), as compared with larvae fed brine shrimp nauplii (higher levels of dietary lipid and protein but low carbohydrates; Harms & Anger 1990; Fig. 8.11a). The difference between the excretion rates in these two experimental groups appears thus to reflect a high carbohydrate content of algal food *vs.* a high protein level in the *Artemia* diet. It was maximum during the postmolt and intermolt stages, i.e. when larval ingestion rate is generally maximal (cf. section 5.3.5). In the phytoplankton-fed group, however, also some catabolization of internal fat reserves from the hepatopancreas may have taken place as a consequence of nutritional stress. During the premolt phase, the diatom-fed larvae showed a continually increasing excretion rate, possibly due to gradually increasing utilization of internal protein reserves following the depletion of metabolically available lipids (cf. section 7.3).

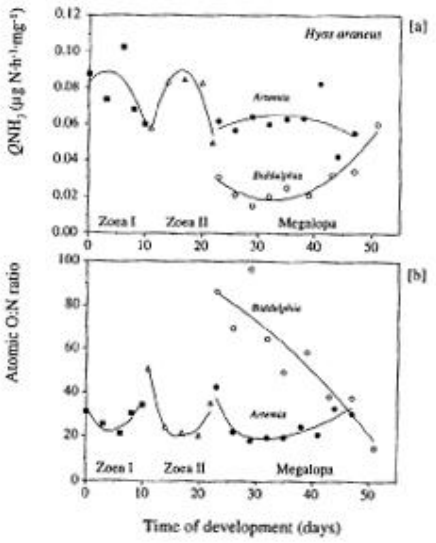


Figure 8.11. Ontogenetic changes [a] in the weight-specific rate of ammonia excretion, [b] in the atomic O:N ratio during the molting cycles of successive larval stages of a brachyuran crab (*Hyas araneus*) reared under constant temperature (12°C); in the megalopa stage, comparison of two feeding regimes is presented (*Artemia* nauplii or diatoms, *Biddulphia*; zoeal stages fed only with *Artemia* (for regression models see text) (redrawn after Anger et al. 1989a, Harms & Anger 1990).

As another key factor, temperature controls the rates of all physiological and biochemical processes, including those of excretion. As in the rates of development and respiration (see sections 6.2.1, 8.3.5), the increase in excretion with increasing temperature is usually quantified with the temperature coefficient Q_{10}. In the literature on the physiology of planktonic crustaceans, inconsistent results suggest a great deal of taxonomic variation as well as interactions with developmental events, geographic range, nutrition, and osmoregulation (for review see Regnault 1987; recent references in Agard 1999). Within the typical range of dry masss observed in decapod crustacean larvae (ca. 10 µg to 1 mg per individual), the weight-specific excretion rate of zooplankton from various climatic regions was found to vary from about 0.01 to 10 µg NH_3-N·mg^{-1}·h^{-1}; it showed a significantly increasing trend from cold to warm-adapted species (Ikeda 1974).

The few existing data measured in decapod larvae under controlled conditions fit well in this scheme. In the larvae of the subarctic-boreal spider crab *Hyas araneus*, measurements varied from ca. 0.04 to 0.1 µg NH_3-N·mg^{-1}·h^{-1} (Anger et al. 1989a), which is comparable with values reported from other boreal zooplankton. In the zoeal stages of a tem-

perate-boreal hermit crab, *Pagurus bernhardus*, the weight-specific rates varied at different temperatures (6-18°C) between ca. 0.04 and 0.14 (Tetzlaff 1995), and in the larvae of the warm-temperate lobster *Homarus americanus*, most values were in the range 0.1-0.2 µg NH_3-N·mg^{-1}·h^{-1} (Logan & Epifanio 1978, Capuzzo & Lancaster 1979a-c, Capuzzo et al. 1984, Sasaki et al. 1986). In the early larval stages of a tropical freshwater shrimp, *Macrobrachium rosenbergii*, weight-specific excretion rates exceeded 1 µg NH_3-N·mg^{-1}·h^{-1} (Agard 1999).

When juvenile or adult euryhaline decapods are exposed to reduced salinities, there is generally an increase in their ammonia production (e.g. Emerson 1969, Rosas et al. 1999). This effect was observed also in larval crabs (*Cancer irroratus*, Johns 1981) and shrimps (*Macrobrachium rosenbergii*, Agard 1999). It is apparently associated with the physiological mechanisms of hyperregulation, possibly indicating a counter-ion exchange of Na^+ for NH_4^+ and Cl^- for HCO_3^- (Armstrong et al. 1978, Regnault 1987).

Excretion may be affected also by toxic pollutants. In lobster larvae, for instance, an increasing tendency was observed during or after an exposure to petroleum hydrocarbons, suggesting a shift in their energy metabolism (Capuzzo & Lancaster 1981, 1982). However, lack of comparative data from other species and with other pollutants does not permit generalizations of this response.

8.5 *The O:N ratio*

The quotient of oxygen respired to nitrogen excreted (either by weight or atoms) is generally accepted as an indicator of the metabolic substrate for energy production. This is based on the fact that variability in the O:N ratio occurs mainly due to changes in the rate of nitrogen excretion, while oxygen consumption tends to remain relatively contant. Hence, this index varies primarily with the N content of the diet, reflecting the biochemical composition of utilized energy reserves originating either from larval biomass or prey (Ikeda 1974, Mayzaud & Conover 1988). According to the average elemental composition of the major compound classes, an atomic O:N ratio in the range 3-16 should theoretically indicate pure protein catabolism, while higher values show an increasing utilization of lipids and/or carbohydrates. Since carbohydrates are quantitatively insignificant within the biomass of most crustaceans (see section 7.3), variability in the O:N quotient of decapod larvae reflects primarily changes in the proportions of protein and lipid degradation; however, dietary carbohydrates should be important in the metabolism of herbivorously feeding species or stages. An O:N ratio of about 50-60 is considered as an indication of approximately equal amounts of protein and lipid degradation, while higher values show a predominant utilization of the latter.

Since metabolism comprises both a utilization of food and a turnover of own body materials, it is sometimes difficult to interpret the O:N ratio in relation to changes in feeding, growth, development, season, or other factors (Mayzaud & Conover 1988). This is easier when larvae are experimentally fed with a monospecific diet of known biochemical composition or kept in absence of food. In starved penaeid prawn (*Metapenaeus ensis*) larvae and "postlarvae", for instance, consistently low O:N ratios were observed, indicating that they utilized proteins as a principal energy source (Chu & Ovsianico-Koulikowsky 1994). Also the nonfeeding early larvae of the palaemonid shrimp *Macrobrachium rosenbergii* showed very low O:N ratios, followed by increasing values in the intermediate (feeding) zoeal stages, and another decrease in the late (premetamorphic) stages where feeding and

growth levelled off (Agard 1999). Again, this pattern indicates a particular importance of proteins as an energy source in larval shrimps. In the lecithotrophic initial stages, the energy originates from remaining yolk lipoproteins (Richard & Ceccaldi 1977, Agard 1999).

In the successive larval stages of the American lobster, *Homarus americanus*, a gradually decreasing O:N ratio (from ca. 28 to about 16) suggested that protein was increasingly utilized as a metabolic substrate, in particular in stage IV (Sasaki et al. 1986). In earlier studies (Capuzzo & Lancaster 1979a-c), similar or lower O:N ratios (13-27) had been observed. This developmental pattern is surprising insofar, as it does not reflect the concurrent biochemical changes occurring in larval biomass (see section 7.3): Late stages of the lobster accumulate lipids, in particular triacylglycerides, at a much faster rate than protein. Apparently, these energy reserves are stored for later use during or after settlement, while dietary proteins largely suffice for growth and developmental reconstruction processes as well as metabolic energy production.

Consistent with trends in the excretion data, the O:N ratio of larval *Homarus americanus* showed an inverse relationship with the protein content of food (Capuzzo & Lancaster 1979a-c). Similarly, spider crab (*Hyas araneus*) megalopae had a lower average O:N ratio when they were fed with zooplankton as compared with siblings eating phytoplankton (Harms & Anger 1990). The difference between these treatments was initially large, but it disappeared during the premolt stages of the molting cycle (Fig. 8.11b). In agreement with changes in the weight-specific excretion rate (Fig. 8.11a), this pattern suggests that herbivorously feeding larvae relied initially on dietary carbohydrates and/or stored lipid reserves, but were subsequently forced to mobilize increasing amounts of protein stores as a metabolic substrate.

Since the rates of larval respiration and excretion vary not only among but also within individual instars, we must expect that molt-cycle related changes occur in the O:N ratio. This was shown in all successive larval stages of *Hyas araneus* (Anger et al. 1989a). The quotient varied between ca. 18 and 45, with a similar average level in each instar (Fig. 8.11b). In *Artemia*-fed larvae of this species, maximal values were measured mostly at the beginning and the end of each molting cycle (i.e. in early postmolt and late premolt), while minima occurred during the intermolt phase. As molt-stage C is characterized by maximal feeding rates (see section 5.3.5), a minimum O:N ratio in intermolt is probably associated with a conversion of protein-rich food. In the postmolt and premolt stages of the molting cycle, high O:N ratios correspond with low ingestion rates, partial utilization of precedingly stored lipid reserves and, presumably, gluconeogenesis and high turnover of carbohydrates associated with cuticular reconstruction processes (section 4.1). Unfortunately, however, there are too few studies with a high temporal resolution of excretion measurements, so that we do not know whether this pattern is typical of decapod larvae or restricted to a particular species or experimental condition.

In crab (*Cancer irroratus*) larvae, O:N ratios between 5 and 47 were measured, without a clear relationship with the developmental stage (Johns 1981). The metabolic quotient was mostly lower when temperature and salinity were unfavourable. This effect was observed also in shrimp (*Macrobrachium rosenbergii*) larvae exposed to various combinations of temperature and salinity (Agard 1999) as well as in juvenile penaeid shrimps under hypoxia (Rosas et al. 1999). Also various pollutants have been shown to reduce the O:N ratio. In *Homarus americanus* larvae, respiration was depressed by toxic stressors, as nitrogen excretion tended to increase (Capuzzo & Lancaster 1981, 1982; see above). These observations suggest that an enhanced degradation of proteins and, consequently,

declining O:N ratios might represent a common unspecific response to physiological stress. On the other hand, a recent study of the metabolism in lead-exposed "postlarvae" of a penaeid shrimp, *Fenneropenaeus indicus*, showed an opposite pattern (Chinni et al. 2000). In this species, ammonia excretion was more depressed than respiration, so that the O:N ratio increased during the exposure to the toxic metal.

Only very few field data of O:N are available for decapod larvae with a known identity. In the shore crab, *Carcinus maenas*, larval nutrition, growth and metabolism were studied *in situ*, together with the occurrence of phytoplankton populations (Meyer 1992, Harms et al. 1994). In various samples taken from the North Sea in early summer, the lowest O:N ratios (12-31) were measured in the zoea I stage, a maximum (115) in the zoea II, and decreasing values in the following stages (68-82, zoea III; 37-43, zoea IV; 53, megalopa). This seemingly inconsistent pattern can be explained with concomitant changes in phytoplankton availability in the field. At the beginning of the study period, the zoea I was probably strongly food-limited, as the plankton community was dominated by *Phaeocystis*. This flagellate is considered to be an exceptionally poor food organism for zooplankton. The low O:N ratio in the zoea I may thus have reflected degradation of body protein, probably as a consequence of a rapid depletion of initially scarce lipid reserves. During the time of development through the two subsequent zoeal stages, diatoms with a high carbohydrate content were available in great quantities, which may explain an enhanced O:N ratio. The ingestion and mechanical maceration of diatoms was confirmed with electron microscopical inspection of the larval gut contents. Later larval stages are known to become increasingly carnivorous, so that an increasing utilization of dietary proteins may explain the final decrease in the larval O:N ratio.

9 ENERGY PARTITIONING

From a biophysical point of view, an organism represents an open system that exchanges energy with its environment. This energy is chemically bound in complex organic molecules that are taken up from food, chemically converted, partially utilized in energy-consuming processes, or accumulated in body tissues. Hence, the concepts of energy and matter may be used as equivalents, and pathways of their transfer can be described quantitatively on the molecular, cellular, or organismic level (Ivlev 1945, Warren & Davis 1967, Welch 1968, Wieser 1986, 1994, Calow 1977a, b, Conover 1978). In this chapter, the partitioning of food materials is treated only on the organismic level, although the compilation of "complete" energy budgets on the level of organisms, populations, and communities has recently been criticized. Davies & Hatcher (1998) argued that this approach is generally too rough and has thus, in most cases, not yielded much new scientific insight into biological systems. I agree with several points of this criticism, namely in relation to mostly poor consideration of developmental changes and effects of extrinsic factors on the uptake and partitioning of energy. Hence, I will pay here special attention to those lesser studied aspects.

The principal components of a bioenergetic budget, i.e. food uptake, fecal losses, growth, and metabolism, have individually been treated before. The goal of this chapter is an integrated view of the major budget parameters and their quantitative relationships. The proportions of energetic gains and losses will be compared among taxa, larval stages, stages within the molting cycle, and betweeen different environmental conditions. Before dealing with specific examples from decapod crustacean larvae, I will give here a brief general account of the major budget parameters and their relationships.

9.1 *Budgets of energy and matter: general aspects*

Throughout this chapter, the following symbols will be used to denote the pricipal components of bioenergetic budgets:

- *feeding*, *F*
- *egestion*, *L*
- *growth*, *G*
- *respiration*, *R*
- *excretion*, *U*

The use of *U* (derived from urine) as a symbol for excretion is consistent with the predominant terminology in the literature. *L* stands here for unspecified mixed *"losses"* through *egestion* (also termed *"rejecta"*; see Mootz & Epifanio 1974, Logan & Epifanio 1978, Levine & Sulkin 1979, Anger & Harms 1989) of feces and leached materials. All other symbols are abbreviations of the corresponding terms (inconsistent terminology in the literature).

When these parameters are used in budgets of energy or matter, they must be expressed in the same unit. In carbon budgets, all parameters are given in µg (or mg) C, while Joules (J) are universally used as a unit in energy budgets (for conversion equivalents of mass and energy see below). An apostroph with the symbol is used here to denote a rate, i.e. a flow per unit of time. *F'*, for instance, is the instantaneous rate of feeding, i.e. the amount

of C or energy consumed per hour or day. Without the apostroph as an indicator for a rate, a budget parameter refers to a given developmental interval, e.g. food uptake, *F*, during the duration of a particular larval stage or throughout the period of larval development from hatching to metamorphosis. *R* as a bioenergetic parameter is always given in units of C or energy loss per unit of time, while the rate of oxygen consumption, from which *R* is estimated, is denoted with the symbol VO_2 (expressed in $\mu g\ O_2 \cdot hour^{-1} \cdot individual^{-1}$; see chapter 8).

9.1.1 *Principal bioenergetic parameters and pathways*

The partitioning of matter or energy taken up from food is schematically depicted in Figure 9.1, showing the principal pathways. The first losses of food materials can be experimentally observed already when larval feeding (*F*) is quantified. Depending on the physical properties of captured food particles, minor or major parts are usually lost due to leaching of liquid and fine particulate matter which cannot be quantitatively ingested (see section 5.3). As a subsequent loss of chemical energy, parts of the ingested materials pass through the larval intestine without being absorbed. These losses include a peritrophic membrane, which encloses the fecal material and is discarded via the anus. In a strict sense, however, this actively secreted membrane represents a part of body growth and thus, should be considered as an exuvial rather than a fecal loss (see Jones et al. 1997a).

The separate quantification of leaching and defecation is, at least in small aquatic animals, technically difficult and unprecise. In larval decapods, it is thus convenient (although not always satisfactory) to consider these losses collectively as unspecified rejecta or egestion, *L*. These losses are usually not measured directly but estimated from the difference between the total amount of food ingested (*F*) and the sum of all other, more precisely measurable budget parameters. These are summarized as *absorption*, *Ab*, which represents the chemical energy of the fraction of food that has crossed the gut wall.

In all higher organisms, the oxydation of absorbed nitrogenous compounds is incomplete, so that not only water and carbon dioxide but also chemically reduced molecules are produced. In aquatic crustaceans including decapod larvae, the major catabolic end product of the nitrogen metabolism is ammonia; it is excreted with the urine (see section 8.4). A fraction of the absorbed energy is thus lost with the excretion of ammonia (*U*). The remaining energy is summarized as assimilation, *A*, comprising the production of body tissues (growth, *G*) and metabolic losses through respiration (*R*). These principal pathways of matter and energy may be described with the following general equations:

$$Ab = F - L \tag{9.1}$$

$$A = Ab - U = F - L - U = G + R \tag{9.2}$$

In the literature, *U* has sometimes been considered as a fraction of *L*, confusing it with the egestion of feces. This is not quite correct because nitrogenous waste products are actually lost only after they have been absorbed with larger molecules. Since they are not further metabolizable in higher organisms, only the difference between total *Ab* and *U* becomes eventually available for growth (*G*) and metabolism (*R*).

Like *U*, *R* represents a loss from energy metabolism, i.e. from the catabolization of energy-rich macromolecules. *R* is usually measured as oxygen consumption, assuming that anaerobic metabolic processes can energetically be ignored (see section 8.3). The oxydation of complex organic molecules delivers chemical energy that is stored in adenylate

nucleotides (ATP and several others). This energy is available for the utilization in maintenance, muscle contractions, and other energy-consuming processes, or it may be reinvested in the synthesis of new macromolecular compounds such as proteins and lipids. Another part of the energy that is obtained from the degradation of food molecules, however, is inevitebly lost as metabolic heat.

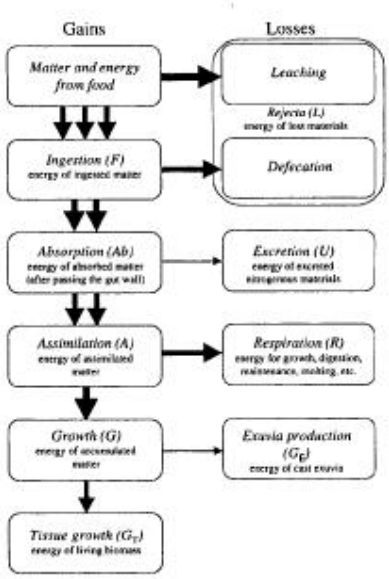


Figure 9.1. Partitioning of energy: the principal parameters of a bioenergetic budget.

The sum of *G* and *R* is termed also the *"metabolizable energy"* or *"physiological fuel value"* of food (Warren & Davis 1967, Wieser 1994). The energy that is ultimately available for body growth (*G*) is thus given as the difference between total ingestion, absorption, or assimilation and the various losses:

$$G = F - L - R - U = Ab - R - U = A - R \tag{9.3}$$

In arthropods, another part of this accumulated matter is lost at the end of each molting cycle. The energy of the cast exoskeleton (exuvia production, G_E) must thus be subtracted from total body growth (G) to obtain the production of living tissues, G_T:

$$G_T = G - G_E \tag{9.4}$$

In addition to this synthesized but eventually discarded exuvial matter, crustaceans produce a chitinous peritrophic membrane which coats the fecal pallet. Although this membrane represents an exuvial loss, it is usually - for technical reasons - considered as a

part of the feces. This implies the following problem (Jones et al. 1997a): *"if the energy content of peritrophic membranes proved to be relatvely high, their inclusion as egesta rather than exuvia would tend to underestimate assimilation efficiency and consequently overestimate net growth efficiency"* (for bioenergetic efficiencies see following section). The actual significance of this generally ignored budget parameter remains to be quantified in decapod larvae.

9.1.2 *Indices of bioenergetic efficiency*

From the above equations, efficiency indices, i.e. input:output ratios, can be derived (Ivlev 1945, Conover 1966, Warren & Davis 1967, Calow 1977b). The quotient of assimilation to ingestion gives the total fraction (or percentage) of the ingested dietary energy that is available for growth and metabolism. This index is termed *assimilation efficiency*, *A/F*:

$$A/F = (G + R)/F = (F - L - U)/F \tag{9.5}$$

Similarly, an *absorption efficiency* (*Ab/F*) may be given as a relative measure of food conversion. The fraction of ingested energy which is eventually converted into body growth represents another frequently used index of food utilization, named *gross growth efficiency*, K_1:

$$K_1 = G/F = (F - L - R - U)/F \tag{9.6}$$

When K_1 is applied to a particular biochemical compound class, it is commonly termed *conversion efficiency* rather than gross growth efficiency. In aquaculture, for instance, the conversion of expensive proteinaceous feeds to body proteins (the protein conversion efficiency) is of particular interest (Capuzzo 1982). The maximally possible efficiency of food conversion to growth is in living systems, in general, about 70-80% (Calow 1977b). Such a high level, however, may be reached only by very young, postnatal animals including larvae. Even in these early life-history stages, several factors such as energy requirements for locomotory and feeding activities or differentiation processes in cells and tissues, mitigate against the achievement of maximum conversion efficiency.

Finally, growth can be related to the total quantity of assimilated energy. The quotient of these two parameters is termed *net growth efficiency*, K_2:

$$K_2 = G/A = (F - L - U - R)/(F - L - U) \tag{Eq. 9.7}$$

Readjusting Eqs. 9.5-9.7, we can see that net growth efficiency equals the quotient of the gross growth and assimilation efficiencies:

$$K_2 = \frac{K_1}{(A/F)} \tag{Eq. 9.8}$$

K_2 may be estimated from the relationship:

$$K_2 = \frac{G}{G + R} \tag{Eq. 9.9}$$

It should be noted that K_1 and K_2 are not identical with the thermodynamic efficiencies of particular synthetic processes. Since they only quantify the overall fractions of ingested or assimilated food, respectively, that an organism invests into body growth, these indices are considered as ecological rather than physiological measures of production efficiency

(Conover 1978). K_1 and K_2 have thus more practical than theoretical significance. In physiological bioenergetics, especially on the cellular and molecular levels, the *partial production efficiency* (K_3), the *absolute caloric production efficiency* (K_4), and the *absolute energetic production efficiency* (K_5) are more meaningful (Wieser 1986).

9.1.3 *Equivalents of mass and energy*

Since direct calorimetric measurements of the energy content and metabolic heat production in pelagic larvae and their food are technically difficult, the various parameters of bioenergetic budgets are usually determined with indirect methods, yielding data in different units. For instance, the biomass of larvae and prey organisms may be quantified as total amounts of organic substances, proximate biochemical compounds, or carbon content, whereas respiratory losses are measured as oxygen consumption (VO_2), and excretion as a quantity of nitrogen excreted with NH_4^+ and NH_3. Hence, all these data must be converted to a common unit before they can be inserted in a budget.

In energy budgets, all measurements must be given in Joules (or calories; 1 J = 0.239 cal), while a carbon budget requires conversions to mass units of C. When particular nitrogenous compounds such as proteins are of interest (mainly in aquaculture), a nitrogen budget can be established, using mass units of N. It should be stressed here that the complete form of a budget (Fig. 9.1; Eqs. 9.1-9.3) applies in aquatic crustaceans only when it is given in energy units. In C budgets, the U term is usually omitted, because the excretion of organic (i.e. C-containing) compounds is generally insignificant or lacking. In N budgets, on the other hand, the respiration term does not occur.

The caloric content of food materials and larval body mass can be measured directly, using bomb calorimetry or a wet oxydation technique (Grodzinski et al. 1975, Newell 1982, Henken et al. 1986). Alternatively, it may be estimated from the average energy contents of the major biochemical compound classes. Although the conversion factors given in the literature may vary slightly among authors, the following caloric equivalents have widely been accepted (Winberg 1971):

- 23.64 J/mg protein
- 17.15 J/mg carbohydrate
- 39.54 J/mg lipid

When no biochemical analyses but only carbon values are available, an estimate of the energy content is possible too, using an empirical regression equation obtained from parallel measurements of the organic C (in % of ash-free dry mass) and the energy content (E, in Joules) in aquatic organisms (Salonen et al. 1976):

- $E = 19.73 + 0.42 \cdot C$ [J/mg organic C]

This conversion takes into consideration that the caloric content of biomass varies significantly not only with the absolute but also with the relative C content of biomass. This shift is caused by the fact that high percentage C values reflect high lipid contents (for correlation between lipid and C see section 7.4). Compared with proteins, lipids contain more C per unit weight (70-80% *vs.* 50-54%; Winberg 1971), and their average energy content per unit C is about 20% higher (Salonen et al. 1976). It must be warned, however, that energy estimates from C data are probably less reliable than those based on analyses of proximate biochemical composition. Likewise, ash-free dry mass (*AFW*) data may be used for rough estimates of the uptake and conversion of organic matter and chemical energy.

Oxygen consumption (VO_2) can be converted quite accurately into an energy loss, because variable utilization of different biochemical substrates in metabolic processes causes only minor variation in the amounts of metabolic heat production. This applies also to the caloric equivalent of nitrogen excretion. In the literature, the following conversion factors are commonly used for the consumption of oxygen and the production of ammonia-nitrogen, respectively, into caloric losses (Elliott & Davison 1975, Gnaiger 1983):

- 14.06 J/mg O_2
- 24.87 J/mg NH_3-N

In contrast to the metabolic energy losses, the quantity of C that is lost with respiratory CO_2 depends on the predominant metabolic substrate. The respiratory quotient, *RQ* (i.e. the molar ratio of produced CO_2 to consumed O_2), equals a value of 1.0 when exclusively carbohydrates are catabolized, while an average of about 0.7 is obtained for the oxydation of fat, and ca. 0.8 for protein catabolization. Since natural food sources are always biochemical mixtures, an intermediate *RQ* of about 0.8-0.9 may generally be assumed (Nelson et al. 1977). If predominantly zooplankton with a similar chemical composition as that of the crustacean larvae is eaten (high dietary protein, low lipid, very low carbohydrate level), an average *RQ* of 0.8 should be a realistic estimate for predatory larvae such as the mysis stages of nephropid lobsters; higher values ($\geq$0.9) may be more representative of phytoplankton feeders, e.g. the protozoeae of penaeid shrimps. From these *RQ* estimates we obtain as conversion factors between oxygen consumption and respiratory carbon losses in carnivores and herbivores:

- 0.30 - 0.34 mg C/mg O_2

9.2 *Ontogenetic shifts in energy partitioning*

Compared with the amount of literature that is available on the bioenergetics of adult crustaceans and other large-sized invertebrates, there exists only a very limited number of studies on the energy partitioning in larval decapods. Most published data allow only for an identification of ontogenetic changes between successive larval stages, but not of those occurring within these stages (Anger 1991a). Since we know, however, that dramatic physiological changes take place during each molting cycle, we must expect significant variation in the uptake and partitioning of dietary energy within individual instars. In the following section, I will thus primarily address molt-cycle related changes in energy or carbon budgets. By integration of these temporal patterns in energy partitioning (rather than from single "representative" measurements taken in successive instars), summary budgets for individual developmental stages can be obtained and analysed for possible ontogenetic trends.

9.2.1 *Instantaneous budgets: changes during the molting cycle*

In order to identify molt-cycle related changes in energy partitioning, we need to measure the various parameters of an energy budget with a sufficiently high temporal resolution. This is generally difficult, as larval molting cycles are short, usually not exceeding a few days. As a particularly well-suited "model species" for bioenergetic research on larval decapods, the spider crab *Hyas araneus* has been studied in much detail, because it shows, from a technical point of view, several advantages: (1) the development duration of the individual larval stages is comparatively long (ca. 10-20 days at ecologically relevant temperatures), allowing for a high resolution with 24 or 48 h sampling intervals; (2) this

species (as all spider crabs) passes through only two zoeal stages and a megalopa, which is the minimum required to study all major larval types of the higher Decapoda, i.e. both anamorphic and metamorphic zoeae, and a decapodid (cf. section 2.2); (3) the larvae are among the largest in the Brachyura, allowing for small sample size and high precision in chemical determinations; (4) the fecundity is high, with >10,000 zoeae hatching from a single female, so that sample size and number of replicate measurements remain limited by bench space and labour rather than by availability of material. These technical advantages of our model species have greatly facilitated the gleaning of an extensive data set, from which we derived descriptive models of bioenergetic and other physiological changes during larval development (see Anger et al. 1989a, Anger & Harms 1989, Anger 1990, 1991a). Hence, this species serves us here as a standard example of molt-cycle related and other ontogenetic changes in energy partitioning.

When we measured absolute energy flows (in Joules per individual and day), we found dramatic changes during each of the larval molting cycles (Fig. 9.2). The instantaneous (daily) rate of food uptake (*F'*) increased rapidly in postmolt, reached a maximum in intermolt (zoea I) or earlier within the molting cycle (zoea II, megalopa), and then tended to decrease throughout the premolt period (Fig. 9.2a). The rate of growth (*G'*) was always maximum in postmolt and early intermolt, decreasing throughout the later parts of the molting cycle (cf. section 6.2.3). The respiratory energy losses (*R'*), in contrast, varied much less, showing a gradually increasing trend throughout the time of larval development. The daily excretory losses (*U'*) changed within each larval stage with an arched pattern, reaching a maximum approximately in the middle of the molting cycle (Fig. 9.2b). Although, similar as in *R'*, the average level of *U'* increased in successive instars, the energetic losses through nitrogen excretion remained always at an order of magnitude below those of the estimated respiratory heat production. Thus, *U'* had only a minor significance in total energy partitioning.

When the sum of respiration, excretion, and growth (i.e. assimilation, *A'*) is compared with total food uptake (*F'*), instantaneous assimilation efficiency is obtained as an index of daily food utilization. In the zoeal stages of *Hyas araneus*, the *A'/F'* quotient was consistently maximum (>80%) in postmolt, minimum (about 50%) during the intermolt period, and increasing again (to ca. 70-80%) in premolt. During major parts of the megalopa molting cycle, however, unrealistically high *A'/F'* values were calculated, indicating that the rates of feeding (*F'*) and egestion (*L*) were in this stage experimentally underestimated (for discussion see Anger & Harms 1989, Anger 1990).

Within total assimilation, the growth parameter (*G'*) was in all larval stages during the postmolt and early intermolt periods consistently higher than *R'*, indicating that the conversion of dietary energy into biomass was particularly efficient during the first half of the molting cycle. These proportions revered consistently in the second half, with *R'* increasingly exceeding the *G'* term. In the late megalopa, i.e. shortly before metamorphosis, the crab larvae respired more energy than they accumulated from food, so that growth became eventually negative (Fig. 9.2a).

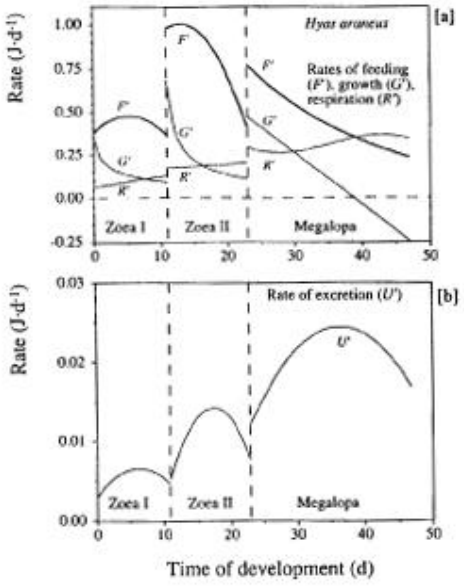


Figure 9.2. Daily rates of feeding, growth, respiration, and nitrogen excretion (all in units of energy, J) during the time of larval development in a spider crab, *Hyas araneus* (redrawn after Anger & Harms 1989).

In comparative research on the bioenergetics of decapod larvae, also biomass-specific rates of feeding, growth, and respiration should be given to enhance the comparability among larvae with different body size. In energy budgets, it is thus convenient to convert the data of food uptake, biomass accumulation, and oxygen consumption into energy-specific rates (*F'/E*, *G'/E*, *R'/E*). In *Hyas araneus*, the specific rate of food uptake was maximum after hatching, reaching an equivalent of about 50% of larval biomass (in energy units) consumed per day. During the zoea I molting cycle, the *F'/E* values decreased to a level below 20% of larval body energy per day; a similar feeding pattern, only at a slightly lower average level, was observed also in the zoea II (Fig.9.3a). The megalopae of *H. araneus* ate, on average, much less than the zoeal stages (mostly corresponding to <10% of their own biomass per day; however, these values probably underestimated the actual feeding rates). During the course of the megalopa molting cycle, the *F'/E* values showed a decreasing tendency, as in the other stages.

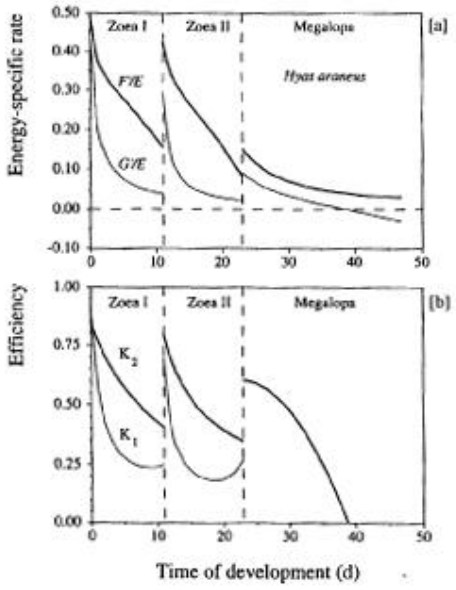


Figure 9.3. Changes in energy partitioning during the time of larval development in a spider crab, *Hyas araneus*; [a] biomass-specific (energy-based) daily rates of feeding (*F'/E*) and growth (*G'/E*); [b] gross growth efficiency, K_1 (given only for zoeal stages), net growth efficiency, K_2 (redrawn after Anger & Harms 1989).

Similar molt-cycle related patterns as in the energy-specific ingestion rates were observed also in the specific growth rates (Fig.9.3a). The highest *G'/E* was measured in postmolt larvae, reaching maximum values of about 30-40%·d^{-1} in the zoeal stages and ca. 9%· d^{-1} in the early megalopa. Compared to the specific rates of feeding and growth, the energy flows into metabolism were smaller and relatively constant, with *R'/E* and *U'/E* values of about 3-8% and 0.2-0.4%·d^{-1}, respectively.

When daily growth rates are compared directly with the concomitant feeding rates, daily gross growth efficiencies can be estimated. In the zoeal stages of *Hyas araneus*, K_1 was clearly maximum in the initial phase of the molting cycle, decreasing thereafter (Fig. 9.3b; no K_1 curve is shown for the megalopa stage, as our data indicate that the rates of feeding and egestion were experimentally underestimated; see above). In late premolt, the instantaneous rate of feeding tended to decrease slightly faster than growth (cf. Fig. 9.3a), so that K_1 increased slightly at the end of the zoeal molting cycles; however, it remains unclear if this trend can be generalized for crab larvae.

Since the quantification of ingestion rates is generally unprecise (see section 5.3) and all parameters of assimilation were in our experiments measured directly (in contrast to *L'*), net growth efficiency should be a more reliable measure of energy conversion than K_1. Similar to K_1, the K_2 index showed in all larval stages of *Hyas araneus* consistently a maximum in postmolt and a clear decreasing trend throughout the later parts of the molting cycle; as a consequence of biomass losses during the premolt stages in the megalopa,

the index became eventually negative (Fig. 9.3b). Decreasing K_2 values were observed also in the larval molting cycles of the hermit crab *Pagurus bernhardus*, especially in the last two zoeal stages (Anger et al. 1990b). Strikingly similar bioenergetic patterns as in the larvae of the brachyuran crab *H. araneus* were recently found also in a caridean shrimp, *Macrobrachium nipponense*, namely in the absolute and biomass-specific rates of feeding, growth, and respiration (Shin & Chin 1994, 1995).

With the exception of the rate of feeding and related parameters (A'/F', L', K_1), our models of molt-cycle related changes in the energy budget of larval *H. araneus* are based on an extensive set of data. Unfortunately, however, very few studies with a similar high temporal resolution have become available for other species, so that it remains uncertain if the patterns shown above are characteristic of decapod crustacean larvae. Their generality is supported by studies where molt-cycle related changes in at least one bioenergetic parameter (usually growth or respiration) were measured in short intervals, showing mostly similar patterns as in *Hyas araneus* and in *Macrobrachium nipponense*.

In summary, I suggest that at least some of the patterns shown above should occur universally in planktivorous marine decapod larvae; however, major deviations must be expected in species with an enhanced endotrophic potentia (facultative lecithotrophy). In particular, the following bioenergetic trends should typically occur during the course of individual larval molting cycles:

- arched curves of ingestion rate (F') with maximum values in intermolt;
- drastically decreasing instantaneous rates of growth (G');
- gradually increasing respiratory energy losses (R');
- G' initially exceeding R', but metabolic losses equal or outbalance in later molt-stages the concomitant rate of biomass accumulation;
- bioenergetically insignificant excretory losses (U'), possibly varying with the same temporal patterns as F';
- A'/F', K_1, and K_2 maximum in the early molt-stages, decreasing through major parts of the molting cycle; A'/F' may increase again during premolt.

Since the predictability of larval feeding and growth has great practical relevance, more comparative bioenergetic studies are necessary to test these putative rules for their general applicability. The available evidence has clearly shown that molt-cycle related changes in energy partitioning may be stronger than those between successive larval stages. Hence, the construction of more realistic bioenergetic models requires an enhanced temporal resolution of sampling and measuring.

9.2.2 *Cumulative budgets: shifts between successive stages*

When the regression curves of molt-cycle related changes in energy partitioning (Fig. 9.2) are integrated over the time of development within each larval instar, cumulative stage-specific energy budgets are obtained. These summary budgets can be compared among successive larval stages to identify ontogenetic shifts.

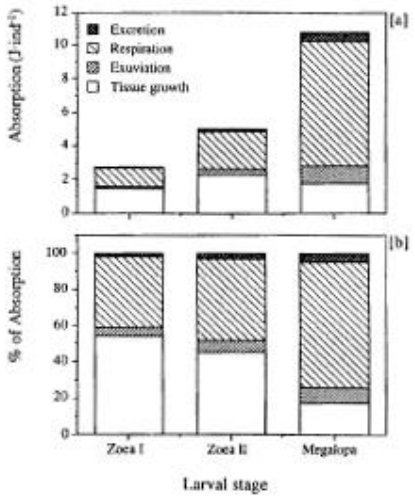


Figure 9.4. Assimilation and partitioning of energy in successive larval stages of a spider crab, *Hyas araneus*; [a] absolute quantities (Joules per individual); [b] relative proportions (in % of total assimilated energy) distributed among tissue growth, exuvia production, respiration, and nitrogen excretion (redrawn after Anger & Harms 1989).

In the successive larval stages of *Hyas araneus*, an exponential increase was observed in assimilation (A), respiration (R), excretion (U), and exuvia production (G_E), but not in total growth or tissue growth (G, G_T) achieved per instar. G increased clearly between the zoea I and II stages, but only little in the megalopa (Fig. 9.4a). In the latter stage, about one third (35%) of total growth was lost again with the shed exoskeleton (G_E), so that the remaining tissue growth (G_T) was lower than in the zoea II (Fig. 9.4a). In the zoeal stages, the exuvial losses amounted to only 9% and 13% of G, respectively. This conspicuous shift in the relation between G_T and G_E reflects the differential degree of cuticle thickness in pelagic *vs.* benthic or semibenthic forms (cf. section 3.1). A gradual increase in the relation between G_E and G_T was found also in the successive larval stages of the caridean shrimp *Macrobrachium nipponense* (Shin & Chin 1995) and in several other decapod taxa (Anger 1991a, 1998). This suggests that a shift towards increasing exuvial losses and decreasing tissue growth represents a growth rule in larval decapods.

Ontogenetic shifts in the overall energy partitioning become better comparable among taxa or stages, when the major energy flows are expressed in percent of total absorption. In the successive larval instars of *Hyas araneus*, these changes were similar to the tendencies observed within individual molting cycles (Fig. 9.4b). Growth exceeded initially the metabolic losses, but this relation declined in later stages. In the zoea I, G and R amounted to 59 and 39% of Ab, respectively, while 52 *vs.* 45% were measured in the zoea II, and an inverse relation (26 *vs.* 69%) occurred in the megalopa. If excretory losses are ignored, these percentage growth figures represent practically net growth efficiencies; hence, K_2 decreased in the successive larval stages of *H. araneus* from about 59 to 26%.

Similar K_2 figures as in *Hyas araneus* were measured in the larval stages of another spider crab, *Libinia ferreirae*, with 57, 36, and 7%, respectively (Anger et al. 1989b). The same trend, only much weaker, was observed also in the hermit crab, *Pagurus bernhardus*, with K_2 values of 58% in the zoea I *vs.* 44-47% in the later zoeal stages (Anger et al. 1990b). In the larval stages of the palaemonid shrimp *Macrobrachium nipponense*, again the same tendency was found, but with generally higher K_2 figures (Shin & Chin 1995). K_2 decreased in this species from 72% in the zoea II (the zoea I is lecithotrophic) to 40-42% in larval instar IX and in the "postlarva" (in this case, probably the first juvenile stage). In the congenor *M. rosenbergii*, however, much lower and ontogenetically increasing rather than decreasing K_2 values were measured, ranging from 21 to 36% (Stephenson & Knight 1980). In a recent study on the same shrimp species, highly variable K_2 values were obtained, which seemed to be influenced more by temperature and salinity variation than by developmental stage (Agard 1999). Similarly as in *M. nipponense*, K_2 decreased in *Penaeus monodon* larvae from initially 88% (protozoea I) to a level of 56-66% (mysis stages, first "postlarva"; Kurmaly et al. 1989a).

In summary, an ontogenetically decreasing trend in K_2 has most frequently, although not always, been observed in studies with a high temporal resolution of measurements, suggesting that this represents a typical pattern in larval decapods (cf. McConaugha 1985, Anger 1991a). The same may apply to K_1. A slight decrease in K_1 was observed between the three successive larval stages of *Hyas araneus*, with cumulative values of 33, 26, and 26%, respectively. This index decreased also throughout the larval development of the shrimp *Palaemon serratus* (from 76 to 41%; Reeve 1969). In another palaemonid species, *Macrobrachium nipponense*, it decreased from initially 63% (zoea II) to a final value of 34% (Shin & Chin 1995). In contrast to K_1, the A/F quotient appears to vary more among taxa than in relation to ontogeny (Anger 1991a).

From the energy flows determined in successive larval stages, an overall cumulative budget may be calculated for the entire larval phase of a species. Average percentage flows into tissue growth, exuviation, respiration, and nitrogen excretion, respectively, may be compared among different species or rearing conditions (McConaugha 1985, Anger 1991a). In all three larval stages of *Hyas araneus* combined, 58% of the absorbed energy was lost with respiratory heat production and about 4% through ammonia excretion; total growth (G) accounted for 38% of Ab, but one fifth of this quantity was lost again with the cast exuviae (G_E in Fig. 9.5).

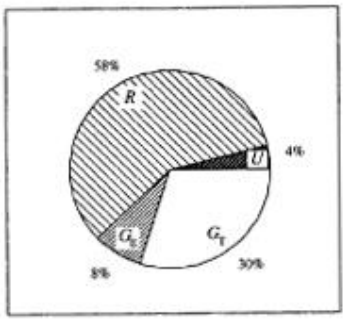


Figure 9.5. Partitioning (% of total energy assimilated) among tissue growth (G_T), exuvia production (G_E), respiration (R), and nitrogen excretion (U) during the complete larval development of a spider crab, *Hyas araneus* (redrawn after Anger & Harms 1989).

As a consequence of ontogenetic shifts in energy partitioning and differential lengths of successive molting cycles, different stages may contribute in quite variable proportions to the overall cumulative energy budget of total larval development. When the absolute energy flows are compared in *Hyas araneus* larvae, *R* is clearly the dominating bioenergetic parameter (Fig. 9.6a). This is principally a consequence of low growth rates and high metabolic losses in the megalopa, which also has a long development duration (approximately equalling that through the two zoeal stages combined). While the zoeal stages contributed only 10 and 21%, respectively, to the respiratory energy losses during the complete phase of larval development, the megalopa was responsible for 69% of total *R*. Similar differences were found in the stage-specific contributions to the excretory and exuvial losses (U, G_E in Fig. 9.6b). In contrast, the proportions of *Ab* that were invested in larval tissue growth (G_T from hatching to metamorphosis) varied less among the successive stages, with contributions of 27% (zoea I), 41% (zoea II), and 32% (megalopa), respectively.

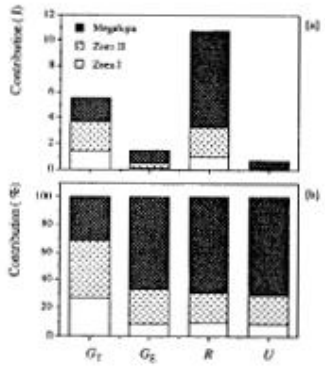


Figure 9.6. Contribution (in %) of the successive larval stages of a spider crab (*Hyas araneus*) to the principal parameters of the larval summary energy budget: tissue growth, G_T; exuvia production, G_E; respiration, R; nitrogen excretion, U (redrawn, after Anger & Harms 1989).

9.3 *Effects of environmental factors*

The assimilation and partitioning of dietary energy changes not only ontogenetically, but may be altered also by extrinsic factors such as the feeding regime, temperature, salinity, oxygen concentration, the action of toxic pollutants, etc. External effects have been extensively studied in isolated budget parameters, while much less is known about changes in the quantitative relations between different energy flows. Isolated environmental effects on larval feeding, growth, respiration, and excretion are reviewed in chapters 5-8 of this volume. In the following sections, I will thus focus on externally induced changes in the bioenergetic efficiencies of assimilation and growth, i.e. in A/F, K_1, and K_2.

9.3.1 *Food*

When energetic efficiencies are compared on different trophic levels within the zooplankton, there appear to exist some typical differences between herbivorous and carnivorous species, implying a negative correlation between A/F and K_2 (Welch 1968). According to the literature, herbivorous species tend to assimilate a smaller proportion of what they ingest (lower A/F), but are able to convert a greater part of the assimilated energy to growth (higher K_2) as compared with carnivores. According to Jones et al. (1997a), *"herbivores tend to show very low assimilation efficiencies, but very rapid throughput of relatively high quantities of ingested material, whereas the carnivores ingest relatively smaller quantities of food but have much longer gut residence times"*. As a result, K_1 may remain roughly the same in these trophic groups.

These differences in A/F and K_2 are believed to reflect differential chemical composition and digestibility of plants and animals as food sources. High A/F values may be explained by relatively easy digestibility of the proteinaceous diets of carnivores as compared to plant matter with large quantities of high molecular weight polysaccharides. It is

possible that the low average net growth efficiency in carnivores has selected for improved enzymatic mechanisms of protein digestion and thus, for an enhanced assimilation efficiency (Calow 1977b). On the other hand, the low average A/F level in herbivores might have selected for mechanisms enhancing the K_2, i.e. for a switch from high metabolic energy investment into activity towards an enhancement of growth.

Similar shifts in the efficiencies of assimilation and growth may be expected in omnivorous larvae exposed to variable feeding regimes. However, when growth was compared in megalopae of *Hyas araneus* fed with either *Artemia* nauplii or diatoms, a much higher K_2 was found in the carnivorous group (13.8 *vs.* 1.5%; Harms & Anger 1990). Since larval energy budgets have only rarely been studied under different conditions, it remains to be checked in future research whether this finding was a rare exception, or if the presumable rule of higher K_2 in herbivores than in carnivores does not generally apply to larval decapods. Probably, the larvae of *H. araneus* are physiologically better adapted to carnivorous feeding, lacking mechanisms for an efficient conversion of assimilated phytoplankton materials to body growth and thus, losing major parts of A with metabolic heat and waste products.

Within a trophic level, A/F, K_1, and K_2 appear to be positively correlated when different levels of availability and uptake of food are compared. When food is scarce or the feeding process is inefficient (for instance, when the average particle size is unsuitably small or large in relation to larval mouthpart morphology; cf. section 5.2.3), changes in the feeding behavior or in the conversion and partitioning of dietary energy may allow for compensatory growth. As a first response to a decreased food level, decapod larvae can increase their feeding activity, enhancing the volume of water searched or filtered per unit of time. As alternative or additional mechanisms, the rate of conversion of ingested food may be adjusted according to the available quantities, or the amounts of metabolizable energy can be upregulated (i.e. A/F enhanced) by means of reducing the fecal losses (for regulation of digestive enzyme activity and gut evacuation time, see section 5.4). As another possible response to poor food availability, a shift within the budget parameter A is possible, switching parts of the absorbed nutrients from metabolic to synthetic pathways; in this case, the metabolic rate is reduced, and the growth efficiencies K_1 and K_2 are enhanced (Calow 1977b). Hence, a low level of available dietary energy may stimulate mechanisms for increasing F, A/F, K_1, and/or K_2.

A more detailed picture of energy partitioning is obtained when conversions of major biochemical compound classes are considered separately. For instance, protein absorption efficiency may remain high under food-limited conditions, while lipid accumulation ceases or fat reserves are reduced (see section 7.5.2.2, Fig. 7.6). The compound-specific conversion efficiencies depend, also in well-fed crustaceans, on the overall biochemical composition and digestibility of food. In lobster and prawn culture, for example, protein conversion may be enhanced (or its catabolism reduced) when certain lipids or carbohydrates are added to the diet (Capuzzo 1982). Similarly, additions of essential fatty acids or cellulose fiber have been shown to increase the efficiency of protein conversion. On the other hand, A/F, K_1 and K_2 may be downregulated at excess levels of food availability (Conover 1978, Heinle 1981, Abreu-Grobois et al. 1991), including a reduced conversion of individual dietary compounds such as proteins or lipids (Capuzzo 1982).

9.3.2 *Temperature and salinity*

Single or combined effects of temperature and salinity on larval survival, development, feeding, growth, or respiration have been described in numerous publications, but environmentally induced shifts in the partitioning of energy flows have been studied only rarely. Even in holozooplankton such as copepods, relatively few and inconsistent observations exist on the quantitative relationships between physical factors and energy partitioning. McLaren (1963) hypothesized that temperature-induced changes in gross or net growth efficiency of zooplankton might explain diurnal vertical migrations in the water column, assuming that the weight-specific rates of respiration and growth should be different functions of temperature. As an adaptation to such a shift in energy partitioning, planktonic grazers should metabolize their food at temperatures different from those at which they eat it, thus enhancing K_1 or K_2. However, these shifts appear to be too small to explain why many species spend considerable amounts of energy for migrating up and down. Recent evidence suggests that both the need for dispersal and pelagic predation pressure are more significant selective forces in the evolution of migration patterns than a possible energetic advantage of increased growth efficiency (see chapter 10).

When the larval stages of the rock crab, *Cancer irroratus*, were reared under several temperature-salinity combinations, A/F was not correlated with the apparent suitability of the various conditions. Rather, K_1 and K_2 (i.e. the channellization of ingested and assimilated energy into tissue growth), tended to decrease under conditions where also survival was particularly low (Johns 1982). In this species, unfavourably low salinities exerted stronger negative effects than unfavourable temperatures. In caridean shrimp (*Palaemon serratus*) larvae, the ingestion rate increased with increasing temperature, but the efficiency of conversion of assimilated energy to growth (K_2) remained roughly the same, which allowed for enhanced growth at higher temperatures (Yúfera & Rodríguez 1985b).

Salinity effects on energy partitioning were recently shown also in the zoea I of the shore crab, *Carcinus maenas* (Anger et al. 1998). Under hyposaline stress, the larvae were not able to assimilate the same amounts of energy as unstressed siblings, so that less metabolizable energy was available for growth and metabolism. Although respiration was significantly reduced by low salinities, this energy-sparing effect did not compensate the depression of total assimilation, and thus, growth was significantly reduced. This was caused not only by a decreased level of A, but also by a dramatical decline in K_2. Interestingly, this drop in net growth efficiency was conspicuous only during the first half of the molting cycle, while a partial compensation (i.e. an increase in K_2 at unfavourably low salinities) was observed during premolt. These data demonstrate once more that future studies of stress effects on larval growth must pay attention to molt-cycle related and other developmental variation in the physiological response and tolerance patterns, i.e. the temporal resolution of sampling and measuring should be increased wherever possible. In the same study, reduced K_2 values were observed after short transitory periods of exposure to hyposaline conditions. When this stress occurred at the beginning of the molting cycle, an exposure of only 24 hours had almost the same negative effect on growth efficiency as longer lasting or continual osmotic stress. This finding shows again the importance of studying short-term in addition to chronic environmental effects.

In summary, unfavourable environmental conditions appear to depress not only single parameters of the energy budget (ingestion, respiration, growth), but in most cases also the efficieny of channelling ingested or assimilated energy into tissue growth. However, too few comparative data from larval decapods have become available to allow for safe gen-

eralizations. In juvenile penaeid shrimps, K_2 was observed to increase under conditions of physical stress (in this case, reduced oxgen concentration), partially compensating for a reduced assimilation of food (Rosas et al. 1998, 1999). This suggests that also compensation mechanisms exist in the partitioning of energy.

9.3.3 *Pollution*

Among the stress factors that may affect larval growth and development in their natural environment, numerous man-made pollutants have been studied in decapod larvae as experimental target organisms. However, the response criteria were mostly limited to the rates of survival and development, more rarely to growth or respiration. In *Cancer irroratus* larvae, toxic water-soluble fuel oil fractions were shown to increase the respiratory energy losses and to depress the rates of feeding and growth (Johns & Pechenik 1980). Similarly as in *Carcinus maenas* larvae exposed to brackish water, the reduction in growth was caused not only by decreased assimilation, but also by reduced efficiency of food conversion, i.e. declining K_1 and K_2. Enhanced respiration, reduced growth, and reduced K_2 were found also in early shrimp (*Palaemonetes pugio*) larvae in the presence of Methoprene, an insect growth regulator (McKenney & Celestial 1993).

When lobster (*Homarus americanus*) larvae were exposed to a mixed toxicant, drilling fluids from oil platforms, a dramatic decline occurred in all major budget parameters, namely F, A, R, G, and K_1 (Smith Derby & Capuzzo 1984). Since G was proportionally more affected than R, also the K_2 index (not given in this paper) must have been reduced under this pollution stress. The same effects can be inferred from the respiration and growth data shown in a paper that described toxic effects of chlorine and chloramine on the physiology of larval lobsters (Capuzzo 1977).

10 ECOLOGY AND BEHAVIOR

Most larval decapods sojourn for a few days or weeks in the pelagic environment, although some may stay there for up to several months before they eventually return to the benthos and recruit to the adult populations (Thorson 1961). The regional patterns of larval dispersal depend largely on major oceanic current systems, coastal morphology, and prevailing wind directions during the reproductive season. This leads to regionally differential recruitment and hence, variation in the degree of genetic exchange among geographically separated populations (Bunch et al. 1998). During their planktonic phase, the larvae are exposed to variations in numerous ecological factors which influence their chances of survival, development, dispersal, and recruitment. These include physical and chemical variables such as temperature, salinity, light, and toxic pollutants, as well as the principal biotic factors food and predation (for exhaustive review, see Sastry 1983b, Pechenik 1987, Morgan 1995a, Epifanio & Garvine 2001). Since the various causes of larval mortality in the plankton determine, directly or indirectly, the stability of benthic fish and invertebrate populations, they are of great general interest also in marine ecology and fisheries biology (Rumrill 1990, Morgan 1995a).

Although they seem to be weak and only passively drifting, planktonic larvae are not entirely subjected to the arbitrariness of locally or temporarily prevailing conditions in the pelagic environment (for recent discussion, see Metaxas 2001). There is a steadily increasing body of evidence that larvae can actively avoid unfavourable physical conditions, reduce predation, and participate in the processes of dispersal and recruitment, namely by choosing a position within the water column or selecting a suitable substratum for settlement. This partial self-determination of larval fate is based upon genetically fixed and environmentally entrained behavioral patterns, and on other evolutionary adaptations to predictable changes in the environment. Within certain limits, there are adaptations even to the lack of predictability in particular habitats, enhancing the likelihood of successful development and metamorphosis under highly variable conditions.

The ecological key factors governing in the pelagic environment as well as principal life-history adaptations to these variables constitute the primary subjects of this chapter. This includes relationships between climatic conditions and larval tolerance, physiological regulation mechanisms, seasonality of reproduction, female energy allocation to offspring production, endogenous rhythms of egg hatching, behavioral responses of larvae to gradients in physical and chemical factors, patterns of larval migration, anti-predatory features, dispersal strategies, examples of larval development in land-locked habitats outside the ancestral environment of the Decapoda, the sea, and eventually, key processes and adaptations involved in settlement and metamorphosis.

Similar as in nutrition, there exists a tremendous amount of publications on larval ecology and behavior, comprising several thousand papers (Young 1990, Rice 1993). It is thus impossible to provide here an exhaustive overview of all relevant literature. An extensive review was recently presented in the book *"Ecology of Marine Invertebrate Larvae"* (McEdward 1995), which deals with all major ecological, behavioral, and evolutionary aspects of larval life in the plankton, in general (including non-crustacean larvae). Here, I concentrate on the principal ecological mechanisms and adaptations in larval decapods, preferentially showing examples from recent and current research.

10.1 *Ecological key factors: selective pressures, adaptations, behavioral responses*

Various effects of ecological key factors such as temperature, salinity, oxygen concentration, and food availability have been treated in the preceding chapters, especially in relation to larval growth and metabolism. The following sections will primarily deal with specific tolerance limits and ontogenetic changes therein, behavioral avoidance mechanisms, and examples of presumable selective pressures and specific adaptations to variability in the most prominent ecological parameters. Adaptations to particular environmental conditions occur in virtually all aspects of larval biology that have been reviewed here, including larval morphology, anatomy, the molting cycle, feeding, growth, biochemical composition, metabolism, and energy partitioning. Thus, there is unavoidably an overlap with information given before, but also among the sections of this chapter, where ecological traits are considered in relation to all other aspects of larval life.

10.1.1 *Temperature*

As an ecological key factor, temperature exerts a paramount influence on all developmental and other physiological processes (Costlow & Bookhout 1969). In particular, this comprises accelerating and delaying effects on rates of larval growth, development and metabolism (see sections 6.4.1 and 8.3.5), as well as seasonal variation in the occurrence of larvae in the plankton; the latter aspect will be treated below (section 10.2). Here, I will concentrate on examples of tolerance limits in relation to climatic adaptation and review behavioral responses to temperature gradients.

In numerous studies on decapod crustacean larvae, rates of survival and development through successive stages, or those of respiration and growth were described as functions of temperature. As a rule, the tolerated range is closely associated with the geographic distribution of a species. While decapods from the tropics and high latitudes show in general a stenothermal response, those living in temperate climates are usually eurythermal. This response is an adaptation to the occurrence of pronounced seasonal and regional temperature variations in the intermediate climatic zones. These patterns are exemplified here with some arbitrarily chosen species differing in their climatic distributions.

The Antarctic shrimp species *Notocrangon antarcticus* and *Chorismus antarcticus* may be considered as typical examples of extremely cold-adapted and stenothermal decapods. In rearing experiments, they developed at 0°C from hatching through metamorphosis, whilst temperatures above 6°C were not tolerated (Bruns 1992). In the subarctic-boreal shrimp *Pandalus borealis*, the upper limit of tolerance is higher. In rearing experiments, the larvae developed well at temperatures below 9°C, but showed signs of physiological stress in warmer water (Paul & Nunes 1983; see section 8.3.5, Fig. 8.7). The larvae of the northern stone crab, *Lithodes maja*, shows a similar temperature optimum, consistent with a similar geographic range (Anger 1996b). Similarly, the spider crab *Hyas araneus* occurs in the subarctic zone of the North Atlantic, although its distribution extends south to the temperate waters of the Channel region (Christiansen 1969). This is consistent with a much wider thermal tolerance range: Larval development, at least to the megalopa stage, is in this species possible at 2°C, while the upper limit was observed at about 18°C (Anger & Nair 1979, Anger 1983b, 1987b). The common shore crab, *Carcinus maenas*, is a typical example of a eurythermal temperate species. It is distributed from northern Norway to subtropical regions in northwestern Africa. In laboratory experiments, its larvae were successfully reared at temperatures ranging from 9-25°C (Dawirs et al. 1986, Dawirs &

Dietrich 1986). By comparison, the optimal range of tropical and subtropical crab species is usually above 25°C, while temperatures below 20°C cause an increase in larval mortality (see e.g. Anger et al. 1981b, Anger 1991b). Similar shifts in the temperature optimum occur also intraspecifically. This has been documented, for instance, in larval and juvenile fiddler crabs (*Uca* spp.) from populations living in different climatic regions (Vernberg & Costlow 1966).

Many researchers chose a multifactorial experimental approach to study effects of temperature in combination with different salinities, pollutants, food concentrations, or other variables. The complex results can be analysed with nonlinear models which show the relative importance of single effects and interactions thereof (Alderdice 1972, 1976; for application in decapod larvae, see e.g. Costlow et al. 1960). Such combined effects can be illustrated in "response surface" diagrams, where rates of survival, development, or metabolism are shown in a two- or multifactorial field (Fig. 10.1; cf. section 8.3.5, Fig. 8.10).

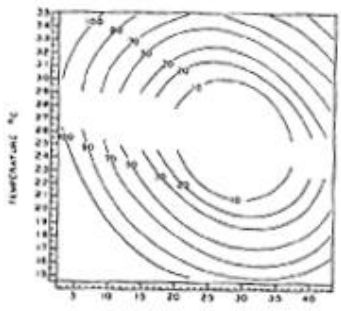


Figure 10.1. Percent mortality of the zoea I of a crab (*Sesarma cinereum*) reared at 12 combinations of temperature and salinity; fitted response surface (from Costlow *et al.* 1960, with permission from MBL, Woods Hole, USA).

As a rule, such investigations showed that the range of tolerance of one factor (e.g. temperature) will narrow when another ecological variable deviates from the optimum. For instance, larval *Carcinus maenas* are sensitive to both low temperatures and low salinities. In consequence, the tolerance of low temperatures is further reduced when also salinity is suboptimally low, or *vice versa* (Nagaraj 1993). Similar response patterns were observed in euryhaline shrimp (*Palaemon serratus*; Yagi et al. 1990) and crab larvae (*Eriocheir sinensis*; Anger 1991b), as well as in juvenile penaeids (Charmantier-Daures et al. 1988). In a tropical shrimp, *Macrobrachium amazonicum*, the upper thermal limit for successful development through metamorphosis was found to be reduced at both unfavourably high and low salinities (Moreira et al. 1986). As a general consequence of such interacting effects of two or more ecological variables, the actual range of a species' distribution is commonly smaller that should be expected from the response to a single key factor (for extensive review, see Kinne 1964b, 1970, 1971).

Although larval stages have generally a narrower range of physiological tolerance than juveniles and adults, also the opposite pattern has been observed in some species. In the Dungeness crab, *Cancer magister*, for example, early juveniles died at high temperatures which were still tolerated by the megalopa (Sulkin et al. 1996). As a consequence, settlement and metamorphosis in regions with warm water (e.g. those between British Columbia and Vancouver Island) may not imply successful recruitment.

Temperature effects were observed not only in seasonal and regional, but also in interannual variability of larval production in the plankton (Lindley 1988, 1998a, Lindley et al. 1993). This implies consequences on the population and community levels. For instance, unfavourably warm summers may cause recruitment failures in economically important decapod species such as *Cancer* crabs and affect the commercial fisheries in subsequent years (Sulkin et al. 1996).

Temperature exerts a direct influence on larval activity and swimming speed; this response is termed *thermokinesis* (for review see Sulkin 1984). While the locomotory activity usually increases with increasing temperature, the opposite effect was recently observed in the megalopa of a deep sea crab species from hydrothermal vent fields, *Bythograea thermydron* (Epifanio et al. 1999). In this case, cold water may indicate an unsuitably large distance from the species-specific habitat, inducing an increased swimming activity and, in effect, a search of warmer vent water. Temperature variation has been suggested also as a possible environmental cue in the reimmigration of crab (*Chasmagnathus granulata*) megalopae returning from the sea into warmer estuaries and coastal lagoons (Ismael et al. 1997).

Indirect temperature effects on larval behavior include changes in the response to other physical factors such as light, gravity, or hydrostatic pressure (Ott & Forward 1976). Hence, thermal discontinuities (thermoclines) may sometimes inhibit vertical migrations of decapod larvae and other plankton in the water column. Zoeae of shallow-water crabs (*Rhithropanopeus harrisii*, *Neopanope sayi*), for instance, were observed to avoid sharp gradients, swimming upward when the temperature decreased and downward when it increased (Forward 1990). With this behavioral adaptation, the larvae appear to maintain their vertical position in a thermally favourable range within the upper part of the water column. In the larvae of coastal and estuarine species such as the blue crab, *Callinectes sapidus*, the ability to penetrate thermoclines depends largely on the developmental stage and on previous temperature acclimatization (McConnaughey & Sulkin 1984). By contrast, the larvae of a deep sea crab, *Geryon quinquedens*, appear to be adapted to the necessity of extensive vertical migrations, showing no difficulties to swim through layers with thermal discontinuities (Kelly et al. 1982). This capability enables the larvae to ascend from the cold and dark deep-water zones to highly productive surface waters, where the nutritional and thermal conditions allow for fast development and growth. In the early larvae of another species from the deep sea, the hydrothermal vent shrimp *Mirocaris fortunata*, the range of vertical distribution within the water column is limited by the tolerance of relatively high temperatures in the upper zones (Tylor & Dixon 2000).

10.1.2 *Salinity tolerance and osmoregulation*

While the salt content remains widely constant in the open ocean, it may fluctuate seasonally, regionally and locally in coastal and estuarine regions. For species living in such variable environments, the salinity factor is thus considered of utmost ecological and physiological importance, and consequently, its effects have extensively been studied.

Since the crustacean integument is, at least in some body regions, permeable for water and inorganic ions, environmental salinity fluctuations may cause rapid changes in the ion concentrations of the blood and other tissues. This will reduce the effectiveness of physiological and biochemical processes, which depend on rather constant osmotic and ionic conditions in the internal medium, and thus, may cause serious physiological and structural damage to tissues and cells. Hence, the salinity tolerance of aquatic species is closely associated with their capability to maintain the internal medium largely independent of the external conditions. The protection of the internal milieu may be achieved, in principle, in two different ways: (a) passively by reducing the permeability of the integument; (b) actively through processes of regulation.

The passive mechanism occurs in adult freshwater crayfish and, to some degree, also in eggs attached to the female pleon of decapods in general. In planktonic larvae, however, a thick and heavy cuticle would not be compatible with the needs for buoyancy and active swimming. In the absence of functional gills, also respiration through the impermeable integument would be impeded, while the costs for swimming would increase as a consequence of heavy sclerotisation and negative buoyancy. Thus, the salinity tolerance of larval decapods depends largely on the alternative mechanism, i.e. the capability to actively regulate the internal concentration.

10.1.2.1 Principal mechanisms of osmoregulation

Ion concentrations in the internal media can be regulated through active physiological processes, both in single ion species (ionic regulation) and in total concentration of osmotically active compounds (osmoregulation). While the regulation and transport of single ions belong to the most widespread processes within the metabolic and nervous functions of cells and tissues, osmoregulation is less common. This, however, is a crucial adaptation to variability in the overall salt concentration (salinity) of the external medium, not in its ionic composition. Osmoregulation is possible on two different levels, implying different physiological mechanisms:

(1) *Intracellular regulation*. Independent of the ion concentration in the blood and the environment, cells have a limited capacity to maintain their volume constant (see Gilles & Péqueux 1983, Péqueux 1995). The underlaying biochemical mechanisms are based on *de novo* synthesis and degradation, respectively, of free amino acids (cf. section 7.5.1). This type of regulation, which is presumed to be evolutionarily old, is comparably slow and thus, inefficient when fast or extensive osmotic changes occur in the extracellular medium.

Among the larval decapods, biochemical evidence of intracellular regulation was shown in the megalopa of the blue crab, *Callinectes sapidus*. This species recruits in estuaries, preferring brackish water for settlement and metamorphosis (Forward et al. 1996). When megalopae were exposed for several days to full-strength seawater (which, in this case, may be considered as a condition of hyperosmotic stress), the free amino acid pool increased substantially, mainly as a consequence of proline synthesis (Burton 1992). Amino acid concentrations increased rapidly also after eyestalk removal, suggesting that intracellular regulation is controlled by neuroendocrine factors from the eyestalk ganglia (Tucker & Costlow 1975). In larval and early juvenile lobsters, *Homarus gammarus*, the amino acid level in muscle cells, especially that of glycine, proline and alanine, responded in all developmental stages to changes in salinity (Haond et al. 1999).

(2) *Extracellular regulation*. Many aquatic organisms are capable of maintaining the osmotic concentration of their blood and other extracellular liquids at a constant level. Within the range in which this regulation process is effective, the organism can tolerate even sudden changes in the environment, at least a rapid decrease in salinity (for instance in small water bodies after precipitation). This fast response is possible because the extracellular regulation mechanisms are more efficient than those of intracellular regulation.

Adult decapods may require one or two days to reach a new osmotic equilibrium relative to the environmental osmolality, while the regulatory response of larval stages is much faster. With their comparably permeable integument, they require usually less than two hours after a salinity change to reach a stable hemolymph osmolality (Felder et al. 1986, Charmantier 1998, Charmantier et al. 1998). Like in intracellular regulation, there is strong evidence for a participation of hormonal factors from the eyestalks in the control of extracellular regulation (for review, see McNamara et al. 1991, Charmantier & Charmantier-Daures 1998).

Depending on the direction of the internal counterreaction to an external change, two types of osmoregulation are differentiated: (a) *hyperregulation*, the internal concentrations are maintained above those in the external medium; (b) *hyporegulation*, the internal concentrations are kept below those in the external medium. The osmolality difference between the internal and external media is termed *"osmoregulatory capacity"* (*OC*). The *OC* can be used as a comparative index of the strength of osmoregulation in different developmental stages or species exposed to different salinity conditions. Its sign indicates the direction of the response, i.e. positive *OC* values show hyper-, negative values hyporegulation.

The physiological basis of extracellular hyper-osmoregulation is mainly an effective ionic regulation, in particular of Na^+ and Cl^- concentrations. In dilute media, passively lost ions are actively replaced by means of an ion pump, in which the enzyme Na^+-K^+-ATPase plays a key role (for review see Péqueux 1995). By contrast, the mechanism of hypo-osmoregulation in hypersaline media is at present not as completely understood; this includes the active excretion of ions and the participation of particular enzymes (see Péqueux 1995, Charmantier 1998).

Extracellular osmoregulation is a widespread and well-studied salinity adaptation in adult estuarine crustaceans; however, comparably little is known about its occurrence and ontogeny in larval stages. The first pioneering investigations on osmoregulation in decapod larvae were conducted already in the mid and late sixties (Kalber & Costlow 1966, 1968, Kalber 1970). A conspicuous upswing of this line of investigations occurred only two decades later, after advanced microtechniques had become available, mostly originating from medical research (for recent review see Charmantier 1998). Meanwhile, about 20 species of larval decapods have been studied as to their osmoregulatory capabilities, although most of these investigations were not complete with respect to the major life-history phases (larval, juvenile, adult).

10.1.2.2 Ontogenetic patterns in the appearance of osmoregulation

In general, early larval stages show weaker regulatory capabilities than conspecific juveniles or adults, and hence, are less tolerant of salinity changes in the environment. This ontogenetic increase in the regulatory capability may occur gradually or stepwise, and its extent varies considerably among species. According to the available data, at least three

categories of ontogenetic patterns may be distinguished (for references, see Charmantier 1998):

(1) The regulatory capabilities increase only little during ontogeny, so that osmoregulation remains weak in both the larval and adult life-cycle stages. The species in this category are largely osmoconformers, i.e. the osmolality of their internal medium changes proportionally with that in the external medium, especially at enhanced salinities; a weak hyperregulatory capability may occur in moderately dilute media though. This pattern is typical of stenohaline marine decapods, for instance species of *Cancer* and most spider crabs (e.g. *Libinia*, *Chionoecetes*, *Hyas* spp.). Their larvae develop in physically stable marine waters where also the adults live, and thus, have in their evolution not adapted to the occurrence of variable salinities. As an example, the osmoregulatory capacities of the postembryonic stages (zoea I to crab I) of *Cancer irroratus* are shown in Figure 10.2a.

Even in full-strength seawater and under hypersaline conditions, the hemolymph concentration remains slightly above that of the external medium ("hyper-osmoconformers"). This is due to the persistence of osmotically active compounds, mostly amino acids. In planktonic larvae, it is probably this osmotic gradient which maintains under variable salinity conditions the turgor and thus, the functionality of the swimming appendages (Foskett 1977, Charmantier 1998). Since their capacity for extracellular regulation is weak and thus, hemolymph osmolality may vary with environmental conditions, the stenohaline species in this category depend widely on less efficient intracellular regulation.

(2) Osmoregulation is strong in both the larval and adult stages, at least in dilute media ("hyper-osmoregulators"); at hypersaline conditions, however, these species are commonly typical hyper-osmoconformers. As in the first category, the regulatory capabilities increase only little and gradually during ontogeny, but on a higher level. This pattern has been observed in palaemonid freshwater shrimps (e.g. *Palaemonetes argentinus*; see Fig. 10.2b). The larvae of these species develop in waters with low salinity, within or adjacent to the oligohaline or limnic adult environment, and thus, they need to hyperregulate. Again, little ontogenetic change in the osmoregulatory capability corresponds here with little ecological change from the larval to the adult habitats.

(3) Osmoregulation is weak in the larvae but strong in juveniles and adults. The adult type of regulation is normally established at metamorphosis to the first juvenile stage. Species in this category show not only a pronounced capability for hyper-osmoregulation in dilute media, but sometimes also hyporegulation at salinities equal to or above those in the ocean. Hypersaline conditions occur in partly land-locked habitats such as salt marshes, mangrove swamps, and supratidal rock pools (see section 10.4).

This ontogenetic pattern of osmoregulation has been reported from penaeid prawns (*Marsupenaeus japonicus*) and clawed lobsters (*Homarus americanus*, *H. gammarus*). Dramatic physiological changes at metamorphosis correspond in this developmental type with sometimes abrupt transitions between larval and juvenile habitat conditions. This pattern should thus be typical of estuarine species that "export" their early larvae to physically more stable marine waters and reimmigrate shortly before or after metamorphosis (section 10.3.1).

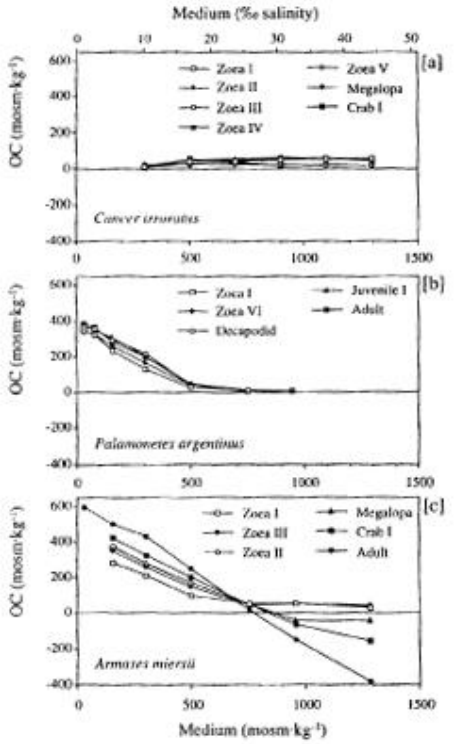


Figure 10.2. Basic osmoregulatory patterns in decapod crustacean larvae: osmoregulatory capacity (*OC*) in relation to the osmolality of the medium; [a] *Cancer irroratus* (stenohaline marine crab, hyper-osmoconformer); [b] *Palaemonetes argentinus* (freshwater and brackish water shrimp, hyper-isoregulator); [c] *Armases miersii* (extremely euryhaline estuarine crab, hyper-hypo-regulator); redrawn to same scale after [a] Charmantier & Charmantier-Daures (1991), [b] Charmantier & Anger (1999), [c] Charmantier *et al.* (1998).

In two semiterrestrial grapsid crab species that reproduce in supratidal rock pools and mangrove swamps, respectively (*Armases miersii*, *Sesarma curacaoense*), an earlier transition from the larval to the adult type has recently been observed (Charmantier et al. 1998, Anger & Charmantier 2000). The larvae of these tropical crabs show already from hatching an unusually strong capacity of hyperregulation in low salinities. The capability for hyporegulation is attained in the megalopa stage. Hence, the ontogeny of osmoregulation in these species (exemplified in Fig. 10.2c with *A. miersii*) must either be considered as an extreme case of the third pattern, or it may be assigned to a new category. This would comprise species whose larvae are adapted to development in physically extreme or highly variable habitats, and thus, show an earlier transition to the adult type of osmoregulation. The fiddler crab *Uca subcylindrica* may also belong to this category, as the pattern of hyper-hyporegulation was in this species observed to appear, although weakly, already in the megalopa stage (Rabalais & Cameron 1985). Like *A. miersii* and *S. curacaoense*, *U.*

subcylindrica "breeds" in land-locked habitats, namely in temporary rainfall puddles in an arid region of the southern United States.

The capability for hypo-osmoregulation is especially important in terrestrial and semi-terrestrial habitats where desiccation occurs (Kinne 1971; for review of water balance in decapods, see Greeaway 1988, 1999, Taylor & Greenaway 1994). This is principally a problem for juvenile and adult decapods living in such habitats rather than for their meroplanktonic larvae. However, it may explain why the capability for hypo-osmoregulation appears in a semiterrestrial crab species, *Chasmagnathus granulata*, already in the megalopa stage (Charmantier et al. in prep.). In this species, the megalopa settles in very shallow water bodies within the amphibious adult habitat, close to the adult burrows (Luppi 1999, Luppi et al., submitted). In this microenvironment, rainfall and evaporation, respectively, are likely to cause hyposaline as well as hypersaline conditions, so that desiccation may cause an osmolality increase in the hemolymph of the megalopa. Although the capability of hyper-hyporegulation is in this stage not as strongly developed as in the conspecific juveniles and adults (see Castilho et al. 2001, and earlier literature cited therein), this physiological trait allows for recruitment in such an unpredictable habitat.

The salinity tolerance of particular species or developmental stages is closely associated with their capacity of osmoregulation and thus, also with the presence or absence of specialized transport epithelia (Charmantier 1998). In juvenile and adult decapods, ion transporting tissues are localized primarily in the gills, but also in the branchiostegites and other parts of the gill chamber. In addition, also the gut walls and the antennary gland might participate in or aid to osmoregulation (Kinne 1971), although this has not been demonstrated in larvae. During ontogeny, *anlagen* of the osmoregulatory organs and tissues may appear at hatching (in penaeid prawns from a protozoeal stage, lacking in the nauplius phase). The gills, in contrast, become infolded and functional only in decapodid stages (Felder et al. 1986, Furigo 1993, Bouaricha et al. 1994; c.f. section 3.2). In species which are already in the zoeal phase capable of osmoregulation, it is probably the branchiostegite region that is mainly responsible for this function. Comparably low initial salinity tolerance indicates that these tissues, although apparently specialized in ion transport, are less efficient than the gills; this is probably also a consequence of their lower surface area. As another indicator (and as a physiological basis) of extracellular osmoregulation, the activity of Na^+-K^+-ATPase increases during ontogeny, parallel to changes in salinity tolerance and the development of transporting tissues (Thuet et al. 1988, Bouaricha et al. 1991a-c, Charmantier 1998).

10.1.2.3 Effects of the molting cycle

The capability for osmoregulation changes not only during development through a sequence of larval stages, but also during the course of each molting cycle (Charmantier 1998, Charmantier et al. 1998). The osmoregulatory capacity (*OC*) is generally minimum in the postmolt stages *A* and *B*. During this phase, the cuticle is thin, structurally incomplete (the endocuticle layer is still lacking; see section 4.1.1), and relatively permeable for water and small ions. Since the osmolality of the hemolymph remains above that of the surrounding medium, the osmotic gradient facilitates, especially during and shortly after ecdysis, a passive uptake of water. This allows for a rapid increase in body size, before the cuticle becomes thicker and less permeable. As a consequence of this sudden "growth" process, the contents of water and minerals within larval biomass increase dramatically during the brief postmolt phase (see section 7.1). In the subsequent intermolt stages, the

cuticle is completed and the *OC* reaches its maximum. In late premolt, the permeability of the integument inceases again, causing a passive ingress of water. As an effect of this mechanism, the larval body will inflate until the old cuticle bursts and ecdysis begins.

10.1.2.4 Environmental factors

Similarly as we have seen in the tolerance of thermal stress, salinity tolerance varies not only with phylogenetic position and developmental stage, but also due to effects of previous acclimatization (or non-genetic resistance adaptation; see Kinne 1964a, 1971) as well as interactions with other physical and chemical parameters, in particular with temperature (for review, see Kinne 1970, 1971; Vernberg & Silverthorn 1979). In portunid crab (*Necora puber*, *Carcinus maenas*) larvae, for instance, the tolerance of hypo-osmotic stress was reduced at unfavourably low temperatures (Nagaraj 1992, 1993). The same response pattern was observed also in other species of larval crabs (*Eriocheir sinensis*, Anger 1991b; *Hemigrapsus sanguineus*, Epifanio et al. 1998) and in juvenile shrimps (*Marsupenaeus japonicus*, *Fenneropenaeus chinensis*, Charmantier-Daures et al. 1988).

As a further example of salinity interactions with additional ecological stress factors, larval growth in the mud crab, *Rhithropanopeus harrisii*, was depressed when hypo-osmotic stress occurred in combination with an exposure to sublethal concentrations of naphthalene, a toxic compound from crude oil (Laughlin & Neff 1981). Also other toxic pollutants such as ammonia, metals, insecticides, and even turbidity may reduce the osmoregulatory capability and salinity tolerance of larval and adult decapods (Vitale et al. 1999, Rebelo et al. 2000; for recent review see Lignot et al. 2000). Likewise, the *OC* can be significantly reduced by parasitic and other forms of disease, for instance by fungal infections (Souheil et al. 1999). As recently shown in lobsters infected with dinoflagellate parasites, this effect may be due to an interference of metabolites released by infectious microorganisms and the neuroendocrine control system (Stentiford et al. 2001).

When decapod crustacean larvae are confronted with unfavourable salinity conditions, they may respond also with an active avoidance behavior. This was observed, for instance, in early lobster larvae (*Homarus gammarus*; Scarratt & Raine 1967) as well as in several species of larval brachyurans (Forward 1989a, Capaldo 1993). Since vertical salinity gradients (haloclines) are common in estuarine and coastal environments, specific response patterns to osmotic changes are believed to exert a great influence on larval distribution and recruitment (Sulkin & van Heukelem 1982, Tankersley et al. 1995). On the other hand, reduced salinities may serve as indicators of estuarine conditions, and hence, help as attracting cues in the "home"-bound navigation of the late developmental stages of estuarine species (see section 10.5).

In the larvae of *Rhithropanopeus harrisii*, Harges & Forward (1982) found different mechanisms for the perception of an increase or decrease in salinity, respectively. Ion substitution experiments showed that the perception of a decrease depends on a change in sodium or in cations of similar size, probably perceived by a classical salt receptor. In the detection of salinity increase, cation size is not an important parameter, but pH and maybe osmolality. The nature of the receptor for an increase in salinity has remained unknown.

10.1.2.5 Population genetics

Since salinity tolerance has also a genetic basis, differential selection pressures in isolated populations of a species may lead to physiologically distinct races with differential larval salinity tolerance and, eventually, to speciation. This evolutionary process has extensively

been studied in shrimp species from Japan, *Macrobrachium nipponense* and *Palaemon paucidens*, which live in freshwater rivers, lakes, and brackish estuaries (Mashiko 1987, 1990, 1992, 1999, Chow et al. 1988, Fidhiany et al. 1991, Ogawa et al. 1991, Mashiko & Numachi 1993, 2000). These estuarine and freshwater environments differ not only in the prevailing salinities but also in nutritional conditions, with low or unreliable plankton production in rivers and streams *vs.* high productivity in estuaries. Thus, genetically isolated and distinguishable freshwater populations show not only a shift in the salinity optimum, but as additional adaptations, also tendencies towards enhanced egg size, longer embryonic incubation period, and an abbreviation of the larval phase.

10.1.3 *The key parameters in larval depth control*

Compared with the effects of temperature and salinity, variations in other physicochemical factors such as light, hydrostatic pressure, turbulence, oxygen concentration, pH, etc. seem to have only minor direct importance for larval survival and development. However, decapod crustacean larvae are able to perceive gradients in most of these parameters (for sensory organs see section 3.3), and hence, may utilize them as orientation cues. Gravity, hydrostatic pressure and light are particularly reliable indicators of depth in the water column, and thus, aid in the control of the vertical position of the larvae. Behavioral responses to these variables are summarized here in a single section, because their significance for larval orientation and for the feedback mechanism of depth regulation is primarily based on interacting rather than isolated effects. Consequently, most investigators studied the influence of these parameters on larval behavior together.

Since the direction and speed of water currents may change with depth, vertical orientation and depth regulation are crucial for the patterns and the extent of larval dispersal, but also for feeding and predator avoidance. In consequence of their general significance in larval ecology, the relationships between variations in physical factors, larval behavior, and dispersal in the plankton have extensively been studied since more than three decades both in the laboratory and field (see Rice 1993). Most of the available data, in total several hundred papers, originate from investigations conducted in North America (e.g. Bigford 1979a, Forward & Buswell 1989, Forward et al. 1997a, Sulkin 1984, 1990, Epifanio 1995, Morgan et al. 1996), Australia (Dall et. al. 1990, Rothlisberg & Church 1994, Rothlisberg et al. 1994, 1996), and Europe (Rice 1966, Schembri 1982, Queiroga 1994, 1996, Paula 1987, 1989, 1993, Queiroga et al. 1997, Zeng & Naylor 1996a-d, 1997, Zeng et al. 1997, Pereira et al. 2000). Naturally, only a few arbitrarily chosen examples from this great diversity of scientific observations can be shown in this section.

10.1.3.1 Gravity

The directed locomotory response to gravitational forces, termed *geotaxis*, is one of the basic components of control of the vertical position in the water column, especially during the absence of light (Sulkin 1973, 1984). In most species tested so far, the early developmental stages show negative geotaxis, so that they tend to concentrate near the surface where plankton productivity is normally highest. This behavior is sometimes enhanced by upward swimming after an increase in hydrostatic pressure or a decrease in light intensity. Later larval stages, in contrast, tend to show positive geotaxis and may thus increasingly accomodate near the bottom. The directions of the responses to light and pressure are often opposed to that of geotaxis, so that a finely tuned control of the vertical position is

possible, and rhythmic diel or tidally induced up-and-down migrations may result from the interactions of these physical cues.

10.1.3.2 Hydrostatic pressure

This factor should be among the ecological key variables for species that live and reproduce in great depth (see e.g. Tylor & Dixon 2000). It has thus generally been presumed that larvae of deep sea species require high pressure for normal development. Among these, a number of new species of shrimps and crabs have been discovered and morphologically described in the past three decades (see e.g. Chevaldonné & Olu 1996, Baba & Williams 1998, and earlier literature cited therein). However, their life histories have remained widely unknown. Epifanio et al. (1999) succeeded recently to capture live megalopae of *Bythograea thermydron*, a crab that lives in hydrothermal vent fields in 2500-2600 m depth, and to rear them at atmospheric pressure through metamorphosis and the first juvenile instars. If more deep sea species show such a surprising independence of high pressure, this would allow for future experimental investigations of life histories and mechanisms of dispersal and recruitment in the deep sea.

While shallow-water species may not be adapted to high pressure, they experience normally great relative changes in hydrostatic pressure, namely during the tidal cycles and vertical migrations. In laboratory experiments with stepwise changes in pressure, zoeae of the mud crab, *Rhithropanopeus harrisii*, perceived differences corresponding to changes of only a few centimetres in water depth (Forward & Buswell 1989, Forward & Wellins 1989). In general (for exceptions, see below), the larvae responded with compensatory vertical movements, i.e. with an active ascend after a pressure increase, and passive sinking or an active descend after a decrease in pressure. When the speed of larval ascend exceeded an upper treshold, the zoeae showed a counterreaction, i.e. a descend. All these experimental results support the negative feedback mechanism proposed by Sulkin (1984) as a basis of larval depth regulation. Interestingly, the larvae of this species reacted about three times more sensitively to an increase than to a decrease in pressure, with lower reaction thresholds of 3 and 8-10 mbar, respectively. This appears plausible, as the larvae are negatively buoyant (Sulkin 1984, Morgan 1989), and unvoluntary sinking is thus more likely to happen and probably also faster than a passive upward transport, e.g. due to turbulent mixture in the water column.

All four zoeal stages of *Rhithropanopeus harrisii* showed an increasing swimming speed when pressure increased (this response is termed *barokinesis*; see Bentley & Sulkin 1977). During darkness, barokinesis was enhanced and accompanied by negative geotaxis, so that even a small increase in pressure lead to a rapid upward migration (Forward & Wellins 1989). This complex response pattern should be important in larval depth regulation at night, when the zoeae, especially the early stages, tend to ascend to the surface layer of the plankton, probably for feeding (Forward & Douglass 1989). Late zoeal stages of brachyuran crabs, by contrast, are often insensitive to pressure changes or show only weak barokinesis. This results in a gradual descend due to positive geotaxis. In the megalopa stage, the kinetic response to pressure variation is high again, and the response threshold is lower (Sulkin 1984).

At different rates of pressure change, not only the intensity of the behavioral response (i.e. barokinesis) may alter, but also the direction of swimming. While a passive sinking of crab larvae was observed during periods of slow pressure decrease, a rapid decrease in pressure induced an active ascend (Forward & Wellins 1989). This reversal in the pressure

response appears paradoxical, unless it is interpreted as a mechanism aiding in predator avoidance rather than larval orientation within the water column. The authors speculated that a rapid pressure decrease might indicate feeding currents produced by filter-feeding benthic predators or suction-feeding fish, which should evoke an escape reaction. Although this interpretation does not fully explain why the escape movement is directed towards the surface, it is supported by recent observations which showed that copepods are able to perceive the differential hydromechanical disturbances generated by prey or predator organisms, respectively (Kiørboe & Visser 1999).

10.1.3.3 Light

Besides gradients in gravity and hydrostatic pressure, also those in the intensity and quality of light are indicators of depth. Hence, the light factor is considered as one of the most important cues for the orientation of meroplanktonic larvae, in general (Thorson 1964). Decapod larvae respond to a broad range of wavelengths, although the response peaks appear to differ among species (Forward 1976a, 1987a, Forward & Douglass 1989). Also the plane of polarization has been shown to influence larval orientation, again with variability in the response of different species and developmental stages (Via & Forward 1975, Bardolph & Stavn 1978). Very importantly, the history of light adaptation modifies not only the intensity but also the direction of light reponses (Sulkin 1984, Forward 1989b). While dark-adapted larvae are generally positively phototactic, light-adapted individuals may switch to negative phototaxis. The same reversal occurs also when the intensity of light changes drastically. In general, high light intensities induce a descend in zoeal stages, while an upward migration occurs at low light levels. The latter response is enhanced when hydrostatic pressure is increased concomitently. Since differential light adaptation modifies also the threshold of the larval response to pressure gradients, it appears that the larvae regulate their vertical position within the water column in relative rather than absolute terms (Forward 1989b).

The response to light is further modulated by variations in temperature and salinity. In addition, the nutritional status of a larva may interfere with its responses to light and pressure. In starved *Rhithropanopeus harrisii* larvae, for instance, the swimming speed is reduced, but phototaxis is enhanced (Cronin & Forward 1980). This alteration of the photoresponse should move the larvae higher in the water column, presumably enhancing their chances to encounter food organisms. These examples may illustrate how larval behavior is, in a complex manner, influenced by numerous intrinsic and extrinsic factors, an exhaustive review of which would exceed the scope of this chapter.

Changes in light serve not only as an orientation cue, but also as an alarm signal. Presumably as a reaction to the appearance of large predators such as fish, most crustacean larvae exhibit a *"shadow response"* (or *"shadow reflex"*), that is the initiation of rapid escape movements when light intensity decreases suddenly (Forward 1976b, 1977, 1986). This reflex may be widespread among planktonic larvae. Young & Chia (1985) observed it, for instance, in ascidian larvae. Moreover, it is known also from adult crabs. These are able to learn, after repetitive triggering of the response, that the cue is no longer associated with danger; recent studies have shown that this behavior is under the control of neuropeptides, namely angiotensins, which are influenced also by environmental factors such as salinity (Delorenzi et al. 1995, 1997, 2000). It should thus be interesting to study the ontogeny of this putative hormonal control system in larval decapods.

In late larval stages approaching the time of settlement and metamorphosis, the behavioral response pattern to the various physical stimuli appears generally more complex (Sulkin 1984). In the megalopa of the blue crab, *Callinectes sapidus*, for instance, an endogenous rhythm induces at daytime a pronounced locomotor activity and an ascend to the surface layers, but inactivity at night (Forward et al. 1997a). This behavioral pattern changes again when the megalopa encounters estuarine conditions: under low salinities, the ascend is not stimulated but inhibited by daylight, so that the risk of a transport back to offshore areas with outflowing surface currents is reduced.

While behavioral responses to light, hydrostatic pressure, and gravity have been documented in numerous investigations, their physiological and structural basis is not as clear. In contrast to the ontogeny of the compound eyes, which has received great attention, the function and even the identity of pressure and gravity detectors have remained largely obscure. Indirect evidence from recent ultrastructural studies suggests that the "sensory dorsal organ" (see section 3.3.3) may be a baroreceptor (Laverack et al. 1996), however, immediate proof is lacking.

Light is not only an effective modulator of larval behavior, but may exert also direct effects on the survival, growth, molting, and development of decapod larvae (Aiken et al. 1981, Minagawa 1994, Mikami & Greenwood 1997b; see section 6.4.3). High light intensity in shallow waters, particularly the ultraviolet component of sunlight, has been shown to cause photodamage in marine organisms (see recent book by De Mora et al. 2000), including decapod crustacean larvae (Damkaer et al. 1980, 1981, Damkaer & Dey 1983, Morgan & Christy 1996, Hovel & Morgan 1999, Miner et al. 2000, Wübben 2000). Diurnal downward migration within the water column has thus been discussed also as a behavioral adaptation to this potential risk, in addition to the avoidance of visually oriented predators (see section 10.1.6). Such vertical migrations reduce the duration of exposure and hence, the severeness of potentially dangerous effects (Rodriguez et al. 2000).

As a passive protection, the larvae of many species are darkly pigmented, blocking with their chromatophores the ultraviolet radiation. This morphological adaptation occurs already in embryonic stages (see Kim et al. 2000). It is especially important in some tropical species whose larvae develop in extremely shallow water bodies, as well as in megalopae returning during daylight in surface waters to their parental onshore environments (see Miner et al. 2000). In addition to chromatophores, various other radiation-absorbing compounds (chemical "suncreens") have been identified in numerous invertebrates (for review see Cockell & Knowland 1999). In spite of avoidance and protection mechanisms, solar UV-B radiation (285-315 nm wave length) has been shown to cause chemical lesions in DNA of larval decapods.

Since UV radiation is a natural factor in the ecology of most organisms, it has selected for the evolution of physiological photorepair systems which attenuate the effects of UV-induced changes in cell structures (see e.g. Kim et al. 2000). Such repair mechanisms are activated by short-wave visible light (Hovel & Morgan 1999). This implies that, depending on the turbidity of the water and the intensity of solar radiation (i.e. also on daytime and latitude), there should be an optimal depth within the euphotic zone of the water column, where photorepair systems are activated while photodamage is reduced. Together with a vertical gradient in predation pressure and indirect effects of the vertical position (related to the horizontal transport and dispersal of larvae), these antagonistic physiological effects of different components of the solar radiation should select for a finely tuned, complex pattern of vertical migrations.

10.1.4 *Oxygen concentration*

In the marine pelagial, where most decapod larvae develop, oxygen is normally available in sufficiently high concentrations near the physical saturation level. Hence, pelagic larvae are, in general, not well adapted to low O_2 levels and react sensitively against variations in oxygen concentration (see section 8.3.4).

As an unspecific response to low-oxygen stress, larvae show enhanced mortality, retarded development, and reduced growth. This was recently shown in a study where field-caught megalopae of the blue crab (*Callinectes sapidus*) were exposed to reduced O_2 concentrations (40 or 60% saturation; Tankersley & Wieber 2000). When this stress was exerted for only 2h each day, it had no significant effect, while longer exposure (4h per day) caused a a significant delay of metamorphosis. The authors conclude *"that the presence of hypoxic and anoxic water in deep water layers and shallow near-shore habitats of estuaries during the summer months may influence the onshore migration, settlement and survival of blue crab megalopae and newly metamorphosed juvenile crabs"*. Also shrimp (*Palaemonetes vulgaris*) larvae exposed to cyclic or constant patterns of hypoxia showed impaired growth and development (Coiro et al. 2000).

10.1.5 *Pollutants*

Survival, development, physiological performance, and behavior of larval crustaceans are affected by numerous anthropogenous chemicals. While some pollutants occur also naturally in the biosphere (e.g. organic wastes and degradation products thereof, metals, petroleum hydrocarbons), others are entirely artificial and very persistant, e.g. some radioactive elements and numerous synthetic organic products such as PCBs, pesticides, herbicides, etc. Many of those substances are highly toxic and hence, exert stress even in low concentrations; although detoxification mechanisms, e.g. cytochrome P-450 proteins, have been found in the Crustacea (Lee et al. 1982, James & Boyle 1998), nothing is know about their ontogeny.

There are numerous studies of pollution effects on survival, development, growth, and metabolism in aquatic invertebrates including decapod crustacean larvae. Since such effects have been reviewed in more specific contexts in chapters 6-9, I will concentrate here on sublethal effects on behavioral and ecological traits, and on interactions with other environmental factors.

10.1.5.1 Toxic metals

In the literature, the commonly used term "heavy metals" is applied in a vague and unduely extended meaning, comprising all metals that are toxic in relatively low concentrations, including zink, aluminum and other elements which chemically do not belong to this category. Also "toxicity" is a relative concept, always depending on the concentration considered and on interacting factors. Among these, salinity is known to exert a particularly great influence on the accumulation and toxicity of metals (see Bianchini & Gilles 2000, and earlier papers cited therein). Moreover, toxicity varies among taxa and developmental stages. Although no ontogenetic changes in the response to toxic metals were observed in successive zoeal stages of a shrimp (*Palaemon serratus*), the larvae of different decapod species showed clear differences in sensitivity; spider crab (*Maja squinado*) and lobster (*Homarus gammarus*) zoeae were more sensitive than those of shrimp (Marino-Balsa et al. 2000).

The truely heavy element mercury (Hg) is a particularly great threat to the environment, and thus, has received special attention. The severeness of its toxic effects depends largely on the chemical compounds in which it occurs and on other environmental variables. In fiddler crab (*Uca pugilator*) zoeae, for instance, survival was greatly reduced, even at low concentrations, when Hg occurred in a combination with suboptimal temperature or salinity (Vernberg et al. 1973). In grass shrimp (*Palaemonetes pugio*) larvae, the survival rate during a 48-h exposure decreased with increasing Hg concentration, and this detrimental effect was further enhanced by starvation (Shealy & Sandifer 1975). Moreover, the duration of development under sublethal concentrations was increased as a consequence of both delayed molting and an occurrence of additional larval instars, and many larvae showed morphological deformities.

Similar toxic effects were observed also in the presence of other metals, for example when the larvae of *Palaemonetes pugio* were exposed to cadmium; these effects were further enhanced by unfavourably low salinities (Middaugh & Floyd 1978). In adult crabs (*Chasmagnathus granulata*), cadmium has recently been shown to inhibit metabolic key enzymes, interfering with ionic regulation and other vital functions and reducing the resistance against osmotic and other stress (Vitale et al. 1999); the same physiological effects should occur also in larvae. When ovigerous females of *C. granulata* were exposed to cadmium, the larvae hatched with morphological abnormalities (Rodríguez & Medesani 1994). In another grapsid crab species, *Sesarma pictum*, zink was observed to delay larval metamorphosis, even when this metal was present only in low concentrations (Pasupathi & Kannupandi 1989). In portunid crab larvae (*Portunus pelagicus*), chromium, nickel and copper caused an inhibition of molting, an increase in the duration of development, and a reduction of juvenile body size (Mortimer & Miller 1994).

10.1.5.2 Petroleum hydrocarbons

The available evidence suggests that both the toxicity and the persistance of water-soluble fractions of crude oil is relatively low compared to some of the toxic metals. Since hydrocarbons are released also from natural sources in the sea floor, it is likely that their continual presence has favoured the evolution of compensating physiological mechanisms in potentially affected organisms. In decapod eggs exposed to oil pollution, the low permeability of the egg membrane protects the developing embryoes, so that viable larvae may be produced (Hartman & Sulkin 1999). Also after hatching, planktonic larvae appear to accumulate only small quantities of oil-derived hydrocarbons within their biomass, due to low rates of uptake and/or high rates of metabolic turnover (Capuzzo 1985).

Most stress effects exerted by pollutants are actually unspecific, occurring also under otherwise unfavourable conditions. This applies also to toxic effects of petroleum hydrocarbons on decapod larvae, namely delayed development and a depression of growth and metabolism (Katz 1973, Capuzzo & Lancaster 1982). In rock crab (*Cancer irroratus*) larvae exposed to the water-soluble fraction of reffined oil, this was due to decreasing uptake and absorption of food and a reduced conversion efficiency (Johns & Pechenik 1980; cf. section 9.3.3)). Lobster (*Homarus americanus*) larvae showed signs of toxic stress not only during direct exposure to oil-seawater dispersions, but also after eating oil-contaminated food (Capuzzo et al. 1984). The toxicity of crude and refined oils is to a great extent associated with their contents of low molecular weight aromatics such as naphthalene (Moore & Dwyer 1974). When larvae of *Rhithropanopeus harrisii* were exposed to sublethal concentrations of naphthalene, they showed enhanced metabolic rates

and depressed growth, especially when the toxicant occurred in combination with unfavourable salinities (Laughlin & Neff 1981).

Even when hydrocarbons are present in very low concentrations (i.e. not acutely toxic), their odors may interfere with chemoreceptive functions that are involded in the control of feeding, orientation, and other behaviors of crustaceans (Atema 1974, Atema et al. 1988). In barnacle larvae, for instance, experimental observations suggest that some components of cruide oil can mimic natural chemical cues that stimulate settlement behavior and metamorphosis (Holland et al. 1984). Hence, such organic pollutants may induce settlement at unfavourable sites and, in consequence, increase postsettlement mortality. So far, however, little is known about hydrocarbon-induced or other pollution-related behavioral changes in decapod larvae.

10.1.5.3 Pesticides

Increasing concern associated with the use of highly persistant and bioaccumulable organochlorine pesticides lead in the seventies to changes in the manufacture and application of synthetic chemicals in the agricultural industry. However, also new generations of pesticides such as organophosphates and pyrethroids were proven to be potentially dangerous to the environment and hence, have stimulated toxicity tests with larval decapods and other aquatic invertebrates. For instance, sublethal concentrations of fenvalerate, a synthetic pyrethroid, were shown to reduce the adaptability to fluctuating salinities in the larvae of a caridean shrimp, *Palaemonetes pugio* (McKenney & Hamaker 1984). Toxic effects were observed also when larvae of *Rhithropanopeus harrisii* were exposed to Methopren, a synthetic juvenile-hormone analog that is used as an insect growth regulator (Celestial & McKenney 1994). When parathion, an extensively used organophosphate insecticide, was present during embryogenesis of the crab *Chasmagnathus granulata*, the larvae hatched with morphological abnormities, similar as those observed after cadmium exposure (Rodríguez & Pisanó 1993; cf. Rodríguez & Medesani 1994). Also acute toxicity of parathion to crab larvae was experimentally shown (Rodríguez & Amin 1991).

More recently, the organophosphorous insecticide azinphosmethyl was shown to inhibit the nervous system of larval *Palaemonetes pugio*, reducing the activity of the key enzyme acetylcholinesterase (Key et al. 1998a). Since this enzyme plays a significant role in numerous metabolic processes of both vertebrates and invertebrates, this inhibitory effect may be a wide-spread cause of pesticide toxicity; malathion, on the other hand, had no such effect (Key et al. 1998b). Fenitrothion, another organophosphorus insecticide, was found to interact with larval osmoregulation in the shrimp *Marsupenaeus japonicus*, and hence, to reduce the tolerance of salinity stress (Lignot et al. 1997). Similar effects were observed when larvae of the same species were exposed to tributyltin oxide, an organometal compound (Lignot et al. 1998). In mud crab (*Rhithropanopeus harrisii*) and fiddler crab (*Uca minax*) larvae, sublethal concentrations of various other pesticides caused behavioral changes in swimming activity and in the response to light (Forward & Costlow 1976, 1978, Capaldo 1987). Among the currently used pesticides, there are also several synthetic insect juvenile hormone analogs (van Leneteren 1999). At least one of these chemical products, Fenoxycarb, has recently been shown to cause reduced larval growth and a suppressed accumulation of lipids (especially triacylglycerides, *TAG*) in the mud crab, *R. harrisii* (Nates & McKenney 2000b).

10.1.5.4 Miscellaneous pollutants

During drilling operations in the ocean, complex mixtures of chemicals are used to lubricate the drill bit, remove cuttings, and equalize hydrostatic pressure. These pollutants are continually discharged to the surrounding waters during drilling and in bulk at the completion of the programme. Since those mixtures contain various toxic substances such as metals and phenolic compounds, which may affect the regional marine fauna and flora, effects of drilling fluids on survival, development, and metabolism were experimentally studied also in decapod larvae. Again, depressed rates of larval survival, feeding, growth, and respiration were observed as unspecific toxic effects (Smith Derby & Capuzzo 1984). As another class of toxicants, halogens such as free chlorine, chloramine, organochlorine, and bromine compounds are released or formed, respectively, during antifouling treatments in coastal power stations. Although the various compounds showed different toxicities, they caused consistently a reduction of growth and metabolic rate in lobster larvae (Capuzzo et al. 1976, Capuzzo 1977). Similarly, mining effluents introduce variable mixtures of pollutants into the sea, where they cause detrimental effects in decapod and fish larvae (Kline & Stekoll 2000).

In summary, pollutants are present in all aquatic environments and may affect all major physiological and behavioral functions in decapod crustacean larvae and other plankton, seriously reducing the chances of survival and successful development through metamorphosis. Hence, man-made chemicals must now be considered as one of the ecological key determinants of recruitment in benthic species with meroplanktonic life-history stages.

10.1.6 *Biotic factors*

In the literature on the ecology, behavior and evolution of larval forms, there has been much dispute about the relative importance of the major physico-chemical and biotic key factors, respectively (see e.g. Ghiselin 1987). While earlier investigators tended to explain behavioral adaptations in meroplanktonic larvae, including their basic responses to light, hydrostatic pressure etc., primarily as mechanisms of dispersal and gene flow, biotic factors were later increasingly considered as selective agents (Strathmann 1982, 1985). Effects of the two predominant biotic factors, food availability and predation, are commonly referred to using the terms *"bottom-up"* and *"top-down"* control, indicating their respective direction between trophic levels. While nutritional factors ("bottom-up" forces) were mostly emphasized throughout the traditional literature, effects of predation ("top-down" forces) have more recently received a growing attention, in particular in studies of estuarine communities (Morgan 1995a, Verity & Smetacek 1996). Since these effects are usually acting in concert and difficult to separate, competition for food and predation are treated here together. As another category of biotic factors, effects of biogenic diseases are reviewed below.

10.1.6.1 Competition for food *vs.* predation

As a potentially important biotic selection force, intra- and interspecific competition among larvae has been discussed (Strathmann 1996). The available data suggest that the significance of competition for food in the plankton tends to increase at higher trophic levels (Olson & Olson 1989, Verity & Smetacek 1996). This implies that food limitation ("bottom-up" control) should predominate in predatory species, while phytoplankton grazers should be primarily controlled by predation ("top-down" forces). Competition for limited food sources and other "bottom-up" forces have been discussed in sections 5.1,

5.2.2 and 5.3.2, and thus, I will here largely concentrate on recent evidence for adaptations to predation. Further examples of potential biotic selection forces in the evolution of decapod larvae will be given below (sections 10.2-10.4).

Most estuarine decapod species follow an export strategy, i.e. their larvae are transported out of the adult environment, develop in coastal marine areas, and recruit only in the decapodid or juvenile phase to the estuarine populations (see section 10.3.1). Recent observations suggest that this life-history pattern is not only an adaptation to the prevalence of physical stress factors (e.g. low salinity), which may inhibit the development of physiologically sensitive larvae in the habitat of origin. The lower estuaries are known also as highly productive systems that have favoured the evolution of specifically adapted, visually oriented predators, in particular planktivorous fish. Their feeding activity is believed to range among the most important causes of mortality in larval decapods and other meroplankton. At least in some decapod species, the export of larval stages is thus considered as a complex avoidance response to high predation pressure in estuarine ecosystems (see Morgan 1990, 1995a, Hovel & Morgan 1997).

The rapid export of the early larvae depends to a great extent on endogenous egg hatching rhythms, with larval release occurring predominantly during nocturnal ebb tides (see section 10.3). These rhythms were previously considered only as components of passive dispersal mechanisms, based on the response to physical factors such as tidal currents, salinity gradients, etc. However, preferential hatching at night indicates that predation pressure should be another important selective force. This is obvious in fully marine species, for instance in coral reefs dwellers, where an advection of the larval stages would be disadvantageous, but larval release rhythms associated with lunar cycles and other environmental cues do exist (see Reyns & Sponaugle 1999). Unlike in estuarine species, this rhythmicity of hatching should thus be related to factors other than physical or nutritional stress in the adult habitat, probably pelagic predation. Nocturnal peaks were observed also in the occurrence of drifting palaemonid larvae in freshwater streams and interpreted as a mechanism of predator avoidance (March et al. 1998). In recent reviews of reproductive adaptations to coastal and estuarine conditions, "top-down" control is thus increasingly emphasized as a selective force (Morgan 1989, 1990, 1995b, Hovel & Morgan 1997, Morgan & Christy 1997, Zeng & Naylor 1997, Christy & Morgan 1998, Pechenik 1999).

Vertical migrations of decapod larvae in the water column are common both in estuarine and coastal environments. Although these behavioral rhythms are primarily triggered by physical parameters (see section 10.1.3), their selective advantage is more immediately related to biotic factors. For instance, it is likely that nocturnal upward migrations have evolved as a response to vertical gradients in food availability, i.e. to a comparably high productivity of the surface layers, whereas the commonly observed diurnal descend should represent a mechanism of predator avoidance. Predation selected also for typical patterns of reimmigration in the megalopae of exporting crab species. They return from the sea into estuarine environments on large-amplitude flood tides, primarily at night. This enhances not only the passive upriver transport, but reduces also the mortality caused by predation (Christy & Morgan 1998).

Synchronized timing of larval molting may be another evolutionary response to the selective pressure that is exerted by visually oriented predators. In a spiny lobster, *Thenus orientalis*, molting of the phyllosoma stages was shown to occur around dawn, while the subsequent nisto and juvenile stages molted only nocturnally, with apparent synchronicity (Mikami & Greenwood 1997b). This synchronization disappeared when the larvae were

reared under continuous light or darkness, indicating that cues from a natural light cycle are important triggers. Also in American lobster (*Homarus americanus*) larvae, the metamorphic molt was shown to occur predominantly in the dark phase of both normal and experimentally reversed photoperiod cycles (Waddy & Aiken 1999).

Nocturnal egg hatching, vertical migrations, and synchronized molting of larvae thus appear to represent adaptive strategies that are, in part, directed towards an avoidance of intense pelagic predation in estuarine and coastal waters. However, there are decapod crustacean species that have adapted their entire life cycle to estuarine conditions, i.e. their larval stages develop successfully near to or within the adult environment ("retention strategies"; see section 10.3.2). This implies that the larvae of such species must be capable of tolerating not only physical stress, but to survive also under enhanced predation pressure. This is based on specific adaptations in behavioral and morphological features.

For a long time, long larval spines had been considered almost exclusively as a morphological adaptation enhancing the buoyancy of planktonic larvae and thus, reducing the energetic costs for swimming. Indirect evidence for this relationship between larval morphology and water density was observed also in the larvae of the Chinese mitten crab, *Eriocheir sinensis* (see section 2.5, Fig. 2.15). On the other hand, experimental studies by Morgan (1987, 1990, 1992) demonstrated that spines do not always retard the sinking of larvae but may reduce predation. Long carapace spines and large body size appear to be effective protections against planktivorous fishes (Fig. 10.3). However, those morphological traits do not protect as effectively against invertebrate predators, especially in the benthos. Early crab (*Uca minax*, *Rhithropanopeus harrisii*) larvae, for instance, were readily eaten by benthic estuarine shrimps, crabs, and amphipods (Morgan 1992). Predation by caridean shrimps such as *Crangon septemspinosa* and *Palaemonetes pugio* was shown also in megalopae of the blue crab, *Callinectes sapidus* (Olmi & Lipcius 1991). During and after metamorphosis, the hiding in refuges becomes thus more important than morphological adaptations (cf. section 10.5).

Besides spination, lack of pigmentation (i.e. transparency of larvae) has been considered as a morphological adaptation to pelagic predation pressure. Although this hypothesis appears to be plausible, it was not supported by a recent experimental study, in which the predation by planktivorous fish on four species of crab larvae was not found to be significantly influenced by larval pigmentation (Morgan & Christy 1997). On the other hand, Jeffs et al. (in press) suggested that transparency is an important defense of the nektonic puerulus of spiny lobsters, which is transported over large distances across the continental shelf. In this case, the need for transparency seems to have selected also for a special biochemical adaptation, namely a storage of transparent phospholipids in the hematocoel instead of an accumulation of triacylglycerides (*TAG*) in the hepatopancreas. After the settlement in coastal regions, these polar compounds appear to be transformed to neutral lipids (*TAG*) which are eventually stored in the R-cells of the hepatopancreas. Further comparative studies of potential antipredatory adaptations in larval coloration, morphology, biochemistry, and behavior should be worth-while.

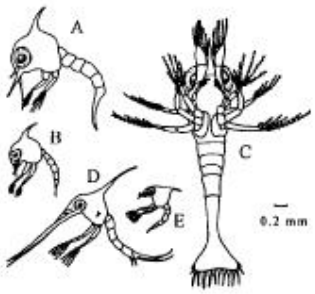


Figure 10.3. Long spines and large body size as putative morphological adaptations to predation pressure in the estuarine plankton; comparison of the zoea I stage of decapod species differing in dispersal strategy and susceptibility to pelagic predation: (A) *Sesarma reticulatum*, (B) *Sesarma cinereum*, (C) *Palaemonetes pugio*, (D) *Rhithropanopeus harrisii*, (E) *Uca minax*; species B and E develop in coastal marine regions (export strategy), the others within estuaries (retention); B and E are preferred prey of pelagic fishes (from Morgan 1990).

As a behavioral response to predation, we have already mentioned the "shadow reflex" (see section 10.1.3.3). A sudden decrease in the intensity of light is apparently interpreted as an indication of an approaching predator, which elicits an immediate escape response. In addition to optical cues, larvae perceive also chemical alarm signals. In the coevolution of grazing and predatory zooplankton, potential prey species have "learned" to smell dominant competitors and potential predators (see Young & Chia 1981). This adaptation is particularly well documented in freshwater plankton (for recent review see Ringelberg 2000). Chemical signals that are released from predatory fish or invertebrates (*kairomones*), or substances that are leached from preyed and damaged conspecifics, have frequently been observed to induce behavioral responses as well as modifications of reproductive and morphological traits in potential prey species. This is particularly well known from cladocerans (e.g. Lampert 1993, Kleiven et al. 1996, Pijanowska 1997, Brewer et al. 1999, Weber 2001), but it occurs also in other invertebrate taxa (Greene 1999). In brine shrimp (*Artemia*), the migratory activity and the response to light is enhanced by exposure to predator odors (Forward 1993, Forward & Rittschof 1993, 1999), and in copepods it was shown that the feeding activity is reduced when exudates from planktivorous fish are released into the water (Cieri & Stearns 1999).

Early juvenile lobsters (*Homarus americanus*; instar IV) and megalopae of a mud crab (*Panopeus herbstii*) are apparently able to perceive chemical signals from benthic predators and respond with a delay of settlement and metamorphosis (Boudreau et al. 1993a, b, Dittel et al. 1996). This capability of predator avoidance appears to be crucial for the chances of survival in the settling stage, where benthic predation (including cannibalism) has repeatedly been identified as a key factor controlling the recruitment success and hence, the local population size of decapods (Eggleston & Armstrong 1995, Hunt & Scheibling 1997). As another avoidance mechanism, settling larvae of many species prefer substrates which offer shelter from predation (see section 10.5). First experimental

evidence for the occurrence of similar adaptations in planktonic zoeal stages could be shown only recently by Forward & Rittschof (2000), who observed that *Rhithropanopeus harrisii* larvae changed their vertical migration response to light variation, when mucus from planktivorous fish was present. We may expect that future research will add many more examples of behavioral responses to kairomones in planktonic decapod larvae.

10.1.6.2 Diseases

Numerous types of diseases have been observed in both adult and larval crustaceans, especially under high-density stocking conditions in aquaculture (for review see Provenzano 1983). Virtually all major organ systems including the integument, hepatopancreas, gut, and hemolymph may be affected by parasitic, viral, bacterial, fungal, and other infections, decreasing the survival, growth, appearance, and commercial value of cultivated species. The high economic significance of diseases as a key factor in aquaculture is reflected in numerous scientific publications and reviews, which can only be examplified in this section, referring primarily to recent papers where the older literature is cited. Naturally, most of the available literature concentrates on commercially important species. This includes in particular: palaemonid and penaeid prawns (reviews: Trimble & Sandifer 1977, Brock 1983, Lightner 1983, Lawrence et al. 1985, Owens 1987, New 1990, Lee & Wickins 1992, Spaargaren 1996; recent papers: e.g. Flegel et al. 1999, Wang et al. 1999, Roque et al. 2000), clawed and spiny lobsters (Fisher et al. 1978, Stewart 1984, D'Abramo & Conklin 1985, Aiken & Waddy 1995, Pahl & Opitz 1999, Diggles et al. 2000), crayfish (Avault & Huner 1985), and large brachyuran and anomuran crab species (Fisher & Nelson 1978, Bigford 1979b, Kuris et al. 1991, Yasunobu et al. 1997, Messick 1998).

Although the widespread incidence of contagious diseases in aquaculture is undoubtly related to the enhanced risk of infections under intensive culture conditions, it is by no means a laboratory artifact. In natural crustacean populations, the reproductive success may greatly be reduced by egg parasites or other diseases (Kuris 1991, Kuris & Lafferty 1992, Shields & Wood 1993), bacterial shell lesions may impair the aspect and cause an accumulation of ecotoxins, or parasitic dinoflagellates invading the hemolymph may deteriorate the taste, and thus, affect the marketability of exploited stocks (Getchell 1989, Sindermann 1991, Meyers et al. 1996). When shore crabs, *Carcinus maenas*, were experimentally inoculated with Gram negative bacteria (*Listonella (= Vibrio) anguillarum*), they showed a temporary reduction in the immunocompetence, i.e. they became less resistant against other infections (Hauton et al. 1997). In a commercially fished portunid crab species, *Necora puber*, a regional population decline was associated with dinoflagellate infections (Wilhelm & Mialhe 1996). These examples show that parasitic and other diseases belong to the key factors also in the field, at least in the benthos.

In the plankton, the diversity of infectious diseases should be lower, due to shorter average life cycles in the potential host species. However, field studies provided circumstantial evidence that viral attack can terminate regional phytoplankton blooms (Bratbak et al. 1993), and it has even been suggested that viruses played an evolutionarily significant role in past extinctions of dominant species (Emiliani 1993). Numerous viral, fungal, bacterial, and parasitic infections were documented also from larval decapods both in laboratory culture and in the field (e.g. Lavilla-Pitogo et al. 1990, Lindley 1992, Hameed 1993, Momoyama & Sano 1996, Abraham et al. 1997, Genthner et. al. 1997, Robertson et al. 1998, Zafran et al. 1998, Harris & Owens 1999, Vandenberghe et al. 1999, Watanabe et al. 1999, Venegas et al. 1999, Chen et al. 2000). The potential role of this biotic control

factor has thus been introduced also in models of population dynamics and fisheries (Kuris & Lafferty 1992).

In artificial rearing, the efficacy and compatibility of several antibiotic or toxic antifouling substances have been tested, although with quite variable success (e.g. Armstrong et al. 1976, Fisher & Nelson 1978, Lino-Po & Sanvictores 1986, Gardner & Northam 1997, Pahl & Opitz 1999). Recently, aquaculturists began to experiment with vaccination against contagious disease (Itami et al. 1992, Zafran et al. 1998, Alabi et al. 1999, 2000). In a study on biochemical composition and energy reserves in shrimp (*Litopenaeus vannamei*) larvae, it was shown that the susceptibility to viral infections in aquaculture may be enhanced not only as a consequence of high stocking density, but also as a "domestication effect" in fattened larvae (Stuck et al. 1996). Likewise, injured larvae are weaker and thus, more susceptible to infections than healthy larvae (Diggles et al. 2000).

Decapod crustaceans, and probably also their larvae, are partially protected by immunoreactive factors in the hemolymph (for recent review, see Roch 1999). This system can be activated by particular dietary components, for instance immunostimulants that have been derived from fungi and yeasts (e.g. Chang et al. 1999), and this immunity can be tranferred from egg-producing females to their larvae (Huang & Song 1999). Since disease resistance reflects also the general health condition of an animal, the bactericidal activity of blood serum samples can be used as a measure of physiological condition (Ueda et al. 1999). Hence, immunological techniques may become useful new tools in studies of larval physiology and ecology. As an additional protection against disease, there are competitive interactions among different microorganisms as well as immunostimulating effects of probiotic bacteria that apparently promote the defense of the gut flora against pathogenic species (Skjermo & Vadstein 1999, Vandenberghe et al. 1999). Antibacterial activity has been observed also in diatoms belonging to the larval food sprectrum both in culture and in the plankton (e.g. Naviner et al. 1999). In lobster embryos, it was shown that epibiotic bacteria produced a fungicide-like antibiotic substance that protected the eggs against *Lagenidium* infections (Gil-Turnes & Fenical 1992). Since this fungus is a widespread problem in larval cultures (Armstrong et al. 1976, Fisher et al. 1978), similar interaction effects should occur there too.

Morphological (including electron-microscopical) studies have allowed for the description of a great variety of viruses and microbial infections. However, extremely small size and little morphological diversity have remained a serious obstacle in the detection and identification of pathogens. Immunohistochemical (e.g. Field & Appleton 1996, Robertson et al. 1998, Roch 1999) and molecular genetical techniques have become promising new diagnostic tools (e.g. Pasharawipas & Flegel 1994, Durnad et al. 1996, Genmoto et al. 1996, Vandenberghe et al. 1999, Tsai et al. 1999, Chen et al. 2000).

10.2 *Seasonality in the plankton*

Since meroplanktonic life-history stages of benthic invertebrates are only sojourners in the pelagic environment, the timing and duration of their occurrence are of utmost ecological interest. Meroplanktonic larvae, in general, are significant as grazers of phytoplankton and as predators of smaller zooplankton, but also as prey organisms of benthic filter feeders (Bingham & Walters 1989, Tamburri & Zimmer-Faust 1996), predatory fish (Paradis et al. 1996, Morgan & Christy 1997), and of innumerable other plankton feeders (Morgan 1992). Decapod larvae may seasonally and regionally dominate within the coastal mero-

plankton, occasionally contributing up to 90% of total zooplankton biomass (Tenore et al. 1982, Williams & Collins 1986). In the following section, I will review the climatic control of and relationships between plankton production, invertebrate reproduction, and larval occurrence in the field. In this context, I will discuss the predictability of planktonic development in the field and show examples of reproductive adaptations to seasonality in the pelagic environment.

10.2.1 *Productivity cycles and seasonality of reproduction*

Water temperature and day length are key determinants of larval occurrence, controlling both the repoductive cycle of aquatic invertebrates and the intensity of primary production. The latter phenomenon, which depends more on light than on temperature conditions, is (directly or indirectly) the nutritional basis for planktonic suspension feeders such as the decapod crustacean larvae. The extent to which temperature and light vary seasonally depends primarily on the geographic latitude. These climatic parameters show little variation near the equator, allowing for relatively constant production of phyto- and zooplankton throughout the year. The seasonality of day length increases continuously from the equator towards the poles, while temperature varies maximally at the intermediate latitudes.

Although seasonal changes in plankton production occur also in tropical regions, meroplanktonic larvae may be found there throughout the year as members of the pelagic community. Major seasonal variations in the tropics are related to the alternation of rainy and dry seasons, for example those associated with the monsoon system of the Indo-West-Pacific. These climatic forces cause periodical changes in the direction and velocity of winds and ocean currents, in the frequency of rains, and in the turbidity and productivity of surface waters (see Paula et al. 1998). All of those cyclic phenomena may significantly affect the chances of larval development and recruitment, and hence, select for seasonal cycles in the reproduction of decapod crustaceans and other aquatic invertebrates. In several equatorial penaeid shrimp species from northern Australia, for example, markedly seasonal patterns in spawning and recruitment were described (Dall et al. 1990). Peak spawning periods occur typically in the dry seasons ("spring" and "autumn"), when winds, ocean currents, and turbidity are minimum.

Compared with the tropics, temperate regions show a more pronounced seasonality in water temperature and day length. Moreover, marked seasonal salinity changes may occur in estuarine and coastal zones, for instance during the melting of snow and ice in spring. As an adaptation to the regular occurrence of a peak plankton productivity and an increase in water temperature during spring and summer (both aiding to a rapid planktonic development), most temperate invertebrate species show clear seasonal cycles in their reproduction. This requires a seasonal timing of egg hatching which, at least in some species, is triggered by environmental cues. Besides an increase in temperature or day length, also chemical signals released from phytoplankton blooms have been shown to stimulate the hatching of marine invertebrate larvae (Himmelman 1975, Starr et al. 1991, 1994). In species whose larvae depend strongly on planktonic food sources, this adaptive response should enhance the chances of optimal larval nutrition and thus, survival in the plankton. Among the Decapoda, this effect has been demonstrated in a boreal spider crab, *Chionoecetes opilio* (Starr et al. 1994).

While the majority of temperate species exhibits a clear peak of hatching in spring or summer, when sufficient planktonic food is available, there are also exceptions that hatch

in winter. Dungeness (*Cancer magister*) and spider crabs (*Hyas araneus*), for instance, release their larvae before the spring bloom begins, i.e. when food is still limited. Both species have experimentally been shown to ingest and convert, as an additional food source, also unicellular algae and protozoans, which may bridge the gap in mesozooplankton availability during late winter in the field (Anger & Nair 1979, Sulkin et al. 1998a).

In high latitudes, significant phytoplankton production occurs only during a short period in late spring and early summer, when day length reaches a maximum. Secondary production follows with a delay of one or two months, reaching its peak in mid or late summer, when temperature is near its maximum. Thus, the productivity peak is short, while the water temperatures remain on average low, even in summer. With increasing latitude, there is consequently a mismatch between prolonged development duration at low temperatures and a shortening period of food production, which should select against a planktotrophic mode of development. This may explain why the pelagic larvae of decapods in high latitudes show a conspicuous tendency toward lecithotrophy and why the total number of Decapoda and other invertebrate species with pelagic development decreases dramatically towards the poles (Thorson 1950, Lindley 1998a).

The spider crab *Hyas araneus* is one of the few decapod species that have retained their planktonic larval phase in high latitudes. This species occurs in subarctic regions of the Atlantic Ocean, extending as far north as to the coasts of Greenland and Spitzbergen (Christiansen 1969). In spite of an extremely long duration of embryonic development (2 years; Petersen 1995), the timing of larval hatching is focussed within a period of only a few weeks, namely in early spring, just before primary production begins to rise. As a control mechanism aiding in this coordination of reproduction with the seasonal cycle of plankton productivity, the embryos of *H. araneus* seem to pass through a period of diapause (Petersen 1995, Petersen & Anger 1997). Coordinated hatching enables the larvae to exploit both the spring bloom of phytoplankton and the subsequently developing zooplankton populations which graze on diatoms and other plankton algae. Since zooplanktonic grazers are on average larger food items, these should become increasingly important for the nutrition of later larval stages (cf. section 5.2.2). A similar seasonal timing of larval hatching appears to occur in snow crab (*Chionoecetes opilio*; Taylor et al. 1985) and king crab species from subarctic regions (*Paralithodes camtschaticus*, *P. platypus*; Jensen & Armstrong 1989). In contrast to members of the closely related genus *Lithodes*, the larvae of *Paralithodes* spp. require planktonic food, and thus, depend on the short bloom in spring and summer (Shirley & Shirley 1989).

Hyas araneus shows, in addition to reproductive coordination with a pronounced seasonality in plankton production, a comparably high maternal energy investment per offspring (large egg size). This reproductive trait should be important in years with a weak or seasonally delayed plankton production. Provided with enhanced energy stores from the egg yolk, early larvae can survive for quite extended periods under conditions of famine. For instance, the zoea I can live in complete absence of food for about 8 days (at 12°C) without losing its capability for later recovery (Anger & Dawirs 1981). At lower, typical spring temperatures in the field (≤6°C), the maximal time of survival under conditions of starvation exceeds one month.

Similar albeit more pronounced adaptations to seasonally low temperatures and short periods of plankton production have been observed also in the larvae of Antarctic deep-water shrimps, *Notocrangon antarcticus* and *Chorismus antarcticus* (Bruns 1992). *N. antarcticus* has, compared with most other decapods, very large eggs and larvae, and an

abbreviated pelagic development with only three larval stages. In rearing experiments at a typical Antarctic spring and summer temperature (2°C), their development took about 28, 30, and 42 days, respectively (Bruns 1992). Hence, the duration of planktonic development is, in spite of a low temperature level, short enough to guarantee successful recruitment before the end of the summer season. As another adaptation to short and unreliable planktonic food production, the zoeal stages show a high degree of facultative lecithotrophy. The zoea I can reach the second stage also in complete absence of food, and when the onset of feeding was experimentally delayed until 24 days after hatching, the larvae did not lose their capability to recover from starvation and to develop successfully to metamorphosis (PNR_{50}>50d). An unusually great inpendence from food was demonstrated also in *PRS* experiments, in which *N. antarcticus* larvae were fed for only short initial periods after hatching, then starved continually. Only 6 days of feeding at the beginning of the zoea I moulting cycle were sufficient to allow for further development in complete absence of food, not only to the zoea II but through all larval stages to metamorphosis (taking in total more than 3 months).

As *Notocrangon antarcticus*, also *Chorismus antarcticus* has a facultatively lecithotrophic zoea I (Bruns 1992). This species passes through four zoeal stages, requiring about 22, 33, 42, and 50 days, respectively (at 0°C). Although the response of *C. antarcticus* larvae to starvation was slightly more sensitive than in *N. antarcticus*, they showed very little nutritional vulnerability as compared with most other decapod species.

Facultative lecithotrophy may be considered as an evolutionary transition from obligatory planktotrophy towards full lecithotrophy, which is reached, for instance, in the northern stone crab, *Lithodes maja* (cf. section 6.3.1, Fig. 6.11). Being nutritionally fully independent of the short season of plankton production, its larvae may hatch throughout the year, including autumn and winter. In the laboratory, the females were observed to release their larvae in small daily numbers, so that hatching occurred over extended periods of up to several weeks per egg mass (Anger 1996b). This reproductive trait should strongly reduce the density of larval aggregations in the plankton and thus, may represent an adaptation to predation pressure in species with relativele large and easily visible larvae. The same pattern has been found also in lobsters (*Homarus* spp.) and some crabs, e.g. the subarctic species *Hyas araneus* (Kunisch & Anger 1984).

Arctic and Antarctic congeners of the stone crab (e.g. *Lithodes aequispinus*, *L. santolla*; the latter species is in the literature often found under the synonym *L. antarcticus*) produce similarly large eggs as *L. maja*. Morphological descriptions of their larvae show conspicuous lipid droplets within their carapace (Campodónico 1971). This suggests that the lecithotrophic mode of development may be a common trait among *Lithodes* species from high latitudes (for discussion see Anger 1996b). This generalization is corroborated by recent experimental evidence for lecithotrophy in the three zoeal stages of *L. aequispinus*, a king crab from Alaska (Shirley & Zhou 1997). Similarly, *Paralomis granulosa*, a lithodid species from subantarctic regions of South America, shows large egg size and an abbreviated development with only two zoeal stages and a megalopa (Campodónico & Guzmán 1981, Comoglio & Vinuesa 1991). Current experimental studies with *L. santolla* and *P. granulosa* (Calcagno, Kaffenberger, Lovrich, Anger, unpubl. data) have shown that the larvae of these species are entirely lecithotrophic from hatching, at least to the megalopa stage. As a final step in the reproductive adaptation to limited food availability in combination with low temperatures, decapods in high latitudes may eventually omit the pelagic larval phase. In the Sclerocrangonidae, for instance, direct development and

some degree of maternal brood protection have been observed, similarly as in crayfish (Wollebaek 1906, Makarov 1968a, b).

In summary, a short season of plankton production in combination with low summer temperatures in high latitudes have selected for an abbreviated larval development and an enhanced female energy allocation per offspring, allowing for a significant reduction of larval dependence on planktonic food. Those species which have retained planktotrophic larval stages, show tendencies towards facultative lecithotrophy and/or a conspicuous coordination of their reproductive cycle with seasonal cycles of day length and temperature.

10.2.2 *Estimating larval development and recruitment in the field: extrapolation of laboratory data*

Variability in water temperature is weak not only in tropical regions, but also in high latitudes. Thus, temperature as an environmental key factor is most important in the temperate zones, where great seasonal variations occur, in some regions exceeding a span of 20°C. Moreover, conspicuous regional differences occur due to differential influences of warm and cold water currents, and in offshore regions there are extreme vertical temperature gradients. Temperature-dependence of pelagic development represents thus a crucial life-history trait, in particular in species from temperate regions; the same should apply to deep sea species, as far as their larvae migrate within the water column.

The duration of larval development as a function of temperature has experimentally been investigated in numerous decapod species, and this relationship was commonly described with non-linear regression equations (see section 6.4.1, Eqs. 6.13-6.15). However, only rarely were those regressions linked with other empirically derived equations that describe the seasonal cycle of in situ water temperatures in the field. When this is done, one may yield a simple simulation model for the estimation of the rate of larval development in the plankton (see Anger 1983b, Harms 1984, Dawirs 1985, Schultze & Anger 1997). The principle of computing is as follows: (1) Beginning from an assumed calendar day of hatching in the field, the theoretical average water temperature (T) is estimated for each successive day; (2) with these T values, the theoretical duration of development (D) through a larval stage is calculated for each on successive day; (3) from these D values, daily fractions of development time ($1/D$) are obtained; (4) these fractions are summed over a period of simulation days, until a cumulative value of $\sum[1/D]=1.0$ is reached, i.e. 100% of the theoretical instar duration, D. This procedure is reiterated for each larval stage (using stage-specific regression equations for the relationship between D and T), until the theoretical day of metamorphosis is reached.

Naturally, such simple models allow only for rough estimates of development duration and timing of recruitment, as they are based on regression equations describing the rate of larval development under laboratory conditions. Hence, they do not take into account the potential effects of food limitation or other adverse conditions, and vertical or local temperature gradients are disregarded. In spite of its simplicity, however, our simulation model allows for the prediction of some interesting effects of seasonality in temperature, which can be tested in laboratory and field studies (see Anger 1983b). Such theoretical effects may have implications for larval nutrition (e.g. match or mismatch with plankton blooms), mortality (differential time of exposure to pelagic predation), and for the expected dispersal and gene flow among geographically separated populations.

This approach is exemplified in Figure 10.4 with the spider crab *Hyas araneus*. Under constant temperature conditions in the laboratory, its development duration is consistently

shortest in the zoea I stage, slightly longer in the zoea II, and more than double as long in the megalopa. In the field, however, the temperature increases from hatching in late winter throughout spring. This change is likely to cause shifts in the proportions of the successive development durations. During the period of maximal hatching (in the southern North Sea mid-February to mid-March), the zoea I develops at low temperatures (about 3-4°C), so that this stage should require a longer time than the subsequent stages (Fig. 10.4a). Later, throughout most of the reproductive season, the three larval stages have similar theoretical development durations in the field. This implies that about two thirds of the total time of larval development (*D*) are spent in the fully planktonic zoeal phase, while only one third of *D* is passed as a semibenthic megalopa (Fig. 10.4b). Only the seasonally latest larvae (hatching from late March to April) pass through a relatively short planktonic and a long megalopa phase, similarly as under constant laboratory conditions.

When a temperature modulation (e.g. a constant addition or subtraction of 1°C) is introduced into the model, effects of interannual variation in average water temperature can be simulated (Anger 1983b). Since the temperature-dependence of development varies among larval stages and with the temperature range, unusually cold or warms years will change the proportions of time spent in successive instars as well as the timing of benthic recruitment. As an example of effects that cannot immediately be expected from laboratory data, the model predicts that the period of recruitment should be shorter than the period of hatching. This "focussing" effect is due to faster development in larvae hatching later within the season. As another theoretical prediction, this effect should be stronger in unusually cold years, due to generally higher Q_{10} values at lower temperatures. Similar effects were predicted also for the larval stages of a caridean shrimp, *Pandalus montagui* (see Schultze & Anger 1997).

Compared with *Pandalus montagui* and *Hyas araneus*, the shore crab, *Carcinus maenas*, has a longer reproductive period, extending from early spring through late summer. In this species, the model predicts also a developmental acceleration in successively later hatching cohorts throughout the spring season (Dawirs 1985). However, the opposite effect should occur in larvae hatching at the end of the reproductive season, in late summer. At that time, the water temperatures begin to decrease, causing an increasing duration of pelagic development. As an additional delaying factor, the production of planktonic food declines through fall and winter. Thus, seasonally decreasing temperatures in temperate regions should substantially deteriorate the conditions for meroplanktonic development, as they prolong the exposure of the larvae to potentially detrimental factors, namely food limitation and pelagic predation. Below a critical temperature limit, which varies with the species and its geographical range, development should eventually cease (Dawirs 1985, Anger 1991b, Ismael et al. 1997).

In summary, the temperature-dependence of larval development duration should select against larval release late in the year, especially in temperate regions where sharp seasonal variations in temperature, day length, and productivity occur. This limits the reproductive season of decapods and other marine invertebrates with a planktotrophic larval phase. An extension of the reproductive season has been achieved by species which have evolved a seasonal dimorphism of eggs and larvae. An example for this special type of adaptation to seasonality in the plankton is shown in the following section.

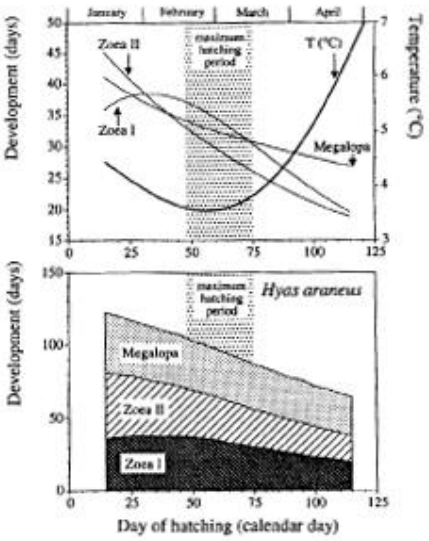


Figure 10.4. Simulated duration of the larval development of a spider crab (*Hyas araneus*) in the field (Helgoland, North Sea); [a] development of successive larval stages in relation to the time of hatching (calendar day) and as a function of seasonal temperature variation; [b] cumulative development and relative proportions of time spent in successive stages (extrapolated from laboratory data) (redrawn after Anger 1983b).

10.2.3 *Summer and winter larvae*

Being the most important species among the commercially fished caridean shrimps in the southern North Sea and adjacent regions, the brown shrimp (*Crangon crangon*) has received considerable interest in fishery biology (Tiews 1970) and in studies of larval ecology (see Moksnes & Wennhage 2001, and earlier papers cited therein). Untypically among the temperate shrimps, this species shows here roughly a bimodal pattern of reproduction, with maximum hatching in late winter and early summer (Boddeke 1982). Eggs that are produced and incubated during winter are up to about 20% larger in terms of both volume and weight as compared to summer eggs (Paschke 1998). Although they do not differ significantly in their relative proximate biochemical and elemental composition or in energy density (Joules per unit of dry mass), the absolute amounts per egg of all major constituents show a pronounced seasonal variation. This phenomenon is *"not uncommon in animals with long breeding season"*, in general (Ghiselin 1987), but it has rarely been documented in decapod crustaceans.

Recent investigations (Linck 1995, Paschke 1998) have shown that the winter and summer eggs of *Crangon crangon* do not represent clearly separated cohorts but extremes in a continuum. An inverse relationship between seasonal temperature and larval size has been documented also in several other decapod species (Lindley 1998a) and may thus represent a fairly general rule (c.f. section 6.4.1). Also the duration of embryonic development decreases throughout the reproductive season, taking about three months in winter (at 6°C) and less than three weeks in summer (at 18°C; Paschke 1998). However, this

gradual acceleration is caused not only by increasing temperatures. It is probably also associated with decreasing egg size. At equal temperatures, the large winter eggs require a significantly longer development time than the small summer eggs.

As a result of these reproductive patterns, there is a gradual decrease in body size, from large winter larvae to smaller summer larvae (Criales 1985, Linck 1995, Paschke 1998). The former contain significantly higher quantities of proteins, lipids, and energy, bestowing them a greater tolerance of nutritional stress. When freshly hatched winter larvae were experimentally exposed to limited periods of feeding and starvation, they reached significantly faster their "Point of reserve saturation", *PRS* (i.e. a state of secondarily reached facultative lecithotrophy), and they took longer to pass the critical "Point of no return", *PNR* (Paschke 1998). Thus, the seasonal variation in the size of eggs and larvae of *C. crangon* may be interpreted as an adaptation to seasonality in planktonic food production.

Although an assignment of seasonal larval cohorts to different generations or phenotypes remains hypothetical until more data on juvenile growth, time to sexual maturation, and other life-history traits of *Crangon crangon* become available (including the possible occurrence of protandric hermaphroditism; see Tiews 1987), we may conclude the following: Enhanced maternal energy investment in the winter eggs allows for an extension of the reproductive season, as the earliest hatching larvae (the "winter cohort") can survive under nutritionally poor conditions until the spring bloom begins. Subsequently, an increase in both food availability and temperature allows for accelerated growth of larvae and juveniles, so that sexual maturity and first egg production may be reached already in the following winter, i.e. with an age of about one year (cf. Detlefsen 1984). Since the later hatching "summer cohort" grows less during the following autumn and winter, due to a decrease in both water temperature and food availability, this cohort should produce its first eggs only in the next summer or in the winter thereafter, i.e. about one year to one year and a half after hatching.

This implies that the winter cohort has, compared with that produced in summer, the advantage of larger initial body size, which may reduce the rate of planktonic larval mortality due to both predation and food limitation. Moreover, the earlier appearance in the pelagial allows for faster growth in the early juvenile phase and an earlier attainment of reproductive maturity. On the other hand, the duration of the planktonic larval phase must be much longer in cold water during spring. This effect may offset some of these selective advantages of the winter larvae, as it increases their time of exposure to pelagic predation. These patterns suggest a bet-hedging strategy, resembling that of seasonal reproduction in anostracan species where two differential temperature-induced cohorts alternate (see Saiah & Perrin 1990). If seasonal flexibility in the size of eggs and larvae of *Crangon crangon* is an adaptation to seasonality in plankton production, then we may expect that similar patterns should occur also in other species with an extended reproductive period.

10.3 *Estuarine life-cycle adaptations: export* vs. *retention*

The numerous physiological and behavioral adaptations to predictable environmental changes that may occur during the development through successive life-history stages form the basis of reproductive strategies. Fully marine species are adapted, throughout their life cycle, to relatively stable environmental conditions and thus, do not tolerate major variations in physico-chemical factors. Species living in coastal or estuarine areas, in contrast, are normally exposed to changes in temperature, salinity, and other parameters.

Compared with both fully marine and true freshwater species, the physiological and behavioral adaptations to variability in the environment are thus particularly pronounced in the inhabitants of estuarine and other transitional habitats. In many of these species, however, the typical adaptations such as euryhalinity or eurythermality are attained only in the benthic juvenile or adult phase, while the larvae remain physiologically fragile. The maintenance of estuarine populations requires thus the evolution of special life-history adaptations, which should somehow protect the larvae from enhanced mortality in the physically unstable adult environment. These adaptations comprise programmed ontogenetic changes in the physiological tolerance of stress factors, endogenous rhythms of egg hatching and larval migration, and numerous behavioral responses to variability in single or combined physico-chemical factors (see above, section 10.1); at least some of these traits, including patterns of larval behavior, are genetically determined and hence, heritable (Zeng & Naylor 1996b).

Two principal strategies occur in the life cycles of estuarine species (Strathmann 1982): (1) export of the larval stages to adjacent coastal or offshore marine areas, where the conditions for larval development are more favourable; (2) adaptation of all life-cycle stages to the estuarine conditions, allowing for larval retention within the parental environment. The latter strategy is considered as a transitional stage in the evolution of limnic and terrestrial species. Examples of these life-history strategies will be reviewed in the following sections.

10.3.1 *The export strategy*

Most estuarine and several freshwater species are known to export rather than retain their larvae within the parental habitat. This is primarily based on rhythms of hatching and larval behavior, namely tidal vertical migrations in the water column, using tidal currents for early larval seaward transport and later reimmigration. A simplified conceptual model for this pattern is shown in Figure 10.5. In the older literature, this life-history pattern has primarily been interpreted as an adaptation to the needs for dispersal and gene flow (Scheltema 1975). However, Strathmann (1982, 1986, 1993) and Pechenik (1999) argued that these potential selective forces do not necessarily play a key role in the evolution of export strategies. The favourability of conditions for life varies among estuaries, and thus, should not favour the spread or dispersal of larvae among estuaries. More important in the evolutionary selection for an export strategy, both the physical and biotic conditions appear to be, on average, more favourable for larval development outside than inside the estuary (Morgan 1995a, Hovel & Morgan 1997). In consequence, the larvae of exporting species did not need to evolve special adaptations against osmotic or thermal stress, or against particularly intense pelagic predation pressure, so that they resemble in most of their traits the larvae of fully marine species.

In exporting estuarine species that release their offspring within the typical parent habitat, the freshly hatched larvae will initially suffer from low salinity and other physical stress factors, and they may be exposed to strong predation pressure in the estuary. However, the time of their exposure to those adverse conditions is shortened by several mechanisms aiding in a rapid downstream transport. These include tidally and diurnally coordinated hatching rhythms as well as a rapid ascend of the larvae to outflowing surface layers, where they profit also from high estuarine plankton production while they are being transported towards the sea. The various active and passive mechanisms of larval export in estuaries can only briefly be summarized and exemplified in this section; they have

been analyzed and discussed in numerous research papers and several reviews (e.g. Paula 1989, 1998, McConaugha 1992, Morgan 1995a, Shanks 1995a, b, Young 1995, Garrison 1999, Pereira et al. 2000, Epifanio & Garvine 2001, Epifanio in press).

Tidal, lunar, and diurnal rhythmicity of egg hatching as well as the underlaying physiological mechanisms have extensively been studied in various estuarine and coastal marine decapod species, mostly brachyuran crabs (for details and review of literature, see De-Coursey 1983, Forward 1987b, Rittschof et al. 1990, De Vries et al. 1991, Morgan 1995b, Saigusa & Kawagoye 1997, Saigusa & Terajima 2000). As a brief summary of the available evidence, one may say that hatching is generally synchronized with the cycles of lunar or solar light and with tidal currents. This coordination is, in principle, based on a combination of endogenous rhythms and environmental entrainment, with variations in light and salinity as primary *zeitgeber* signals. The hatching process itself is controlled by chemical and behavioral interactions between late embryos and the mother animal. Shortly before hatching, the embryos release not only proteolytic enzymes aiding in the fracture of the egg membrane, but also proteinaceous pheromones which induce a particular "pumping" or "ovigerous hair-stripping" behavior in the female. This, on the other hand, stimulates the embryos to initiate the hatching process. Some of the communication substances that are released by the embryos could already be concentrated, partially purified, and chemically characterized (see Forward et al. 1987, Pettis et al. 1993, Saigusa 1996). Although several details of the egg hatching mechanisms have already been elucidated, there is still dispute as to the hierarchy of the involved control factors, including the relative importance of the embryos and the mother animals.

At the American east coast, the occurrence of hatching peaks is usually synchronized with nocturnal high tides, especially when spring tides co-occur with full or, preferably, new moon, i.e. when the tidal amplitude is maximum (Morgan 1995b, and earlier papers cited therein). This pattern of tidally controlled hatching rhythms makes sure that the freshly hatched larvae will immediately begin their passive horizontal migration towards the mouth of the estuary, leaving the parent environment normally within the time of a single ebb tide. As an additional benefit from this strategy, hatching during high tide will expose the larvae to a water body which originates from the adjacent sea, and thus, has a relatively high salinity and moderate temperature. Furthermore, nocturnal hatching will minimize the initial mortality by visually oriented predators, especially when the entire ebb tide occurs during darkness. Thus, the timing of larval release is here optimal when a new moon spring high tide coincides with sunset.

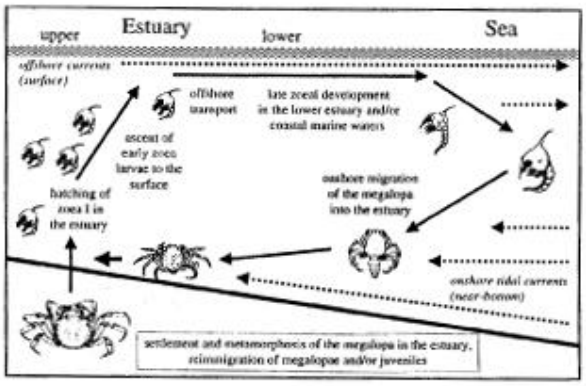


Figure 10.5. Conceptual model of the export strategy, with patterns of ontogenetic migrations (solid arrows) and principal currents (dashed); model simplified, showing only ontogenetic but no diel or tidal vertical migrations of larvae; zoeae are released within the estuary but soon transported seaward using near-surface offshore currents; most of the zoeal development takes place near the mouth of the estuary or in adjacent coastal marine waters; late stages descend to deeper zones, the megalopa reimmigrates into the upper estuarine zones using near-bottom tidal onshore currents. Examples: many grapsid crabs, e.g. *Eriocheir sinensis*, *Chasmagnathus granulata*, *Sesarma cinereum* (for references see text) (redrawn after Anger 1991b).

Since the type of the tidal regime varies regionally, the timing system of hatching control may vary inter- and intraspecifically, reflecting regionally different periodicity in the physical conditions. At the southern European Atlantic coast (Portugal), for instance, peaks of larval release have consistently been observed during the first half of the night, although this timing coincides here with neap ebb tides (Paula 1989, 1993; Queiroga et al. 1994, Queiroga 1998, Pereira et al. 2000). This suggests that, at least in this region and in the species predominating here, the crepuscular decrease in light intensity may be a more important hatching trigger than the tidal cycle. The relative significance of these environmental factors in the control of hatching rhythms has remained under dispute (see e.g. Paula 1998), which shows that more comparative studies from regions with different tidal regimes are required before further generalizations become possible.

Comparable with estuarine decapods, also species in the surf zone of open marine beaches may show export-enhancing hatching rhythms. In a sand-dwelling mole crab, *Emerita talpoida*, rapid transport out of the reach of the surf zone with its mechanical stress and a high frequency of benthic predators is achieved by maximal hatching about one day after strong onshore wind stress with heavy wave action, followed by an offshore-directed net flow (Amend & Shanks 1999).

In spite of all those complex life-history adaptations, the first larval stage is still, at least for a few hours, exposed to unfavourable estuarine conditions. Hence, some larval adaptations, in particular to hypoosmotic stress, should be expected to occur also in exporting estuarine species, namely in the first larval stage. This was observed, for instance, in the zoea I of an estuarine grapsid crab, *Armases (= Sesarma) angustipes*. After hatch-

ing, its zoea I larvae were found to stay alive and remain actively swimming in freshwater for up to two days (Anger et al. 1990c). Similarly, we observed an unusually strong tolerance of low salinity in the zoea I of other grapsid crab species, which also can live as adults under oligohaline or freshwater conditions but require higher salinities for their larval development (e.g. *Eriocheir sinensis*, *Chasmagnathus granulata*, *Cyrtograpsus angulatus*; unpubl. data).

The physiological basis of this tolerance of hypo-osmotic stress in the zoea I is an early appearance of osmoregulatory functions, namely a strong hyper-osmoregulatory capacity in dilute media. This could recently been observed in laboratory-reared larvae of *Chasmagnathus granulata*. In this species, the first zoeal stage is a significantly stronger hyperregulator than the subsequent stages II-IV (Fig. 10.6). This ontogenetic pattern matches the changes in larval ecology in the field (Anger et al. 1994), i.e. hatching within brackish lagoons, followed by an export to lower estuarine or coastal zones with higher saline water. The hyper-*OC* increases again in the megalopa and throughout juvenile development, again corresponding with the typical ecological changes occurring in these life-history stages in the field, i.e. reimmigration and recruitment to estuarine populations.

This pattern of a transitory decrease in the *OC* is remarkable, because regulatory capabilities have normally been found to increase throughout postembryonic development, but never to decrease (see Charmantier et al. 1998, Charmantier & Anger 1999). This implies that ion transporting tissues are present at hatching, apparently degenerating or deactivated in the second and subsequent zoeal stages, and later (from the megalopa) they are rebuilt or reactivated. The histological, ultrastructural, and biochemical (enzymatic) correlates of this complex ontogenetic pattern in *C. granulata*, and maybe in other species with an export strategy, deserve further investigations.

Even stronger tolerance of hypo-osmotic conditions was reported from the early larvae of several South American palaemonid freshwater shrimps (*Macrobrachium olfersii*, *M. carcinus*, *M. acanthurus*, *Palaemon pandaliformis*; for references see Anger & Moreira 1998). Although these species cannot develop in freshwater to the second zoeal stage, the zoea I larvae can survive there for up to about one week, which gives them sufficient time to emigrate from the limnic parental habitats to adjacent brackish waters. As an alternative mechanism, some species show migrations of ovigerous females to the lower parts of the estuary, where the larvae hatch and are subsequently retained (e.g. *Palaemon longirostris*; see Cartaxana 1994, Paula 1998).

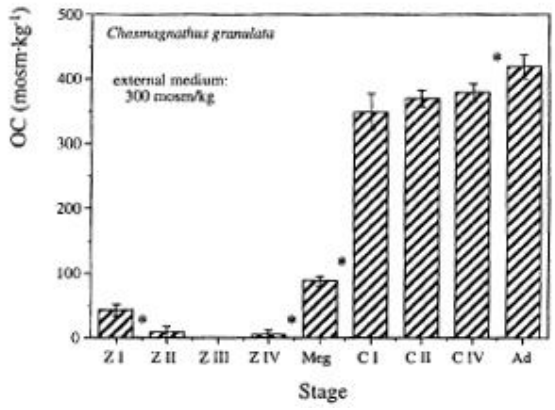


Figure 10.6. Osmoregulatory capacity (*OC*, osmolality difference between the external medium and the haemolymph; mean ± SD) of various ontogenetic stages of an estuarine crab (*Chasmagnathus granulata*) exposed for 20 hours to hyposaline stress (300 mosm/kg or 10.2 ‰ salinity); ZI-ZIV: zoeal stages I-IV; Meg: megalopa, CI-CIV: juvenile crab instars I-IV; ad: adult; *: statistically significant differences between mean *OC* values of successive stages, $P<0.001$; zoea III: complete mortality during the experiment (after Charmantier, Giménez, Charmantier-Daures & Anger, in prep.).

Riverine habitats, where many palaemonid shrimp species live, do not normally show a sufficiently high or regular plankton production. Thus, larval release in the adult habitat implies not only an initial exposure to hypo-osmotic stress but also nutritional incertainty. This should select for lecithotrophy, at least in the first larval stage. This hypothesis is corroborated by experimental observations in several palaemonid species, for instance in *Macrobrachium olfersii*, where the zoea I is a nonfeeding stage (McNamara et al. 1980). Also in *Palaemon pandaliformis* and in a closely related species with a very similar ecology, *Palaemonetes argentinus*, we observed a nonfeeding or facultatively lecithotrophic zoea I, respectively; this is in both species followed by about 6-10 feeding larval stages. Similar developmental patterns were reported from *Palaemonetes pugio* (Broad 1957a), *Palaemon paucidens* (Mashiko 1985), *P. elegans* (Magiera 1993, Kumlu & Jones 1995a), *P. adspersus* (Magiera 1993), *Macrobrachium amazonicum* (McNamara et al. 1983), *M. vollenhovenii* (Willführ-Nast et al. 1993), *M. heterochirus* (McNamara et al. 1985), *M. nipponense* (Kwon & Uno 1969, Shin & Chin 1994), and *M. rosenbergii* (Agard 1999). All these species follow an export strategy, and all have an at least facultatively lecithotrophic zoea I stage. Thus, their first larval stage has sufficient time to leave, transported by outflowing currents, the parental freshwater habitat and reach adjacent estuaries or coastal marine waters, where plankton production is generally higher and more stable. Since the selective pressure of food limitation acts only on the initial phase of larval development, the endotrophic potential has not evolved to a higher level that would allow for fully lecithotrophic development through subsequent stages. This pattern is in contrast to that in several palaemonid species which live in inland freshwater systems, for instance

in Australia (Fielder 1970), southeast Asia (Wong 1989), the Amazon (e.g. Magalhães & Medeiros 1998, and earlier papers cited therein), or in Central American streams (Villalobos & Álvarez 1999, Román et al 2000, Signoret et al. 2000). In all these cases, the larval development is abbreviated, benthic, and lecithotrophic (cf. section 2.4).

Special physiological adaptations in the first larval stage (Fig. 10.6) appear to be the most immediate evolutionary response to the particular selective pressures that the early larvae must face. Additionally, some freshwater and estuarine species mitigate non-marine stress factors with catadromous migrations of the reproducing females. The blue crab, *Callinectes sapidus*, is certainly the best studied example of this variant of the export strategy (Fig. 10.7); approximately a thousand research papers have been published on the life history of this species, including several recent reviews and mathematical models (e.g. Metcalf & Lipcius 1992, Smith & Stoner 1993, Olmi 1994, Epifanio 1995, Jones & Epifanio 1995, Johnson 1995, Morgan et al. 1996, Prager 1996, Tankersley et al. 1998). The Chinese mitten crab, *Eriocheir sinensis*, is another, even more extreme example of this strategy. It lives in rivers and other freshwater habitats, including inland waters that are far from the sea (reportedly up to 1300 km; see Panning 1938). This implies that the females must migrate downriver over large distances to reach estuarine or coastal waters where the larvae are eventually released; these require at least ca. 15‰ salinity for a successful development (Anger 1991b).

Migrations of ovigerous females and subsequent larval hatching in an estuary or in the sea represent a typical reproductive trait of terrestrial decapods. With a few exceptions (see Hartnoll 1988a), the terrestrial Brachyurans (Grapsidae, Ocypodidae, Gecarcinidae) and hermit crabs (Coenobitidae, Diogenidae) export their larvae by means of female migrations. Since larval development on dry land is impossible for crustaceans, and even the adults of these species have adapted to terrestrial but not usually to freshwater conditions, this strategy appears as the only solution.

As a major advantage of an estuarine export strategy with seaward migrations of females, the exposure of freshly hatched larvae to various stress factors prevailing in the adult habitat is minimized. As a disadvantage, however, the larvae of such species run an enhanced risk of irreversible advection to distant offshore waters, where the conditions are quite different from those in the parent habitat and thus, may be favourable only for the pelagic larvae but not for the postsettlement stages. Consequently, the need for successful recruitment to estuarine or freshwater populations has selected for complex mechanisms of coastal retention and onshore transport in the late larval stages. This implies that mechanisms for both larval export and retention may occur in different stages of one and the same species, which shows that this classification of life-cycle strategies is not always as clear and unambiguous as it generally appears from the literature.

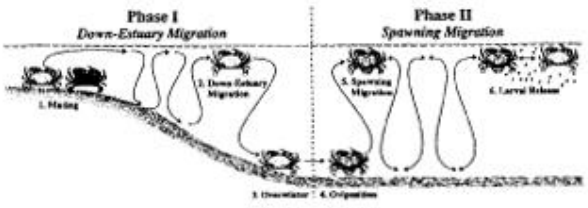


Figure 10.7. Conceptual model of reproductive migrations in adult female blue crabs (*Callinectes sapidus*) aiding in larval export from estuaries (from Tankersley *et al.* 1998, with permission from MBL, Woods Hole, USA). Phase I: adult crabs mate in the brackish regions of the estuary (1); following insemination, the females migrate seaward using selective tidal-stream transport (STST) on nocturnal ebb tides (2), while the males remain in low-salinity areas; after reaching euhaline regions, the females may overwinter near the mouth of the estuary (3); phase II: eggs are attached to the pleon (4); about 10-12 days after oviposition, females with late-stage eggs migrate to the mouth of the estuary or into coastal waters, using STST on nocturnal ebb tides (5); near the time of high tide at night, larvae are released at the entrance of the estuary (6); the females return soon after larval hatching into the estuary using STST on flood tides; steps 4-6 may be repeated several times during a single spawning season.

Mechanisms of cross-shelf transport and subsequent reimmigration have recently been reviewed and modeled for blue crab megalopae in coastal and estuarine areas of the western mid-Atlantic region and the northern Gulf of Mexico (Olmi 1994, Epifanio 1995, van Montfrans et al. 1995, Morgan et al. 1996, Prager 1996, Roman & Boicourt 1999). Comparable studies have been conducted on the dispersal and recruitment of Dungeness and rock crab (*Cancer magister*, *C. irroratus*; Moloney et al. 1994, Clancy & Cobb 1997), the common shore crab (*Carcinus maenas*; Queiroga et al. 1997, Queiroga 1998, Zeng & Naylor 1996a-d, Zeng et al. 1997), penaeid shrimps (Rothlisberg & Church 1994, Rothlisberg et al. 1996), homarid lobsters (Katz et al. 1994), and spiny lobsters (Booth 1997, Phillips & Pearce 1997). In the latter, teleplanic ("long-distance") larvae pass through several months of planktonic life, but their dispersal is apparently limited by large-scale oceanic circulation patterns (Pollock 1993, Polovina et al. 1999). The phenomenon of larval retention in offshore eddies has been described from several regions, reducing the loss of larvae due to irreversible advection (e.g. Chiswell & Roemmich 1998, Perry et al. 1998, Chiswell & Booth 1999, Lee & Williams 1999).

There exists a tremendous amount of data and conceptual models for the complex patterns and mechanisms of larval dispersal and subsequent reimmigration in coastal and estuarine decapods, demonstrating considerable variation among taxa and geographic regions. It must be cautioned, however, that the predictability of larval transport patterns is reduced by small-scale physical effects such as turbulent mixing, which cause patchiness and enhance the variability in larval distribution (Garrison 1999). Besides active migratory responses to several physical factors, numerous passive mechanisms are involved in larval transport. Among these, surface slicks, internal waves, and several other oceanographic processes have been shown to facilitate a directed onshore transport of decapodid stages (Shanks 1995a). This is frequently associated with regional circulation patterns in shelf areas. Off Delaware Bay (USA), for instance, gravitationally driven onshore flows are detectable at least 40 km from the mouths of the large estuaries (Epifanio 1995). In addition, there are wind-driven transport mechanism and interactions with tidal flows (Xie & Eggleston 1999), as well as interfering effects of the shore morphology, which may cause local variation in the subtidal sea level at the coast and consequent subtidal flow into estuaries (Epifanio 1995). When megalopae are recycled within regional gyres, their success of returning to coastal settlement areas depends largely on wind stress and the seasonal timing of the break-off of loop current eddies (Perry et al. 1998).

The return of megalopae from offshore waters into the estuary is facilitated by increased tidal flow at spring tides, while active, apparently directed swimming behavior is stimulated by gradients in physical and chemical cues such as temperature, salinity, and organic compounds of estuarine origin. In contrast to the zoea I larvae, which leave the estuary most efficiently with nocturnal ebb tides, megalopae or equivalent stages utilize preferably spring flood tides for their ingress (e.g. Wenner et al. 1998). As an active behavioral mechanism, some crab species show an oriented swimming of megalopae, using the direction of the sun's bearing as an orientation cue (Shanks 1995b). Furthermore, megalopa larvae show diurnally and tidally controlled vertical migrations aiding in coastal retention or onshore transport.

In tropical estuaries, riding of shrimp and crab megalopae on floating mangrove leaves has repeatedly been observed during inflowing flood tides, indicating another interesting mechanism of reimmigration (Wehrtmann & Dittel 1990, Schwamborn & Bonecker 1996). This behavior resembles the riding of *Cancer magister* megalopae on hydroid medusae (Wickham 1979) or that of phyllosoma larvae on large scyphomedusae (Shojima 1963, Thomas 1963, Herrnkind et al. 1976), suggesting that "hitch-hiking" might be a common means of larval transport. Within estuaries, patches of larvae may be maintained by tidal fronts, and several physical and chemical cues stimulate settlement behavior, metamorphosis, and eventually the recruitment to benthic populations (Epifanio 1987; see below, section 10.5).

10.3.2 *The retention strategy*

In estuarine species showing this life-history pattern, the larvae are not only released but also retained in or close to the parent habitat. As a major precondition for this strategy, physiological adaptations similar to those in the benthic juveniles and adults must have evolved in the planktonic larval stages, so that these can tolerate osmotic, thermal and other estuarine stress. Only a comparably low number of taxa shows this life-cycle strategy, suggesting that its evolutionary attainment is limited by phylogenetic constraints.

In field studies of larval distribution, the question which species follow a retention strategy and which others export their larvae can be solved most easily in relatively small and closed estuarine systems. In species with larval retention, all of the developmental stages occur typically together in the same area of the estuary, without significantly different horizontal distributions in early and late stages (see Cronin 1982, Lambert & Epifanio 1982, Anger et al. 1994, Paula 1998, Chen et al. 1997). As in the export strategy, the distributional patterns of the retention strategy are based upon behavioral responses to numerous physical parameters such as gravity, light, pressure, salinity, and current speed (see section 10.1).

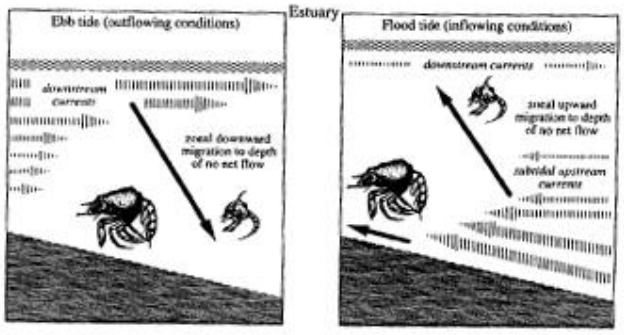


Figure 10.8. Conceptual model of the retention strategy. Larvae are released and retained within the estuary; seaward advection is reduced or inhibited by tidally induced vertical migrations in the water column: downward during ebb tides (avoidance of outflowing surface waters) and upward during flood tides (feeding in the highly productive surface-near zone, preferably at night); the megalopa migrates upstream using near-bottom tidal onshore currents. Eexamples: the mud crab *Rhithropanopeus harrisii*, the grapsid crab *Sesarma reticulatum* (for references see text).

The mechanisms preventing an unvoluntary export from the parent estuary have been investigated in particular detail in the mud crab, *Rhithropanopeus harrisii*, as a model species. These comprise endogenous, tidally entrained rhythms of larval release (see Forward et al. 1982, Forward & Lohmann 1983), behavioral responses of the larvae to ecological key factors, and diurnal and tidal changes in the horizontal or vertical distribution (Cronin 1982, Lambert & Epifanio 1982, Cronin & Forward 1982, 1983, 1986). Based on those data, models of the principal retention mechanisms have been proposed, with particular consideration of passive hydrographical transport processes (Chen et al. 1997, Shen et al. 1999).

Egg hatching rhythms are an especially important component of both the the export and the retention strategy. In the former, a fast downstream transport of freshly hatched larvae with outflowing ebb tides is essential to reduce the exposure to physiological stress and/or predation pressure, whereas the retention strategy implies preferential hatching during incoming flood tides. Nevertheless, also some species that are considered as typical examples of a retention pattern (for instance *Rhithropanopeus harrisii*) may initially show a downstream export of their larvae, although to a lesser extent than the typical exporting species. Adult mud crabs live commonly in oligohaline zones, at salinities below 5‰. Although the larvae of this species are quite euryhaline, the osmotic conditions in the parent habitat are physiologically too stressful to allow for a successful development to metamorphosis (Costlow et al. 1966). As an evolutionary adaptation to this situation, the larval exposure to unfavourably low salinities is minimized by circatidal rhythms of egg hatching. Maximum rates of larval release were observed at high tide, ensuring a limited initial downstream transport of the zoea I (Forward et al. 1982). Later, this partial export is terminated through vertical migrations of the larvae in the water column, which tend to cen-

ter on depths of no net flow, reducing the horizontal transport during the period of planktonic development. This mixed pattern of partial export and subsequent retention is noteworthy, as it shows again that there are transitions between the principal strategies, which thus appear to represent extremes in a continuum rather than strictly dichotomous life-history patterns.

A simple conceptual model of larval retention in estuaries is shown in Figure 10.8. Retained larvae show behavioral patterns of vertical migration that are opposed to those of exported species. In general terms, the vertical position is primarily controlled by tidal cycles and associated factors. During ebb tide, the larvae tend to avoid the outflowing surface layers, staying closer to the bottom where the currents are usually weaker. An ascend follows during flood tide when inflowing currents predominate, transporting the larvae in an upstream direction. These vertical and horizontal migration patterns are in phase with and appear to be reinforced by tidally induced vertical water movements. As a result of this combination of active and passive mechanisms, the zoeae are transported back and forth within the estuary, without leaving it. One might expect that, during the time of development through successive stages, the planktonic larvae should gradually move towards the mouth of the estuary. However, the retention mechanisms in *Rhithropanopeus harrisii* are actually so effective that its larvae are increasingly concentrated in upstream areas (Cronin 1982). Eventually, the megalopa switches to a semibenthic behavior, further enhancing the tendency of upstream transport with inflowing near-bottom currents.

In addition to circatidal egg hatching rhythms, there are also circadian rhythms in larval release of *Rhithropanopeus harrisii* (Forward et al. 1982). Most larvae hatch at night, reducing the immediate mortality by fish predation. However, this mechanism helps the freshly hatched zoeae to survive only during the first few hours of their pelagic life. Later, this problem must be resolved by means of diurnal vertical migrations, resulting in an avoidance of the surface layer during daylight. As an additional, morphological adaptation to intense predation pressure in estuarine environments, the larvae of *R. harrisii* and other species of the retention type have evolved long carapace spines, hindering small planktivorous species and early developmental stages of fish to catch and swallow them (Morgan 1990, 1995a; cf. section 10.1.6; Fig. 10.3).

Palaemonid shrimps are another example of decapod crustaceans that commonly live in estuarine habitats. World-wide, numerous palaemonid species have invaded the upper parts of estuaries, rivers, and various other brackish and freshwater environments. Although most of them follow an export strategy, some species retain their larvae in estuarine zones, and a few have fully adapted to freshwater. It appears that the retention strategy is a transitional step in the life-history adaptation to non-marine conditions, and hence, in the evolutionary conquest of freshwater systems by originally marine decapods.

In fully riverine species, a potentially irreversible advection of pelagic larvae and a low or unreliable plankton production are considered as important selection factors against a planktonic and planktotrophic mode of larval development (for review see Anger 1995a). Thus, limnic conditions have favoured the evolution of abbreviated types of larval development, lecithotrophy, and eventually, direct development (see sections 2.4, 5.1). In palaemonid shrimps of the Amazon basin, for instance, larval development occurs in freshwater, but it is generally abbreviated (or highly "advanced"; Gore 1985). The few remaining larval stages are lecithotrophic and show benthic (or demersal) rather than pelagic behavior (see Magalhães & Medeiros 1998, and earlier papers cited therin). The same type of development was observed also in freshwater shrimps from several other

geographical regions including Australia (Fielder 1970), southeast Asia (Wong 1989), and Mexico (Villalobos & Álvarez 1999, Román et al. 2000, Signoret et al. 2000), which suggests similar selective pressures.

Palaemonetes argentinus is in this context a particularly interesting species. In a population that lives in freshwater rivers and ditches adjacent to a brackish coastal lagoon (Mar Chiquita, Argentina; see Spivak 1997), as well as in an inland population from a freshwater lake, preliminary laboratory experiments (unpubl. data) have shown that the larvae develop successfully under brackish conditions ranging from 1 to 25‰ salinity, in both cases with an apparent optium at about 5-15‰. In seawater (32‰), both populations show complete mortality already in first zoeal stage. In freshwater (<0.5‰), the larvae from Mar Chiquita are able to survive for a few weeks and to develop through several stages, but without reaching the juvenile phase. These observations suggest that a limited export of the early zoeae out of the limnic or oligohaline parent habitat into Mar Chiquita logoon must take place, without reaching the adjacent sea (similarly as in *Rhithropanopeus harrisii*). This is confirmed by field observations (Anger et al. 1994), which show that the larvae of *P. argentinus* are generally retained within the brackish zone (1-25‰). Larvae of the lake population, in contrast to those from Mar Chiquita, can survive and develop to metamorphosis in freshwater, although with an enhanced mortality and delayed development as compared to brackish conditions. In freshwater lakes where no larval export is possible, there may thus be an incipient evolution of a truely limnic clade with freshwater-tolerant larvae, similar as in some palaemonid species from Japan (see Mashiko & Numachi 2000; cf. section 10.1.2). However, also the lake population of *P. argentinus* shows a conspicuous preference for larval development under brackish conditions, which suggests that this shrimp species has only recently invaded freshwater. Thus, a possible process of adaptive radiation is here, on an evolutionary scale, in a very early stage.

10.4 *Development in land-locked habitats*

We should recall here that about 1,000 among the approximately 10,000 known decapod species have conquered freshwater environments, and ca. 100 have adapted to life on firm land (Burggren & McMahon 1988, Hartnoll 1988a). However, many limnic and most of the terrestrial forms have not fully emancipated from the ancestral environment of the Decapoda, the sea. Most of these species follow a typical export strategy, i.e. their recruitment depends on a successful return of late larval or early juvenile stages from adjacent coastal marine regions and thus, on a recurrent conquest of the parental habitat by successive generations. This is in contrast to the alternative strategy evolved by most of the fully limnic decapods, including all crayfishes (Astacidae, Cambaridae, Parastacidae) and the true freshwater crabs (all 11 families of the Potamoidea). These develop within the attached eggs to juveniles, i.e. without passing through pelagic larval stages, remaining in the parental benthic habitat.

In order to better understand, or at least to imagine, the possible course of life-history evolution in, by origin, marine decapod crustaceans that have conquered freshwater or land, it should be interesting to look at transitional developmental patterns rather than only at the extremes of marine planktonic *vs.* direct development. Intermediate life-history patterns occur in several limnic shrimp species that have retained a larval phase in freshwater, although with a tendency towards an abbreviation. Examples of a complete emancipation from the sea in combination with a conserved larval phase have been found also

among the terrestrial and semiterrestrial crabs (Hartnoll 1988a, Anger 1995a). Since this life style excludes a larval development in the adult habitat, i.e. on dry land, these species must have evolved special reproductive and developmental adaptations. As a typical trait, they may release their larvae in particular land-locked "breeding" habitats with small water reservoirs. Unlike estuaries, those aquatic microhabitats are isolated from the sea and often characterized by physically and nutritionally extreme conditions. Since such unusual environments select for non-marine adaptations in the larval stages, the life histories of these species show traits of a retention strategy. On the other hand, the "breeding" habitats are not necessarily identical with those where the adults normally thrive in, and hence, this life-history pattern has also some characteristics in common with an export strategy. Hence, this particular type of life-history does not appear to fit into the classical scheme of export and retention.

10.4.1 *Supratidal rock pools*

Among the Decapoda, the brachyuran crabs show the greatest variability in life style, including freely living and commensal as well as marine, estuarine, freshwater, and terrestrial forms. The crab family Grapsidae (recently proposed to split in several new families comprising the taxon Grapsoidea; see Schubart et al. 2000) is a particularly good example of this biological diversity and adaptability. Being among the most successful invaders of non-marine habitats, the grapsids belong to the typical inhabitants of amphibious environments such as the intertidal fringe of oceans and estuaries, salt marshes, and mangrove swamps (for refences see Anger 1995a). Many species in this taxon tend to follow a retention rather than an export strategy, i.e. to adapt their entire life cycle to stressful or variable physical conditions.

Among the grapsid crabs, the semiterrestrial species *Armases miersii* is an example of extreme adaptability in physiological and life-history traits. This species was morphologically described one century ago (Rathbun 1897), but its life history has remained widely unknown until recently. On the fissured limestone coast of northern Jamaica, the adult crabs live hidden in crevices, between mangrove roots, and in other cryptic habitats near the water edge. They occur also on subtidal rocks, i.e. submerged in oceanic water, as well as in coastal limestone caves with brackish or freshwater. *A. miersii* is active at night, foraging in rock pools that remain largely isolated from the sea, well above the high water mark. This type of habitat is characterized by unpredictable, sometimes extreme short-term and small-scale local variability in salinity, temperature, oxygen concentration, pH, solar radiation, and productivity. These conditions depend primarily on the height above the water level (i.e. the frequency of seawater spray or intrusion), the local position (duration of shadow from mangrove trees or exposure to direct sunlight), and current meteorological conditions (evaporation, rainfall). Variations in temperature and salinity observed in one of these rock pools during a 10-days period are shown as an example in Figure 10.9. Only recently, the ovigerous females of *A. miersii* were observed to release their larvae not into the adjacent sea, as could be expected, but in those supratidal rock pools (Anger & Schultze 1995, Anger 1995b, c, Schuh & Diesel 1995a).

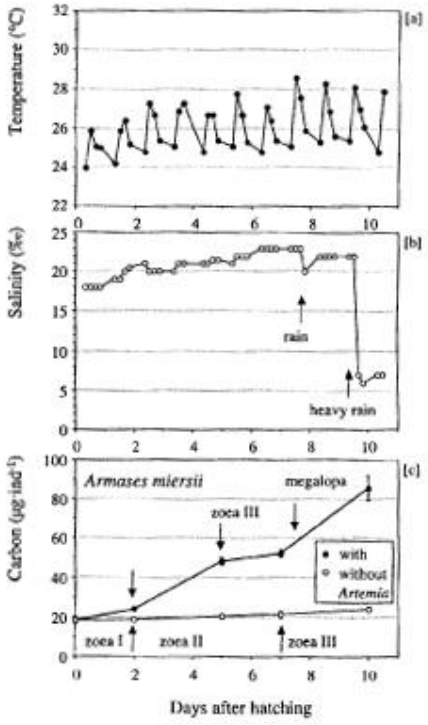


Figure 10.9. Physical conditions and *in-situ* larval development in the land-locked "breeding" habitat of a grapsid crab, *Armases miersii* (supratidal rock pool, Discovery Bay, Jamaica; April 1993); [a] water temperature, [b] salinity, [c] larval development (molts indicated by arrows) and growth (carbon content per individual), with and without experimental addition of *Artemia* spec. nauplii (redrawn after Anger 1995c).

Highly variable and often extreme physico-chemical conditions in this foraging and "breeding" habitat must have selected for physiological adapations in all life-cycle stages of this crab species. Recent investigations have shown that adult *Armases miersii* belong to the most efficient osmoregulators among the decapod crustaceans, being able to maintain an almost constant hemolymph osmolality at salinities ranging from at least 10 to 33‰ (Charmantier et al. 1998, Schubart & Diesel 1998). The regulatory mechanisms develop early in ontogeny: when the zoea I hatches from the egg, it is already a strong hyperregulator, and the adult pattern (hyper-hypo-osmoregulation) is acquired at the megalopa stage (Charmantier et al. 1998; for details, see section 10.1.2). Consequently, the larvae and early juveniles of this species can develop within a wide range of salinities (5-50‰; Anger 1995c, 1996a, Schuh & Diesel 1995b). Moreover, the larvae are tolerant of

low oxygen concentrations (down to 30% saturation) and high temperatures (up to 38°C; Schuh & Diesel 1995a).

The bottom of the rock pools, where adult and juvenile crabs were observed foraging at night, is often overgrown by small, fast-growing filamentous algae and, in deeper parts and crevices, it is covered with a layer of detritus from decaying mangrove leaves, soil particles, dead insects, etc. However, the ephemeral character (i.e. short or variable duration) of such habitats and high variability in physico-chemical conditions preclude a predictable development of plankton communities. In the water column where the pelagic zoeae of *Armases miersii* are normally observed swimming, evenly distributed or concentrated near the surface (Schuh & Diesel 1995a), planktonic organisms that might serve as a potential food source for crab larvae were found only rarely. As an exception, shortly after rainfalls appeared occasionally dense populations of freshwater cladocerans in previously dry rock pools, most probably originating from resting eggs. However, *A. miersii* larvae have not been observed to occur in those recently rain-filled rock pools.

These observations of generally severe planktonic food limitation and extreme nutritional and physical incertainty were confirmed in a study of ten Jamaican nursery rock pools (Schuh & Diesel 1995a). Although the authors drew quite surprising conclusions from their results (claiming *"generally high food availability"* and interpreting lecithotrophy as an adaptation to a variable salinity regime), their own data confirm clearly that the water column lacks in general potentially suitable and accessible food items for planktotrophic crab larvae. Among the potential food organisms observed, cladocerans showed a suitable size, but these were found only occasionally (in one out of ten rock pools studied), and they occurred not in the water column but exclusively in the detritus layer on the bottom, hardly accessible to the planktonic crab larvae. Moreover, cladocerans (presumably limnic species with resting eggs) were observed exclusively at extremely low salinities (ca. 2‰), which excludes a coexistence with developing *A. miersii* zoeae (see Anger 1996a, Schuh & Diesel 1995b). Similarly, most of the other potential prey organisms occurred, if at all, in the benthic detritus layer rather than in the water column (e.g. ostracodes), or they were too small and fast-swimming to be efficiently captured by relatively large and slow zoeae (e.g. benthic harpacticoids; for constraints of functional mouthpart morphology, prey size, and prey behavior, see section 5.2.2).

It is generally accepted that such extremely patchy and, on average, poor nutritional conditions select for the production of fewer and larger offspring, and an enhanced maternal investment in the energy reserves of eggs and larvae (see e.g. Gliwicz & Lampert 1993, Winemiller & Rose 1993, Anger 1995a). Hence, it is not surprising that special reproductive adaptations have evolved in this peculiar nursery habitat (Anger 1995b, c, Schuh & Diesel 1995b). Compared with its closest relatives, *Armases miersii* produces fewer but larger eggs with greater amounts of yolk (i.e. enhanced female energy investment per offspring), and the larvae pass rapidly through only three zoeal stages, whereas all other known *Armases* species have four (abbreviated larval development in terms of both the number of stages and duration of development (cf. Anger 1995a, Zimmermann-Ruf 1997, Cuesta et al. 1999, Cuesta & Anger 2001). Thus, enhanced energy reserves remaining from the egg yolk reduce the dependence on planktonic food, while an abbreviated mode and a fast rate of development reduce the duration of exposure to nutritional and physical stress. By comparison, other crab species which co-occur as adults but do not reproduce in the same habitat lack comparable reproductive adaptations (e.g. *Pachygrapsus* spp., *Grapsus grapsus*, *Cyclograpsus integer*, *Geograpsus lividus*, *Armases ricordi*,

Aratus pisonii). None of these species, which produce large numbers of small eggs, has been observed to release larvae in supratidal rock pools, not even in those with temporarily suitable salinities (Schuh & Diesel 1995a).

Laboratory experiments showed that the degree of nutritional independence in the first two zoeal stages of *Armases miersii* comes close to full lecithotrophy; under conditions of starvation, the larvae were able to develop from hatching to the zoea III stage, exclusively relying on their remaining yolk reserves (Anger 1995b). The zoea III and the megalopa, in contrast, depend increasingly on food. When some prey is available, at least for a short transitory period in one of the preceding instars, also the zoea III and the megalopa attain the capability to develop without further food supply through metamorphosis. With this high endotrophic potential, the larvae of *A. miersii* are well adapted to development in a "breeding" habitat with typically scarce and variable food production.

Recent observations suggest that this far-reaching, yet limited reproductive adaptation to food limitation is complemented by further adaptative traits. Firstly, the megalopa is only during the initial phase of its molting cycle an active swimmer; it shows soon an increasingly benthic behavior. Hence, the terminal larval stage has in its natural habitat access to the detritus layer with its associated microfauna and microflora. Secondly, the zoea III stage and the megalopa show an increasing tendency of cannibalism, especially when earlier zoeae are available as prey (Anger 1995c). This occurs quite frequently in the natural "breeding" habitat, due to multiple and successive release of larvae from different females. During scarcity of other prey, younger larvae may thus be a common food source for older conspecifics, so that intraspecific predation becomes a nutritional buffer, comparable with nurse eggs. A multiple utilization of a single rock pool as a breeding habitat for several females should occur more frequently when the density of the adult population exceeds a critical level. Thus, the intraspecific competition for rock pools and, consequently, larval cannibalism of older on younger stages should be density-dependent processes that may be important in the regulation of *Armases miersii* populations.

As to the evolution of this peculiar life-history pattern, it can be speculated that adult foraging in supratidal rock pools may have played a key role during the initial phase. This semiterrestrial habitat offers a mixture of continually trapped and deposited detritus with an associated microfauna, benthic algae, and larger food items such as leaf fragments, dead insect bodies etc., representing a reliable and concentrated benthic food source that is normally unaccessible to marine species. The exploitation of this niche might thus have evolved in response to predation pressure and/or high competition for food among crabs in the upper intertidal zone.

Larval release within this foraging habitat should have been the next step in the terrestrialization of this omnivorous and highly adaptable species. While the feeding conditions in supratidal rock pools remained suitable for juvenile and adult crabs, the lack of a reliable plankton production selected for larger egg size (implying reduced fecundity), abbreviated and accelerated development, and an enhanced endotrophic potential in the early larval stages. The intermediate developmental mode of facultative lecithotrophy appears to be a finely tuned evolutionary adjustment to conditions of scarce and unreliable but in principle existing food sources. It provides the larvae with sufficient tolerance of nutritional stress, without requiring the maximum female energy investment into offspring production. Full lecithotrophy would require a further enhanced energy investment into reproduction, and it would constrain larval growth (see section 6.3.2), probably without increasing the chance of survival. In a highly unpredictable habitat like supratidal rock

pools, facultative lecithotrophy gives the larvae the maximal nutritional flexibility, allowing for successful development when food is scarce, but also for successful resource exploitation and maximal larval growth when food is transitorily or locally abundant. Facultative lecithotrophy, intraspecific variability in starvation tolerance (Anger 1995b), as well as density- and resource-dependent cannibalism of older on younger larvae (Anger 1995c) represent traits of a bet-hedging strategy (see Philippi Seger 1989; for recent review see Schwartz & Jenkins 2000). I suggest that such highly flexible strategies are crucial in transitional steps of the evolution of non-marine decapod species.

In addition to facultative lecithotrophy, euryhalinity, and eurythermality, the larvae of *Armases miersii* evolved, presumably as another adaptation to the physical conditions in their demanding land-locked "nursery" habitat, also an unusually strong pigmentation. This should protect the larvae against intense solar UV radiation (see section 10.1.3.3). While all these traits undoubtly aid to increase the survival of larvae in supratidal rock pools, they would severely decrease the chances of survival in the adjacent coastal plankton. Most other crab species which live in the same habitat as *A. miersii* but release their larvae into the sea, produce high numbers of small, transparent, and fast-swimming larvae, most probably in response to selective pressure by continuously high abundance of planktivorous fishes (Anger 1995a). It is thus likely that pelagic predation pressure in shallow coastal waters participated in the evolution of this particular reproductive mode. After the appearance of special larval adaptations to the conditions in supratidal rock pools (in particular after attaining large egg size and abbreviated larval development), this selective force should have precluded a return of this species to, or a simulaneous occurrence of, the marine planktotrophic mode of development. Concomitantly persisting selection pressure from physically extreme and nutritionally unpredictable conditions in the "breeding" rock pools should have stabilized the direction of this evolutionary trajectory.

Armases miersii has been used here as an example of transitional life-histories in crabs that reproduce in land-locked habitats, because numerous observations have recently become available for this species. Similar traits have been found in another grapsid crab, *Sesarma curacaoense*, which lives and reproduces in mangrove swamps on Jamaica and other Caribbean islands (Anger 1995d, Anger & Schultze 1995, Schuh & Diesel 1995c). According to preliminary observations, this applies also to another closely related species from coastal mangrove swamps of continental South America, *S. rectum* (see Table 5.1). Within the subfamily Sesarminae (or family Sesarmidae; Schubart et al. 2000), these species are phylogenetically close to the ancestor that gave rise, about four million years ago, to the adaptive radiation of endemic crabs on Jamaica (Schubart et al. 1998). Hence, the reproductive and developmental adaptations found in *A. miersii*, *Sesarma* spp. and, possibly, in other species reproducing in land-locked habitats may serve us here as a model of intermediate stages that may have been passed during the course of an evolutionary process which produced various fully limnic and terrestrial species. Their unusual life histories will be discussed in the following section.

10.4.2 *Adaptive radiation: the Jamaican case*

There are at least two geographical regions world-wide where grapsid crabs have undergone a conspicuous adaptive radiation, one in the Indo-Pacific (Malaysia, Indonesia), the other on the island of Jamaica. In both regions, a number of endemic species live and breed in limnic or terrestrial habitats, entirely emancipated from the ancestral environment, the sea. While little is known about the biology of the endemic southeast Asian

crabs (for taxonomy, adult ecology, and distribution see Sèrene & Soh 1970, Ng 1988, 1992), the Jamaican grapsids have been studied in more detail since a few decades (e.g. Hartnoll 1964, 1971b, 1988a, Abele & Means 1977, Anger & Schuh 1992, Anger 1995a, Schubart et al. 1998, 2000). Their special life-history adaptations may serve us here as an illustrative model of at least one possible, or maybe typical, trajectory in the evolution of non-marine decapods in general.

According to morphological analyses, all endemic Jamaican species of *Sesarma* as well as the genus *Metopaulias* (comprising a single species, *M. depressus*) originate from a common ancestor which was closely related to the extant species *Sesarma curacaoense* (Hartnoll 1964). This is corroborated by similarities in their life-history traits. *S. curacaoense*, *M. depressus*, as well as all endemic *Sesarma* species have, as far as this is known, an abbreviated mode of larval development with only two zoeal stages, while all other West Atlantic *Sesarma* species have three (Rabalais & Gore 1985, Anger et al. 1995).

The monophyly of this group of species is supported by recent evidence from molecular genetics. Since also regional geological events such as the closure of the Panama landbridge and the emergence of Jamaica are well documented and dated, the now available data of genetic distances allowed for calibrating a "molecular clock" (Schubart et al. 1998). This technique suggests that the separation of the endemic Jamaican lineage from a marine ancestor occurred approximately 4.5 million years ago. The speciation process on the island began about 1.1 million years later, continuing throughout the Late Pliocene and Pleistocene epochs. At present, nine endemic Jamaican grapsid crab species are distinguished, eight of which are assigned to the genus *Sesarma*, one to *Metopaulias*. The latter, however, is so closely related with the other species in this group that it should probably better be included in the genus *Sesarma* (Hartnoll 1964, Schubart et al. 1998). The absence of similar adaptive radiations on comparable islands such as Cuba or Hispaniola and in continental South and Central America may be explained by competition or predation by potamid freshwater crabs, which are absent on Jamaica.

Four of the endemic species have been found exclusively in streams (*Sesarma dolphinum*, *S. fossarum*, *S. bidentatum*, one yet undescribed *Sesarma* species), one occurs in both streams and limestone caves (*S. windsor*), one is exclusively cavernicolous (*S. verleyi*), and the others are largely terrestrial *(Metopaulias depressus*, *S. jarvisi*, *S. cookei*). Except for a brief description of larval morphology in *S. bidentatum* (Hartnoll 1964), next to nothing is kown about the life-histories of the limnic *Sesarma* species from Jamaica. It is likely that their larvae develop inside the maternal caves that are dug in river banks, but direct evidence is lacking. In future studies, the application of endoscopic techniques (see Walters et al. 1999) may virtually allow for deeper insights.

Since *Sesarma curacaoense* is considered as the closest relative of the ancestor, from which the adaptive radiation on Jamaica took its origin, we should briefly review the salient traits of its life-history. This semiterrestrial species occurs on several islands in the Caribbean region, living mostly in coastal mangrove swamps with a limited exchange with the adjacent sea. As far as we know, its larvae are retained within the amphibious parental habitat, where ample variations in temperature and salinity occur and plankton production is unpredictable (Schuh & Diesel 1995c). Hence, their typical habitat shows similarities with that of *Armases miersii* and, in consequence, has selected for similar adaptatve traits. This includes large egg size, an abbreviated and rapid larval development, facultative lecithotrophy throughout the zoeal phase, and intraspecific variability in the quantity of yolk reserves (see Anger & Schultze 1995, Anger 1995d). Moreover, the on-

togeny of osmoregulation is similar as in *A. miersii*, with a conspicuous capability of hyperregulation from hatching and the appearance of the adult hyper-hyporegulation pattern in the megalopa (Anger & Charmantier 2000).

These flexible reproductive and developmental traits (consistent with bet-hedging strategies) should have been crucial in the evolution of the endemic Jamaican crab species. As suggested for *Armases miersii*, the invasion of isolated terrestrial and limnic habitats by the ancestral stock implied presumably a continued selection for successively enhanced female energy allocation per offspring (i.e. increasing size of eggs and larvae, increasing lecithotrophy), an early attainment of osmoregulatory capabilities, and dark larval pigmentation as a protection against UV-radiation in the very shallow aquatic habitats of the mangrove zone. Once the larvae showed those non-marine adaptations, predation pressure from planktivorous coastal fish as well as other marine factors selected against an export strategy and thus, must have stabilized this evolutionary trajectory.

In the newly evolved species, the advanced adaptation of all life-cycle stages to non-marine conditions reduced their dispersal capabilities and hence, their spread to other Caribbean islands; as a consequence, they remained endemic on Jamaica. Interestingly, however, the coastal species *Sesarma curacaoense* and *A. miersii* show a wide geographic distribution, although the short duration of their pelagic larval phase as well as other reproductive traits should preclude a dispersal by means of oceanic larval transport. Hence, it is likely that the dispersal of these species depends on an occasional transport of juvenile or adult crabs clinging to floating mangrove branches, drifting algae or other debris, rather than by freely swimming larvae (cf. observations by Wehrtmann & Dittel 1990, Holmquist 1994, Schwamborn & Bonecker 1996). Also in other Caribbean species, including terrestrial forms, has "island-hopping" been a frequent mechanism of dispersal (Donelly 1989).

Among the terrestrial species, the "bromeliad crab", *Metopaulias depressus*, has been studied most intensively. It lives on forest-covered karst hills in the interior of Jamaica, normally associated with large bromeliad plants (*Achmea paniculigera*, occasionally *Hohenbergia* spp.; see Fig. 10.10). Its reproduction takes place during the rainy season (mainly February through April), when the leaf axils of the bromeliads are filled with water. The larvae are released in these small natural "aquaria", where they develop through two nonfeeding zoeal stages and a facultatively lecithotrophic megalopa (Anger & Schuh 1992). Full lecithotrophy in the freely swimming zoeae is clearly an adaptation to practically complete lack of plankton production in the small water reservoirs that are temporarily collected in leaf axils. The megalopa, in contrast, shows exclusively benthic behavior and thus, has access to sessile protozoans and decaying plant and animal debris. In addition, the mother animal has been reported to carry sometimes food items into the brood axils (Diesel 1992). Yet, an extremely high maternal energy investment into offspring production and, consequently, high amounts of yolk persisting throughout larval development suggest that the availability of suitable food sources is generally unreliable in this "nursery" habitat. With its enhanced endotrophic potential, the megalopa can reach metamorphosis in complete absence of food, although with greatly reduced lipid reserves (Anger & Schuh 1992). Severe planktonic food limitation selected for additional bioenergetic adaptations. Compared with most other decapod larvae, the zoeae of *M. depressus* show an economical production (or an enhanced resorption) of cuticle material (Anger & Schuh 1992). The megalopa, in contrast, which depends less on the saving of internal energy re-

serves, as it can rely on some external benthic food sources, shows a higher energetic investment in its exoskeleton.

As another adaptation to their physically harsh habitat, the larvae of *Metopaulias depressus* have evolved a strong tolerance of low pH values (≤6); on the other hand, they became sensitive of slightly basic condidions (pH 8), which are typical of both seawater and the freshwater in karst regions, where the ancestors of this species should have lived successively (Anger & Schuh 1992, Diesel & Schuh 1993). This unusual response pattern reflects the physico-chemical conditions that the larvae typically encounter in rain water with decaying debris and large amounts of tannin and other acidic organic substances. As an additional (behavioral) adaptation to this chemically extreme milieu, the adult females were reported to carry empty snail shells into the leaf axils, presumably mitigating the conditions of low pH (Diesel & Schuh 1993, Diesel 1997).

The evolution of maternal brood care is favoured, in general, in habitats where the early life-cycle stages are particularly endangered and where the competition for limited food resources is high (Wilson 1975, Grant 1983). Since these selective forces prevail also in land-locked habitats where the endemic grapsid crabs on Jamaica reproduce, this trait should be widespread within this group. This presumption is supported by observations on the terrestrial species *Ssesarma jarvisi*, which breeds in empty shells of the snail *Pleurodonte* spp. (Diesel & Horst 1995). The larvae develop in very small amounts (a few drops) of rain water that the females collect and carry into the shell. In occasional rearing experiments, I observed two nonfeeding zoeal stages and a juvenile-like megalopa, which seems to eat decaying plant materials provided by the females. This suggests a similar developmental pattern as in *Metopaulias depressus*.

In summary, the radiation of terrestrial and limnic grapsid crabs on the island of Jamaica, with an abbreviation but not a complete suppression of the larval phase, was possible with the evolution of various special life-history adaptations. These include modifications in both adult and larval behavior (including maternal brood care), an enhanced female energy investment in a reduced number of offspring (enlarged size of eggs and enhanced larval lipid reserves, allowing for various degrees of lecithotrophy), fully benthic megalopae (providing access to non-planktonic food sources), an early expression of osmoregulatory mechanisms (salinity tolerance), and tolerance of unusual and extreme chemical conditions (low pH, low calcium and oxygen concentrations). These traits highlight the great adaptability of decapod crustaceans, in particular of grapsid crabs, explaining the great evolutionary success of this originally marine taxon in brackish, limnic, and terrestrial environments.

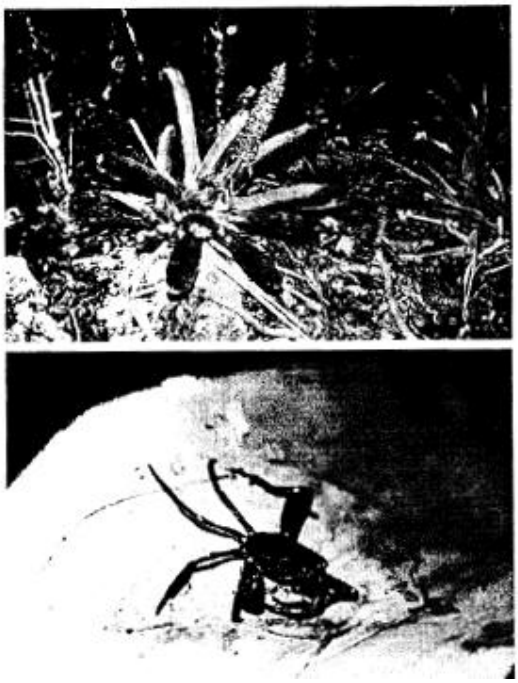


Figure 10.10. The bromeliad crab (*Metopaulias depressus*) in its typical habitat; top: large bottom-living bromeliad plant in a dry forest-covered carst montain (Windsor, Jamaica); bottom: crab on a bromeliad leaf (photos: Anger).

10.5 *Settlement and metamorphosis*

Most of the presumably adaptive traits that we have identified in larval decapods appear to enhance the chance of survival in the plankton. However, there is another highly critical phase at the end of larval development, comprising the processes of settlement and metamorphosis. Only when the transition from the pelagic to the benthic environment has been passed successfully, can larvae contribute to recruitment and maintenance of adult populations.

In most marine invertebrate larvae, the time of metamorphosis depends primarily on the duration of development from hatching to the onset of metamorphic competence, i.e. on the duration of the precompetent phase. This is principally controlled by genetic factors, but strongly influenced also by extrinsic variables such as temperature and food. The final developmental event, metamorphosis, is in many species induced by specific physical or chemical cues associated with the adult habitat. In the absence of such signals, settling larvae may resume swimming and, within certain limits, delay their metamorphosis

to search for a more suitable substratum (e.g. Crisp 1974, 1976; Chia & Rice 1978, Pechenik 1990, 1999; Zimmer-Faust & Tamburri 1994).

A settlement response to habitat-specific cues has been observed especially in competent larvae of sessile animals such as cirripedes, ascidians, or sessile polychaetes (for recent references, see Lau & Qian 2001). After fixation to a substrate, these organisms cannot possibly emigrate from a chosen site and, hence, their postsettlement survival depends crucially on the "right choice" of the time and place of metamorphosis. Although motile animals depend much less on a specific site of settlement, there is a rapidly growing body of evidence for a wide-spread occurrence of environmental cues that influence also their settlement and metamorphosis (McCormick 1999). In the following sections, I show examples of factors affecting the final phase of larval development in decapod crustaceans and discuss possible consequences for later (postsettlement) fitness of the benthic recruits.

10.5.1 *Settlement cues and timing of metamorphosis*

Behavioral and developmental responses to cues from potential sites of settlement have been studied relatively little in decapod crustacean larvae, probably because no such clear effects as in sessile marine invertebrates were expected. Recent investigations, however, have shown that also several species of larval decapods are able to delay their metamorphosis when specific stimuli are absent. For instance, some hermit crab species require a particular type and size of empty snail shell, otherwise they tend to postpone their metamorphosis and show an enhanced mortality (e.g. Harms 1992b, Harvey 1996, Brodie 1999). The megalopae of *Clibanarius longitarsus* appear to represent an extreme case, being able to postpone their metamorphic molt for up to six weeks (Harvey 1992). In a porcellain crab, *Petrolisthes cinctipes*, metamorphosis may be delayed by about three weeks when stimulating cues are absent (in this case, chemical substances released by conspecific adults; Jensen 1991).

Several physical and chemical properties of specific settlement substrates or of a type of environment (e.g. estuaries) have been identified as potential stimuli. In estuarine decapod species such as the blue crab (*Callinectes sapidus*), low or decreasing salinity and several chemical cues associated with water of riverine origin, e.g. humic acids, were found to stimulate metamorphosis (Costlow 1967, Wolcott & de Vries 1994, Forward et al. 1997a, b, Fitzgerald et al. 1998). Also chemical cues from typical estuarine seagrasses, saltmarsh cordgrass and macroalgae had accelerating effects, while structural characteristics of several other substrates (clean oyster shells, plastic rods or ribbons, glass rods) had no such influence (Brumbaugh & McConaugha 1995, Forward et al. 1996). In other species, however, the structure of the substrate may be an important cue (Kenyon et al. 1999).

In experiments with megalopae of mud crabs (*Panopeus herbstii*; Dittel et al. 1996, Weber & Epifanio 1996), fiddler crabs (*Uca pugilator*, *U. pugnax*; Christy 1989, O'Connor & Judge 1997), salt marsh crabs (*Chasmagnathus granulata*; Gebauer et al. 1998), and mangrove crabs (*Sesarma curacaoense*; Walter 1993; Gebauer et al., submitted), metamorphosis occurred earlier in the presence of the type of sediment that was typical of the adult habitat. When megalopae of a fiddler crab species, *Illyoplax pusilla*, were experimentally kept without the preferred substrate (sandy mud), the rate of mortality increased and many of the resulting juvenile crabs showed malformations (Lim 1997).

In an anomuran sand crab, *Emerita talpoida*, the settling stage is apparently not the megalopa but the last zoeal stage (Harvey 1993). When sandy substrates were lacking, it lengthened its molting cycle and showed reduced survival. Similar observations were

made in sand-dwelling thalassinid shrimps (*Callichirus* spp.; Strasser & Felder 1998, 1999a, b). This suggests that, particularly in species living burried in sand of the shallow beach zone, the late zoeal phase might generally be more involved in the settlement process than has been expected.

Cues from the type of substrate that is preferred by adult conspecifics should, in general, indicate favourable conditions for juvenile and adult life. In some cases, the decisive feature of the settlement substratum appears to be its suitability as a shelter from benthic or demersal predation, including cannibalism among newly recruited juveniles (Eggleston & Armstrong 1995, Hunt & Scheibling 1997). The first juvenile or "postlarva" (stage IV) of clawed lobsters (*Homarus* spp.), for instance, settles preferentially in dark crevices, especially on macroalgal-covered rocks (Botero & Atema 1982, Johns & Mann 1987, Boudreau et al. 1993a, Wahle & Incze 1997); unsuitable substrates cause a delay in settlement and molting to instar V (Cobb 1968). Thereafter, burrows are used as a refuge from benthic predators (Lavalli & Barshaw 1986, Barshaw & Lavalli 1988). Another lobster species, *Nephrops norvegicus*, settles preferentially on soft sediments, where it soon begins to dig in (Cobb & Wahle 1994).

Similarly as in the settling stage of the clawed lobsters, the puerulus of spiny lobsters (e.g. *Panulirus argus*) settles preferentially at sites that are covered by macroalgae; these early juvenile habitats are in later juvenile instars exchanged for rock crevices (Butler et al. 1997). Also in the blue crab (*Callinectes sapidus*), the megalopa and the earliest juvenile stages prefer benthic macroalgae as an effective shelter; only later stages were found on vegetation free sediments where the adults live (Pile et al. 1996). In the absence of refuges, the megalopae and early juveniles of this species were observed to suffer heavy mortality due to predation by caridean shrimps, older conspecifics, and other benthic predators (Olmi & Lipcius 1991, Moksnes et al. 1997). Likewise, the megalopae of a mud crab (*Panopeus herbstii*) were readily eaten by juvenile blue crabs, killifish, and grass shrimp when shelter was lacking, while they showed lower mortality after settlement in structurally complex habitats (Dittel et al. 1996). In the shore crab (*Carcinus maenas*), maximum settlement was observed on filamentous algae and in crevices of mussel clumps, where predation pressure was mitigated (Gottschalk 1994, Thiel & Dernedde 1994, Moksnes et al. 1998). A protective effect of vegetation against fish predators was shown also in "postlarval" penaeid prawns (*Penaeus esculentus*; Kenyon et al. 1995).

Predator avoidance is thus one of the principle aspects of substrate selection. This was shown also in field studies of substrate-specific recruitment and survival patterns in Dungeness crab (*Cancer magister*; Eggleston & Armstrong 1995, Banks & Dinnel 2000) and in a thalassinid shrimp (*Neotrypaea californiensis*; Feldman et al. 1997). Further evidence of predation as a key factor at settlement was provided in laboratory studies, where stage IV lobsters (*Homarus americanus*) responded with a delay of settlement to the presence of odors from predatory demersal fish (Boudreau et al. 1993a, b).

While a negative response to the presence of predators is plausible as an evolutionary adaptation to predation pressure, also the opposite effect is conceivable. In a recent review, Pechenik (1999) argued that the metamorphic response to particular chemical cues has the disadvantage that predators could adapt to this bevaviour and mimic such cues, so that competent larvae could be attracted as a potential prey. Some spiders, for example, can mimick sex pheromones of their insect prey (Stowe et al. 1987). Although comparable interactions with predators have not been found in decapod larvae or other marine inver-

tebrates, similar examples of predator-prey coevolution might be discovered in future research.

As another important cue, chemical substances released by conspecific adult odors (pheromones) may stimulate metamorphosis (Jensen 1991, O'Connor 1991, Harvey 1996, O'Connor & Judge 1997, O'Connor & Gregg 1998, Fitzgerald et al. 1998, Gebauer et al. 1998, Strasser & Felder 1998). In general, this mechanism should occur in species that prefer to settle near conspecific adults (gregarious settlement). Similar as in other, less specific odors originating from the adult habitat (e.g. from sediments or macroalgae), these signals indicate favourable conditions for growth and maturation. On the other hand, density-dependent cannibalism should select against this mechanism (Eggleston & Armstrong 1995, Hunt & Scheibling 1997, Moksnes et al. 1998), and thus, gregarious settlement should not be expected to occur in highly aggressive and cannibalistic species such as the crab *Chasmagnathus granulata*. In this species, however, metamorphosis is stimulated by contact with muddy sediments similar to those in the adult habitat, and this effect is further enhanced when it co-occurs with waterborne cues from adult conspecifics (Gebauer et al. 1998). This response pattern reflects the ecology of this crab, which lives in dense aggregations in intertidal salt marshes with fine sediments (Spivak et al. 1994). The coexistence of early and late life-history stages, in spite of strong cannibalistic tendencies in this species, may be explained by fine-scale spatial segregation. Large juveniles and adult crabs live in deep burrows dug in muddy sediments, while the megalopae and early juveniles occur in shallow, usually wet depressions on the surface of the same habitat, usually near the adult burrows (Luppi 1999, Luppi et al., submitted). This segregation into ontogenetically changing microhabitats may reduce the chance of encounter and thus, the significance of intraspecific predation of adults and medium-sized juveniles on recruits. Intra-cohort cannibalism among recruits remains as a potential cause of mortality, but recent experimental observations suggest that this is insignificant (Luppi 1999, Luppi et al., in press).

The chemical nature of pheromones and other metamorphosis-stimulating cues has been studied for a long time in barnacles, molluscs, polychetes, decapods, and several other marine invertebrate taxa (Crisp 1974, 1976, Burke 1986, Rittschof & Buenaventura 1986, Rittschof 1993, Boettcher & Tagett 1998). Only recently could, for the first time, the molecular structure of a water-borne invertebrate pheromone be elucidated in great detail. "Attractin", a cue involved in the reproduction of a marine gastropod, was chemically identified as a polypeptide with N-linked glycosylation, containing 21 % carbohydrates (Painter et al. 1998). Also recently, HPLC analyses revealed that the larvae of a sessile polychete species responded in the laboratory to dissolved free amino acids which had been identified in crude samples of conspecific colonies (Harder & Qian 1999). In barnacles, the neurotransmitters serotonin and dopamin, as well as certain peptides were shown to participate in the regulation of cyprid settlement (Yamamoto et al. 1999, Browne & Zimmer 2001). In decapods, to my knowledge only some substances involved in the chemical communication between the females and embryos at hatching were roughly characterized (see Rittschof 1992, Saigusa & Iwasaki 1999), while very little is known about pheromones that may stimulate settlement and metamorphosis.

In a recent study with larvae of the mangrove crab *Sesarma curacaoense* (Gebauer et al., submitted), the duration of megalopa development was compared between experimental treatments, in which the water was previously conditioned either with adult conspecific (*S. curacaoense*), congeneric (*S. rectum*), or other related crabs belonging to the

same family (Grapsidae) but to different genera (*Armases miersii*, *Chasmagnathus granulata*). Metamorphosis to the first juvenile crab occurred fastest in the megalopae that were exposed to conspecific adult-conditioned water, while it was delayed in the other treatments, increasing in an order from *S. curacaoense* to *S. rectum*, *A. miersii*, *C. granulata*, and untreated control water. This pattern of decreasing response to metamorphosis-stimulating adult odors is congruent with an increasing phylogenetic distance between these species (for phylogenetic relationships among the American grapsids, see Schubart et al. 2000). Thus, our observations suggest that chemically similar attracting factors (pheromones) are produced by closely related species, so that the chemical structure and the effectiveness of these cues may reflect the phylogenetical relationships within a clade.

The capability of delaying metamorphosis in crustacean larvae is remarkable, as it implies a modulation of the molting cycle. In laboratory experiments with several decapod species, the response to stimulating substrates was studied during differential periods within the molting cycle of the megalopa (Harms 1992b, Walter 1993, Wolcott & de Vries 1994). In general, the megalopa responded to the cue already during the postmolt or intermolt stages, i.e. when it was still in the precompetent phase, showing an acceleration of the molting cycle. In most other marine invertebrate larvae, habitat-specific stimuli can be perceived only when the larvae have become competent and can react with an immediate initiation of metamorphosis (Pechenik 1990). Similarly as in previously described effects of nutrition and other extrinsic factors (e.g. temperature, salinity), molt-stage D_0 might be a critical point also in the response of decapod larvae to metamorphosis-stimulating cues (see Wolcott & de Vries 1994).

10.5.2 *Delayed metamorphosis and postmetamorphic fitness*

In benthic species with particular habitat requirements, a flexibility in the timing of larval metamorphosis has primarily been considered as an advantageous selective trait, because it enhances the probability of locating a favourable settlement site (Thorson 1950, Crisp 1974, Obrebski 1979). However, these potential benefits might be reduced or outweighed, when a delay of metamorphosis has also negative consequences for the postmetamorphic fitness, for example a reduction of juvenile survival or growth, or a delay in the onset of sexual maturity (Pechenik 1990, 1999).

Effects of delayed metamorphosis have been experimentally studied in several marine invertebrate species, although very little in decapod crustaceans. Not surprisingly, negative consequences were observed in species with lecitotrophic larvae, for instance in bryozoans, where a delay of larval metamorphosis implies a continued degradation of energy reserves and thus, causes retarded postsettlement development (Woollacott et al. 1989, Wendt 1996). Reduced survival and growth were observed also in juvenile polychaetes (Pechenik & Cerulli 1991) and barnacles (Pechenik et al. 1993). In species with feeding larvae, in contrast, a prolonged premetamorphic period does not necessarily affect the survival and growth of juveniles, because the settling stage may continue to take up food. This is corroborated by studies of metamorphosis in several marine vertebrate and invertebrate species with planktivorous larvae (Victor 1986, Pechenik & Eyster 1989, Miller & Hadfield 1990, Cowen 1991). In a spionid polychaete, however, a reduction of juvenile growth after delayed metamorphosis indicated that postmetamorphic effects may occur also in species with planktivorous larvae (Qian et al. 1990).

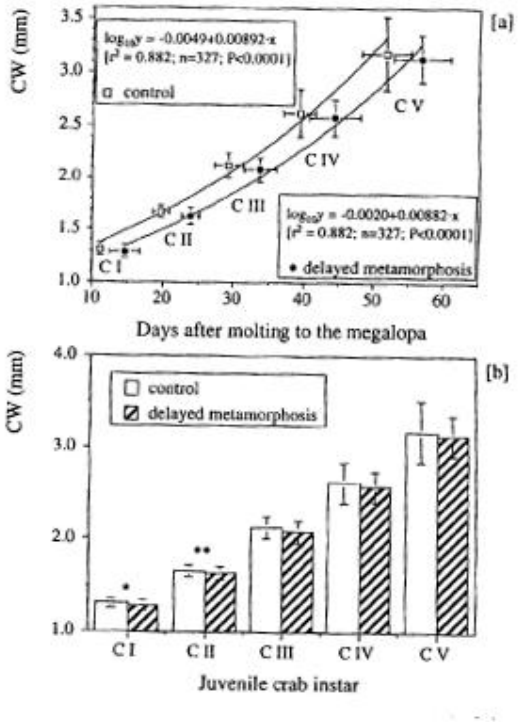


Figure 10.11. Late effects of delayed metamorphosis, due to the absence of stimulating chemical cues during the megalopa stage, on juvenile growth in a grapsid crab, *Chasmagnathus granulata*; [a] carapace width (*CW*) in relation to the time of development after reaching the megalopa stage; [b] *CW* in successive juvenile crab instars; asteriscs: statistically significant differences in mean *CW* of crab instars I and II (*= $P<0.05$; **= $P<0.01$) (redrawn after Gebauer et al. 1999).

Among the decapod crustaceans, a reduction of early juvenile growth was observed in a hermit crab species (*Clibanarius longitarsus*) reared in the absence of suitable snail shells (Harvey 1992). More recently, the costs of delayed metamorphosis were investigated in the crab *Chasmagnathus granulata* (Gebauer et al. 1999). In the absence of metamorphosis-stimulating signals, mortality and molt-cycle duration were significantly enhanced not only in the megalopa, but also in the first juvenile instar. In addition, the body size of early juvenile crabs was reduced after delayed metamorphosis, indicating that a prolongation of the larval phase represents a condition of physiological stress. Although the reduction of body size was only small, it was statistically significant in the first two instars, and it persisted consistently through the subsequent crab stages (Fig. 10.11).

Reduced postmetamorphic body size shows that the megalopa lost during the additional time of development significant amounts of energy, although it is a feeding stage. As a possible explanation, we must consider that the rates of both food uptake and growth decrease in most decapod larvae during the premolt phase of the molting cycle, even under constant and optimal conditions of food availability; these intrinsic patterns are presumably controlled by endocrine factors (see section 6.3.1). As a consequence, competent megalopae may fully "concentrate" on searching a suitable habitat rather than food. In extreme cases, for instance in some hermit crabs and spiny lobsters, the settling stage (megalopa, puerulus) is secondarily lecithotrophic, i.e. entirely nonfeeding. A prolonged premetamorphic period with a reduced or ceasing feeding activity implies an increasing utilization of internally stored reserves and, in consequence, will reduce the postmetamorphic body size. Insofar, delayed metamorphosis may represent a condition of nutritional stress in decapod crustacean larvae.

In later juvenile instars of *Chasmagnathus granulata*, crabs with delayed metamorphosis were not able to catch up in development and growth with unstressed siblings, molting consistently later and with a slightly smaller body size. Laboratory observations have shown that juvenile *C. granulata* are highly cannibalistic, especially during ecdysis, and this behavior increases during growth through later instars (Luppi 1999, Luppi et al., in press). As an indirect consequence of delayed metamorphosis, delayed crabs are thus particularly vulnerable to intraspecific predation by earlier molted (i.e. already hardened) and larger-sized conspecifics (cf. Eggleston & Armstrong 1995, Hunt & Scheibling 1997, Moksnes et al. 1998). In addition, smaller juveniles are probably weaker competitors for food and refuges, which should further reduce their chances of survival and growth in the natural habitat (Hines 1986). Cannibalism among the "young-of-the-year", especially of already settled juveniles on later settling megalopae, has recently been suggested as an important factor regulating recruitment in natural populations of commercially exploited Dungeness crab, *Cancer magister* (Fernández 1999). Also in more general terms, settling larvae and newly metamorphosed juveniles are at a particularly great risk during substrate exploration and immediately thereafter (Hines 1986, Morgan 1995a, Hunt & Scheibling 1997), so that weakened individuals should be especially vulnerable to benthic predation. Thus, there are negative consequences of delayed metamorphosis which should select against it and, in consequence, constrain the limits of flexibility in the timing of metamorphosis.

11 CONCLUDING REMARKS

In the concluding chapter of this volume, I will summarize open questions and prominent advances in our knowledge about the larval biology of the Decapoda. Traditional, extensively studied aspects and recent discoveries in this wide, multidisciplinary field of life science will be contrasted with what I consider as major remaining gaps that deserve, or are likely, to become subjects of increasing efforts in future investigations.

11.1 *Morphology*

Within larval biology, the morphological study of developmental forms and pathways is the oldest line of research; it still continues to contribute significantly to our knowledge. Innumerable papers and several books have been published over the past two centuries, and new larval descriptions are added continually. Since improved cultivation techniques have become available in laboratories all over the world, we are now increasingly accumulating morphological descriptions of the larvae of rare and "exotic" species from all climatic regions. This includes the tropical seas, where high species diversity has always been in contrast to relatively few data on larval biology; this gap has considerably decreased in recent years. Although larval descriptions are now available for numerous species, especially from temperate regions of North America and Europe, we still need more studies of this kind, because many of the older papers lack details or do not comply with modern standards (Rice 1979, Clark et al. 1998). Standardization of larval descriptions becomes thus increasingly important, also in order to allow for including larval characters in taxonomic analyses of speciation, biogeography, and phylogenetic relationships (see e.g. Pohle & Marques 2000).

As a remaining gap and as a challenge for future experimental researchers, the early postembryonic development of deep sea species is still little known. This is mainly due to logistic and technical difficulties in the experimental study of species that are adapted to enormous hydrostatic pressures. Recent success in rearing crab larvae from hydrothermal vent fields (Epifanio et al. 1999), however, shows that this problem may not generally be as great as we believed. This should encourage larval biologists who have access to such materials to try further experimental studies. We may expect to discover interesting new adaptive features in larval morphology, ecology and physiology of deep sea species.

In the traditional research on larval morphology, developmental pathways and stage numbers have mostly been treated as constant, species-specific traits, although also developmental variability has frequently been reported, in particular for shrimps, prawns, and spiny lobsters. This had often been interpeted as an artifact of laboratory cultivation; meanwhile, however, we know that variability in the larval development of decapod crustaceans is much more widespread than previously acknowledged, both in the field and in the laboratory (see section 2.5). Arthur (2000) stessed the evolutionary significance of intraspecific variability in developmental characters *"both within and between geographic populations"*, saying that *"this area is crucial, as all evolutionary novelties ultimately arise from intraspecific variation."* Naturally, this applies not only to morphological but also to physiological traits. They all underly selective pressures, and thus, are highly important in considerations of speciation and other evolutionary mechanisms.

Besides genetic variability among larvae originating from different females or populations, also environmental effects have been identified, indicating phenotypic plasticity. Hence, available larval descriptions must often be treated with caution, as in most cases we do not know the degree of intraspecific variability. In future research, it will thus be necessary to pay more attention to this potential source of error or premature generalization, especially in caridean and penaeoid shrimp species, where the number and morphology of larval stages may vary greatly within a single species. Once we know more about morphogenetic effects of environmental factors such as temperature, salinity, and nutrition, larval morphology might become another tool, in addition to physiological and biochemical indices, for the evaluation of larval condition in the field.

Variable and transitional patterns occur not only in developmental pathways of individual taxa but also among modes of larval development, e.g. in the continuum between lecithotrophy and planktotrophy (see section 5.1). The occurrence of various degrees of facultative lecithotrophy (e.g. in some grapsid crab species), nonfeeding early larval stages (many palaemonid shrimps), and secondary lecithotrophy in late stages (some hermit crabs and spiny lobsters) shows that developmental patterns may be more complex and less constant than often believed. Also morphological transitions between zoeal and decapodid, or those between decapodid and juvenile stages, appear to be common in some taxa (especially in caridean shrimps), causing problems of definition of important terms such as "metamorphosis". Such transitions are significant not only for our terminology, but also for considerations of life-history evolution and phylogenetic relationships.

11.2 *Anatomy, morphogenesis, molting cycle*

The anatomy of decapod larvae shows simpler features but is otherwise, in general, similar to that of the juvenile and adult life-history stages. An ontogenetically late appearance in advanced stages, or a gradual increase in complexity, is typical of all those traits which are not strictly necessary during the early planktonic phase of the life cycle, at least not with full functionality. This is obvious in the development of the reproductive system, but it applies to some extent also to gills, musculature and connective tissues, the circulatory system, parts of the digestive tract, and some cuticular and other integumentary structures. For various anatomical features such as the excretory organs, the organ of Bellonci, the mandibular organ, and the hemocytes, future studies should further elucidate the ontogeny of their structures, functions, and significance for larval life.

The appearance of new tissues and organs is often associated either with the morphogenesis of new appendages (e.g. new muscles and nerves in newly appearing pereiopods and pleopods), or with changes in the function of already existing appendages (e.g. tissue reorganization in natatory cephalic or thoracopodal appendages that are becoming mouthparts), with new patterns of behavior (e.g. development of walking legs, concomitant with the semibenthic life style of the megalopa), or with the availability of new food sources (e.g. access to hard benthic food items, appearance of chelae and the gastric mill in megalopae or juveniles). In all those developmental processes, neurogenesis and the expression of genes coding for ontogenetically new features are becoming increasingly important subjects in the anatomical research on larvae (see Harzsch et al. 1998, 1999b; Chan et al. 1998).

Among the organ systems that, in most Decapoda, develop gradually or become functional only in late larval or early juvenile stages, gills and associated structures should be

among the prime subjects of future research. These anatomical features bear ion-transporting tissues and cells, and thus, are of utmost importance for the appearance of osmoregulatory functions. The study of their ontogeny is crucial for the understanding of life-history adaptations to non-marine (brackish, freshwater, and terrestrial) environments, especially in estuarine, semiterrestrial, and terrestrial species (Morris 2001). Significant advances should be possible through the application of histology, electron microscopy, and immunolocalization of key enzymes such as Na^+-K^+-ATPase (see Bouaricha et al. 1994, Lignot et al. 1999, McNamara & Torres 1999).

In spite of their comparably low anatomical complexity, larval decapods show numerous special adaptations to the pelagic environment. This is most conspicuously in their locomotory and sensory organs, which differ significantly from the corresponding features of benthic juveniles and adults. Other specific larval traits can be found in the feeding appendages and in the digestive tract. Small protozoeal stages of penaeoid shrimps, for instance, are largely confined to small algal food, which has generally a low protein content. Unlike in most other decapod larvae, exclusively or predominantly herbivorous feeding is, in this case, energetically efficient. This is partly due to special features in the functional morphology of the protozoeal mouthparts which allow filter-feeding. In addition, the protozoeae possess anterior midgut caeca, where proteolytic (mostly trypsin-like) digestive enzymes are produced. Together, these special morphological, anatomical and physiological features compensate for an incomplete development of the hepatopancreas, scarcity of dietary proteins, and short gut evacuation time (Jones 1997a, b). Similarly, in euryhaline larvae an initially poor development of the gills may be compensated by other osmoregulatory tissues, which are predominantly located in the branchiostegites (Charmantier et al. 1998).

Another example of special adaptations to the planktonic life style can be seen in the construction of the compound eyes of early larval stages. At hatching, decapod larvae have in general apposition eyes (see section 3.3.5, Fig. 3.9). At least in shrimp and anomuran larvae, these eyes appear to have a particularly high resolution in the dorsal and posterior parts. These are facing upwards in the normal swimming position, allowing to scan the water column above. The anterior and ventral parts, in contrast, have a lower resolution but an enhanced sensitivity (in some species using superposition optics), which allows planktonic larvae to perceive weaker light signals from the water column below. These features are believed to aid in larval depth control and in the avoidance of pelagic predators (see Fincham 1988, Gaten & Herring 1995).

The functions of several other presumable larval sensory organs, for instance those of Laverack's "sensory dorsal organ", and even the existence of detectors for salinity, pressure, and gravity have remained subjects of speculation. Further comparative studies of anatomical and neuronal adaptations in relation to larval behavior (feeding, vertical migrations, escape reactions) would thus be worth-while.

Anatomical and, more conspicuously, morphogenetic changes are closely associated with the occurrence of successive molting cycles. Although this phenomenon has only little been studied in larval crustaceans, we may assume that both the sequence of integumentary changes and its hormonal control are similar as in juveniles and adults. The available evidence suggests that an antagonistic balance of neuropeptides from the eye stalk system, ecdysteroids from the Y-organ and, very likely, juvenoid substances from the mandibular organs are present at hatching, controlling the molting cycle and associated developmental processes throughout the larval phase. This generalization, however,

requires further experimental scrutiny, in particular as to the role of juvenile-hormone like compounds in larval development and metamorphosis, and possibly, also in osmoregulation (for recent evidence in adult crabs, see Lovett et al. 2001). Gene probes and other molecular biological techniques should soon play an important role in their investigation (see e.g. Chan et al. 1998).

In addition to descriptive analyses of the larval molting cycle and its hormonal control, the interference with other aspects of larval biology requires further investigation. This is particularly important for molt-cycle related and environmentally induced variations in behavior or in the rates of feeding, growth, metabolism, and energy partitioning. Studies of interrelationships between those aspects will greatly enhance our understanding of critical points within the molting cycle, and they may allow to construct more realistic stage-based rather than time-based models of developmental changes in bioenergetic and other physiological parameters of larval life.

11.3 *Bioenergetics*

Nutrition, growth, chemical composition, and metabolism belong to the most extensively studied aspects of larval biology. However, they were mostly studied as isolated parameters rather than in the context of overall energy partitioning. Information on changes in larval energy budgets is scarce, especially as to the efficiencies of conversion, assimilation and growth in response to environmental variables. This is in contrast to a great amount of available data on juvenile and adult bioenergetics, in particular for species with a high economic value for fisheries or aquaculture. In "postlarval" penaeoid shrimps, for instance, numerous experimental studies of the uptake and partitioning of energy have greatly increased our basic understanding of growth and reproduction in relation to diet and several other factors (see e.g. recent papers by Rosas, Palacios, and their respective collaborators). Hence, one of the principal gaps in the available data on larval bioenergetics is the lack of integrated studies of interrelationships among the major budget parameters; this applies in particular to effects of interacting environmental factors such as temperature, salinity or food, on bioenergetic efficiencies. Since such relationships may vary greatly among taxa, comparative studies are in this context particularly important, including those on species with little or no economic interest.

As another major gap, very little is known about molt-cycle related and other developmental changes in single bioenergetic parameters, and even less on intrinsic changes in bioenergetic efficiencies. The variation of these parameters within a single molting cycle may be greater than the differences between the average levels in successive stages or even among different species. Hence, more attention should be paid to short-term ontogenetic changes which are overlaying – and occasionally overriding – the effects of environmental factors such as temperature, salinity, pollution stress, etc.

Furthermore, bioenergetic data obtained in the laboratory have hardly been compared with those measured under field conditions. The species- and stage-specific natural food spectrum, needs for micronutrients, shifts in selectivity, and possible ontogenetic changes in the conversion of different food sources are little known, even from laboratory studies. Especially the nutritional significance of detrital aggregates ("marine snow"), the capture of large prey items, and possibly ectoparasitic behavior of phyllosoma larvae "riding" on medusae or fish fry should be interesting questions in future research on the natural larval feeding habits. As another little known phenomenon, comparative studies of larval growth

and biochemical composition suggest that "domestication effects" may occur in laboratory cultures (see Harms et al. 1994, Palacios et al. 2000). Potential differences between wild-caught and artificially reared larvae should thus be studied in more detail and considered when extrapolations of laboratory data to field conditions are attempted.

The bioenergetics, feeding, and behavior of deep sea species represent further open, and hence, promising subjects for future research. There are indications of lecithotrophic development and of unusual patterns of lipid composition in the larvae of hydrothermal vent shrimps (e.g. storage of wax esters instead of triacylglycerides; Pond et al. 1997). These traits were tentatively interpreted as adaptations to the combination of food-limited conditions, enhanced hydrostatic pressure, and low temperatures prevailing in this environment. In vent crabs (*Bythograea thermydron*), on the other hand, a significant increase in body size from hatching to the megalopa stage (Van Dover et al. 1984, 1985) and tolerance of low hydrostatic pressure (Epifanio et al. 1999) indicate that larval development takes place in the water column, probably through an extended sequence of feeding stages and implying the utilization of photosynthetically produced energy. The same appears to apply to the vent shrimp *Mirocaris fortunata* (Tylor & Dixon 2000). The application of stable isotope techniques and analyses of stomach contents and gut pigments (see Schwamborn et al. 1999, Schwamborn & Criales 2000, Dittel et al. 2000, Vereshchaka et al. 2000, Chong et al. 2001, Perissinotto et al. 2001), as well as feeding experiments may show whether deep sea larvae depend, directly or indirectly, on the consumption of phytoplankton produced near the ocean surface, or rather on chemoautotrophic microorganisms associated with hydrothermal vents.

Among the most poorly studied aspects of larval nutrition, we still know little about the extent and the mechanisms of digestive enzyme regulation in relation to rates of ingestion, assimilation, and gut evacuation. Also, the potential role of endosymbiontic microorganis in the larval digestive tract remains unknown. Newly developed immunological and other molecular techniques (see Bilodeau et al. 1999, MaKinster et al. 1999, Makridis et al. 2000; for discussion of methodological limitations and failures see Mayfield et al. 2000) will facilitate the identification of prey items in larval stomachs or that of decapod larvae in the guts of higher predators, and they may show the presence of symbiontic bacteria in the gut or hepatopancreas tubules of larval decapods. As in deep sea species, the trophic role of decapod larvae and other meroplankton within pelagic communities, in general, may further be clarified using stable isotope techniques.

As to larval growth, more comparative biochemical studies of the accumulation or loss of energy reserves are needed. Such investigations will show stage- and species-specific variation of nutritional vulnerability (or flexibility), and they will aid to quantitative estimates of the physiological condition of larvae both in cultures and in the natural plankton. Potential condition indices can be derived from elemental (C:N) or lipid class composition (e.g. neutral lipids in relation to polar or total lipids), from concentrations and proportions of adenylate nucleotides (ATP, energy charge), nucleic acids (RNA:DNA ratio), or from measurements of the electron-transport system activity (*ETSA*) in relation to oxygen consumption ("respiratory efficiency"). Metabolic quotients such as the O:N ratio and the Q_{10} provide information on metabolic substrates or temperature dependence of metabolic processes, respectively. So far, most of these indices have been applied to holoplanktonic and benthic organisms, but hardly to meroplankton. Their experimental evaluation in larval decapods represents thus another open and promising field for future ecophysiological investigations.

As in morphology, larval growth and biochemistry vary intraspecifically. Besides genetic variability within and among hatches, there are maternal effects associated with the previous feeding history, age, size, or reproductive condition of the female, or with environmental conditions prevailing during vitellogenesis (see Cahu et al. 1995, Palacios et al. 1998, 1999). Also the environmental conditions experienced during embryogenesis are known to cause late effects on larval condition, for instance acclimatization to a particular level of temperature or salinity (Kinne 1970, 1971). Recent observations have shown that the initial larval size and biomass at hatching and, in consequence, later chances of development through metamorphosis are significantly influenced by the salinity conditions prevailing during the preceding egg development (Giménez 2000, Giménez & Anger 2001). Since such effects persist through successive developmental phases, they are potentially confounding with other intrinsic or extrinsic effects, and thus, should be considered as an important aspect of larval physiology.

11.4 *Ecology and behavior*

Besides in larval morphology and taxonomy, most progress has been achieved in the research on larval ecology and behavior. This is reflected in several recent review papers, book chapters, and in an increasing number of predictive models of larval hatching, dispersal, settlement, and recruitment (for recent references, see Epifanio & Garvine 2001). Most of this information deals with estuarine and coastal species, while less is known about the larval ecology of fully marine, freshwater, and deep-sea species. While we may recently notice an increasing interest in freshwater decapods (see papers by Moreira & Odinetz Collart 1993, Fièvet 1998, March et al. 1998, Benstead et al. 1999), the study of deep sea species has remained logistically and technically difficult (Epifanio et al. 1999). New insights in larval ecology and behavior, including fine-scale transport, may be expected from an inceasing application of molecular techniques such as PCR amplification of highly repetitive DNA sequences (see Bilodeau et al. 1999), or methods of chemical fingerprinting (trace element composition; see DiBacco & Levin 2000).

An enormous number of publications deals with effects of single or combined physical and chemical key variables such as temperature, salinity, light, or toxic pollutants. Less, however, is known about the role of biotic factors, e.g. predation, food limitation, larval disease, and chemical communication, including the perception of and the response to pheromones and kairomones. Advances have recently been made in studies of behavioral, morphological, and chemical responses to pelagic predation (see Morgan & Christy 1997, and earlier papers cited therein), as well as in pheromone research (see Rittschof 1992, Hallberg et al. 1997, Rittschof et al. 1998, Fitzgerald et al. 1998, Strasser & Felder 1999). Kairomones, on the other hand, have been studied almost exclusively in non-decapod freshwater zooplankton. Only recently could experimental evidence be shown for a behavioral response of larval decapods to chemical factors associated with predators (Forward & Rittschof 2000). Hence, the significance of kairomones for larval behavior and, in consequence, for dispersal and recruitment patterns remain rewarding new fields of research. This includes the study of coevolution in predator-prey and parasite-host systems, for instance the possible mimicking of attracting pheromones by predators or parasites, or that of reppelling kairomones by potential prey species.

As in the case of regional intraspecific variability of reproductive traits, seasonal variability has only little been studied in larval traits. In species living in temperate regions

with strong seasonal variation in physical factors and productivity, the reproductive season may be extended with bet-hedging strategies. In the brown shrimp, *Crangon crangon*, for instance, seasonal variation in egg size and larval provisioning with energy reserves has been observed, allowing the species to reproduce successfully not only in summer, but also in late winter and early spring (see section 10.2.3); recent observations suggest that a similar phenomenon may occur also in the crab *Chasmagnathus granulata* (Spivak, pers. comm.). Further studies of this phenomenon should thus be scientifically interesting and, in exploited species, relevant for considerations of population dynamics and fisheries management.

Through several decades and in numerous species, estuarine life-cycle adaptations have extensively been studied and described in much detail, including the behavioral patterns aiding to larval retention or export, respectively, ontogenetic patterns of osmoregulation, and special morphological traits that may reduce mortality by estuarine predation. On the other hand, traits of larval development in land-locked limnic habitats are far less known. This applies also to the reproduction of species which "breed" in small ephemeral water bodies such as supratidal rock pools (e.g. *Armases miersii*), in mangrove swamps (*Sesarma curacaoense*, *S. rectum*), or in bremeliad leaf axils temporarily filled with rain water (*Metopaulias depressus*). The conditions in such unusual non-marine habitats are known to be highly variable and physically extreme, selecting for special adaptations in the earliest freely living life-history stages, for instance an early appearance of osmoregulatory functions, lecithotrophy, or abbreviated development. Since such adaptations should have appeared also during the early evolutionary steps towards the invasion of freshwater and land, their comparative study will increase our understanding of the evolution of limnic and terrestrial species, in general. As rewarding new subjects for such life-cycle studies, there are little known endemic grapsid crab species in Southeast Asia, other sesarminid crabs in the Central American and Caribbean regions, and palaemonid shrimps in the Amazon and Orinoco basins or in Central America (see sections 10.3.2, 10.4). Studies of their larval biology may provide significant contributions to phylogeny, biogeography, and evolutionary theory.

As another remaining frontier for studies in larval biology, there are "historical" effects of previous conditions persisting through two or more phases of the life cycle. For instance, maternal nutrition and reproductive condition have been shown to affect the "quality" (i.e. the physiological condition) of embryos and larvae (Palacios et al. 1998, 1999; Cavalli et al. 1999), and the physico-chemical conditions prevailing during the period of egg development may either cause effects of cumulative physiological stress, or contrarily, may lead to acclimatization and thus, to an enhanced stress tolerance of the larvae (see Kinne 1964a, 1967, 1970, 1971). Likewise, larval condition may subsequently exert an influence on the chances of benthic juvenile survival, growth, and maturation (e.g. Lim 1997, Gebauer et al. 1999, Pechenik 1990, 1999). Future research should thus strive for an increasingly holistic approach of integrated life-cycle studies, considering that larval biology addreses only one out of several successive but interacting phases within a complex life history.

REFERENCES

Abdu, U., Takac, P., Laufer, H. & Sagi, A. 1998a. Effect of methyl farnesoate on late larval development and metamorphosis in the prawn *Macrobrachium rosenbergii* (Decapoda, Palaemonidae): a juvenoid-like effect? *Biol. Bull.* 195: 112-119.

Abdu, U., Takac, P., Yehezkel, G., Chayoth, R. & Sagi, A. 1998b. Administration of methyl farnesoate through the *Artemia* vector, and its effect on *Macrobrachium rosenbergii* larvae. *Isr. J. Aquacult-Bamid.* 50: 73-81.

Abele, L.G. 1991. Comparison of morphological and molecular phylogeny of the Decapoda. *Mem. Queensland Mus.* 31: 101-108.

Abele, L.G. 1992. A rewiev of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus. *Smithsonian Contr. Zool.* 527: 1-60.

Abele, L.G. & Means, D.B. 1977. *Sesarma jarvisi* and *Sesarma cookei:* montane, terrestrial grapsid crabs in Jamaica (Decapoda). *Crustaceana* 32: 91-93.

Abraham, T.J., Palaniappan, R. & Dhevendaran, K. 1997. Epibiotic infestation of luminous bacteria in penaeid shrimp *Penaeus indicus* (H. Milne-Edwards) larvae. *Ind. J. Mar. Sci.* 26: 209-212.

Abreu-Grobois, F.A., Flores-Campaña, L.M., Briseño-Dueñas, R. & Herrera-Vega, M.A. 1991. Growth and gross growth efficiencies of *Penaeus stylirostris* fed controlled rations of *Artemia* nauplii. In: Lavens, P., Sorgeloos, P., Jaspers, E. & Ollevier, F. (eds), *Larvi '91. Symposium on Fish and Crustacean Larviculture*, *Gent, Belgium, August 27-30,1991*. Gent: European Aquaculture Soc.

Abrunhosa, F.A. & Kittaka, J. 1997a. Functional morphology of mouthparts and foregut of the last zoea, glaucothoe and first juvenile of the king crabs *Paralithodes camtschaticus*, *P. brevipes* and *P. platypus*. *Fisheries Sci.* 63: 923-930.

Abrunhosa, F.A. & Kittaka, J. 1997b. Morphological changes in the midgut, midgut gland and hindgut during the larval and postlarval development of the red king crab *Paralithodes camtschaticus*. *Fisheries Sci.* 63 (5): 746-754.

Abrunhosa, F.A. & Kittaka, J. 1997c. Effect of starvation on the first larvae of *Homarus americanus* (Decapoda, Nephropidae) and phyllosomas of *Jasus verreauxi* and *J. edwardsii* (Decapoda, Palinuridae). *Bull. Mar. Sci.* 61: 73-80.

Abubakr, M.A. & Jones, D.A. 1992. Functional morphology and ultrastructure of the anterior midgut diverticulae of larvae of *Penaeus monodon* Fabricius, 1798 (Decapoda, Natantia). *Crustaceana* 62: 142-158.

Ache, B.W. 1982. Chemoreception and thermoreception. In: Atwood, H.L. & Sandeman, D.C. (eds), *The Biology of Crustacea 3*; *Neurobiology: Structure and Function*: 369-398. New York: Academic Press.

Agard, J.B.R. 1999. A four-dimensional response surface analysis of the ontogeny of physiological adaptation to salinity and temperature in larvae of the palaemonid shrimp *Macrobrachium rosenbergii* (de Man). *J. Exp. Mar. Biol. Ecol.* 236: 209-233.

Aguilar, M., Díaz, F. & Bückle, L.F. 1998. The effect of salinity on oxygen consumption and osmoregulation of *Macrobrachium tenellum*. *Mar. Freshw. Behav. Phy.* 31 (2): 105-113.

Ahl, J.S.B., Laufer, H., Ahl, A.J. & Takac, P. 1996. Exoskeletal abrasion as an indicator of reproductive readiness in the spider crab *Libinia emarginata*. *J. Crust. Biol.* 16: 443-447.

Aiken, D.E. 1969. Photoperiod, endocrinology and the crustacean molt cycle. *Science* 164: 149-155.

Aiken, D.E. 1973. Proecdysis, setal development and molt prediction in the American lobster, *Homarus americanus*. *Fish. Res. Bd. Can.* 30: 1337-1344.

Aiken, D.E., Martin, D.J., Meisner, J.D. & Sochasky, J.B. 1981. Influence of photoperiod on survival and growth of larval American lobsters (*Homarus americanus*). *J. World Maricul. Soc.* 12: 225-230.

Aiken, D.E. & Waddy, S.L. 1976. Controlling growth and reproduction in the American lobster. *Proc. Meet. Wld. Maricult. Soc.* 7: 415-429.

Aiken, D.E. & Waddy, S.L. 1995. Aquaculture. In: Factor, J.R. (ed), *Biology of the Lobster Homarus americanus*: 153-175. San Diego, CA: Academic Press.

Al-Mohanna, S.Y. & Nott, J.A. 1989. Functional cytology of the hepatopancreas of *Penaeus semisulcatus* (Crustacea: Decapoda) during the moult cycle. *Mar. Biol.* 101: 535-544.

Al-Mohanna, S.Y., Nott, J.A. & Lane, D.J.W. 1985. M-"midget" cells in the hepatopancreas of the shrimp *Penaeus semisulcatus* de Haan 1844 (Decapoda: Natantia). *Crustaceana* 48: 260-268.

Alabi, A.O., Jones, D.A. & Latchford, J.W. 1999. The efficacy of immersion as opposed to oral vaccination of *Penaeus indicus* larvae against *Vibrio harveyi*. *Aquaculture* 178: 1-11.

Alabi, A.O., Latchford, J.W. & Jones, D.A. 2000. Demonstration of residual antibacterial activity in plasma of vaccinated *Penaeus vannamei*. *Aquaculture* 187 (1-2): 15-34.

Alcaraz, M. 1997. Copepods under turbulence: grazing, behavior and metabolic rates. *Scient. Mar.* 61 (Suppl.): 177-195.

Alderdice, D.F. 1972. Factor combinations: responses of marine poikilotherms to environmental factors acting in concert. In: Kinne, O. (ed), *Marine Ecology 1 (3); Environmental Factors*: 1659-1722. Chichester: Wiley.

Alderdice, D.F. 1976. Some concepts and descriptions of physiological tolerance: rate-temperature curves of response surfaces. *J. Fish. Res. Bd. Can.* 33: 299-307.

Alford, R.A. & Jackson, G.D. 1993. Do cephalopods and larvae of other taxa grow asymptotically? *Am. Nat.* 141: 717-728.

Amend, M. & Shanks, A. 1999. Timing of larval release in the mole crab *Emerita talpoida*. *Mar. Ecol. Prog. Ser* 183: 295-300.

Anderson, D.T. (ed) 1973. *Embryology and phylogeny in Annelids and Arthropods.* Oxford: Pergamon.

Anger, K. 1983a. Moult cycle and morphogenesis in *Hyas araneus* larvae (Decapoda, Majidae), reared in the laboratory. *Helgoländer Meeresunters.* 36: 285-302.

Anger, K. 1983b. Temperature and the larval development of *Hyas araneus* L. (Decapoda: Majidae); extrapolation of laboratory data to field conditions. *J. Exp. Mar. Biol. Ecol.* 69: 203-215.

Anger, K. 1984a. Influence of starvation on moult cycle and morphogenesis of *Hyas araneus* larvae (Decapoda, Majidae). *Helgoländer Meeresunters.* 38: 21-33.

Anger, K. 1984b. Gain and loss of particulate organic and inorganic matter in larval and juvenile spider crabs (*Hyas araneus*) during growth and exuviation. *Helgoländer Meeresunters.* 38: 107-122.

Anger, K. 1985. Influence of salinity on larval development of the spider crab, *Hyas araneus*, reared in the laboratory. In: Gray, J.S. & Christiansen, M.E. (eds), *Marine biology of polar regions and effects of stress on marine organisms*: 463-474. Chichester: Wiley.

Anger, K. 1986. Changes of respiration and biomass of spider crab (*Hyas araneus*) larvae during starvation. *Mar. Biol.* 90: 261-269.

Anger, K. 1987a. The D_o threshold: a critical point in the larval development of decapod crustaceans. *J. Exp. Mar. Biol. Ecol.* 108: 15-30.

Anger, K. 1987b. Energetics of spider crab *Hyas araneus* megalopa in relation to temperature and the moult cycle. *Mar. Ecol. Prog. Ser.* 36: 115-122.

Anger, K. 1989. Growth and exuvial loss during larval and early juvenile development of the hermit crab *Pagurus bernhardus*, reared in the laboratory. *Mar. Biol.* 103: 503-511.

Anger, K. 1990. Modelling developmental changes in the carbon and nitrogen budgets of larval brachyuran crabs. *Helgoländer Meeresunters.* 44: 53-80.

Anger, K. 1991a. Developmental changes in the bioenergetics of decapod larvae. *Mem. Queensl. Mus.* 31: 289-308.

Anger, K. 1991b. Effects of temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda: Grapsidae). *Mar. Ecol. Prog. Ser.* 72: 103-110.

Anger, K. 1992. Decapoda: Ablauf und Nahrungsabhängigkeit des Häutungszyklus im ersten Larvenstadium. In: Emschermann, P., Hoffrichter, O., Körner, H. & Zissler, D. (eds), *Meeresbiologische Exkursion. Beobachtung und Experiment*: 127-131. Stuttgart: G. Fischer.

Anger, K. 1995a. The conquest of freshwater and land by marine crabs: adaptations in life-history patterns and larval bioenergetics. *J. Exp. Mar. Biol. Ecol.* 193: 119-145.

Anger, K. 1995b. Dev. Biol. of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. 1. Facultative lecithotrophy of larval stages. *Mar. Ecol. Prog. Ser.* 117: 75-81.

Anger, K. 1995c. Dev. Biol. of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. 2. Food limitation in the nursery habitat and larval cannibalism. *Mar. Ecol. Prog. Ser.* 117: 83-89.

Anger, K. 1995d. Starvation resistance in larvae of a semiterrestrial crab, *Sesarma curacaoense* (Decapoda: Grapsidae). *J. Exp. Mar. Biol. Ecol.* 187: 161-174.

Anger, K. 1996a. Salinity tolerance of the larvae and first juveniles of a semiterrestrial grapsid crab, *Armases miersii* (Rathbun). *J. Exp. Mar. Biol. Ecol.* 202: 205-223.

Anger, K. 1996b. Physiological and biochemical changes during lecithotrophic larval development and early juvenile growth in the northern stone crab, *Lithodes maja* (Decapoda: Anomura). *Mar. Biol.* 126: 283-296.

Anger, K. 1998. Patterns of growth and chemical composition in decapod crustacean larvae. *Inv. Reprod. Develop.* 33: 159-176.

Anger, K. & Charmantier, G. 2000. Ontogeny of osmoregulation and salinity tolerance in a mangrove crab, *Sesarma curacaoense* (Decapoda: Grapsidae). *J. Exp. Mar. Biol. Ecol.* 251 (2): 265-274.

Anger, K. & Dawirs, R.R. 1981. Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae). *Helgoländer Wiss. Meeresunters.* 34: 287-311.

Anger, K. & Dawirs, R.R. 1982. Elemental composition (C, N, H) and energy in growing and starving larvae of *Hyas araneus* (Decapoda, Majidae). *Fish. Bull.* 80: 419-433.

Anger, K., Dawirs, R.R., Anger, V. & Costlow, J.D. 1981a. Effects of early starvation periods on zoeal development of brachyuran crabs. *Biol. Bull.* 161: 199-212.

Anger, K., Dawirs, R.R., Anger, V., Goy, J.W. & Costlow, J.D. 1981b. Starvation resistence in first stage zoeae of brachyuran crabs in relation to temperature. *J. Crust. Biol.* 1: 518-525.

Anger, K. & Dietrich, A. 1984. Feeding rates and gross growth efficiencies in *Hyas araneus* L. larvae (Decapoda: Majidae). *J. Exp. Mar. Biol. Ecol.* 77: 169-181.

Anger, K. & Harms, J. 1989. Changes in the energy budget of a decapod crustacean from the North Sea during planktonic larval development. In: Brandini, F.P. (ed), *Memórias do III Encontro Brasileiro de Plâncton Caiobá, (PR) 5-9 de dezembro de 1988*. Curitiba, Paraná, Brazil: Universiade Federal do Paraná.

Anger, K. & Harms, J. 1990. Elemental (CHN) and proximate biochemical composition of decapod crustacean larvae. *Comp. Biochem. Physiol.* 97B: 69-80.

Anger, K., Harms, J., Christiansen, M.E., Suesens, U. & Wilmes, B. 1992. Growth patterns, chemical composition and oxygen consumption in early juvenile *Hyas araneus* (Decapoda: Majidae) reared in the laboratory. *Helgoländer Meeresunters.* 46: 9-28.

Anger, K., Harms, J., Montú, M. & Bakker, C. 1989b. Growth and respiration during the larval development of a tropical spider crab, *Libinia ferreirae* (Decapoda: Majidae). *Mar. Ecol. Prog. Ser.* 54: 43-50.

Anger, K., Harms, J., Montú, M. & Bakker, C.d. 1990c. Effects of salinity on the larval development of a semiterrestrial tropical crab, *Sesarma angustipes* (Decapoda: Grapsidae). *Mar. Ecol. Prog. Ser.* 62: 89-94.

Anger, K., Harms, J., Püschel, C. & Seeger, B. 1989a. Physiological and biochemical changes during the larval development of a brachyuran crab reared under constant conditions in the laboratory. *Helgoländer Meeresunters.* 43: 225-244.

Anger, K. & Hirche, H.J. 1990. Nucleic acids and growth of larval and early juvenile spider crab, *Hyas araneus*. *Mar. Biol.* 105: 403-411.

Anger, K. & Ismael, D. 1997. Growth and elemental composition (C, N, H) in larvae and early juveniles of a South American salt marsh crab, *Chasmagnathus granulata* (Decapoda: Grapsidae). *Mangroves and Salt Marshes* 1: 219-227.

Anger, K. & Jacobi, C.C. 1985. Respiration and growth of *Hyas araneus* L. larvae (Decapoda: Majidae) from hatching to metamorphosis. *J. Exp. Mar. Biol. Ecol.* 88: 257-270.

Anger, K., Laasch, N., Püschel, C. & Schorn, F. 1983. Changes in biomass and chemical composition of spider crab (*Hyas araneus*) larvae reared in the laboratory. *Mar. Ecol. Prog. Ser.* 12: 91-101.

Anger, K., Montú, M. & Bakker, C.d. 1990b. Energy partitioning during larval development of the hermit crab *Pagurus bernhardus* reared in the laboratory. *J. Exp. Mar. Biol. Ecol.* 141: 119-129.

Anger, K., Montu, M., Bakker, C.d. & Loureiro Fernandes, L.L. 1990a. Larval development of *Uca thayeri* Rathbun, 1900 (Decapoda: Ocypodidae) reared in the laboratory. *Meeresforschung* 32: 276-294.

Anger, K. & Moreira, G.S. 1998. Morphometric and reproductive traits of tropical Caridean shrimps. *J. Crust. Biol.* 18: 823-838.

Anger, K. & Nair, K.K.C. 1979. Laboratory experiments on the larval development of *Hyas araneus* (Decapoda, Majidae). *Helgoländer Wiss. Meeresunters.* 32: 36-54.

Anger, K. & Püschel, C. 1986. Growth and exuviation of Norway lobster (*Nephrops norvegicus)* larvae reared in the laboratory. *Ophelia* 25: 157-167.

Anger, K., Riesebeck, K. & Püschel, C. 2000. Effects of salinity on larval and early juvenile growth of an extremely euryhaline crab species, *Armases miersii* (Decapoda: Grapsidae). *Hydrobiologia* 426 (1): 159-166.

Anger, K., Schreiber, D. & Montú, M. 1995. Abbreviated larval development of *Sesarma curacaoense* (Rathbun, 1897) (Decapoda: Grapsidae) reared in the laboratory. *Nauplius, Rio Grande (Brazil)* 3: 127-154.

Anger, K. & Schuh, M. 1992. Bioenergetics of abbreviated larval development in the bromelid crab, *Metopaulias depressus* (Decapoda: Grapsidae). *Comp. Biochem. Physiol.* 103A: 507-518.

Anger, K. & Schultze, K. 1995. Elemental composition (CHN), growth, and exuvial loss in the larval stages of two semiterrestrial crabs, *Sesarma curacaoense* and *Armases miersii* (Decapoda: Grapsidae). *Comp. Biochem. Physiol.* 111A: 615-623.

Anger, K. & Spindler, K.-D. 1987. Energetics, moult cycle, and ecdysteroid titers in spider crab (*Hyas araneus*) larvae starved after the D_o threshold. *Mar. Biol.* 94: 367-375.

Anger, K., Spivak, E., Bas, C., Ismael, D. & Luppi, T. 1994. Hatching rhythms and dispersion of decapod crustacean larvae in a brackish coastal lagoon in Argentina. *Helgoländer Meeresunters.* 48: 445-466.

Anger, K., Spivak, E. & Luppi, T. 1998. Effects of reduced salinities on development and bioenergetics of early larval shore crab, *Carcinus maenas*. *J. Exp. Mar. Biol. Ecol.* 220: 287-304.

Anger, K., Storch, V., Anger, V. & Capuzzo, J.M. 1985. Effects of starvation on moult cycle and hepatopancreas of stage I lobster (*Homarus americanus*) larvae. *Helgoländer Meeresunters.* 39: 107-116.

Aoto, T., Kamiguchi, Y. & Hisano, S. 1974. Histological and ultrastructural studies on the Y organ and the mandubular organ of the freshwater prawn, *Palaemon paucidens,* with special reference to their relation with the molting cycle. *J. Fac. Sci. Hokkaido Univ. (Ser. Zool.)* 19: 295-308.

Armstrong, D.A., Buchanan, D.V. & Caldwell, R.S. 1976. A mycosis caused by *Lagenidium sp* in laboratory-reared larvae of the Dungeness crab, *Cancer magister,* and possible chemical treatments. *J. Invert. Pathol.* 28: 329-336.

Armstrong, D.A., Chippendale, D., Knight, A.W. & Colt, J.E. 1978. Interaction of ionized ammonia on short-term survival and growth of prawn larvae, *Macrobrachium rosenbergii*. *Biol. Bull.* 154: 15-31.

Arthur, W. 2000. Intraspecific variation in developmental characters: the origin of evolutionary novelties. *Amer. Zool.* 40 (5): 811–818.

Arts, M.T., Ackman, R.G. & Holub, B.J. 2001. "Essential fatty acids" in aquatic ecosystems: a crucial link between diet and human health and evolution. *Can. J. Fish. Aquat. Sci.* 58: 122-137.

Arun, S. & Subramanian, P. 1998. Antioxidant enzymes in freshwater prawn *Macrobrachium malcolmsonii* during embryonic and larval development. *Comp. Biochem. Phys. A.* 121B(3): 273-277.

Atema, J. 1974. Effects of cruide oil on the feeding behaviour of the lobster *Homarus americanus*. *Enviro. Pollut.* 6: 77-86.

Atema, J., Fay, R.R., Popper, A.N. & Tavolga, W.N. (eds) 1988. *Sensory Biology of Aquatic Animals.* New York: Springer.

Atkinson, D.E. 1968. The energy charge of the adenylate pools as a regulatory parameter with feedback modifiers. *Biochemistry* 7: 4030-4034.

Atkinson, D.E. & Walton, G.M. 1967. Adenosine trisphosphate conservation in metabolic regulation. *J. Biol. Chem.* 242: 3239-3241.

Avault, J.W. & Huner, J.V. 1985. Crawfish culture in the United States. In: Huner, J.V. & Brown, E.E. (eds), *Crustacean and mollusk aquaculture in the United States*: 1-61. Westport, Connecticut: AVI Publishing Company.

Ax, P. 1987. *The phylogenetic system. The systematization of organisms on the basis of their phylogenies.* Chichester: Wiley.

Baba, K. & Williams, A.B. 1998. New Galatheoidea (Crustacea, Decapoda, Anomura) from hydrothermal systems in the West Pacific Ocean: Bismarck Archipelago and Okinawa Trough. *Zoosystema* 20: 143-156.

Båmstedt, U. 1980. ETS activity as an estimator of repiratory rate of zooplankton populations. The significance of variatons in environmental factors. *J. Exp. Mar. Biol. Ecol.* 42: 267-283.

Båmstedt, U. & Skjoldal, H.R. 1980. RNA concentration of zooplankton: relationship with size and growth. *Limnol. Oceanogr.* 25: 304-316.

Banks, J. & Dinnel, P. 2000. Settlement behavior of dungeness crab (*Cancer magister* Dana, 1852) megalopae in the presence of the shore crab, *Hemigrapsus* (Decapoda, Brachyura). *Crustaceana* 73 (2): 223-234.

Bardolph, M. & Stavn, R.H. 1978. Polarized light sensitivity in the stage 1 zoea of the mud crab *Panopeus herbstii*. *Mar. Biol.* 46: 327-333.

Barker, P.L. & Gibson, R. 1977. Observations on the feeding mechanism, structure of the gut, and digestive physiology of the European lobster *Homarus gammarus* (L.) (Decapoda: Nephropidae). *J. Exp. Mar. Biol. Ecol.* 26: 297-324.

Barrientos, Y. & Laverack, M.S. 1986. The larval crustacean dorsal organ and its relationship to the trilobite median tubercle. *Lethaia* 19: 309-313.

Barshaw, D.E. & Lavalli, K.L. 1988. Predation upon postlarval lobsters *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crabs *Neopanope sayi* on three different substrates: eelgrass, mud and rocks. *Mar. Ecol. Prog. Ser.* 48: 119-123.

Batham, E.J. 1967. The first three larval stages and feeding behaviour of Phyllosoma of the New Zealand palinurid crayfish *Jasus edwardsii* (Hutton 1875). *Trans. Roy. Soc. N.Z., Zool.* 9: 53-64.

Beers, J.R. 1966. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. *Limnol. Oceanogr.* 11: 520-528.

Belchier, M., Edsman, L., Sheehy, M.R.J. & Shelton, P.M.J. 1998. Estimating age and growth in long-lived temperate freshwater crayfish using lipofuscin. *Freshwater Biol.* 39 (3): 439-446.

Belehradek, J. (ed) 1935. *Temperature and living matter.* Protoplasma Monographien 8. Berlin: Borntraeger.

Belehradek, J. 1957. Physiological aspects of heat and cold. *Ann. Rev. Physiol.* 19: 59-82.

Bell, T.A. & Lightner, D.V. (eds) 1988. *A handbook of normal penaeid shrimp histology.* Baton Rouge, LA: World Aquaculture Society.

Bellon-Humbert, C. & Chaigneau, J. 1982. Caractères ultrastructur-aux de l'organe de Bellonci de la crevette *Palaemon serratus* Pennant. Influence de l'ablation de l'organe X de la medulla externa. *Ann. Sci. Natur. Zool. Paris* 4: 63-76.

Bellon-Humbert, C., Thijssen, M.J.P. & Van Herp, F. 1978. Development, location and relocation of sensory and neurosecretory sites in the eyestalks during the larval and postlarval life of *Palaemon serratus* (Pennant). *J. Mar. Biol. Ass. U.K.* 58: 851-868.

Bellonci, G. 1881. Sistema nervoso e organi dei sensi dello *Sphaeroma serratum*. *Atti Accad. Real. Lincei, Roma* 3: 91-104.

Belman, B.W. & Childress, J.J. 1973. Oxygen consumption of the larvae of the lobster *Panulirus interruptus* (Randall) and the crab *Cancer productus* (Randall). *Comp. Biochem. Physiol.* 44 A: 821-828.

Beltz, B.S., Helluy, S.M., Ruchhoeft, M.L. & Gammill, L.S. 1992. Aspects of the embryology and neural development of the American lobster. *J. Exp. Zool.* 261: 288-297.

Benstead, J.P., March, J.G., Pringle, C.M. & Scatena, F.N. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. *Ecol. Appl.*9 (2): 656-668.

Bentley, E. & Sulkin, S.D. 1977. The ontogeny of barokinesis during the zoeal development of the Xanthid crab *Rhithropanopeus harrisii* (Gould). *Mar. Behav. Physiol.* 4: 275-282.

Bergeron, J.-P. & Boulhic, M. 1994. Rapport ARN/ADN et évaluation de l'état nutritionnel et de la croissance des larves de poissons marins: un essai de mise au point expérimentale chez la sole (*Solea solea* L.). *ICES J. Mar. Sci.* 51: 181-190.

Bergeron, J.-P., Person-Le Ruyet, J. & Koutsikopoulos, C. 1997. Use of carbon rather than dry weight to assess the DNA content and nutritional condition index of sole larvae. *ICES J. Mar. Sci.* 54: 148-151.

Bernard, F. 1953. Decapoda Eryonidae. *Dana Reports* 37: 1-93.

Bertalanffy, L.v. 1957. Quantitative laws in metabolism and growth. *Q. Rev. Biol.* 32: 217-231.

Bertram, D.F. & Strathmann, R.R. 1998. Effects of maternal and larval nutrition on growth and form of planktotrophic larvae. *Ecology* 79: 315-327.

Bianchini, A. & Gilles, R. 2000. Is the digestive tract an important access route for mercury in the Chinese crab *Eriocheir sinensis* (Crustacea, Decapoda)? *B. Environ. Contam. Tox.* 64: 412-417.

Biddanda, B.A. 1986. Structure and function of marine microbial aggregates. Oceanlogica Acta. 9: 209-211.

Bidigare, R.R. 1983. Nitrogen excretion by marine zooplankton. In: Carpenter, E.J. & Capone, D.G. (eds), *Nitrogen in the Marine Environment*: 385-409. New York: Academic Press.

Biesiot, P. & McDowell Capuzzo, J. 1990. Digestive protease, lipase and amylase activities in stage I larvae of the American lobster, *Homarus americanus*. *Comp. Biochem. Physiol.* 95A: 47-54.

Biesiot, P.M. & McDowell, J.E. 1995. Midgut-gland development during early life-history stages of the American lobster *Homarus americanus*. *J. Crust. Biol.* 15: 679-685.

Bigford, T.E. 1978. Effect of several diets on survival, development time, and growth of laboratory-reared spider crab, *Libinia emarginata,* larvae. *Fish. Bull. U.S.* 76: 59-64.

Bigford, T.E. 1979a. Ontogeny of light and gravity responses in rock crab larvae (*Cancer irroratus*). *Mar. Biol.* 52: 69-76.

Bigford, T.E. 1979b. Synopsis of biological data on the rock crab *Cancer irroratus* Say. *NOAA Techn. Rep., NMFS Circular* 426: 26 pp.

Bilodeau, A.L., Lankford, W.S., Kim, T.J., Felder, D.L. & Neigel, J.E. 1999. An ultrasensitive method for detection of single crab larvae (*Sesarma reticulatum*) by PCR amplification of a highly repetitive DNA sequence. *Mol. Ecol.*8: 683-684.

Bingham, B.L. & Walters, L.J. 1989. Solitary ascidians as predators of invertebrate larvae: evidence from gut analyses and plankton samples. *J. Exp. Mar. Biol. Ecol.* 131: 147-159.

Birkenbeil, H. 1990. Die ultrastrukturellen Grundlagen der Ecdysonbildung in den Häutungsdrüsen von Crustaceen und Insekten. *Zool. Jb. Physiol.* 94: 409-444.

Blaxter, J.H.S. & Hempel, G. 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). *J. Cons. Perm. Int. Explor. Mer.* 28: 211-240.

Bochdansky, A.B. & Leggett, W.C. 2001. Winberg revisited: convergence of routine metabolism in larval and juvenile fish. *Can. J. Fish. Aquat. Sci.* 58: 220-230.

Boddeke, R. 1982. The occurrence of winter and summer eggs in the brown shrimp (*Crangon crangon*) and the pattern of recruitment. *Neth. J. Sea Res.* 16: 151-162.

Boettcher, A.A. & Targett, N.M. 1998. Role of chemical inducers in larval metamorphosis of queen conch, *Strombus gigas* Linnaeus: relationship to other marine invertebrate systems. *Biol. Bull.* 194: 132-142.

Boidron-Métairon, I.F. 1995. Larval nutrition. In: McEdward, L.R. (ed), *Ecology of Marine Invertebrate Larvae*: 223-248. Boca Raton: CRC Press.

Bookhout, C.G., Wilson, A.J., Duke, T.W. & Lowe, J.I. 1972. Effects of mirex on the larval development of two crabs. *Water, Air, Soil Pollution* 1: 165-180.

Booth, J.D. 1997. Long-distance movements in *Jasus* spp. and their role in larval recruitment. *Bull. Mar. Sci.* 61: 111-128.

Booth, J.D. & Phillips, B.F. 1994. Early life history of spiny lobster. *Crustaceana* 66: 271-294.

Borst, D.W., Laufer, H., Landau, M., Chang, E.S., Hertz, W.A., Baker, F.C. & Schooley, D.A. 1987. Methyl farnesoate and its role in crustacean reproduction and development. *Insect Biochemistry* 17 (7): 1123-1127.

Borst, D.W., Tsukimura, B., Laufer, H. & Couch, E.F. 1994. Regional differences in methyl farnesoate production by the lobster mandibular organ. *Biol. Bull.* 186: 9-16.

Bosc, L.A.G. 1802. *Manuel de l'histoire naturelle des crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature.* 1. Paris: Deterville.

Boschi, E.E., Scelzo, M.A. & Goldstein, B. 1967. Desarrollo larval de dos especies de Crustáceos Decápodos en el laboratorio. *Pachycheles haigae* Rodrigues Da Costa (Porcellanidae) y *Chasmagnathus granulata* Dana (Grapsidae). *Bol. Inst. Biol. Mar., Mar Del Plata* 12: 3-46.

Botero, L. & Atema, J. 1982. Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. *J. Crust. Biol.* 2 (1): 59-69.

Botsford, L.W. 1985. Models of growth. In: Wenner, A.M. (ed), *Crustacean Issues 3*; *Factors in Adult Growth*: 171-188. Rotterdam: Balkema.

Bouaricha, N., Charmantier-Daures, M., Thuet, P., Trilles, J.-P. & Charmantier, G. 1994. Ontogeny of osmoregulatory structures in the shrimp *Penaeus japonicus* (Crustacea, Decapoda). *Biol. Bull.* 186: 29-40.

Bouaricha, N., Charmantier, G., Charmantier-Daures, M., Thuet, P. & Trilles, J.-P. 1991a. Ontogénèse de l'osmorégulation chez la crevette *Penaeus japonicus*. *Cah. Biol. Mar.* 32: 149-158.

Bouaricha, N., Charmantier, G., Charmantierdaures, M., Thuet, P. & Trilles, J.P. 1991b. Ontogeny of osmoregulation in the shrimp *Penaeus japonicus*. *Cahiers De Biologie Marine* 32 (2): 149-158.

Bouaricha, N., Thuet, P., Charmantier, G., Charmantier-Daures, M. & Trilles, J.-P. 1991c. Na^+-K^+ ATPase and carbonic anhydrase activities in larvae, postlarvae and adults of the shrimp, *Penaeus japonicus* (Decapoda, Penaeidea). *Comp. Biochem. Physiol.* 100A: 433-437.

Boudreau, B., Bourget, E. & Simard, Y. 1993a. Effect of age, injury, and predator odors on settlement and shelter selection by lobster *Homarus americanus* postlarvae. *Mar. Ecol. Prog. Ser.* 93: 119-129.

Boudreau, B., Bourget, E. & Simard, Y. 1993b. Behavioural responses of competent lobster postlarvae to odor plumes. *Mar. Biol.* 117: 63-69.

Bowman, T.E. & Abele, L.G. 1982. Classification of the recent Crustacea. In: Abele, L.G. (ed), *The Biology of Crustacea 1*; *Systematics, the Fossil Record and Biogeography*: 1-27. New York: Academic Press.

Bratbak., G., Egge, J.K. & Heldal, M. 1993. Viral mortality of the marine alga *Emiliania huxleyi* (Haptophyceae) and termination of algal blooms. *Mar. Ecol. Prog. Ser.* 93: 39-48.

Bressac, C. 1976a. Étude ultrastructural de la glande du sinus du crab *Pachygrapsus marmoratus*. *C.R. Acad. Sci. Paris* 282 (D): 1529-1531.

Bressac, C. 1976b. Effects de l'ablation des pédoncules oculaires sur les organes Y du crab *Pachygrapsus marmoratus*. *C.R. Acad. Sci. Paris* 282 (D): 1873-1875.

Bressac, C. 1978. L' activité mitotique au niveau de l' organe Y du Crabe *Pachygrapsus marmoratus* (Fabricius). *C.R. Acad. Sc. Paris* t. 286 (Série D): 289-291.

Bressac, C. 1988. Les organes neurohemaux et les glandes endocrines de *Pachygrapsus marmoratus* (Fabricius) (Decapoda, Brachyura). II. Les glandes endocrines: organe Y et glande mandibulaire. *Crustaceana* 55: 103-119.

Brewer, M.C., Dawidowicz, P. & Dodson, S.I. 1999. Interactive effects of fish kairomone and light on *Daphnia* escape behavior. *J. Plankton Res.* 21: 1317-1335.

Briggs, M.R.P., Jauncey, K. & Brown, J.H. 1988. The cholesterol and lecithin requirements of juvenile prawn (*Macrobrachium rosenbergii*) fed semi-purified diets. *Aquaculture* 70: 121-129.

Broad, A.C. 1957a. The relationship between diet and larval development of *Palaemonetes*. *Biol. Bull.* 112: 162-170.

Broad, A.C. 1957b. Larval development of *Palaemonetes pugio* Holthuis. *Biol. Bull.* 112: 144-161.

Broad, A.C. & Hubschman, J.H. 1963. The larval development of *Palaemonetes kadiakensis* M.J. Rathbun in the laboratory. *Trans. Amer. Microsc. Soc.* 82: 185-197.

Broch, E.S. 1960. Endocrine control of the chromatophores of the zoeae of the prawn *Palaemonetes vulgaris*. *Biol. Bull.* 119: 305-306.

Brock, J.A. 1983. Diseases (infectious and noninfectious), metazoan parasites, predators, and public health considerations in *Macrobrachium* culture and fisheries. In: McVey, J.P. (ed), *Handbook of Mariculture 1, Crustacean Aquaculture*: 329-370. Boca Raton, FL: CRC Press.

Brodie, R.J. 1999. Ontogeny of shell-related behaviors and transition to land in the terrestrial hermit crab *Coenobita compressus* H. Milne Edwards. *J. Exp. Mar. Biol. Ecol.* 241 (1): 67-80.

Brown, A.C. & Terwilliger, N.B. 1992. Developmental changes in ionic and osmotic regulation in the dungeness crab, *Cancer magister*. *Biol. Bull.* 182: 270-277.

Brown, A.C. & Terwilliger, N.B. 1998. Ontogeny of hemocyanin function in the dungeness crab *Cancer magister:* hemolymph modulation of hemocyanin oxygen-binding. *J. Exp. Biol.* 201: 819-826.

Browne, K.A. & Zimmer, R. 2001. Controlled field release of a waterborne chemical signal stimulates planktonic larvae to settle. *Biol. Bull.* 200 (1): 87-91.

Brumbaugh, R.D. & McConaugha, J.R. 1995. Time to metamorphosis of blue crab *Callinectes sapidus* megalopae: effects of benthic macroalgae. *Mar. Ecol. Prog. Ser.*129 (1-3): 113-118.

Brun, G.L. & Wojtowicz, M.B. 1976. A comparative study of the digestive enzymes in the hepatopancreas of Jonah crab (*Cancer borealis*) and rock crab (*Cancer irroratus*). *Comp. Biochem. Physiol.* 51B: 387-391.

Bruns, T. 1992. Experimentelle Untersuchungen zur Larvalentwicklung antarktischer Garnelen (Decapoda, Natantia). M.Sc. Thesis, Universität Osnabrück, Germany, 129 pp.

Brusca, R.C. & Brusca, G.J. 1990. *Invertebrates.* Sunderland, Massachussetts: Sinauer Ass.

Buchholz, C. 1984. Die Häutungsdrüse larvaler decapoder Crustaceen. Untersuchungen der Struktur und Funktion am Beispiel der Schlammkrabbe *Rhithropanopeus harrisii* (Gould). Dissertation, Universität Kiel, Germany, 135 pp.

Bulow, F.J. 1987. RNA-DNA ratios as indicators of growth in fish: a review. In: Summerfelt, R.C. & Hall, G.E. (eds), *The age and growth of fish*: 45-64. Ames, Iowa: Iowa State University Press.

Bunch, T., Highsmith, R.C. & Shields, G.F. 1998. Genetic evidence for dispersal of larvae of Tanner crabs (*Chionoecetes bairdi*) by the Alaskan Coastal Current. *Molecular Mar. Biol. and Biotechnology* 7: 153-159.

Burggren, W.W. & McMahon, B.R. (eds) 1988. *Biology of the land crabs.* New York: Cambridge University Press.

Burggren, W.W. & Roberts, J.L. 1991. Respiration and metabolism. In: Prosser, C.L. (ed), *Environmental and metabolic animal physiology*: 353-435. New York: Wiley.

Burghause, F. 1975. Das Y-Organ von *Orconectes limosus* (Malacostraca, Astacura). *Z. Morphol. Tiere* 80: 41-57.

Burke, R.D. 1986. Pheromones and the gregarious settlement of marine invertebrate larvae. *Bull. Mar. Sci.* 39: 323-346.

Burkenroad, M.D. 1981. The higher taxonomy of the Eucarida (Crustacea, Eumalacostraca), in relation to the fossil record. *Transactions of the San Diego Society of Natural History* 19: 251-268.

Burkenroad, M.D. 1983. Natural classification of Dendrobranchiata, with a key to recent genera. In: Schram, F.R. (ed), *Crustacean Issues 1*; *Crustacean phylogeny*: 279-290. Rotterdam: Balkema.

Burton, R.S. 1992. Proline synthesis during osmotic stress in megalopa stage larvae of the blue crab, *Callinectes sapidus*. *Biol. Bull.* 182: 409-415.

Bush, B.M.H. & Laverack, M.S. 1982. Mechanoreception. In: Atwood, H.L. & Sandeman, D.C. (eds), *The Biology of Crustacea 3*; *Neurobiology: Structure and Function*: 399-468. New York: Academic Press.

Butenandt, A. & Karlson, P. 1954. Über die Isolierung eines Metamorphose-Hormons der Insekten in kristallisierter Form. *Z. Naturforsch.* 9: 389-391.

Butler, M.J., Herrnkind, W.F. & Hunt, J.H. 1997. Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bull. Mar. Sci.* 61: 3-19.

Byard, E.H., Shivers, R.R. & Aiken, D.E. 1975. The mandibular organ of the lobster, *Homarus americanus*. *Cell Tiss. Res.* 162, 13-22.

Cahu, C.L., Cuzon, G. & Quazuguel, P. 1995. Effect of highly unsaturated fatty acids, □-tocopherol and ascorbic acid in broodstock diet on egg composition and development of *Penaeus indicus*. *Comp. Biochem. Physiol.* 112A: 417-424.

Calow, P. 1976. *Biological machines: a cybernetic approach to life.* London: Edward Arnold.

Calow, P. 1977a. Ecology, evolution and energetics: a study in metabolic adaptation. In: MacFadyen, A. (ed), *Advan. Ecol. Res. 10*: 1-62.

Calow, P. 1977b. Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* 52: 385-409.

Campodónico, G.I. 1971. Desarrollo larval de la centolla *Lithodes antarctica* Jacquinot en condiciones de laboratorio (Crustácea Decapoda, Anomura: Lithodidae). *Anales Inst. Patagonia Punta Arenas* 2: 181-190.

Campodónico, G.I. & Guzmán, L. 1981. Larval development of *Paralomis granulosa* (Jacquinot) under laboratory conditions (Decapoda, Anomura, Lithodidae). *Crustaceana* 40: 272-285.

Capaldo, P.S. 1987. Effects of Carbaryl (SEVIN) on the stage I zoeae of the red-jointed fiddler crab, *Uca minax* (LeConte). *Estuaries* 10: 132-135.

Capaldo, P.S. 1993. Salinity preferences in the stage-I-zoeae of 3 temperate zone fiddler-crabs, genus *Uca*. *Estuaries* 16: 784-788.

Capuzzo, J.M. 1977. The effect of free chlorine and chloramine on growth and respiration rates of larval lobsters (*Homarus americanus*). *Water Res.* 11: 1021-1024.

Capuzzo, J.M. 1982. Crustacean bioenergetics: the role of environmental variables and dietary levels of macronutrients on energetic efficiencies. In: Pruder, G.D., Langdon, C.J. & Conklin, D.E. (eds), *Proceedings of the second international conference on Aquacult. Nutr.: Biochemical and physiological approaches to shellfish nutrition*: 71-86. Baton Rouge, Louisiana, USA:

Capuzzo, J.M. 1985. Biological effects of petroleum hydrocarbons on marine organisms: integration of experimental results and predictions of impacts. *Mar. Environ. Res.* 17: 272-276.

Capuzzo, J.M. & Lancaster, B.A. 1979a. The effects of dietary carbohydrate levels on protein utilization in the American lobster (*Homarus americanus*). *Proc. World Maric. Soc.* 10: 689-700.

Capuzzo, J.M. & Lancaster, B.A. 1979b. Some physiological and biochemical considerations of larval development in the American lobster, *Homarus americanus* Milne Edwards. *J. Exp. Mar. Biol. Ecol.* 40: 53-62.

Capuzzo, J.M. & Lancaster, B.A. 1979c. Larval development in the American lobster: changes in metabolic activity and the O:N ratio. *Can. J. Zool.* 57: 1845-1848.

Capuzzo, J.M. & Lancaster, B.A. 1981. Physiological effects of south Louisiana crude oil on larvae of the American lobster (*Homarus americanus*). In: Vernberg, F.J., Calabrese, A., Thurberg, F.P. & Vernberg, W.B. (eds), *Biological Monitoring of Marine Pollutants*: 405-423. New York: Academic Press.

Capuzzo, J.M. & Lancaster, B.A. 1982. Physiological effects of petroleum hydrocarbons on larval lobsters (*Homarus americanus*): hydrocarbon accumulation and interference with metabolism. In: Vernberg, F.J. (ed), *Mechanisms of Marine Pollutant Toxicity*: 477-501. New York: Academic Press.

Capuzzo, J.M., Lancaster, B.A. & Sasaki, G.C. 1984. The effects of petroleum hydrocarbons on lipid metabolism and energetics of larval development and metamorphosis in the American lobster (*Homarus americanus*) Milne Edwards. *Mar. Environ. Res.* 14: 201-228.

Capuzzo, J.M., Lawrence, S.A. & Davidson, J.A. 1976. Combined toxicity of free chlorine, chloramine and temperature to stage I larvae of the American lobster *Homarus americanus*. *Water Res.* 10: 1093-1099.

Carlberg, J.M. & Van Olst, J.C. 1976. Brine shrimp (*Artemia salina*) consumption by the larval stages of the American lobster (*Homarus americanus*) in relation to food density and water temperature. In: *Proc. 7th Annual Meeting World Mariculture Society.*

Carlisle, D.B. & Connick, R.O. 1973. Crustecdysone (20-hydroxyecdysone): site of storage in the crayfish *Orconectes propinquus*. *Can. J. Zool.* 51: 417-420.

Carlisle, D.B. & Knowles, F. 1959. *Endocrine control in crustaceans.* London, New York: Cambridge Univ. Press.

Cartaxana, A. 1994. Distribution and migrations of the prawn *Palaemon longirostris* in the Mira River estuary (Southwest Portugal). *Estuaries* 17: 685-694.

Castell, J.D. & Kean, J.L. 1986. Evaluation of the role of nutrition in lobster recruitment. *Can. J. Fish. Aquat. Sci.* 43: 2320-2327.

Castilho, P.C., Martins, I.A. & Bianchini, A. 2001. Gill Na^+,K^+-ATPase and osmoregulation in the estuarine crab, *Chasmagnathus granulata* Dana, 1851 (Decapoda, Grapsidae). *J. Exp. Mar. Biol. Ecol.* 256 (2): 215-227.

Catacutan, M.R. 1991. Growth and fatty acid composition of *Penaeus monodon* juveniles fed various lipids. *Israeli J. Aquaculture Bamidgeh* 43: 47-56.

Cavalli, R.O., Berghe, E.V., Lavens, P., Thuy, N.T.T., Wille, M. & Sorgeloos, P. 2000. Ammonia toxicity as a criterion for the evaluation of larval quality in the prawn *Macrobrachium rosenbergii*. *Comp. Biochem. Phys. A.* 125C(3): 333-343.

Cavalli, R.O., Lavens, P. & Sorgeloos, P. 1999. Performance of *Macrobrachium rosenbergii* broodstock fed diets with different fatty acid composition. *Aquaculture* 179: 387-402.

Cavolini, P. 1792. *Abhandlungen über die Erzeugnisse der Fische und der Krebse. Aus dem Italiänischen übersetzt. Mit Anmerkungen herausgegeben von E.A.W. Zimmermann.* Berlin.

Ceccaldi, H.J. 1994. Appareil digestif: anatomie et physiologie. In: Forest, J. (ed), Traité De Zoologie 1 (6); Crustacés. Morphologie, Physiologie, Reproduction, Systématique: 487-527.

Celestial, D.M. & McKenney, C.L. 1994. The influence of an insect growth-regulator on the larval development of the mud crab *Rhithropanopeus harrisii*. *Environm. Poll.* 85: 169-173.

Chace, F.A. 1992. On the classification of the Caridea (Decapoda). *Crustaceana* 63: 71-80.

Chaigneau, J. 1978. L'organe de Bellonci des Crustacés. Historique et état actuel des connaissance. *Arch. Zool. Exp. Gen.* 119: 185-199.

Chaigneau, J. 1994a. Système nerveux. I. Cytologie, histologie et anatomie. In: Forest, J. (ed), Traité De Zoologie; Crustacés. Morphologie, Physiologie, Reproduction, Systématique 1: 235-344.

Chaigneau, J. 1994b. Les organes des sens autres que ceux de la vision. In: Forest, J. (ed), Traité De Zoologie; Crustacés. Morphologie, Physiologie, Reproduction, Systématique 1: 345-410.

Chamberlain, N.A. 1957. Larval development of the mud crab *Neopanope texana sayi* (Smith). *Biol. Bull. Mar. Biol. Lab. Woods Hole* 113: 338.

Chan, S.-M., Chen, X.G. & Gu, P.L. 1998. PCR cloning and expression of the molt-inhibiting hormone gene for the crab (*Charybdis feriatus*). *Gene* 224 (1-2): 23-33.

Chandumpai, A., Dall, W. & Smith, D.M. 1991. Lipid-class composition of organs and tissues of the tiger prawn *Panaeus esculentus* during the moulting cycle and during starvation. *Mar. Biol.* 108: 235-245.

Chang, C.-F., Su, M.-S., Chen, H.-Y., Kou, G.-H. & Liao, I.-L. 1999. Effect of dietary □-1,3-glucan on resistance to white spot syndrome virus (WSSV) in postlarval and juvenile *Penaeus monodon*. *Deseases of Aquatic Organisms* 36: 163-168.

Chang, E.S. 1995. Physiological and biochemical changes during the molt cycle in decapod crustaceans: an overview. *J. Exp. Mar. Biol. Ecol.* 193: 1-14.

Chang, E.S. & Bruce, M.J. 1981. Ecdysteroid titers of larval lobsters. *Comp. Biochem. Physiol.* 70: 239-241.

Chang, E.S., Bruce, M.J. & Newcomb, R.W. 1987. Purification and amino acid composition of a peptide with molt-inhibiting activity from the lobster, *Homarus americanus. Gen. Comp. Endocrinol.* 65: 56-64.

Chang, E.S., Bruce, M.J. & Tamone, S.L. 1993. Regulation of crustacean molting: a multi-hormonal system. *Amer. Zool.* 33: 324-329.

Chang, E.S., Prestwich, G.D. & Bruce, M.J. 1990. Amino acid sequence of a peptide with both molt-inhibiting and hyperglycemic activities in the lobster, *Homarus americanus*. *Biochem. Biophys. Res. Commun.* 171: 818-826.

Chang, E.S., Sage, B.A. & O'Connor, J. 1976. The qualitative and quantitative determinations of ecdysones in tissues of the crab, *Pachygrapsus crassipes,* following molt induction. *Gen. Comp. Endocrinol.* 30: 21-33.

Chapelle, S. 1986. Aspects of phospholipid metabolism in crustaceans as related to changes in environmental temperature and salinity. *Comp. Biochem. Physiol.* 84B: 423-439.

Charmantier-Daures, M. & Charmantier, G. 1994. Les organes endocrines. In: Forest, J. (ed), Traité De Zoologie 6 (1); Crustacés. Morphologie, Physiologie, Reproduction, Systématique: 595-629.

Charmantier-Daures, M., Charmantier, G., Janssen, K.P.C., Aiken, D.E. & van Herp, F. 1994. Involvement of eyestalk factors in the neuroendocrine control of osmoregulation in adult American lobster *Homarus americanus*. *Gen. Comp. Endocrinol.* 94: 281-293.

Charmantier-Daures, M. & Segonzac, M. 1998. Organ of Bellonci and sinus gland in three decapods from Atlantic hydrothermal vents: *Rimicaris exoculata*, *Chorocaris chacei*, and *Segonacia mesatlantica*. *J. Crust. Biol.* 18: 213-223.

Charmantier-Daures, M., Thuet, P., Charmantier, G. & Trilles, J.-P. 1988. Tolérance à la salinité et osmorégulation chez les post-larves de *Penaeus japonicus* et *P. chinensis.* Effect de la température. *Aquat. Living Resour.* 1: 267-276.

Charmantier, G. 1998. Ontogeny of osmoregulation in crustaceans: a review. *Int. J. Inver. Rep. Dev.* 33: 177-190.

Charmantier, G. & Aiken, D.E. 1987. Intermediate larval and postlarval stages of *Homarus americanus* H. Milne Edwards, 1837 (Crustacea: Decapoda). *J. Crust. Biol.* 7: 525-535.

Charmantier, G. & Anger, K. 1999. Ontogeny of osmoregulation in the palaemonid shrimp *Palaemonetes argentinus* (Crustacea: Decapoda). *Mar. Ecol. Prog. Ser.* 181: 125-129.

Charmantier, G. & Charmantier-Daures, M. 1991. Ontogeny of osmoregulation and salinity tolerance in *Cancer irroratus;* elements of comparison with *C. borealis* (Crustacea, Decapoda). *Biol. Bull.* 180: 125-134.

Charmantier, G. & Charmantier-Daures, M. 1994. Ontogeny of osmoregulation and salinity tolerance in the isopod crustacean *Sphaeroma serratum*. *Mar. Ecol. Prog. Ser.* 114: 93-102.

Charmantier, G. & Charmantier-Daures, M. 1998. Endocrine and neuroendocrine regulations in embryos and larvae of crustaceans. *Int. J. Inver. Rep. Dev.* 33: 273-287.

Charmantier, G., Charmantier-Daures, M. & Aiken, D.E. 1988. Larval development and metamorphosis of the American lobster *Homarus americanus* (Crustacea, Decapoda): effect of eyestalk ablation and juvenile hormone injection. *Gen. Comp. Endocrinol.* 70: 319-333.

Charmantier, G., Charmantier-Daures, M. & Aiken, D.E. 1991. Metamorphosis in the lobster *Homarus* (Decapoda): a review. *J. Crust. Biol.* 11: 481-495.

Charmantier, G., Charmantier-Daures, M. & Anger, K. 1998. Ontogeny of osmoregulation in the grapsid crab *Armases miersii* (Crustacea, Decapoda). *Mar. Ecol. Prog. Ser.* 164: 285-292.

Charmantier, G., Charmantier-Daures, M. & Van Herp, F. 1996. Hormonal regulation of growth and reproduction in Crustaceans. In: Fingerman, M., Nagabhushanam, R. & Thompson, M.-F. (eds), *Mar. Biotechnol. 1*; *Endocrinology and Reproduction*: 109-161. New Delhi: Oxford & IBH Publ.

Charniaux-Cotton, H. 1954. Découverte chez un Crustacé Amphipode *(Orchestia gammarella)* d'une glande endocrine responsable de la différenciation de caractères sexuels primaires et secondaires mâles. *C.R. Acad. Sci. Paris* 239: 780-782.

Charniaux-Cotton, H. & Payen, G. 1985. Sexual differentiation. In: Bliss, D.E. & Mantel, L.H. (ed), *The Biology of Crustacea 9*; *Integument, Pigments, and Hormonal Processes*: 217-299. New York: Academic Press.

Charniaux-Legrand, H. 1952. Le cycle d'intermue des amphipodes et ses particularités chez les formes terrestres (Talitridae). *Arch. Zool. Exp.* 88: 178-204.

Chaudonneret, J. 1978. Evolution de la chaîne nerveuse láterale chez quelques Malacostracés. *Archs. Zool. Exp. Gén.* 119: 163-184.

Chaves, A.R. 2001. Effects of sinus gland extract on mandibular organ size and methyl farnesoate synthesis in the crayfish. *Comp. Biochem. Physiol.* 128A(2): 327-333.

Chen, J.-C. & Lai, S.-H. 1993. Effects of temperature and salinity on oxygen consumption and ammonia-N excretion of juvenile *Penaeus japonicus* Bate. *J. Exp. Mar. Biol. Ecol.* 165: 161-170.

Chen, J.-C. & Nan, F.-H. 1991. Lethal effect of nitrite on *Metapenaeus ensis* larvae. *J. World Aquacult Soc.* 22: 51-56.

Chen, L.-L., Lo, C.-F., Chiu, Y.-L., Chang, C.-F. & Kou, G.-H. 2000. Natural and experimental infection of white spot syndrome virus (WSSV) in benthic larvae of mud crab *Scylla serrata*. *Dis. Aquat. Org.* 40: 157-161.

Chen, Y.-H., Shaw, P.-T. & Wolcott, T.G. 1997. Enhancing estuarine retention of planktonic larvae by tidal currents. *Est. Coast. Shelf Sci.* 45: 525-533.

Cheng, J.-H. & Chang, E.S. 1993. Determinants of postmolt size in the lobster (*Homarus americanus*). III. Scute density. *Inv. Reprod. Develop.* 24: 169-178.

Chevaldonné, P. & Olu, K. 1996. Occurrence of anomuran crabs (Crustacea: Decapoda) in hydrothermal vent and cold-seep communities: a review. *Proc. Biol. Soc. Wash.* 109: 286-298.

Chia, F.-S. & Rice, M.E. 1978. *Settlement and metamorphosis of marine invertebrate larvae.* New York: Elsevier.

Childress, J.J. & Nygaard, M. 1974. Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off Southern California. *Mar. Biol.* 27: 225-238.

Chin, T.-S. & Chen, J.-C. 1987. Acute toxicity of ammonia to larvae of the tiger prawn, *Penaeus monodon*. *Aquaculture* 66: 247-253.

Chinni, S., Khan, R.N. & Yallapragada, P.R. 2000. Oxygen consumption, ammonia-N excretion, and metal accumulation in *Penaeus indicus* postlarvae exposed to lead. *Bull. Environ. Contam. Toxicol.* 64: 144-151.

Chiswell, S.M. & Booth, J.D. 1999. Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Mar. Ecol. Prog. Ser.*183: 227-240.

Chiswell, S.M. & Roemmich, D. 1998. The East Cape Current and two eddies: a mechanism for larval retention? *New Zeal. J. Mar. Fresh.* 32: 385-397.

Chong, V.C., Low, C.B. & Ichikawa, T. 2001. Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. *Mar. Biol.* 138 (1): 77-86.

Chow, S., Fujio, Y. & Nomura, T. 1988. Reproductive isolation and distinct population structures in two types of freshwater shrimp *Palaemon paucidens*. *Evolution* 42: 804-813.

Christiansen, M.E. 1969. *Crustacea Decapoda Brachyura.* Marine Invertebrates of Scandinavia 2. Oslo: Universitetsforlaget.

Christiansen, M.E. 1986. Effect of diflubenzuron on the cuticle of crab larvae. In: Muzzarelli, R., Jeuniaux, C. & Gooday, G.W. (eds), *Chitin in Nature and Technology*: 175-181. Plenum Publishing Corporation.

Christiansen, M.E. 1988. Hormonal processes in decapod crustacean larvae. In: Fincham, A.A. & Rainbow, P.S. (eds), *Symposia of the Zoological Society of London 59*; *Aspects of Decapod Crustacean Biology 59*: 47-68. Oxford: Clarendon Press, Oxford.

Christiansen, M.E. & Anger, K. 1990. Complete larval development of *Galathea intermedia* Lilljeborg reared in laboratory culture (Anomura: Galatheidae). *J. Crust. Biol.* 10: 87-111.

Christiansen, M.E. & Costlow, J.D. 1982. Ultrastructural study of the exoskeleton of the estuarine crab *Rhithropanopeus harrisii:* effect of the insect growth regulator Dimilin® (Diflubenzuron) on the formation of the larval cuticle. *Mar. Biol.* 66: 217-226.

Christiansen, M.E., Gosling, E. & Williams, M.A. 1984. Effect of the insect growth regulator diflubenzuron (Dimilin)® on the uptake of glucose and N-acetylglucosamine into the cuticle of crab larvae. *Mar. Biol.* 83: 225-230.

Christy, J.H. 1989 Mar. Rapid development of megalopae of the fiddler crab *Uca pugilator* reared over sediment: implications for models of larval recruitment. *Mar. Ecol. Prog. Ser.* 57: 259-265.

Christy, J.H. & Morgan, S.G. 1998. Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. *Mar. Ecol. Prog. Ser.* 174: 51-65.

Chu, K.H. & Ovsianico-Koulikowsky, N.N. 1994. Ontogenetic changes in metabolic activity and biochemical composition in the shrimp, *Metapenaeus ensis*. *J. Exp. Mar. Biol. Ecol.* 182: 11-26.

Chu, K.H. & Shing, C.K. 1986. Feeding behavior of the shrimp, *Metapenaeus ensis*, on *Artemia* nauplii. *Aquaculture* 58: 175-184.

Cieri, M.D. & Stearns, D.E. 1999. Reduction of grazing activity of two estuarine copepods in response to the exudate of a visual predator. *Mar. Ecol. Prog. Ser.* 177: 157-163.

Cisne, J.L. 1982. Origin of the Crustacea. In: Abele, L.G. (ed), *The Biology of Crustacea 2*; *Embryology, Morphology and Genetics*: 65-92. New York: Academic Press.

Clancy, M. & Cobb, J.S. 1997. Effect of wind and tidal advection on distribution patterns of rock crab *Cancer irroratus* megalopae in block island sound, Rhode Island. *Mar. Ecol.-Progress Series* 152 (1-3): 217-225.

Clare, A.S. & Lumb, G. 1994. Identification of haemocytes and their role in clotting in the blue crab, *Callinectes sapidus*. *Mar. Biol.* 118: 601-610.

Clark, P.F., Calazans, D.K. & Pohle, G.W. 1998. Accuracy and standardization of Brachyuran larval descriptions. *Int. J. Inver. Rep. Dev.* 33 (2-3): 127-144.

Clarke, A. 1993a. Egg size and egg composition in polar shrimps (Caridea, Decapoda). *J. Exp. Mar. Biol. Ecol.* 168 (2): 189-203.

Clarke, A. 1993b. Reproductive trade-offs in caridean shrimps. *Funct. Ecol.* 7 (4): 411-419.

Clarke, A., Brown, J.H. & Holmes, L.J. 1990. The biochemical composition of eggs from *Macrobrachium rosenbergii* in relation to embryonic development. *Comp. Biochem. Physiol.* 96B: 505-511.

Claybrook, D.L. 1983. Nitrogen metabolism. In: Mantel, L.H. (ed), *The Biology of Crustacea 5*; *Internal Anatomy and Physiological Regulation*: 163-213. New York: Academic Press.

Clemens, S., Massbuau, J.-C., Meyrand, P. & Simmers, J. 1999. Changes in motor network expression related to moulting behaviour in lobster: role of moult-induced deep hypoxia. *J. Exp. Biol.* 202: 817-827.

Clemmesen, C. 1987. Laboratory studies on RNA/DNA ratios of starved and fed herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. *J. Cons. Int. Explor. Mer* 43: 122-128.

Clemmesen, C. 1989. RNA/DNA ratios of laboratory-reared and wild herring larvae determined with a highly sensitive fluorescence method. *J. Fish. Biol. 35 (Suppl. A):* 331-333.

Clemmesen, C. 1994. The effect of food availability, age or size on the RNA/DNA ratio of individually measured herring larvae: laboratory calibration. *Mar. Biol.* 118 (3): 377-382.

Cobb, J.S. 1968. Delay of moult by the larvae of *Homarus americanus*. *J. Fish. Res. Bd. Can.* 25: 2251-2253.

Cobb, J.S. & Wahle, R.A. 1994. Early-life history and recruitment processes of clawed lobsters. *Crustaceana* 67: 1-25.

Coffin, H.G. 1958. The laboratory culture of *Pagurus samuelis* (Stimpson) (Crustacea, Decapoda). *Walla Walla College Publications Dept. Biol. Sci. and Biol. Stn.* 22: 1-5.

Coiro, L.L., Poucher, S.L. & Miller, D.C. 2000. Hypoxic effects on growth of *Palaemonetes vulgaris* larvae and other species: using constant exposure data to estimate cyclic exposure response. *J. Exp. Mar. Biol. Ecol.* 247 (2): 243-255.

Coleman, D.C. & Fry, B. 1991. *Carbon Isotope Techniques.* San Diego: Academic Press.

Collocott, T.C. 1971. *Dictionary of science and technology.* Edinburgh: W. & R. Chambers.

Colorni, A. 1985. A study on the bacterial flora of giant prawn, *Macrobrachium rosenbergii,* larvae fed with *Artemia salina* nauplii. *Aquaculture* 49: 1-10.

Comoglio, L.I. & Vinuesa, J. 1991. Larval culture of southern king crab *Lithodes santolla* and false king crab *Paralomis granulosa* under laboratory conditions. In: Lavens, P., Sorgeloos, P., Jaspers, E. & Ollevier, F. (eds), *Larvi '91. Symposium on Fish and Crustacean Larviculture*, *Gent, Belgium, August 27-30,1991*. Gent, Belgium: European Aquacult. Soc.

Conklin, D.E. 1980. Nutrition. In: Cobb, J.S. & Phillips, B.F. (eds), *The biology and management of lobsters. Vol. 1*: 277-300. New York: Acad. Press.

Conover, R.J. 1966. Factors affecting the assimilation of organic matter by zooplankton and the question of superfluous feeding. *Limnol. Oceanogr.* 11: 346-354.

Conover, R.J. 1978. Transformation of organic matter. In: Kinne, O. (ed), *Marine Ecology 4*; *Dynamics*: 221-499. Chichester: Wiley.

Cooke, I.M. & Sullivan, R.E. 1982. Hormones and Neurosecretion. In: Atwood, H.L. & Sandeman, D.C. (eds), *The Biology of Crustacea 3*; *Neurobiology: Structure and Function*: 206-290. New York: Academic Press.

Costlow, J.D. 1961. Fluctuations in hormone activity in Brachyuran larvae. *Nature* 192: 183-184.

Costlow, J.D. 1963a. The effect of eyestalk extirpation on metamorphosis of megalops of the blue crab, *Callinectes sapidus* Rathbun. *Gen. Comp. Endocrinol.* 3: 120-130.

Costlow, J.D. 1963b. Regeneration and metamorphosis in larvae of the blue crab, *Callinectes sapidus* Rathbun. *J. Exp. Zool.* 152: 219-228.

Costlow, J.D. 1963c. Larval development. *Aibs Bull.* 13: 63-65.

Costlow, J.D. 1967. The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus*. *Helgoländer Wiss. Meeresunters.* 15: 84-97.

Costlow, J.D. 1968. Metamorphosis in crustaceans. In: Etkin, W. & Gilbert, L.I. (eds), *Metamorphosis: a problem in developmental biology*: 3-41. New York: Appleton-Century-Crofts.

Costlow, J.D. & Bookhout, C.G. 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull. Mar. Biol. Lab. Woods Hole* 116: 373-396.

Costlow, J.D. & Bookhout, C.G. 1962. The larval development of *Sesarma reticulatum* Say reared in the laboratory. *Crustaceana* 4: 281-294.

Costlow, J.D. & Bookhout, C.G. 1964. An approach to the ecology of marine invertebrate larvae. In: *Proceedings of Symposium on Experimental Mar. Ecol.*. Kingston, RI: Graduate school of Oceanography, University of Rhode Island.

Costlow, J.D. & Bookhout, C.G. 1969. Temperature and meroplankton. *Chesapeake Sci.* 10: 252-257.

Costlow, J.D. & Bookhout, C.G. 1970. Marine larvae - the neglected link in biological resources. In: *Proceedings of the Symposium on Hydrobiology*, *Miami Beach, Florida, June 24-27, 1970*

Costlow, J.D., Bookhout, C.G. & Monroe, R. 1960. The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. *Biol. Bull.* 118: 183-202.

Costlow, J.D., Bookhout, C.G. & Monroe, R. 1966. Studies on the larval development of the crab, *Rhithropanopeus harrisii* (Gould). I. The effect of salinity and temperature on larval development. *Physiol. Zool.* 39: 81-100.

Costlow, J.D. & Sandeen, M.I. 1961. The appearance of chromatophorotropic activity in the developing crab, *Sesarma reticulatum*. *Am. Zool.* 1: 443.

Costlow, J.D. & Sastry, A.N. 1966. Free amino acids in developing stages of two crabs, *Callinectes sapidus* Rathbun and *Rhithropanopeus harrisii* (Gould). *Acta Embryol. Morphol. Exp.* 9: 44-55.

Cournil, I., Casanovas, B., Helluy, S.M. & Beltz, B.S. 1995. Dopamine in the lobster *Homarus gammarus:* II. Dopamine-immunoreactive neurons and development of the nervous system. *J. Comp. Neurol.* 362: 1-16.

Coutteau, P., Geurden, I., Camara, M.R., Bergot, P. & Sorgeloos, P. 1997. Review on the dietary effects of phospholipids in fish and crustacean larviculture. *Aquaculture* 155: 153-168.

Cowart, J.D., Fielman, K.T., Woodin, S.A. & Lincoln, D.E. 2000. Halogenated metabolites in two marine polychaetes and their planktotrophic and lecithotrophic larvae. *Mar. Biol.* 136 (6): 993-1002.

Cowen, R.K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. *Mar. Ecol. Prog. Ser.* 69: 9-15.

Cowles, T.J., Olson, R.J. & Chisholm, S.W. 1988. Food selection by copepods: discrimination on the basis of food quality. *Mar. Biol.* 100: 41-49.

Criales, M.M. 1985. Untersuchungen zur Larvalentwicklung von *Crangon crangon* L. und *Crangon allmanni* Kinahan (Decapoda, Natantia, Caridea). Dissertation, Universität Kiel, Germany, 223 pp.

Criales, M.M. & Anger, K. 1986. Experimental studies on the larval development of the shrimps *Crangon crangon* and *C. allmanni*. *Helgoländer Meeresunters.* 40: 241-265.

Cripps, G.C. & Atkinson, A. 2000. Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. *Can. J. Fish. Aquat. Sci.* 57: 31-37.

Crisp, D.J. 1974. Energy relations of marine invertebrate larvae. *Thalassia Jugoslavica* 10: 103-120.

Crisp, D.J. 1976. Settlement responses in marine organisms. In: Newell, R.C. (ed), *Adaptation in Environment*: 83-124. London: Butterworths.

Cronin, L.E. 1947. Anatomy and histology of the male reproductive system of *Callinectes sapidus* Rathbun. *J. Morphol.* 81: 209-239.

Cronin, T.W. 1982. Estuarine retention of larvae of the crab *Rhithropanopeus harrisii*. *Est. Coast. Shelf Sci.* 15 (2): 207-220.

Cronin, T.W. 1986. Photoreception in marine invertebrates. *Am. Zool.* 26 (2): 403-415.

Cronin, T.W. 1988. Vision in marine invertebrates. In: Atema, J., Fay, R.R., Popper, A.N. & Tavolga, W.N. (eds), *Sensory Biology of Aquatic Animals*: 403-418. New York: Springer.

Cronin, T.W. 1990. Pigments in crustacean compound eyes. In: Wiese, K., Krenz, W.D., Tautz, J., Reichert, H. & Mulloney, B. (eds), *Frontiers in Crustacean Neurobiology, Advances in Life Sciences*: 58-65. Basel: Birkhäuser.

Cronin, T.W. & Forward, R.B. 1980. The effects of starvation on phototaxis and swimming of larvae of the crab *Rhithropanopeus harrisii*. *Biol. Bull.* 158: 283-294.

Cronin, T.W. & Forward, R.B. 1982. Tidally timed behavior: effects on larval distributions in estuaries. In: Kennedy, V.S. (ed), *Estuarine Comparisons*: 505-520. New York: Academic Press.

Cronin, T.W. & Forward, R.B. 1983. Vertical migration rhythms of newly hatched larvae of the estuarine crab, *Rhithropanopeus harrisii*. *Biol. Bull.* 165: 139-153.

Cronin, T.W. & Forward, R.B. 1986. Vertical migration cycles of crab larvae and their role in larval dispersal. *Bull. Mar. Sci.* 39: 192-201.

Cronin, T.W., Marshall, N.J., Caldwell, R.L. & Pales, D. 1995. Compound eyes and ocular pigments of crustacean larvae (Stomatopoda and Decapoda, Brachyura). *Mar. Freshw. Behav. Phy.* 26 (2-4): 219-231.

Cuesta, J.A., Schuh, M., Diesel, R. & Schubart, C.D. 1999. Abbreviated development of *Armases miersii* (Grapsidae: Sesarminae), a crab that breeds in supralittoral rock pools. *J. Crust. Biol.* 19: 26-41.

Cuesta, J.A. & Anger, K. 2001. Larval morphology of the sesarmid crab *Armases angustipes* Dana, 1852 (Decapoda, Brachyura, Grapsoidea). *J. Crust. Biol.* 21 (3): 821-838.

Curl, H. 1962. Analyses of carbon in marine plankton organisms. *J. Mar. Res.* 20: 181-188.

D'Abramo, L.R. & Conklin, D.E. 1985. Lobster aquaculture. In: Huner, J.V. & Brown, E.E. (eds), *Crustacean and mollusk aquaculture in the United States*: 159-201. Westport, Connecticut: AVI Publishing Co.

D'Abramo, L.R., Conklin, D.E. & Akiyama, D.M. (eds) 1997. *Crustacean Nutrition.* Advances in World Aquaculture 6. Baton Rouge, LA: World Aquaculture Society, Louisiana State University.

D'Souza, F.M.L. & Kelly, G.J. 2000. Effects of a diet of a nitrogen-limited alga (*Tetraselmis suecica*) on growth, survival and biochemical composition of tiger prawn (*Penaeus semisulcatus*) larvae. *Aquaculture* 181: 311-329.

D'Souza, F.M.L. & Loneragan, N.R. 1999. Effects of monospecific and mixed-algae diets on survival, development and fatty acid composition of penaeid prawn (*Penaeus* spp.) larvae. *Mar. Biol.* 133: 621-633.

Dadd, R.H. 1977. Qualitative requirements and utilization of nutrients: arthropods other than insects. In: *CRC Handbook Series in Nutrition and Food 1*; 347-352. Cleveland, Ohio: CRC Press.

Dagg, M.J. 1974. Loss of prey body contents during feeding by an aquatic predator. *Ecology* 55: 903-906.

Dagg, M.J. 1977. Some effects of patchy food environments on copepods. *Limnol. Oceanogr.* 22: 99-107.

Dahl, E. 1957. Embryology of X organs in *Crangon allmanni*. *Nature* 179: 482.

Dahms, H.U. 2000. Phylogenetic implications of the Crustacean nauplius. *Hydrobiologia* 417: 91-99.

Dall, W. 1995. Carotenoids versus retinoids (vitamin A) as essential growth factors in penaeid prawns (*Penaeus semisulcatus*). *Mar. Biol.* 124 (2): 209-213.

Dall, W., Chandumpai, A. & Smith, D.M. 1992. Fatty acid composition of organs and tissues of the tiger prawn *Penaeus esculentus* during the moulting cycle and during starvation. *Mar. Biol.* 113 (1): 45-55.

Dall, W., Hill, B.J., Rothlisberg, P.C. & Staples, D.J. 1990. The Biology of the Penaeidae. *Advances in Mar. Biol.* 27: 1-461.

Dall, W. & Moriarty, D.J.W. 1983. Functional aspects of nutrition and digestion. In: Mantel, L.H. (ed), *The Biology of Crustacea 5*; *Internal Anatomy and Physiological Regulation*: 215-261. New York: Academic Press.

Damkaer, D.M. & Dey, D.B. 1983. UV damage and photoreactivation potentials of larval shrimp, *Pandalus platyceros*, and adult euphausiids, *Thysanoessa raschii*. *Oecologia* 60: 169-175.

Damkaer, D.M., Dey, D.B. & Heron, G.A. 1981. Dose/dose-rate response of shrimp larvae to UV-B radiation. *Oecologia* 48: 178-182.

Damkaer, D.M., Dey, D.B., Heron, G.A. & Prentice, E.F. 1980. Effects of UV-B radiation on near-surface zooplankton of Puget Sound. *Oecologia* 44: 149-158.

Daniel, R.J. 1930. The abdominal musculature system of the zoea and mysis stages of the shrimp (*Crangon vulgaris* Fabr.) and their bearing on phylogeny. *Proc. Trans. Liverpool Biol. Soc.* 44: 95-149.

Daniel, R.J. 1931. The abdominal muscles of the shore crab (*Carcinus maenas*) and of the zoea and megalopa stages. *Proc. Trans. Liverpool Biol. Soc.* 45: 50-56.

Davies, M.S. & Hatcher, A.M. 1998. The energy budget: a useful tool? *Ann. Zool. Fenn.* 35: 231-240.

Davis, C.S., Flierl, G.R., Wiebe, P.H. & Franks, P.J.S. 1991. Micropatchiness, turbulence and recruitment in plankton. *J. Mar. Res.* 49: 109-151.

Dawirs, R.R. 1981. Elemental composition (C, N, H) and energy in the development of *Pagurus bernhardus* (Decapoda: Paguridae) megalopa. *Mar. Biol.* 64: 117-123.

Dawirs, R.R. 1982. Methodical aspects of rearing decapod larvae, *Pagurus bernhardus* (Paguridae) and *Carcinus maenas* (Portunidae). *Helgoländer Meeresunters.* 35: 439-464.

Dawirs, R.R. 1983. Respiration, energy balance and development during growth and starvation of *Carcinus maenas* L. larvae (Decapoda: Portunidae). *J. Exp. Mar. Biol. Ecol.* 69: 105-128.

Dawirs, R.R. 1984a. Influence of starvation on larval development of *Carcinus maenas* L. (Decapoda: Portunidae). *J. Exp. Mar. Biol. Ecol.* 80: 47-66.

Dawirs, R.R. 1984b. Respiratory metabolism of *Pagurus bernhardus* (Decapoda: Paguridae) megalopa. *Mar. Biol.* 83: 219-223.

Dawirs, R.R. 1985. Temperature and larval development of *Carcinus maenas* (Decapoda) in the laboratory; predictions of larval dynamics in the sea. *Mar. Ecol. Prog. Ser* 24: 297-302.

Dawirs, R.R. 1986. Influence of limited food supply on growth and elemental composition (C, N, H) of *Carcinus maenas* (Decapoda) larvae, reared in the laboratory. *Mar. Ecol. Prog. Ser* 31: 301-308.

Dawirs, R.R. 1987. Influence of limited starvation periods on growth and elemental composition (C, N, H) of *Carcinus maenas* (Decapoda: Portunidae) larvae reared in the laboratory. *Mar. Biol.* 93: 543-549.

Dawirs, R.R. & Dietrich, A. 1986. Temperature and laboratory feeding rates in *Carcinus maenas* L. (Decapoda: Portunidae) larvae from hatching through metamorphosis. *J. Exp. Mar. Biol. Ecol.* 99: 133-147.

Dawirs, R.R., Püschel, C. & Schorn, F. 1986. Temperature and growth in *Carcinus maenas* L. (Decapoda: Portunidae) larvae reared in the laboratory from hatching through metamorphosis. *J. Exp. Mar. Biol. Ecol.* 100: 47-74.

Day, R. & McEdward, L. 1984. Aspects of the physiology and ecology of pelagic larvae of marine benthic invertebrates. In: Steidinger, K.A. & Walker, L.M. (eds), *Marine Plankton Life Cycle Strategies*: 94-120. Boca Raton, FL: CRC Press.

Day, T. & Taylor, P.D. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am. Nat.* 149: 381-393.

De Mora, S., Demers, S. & Vernet, M. (eds) 2000. *The effects of UV radiation in the marine environment.* Cambridge: Cambridge University Press.

De Vries, M.C., Rittschof, D. & Forward, R.B. 1991. Chemical mediation of larval release behaviors in the crab *Neopanope sayi*. *Biol. Bull.* 180: 1-11.

De Wolf, P. 1989. The price of patchiness. *Helgoländer Meeresunters.* 43: 263-273.

Dechancé, M. 1963. Développement direct chez un paguride, *Paguristes abbreviatus* Dechancé, et remarques sur le développement des *Paguristes*. *Bull. Mus. Natn. Hist. Nat., Paris* 35: 488-495.

DeCoursey, P.J. 1983. Biological timing. In: Vernberg, F.J. & Vernberg, W.B. (eds), *The Biology of Crustacea 7*; *Behavior and Ecology*: 107-162. Academic Press: New York:

DeCoursey, P.J. & Vernberg, W.B. 1972. Effect of mercury on survival, metabolism and behaviour of larval *Uca pugilator* (Brachyura). *Oikos* 23: 241-247.

DeFreese, D.E. & Clark, K.B. 1983. Analysis of reproductive energetics of Florida Opistobranchia (Mollusca: Gastropoda). *Int. J. Inv. Reprod.* 6: 1-10.

Dehn, P.F., Haya, K. & Aiken, D.E. 1985. Adenylate energy charge, arginine phosphate and AT-Pase activity in juvenile *Homarus americanus* during the molt cycle. *Comp. Biochem. Physiol.* 81 B: 629-633.

Dehnel, P.A. 1967. Osmotic and ionic regulation in estuarine crabs. In: Lauff, H.H. (ed), *Publ. American Association for the Advancement of Science 83*; *Estuaries*: 541-547. Washington, DC: American Association for the Advancement of Science.

Del Giorgio, P.A. 1992. The relationship between ETS (electron transport system) activity and oxygen consumption in lake plankton: a cross-system calibration. *J. Plankton Res.* 14: 1723-1741.

Delorenzi, A., Dimant, B., Frenkel, L., Nahmod, V.E., Nässel, D.R. & Maldonado, H. 2000. High environmental salinity induces memory enhancement and increases levels of brain angiotensin-like peptides in the crab *Chasmagnathus granulatus*. *J. Exp. Biol.* 203 (22): 3369-3379.

Delorenzi, A., Locatelli, F., Romano, A., Nahmod, V. & Maldonado, H. 1997. Angiotensin II (3-8) induces long-term memory improvement in the crab *Chasmagnathus*. *Neurosci. Lett.* 226: 143-146.

Delorenzi, A., Pedreira, M.E., Romano, A., Pirola, C.J., Nahmod, V.E. & Maldonado, H. 1995. Acute administration of angiotensin II improves long-term habituation in the crab *Chasmagnathus*. *Neurosci. Lett.* 196: 193-196.

Démeusy, N. 1975. Observations sur le fonctionement des glandes mandibulaires de Décapode Brachyoure *Carcinus maenas* L.: Animaux témoins et animaux sans pédoncles oculaires. *C.R. Acad. Sci. Paris* 281D: 1887-1889.

Depledge, M.H. 1984. Disruption of circulatory and respiratory activity in shore crabs (*Carcinus maenas* (L.)) exposed to heavy metal pollution. *Comp. Biochem. Physiol.* 78C: 445-459.

Derby, C.D. 1989. Physiology of sensory neurons in morphologically identified cuticular sensilla of crustaceans. In: Felgenhauer, B.E., Watling, L. & Thistle, A.B. (eds), *Crustacean Issues 6*; *Functional morphology of feeding and grooming in Crustacea*: 27-47. Rotterdam: Balkema.

Derby, C.D. & Atema, J. 1988. Chemoreceptor cells in aquatic invertebrates: peripheral mechanisms of chemical signal processing in Decapod Crustaceans. In: Atema, J., Fay, R.R., Popper, A.N. & Tavolga, W.N. (eds), *Sensory Biology of Aquatic Animals*: 365-385. New York: Springer.

Detlefsen, G.U. 1984. *Krabben. Garnelen - Granate.* Husum: Husum Druck- u. Verlagsgesellschaft.

Dexter, B.L. 1981. Setogenesis and molting in planktonic crustaceans. *J. Plankton Res.* 3: 1-13.

Díaz, G.G. & Kasahara, S. 1987. The morphological development of *Macrobrachium rosenbergii* (de Man) larvae. *J. Fac. Appl. Biol. Sci., Hiroshima Univ.* 26: 43-56.

Díaz, H. & Bevilacqua, M. 1987. Early developmental sequences of *Aratus pisonii* (H. Milne Edwards) (Brachyura, Grapsidae) under laboratory conditions. *J. Coast. Res.* 3: 63-70.

DiBacco, C. & Levin, L. 2000. Development and application of elemental fingerprinting to track the dispersal of marine invertebrate larvae. *Limnol. Oceanogr.* 45 (4): 871-880.

Dickson, G.W. & Giesy, J.P. 1982. The effects of starvation on muscle phosphoadenylate concentration and adenylate energy charge of surface and cave crayfish. *Comp. Biochem. Physiol.* 71A: 357-361.

Diesel, R. 1992. Managing the offspring environment: brood care in the bromeliad crab, *Metopaulias depressus*. *Behav. Ecol. Sociobiol.* 30 (2): 125-134.

Diesel, R. 1997. Maternal control of calcium concentration in the larval nursery of the Bromeliad Crab, *Metopaulias depressus* (Grapsidae). *P. Roy. Soc. Lond. B. Bio.* 264: 1403-1406.

Diesel, R. & Horst, D. 1995. Breeding in a snail shell: ecology and biology of the Jamaican montane crab *Sesarma jarvisi* (Decapoda: Grapsidae). *J. Crust. Biol.* 15: 179-195.

Diesel, R. & Schuh, M. 1993. Maternal care in the bromeliad crab *Metopaulias depressus*(Decapoda): maintaining oxygen, pH and calcium levels optimal for the larvae. *Behav. Ecol. Sociobiol.* 32 (1): 11-15.

Diesel, R. & Schuh, M. 1998. Effects of salinity and starvation on larval development of the crabs *Armases ricordi* and *A. roberti* (Decapoda: Grapsidae) from Jamaica, with notes on the biology and ecology of adults. *J. Crust. Biol.* 18 (3): 423-436.

Dietrich, A. & Uhlig, G. 1984. Stage-specific classification of copepods with automatic image analysis. *Crustaceana Suppl.* 7: 159-165.

Diggles, B.K., Moss, G.A., Carson, J. & Anderson, C.D. 2000. Luminous vibriosis in rock lobster *Jasus verreauxi* (Decapoda: Palinuridae) phyllosoma larvae associated with infection by *Vibrio harveyi*. *Dis. Aquat. Organ.* 43: 127-137.

Dilling, L., Wilson, J., Steinberg, D. & Alldredge, A. 1998. Feeding by the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow. *Mar. Ecol. Prog. Ser.* 170: 189-201.

Dittel, A., Epifanio, C.E. & Natunewicz, C. 1996. Predation on mud crab megalopae, *Panopeus herbstii* H. Milne Edwards: effect of habitat complexity, predator species and postlarval densities. *J. Exp. Mar. Biol. Ecol.* 199: 191-202.

Dittel, A.I., Epifanio, C.E., Cifuentes, L.A. & Kirchman, D.L. 1997. Carbon and nitrogen sources for shrimp postlarvae fed natural diets from a tropical mangrove system. *Est. Coast. Shelf Sci.* 45 (5): 629-637.

Dittel, A.I., Epifanio, C.E., Schwalm, S.M., Fantle, M.S. & Fogel, M.L. 2000. Carbon and nitrogen sources for juvenile blue crabs *Callinectes sapidus* in coastal wetlands. *Mar. Ecol. Prog. Ser.* 194: 103-112.

Dobkin, S. 1961. Early developmental stages of pink shrimp, *Penaeus duorarum,* from Florida waters. *Fish. Bull. U.S.* 61: 321-349.

Dobkin, S. 1968. The larval development of a species of *Thor* (Caridea, Hippolytidae) from South Florida. *Crustaceana* Suppl. 2: 1-18.

Dobkin, S. 1969. Abbreviated larval development in caridean shrimps and its significance in the artificial culture of these animals. *FAO Fisheries Rep.* 57: 935-945.

Donelly, T.W. 1989. History of marine barriers and terrestrial connections: Caribbean palaeogeographic inference from pelagic sediment analyses. In: Woods, C.A. (ed), *Biogeography of the West Indies. Past, Present, and Future*: 103-118. Gainesville, FL: Sandhill Crane Press.

Douglass, J.K. & Forward, R.B. 1989. The ontogeny of facultative superposition optics in a shrimp eye: hatching through metamorphosis. *Cell Tissue Res.* 258: 289-300.

Drach, P. 1939. Mue et cycle d'intermue chez les Crustacés Décapodes. *Annls. Inst. Océanogr., Monaco* 19: 103-391.

Drach, P. & Tchernigovtzeff, C. 1967. Sur la méthode de détermination des stades d'intermue et son application générale aux crustacés. *Vie Et Milieu Serie A - Biologie Marine* 18: 595-609.

Dubois, D.M. 1975. Simulation of the spatial structuration of a patch of prey-predator plankton populations in the Southern Bight of the North Sea. *Mém. Soc. Roy. Sci. Liège* 6, 7: 75-82.

Dupré, E.M. & Guisado, C.A. 1996. Identificación de los primeros estados de phyllosoma de la langosta de Juan Fernández (*Jasus frontalis*) mantenidos en laboratorio. *Invest. Mar. Valparaíso* 24: 39-50.

Durnad, S., Lightner, D.V., Nunan, L.M., Redman, R.M., Mari, J. & Bonami, J.-R. 1996. Application of gene probes as diagnostic tools for white spot baculovirus (WSBV) of penaeid shrimp. *Dis. Aquat. Org.* 27: 59-66.

Ebert, E.E., Haseltine, A.W., Houk, J.L. & Kelly, R.O. 1983. Laboratory cultivation of the dungeness crab, *Cancer magister*. *Fish. Bull.* 172: 259-309.

Echalier, G. 1954. Recherches expérimentales sur le rôle de "l'organe Y" dans le mue de *Carcinus maenas* (L.) (Crustacés Décapodes). *C.R. Acad. Sci. Paris* 238: 523-525.

Echalier, G. 1955. Rôle de l'organe Y dans le déterminisme de la mue de *Carcinus (Carcinides) maenas* (L.) (Crustacés Décapodes): Experiences d'implantation. *C.R. Acad. Sci. Paris* 240: 1581-1583.

Eggleston, D.B. & Armstrong, D.A. 1995. Pre- and post-settlement determinants of estuarine dungeness crab recruitment. *Ecol. Monogr.* 65: 193-216.

Elliott, J.K. & Leggett, W.C. 2000. Larval condition and vulnerability to predation: reply to comment by Suthers. *Can. J. Fish. Aquat. Sci.* 57 (7): 1537-1538.

Elliott, J.M. & Davison, W. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia* 19: 195-201.

Elofsson, R. 1963. The nauplius eye and frontal organs in Decapoda (Crustacea). *Sarsia* 12: 1-68.
Elofsson, R. 1966. Notes on the development of the nauplius eye and frontal organs of decapod crustaceans. *Acta Univ. Lundensis II* 27: 1-23.
Elofsson, R. 1969. The development of the compound eyes of *Penaeus duorarum* (Crustacea: Decapoda) with remarks on the nervous system. *Z. Zellforsch.* 97: 323-350.
Emerson, D.N. 1969. Influence of salinity on ammonia excretion rates and tissue constituents of euryhaline invertebrates. *Comp. Biochem. Physiol.* 29: 1115-1133.
Emiliani, C. 1993. Viral extinctions in deep-sea species. *Nature* 366: 217-218.
Emmerson, W.D. 1980. Ingestion, growth and development of *Penaeus indicus* larvae as a function of *Thalassiosira weissflogii* cell concentration. *Mar. Biol.* 58 (1): 65-73.
Emmerson, W.D. 1984. Predation and energetics of *Penaeus indicus* (Decapoda: Penaeidae) larvae feeding on *Brachionus plicatilis* and *Artemia* nauplii. *Aquaculture* 38 (3): 201-209.
Ennis, G.P. 1995. Larval and postlarval ecology. In: Factor, J.R. (ed), *Biology of the lobster Homarus americanus*: 23-46. San Diego, New York: Academic Press.
Epifanio, C.E. 1971. Effects of dieldrin in seawater on the development of two species of crab larvae, *Leptodius floridanus* and *Panopeus herbstii*. *Mar. Biol.* 11 (4): 356-362.
Epifanio, C.E. 1972. Effects of dieldrin-contaminated food on the development of *Leptodius floridanus* larvae. *Mar. Biol.* 13 (4): 292-297.
Epifanio, C.E. 1987. The role of tidal fronts in maintaining patches of Brachyuran zoeae in estuarine waters. *J. Crust. Biol.* 7 (3): 513-517.
Epifanio, C.E. 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off Mid-Atlantic States. *B. Mar. Sci.* 57: 713-725.
Epifanio, C.E. (in press). Larval biology. In: Kennedy, V.S. & Cronin, L.E. (eds), *The Blue Crab Callinectes sapidus*. College Park, MD: Maryland Sea Grant.
Epifanio, C.E. & Dittel, A.I. 1982. Comparison of dispersal of crab larvae in Delaware Bay, USA, and the Gulf of Nicoya, Central America. In: Kennedy, V.S. (ed), *Estuarine Comparisons*: 477-487. New York: Academic Press.
Epifanio, C.E., Dittel, A.I., Park, S., Schwalm, S. & Fouts, A. 1998. Early life history of *Hemigrapsus sanguineus*, a non-indigenous crab in the Middle Atlantic Bight (USA). *Mar. Ecol. Prog. Ser.*170: 231-238.
Epifanio, C.E. & Garvine, R.W. 2001. Larval transport on the Atlantic continental shelf of North America: a review. *Est. Coast. Shelf Sci.* 52 (1): 51-77.
Epifanio, C.E., Perovich, G., Dittel, A.I. & Cary, S.C. 1999. Development and behavior of megalopa larvae and juveniles of the hydrothermal vent crab *Bythograea thermydron*. *Mar. Ecol. Prog. Ser.* 185: 147-154.
Epifanio, C.E., Valenti, C.C. & Pembroke, A.E. 1984. Dispersal and recruitment of blue crab larvae in Delaware Bay, USA. *Est. Coast. Shelf Sci.* 18 (1): 1-12.
Erri Babu, D. & Anger, K. 1987. The structure and modification of integumental tissues in *Pagurus bernhardus* (L.) (Decapoda: Anomura). *J. Exp. Mar. Biol. Ecol.* 112: 267-281.
Escribano, R., Rodriguez, L. & Irribarren, C. 1998. Temperature-dependent development and growth of *Calanus chilensis* Brodsky from Northern Chile. *J. Exp. Mar. Biol. Ecol.* 229: 19-34.
Ettershank, G. 1983. Age structure and cyclical annual size change in the Antarctic krill, *Euphausia superba*, Dana. *Polar Biology* 2: 189-193.
Ettershank, G. 1984. A new approach to the assessment of longevity in the Antarctic krill, *Euphausia superba*. *J. Crust. Biol.* 4: 295-305.
Ewald, J.J. 1969. Observations on the biology of *Tozeuma carolinense* (Decapoda, Hippolytidae) from Florida, with special reference to larval development. *Bull. Mar. Sci.* 19: 510-549.
Factor, J.R. 1981a. Unusually complex basement membranes in the midgut of two Decapod Crustaceans, the stone crab (*Menippe mercenaria*) and the lobster (*Homarus americanus*). *The Anatomical Record* 200: 253-258.

Factor, J.R. 1981b. Development and metamorphosis of the digestive system of larval lobsters, *Homarus americanus* (Decapoda: Nephropidae). *J. Morphol.* 169: 225-242.

Factor, J.R. 1989. Development of the feeding apparatus in decapod crustaceans. In: Felgenhauer, B.E., Watling, L. & Thistle, A.B. (eds), *Crustacean Issues 6*; *Functional morphology of feeding and grooming in Crustacea*: 185-203. Rotterdam: Balkema.

Factor, J.R. 1995a. Introduction, anatomy, and life history. In: Factor, J.R. (ed), *Biology of the lobster Homarus americanus*: 1-11. San Diego, New York: Academic Press.

Factor, J.R. (ed) 1995b. *Biology of the lobster Homarus americanus.* San Diego: Academic Press.

Fagetti, E.G. & Campodonico, I. 1971. Larval development of the red crab *Pleuroncodes monodon* (Decapoda Anomura: Galatheidae) under laboratory conditions. *Mar. Biol.* 8: 70-81.

Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A. & Sargent, J. 2000. Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Can. J. Fish. Aquat. Sci.* 57: 178-191.

Fang, L.-S. & Lee, B.-N. 1992. Ontogenic change of digestive enzymes in *Penaeus monodon*. *Comp. Biochem. Physiol.* 103B: 1033-1037.

Farmer, A.S.D. 1974. The development of the external sexual characters of *Nephrops norvegicus* (L.) (Decapoda: Nephropidae). *J. Nat. Hist.* 8: 241-255.

Felder, D.L. & Felgenhauer, B.E. 1993. Morphology of the midgut-hindgut juncture in the ghost shrimp *Lepidophthalmus lousianensis* (Schmitt) (Crustacea: Decapoda: Thalassinidea). *Acta Zoologica* 74 (4): 263-276.

Felder, D.L., Martin, J.W. & Goy, J.W. 1985. Patterns in early postlarval development of Decapods. In: Wenner, A.M. (ed), *Crustacean Issues 2*; *Larval Growth*: 163-225. Rotterdam: Balkema.

Felder, J.M., Felder, D.L. & Hand, S.C. 1986. Ontogeny of osmoregulation in the estuarine ghost shrimp *Callianassa jamaicense* var. *louisianensis* Schmitt (Decapoda, Thalassinidae). *J. Exp. Mar. Biol. Ecol.* 99: 91-105.

Feldman, K.L., Armstrong, D.A., Eggleston, D.B. & Dumbauld, B.R. 1997. Effects of substrate selection and post-settlement survival on recruitment success of the thalassinidean shrimp *Neotrypaea californiensis* to intertidal shell and mud habitats. *Mar. Ecol. Prog. Ser.*150: 121-136.

Felgenhauer, B.E. 1987. Techniques for preparing crustaceans for scanning electron microscopy. *J. Crust. Biol.* 7: 71-76.

Felgenhauer, B.E. 1992a. External anatomy and integumentary structures. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates, Vol. 10: Decapod Crustacea*: 7-43. New York: Wiley-Liss.

Felgenhauer, B.E. 1992b. Internal anatomy of the Decapoda: an overview. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates, Vol. 10: Decapod Crustacea*: 45-75. New York: Wiley-Liss.

Felgenhauer, B.E. & Abele, L.G. 1983a. Ultrastructure and functional morphology of feeding and associated appendages in the tropical freshwater shrimp, *Atya innocuous* (Herbst), with notes on its ecology. *J. Crust. Biol.* 3 (3): 336-363.

Felgenhauer, B.E. & Abele, L.G. 1983b. Phylogenetic relationships among shrimp-like decapods. In: Schram, F.R. (ed), *Crustacean Issues 1*; *Crustacean phylogeny*: 291-309. Rotterdam: Balkema.

Felgenhauer, B.E. & Abele, L.G. 1989. Evolution of the foregut in the lower Decapoda. In: Felgenhauer, B.E., Watling, L. & Thistle, A.B. (eds), *Crustacean Issues 6*; *Functional Morphology of Feeding and Grooming in Crustacea*: 205-218. Rotterdam: Balkema.

Fernández de Puelles, M.L. 1985. Estudio preliminar de la alimentación y mortalidad larvaria del Decápodo *Pisidia longicornis* (Linne) en condiciones de laboratorio. *Bol. Inst. Esp. Oceanogr.* 2: 100-107.

Fernández, M. 1999. Cannibalism in Dungeness crab *Cancer magister*: effects of predator-prey size ratio, density, and habitat type. *Mar. Ecol. Prog. Ser* 182: 221-230.

Ferron, A. & Leggett, W.C. 1994. An appraisal of condition measures for marine fish larvae. *Adv. Mar. Biol.* 30: 217-303.

Fidhiany, L.K.A. & Fujio, Y. 1991. Adult salinity tolerance and larval salinity requirement of the freshwater shrimp *Palaemon paucidens* in Japan. *Tohoku J. Agricult. Res.* 42: 17-24.

Field, R.H. & Appleton, P.L. 1996. An indirect fluorescent antibody technique for the diagnosis of *Hematodinium* sp. infection of the Norway lobster *Nephrops norvegicus*. *Dis. Aquat. Org.* 24: 199-204.

Fielder, D.R. 1970. The larval development of *Macrobrachium australiense* Holthuis, 1950 (Decapoda, Palaemonidae), reared in the laboratory. *Crustaceana* 18: 60-74.

Fielder, D.R., Greenwood, J.G. & Ryall, J.C. 1975. Larval development of the tiger prawn, *Penaeus esculentus* Haswell, 1879 (Decapoda, Penaeidae) reared in the laboratory. *Aust. J. Mar. Fresh. Res.* 26: 155-175.

Fièvet, E. 1998. Distribution et capacits d'expansion des crevettes d'eau douce de la région Caraibe: exemple des genres *Macrobrachium* et *Atya* (Crustacea: Caridea). *Biogeographica* 74 (1): 1-22.

Fincham, A.A. 1980. Eyes and classification of malacostracan crustaceans. *Nature, London* 287: 729-731.

Fincham, A.A. 1983. Larval development of British prawns and shrimps (Crustacea, Decapoda, Natantia). IV. *Palaemon* (Palaemon) *serratus* (Pennant,1777) and functional morphology of swimming. *Bull. Br. Mus. Nat. Hist. (Zool.)* 44: 125-161.

Fincham, A.A. 1984. Ontogeny and optics of the eyes of the common prawn *Palaemon* (*Palaemon*) *serratus* (Pennant, 1777). *Zool. J. Linnean Soc.* 81: 89-113.

Fincham, A.A. 1985. Larval development of British prawns and shrimps (Crustacea, Decapoda, Natantia). V. *Palaemon* (*Palaemon*) *adspersus* Rathke, 1837). *Bull. Br. Mus. Nat. Hist. (Zool.)* 48: 215-231.

Fincham, A.A. 1988. Ontogeny of anomuran eyes. In: Fincham, A.A. & Rainbow, P.S. (eds), *Aspects of Decapod Crustacean Biology, Symposia of the Zoological Society of London 59*. Oxford: Clarendon Press.

Fingerman, M. 1992. Glands and secretion. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates 10*; *Decapod Crustacea*: 345-394. New York: Wiley-Liss.

Fingerman, M., Hanumante, M.M., Kulkarni, G.K., Ikeda, R. & Vacca, L.L. 1985. Localization of substance P-like, leucine-enkephalin-like, methionine-enkephalin-like, and FMRF-amide-like immunoreactivity in the eyestalk of the fiddler crab, *Uca pugilator*. *Cell Tissue Res.* 241: 473-477.

Finn, R.N., Fyhn, J.H. & Evjen, M.S. 1995. Physioloical energetics of developing embryos and yolk-sac larvae of Atlantic cod (*Gadus morhua*). I. Respiration and nitrogen metabolism. *Mar. Biol.* 124: 355-369.

Fisher, L.R. 1960. Vitamins. In: Watermann, T.H. (ed), *The Physiology of Crustacea 1*; *Metabolism and growth*: 259-289. New York: Academic Press.

Fisher, W.S. & Nelson, R.T. 1978. Application of antibiotics in the cultivation of Dungeness crab, *Cancer magister*. *J. Fish. Res. Bd. Can.* 35: 1343-1349.

Fisher, W.S., Nilson, E.H., Steenbergen, J.F. & Lightner, D.V. 1978. Microbial diseases of cultured lobsters: a review. *Aquaculture* 14: 115-140.

Fitzgerald, T.P., Forward, R.B. & Tankersley, R.A. 1998. Metamorphosis of the estuarine crab *Rhithropanopeus harrisii:* effect of water type and adult odor. *Mar. Ecol. Prog. Ser.* 165: 217-223.

Flegel, T.W., Thamavit, V., Pasharawipas, T. & Alday-Sanz, V. 1999. Statistical correlation between severity of hepatopancreatic parvovirus infection and stunting of farmed black tiger shrimp (*Penaeus monodon*). *Aquaculture* 174: 197-206.

Fletcher, B.L., Dillard, C.J. & Tappel, A.L. 1973. Measurements of fluorescent lipid peroxidation products in biological systems and tissues. *Analyt. Biochem.* 52: 1-9.

Floreto, E.A.T., Prince, D.L., Brown, P.B. & Bayer, R.C. 2000. The biochemical profiles of shell-diseased American lobsters, *Homarus americanus* Milne. *Aquaculture* 188 (3-4): 247-262.

Florkin, M. 1960. Blood chemistry. In: Waterman, T.H. (ed), *The Physiology of Crustacea 1*: 141-160. New York: Academic Press.

Fordyce, D. & Cronin, T.W. 1989. Comparison of fossilized schizochroal compound eyes of phacopid trilobites with eyes of modern marine crustaceans and other arthropods. *J. Crust. Biol.* 9: 554-569.

Forest, J. 1994. Crustacés. Vol. 1. Morphologie, Physiologie, Reproduction, Systématique. In: Grassé, P.-P. (ed), *Traité de Zoologie. 6*: 1-917.

Forss, C.A. & Coffin, H.G. 1960. The use of the brine shrimp nauplii, *Artemia salina,* as food for the laboratory culture of decapods. *Walla Walla College Publications Dept. Biol. Sci. and Biol. Stn.* 26: 1-17.

Forward, R.B. 1974. Negative phototaxis in crustacean larvae: possible functional significance. *J. Exp. Mar. Biol. Ecol.* 16: 11-17.

Forward, R.B. 1976a. Light and diurnal vertical migration: Photobehavior and photophysiology of plankton. In: Smith (ed), *Photochemical and Photobiological Review 1*: 157-209.

Forward, R.B. 1976b. A shadow response in a larval crustacean. *Biol. Bull.* 151: 126-140.

Forward, R.B. 1977. Occurence of a shadow response among brachyuran larvae. *Mar. Biol.* 39: 331-341.

Forward, R.B. 1986. A reconsideration of the shadow response of a larval crustacean. *Mar. Fresh. Behav. Physiol.* 12 (2): 99-113.

Forward, R.B. 1987a. Comparative study of crustacean larval photoresponses. *Mar. Biol.* 94: 589-595.

Forward, R.B. 1987b. Larval release rhythms of decapod crustaceans: an overview. *Bull. Mar. Sci.* 41: 165-176.

Forward, R.B. 1989a. Behavioral responses of crustacean larvae to rates of salinity change. *Biol. Bull.* 176: 229-238.

Forward, R.B. 1989b. Depth regulation of larval marine decapod crustaceans: test of an hypothesis. *Mar. Biol.* 102: 195-201.

Forward, R.B. 1990. Behavioral responses of crustacean larvae to rates of temperature change. *Biol. Bull.* 178: 195-204.

Forward, R.B. 1993. Photoresponses during diel vertical migration of brine shrimp larvae: Effect of predator exposure. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 39: 37-44.

Forward, R.B. & Buswell, C.U. 1989. A comparative study of behavioural responses of larval decapod crustaceans to light and pressure. *Mar. Behav. Physiol.* 16: 43-56.

Forward, R.B. & Costlow, J.D. 1974. The ontogeny of phototaxis by larvae of the crab *Rhithropanopeus harrisii*. *Mar. Biol.* 26: 27-33.

Forward, R.B. & Costlow, J.D. 1976. Crustacean larval behavior as an indicator of sublethal effects of an insect juvenile hormone mimic. In: Wiley, M. (ed), *Estuarine processes 1*: 279-289. New York: Academic Press.

Forward, R.B. & Costlow, J.D. 1978. Sublethal effects of insect growth regulators upon crab larval behavior. *Wat. Air Soil Pollut.* 9: 227-238.

Forward, R.B., De Vries, M.C., Rittschof, D., Frankel, D.A.Z., Bischoff, J.P., Fisher, C.M. & Welch, J.M. 1996. Effects of environmental cues on metamorphosis of the blue crab *Callinectes sapidus*. *Mar. Ecol. Prog. Ser.* 131: 165-177.

Forward, R.B. & Douglass, J.K. 1989. Crustacean larval visual sensitivity during diel vertical migration. In: Klekowski, R.Z., Styczynska-Jurewicz, E. & Falkowski, L. (eds), *Proceedings of the twenty first European Mar. Biol. Symposium, Gdansk, Poland, 14-19 Sept. 1986*

Forward, R.B., Lohmann, K. & Cronin, T.W. 1982. Rhythms in larval release by an estuarine crab (*Rhithropanopeus harrisii*). *Biol. Bull.* 163: 287-300.

Forward, R.B. & Lohmann, K.J. 1983. Control of egg hatching in the crab *Rhithropanopeus harrisii* (Gould). *Biol. Bull.* 165: 154-166.

Forward, R.B. & Rittschof, D. 1993. Activation of photoresponses of brine shrimp nauplii involved in diel vertical migration by chemical cues from fish. *J. Plankton Res.* 15: 693-701.

Forward, R.B. & Rittschof, D. 1999. Brine shrimp larval photoresponses involved in diel vertical migration: activation by fish mucus and modified amino sugars. *Limnol. Oceanogr.* 44 (8): 1904-1916.

Forward, R.B. & Rittschof, D. 2000. Alteration of photoresponses involved in diel vertical migration of a crab larva by fish mucus and degradation products of mucopolysaccharides. *J. Exp. Mar. Biol. Ecol.* 245 (2): 277-292.

Forward, R.B., Rittschof, D. & De Vries, M.C. 1987. Peptide pheromones synchronize crustacean egg hatching and larval release. *Chem. Senses* 12: 491-498.

Forward, R.B., Swanson, J., Tankersely, R.A. & Welch, J.M. 1997a. Endogenous swimming rhythms of blue crab, *Callinectes sapidus,* megalopae: effects of offshore and estuarine cues. *Mar. Biol.* 127: 621-628.

Forward, R.B., Tankersley, R.A., Blondel, D. & Rittschof, D. 1997b. Metamorphosis of the blue crab *Callinectes sapidus:* effects of humic acids and ammonium. *Mar. Ecol. Prog. Ser.* 157: 277-286.

Forward, R.B. & Wellins, C.A. 1989. Behavioral responses of a larval crustacean to hydrostatic pressure: *Rhithropanopeus harrisii* (Brachyura: Xanthidae). *Mar. Biol.* 101: 159-172.

Foskett, J.K. 1977. Osmoregulation in the larvae and adults of the grapsid crab *Sesarma reticulatum* Say. *Biol. Bull. Mar. Biol. Lab. Woods Hole* 153: 505-526.

Fraser, A.J. 1989. Triacylglycerol content as a condition index for fish, bivalve, and crustacean larvae. *Can. J. Fish. Aquat. Sci.* 46: 1868-1873.

Freeman, J.A. 1990. Molt increment, molt cycle duration, and tissue growth in *Palaemonetes pugio* Holthuis larvae. *J. Exp. Mar. Biol. Ecol.* 143: 47-61.

Freeman, J.A. 1991. Growth and morphogenesis in crustacean larvae. *Mem. Queensl. Mus.* 31: 309-319.

Freeman, J.A. 1993. The crustacean epidermis during larval development. In: Horst, M.N. & Freeman, J.A. (eds), *The crustacean integument. Morphology and biochemistry*: 193-219. Boca Raton, FL: CRC Press.

Freeman, J.A. 1995. Epidermal cell cycle and region-specific growth during segment development in *Artemia*. *J. Exp. Zool.* 271: 285-295.

Freeman, J.A., Cheshire, L.B. & MacRae, T.H. 1992. Epithelial morphogenesis in developing *Artemia:* the role of cell replication, cell shape change, and the cytoskeleton. *Dev. Biol.* 152: 279-292.

Freeman, J.A. & Costlow, J.D. 1980. The molt cycle and its hormonal control in *Rhithropanopeus harrisii* larvae. *Roux´s Archives of Dev. Biol.* 74: 479-485.

Freeman, J.A. & Costlow, J.D. 1983. Endocrine control of spine epidermis resorption during metamorphosis in crab larvae. *Roux´s Archives of Dev. Biol.* 192: 362-365.

Freeman, J.A. & Costlow, J.D. 1984. Endocrine control of apolysis in *Rhithropanopeus harrisii* larvae. *J. Crust. Biol.* 4: 1-6.

Freeman, J.A. & Porterfield, M. 1996. Nutrient stimulation of epidermal growth in developing *Artemia*. *Aquacult. Nutr.* 2: 201-206.

Freeman, J.A., West, T.L. & Costlow, J.D. 1983. Postlarval growth in juvenile *Rhithropanopeus harrisii*. *Biol. Bull.* 165: 409-415.

Frost, B.W. 1977. Feeding behavior of *Calanus pacificus* in mixtures of food particles. *Limnol. Oceanogr.* 22: 472-491.

Frydel, M.B. 1979. Ontogenesis of the neurosecretory system in the crab *Rhithropanopeus harrisii* (Gould) subspecies *tridentatus* (Maitland). *Zool. Pol.* 27: 255-277.

Furigo, F. 1993. Kiemenentwicklung der chinesischen Wollhandkrabbe, *Eriocheir sinensis,* unter besonderer Berücksichtigung osmoregulatorischer Funktionen. M. Sc. Thesis, Universität Gießen, Germany, 86 pp.

Furota, T. 1996. Life cycle studies on the introduced spider crab *Pyromaia tuberculata* (Lockington) (Brachyura: Majidae). I. Egg and larval stages. *J. Crust. Biol.* 16: 71-76.

Gabe, M. 1953. Sur l'existence, chez quelques Crustacés Malacostracés, d'un organe comparable à la glande de la mue des insectes. *C. R. Acad. Sci. Paris* 237: 1111-1113.

Galgani, F.G. & Benyamin, Y. 1985. Radioimmunoassay of shrimp trypsin: application to the larval development of *Penaeus japonicus* Bate, 1888. *J. Exp. Mar. Biol. Ecol.* 87: 145-151.

Galgani, F.G., Benyamin, Y. & Ceccaldi, H.J. 1984. Identification of digestive proteinases of *Penaeus kerathurus* (Forskal): a comparison with *Penaeus japonicus* Bate. *Comp. Biochem. Physiol.* 78: 355-361.

Galindo, R.J.G., Medina, J.A. & Villagrana, L.C. 1996. Physiological and biochemical changes in shrimp larvae (*Penaeus vannamei*) intoxicated with organochlorine pesticides. *Mar. Poll. Bull.* 32: 872-875.

Galois, R. 1987. Les lipides neutres chez les Crustaces Decapodes: metabolisme et besoins. *Océanis* 13: 197-215.

Gardner, C. & Maguire, G.B. 1998. Effect of photoperiod and light intensity on survival, development and cannibalism of larvae of the Australian giant crab *Pseudocarcinus gigas* (Lamarck). *Aquaculture* 165: 51-63.

Gardner, C. & Northam, M. 1997. Use of prophylactic treatments for larval rearing of giant crabs *Pseudocarcinus gigas* (Lamarck). *Aquaculture* 158 (3-4): 203-214.

Garrison, L.P. 1999. Vertical migration behavior and larval transport in brachyuran crabs. *Mar. Ecol. Prog. Ser.*176: 103-113.

Gaten, E. 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contr. Zool.* 67: 223-235.

Gaten, E. & Herring, P.J. 1995. Morphology of the reflecting superposition eyes of larval ophlophorid shrimps. *J. Morphol.* 225: 19-29.

Gaten, E., Herring, P.J., Shelton, P.M.J. & Johnson, M. 1998a. The development and evolution of the eyes of vent shrimps (Decapoda: Bresiliidae). *Cah. Biol. Mar.* 39: 287-290.

Gaten, E., Herring, P.J., Shelton, P.M.J. & Johnson, M.L. 1998b. Comparative morphology of the eyes of postlarval bresiliid shrimps from the region of hydrothermal vents. *Biol. Bull.* 194: 267-280.

Gaudy, R. & Boucher, J. 1983. Relation between respiration, excretion (ammonia and inorganic phosphorus) and activity of amylase and trypsin in different species of pelagic copepods from an Indian Ocean equatorial area. *Mar. Biol.* 75: 37-45.

Gebauer, P., Paschke, K. & Anger, K. 1999. Costs of delayed metamorphosis: reduced growth and survival in early juveniles of an estuarine grapsid crab, *Chasmagnathus granulata*. *J. Exp. Mar. Biol. Ecol.* 238: 271-281.

Gebauer, P., Paschke, K. & Anger, K., submitted. Metamorphosis in a semiterrestrial crab, *Sesarma curacaoense*: intra- and interspecific settlement cues from adult odors. *J. Exp. Mar. Biol. Ecol.*

Gebauer, P., Walter, I. & Anger, K. 1998. Effects of substratum and conspecific adults on the metamorphosis of *Chasmagnathus granulata* (Dana) (Decapoda: Grapsidae) megalopae. *J. Exp. Mar. Biol. Ecol.* 223: 185-198.

Gellissen, G., Hennecke, R. & Spindler, K.-D. 1991. The site of synthesis of hemocyanin in the crayfish, *Astacus leptodactylus*. *Experientia* 47: 194-195.

Genmoto, K., Nishizawa, T., Nakai, T. & Muroga, K. 1996. 16S rRNA targeted RT-PCR for the detection of *Vibrio penaeicida,* the pathogen of cultured kuruma prawn *Penaeus japonicus*. *Dis. Aquat. Org.* 24: 185-189.

Genthner, F.J., Foss, S.S. & Glas. P.S. 1997. Virulence of *Metarhizium anisopliae* to embryos of the grass shrimp *Palaemonetes pugio*. *J. Invert. Pathol.* 69 (2): 157-164.

Gerritsen, J. & Strickler, J.R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Bd. Can.* 14: 73-82.

Getchell, R.G. 1989. Bacterial shell disease in crustaceans: a review. *J. Shellfish Res.* 8: 1-6.

Gharrett, J.A., Rice, S.D. & Stekoll, M.S. 1985. Influence of an oil-contaminated diet on feeding rates, growth, and molting success of juvenile red king crabs, *Paralithodes camtschatica*. In: Melteff, B.R. (ed), *Proc. Int. King Crab Symp., Lowell Wakefield Fisheries Symposium Series*. Alaska, Fairbanks: University of Alaska, Fairbanks.

Ghiselin, M.T. 1987. Evolutionary aspects of marine invertebrate reproduction. In: Giese, A.C., Pearse, J.S. & Pearse, V.B. (eds), *Reproduction of Marine Invertebrates 9*; *General Aspects: Seeking Unity in Diversity*: 609-665. Palo Alto and Pacific Grove, California: Blackwell Scientific Publications and The Boxwood Press.

Gibson, R. & Barker, P.L. 1979. The decapod hepatopancreas. *Oceanogr. Mar. Biol. Annu. Rev.* 17: 285-346.

Gil-Turnes, M.S. & Fenical, W. 1992. Embryos of *Homarus americanus* are protected by epibiotic bacteria. *Biol. Bull.* 182: 105-108.

Gilles, R. & Péqueux, A. 1983. Interactions of chemical and osmotic regulation with the environment. In: Vernberg, F.J. & Vernberg, W.B. (eds), *The Biology of Crustacea 8*; *Environmental Adaptations*: 109-177. New York: Academic Press.

Giménez, L. 2000. El efecto de la salinidad y la biomasa inicial en el desarrollo larval del cangrejo estuarino *Chasmagnathus granulata* (Crustacea, Decapoda). Dissertation, Universidad de la República, Montevideo, Uruguay, 145 pp.

Giménez, L. & Anger, K. 2001. Relationships among egg size, embryonic development, and larval biomass in the estuarine crab *Chasmagnathus granulata* Dana, 1851. *J. Exp. Mar. Biol. Ecol.* 260: 241-257.

Ginsburger-Vogel, T. & Charniaux-Cotton, H. 1982. Sex determination. In: Abele, L.G. (ed), *The Biology of Crustacea 2*; *Embryology, Morphology and Genetics*: 257-281. New York: Academic Press.

Giulianini, P.G., Smullen, R.P., Bentley, M.G. & Ferrero, E.A. 2000. Localisation of crustacean hyperglycemic hormone in late embryonic and first larval stage of *Nephrops norvegicus* (Astacoidea, Nephropidae). *Ital. J. Zool.* 67: 339-341.

Glaessner, M.F. 1969. Decapoda. In: Moore, R.C. (ed), Treatise on Invertebrate Palaeontology 4 (2); Part R, Arthropoda: 399-533. Lawrence, Kansas: Geol. Soc. Am. and Kansas Press.

Gliwicz, Z.M. & Lampert, W. 1993. Body-size related survival of cladocerans in a trophic gradient: an enclose study. *Arch. Hydrobiol.* 129: 1-23.

Gnaiger, E. 1983. Calculation of energetic and biochemical equivalents of respiratory oxygen consumption. In: Gnaiger, E. & Forstner, H. (eds), *Polarographic oxygen sensors*: 337-345. Berlin: Springer.

Gnaiger, E. & Bitterlich, G. 1984. Proximate biochemical composition and caloric content calculated from elemental CHN analysis: a stoichiometric concept. *Oecologia* 62: 289-298.

Gonor, S.L. & Gonor, J.J. 1973. Feeding, cleaning, and swimming behavior in larval stages of porcellanid crabs (Crustacea: Anomura). *Fish. Bull.* 71: 225-234.

González-Gordillo, J.I. & Rodríguez, A. 2000. Larval development of *Philocheras fasciatus* (Risso, 1816) (Decapoda, Caridea) reared in the laboratory, comparison with plankton larvae and occurrence of accelerated development. *J. Plankton Res.* 22 (10): 1909-1924.

Gore, R.H. 1979. Studies on decapod crustacea from the Indian River region of Florida. 9. Larval development of *Galathea rostrata* under laboratory conditions, with a discussion of larval development in the Galatheidae (Crustacea Anomura). *Fish. B-Noaa* 76 (4): 781-806.

Gore, R.H. 1985. Molting and growth in Decapod larvae. In: Wenner, A.M. (ed), *Crustacean Issues 2*; *Larval Growth*: 1-65. Rotterdam: Balkema.

Gorgels-Kallen, J.L. & Meij, J.T.A. 1985. Immunocytochemical study of the hyperglycemic hormone (CHH)-producing system in the eyestalk of the crayfish *Astacus leptodactylus* during larval and postlarval development. *J. Morphol.* 183: 155-163.

Gorsky, G., Dallot, S., Sardou, J., Fenaux, R., Carré, C. & Palazzoli, I. 1988. C and N composition of some northwestern Mediterranean zooplankton and micronekton species. *J. Exp. Mar. Biol. Ecol.* 124: 133-144.

Gottschalk, C. 1994. Feldökologische und experimentelle Untersuchungen zum Siedeln und zur Substratpräferenz von *Carcinus maenas* (L.) (Decapoda, Portunidae). M. Sc. Thesis, Freie Universität Berlin, Germany, 139 pp.

Goudeau, M., Lachaise, F., Carpentier, G. & Goxe, B. 1990. High titers of ecdysteroids are associated with the secretory process of embryonic envelopes in the European lobster. *Tissue Cell* 22: 269-281.

Govind, C.K. 1992. Nervous System. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates 10*; *Decapod Crustacea*: 395-438. New York: Wiley-Liss.

Graf, F. 1986. Fine determination of the molt cycle stages in *Orchestia cavimana* Heller (Crustacea: Amphipoda). *J. Crust. Biol.* 6: 666-678.

Grahame, J. 1983. Adaptive aspects of feeding mechanisms. In: Vernberg, F.J. & Vernberg, W.B. (eds), *The Biology of Crustacea 8*; *Environmental Adaptations*: 65-107. New York: Academic Press.

Grant, A. 1983. On the evolution of brood protection in marine benthic invertebrates. *Am. Nat.* 122: 549-555.

Greenaway, P. 1988. Ion and water balance. In: Burggren, W.W. & McMahon, B.R. (eds), *Biology of the Land crabs*: 211-248. New York: Cambridge University Press.

Greenaway, P. 1991. Nitrogenous excretion in aquatic and terrestrial crustaceans. *Mem. Queensland Mus.* 31: 215-227.

Greenaway, P. 1999. Physiological diversity and the colonization of land. In: Schram, F.R. & von Vaupel Klein, J.C.; *Crustaceans and the Biodiversity Crisis* 1: 823-842. Leiden: Brill.

Greene, E. 1999. Phenotypic variation in larval development and evolution: polymorphism, polyphenism, and developmental reaction norms. In: Hall, B.K. & Wake, M.H. (eds), *The origin and evolution of larval forms*: 379-410. San Diego: Academic Press.

Gribble, N.A. 1994. Static and functional anatomy of the cardiovascular system of the portunid crab *Portunus pelagicus* (Linnaeus). Part A. Static anatomy. *J. Crust. Biol.* 14: 627-640.

Griffith, C.D.G. 1973. Some fundamental problems in biological classification. *Syst. Zool* 22: 338-343.

Griffith, C.D.G. 1976. The future of the Linnean nomenclature. *Syst. Zool* 25: 168-173.

Grodzinski, W., Klekowski, R.Z. & Duncan, A. 1975. *Methods for Ecological Bioenergetics.* IBP Handbook 24. Oxford: Blackwell.

Gross, P.S. & Knowlton, R.E. 1997. Effects of timed eyestalk ablation on molting in larvae of the snapping shrimp, *Alpheus heterochaelis* Say. *Int. J. Inver. Rep. Dev.* 32 (2): 119-126.

Gross, P.S. & Knowlton, R.E. 1999. Variation in larval size after eyestalk ablation in larvae of the snapping shrimp *Alpheus heterochaelis*. *J. Crust. Biol.* 19 (1): 8-13.

Gu, H., Anderson, A.J., Mather, P.B. & Capra, M.F. 1996. Effects of feeding level and starvation on growth and water and protein content in juvenile redclaw crayfish, *Cherax quadricarinatus* (von Martens). *Mar. Fershwater Res.* 47: 745-748.

Guerao, G., Perezbaquera, J. & Ribera, C. 1994. Growth and reproductive biology of *Palaemon xiphias* Risso, 1816 (Decapoda: Caridea: Palaemonidae). *J. Crust. Biol.* 14 (2): 280-288.

Gurney, R. 1939. *Bibliography of the larvae of decapod Crustacea.* London: Ray Society.

Gurney, R. 1942. *Larvae of decapod Crustacea.* London: Ray Society.

Gurney, R. & Lebour, M.V. 1941. On the larvae of certain Crustacea Macrura mainly from Bermuda. *J. Linn. Soc.* 41: 89-181.

Hadley, P.B. 1906. Regarding the rate of growth of the American lobster (*Homarus americanus* Milne Edwards). *Ann. Report R.I. Comm. Inland Fish.* 36: 153-235 + plates XXVI-XXXVII.

Haeckel, E. 1866. *Generelle Morphologie der Organismen, 1: Allgemeine Grundzüge der organischen Formen. Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie.* Berlin: Riemer.

Hafner, G.S., Tokaski, T. & Hammond-Soltis, G. 1982. Development of the crayfish retina: a light and electron microscopy study. *J. Morphol.* 173: 101-118.

Hagerman, L. 1976. The respiration during the moult cycle of *Crangon vulgaris* (Fabr.) (Crustacea, Natantia). *Ophelia* 15: 15-21.

Hale, H.M. 1925. The development of two Australian sponge crabs. *Proc. Linn. Soc. NSW* 50: 405-413.

Hale, H.M. 1931. The post-embryonic development of an Australian xanthid crab (*Pilumnus vestitus* Haswell). *Rec. South Austr. Mus.* 4: 321-331.

Hall, B.K. & Wake, M.H. 1999. Introduction: Larval development, evolution, and ecology. In: Hall, B.K. & Wake, M.H. (eds), *The origin and evolution of larval forms*: 1-19. San Diego: Academic Press.

Hallberg, E. & Elofsson, R. 1989. Construction of the pigment shield of the crustacean compound eye: a review. *J. Crust. Biol.* 9: 359-372.

Hallberg, E., Johansson, K.U.I. & Elofsson, R. 1992. The aesthetasc concept - structural variations of putative olfactory receptor cell complexes in crustacea. *Microsc. Res. Techniq.* 22 (4): 325-335.

Hallberg, E., Johansson, K.U.I. & Wallen, R. 1997. Olfactory sensilla in crustaceans: morphology, sexual dimorphism, and distribution patterns. *Int. J. Insect Morphol. Embryol.* 26: 173-180.

Hallberg, E. & Kauri, T. 1992. Evidence of a non-photoreceptive function of the sensory units of the organ of Bellonci in *Macrobrachium rosenbergii* (Decapoda, Caridea). *Crustaceana* 62: 137-141.

Hamasaki, K., Takeuchi, T. & Sekiya, S. 1998. Dietary value for larval swimming crab *Portunus trituberculatus* of marine rotifer *Brachionus rotundiformis* cultured with several feeds. *Nippon Suisan Gakk.* 64 (5): 841-846.

Hameed, A.S.S. 1993. A study of the aerobic heterotrophic bacterial flora of hatchery-reared eggs, larvae and postlarvae of *Penaeus indicus*. *Aquaculture* 117: 195-204.

Hampshire, R. & Horn, D.H.S. 1966. Structure of crustecdysone, a crustacean moulting hormone. *Chem. Commun.* 1966: 37-38.

Hansen, B.W. 1999. Cohort growth of planktotrophic polychaete larvae - are they food limited? *Mar. Ecol. Prog. Ser.*178: 109-119.

Hanström, B. 1937. Die Sinusdrüse und der hormonal bedingte Farbwechsel der Crustaceen. *Kungl. Svenska Vetenskap. Handl.* 16: 1-99.

Haond, C., Bonnal, L., Sandeaux, R., Charmantier, G. & Trilles, J.P. 1999. Ontogeny of intracellular isosmotic regulation in the European lobster *Homarus gammarus* (L.). *Physiol. Biochem. Zool.* 72 (5): 534-544.

Harder, T. & Qian, P.-Y. 1999. Induction of larval attachment and metamorphosis in the serpulid polychaete *Hydroides elegans* by dissolved free amino acids: isolation and identification. *Mar. Ecol. Prog. Ser.*179: 259-271.

Harding, G.C., Drinkwater, K.F. & Vass, W.P. 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Marine: an new synthesis. *Can. J. Fish. Aquat. Sci.*40 (2): 168-184.

Harding, G.C. & Fraser, A.J. 1999. Application of the triacylglycerol/sterol condition index to the interpretation of larval lobster *Homarus americanus* distribution in close proximity to Georges Bank, Gulf of Maine. *Mar. Ecol. Prog. Ser.* 186: 239-254.

Harges, P.L. & Forward, R.B. 1982. Salinity perception by larvae of the crab *Rhithropanopeus harrisii* (Gould). *Mar. Behav. Physiol.* 8: 311-331.

Harms, J. 1982. Untersuchungen zur Larvalentwicklung und zum Wachstum von Seepocken der Deutschen Bucht. M.Sc. Thesis, Technische Hochschule Darmstadt, Germany, 118 pp.

Harms, J. 1984. Influence of water temperature on larval development of *Elminius modestus* and *Semibalanus balanoides* (Crustacea, Cirripedia). *Helgoländer Meeresunters.* 38: 123-134.

Harms, J. 1986. Effects of temperature and salinity on larval development of *Elminius modestus* (Crustacea, Cirripedia) from Helgoland (North Sea) and New Zealand. *Helgoländer Meeresunters.* 40: 355-376.

Harms, J. 1990. Accumulation and loss of biomass in *Liocarcinus holsatus* larvae during growth and exuviation. *Mar. Biol.* 104: 183-190.

Harms, J. 1992a. Effects of nutrition (herbivore *vs* carnivore) on energy charge and nucleotide composition in *Hyas araneus* larvae. *Helgoländer Meeresunters.* 46: 29-44.

Harms, J. 1992b. Larval development and delayed metamorphosis in the hermit crab *Clibanarius erythropus* (Latreille) (Crustacea, Diogenidae). *J. Exp. Mar. Biol. Ecol.* 156: 151-160.

Harms, J. & Anger, K. 1990. Effects of nutrition (herbivore *vs.* carnivore) on the energy budget of a brachyuren megalopa. *Thermochimica Acta* 172: 229-240.

Harms, J., Anger, K., Klaus, S. & Seeger, B. 1991. Nutritional effects on ingestion rate, digestive enzyme activity, growth, and biochemical composition of *Hyas araneus* L. (Decapoda: Majidae) larvae. *J. Exp. Mar. Biol. Ecol.* 145: 233-265.

Harms, J., Meyer-Harms, B., Dawirs, R.R. & Anger, K. 1994. Growth and physiology of *Carcinus maenas* (Decapoda, Portunidae) larvae in the field and in laboratory experiments. *Mar. Ecol. Prog. Ser.* 108: 107-118.

Harms, J., Moal, J., Le Coz, J.R., Daniel, J.Y. & Samain, J.F. 1990. Nucleotide composition and energy charge in growing and starving zoea I of *Carcinus maenas* (Decapoda: Portunidae). *Comp. Biochem. Physiol.* 96B: 405-414.

Harms, J. & Seeger, B. 1989. Larval development and survival in seven decapod species (Crustacea) in relation to laboratory diet. *J. Exp. Mar. Biol. Ecol.* 133: 129-139.

Harris, J.M. 1993. The presence, nature and role of gut microflora in aquatic invertebrates: a synthesis. *Microb. Ecol.* 25: 195-231.

Harris, L.J. & Owens, L. 1999. Production of exotoxins by two luminous *Vibrio harveyi* strains known to be primary pathogens of *Penaeus monodon* larvae. *Dis. Aquat. Organ.* 38 (1): 11-22.

Harris, R.P., Samain, J.-F., Moal, J., Martin-Jézéquel, V. & Poulet, S.A. 1986. Effects of algal diet on digestive enzyme activity in *Calanus helgolandicus*. *Mar. Biol.* 90: 353-361.

Harris, R.R. & Santos, M.C.F. 2000. Heavy metal contamination and physiological variability in the Brazilian mangrove crabs *Ucides cordatus* and *Callinectes danae* (Crustacea: Decapoda). *Mar. Biol.* 137 (4): 691-703.

Harrison, F.W. & Humes, A.G. (eds) 1992. *Decapod Crustacea.* Microscopic Anatomy of Invertebrates 10. New York: Wiley-Liss.

Harrison, K.E. 1990. The role of nutrition in maturation, reproduction and embryonic development of decapod crustaceans: a review. *J. Shellfish Res.* 9: 1-28.

Hart, J.F.L. 1935. The larval development of the British Columbia Brachyura. I. Xanthidae, Pinnotheridae (in part) and Grapsidae. *Can. J. Res.* 12: 411-432.

Hartman, M.J. & Sulkin, S. 1999. Effects of prior exposure to petroleum hydrocarbon contamination during brooding on the subsequent larval development of the brachyuran crab *Hemigrapsus oregonensis*. *J. Crust. Biol.* 19: 690-698.

Hartnoll, R.G. 1964. The freshwater grapsid crabs of Jamaica. *Proc. Linn. Soc. Lond.* 175: 145-169.

Hartnoll, R.G. 1971a. The occurrence, methods and significance of swimming in the Brachyura. *Anim. Behav.* 19: 34-50.

Hartnoll, R.G. 1971b. *Sesarma cookei* n.sp., a grapsid crab from Jamaica. *Crustaceana* 20: 257-262.

Hartnoll, R.G. 1982. Growth. In: Abele, L.G. (ed), *The Biology of Crustacea 2*; *Embryology, Morphology and Genetics*: 111-196. New York: Academic Press.

Hartnoll, R.G. 1985. Growth, sexual maturity and reproductive output. In: Wenner, A.M. (ed), *Crustacean Issues 3*; *Factors in adult growth*: 101-128. Rotterdam: Balkema.

Hartnoll, R.G. 1988a. Evolution, systematics, and geographical distribution. In: Burggren, W.W. & McMahon, B.R. (eds), *Biology of the land crabs*: 6-54. New York: Cambridge University Press.

Hartnoll, R.G. 1988b. Growth and molting. In: Burggren, W.W. & McMahon, B.R. (eds), *Biology of the land crabs*: 186-210. New York: Cambridge University Press.

Hartnoll, R.G. & Dalley, R. 1981. The control of size variation within instars of a crustacean. *J. Exp. Mar. Biol. Ecol.* 53 (2-3): 235-239.

Hartnoll, R.G. & Mohamedeen, H. 1987. Laboratory growth of the larvae of six British crabs. *J. Exp. Mar. Biol. Ecol.* 107 (2): 155-170.

Harvey, A.W. 1992. Costs and benefits of delayed metamorphosis in the hermit crab *Clibanarius longitarsus*. *Am. Zool.* 32: 114.

Harvey, A.W. 1993. Larval settlement and metamorphosis in the sand crab *Emerita talpoida* (Crustacea, Decapoda, Anomura). *Mar. Biol.* 117 (4): 575-581.

Harvey, A.W. 1996. Delayed metamorphosis in Florida hermit crabs: multiple cues and constraints (Crustacea: Decapoda: Paguridae and Diogenidae). *Mar. Ecol. Prog. Ser.*141 (1-3): 27-36.

Harvey, A.W. & Colasurdo, E.A. 1993. Effects of shell and food availability on metamorphosis in the hermit crabs *Pagurus hirsutiusculus* (Dana) and *Pagurus granosimanus* (Stimpson). *J. Exp. Mar. Biol. Ecol.* 165 (2): 237-249.

Harvey, E.A. & Epifanio, C.E. 1997. Prey selection by larvae of the common mud crab *Panopeus herbstii* Milne-Edwards. *J. Exp. Mar. Biol. Ecol.* 217: 79-91.

Harzsch, S., Benton, J., Dawirs, R.R. & Beltz, B. 1999a. A new look at embryonic development of the visual system in decapod crustaceans: neuropil formation, neurogenesis, and apoptotic cell death. *J. Neurobiol.* 39: 294-306.

Harzsch, S. & Dawirs, R.R. 1993. On the morphology of the central nervous system in larval stages of *Carcinus maenas* L. (Decapoda, Brachyura). *Helgoländer Meeresunters.* 47: 61-79.

Harzsch, S. & Dawirs, R.R. 1994. Neurogenesis in larval stages of the spider crab *Hyas araneus* (Decapoda, Brachyura): proliferation of neuroblasts in the ventral nerve cord. *Roux's Archives of Dev. Biol.* 204: 93-100.

Harzsch, S. & Dawirs, R.R. 1995a. Maturation of the compound eyes and eyestalk ganglia during larval development of the brachyuran crustaceans *Hyas araneus* L. (Decapoda, Majidae) and *Carcinus maenas* L. (Decapoda, Portunidae). *Zoology* 99: 189-204.

Harzsch, S. & Dawirs, R.R. 1995b. A developmental study of serotonin-immunoreactive neurons in the larval central nervous system of the spider crab *Hyas araneus* (Decapoda, Brachyura). *Invertebr. Neurosci.* 1: 53-65.

Harzsch, S. & Dawirs, R.R. 1996a. Neurogenesis in the developing crab brain: postembyonic generation of neurons persits beyond metamorphosis. *J. Neurobiol.* 29: 384-398.

Harzsch, S. & Dawirs, R.R. 1996b. Development of neurons exhibiting FMRFamide-related immunoreactivity in the central nervous system of larvae of the spider crab *Hyas araneus* L. (Decapoda: Majidae). *J. Crust. Biol.* 16: 10-19.

Harzsch, S., Miller, J., Benton, J. & Beltz, B. 1999b. From embryo to adult: persistent neurogenesis and apoptotic cell death shape the lobster deutocerebrum. *J. Neuroscience* 19: 3472-3485.

Harzsch, S., Miller, J., Benton, J., Dawirs, R.R. & Beltz, B. 1998. Neurogenesis in the thoracic neuromeres of two crustaceans with different types of metamorphic development. *J. Exp. Biol.* 201: 2465-2479.

Hashizume, K. 1999. Larval development of seven species of *Lucifer* (Dendrobranchiata, Sergestoidea), with a key for the identifcation of their larval forms. In: Schram, F.R. & von Vaupel Klein, J.C. (eds), *Crustaceans and the Biodiversity Crisis 1*: 753-804. Leiden: Brill.

Hatfield, S.E. 1983. Intermoult staging and distribution of dungeness crab, *Cancer magister*, megalopae. *Fish. Bull.* 172: 85-96.

Haug, A. & Myklestadt, S. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. I. The chemical composition of phytoplankton populations. *J. Exp. Mar. Biol. Ecol.* 11: 15-26.

Hauton, C., Williams, J.A. & Hawkins, L.E. 1997. The effects of a live in vivo pathogenic infection on aspects of the immunocompetence of the common shore crab, *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.* 211: 115-128.

Haynes, E. 1979. Description of larvae of the northern shrimp, *Pandalus borealis,* reared in situ in Kachemak Bay, Alaska. *Fish. B-Noaa* 77 (1): 157-173.

Haynes, E. 1979. Larval morphology of *Pandalus tridens* and a summary of the principal morphological characteristics of North Pacific pandalid shrimp larvae. *Fish. B-Noaa* 77 (3): 625-640.

Heinle, D.R. 1981. Zooplankton. In: Vernberg, F.J. & Vernberg, W.B. (eds), *Functional Adaptations of Marine Organisms*: 85-145. London: Academic Press.

Helluy, S.M. & Beltz, B.S. 1990. Stages in the embryonic development of the American lobster *Homarus americanus* with special emphasis on its nervous system. In: Wiese, K., Krenz, W.D., Tautz, J., Reichert, H. & Mulloney, B. (eds), *Frontiers in Crustacean Neurobiology. Advances in Life Sciences*: 530-536. Basel: Birkhäuser.

Helluy, S.M. & Beltz, B.S. 1991. Embryonic development of the American lobster (*Homarus americanus*): quantitative staging and characterization of an embryonic molt cycle. *Biol. Bull.* 180: 355-371.

Helluy, S.M., Ruchhoeft, M.L. & Beltz, B.S. 1995. Development of the olfactory and accessory lobes in the American lobster: An allometric analysis and its implications for the deuterocerebral structure of decapods. *J. Comp. Neur.* 357: 433-445.

Helluy, S.M., Sandeman, R., Beltz, B. & Sandeman, D. 1993. Comparative brain ontogeny of the crayfish and lawed lobster - Implications of direct and larval development. *J. Comp. Neurol.* 335 (3): 343-354.

Henken, A.M., Lucas, H., Tijssen, P.A.T. & Machiels, M.A.N. 1986. A comparison between methods used to determine the energy content of feed, fish and faeces samples. *Aquaculture* 58: 195-201.

Henry, R.P. 2001. Environmentally mediated carbonic anhydrase induction in the gills of euryhaline crustaceans. *J. Exp. Biol.* 204 (5): 991-1002.

Herring, P.J. & Dixon, D.R. 1998. Extensive deep-sea dispersal of postlarval shrimp from a hydrothermal vent. *Deep Sea Res. Part I-Oceanographic Research Papers* 45: 2105-2118.

Herrnkind, W.F. 1968. The breeding of *Uca pugilator* (Bosc) and mass rearing of the larvae with comments on the behavior of the larval and early crab stages (Brachyura, Ocypodidae). *Crustaceana Suppl.* 2: 214-224.

Herrnkind, W.F., Halusky, J. & Kanciruk, P. 1976. A further note on phyllosoma larvae associated with medusae. *B. Mar. Sci.* 26: 110-112.

Hessen, D.O. & Lyche, A. 1991. Inter- and intraspecific variations in zooplanktion element composition. *Arch. Hydrobiol.* 121: 343-353.

Hiatt, R.W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pacif. Sci.* 2: 135-213.

Higgins, L.E. & Rankin, M.A. 1996. Different pathways in arthropod postembryonic development. *Evolution* 50 (2): 573-582.

Hill, B.J. & Wassenberg, T.J. 1992. Preferences and amount of food eaten by the prawn *Penaeus esculentus* over the moult cycle. *Aust. J. Mar. Fresh. Res.*43: 727-735.

Hiller-Adams, P. & Childress, J.J. 1983. Effects of prolonged starvation on O_2 consumption, NH_4^+ excretion, and chemical composition of the bathypelagic mysid *Gnathophausia ingens*. *Mar. Biol.* 77: 119-127.

Himmelman, J.H. 1975. Phytoplankton as a stimulus for spawning in three marine invertebrates. *J. Exp. Mar. Biol. Ecol.* 20: 199-214.

Hines, A.H. 1986. Larval patterns in the life histories of brachyuran crabs (Crustacea, Decapoda, Brachyura). *B. Mar. Sci.* 39 (2): 444-466.

Hinsch, G.W. 1990. Morphology, histology, ultrastructure and functions of the mandibular glands in crustaceans. In: Gupta, A.P. (ed), *Morphogenetic Hormones of Arthropods 1-2*: 495-515. New Brunswick: Rutgers University Press.

Hinsch, G.W., Spaziani, E. & Vensel, W.H. 1980. Ultrastructure of the Y-organ of *Cancer antennarius* in normal and de-eyestalked crabs. *J. Morphol.* 163: 167-174.

Hinton, D.J. & Corey, S. 1979. The mouthparts and digestive tract in the larval stages of *Homarus americanus*. *Can. J. Zool.* 57: 1413-1423.

Hirata, H., Anastasios, M. & Yamasaki, S. 1985. Evaluation of the use of *Brachionus plicatilis* and *Artemia nauplii* for rearing prawn *Penaeus japonicus* larvae on a laboratory scale. *Mem. Fac. Fish. Kagoshima Univ.* 34: 27-36.

Hirche, H.J. & Anger, K. 1987a. Digestive enzyme activities during larval development of *Hyas araneus* (Decapoda, Majidae). *Comp. Biochem. Physiol.* 87B: 297-302.

Hirche, H.J. & Anger, K. 1987b. The accumulation of age pigments during larval development of the spider crab, *Hyas araneus* (Decapoda, Majidae). *Comp. Biochem. Physiol.* 88B: 777-782.

Hirota, J. & Szyper, J.P. 1975. Separation of total particulate carbon into inorganic and organic components. *Limnol. Oceanogr.* 20: 896-900.

Hirota, R. & Fukuda, Y. 1985. Dry weight and chemical composition of the larval forms of crabs (Decapoda: Brachyura). *Bull. Plank. Soc. Jap.* 32: 149-153.

His, E. & Seaman, M.N.L. 1992. Effects of temporary starvation on the survival, and on subsequent feeding and growth, of oyster (*Crassostrea gigas*) larvae. *Mar. Biol.* 114: 277-279.

Hobbs, H.H. 1991. Decapoda. In: Thorp, J.H. & Covich, A.P. (eds), *Ecology and Classification of North American Freshwater Invertebrates*: 823-858. New York: Academic Press.

Hochachka, P.W. 1997. Oxygen - a key regulatory metabolite in metabolic defense against hypoxia. *Am. Zool.* 37: 595-603.

Hochachka, P.W. & Somero, G.N. 1984. *Biochemical Adaptation.* Princeton, N.J.: University Press.

Höcker, B. 1988. Licht- und elektronenmikroskopische Untersuchungen zur Larval- und Juvenilentwicklung der Seespinne (*Hyas araneus*) unter besonderer Berücksichtigung des Y-Organs. M. Sc. Thesis, Universität Hamburg, Germany, 111 pp.

Holland, D.L. 1978. Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates. In: Malins, D.C. & Sargent, J.R. (eds), *Biochemical and biophysical perspectives in marine biology 4*: 85-123. New York: Academic Press.

Holland, D.L., Crisp, D.J., Huxley, R. & Sisson, J. 1984. Influence of oil shale on intertidal organisms: effects of oil shale extract on settlement of the barnacle *Balanus balanoides* (L.). *J. Exp. Mar. Biol. Ecol.* 75: 245-255.

Holland, D.L. & Gabbott, P.A. 1971. A micro-analytical scheme for the determination of protein, carbohydrate, lipid and RNA levels in marine invertebrate larvae. *J. Mar. Biol. Assoc. Uk.* 51: 659-668.

Holliday, C.W. & Miller, D.S. 1984. Cellular mechanisms of organic anion transport in crustacean renal tissue. *Amer. Zool.* 24: 275-284.

Holmquist, J.G. 1994. Benthic macroalgae as a dispersal mechanism for fauna - influence of a marine tumbleweed. *J. Exp. Mar. Biol. Ecol.* 180 (2): 235-251.

Hong, S.Y. 1988a. The prezoal stage in various decapod crustaceans. *J. Nat. Hist.* 22: 1041-1075.

Hong, S.Y. 1988b. Development of epipods and gills in some pagurids and brachyurans. *J. Nat. Hist.* 22: 1005-1040.

Hopkin, S.P. & Nott, J.A. 1980. Studies of the digestive cycle of the shore crab *Carcinus maenas* (L.) with special reference to the B cells in the hepatopancreas. *J. Mar. Biol. Ass. U.K.* 60: 891-907.

Horn, D.H.S., Middleton, E.J., Wunderlich, J.A. & Hampshire, F. 1966. Identity of the moulting hormones of insects and crustaceans. *Chem. Commun.* 1966: 339-340.

Horn, R. & Harms, J. 1988. Larval development of *Halicarcinus varius* (Decapoda: Hymenosomatidae). *New Zeal. J. Mar. Fresh.* 22: 1-8.

Horst, M.N. & Freeman, J.A. (eds) 1993. *The crustacean integument. Morphology and biochemistry.* Boca Raton, FL: CRC Press.

Hovel, K.A. & Morgan, S.G. 1997. Planktivory as a selective force for reproductive synchrony and larval migration. *Mar. Ecol. Prog. Ser.*157: 79-95.

Hovel, K.A. & Morgan, S.G. 1999. Susceptibility of estuarine crab larvae to ultraviolet radiation. *J. Exp. Mar. Biol. Ecol.* 237 (1): 107-125.

Huang, C.C. & Song, Y.L. 1999. Maternal transmission of immunity to white spot syndrome associated virus (WSSV) in shrimp (*Penaeus monodon*). *Dev. Comp. Immunol.* 23 (7-8): 545-552.

Hubbel, S.P. 1971. Of sowbugs and systems: The ecological bioenergetics of a terrestrial isopod. In: Patten, B.C. (ed), *Systems Analysis and Simulation Ecology*: 269-324. New York: Academic Press.

Hubschman, J.H. 1963. Development and function of neurosecretory sites in the eyestalks of larval *Palaemonetes* (Decapoda, Natantia). *Biol. Bull. Mar. Biol. Lab. Woods Hole* 125: 96-113.

Hubschman, J.H. 1971. Transient larval glands in *Palaemonetes*. In: Crisp, D.J. (ed), *Fourth European Mar. Biol. Symposium*: 295-300. Cambridge: University Press.

Hudon, C. 1987. Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Iles-de-la-Madeleine (Québec). *Can. J. Fish. Aquat. Sci.*44: 1855-1869.

Huner, J.V. 1990. Biology, fisheries, and cultivation of freshwater crawfishes in the U.S. *Reviews in Aquatic Sciences* 2 (2): 229-254.

Huner, J.V. & Colvin, L.B. 1979. Observations on the molt cycle of two species of juvenile shrimp, *Penaeus californiensis* and *Penaeus stylirostris* (Decapoda, Crustacea). *Proc. Natn. Shellfish. Ass.* 69: 77-84.

Hunt, H.L. & Scheibling, R.E. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser* 155: 269-301.

Huntley, M. & Boyd, C. 1984. Food-limited growth of marine zooplankton. *Am. Nat.* 124: 455-478.

Huong, D.T.T., Yang, W.-J., Okuno, A. & Wilder, M.N. 2001. Changes in free amino acids in the hemolymph of giant freshwater prawn *Macrobrachium rosenbergii* exposed to varying salinities: relationship to osmoregulatory ability. *Comp. Biochem. Physiol.* 128A (2): 317-326.

Icely, J.D. & Nott, J.A. 1992. Digestion and absorption: digestive system and associated organs. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates 10*; *Decapod Crustacea*: 147-201. New York: Wiley-Liss.

Ikeda, T. 1974. Nutritional ecology of marine zooplankton. *Mem. Fac. Fish. Hokkaido Univ* 22: 1-97.

Ikeda, T. 1977. Feeding rates of planktonic copepods from a tropical sea. *J. Exp. Mar. Biol. Ecol.* 29: 263-277.

Ikeda, T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Mar. Biol.* 85: 1-11.

Ikeda, T. & Aritaki, M. 1991. Dry weight and elemental composition (C and N) of the cast moults of the larvae of the pink shrimp *Pandalus borealis* Krøyer. *Bull. Japan Sea Natl. Fish. Res. Inst.* 41: 73-76.

Ikeda, T., Hing Fay, E., Hutchinson, S.A. & Boto, G.M. 1982. Ammonia and inorganic phosphate excretion by zooplankton from inshore waters of the Great Barrier Reef, Queensland. I. Relationship between excretion rates and body size. *Aust. J. Mar. Freshw. Res.* 33: 55-70.

Imam, F.S. 1982. Formation, growth, and spatial relationship of eyestalk neuroendocrine structures in *Alpheus heterochaelis* Say (Crustacea, Decapoda, Alphaeidae). *Am. Zool.* 22: 911.

Incze, L.S. & Paul, A.J. 1983. Grazing and predation as related to energy needs of stage I zoeae of the tanner crab *Chionoecetes bairdi* (Brachyura: Majidae). *Biol. Bull. Mar. Biol. Lab. Woods Hole* 165 (1): 197-208.

Ingle, R.W. 1992. *Larval stages of northeastern Atlantic crabs. An illustrated key.* London: Chapman & Hall.

Ingle, R.W. 1998. Decapod larval taxonomic research in the North Eastern Atlantic and Mediterranean: past achievements and future prospects. *Inv. Reprod. Develop.* 33 (2-3): 97-107.

Inoue, M. 1978. Studies on the cultured phyllosma larvae of the Japanese spiny lobster. *Panulirus japonicus*. - I. Morphology of the phyllosma. *Bull. Jap. Soc. Scient. Fish.* 44: 457-475.

Irigoien, X., Harris, R.P. & Head, R.N. 2000. Does turbulence play a role in feeding and reproduction of *Calanus finmarchicus*? *J. Plankton Res.* 22 (2): 399-407.

Ismael, D. 1995. Influência de parâmetros ambientais no desenvolvimento, consumo de oxigênio e crecimento larval de duas espécies de Braquiúros. Dissertation, Universidade de São Paulo, Brazil, 143 pp.

Ismael, D., Anger, K. & Moreira, G.S. 1997. Influence of temperature on larval survival, development, and respiration in *Chasmagnathus granulata* (Crustacea, Decapoda). *Helgoländer Meeresunters.* 51: 463-475.

Itami, T., Yan, Y. & Takahashi, Y. 1992. Studies on vaccination against vibriosis in cultured Kuruma prawn *Penaeus japonicus.* I. Effect of vaccine concentration and duration of vaccination efficacy. *J. Shimonoseki Univ. Fish.* 40: 83-87.

Ito, M. & Lucas, J.S. 1990. The complete larval development of the scyllarid lobster, *Scyllarus demani* Holthius, 1946 (Decapoda, Scyllaridae), in the laboratory. *Crustaceana* 58: 144-167.

Ivanovici, A.M. 1980. Application of adenylate energy charge to problems of environmental impact assessment in aquatic organisms. *Helgoländer Meeresunters.* 33: 556-565.

Ivlev, U. 1945. The biological productivity of waters (Translation, Fisheries Research Board of Canada, No. 394). *Uspekhi Soureminnoi Biologii* 19: 98-120.

Ivleva, I.V. 1970. The influence of temperature on the transformation of matter in marine invertebrates. In: Steele, J.H. (ed), *Marine food chains*: 96-112. Edinbourgh: Oliver & Boyd.

Ivleva, I.V. 1980. The dependence of Crustacean respiration rate on body mass and habitat temperature. *Int. Revue Ges. Hydrobiol.* 65: 1-47.

Jacobi, C.C. & Anger, K. 1985a. Growth and respiration during the larval development of *Hyas coarctatus* (Decapoda: Maijdae). *Mar. Biol.* 87: 173-180.

Jacobi, C.C. & Anger, K. 1985b. Effect of temperature on respiration of larval stages of *Hyas araneus* and *H. coarctatus* (Decapoda, Majidae). *Mar. Ecol. Prog. Ser.* 26: 181-186.

Jaeckle, W.B. 1994. Rates of energy consumption and acquisition by lecithotrophic larvae of *Bugula neritina* (Bryozoa: Cheilostomata). *Mar. Biol.* 119: 517-523.

Jägersten, G. 1972. *Evolution of the Metazoan Life Cycle.* London, New York: Academic Press.

James, M.O. & Boyle, S.M. 1998. Cytochromes P450 in crustacea. *Comp. Biochem. Phys. A.* 121C(1-3): 157-172.

James-Pirri, M.J. & Cobb, J.S. 1997. Growth rates of planktonic and newly settled American lobsters *Homarus americanus*. *Mar. Ecol.-Progress Series* 160: 233-240.

Jarminowski, H. 1990. Histologische und elektronenmikroskopische Untersuchungen zur Larvalentwicklung von *Pagurus bernhardus* unter besonderer Berücksichtigung der Funktionsfähigkeit des Verdauungstraktes der Megalopa. M. Sc. Thesis, Universität Freiburg i. Br., Germany, 60 pp.

Jaros, P.P. 1986. Neuropeptides in crustaceans with special reference to opioid-like peptides. In: *CRC Handbook of Comparative Opioid and Related Neuropeptide Mechanisms 1*: 181-195.

Jaros, P.P. 1990. Enkephalins, biologically active neuropeptides in invertebrates, with special reference to crustaceans. In: Wiese, K., Krenz, W.D., Tautz, J., Reichert, H. & Mulloney, B. (eds), *Frontiers in Crustacean Neurobiology. Advances in Life Sciences*: 471-482. Basel: Birkhäuser.

Jayaprakas, V. & Sambhu, C. 1996. Growth response of white prawn, *Penaeus indicus,* to dietary L-carnitine. *Asian Fish. Sci.* 9: 209-219.

Jeckel, W.H., Aizpun de Moreno, J.E. & Moreno, V.J. 1989a. Biochemical composition, lipid classes and fatty acids in the male reproductive system of the shrimp *Pleoticus muelleri* Bate. *Comp. Biochem. Physiol.* 93B: 807-811.

Jeckel, W.H., Aizpun de Moreno, J.E. & Moreno, V.J. 1989b. Biochemical composition, lipid classes and fatty acids in the ovary of the shrimp *Pleoticus muelleri* Bate. *Comp. Biochem. Physiol.* 92B: 271-276.

Jeffs, A., Nichols, P.D. & Bruce, M.P. in press. Lipid reserves used by the puerulus of the spiny lobster *Jasus edwardsii* in crossing the continental shelf of New Zealand. *Mar. Biol.*

Jeffs, A., Willmott, M.E. & Wells, R.M.G. 1999. The use of energy stores in the puerulus of the spiny lobster *Jasus edwardsii* across the continental shelf of New Zealand. *Comp. Biochem. Physiol.* 123A: 351-357.

Jenkin, P.M. & Hinton, H.E. 1966. Apolysis in arthropod moulting cycles. *Nature* 211: 871.

Jensen, G.C. 1991. Competency, settling behavior, and postsettlement aggregation by porcelain crab megalopae (Anomura: Porcellanidae). *J. Exp. Mar. Biol. Ecol.* 153: 49-61.

Jensen, G.C. & Armstrong, D.A. 1989. Biennial reproductive cycle of blue king crab, *Paralithodes platypus,* at the Pribilof Islands, Alaska and comparison to a congener, *P. camtschatica*. *Can. J. Fish. Aquat. Sci.* 932-940.

Johns, D.M. 1981. Physiological studies on *Cancer irroratus* larvae. I. Effects of temperature and salinity on survival, development rate and size. *Mar. Ecol. Prog. Ser.* 5: 75-83.

Johns, D.M. 1982. Physiological studies on *Cancer irroratus* larvae. III. Effects of temperature and salinity on the partitioning of energy resources during development. *Mar. Ecol. Prog. Ser.* 8: 75-85.

Johns, D.M. & Pechenik, J.A. 1980. Influence of water-accomodated fraction no. 2 fuel oil on energetics of *Cancer irroratus* larvae. *Mar. Biol.* 55 (4): 247-254.

Johns, P.M. & Mann, K.H. 1987. An experimental investigation of juvenile lobster habitat preference and mortality among habitats of varying structural complexity. *J. Exp. Mar. Biol. Ecol.* 109: 275-285.

Johnson, D.M., Akre, B.G. & Crowley, P.H. 1975. Modeling arthropod predation: wasteful killing by damselfly naiads. *Ecology* 56: 1081-1093.

Johnson, D.R. 1995. Wind forced surface currents at the entrance to Chesapeake Bay: their effect on blue crab larval dispersion and post-larval recruitment. *B. Mar. Sci.* 57: 726-738.

Johnson, K.B. & Shanks, A.L. 1997. The importance of prey densities and background plankton in studies of predation on invertebrate larvae. *Mar. Ecol. Prog. Ser.*158: 293-296.

Johnson, P.T. 1980. *Histology of the blue crab Callinectes sapidus. A model for the Decapoda.* New York: Praeger Publishers.

Jones, D.A., Kamarudin, M.S. & Le Vay, L. 1993. The potential for replacement of live feeds in larval culture. *J. World Aquacult Soc.* 24: 199-210.

Jones, D.A., Kanazawa, A. & Ono, K. 1979. Studies on the nutritional requirements of the larval stages of *Penaeus japonicus* using microencapsulated diets. *Mar. Biol.* 54: 261-267.

Jones, D.A., Kumlu, M., Le Vay, L. & Fletcher, D.J. 1997b. The digestive physiology of herbivorous, omnivorous and carnivorous crustacean larvae: a review. *Aquaculture* 155: 285-295.

Jones, D.A., Yule, A.B. & Holland, D.L. 1997a. Larval nutrition. In: D'Abramo, L.R., Conklin, D.E. & Akiyama, D.M. (eds), *Advances in World Aquaculture 6*; *Crustacean Nutrition*: 353-389. Baton Rouge, Louisiana, USA: World Aquaculture Society, Louisiana State University.

Jones, M.B. & Epifanio, C.E. 1995. Settlement of brachyuran megalopae in Delaware Bay: an analysis of time series data. *Mar. Ecol. Prog. Ser.*125 (1-3): 67-76.

Juberthie-Jupeau, L. & Chaigneau, J. 1975. Les phaosomes de l'organe de Bellonci et leur genèse chez deux Atyidae (Crustacé, Décapodes). *C.R. Acad. Sci. Paris* 280D: 1873-1876.

Juinio, M.A.R. & Cobb, J.S. 1994. Estimation of recent growth of field-caught postlarval American lobsters, *Homarus americanus,* from RNA:DNA ratios. *Can. J. Fish. Aquat. Sci.*51 (2): 286-294.

Kaestner, A. 1980. *Invertebrate Zoology. Vol. III. Crustacea.* Huntington, N.Y.: Krieger.

Kalber, F.A. & Costlow, J.D. 1966. The ontogeny of osmoregulation and its neurosecretory control in the decapod crustacean, *Rhithropanopeus harrisii* (Gould). *Am. Zoologist* 6: 221-229.

Kalber, F.A. & Costlow, J.D. 1968. Osmoregulation in larvae of the land-crab, *Cardisoma guanhumi* Latreille. *Am. Zoologist* 8: 411-416.

Kamarudin, M.S., Jones, D.A. & Levay, L. 1994. Ontogenic change in digestive enzyme-activity during larval development of *Macrobrachium rosenbergii*. *Aquaculture* 123 (3-4): 323-333.

Kanazawa, A. 1990. Microparticulate feeds for penaeid larvae. In: *Actes De Colloque 9*; *Advances in tropical aquaculture*: 395-404. Tahiti: Aquacop. Ifremer.

Kanazawa, A. & Koshio, S. 1994. Lipid nutrition of the spiny lobster *Panulirus japonicus* (Decapoda, Palinuridae). A review. *Crustaceana* 67: 226-232.

Kanazawa, A., Teshima, S., Tokiwa, S., Kayama, M. & Hirata, M. 1979b. Essential fatty acids in the diet of prawn. II. Effect of docosahexaenoic acid on growth. *Bull. Jpn. Soc. Sci. Fish.* 45: 1151-1153.

Kanazawa, A., Teshima, S.-I. & Sakamoto, M. 1985. Effects of dietary lipids, fatty acids, and phospholipids on growth and survival of prawn (*Penaeus japonicus*) larvae. *Aquaculture* 50: 39-49.

Kanazawa, A., Teshina, S. & Ono, K. 1979a. Relationship between essential fatty acid requirements of aquatic animals and the capacity for bioconversion of linolenic acid to highly unsaturated fatty acids. *Comp. Biochem. Physiol.* 63B: 295-298.

Kattner, G., Wehrtmann, I.S. & Merck, T. 1994. Interannual variations of lipids and fatty acids during larval development of *Crangon* spp in the German bight, North sea. *Comp. Biochem. Phys. A.* 107B(1): 103-110.

Katz, C.H., Cobb, J.S. & Spaulding, M. 1994. Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. *Mar. Ecol. Prog. Ser.*103 (3): 265-273.

Katz, L.M. 1973. The effects of water soluble fraction of crude oil on larvae of the decapod crustacean *Neopanope texana* (Sayi). *Environm. Pollut.* 5: 199-204.

Keller, R. 1992. Crustacean neuropeptides: structures, functions and comparative aspects. *Experientia* 48: 439-448.

Keller, R. & Willig, A. 1976. Experimental evidence of the molt controlling function of the Y-Organ of a macruran decapod, *Orconectes limosus*. *J. Comp. Physiol.* 108: 271-278.

Kelly, P., Sulkin, S.D. & Van Heukelem, W.F. 1982. A dispersal model for larvae of the deep sea red crab *Geryon quinquedens* based upon behavioral regulation of vertical migration in the hatching stage. *Mar. Biol.* 72 (1): 35-43.

Kenyon, R.A., Haywood, M.D.E., Heales, D.S., Loneragan, N.R., Pendrey, R.C. & Vance, D.J. 1999. Abundance of fish and crustacean postlarvae on portable artificial seagrass units: daily sampling provides quantitative estimates of the settlement of new recruits. *J. Exp. Mar. Biol. Ecol.* 232: 197-216.

Kenyon, R.A., Loneragan, N.R. & Hughes, J.M. 1995. Habitat type and light affect sheltering behaviour of juvenile tiger prawns (*Penaeus esculentus* Haswell) and success rates of their fish predators. *J. Exp. Mar. Biol. Ecol.* 192: 87-105.

Key, P.B., Fulton, M.H., Layman, S.L. & Scott, G.I. 1998a. Azinphosmethyl exposure to grass shrimp (*Palaemonetes pugio*) life stages with emphases on larval acetylcholinesterase activity. *Bull. Environ. Contam. Toxicol.* 60: 645-650.

Key, P.B., Fulton, M.H., Scott, G.I., Layman, S.L. & Wirth, E.F. 1998b. Lethal and sublethal effects of malathion on three life stages of the grass shrimp, *Palaemonetes pugio*. *Aquat. Toxicol.* 40: 311-322.

Kilman, V., Fenelon, V.S., Richards, K.S., Thirumalai, V., Meyrand, P. & Marder, E. 1999. Sequential developmental acquisition of cotransmitters in identified sensory neurons of the stomatogastric nervous system of the lobsters, *Homarus americanus* and *Homarus gammarus*. *J. Comp. Neurol.* 408 (3): 318-334.

Kim, G.B., Lee, R.F. & Mitchell, D.L. 2000. Damage to grass shrimp (*Palaemonetes pugio*) embryo DNA by summer sunlight followed by DNA repair in the dark. *Mar. Biol.* 137 (4): 675-682.

Kinne, O. 1964a. Non-genetic adaptation to temperature and salinity. *Helgoländer Wiss. Meeresunters.* 9: 433-458.

Kinne, O. 1964b. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. *Oceanogr. Mar. Biol. Ann. Rev.* 2: 281-339.

Kinne, O. 1967. Physiology of estuarine organisms with special referance to salinity and temperature: general aspects. In: Lauff, H.H. (ed), *Estuaries*: 525-540. Washington, DC: American Association for the Advancement of Science.

Kinne, O. 1970. Invertebrates. In: Kinne, O. (ed), *Marine Ecology 1*; *Temperature*: 407-514. Chichester: Wiley.

Kinne, O. 1971. Salinity. In: Kinne, O. (ed), *Marine Ecology 1*: 683-1244. Chichester: Wiley.

Kinne, O. 1977. Research cultivation. In: Kinne, O. (ed), *Marine Ecology 3*: 579-1293. Chichester: Wiley.

Kiørboe, T. 2000. Colonization of marine snow aggregates by invertebrate zooplankton: abundance, scaling, and possible role. *Limnol. Oceanogr.* 45 (2): 479–484.

Kiørboe, T., Andersen, K.P. & Dam, H.G. 1990. Coagulation efficiency and aggregate formation in marine phytoplankton. *Mar. Biol.* 107: 235-245.

Kiørboe, T. & Visser, A.W. 1999. Predator and prey perception in copepods due to hydromechanical signals. *Mar. Ecol. Prog. Ser.* 179: 81-95.

Kirk, M.D. & Govind, C.K. 1992. Early innervation of abdominal swimmeret muscles in developing lobsters. *J. Exp. Zool.* 261: 298-309.

Kittaka, J. 1994. Culture of phyllosomas of spiny lobster and its application to studies of larval recruitment and aquaculture. *Crustaceana* 66: 258-270.

Kittaka, J. 1997. Culture of larval spiny lobsters: a review of work done in northern Japan. *Mar. Freshwater. Res.* 48: 923-930.

Kittaka, J. & Kimura, K. 1989. Culture of the Japanese spiny lobster *Panulirus japonicus* fromm egg to juvenile stage. *Nippon Suisan Gakk.* 55: 963-970.

Kleinholz, L.H. 1985. Biochemistry of crustacean hormones. In: Bliss, D.E. & Mantel, L.H. (eds), *The Biology of Crustacea 9*; *Integument, Pigments, and Hormonal Processes*: 464-522. New York: Academic Press.

Kleiven, O.T., Larsson, P. & Hobæk, A. 1996. Direct distributional response in *Daphnia pulex* to a predator kairomone. *J. Plankt. Res.* 18: 1341-1348.

Kline, E.R. & Stekoll, M.S. 2000. Relative sensitivity of marine species to an effluent with elevated total dissolved solids. *Environmental Toxicology and Chemistry* 19 (1): 228-233.

Knight, M.D. 1968. The larval development of *Blepharipoda occidentalis* Randall and *B. spinimana* (Philippi) (Decapoda, Albuneidae). *Proc. Calif. Academy of Science* 35: 337-370.

Knowles, F.G.W. & Carlisle, D.B. 1956. Endocrine control in the Crustacea. *Biol. Rev.* 31: 396-473.

Knowlton, R.E. 1965. Effects of some environmental factors on the larval development of *Palaemonetes vulgaris* (Say). *J. Elisha Mitchell Scient. Soc.* 81: 87.

Knowlton, R.E. 1974. Larval developmental processes and controlling factors in decapod Crustacea, with emphasis on Caridea. *Thalassia Jugoslavica* 10: 139-158.

Knowlton, R.E. 1994. Effects of larval eyestalk extirpation on morphogenesis and molting in the snapping shrimp *Alpheus heterochaelis* Say. *J. Exp. Zool.* 270 (2): 162-174.

Knudsen, J.W. 1958. Life cycle studies of the Brachyura of western North America, I. General culture methods and the life cycle of *Lophopanopeus leucomanus leucomanus* (Lockington). *Bull. So. Calif. Academy of Science* 57: 51-59.

Knudsen, J.W. 1960. Reproduction, life history, and larval ecology of the California Xanthidae, the pebble crabs. *Pac. Sci.* 14: 3-17.

Komai, T. & Mizushima, T. 1993. Advanced larval development of *Pandalopsis japonica* Balss, 1914 (Decapoda, Caridea, Pandalidae) reared in the laboratory. *Crustaceana* 64: 24-39.

Kon, T. 1979. Ecological studies on larvae of the crabs belonging to the genus *Chionoecetes*. *Bull. Japan. Soc. Sci. Fish.* 45: 7-9.

Konishi, K. & Quintana, R. 1987. Notes on the prezoea stage of decapod crustaceans. *Aquabiology* 52: 372-378.

Koolman, J. (ed) 1989. *Ecdysone, from Chemistry to Mode of Action.* Stuttgart: Thieme.

Kozlovskaya, E.P. & Vaskovsky, V.E. 1970. A comparative study of proteinases of marine invertebrates. *Comp. Biochem. Physiol.* 34: 137-142.

Kristensen, J.H. 1972. Carbohydrases of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrates studied. *Mar. Biol.* 14: 130-142.

Krol, R.M., Hawkins, W.E. & Overstreet, R.M. 1992. Reproductive components. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates 10*; *Decapod Crustacea*: 295-343. New York: Wiley –Liss.

Kumlu, M. & Jones, D.A. 1995a. Feeding and digestion in the caridean shrimp larva of *Palaemon elegans* Rathke and *Macrobrachium rosenbergii* (De Man) (Crustacea, Palaemonidae) on live and artificial diets. *Aquacult. Nutr.* 1 (1): 3-12.

Kumlu, M. & Jones, D.A. 1995b. The effect of live and artificial diets on growth, survival and trypsin activity of larvae of *Penaeus indicus*. *J. World Aquacult. Soc.* 26: 406-415.

Kumlu, M. & Jones, D.A. 1997. Digestive protease activity in planktonic crustaceans feeding at different trophic levels. *J. Mar. Biol. Ass. U.K.* 77 (1): 159-165.

Kumlu, M., Sarihan, E. & Tekelioglu, N. 1992. Trypsin activity in larvae of *Penaeus monodon* Fabricius, 1789 (Decapoda; Penaeidae) in relation to their diet. *Isr. J. Aquacult.-Bamid.* 44 (4): 103-110.

Kunisch, M. & Anger, K. 1984. Variation in development and growth rates of larval and juvenile spider crabs *Hyas araneus* reared in the laboratory. *Mar. Ecol. Prog. Ser.* 15: 293-301.

Kurata, H. 1960. Studies on the larva and post-larva of *Paralithodes camtschatica.* II. Feeding habits of the zoea. *Bull. Hokk. Reg. Fish. Res. Lab.* 21: 1-8.

Kurata, H. 1962. Studies on the age and growth of Crustacea. *Bull. Hokkaido Reg. Fish. Lab.* 24: 1-115.

Kuris, A.M. 1991. A review of patterns and causes of crustacean brood mortality. In: Wenner, A. & Kuris, A. (eds), *Crustacean Iss. 7*; *Crustacean Egg Production*: 117-141. Balkema, Rotterdam:

Kuris, A.M., Blau, S.F., Paul, A.J., Shields, J.D. & Wickham, D.E. 1991. Infestation by brood symbionts and their impact on egg mortality of the red king crab, *Paralithodes camtschatica,* in Alaska: Geographic and temporal variation. *Can. J. Fish. Aquat. Sci.*48 (4): 559-568.

Kuris, A.M. & Lafferty, K.D. 1992. Modelling crustacean fisheries: effects of parasites on management strategies. *Can. J. Fish. Aquat. Sci.*49 (2): 327-336.

Kurmaly, K., Jones, D.A. & Yule, A.B. 1990. Acceptability and digestion of diets fed to larval stages of *Homarus gammarus* and the role of dietary conditioning behaviour. *Mar. Biol.* 106: 181-190.

Kurmaly, K., Jones, D.A., Yule, A.B. & East, J. 1989b. Comparative analysis of the growth and survival of *Penaeus monodon* (Fabricius) larvae, from protozoa 1 to postlarva 1, on live feeds, artificial diets and on combinations of both. *Aquaculture* 81: 27-45.

Kurmaly, K., Yule, A.B. & Jones, D.A. 1989a. An energy budget for the larvae of *Penaeus monodon* (Fabricius). *Aquaculture* 81: 13-25.

Kurmaly, K., Yule, A.B. & Jones, D.A. 1989c. Effects of body size and temperature on the metabolic rate of *Penaeus monodon*. *Mar. Biol.* 103: 25-30.

Kwon, C.S. & Uno, Y. 1969. The larval development of *Macrobrachium nipponense* (De Haan) reared in the laboratory. *La Mer (Bulletin De La Société Franco-Japonaise D´Océanographie)* 7: 278-294.

Lachaise, F., Le Roux, A., Hubert, M. & Lafont, R. 1993. The molting gland of crustaceans: localization, activity, and endocrine control. *J. Crust. Biol.* 13: 198-234.

Lake, P.S. & Ong, J.E. 1970. Ultrastructure of the "onion bodies" of the sensory pore X-organ of *Paratya tasmanensis* Reik (Crustacea, Decapoda). *Experientia* 26: 1129-1130.

Lambert, R. & Epifanio, C.E. 1982. A comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. *Estuaries* 5 (3): 182-188.

Lampert, W. 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 39: 79-88.

Lampitt, R.S., Wishner, K.F., Turley, C.M. & Angel, M.W. 1993. Marine snow studies in the northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. *Mar. Biol.* 116: 689-702.

Land, M.F. 1980. Compound eyes: old and new optical mechanisms. *Nature, London* 287: 681-686.

Lau, S.C.K. & Qian, P.-Y. 2001. Larval settlement in the serpulid polychaete *Hydroides elegans* in response to bacterial films: an investigation of the nature of putative larval settlement cue. *Mar. Biol.* 138 (2): 321-328.

Laufer, H., Borst, D.W., Baker, F.B. & Schooley, D.A. 1986. Juvenile hormone-like compounds in crustacea. *Biol. Bull.* 170 (3): 539.

Laughlin, R.A., Rodriguez, P.J. & Marval, J.A. 1983. Zoeal stages of the coral crab *Carpilius corallinus* (Herbst) (Decapoda, Xanthidae) reared in the laboratory. *Crustaceana* 44: 169-186.

Laughlin, R.B. & French, W. 1989a. Differences in responses to factorial combinations of temperature and salinity by zoeae from two geographically isolated populations of the mud crab *Rhithropanopeus harrisii*. *Mar. Biol.* 102: 387-395.

Laughlin, R.B. & French, W. 1989b. Interactions between temperature and salinity during brooding on subsequent zoeal development of the mud crab *Rhithropanopeus harrisii*. *Mar. Biol.* 102: 377-386.

Laughlin, R.B., French, W. & Guard, H.E. 1985. On the correlation between acute and sublethal stress in mud crab larvae, *Rhithropanopeus harrisii:* the example of triorganotin compounds. In: Gray, J.S. & Christiansen, M.E. (eds), *Mar. Biol. of polar regions and effects of stress on marine organisms*: 513-526. Chichester: Wiley.

Laughlin, R.B. & Neff, J.M. 1981. Ontogeny of respiratory and growth responses of larval mud crabs *Rhithropanopeus harrisii* exposed to different temperatures, salinities and naphthalene concentrations. *Mar. Ecol. Prog. Ser.*5 (3): 319-332.

Laughlin, R.B., Neff, J.M., Hrung, Y.C., Goodwin, T.C. & Giam, C.S. 1978b. Effects of 3 phthalate esters on larval development of grass shrimp *Palaemonetes pugio* (Holthuis). *Water Air Soil Poll.* 9 (3): 323-336.

Laughlin, R.B., Ng, J. & Guard, J.N. 1981. Hormesis: a response in low environmental concentrations of petroleum hydrocarbons. *Science* 211: 705-707.

Laughlin, R.B., Young, L.G.L. & Neff, J.M. 1978a. A long-term study of the effects of water-soluble fractions of No. 2 fuel oil on the survival, development rate, and growth of the mud crab *Rhithropanopeus harrisii*. *Mar. Biol.* 47: 87-95.

Lavalli, K.L. & Barshaw, D.E. 1986. Burrows protect postlarval lobster *Homarus americanus* from predation by the non-burrowing cunner *Tautogolabrus adspersus*, but not from the burrowing mud crab *Neopanope texani*. *Mar. Ecol. Prog. Ser.* 32: 13-16.

Laverack, M.S. 1988a. The diversity of chemoreceptors. In: Atema, J., Fay, R.R., Popper, A.N. & Tavolga, W.N. (eds), *Sensory Biology of Aquatic Animals*: 287-312. New York: Springer.

Laverack, M.S. 1988b. Larval locomotion, sensors, growth and their implications for the nervous system. In: Fincham, A.A. & Rainbow, P.S. (eds), *Aspects of Decapod Crustacean Biology, Symposia of the Zoological Society of London 59*: 103-122. Oxford: Clarendon Press.

Laverack, M.S. 1988c. The numbers of neurones in decapod Crustacea. *J. Crust. Biol.* 8: 1-11.

Laverack, M.S. 1990. External sensors and the dorsal organ of Crustacea. In: Wiese, K., Krenz, W.D., Tautz, J., Reichert, H. & Mulloney, B. (eds), *Frontiers in Crustacean Neurobiology, Advances in Life Sciences*: 90-96. Basel: Birkhäuser.

Laverack, M.S., Macmillan, D.L. & Neil, D.M. 1976. A comparison of beating parameters in larval and post-larval locomotor systems of the lobster *Homarus gammarus* (L.). *Philos. T. Roy. Soc. B.*274 (929): 87-99.

Laverack, M.S., Macmillan, D.L., Ritchie, G. & Sandow, S.L. 1996. The ultrastructure of the sensory dorsal organ of Crustacea. *Crustaceana* 69: 636-651.

Laverack, M.S. & Saier, B. 1993. Morphology and ultrastructure of a presumptive oxygen receptor in the gills of the Norway lobster *Nephrops norvegicus* (Decapoda). *J. Crust. Biol.* 13: 504-510.

Laverack, M.S. & Sinclair, A. 1994. Innervation of the dorsal organ of the shrimp *Macrobrachium intermedium* (Decapoda: Natantia). *J. Crust. Biol.* 14: 1-5.

Lavilla-Pitogo, C.R., Baticados, M.C.L., Cruz-Lacierda, E.R. & de la Pena, L.D. 1990. Occurrence of luminous bacterial disease of *Penaeus monodon* larvae in the Philippines. *Aquaculture* 91: 1-13.

Lawrence, A.L., McVey, J.P. & Huner, J.V. 1985. Penaeid shrimp culture. In: Huner, J.V. & Brown, E.E. (eds), *Crustacean and mollusk aquaculture in the United States*: 127-157. Westport, Connecticut: AVI Publishing Company.

Lawton, P. & Lavalli, K.L. 1995. Postlarval, juvenile, adolescent, and adult ecology. In: Factor, J.R. (ed), *Biology of the Lobster Homarus americanus*: 47-88. San Diego, CA: Academic Press.

Le Roux, A. 1968. Description d'organes mandibulaires nouveaux chez les Crustacés décapodes. *C.R. Acad. Sci., Sér.* D 266: 1414-1417.

Le Roux, A. 1969. Aspects histologiques et histochimiques des organes mandibulaires chez les Crustacés Décapodes. *Bull. Soc. Zool. Fr.* 94: 299-300.

Le Roux, A. 1971. Étude anatomique et fonctionelle du proventricule des larves et des juvéniles du premier stade de *Palaemonetes varians* (Leach) (Décapode, Natantia). I. - Données anatomiques. *Bull. Soc. Zool. France* 96: 127-140.

Le Roux, A. 1974. Mise au point à propos de la distinction entre l´organe Y et l'organe mandibulaire chez les Crustacés eucarides. *C.R. Acad. Sci., Sér.* D 278: 1261-1264.

Le Roux, A. 1976. Aspects de la différenciation sexuelle chez *Pisidia longicornis* (Linné) (Crustacea, Decapoda). *C.R. Acad. Sc. Paris* 283: 959-962.

Le Roux, A. 1977. L'organe Y de *Palaemon serratus* (Pennant) (Décapod, Natantia): Localisation et aspects histologiques. *Cah. Biol. Mar.* 18: 413-425.

Le Roux, A. 1982a. L'organe Y des larves de *Pisidia longicornis* (Linné) (Crustacé, Décapode, Anomoure). Ses modifications au cours de la phase zoé. *Arch. Zool. Exp. Gén.* 122: 441-455.

Le Roux, A. 1982b. Les organes endocrines chez les larves des Crustacés Eucarides. Intervention dans la croissance au cours de la vie larvaire et des premiers stades juvéniles. *Oceanis* 8: 505-531.

Le Roux, A. 1983a. Histogenese de l'organe Y (glande de mue) chez l´embryon de la crevette *Palaemon serratus* (Pennant) (Crustace Décapode Natantia). *IFREMER, Actes De Colloques* 1: 255-262.

Le Roux, A. 1983b. Réactions de l'organe mandibulaire à l'ablation des pédoncules oculaires chez les larves et les juvéniles de *Palaemonetes varians* (Leach) (Decapoda, Natantia). *C.R. Acad. Sc. Paris* 296: 697-700.

Le Roux, A. 1984. Quelques effects de l'ablation des pédoncules oculaires sur les larves et les premiers stades juvéniles de *Palaemonetes varians* (Leach) (Decapoda, Palaemonidae). *Bull. Soc. Zool. France* 109: 43-60.

Le Roux, A. 1989. Contribution à l'étude du développement larvaire et de la métamorphose chez des Crustacés Eucarides. Dissertation, Université de Rennes, 373 pp.

Le Roux, A. 1991. Le système endocrine larvaire des Crustacés Décapodes. *Bull. Soc. Zool. Fr.* 116: 63-65.

Le Roux, A. 1992. Eléments de morphogenèse sexuelle du homard *Homarus gammarus* (Linné). *Bull. Soc. Zool. Fr.* 117: 189-202.

Le Vay, L., Rodríguez, A., Kamarudin, M.S. & Jones, D.A. 1993. Influence of live and artificial diets on tissue composition and trypsin activity in *Penaeus japonicus* larvae. *Aquaculture* 118 (3-4): 287-297.

Leach, W.E. 1815. A tabular view of the external characters of four classes of animals, which Linne arranged under Insects. *Actes De Colloques* 11: 306-400.

Lebour, M.V. 1922. The food of plankton organisms. *J. Mar. Biol. Ass. U.K.* 12: 644-677.

Lebour, M.V. 1925. Young anglers in captivity and some of their enemies. A study in a plunger jar. *J. Mar. Biol. Ass.* 14: 721-734.

Lebour, M.V. 1927. Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity, with a description of the larval stages of *Inachus dorsettensis, Macropodia longirostris* and *Maia squinado*. *J. Mar. Biol. Ass.* 14: 795-821.

Lebour, M.V. 1947. Notes on the inshore plankton of Plymouth. *J. Mar. Biol. Ass. U.K.* 26: 527-547.

Lee, D.O.C. & Wickins, J.F. (eds) 1992. *Crustacean Farming.* London: Blackwell Scientific Publications.

Lee, R.F., Conner, J.W., Page, D., Ray, L.E. & Giam, C.S. 1982. Cytochrome P-450 dependent mixed-function oxygenase systems in marsh crabs. In: Vernberg, W.B., Calabrese, A., Thurnberg, F.P. & Vernberg, F.J. (eds), *Physiological Mechanisms of Marine Pollutant Toxicity*: 145-159. New York: Academic Press.

Lee, R.F. & Puppione, D.L. 1988. Lipoproteins I and II from the hemolymph of the blue crab *Callinectes sapidus:* Lipoprotein II associated with vitellogenesis. *J. Exp. Zool.* 248: 278-289.

Lee, T.N. & Williams, E. 1999. Mean distribution and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. *B. Mar. Sci.* 64: 35-56.

Leeuwenhoek, A.v. 1807. The select works of A. v. Leeuwenhoek, containing his microscopical discoveries in many of the works of nature. Translated by Samuel Hoole, London. 266-267.

Lehninger, A.L., Nelson, D.L. & Cox, M.M. 1993. *Principles of biochemistry.* 2 ed. New York: Worth Publishers.

Lehto, J., Sulkin, S., Strom, S. & Johnson, D. 1998. Protist and detrital particles as prey for the first larval stage of the brachyuran crab, *Hemigrapsus oregonensis*. *J. Exp. Mar. Biol. Ecol.* 230: 213-224.

Leibovitz, M.S. & Siegel, B.V. 1980. Aspects of free radical reactions in biological systems: aging. *J. Gerontol.* 35: 45-56.

Lemcke, H.W. & Lampert, W. 1975. Veränderungen im Gewicht und der chemischen Zusammensetzung von *Daphnia pulex* im Hunger. *Arch. Hydrobiol. (Suppl.)* 48: 108-137.

Lemmens, J.W.T.J. 1994. Biochemical evidence for absence of feeding in puerulus larvae of the western rock lobster *Panulirus cygnus* (Decapoda: Palinuridae). *Mar. Biol.* 118 (3): 383-391.

Lemmens, J.W.T.J. 1995. Nucleic acid levels, cellular activity and growth during the puerulus stage of the western rock lobster (*Panulirus cygnus;* Decapoda: Palinuridae). *J. Exp. Mar. Biol. Ecol.* 194 (2): 143-156.

Lemmens, J.W.T.J. & Knott, B. 1994. Morphological changes in external and internal feeding structures during the transition phyllosoma-puerulus-juvenile in the western rock lobster (*Panulirus cygnus,* Decapoda: Palinuridae). *J. Morphol.* 220 (3): 271-280.

Lemos, D., Ezquerra, J.M. & Garcia-Carreño, F.L. 2000. Protein digestion in penaeid shrimp: digestive proteinases, proteinase inhibitors and feed digestibility. *Aquaculture* 186 (1-2): 89-105.

Lemos, D., Hernández-Cortés, M.P., Navarrete, A., Garcia-Carreño, F.L. & Phan, V.N. 1999. Ontogenetic variation in digestive proteinase activity of larvae and postlarvae of the pink shrimp *Farfantepenaeus paulensis* (Crustacea: Decapoda: Penaeidae). *Mar. Biol.* 135: 653-662.

Lennert-Cody, C.E. & Franks, P.J.S. 1999. Plankton patchiness in high-frequency internal waves. *Mar. Ecol. Prog. Ser* 186: 59-66.

Leong, K.K., Chu, K.H. & Wong, C.K. 1991. Feeding behavior during development of the penaeid shrimp *Metapenaeus ensis*. In: Lavens, P., Sorgeloos, P., Jaspers, E. & Ollevier, F. (eds), *Spec. Publ. 15*; *Larvi '91. Symposium on Fish and Crustacean Larviculture. Gent, Belgium, August 27-30*: 122-124. Gent, Belgium: Eur. Aquacult. Soc.

Leslie, I. 1955. The nucleic acid content of tissues and cells. In: Chargaff, E. & Davidson, J.-N. (eds), *The Nucleic Acids: Chemistry and Biology 2*: 1-50. New York: Academic Press.

Levine, D.M. & Sulkin, S.D. 1979. Partitioning and utilization of energy during the larval development of the xanthid crab, *Rhithropanopeus harrisii* (Gould). *J. Exp. Mar. Biol. Ecol.* 40: 247-257.

Levine, D.M. & Sulkin, S.D. 1984. Nutritional significance of long-chain polyunsaturated fatty acids to the zoeal development of the Brachyuran crab, *Eurypanopeus depressus* (Smith). *J. Exp. Mar. Biol. Ecol.* 81: 211-223.

Levine, D.M., Sulkin, S.D. & Van Heukelem, L. 1983. The design and development of microencapsulated diets for the study of nutritional requirements of Brachyuran crab larvae. In: Berg, C.J. (ed), *Culture of Marine Invertebrates*: 193-204. Stroudsburg, Pennsylvania: Hutchinson Ross.

Li, F. & Li, S. 1995. Comparative study on the development of gastric mill of the larvae of *Scylla serrata*. *Marine Science* 5: 38-41.

Li, F. & Li, S. 1998. Studies on the hepatopancreas of larval *Scylla serrata*. *Oceanologia Et Limnologia Sinica* 29: 29-34.

Li, S., Wang, G., Tan, H. & Lin, Q. 1995. Comparative studies on the hydrolytic enzyme activities for the mud crab, *Scylla serrata* (Forskal) during embryonic development. *Journal of Xiamen University (Natural Science)* 39 (6): 970-974.

Lightner, D.V. 1983. Diseases of cultured penaeid shrimp. In: McVey, J.P. (eds), *Handbook of Mariculture I, Crustacean Aquaculture*: 289-320. Boca Raton, Florida: CRC Press.

Lignot, J.-H., Charmantier-Daures, M. & Charmantier, G. 1999. Immunolocalization of Na^+K^+-ATPase in the organs of the branchial cavity of the European lobster *Homarus gammarus* (Crustacea, Decapoda). *Cell Tissue Res.* 296: 417-426.

Lignot, J.-H., Pannier, F., Trilles, J.-P. & Charmantier, G. 1998. Effects of tributyltin oxide on survival and osmoregulation of the shrimp *Penaeus japonicus* (Crustacea, Decapoda). *Aquat. Toxicol.* 41: 277-299.

Lignot, J.-H., Spanings-Pierrot, C. & Charmantier, G. 2000. Osmoregulatory capacity as a tool in monitoring the physiological condition and the effect of stress in crustaceans. *Aquaculture* 191 (1-3): 209-245.

Lignot, J.-H., Trilles, J.-P. & Charmantier, G. 1997. Effect of an organophosphorus insecticide, fenitrothion, on survival and osmoregulation of various developmental stages of the shrimp *Penaeus japonicus* (Crustacea: Decapoda). *Mar. Biol.* 128: 307-316.

Lim, B.K. 1997. Preliminary results on the effects of salinity and settling conditions on megalopal metamorphosis of fiddler crab *Ilyoplax pusilla*. *Hydrobiologia* 358: 297-299.

Lim, B.K. & Hirayama, K. 1991. Growth and elemental composition (C, N, P) during larval developmental stages of mass-cultured swimming crab *Portunus trituberculatus*. *Mar. Ecol. Prog. Ser.*78: 131-137.

Lim, B.K. & Hirayama, K. 1993. Adenosine-triphosphate (ATP) content of swimming crab *Portunus trituberculatus* mass cultured larvae in their early developmental stages. *Nippon Suisan Gakk.* 59 (4): 735.

Lin, H.-P., Thuet, P., Trilles, J.-P., Mounet-Guillaume, R. & Charmantier, G. 1993. Effects of ammonia on survival and osmoregulation of various development stages of the shrimp *Penaeus japonicus*. *Mar. Biol.* 117: 591-598.

Linck, B.M. 1995. Einfluß von Temperatur und Salzgehalt auf die Larven der Nordseegarnele *Crangon crangon*. M.Sc. Thesis, Universität Oldenburg, Germany, 174 pp.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399-418.

Lindley, J.A. 1988. Estimating biomass and production of pelagic larvae of brachyuran decapods in western European shelf waters. *J. Exp. Mar. Biol. Ecol.* 122 (3): 195-211.

Lindley, J.A. 1990. Regressions for estimating development times of the pelagic larvae of Paguridae and Porcellanidae. *J. Plankton Res.* 12 (3): 673-678.

Lindley, J.A. 1992. A nematode parasite in a zoea of *Pisidia longicornis* (Linnaeus, 1767) (Decapoda, Anomura). *Crustaceana* 63: 322-323.

Lindley, J.A. 1998a. Diversity, biomass and production of decapod crustacean larvae in a changing environment. *Int. J. Inver. Rep. Dev.* 33 (2-3): 209-219.

Lindley, J.A. 1998b. Dry weights, carbon and nitrogen content of decapod larvae from the plankton. *J. Mar. Biol. Assoc. Uk.* 78 (1): 341-344.

Lindley, J.A., Williams, R. & Conway, D.V.P. 1994. Variability in dry weight and vertical distributions of decapod larvae in the Irish Sea and North Sea during the spring. *Mar. Biol.* 120 (3): 385-395.

Lindley, J.A., Williams, R. & Hunt, H.G. 1993. Anomalous seasonal cycles of decapod crustacean larvae in the North Sea plankton in an abnormally warm year. *J. Exp. Mar. Biol. Ecol.* 172 (1-2): 47-65.

Linné, C. 1767. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, fifferentiis, synonymus, locis.* 12th ed. Stockholm.

Lino-Po, G. & Sanvictores, E.G. 1986. Tolerance of *Penaeus monodon* eggs and larvae to fungicides against *Lagenidium* sp. and *Haliphthoros philippinensis*. *Aquaculture* 51: 161-168.

Little, G. 1969. The larval development of the shrimp, *Palaemon macrodactylus* Rathbun, reared in the laboratory, and the effect of eyestalk extirpation on development. *Crustaceana* 17: 69-87.

Livingstone, D.R. 1991. Origins and evolution of pathways of anaerobic metabolism in the animal kingdom. *Amer. Zool.* 31: 522-534.

Lockwood, A.P.M. 1976. Physiological adaptation to life in estuaries. In: Newell, R.C. (ed), *Adaptation to Environment: Essays on the Physiology of Marine Animals*: 315-392. London: Butterworths.

Logan, D.T. & Epifanio, C.E. 1978. A laboratory energy balance for the larvae and juveniles of the American lobster *Homarus americanus*. *Mar. Biol.* 47 (4): 381-389.

Londershausen, M., Kuppert, P. & Spindler, K.-D. 1982. Ecdysteroid receptors: a comparison of cytoplasmic and nuclear receptors from crayfish hypodermis. *Hoppe-Seyler's Z. Physiol. Chem.* 363: 797-802.

Loneragan, N.R., Bunn, S.E. & Kellaway, D.M. 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. *Mar. Biol.* 130: 289-300.

Loo, L.-O., Pihl Baden, S. & Ulmestrand, M. 1993. Suspension feeding in adult *Nephrops norvegicus* (L.) and *Homarus gammarus* (L.) (Decapoda). *Neth. J. Sea Res* 31: 291-297.

Lopez, M.D.G. 1996. Effect of starvation on development and survivorship of naupliar *Calanus pacificus* (Brodsky). *J. Exp. Mar. Biol. Ecol.* 203: 133-146.

Lovett, D.L. & Felder, D.L. 1989. Ontogeny of gut morphology in the white shrimp *Penaeus setiferus* (Decapoda, Penaeidae). *J. Morphol.* 201: 253-272.

Lovett, D.L. & Felder, D.L. 1990a. Ontogenetic change in digestive enzyme activity of larval and postlarval white shrimp *Penaeus setiferus* (Crustacea, Decapoda, Penaeidae. *Biol. Bull.* 178: 144-159.

Lovett, D.L. & Felder, D.L. 1990b. Ontogenetic changes in enzyme distribution and midgut function in developmental stages of *Penaeus setiferus* (Crustacea, Decapoda, Penaeidae). *Biol. Bull.* 178: 160-174.

Lovett, D.L. & Felder, D.L. 1990c. Ontogeny of kinematics in the gut of the white shrimp *Penaeus setiferus* (Decapoda: Penaeidae). *J. Crust. Biol.* 10: 53-68.

Lovett, D.L., Verzi, M.P., Clifford, P.D. & Borst, D.W. 2001. Hemolymph levels of methyl farnesoate increase in response to osmotic stress in the green crab, *Carcinus maenas*. *Comp. Biochem. Physiol.* 128A (2): 299-306.

Lovrich, G.A. & Ouellet, P. 1994. Patterns of growth and triacylglycerol content in snow crab *Chionoecetes opilio* (Brachyura: Majidae) zoeal stages reared in the laboratory. *Mar. Biol.* 120 (4): 585-591.

Lumb, G., Clare, A.S. & Costlow, J.D. 1991. Cheliped regeneration in the megalopa of the mud crab, *Rhithropanopeusn harrisii* (Gould). *Int. J. Inver. Rep. Dev.* 20 (2): 87-96.

Luppi, T.A. 1999. La coexistencia de dos especies de cangrejos en el ecosistema del cangrejal: estudio comparativo del asentamiento y el reclutamiento. Dissertation, Universidad Nacional de Mar del Plata, Argentina, 101 pp.

Luppi, T.A., Spivak, E.D. & Anger, K., in press. Experimental studies of predation and cannibalism in recruits of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Brachyura: Grapsidae). *J. Exp. Mar. Biol. Ecol.*

Luppi, T.A., Spivak, E.D., Anger, K. & Valero, J.L., submitted. Patterns and processes of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Brachyura: Grapsidae) recruitment in Mar Chiquita Coastal Lagoon, Argentina. *Est. Coast. Shelf Sci.*

Lynch, M., Weider, L.J. & Lampert, W. 1986. Measurement of the carbon balance in *Daphnia*. *Limnol. Oceanogr* 31: 17-33.

MacDonald, N.L., Stark, J.R. & Keith, M. 1989. Digestion and nutrition in *Penaeus monodon*. *J. World Aquacult. Soc.* 20: 53A.

MacKenzie, B.R. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality, and growth in laboratory-reared *Homarus americanus* Milne Edwards larvae. *J. Exp. Mar. Biol. Ecol.* 116: 87-98.

MacKenzie, B.R., Leggett, W.C. & Peters, R.H. 1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? *Mar. Ecol. Prog. Ser.* 67: 209-225.

MacMillan, D.L., Neil, D. & Laverack, M.S. 1976. A quantitative analysis of exopodite beating in the larvae of the lobster *Homarus gammarus* (L.). *Philos. T. Roy. Soc. B.*274 (929): 69-85.

Maeda, M. & Liao, I.C. 1994. Microbial processes in aquaculture environment and their importance for increasing crustacean production. *Jarq-Jpn. Agr. Res. Q.* 28 (4): 283-288.

Magalhães, C. 1987. The larval development of palaemonid shrimps from the Amazon Region reared in the laboratory. V. Abbreviated development of *Pseudopalaemon chryseus* Kensley & Walker, 1982 (Crustacea: Decapoda: Palaemonidae). *Acta Amazonica* 16/17: 95-108.

Magalhães, C. & Medeiros, N. 1998. The larval development of palaemonid shrimps from the Amazon region reared in the laboratory. VII. Abbreviated development of *Pseudopalaemon amazonensis* Ramos-Porto, 1979 (Crustacea: Decapoda: Caridea). *Acta Amazonica* 28 (4): 433-448.

Magiera, U. 1993. Experimentelle Laboruntersuchungen zur Larvalentwicklung von *Palaemon adspersus,* Rathke 1837 und *Palaemon elegans,* Rathke 1837 (Decapoda: Natantia: Palaemonidae). M. Sc. Thesis, Universität Osnabrück, Germany, 120 pp.

Makarov, R.R. 1968a. On the larval development of the genus *Sclerocrangon* G.O. Sars (Caridea, Crangonidae). *Crustaceana (Suppl.)* 2: 27-37.

Makarov, R.R. 1968b. The abbreviation of the larval development in decapods (Crustacea, Decapoda). *Zool. Zh.* 47: 348-359.

Makarov, R.R. 1974. Dominance of larval forms in euphausiid (Crustacea: Eucarida) ontogenesis. *Mar. Biol.* 27: 93-100.

Makarov, R.R. & Maslennikov, V.V. 1981. Ecology of larval development of the crustacean *Euphausia superba.* Change in dominant larval forms as a function of environmental conditions. *Mar. Ecol. Prog. Ser.* 4: 265-271.

MaKinster, J.G., Roberts, J.E., Felder, D.L., Chlan, C.A., Boudreaux, M., Bilodeau, A.L. & Neigel, J.E. 1999. PCR amplification of a middle repetitive element detects larval stone crabs (Crustacea: Decapoda: Menippidae) in estuarine plankton samples. *Mar. Ecol. Prog. Ser.* 188: 161-168.

Makridis, P., Fjellheim, A.J., Skjermo, J. & Vadstein, O. 2000. Control of the bacterial flora of *Brachionus plicatilis* and *Artemia franciscana* by incubation in bacterial suspensions. *Aquaculture* 185 (3-4): 207-218.

Mallasen, M. & Valenti, W.C. 1998. Efeito da composição iónica da agua do mar artificial no desenvolvimento de larvas de *Macrobrachium rosenbergii* (De Man, 1879)(Crustacea, Decapoda) no estagio II. *Acta Sci.* 20 (2): 195-200.

Malloy, K.D. & Targett, T.E. 1994. The use of RNA:DNA ratios to predict growth limination of juvenile summer flounder (*Paralichthys dentatus*) from Delaware and North Carolina estuaries. *Mar. Biol.* 118: 367-375.

Manahan, D.T. 1990. Adaptations by invertebrate larvae for nutrient acquisition from seawater. *Amer. Zool.* 30: 147-160.

Manahan, D.T., Jaeckle, W.B. & Nourizadeh, S.D. 1989. Ontogenetic changes in the rates of amino acid transport from seawater by invertebrate larvae (Echinodermata, Echiura, Mollusca). *Biol. Bull.* 176: 161-168.

Mancillas, J.R., McGinty, J.F., Selverston, A.I., Karten, H. & Bloom, F.E. 1981. Immunocytochemical localization of enkephalin and substance P in retina and eyestalk neurones of lobster. *Nature* 293: 576-578.

Mantel, L.H. 1985. Neurohormonal integration of osmotic and ionic regulation. *Amer. Zool.* 25: 253-263.

Mantel, L.H. & Farmer, L.L. 1983. Osmotic and ionic regulation. In: Mantel, L.H. (ed), *The Biology of Crustacea* 5; *Internal Anatomy and Physiological Regulation*: 53-161. New York: Academic Press.

Marangos, C., Barbosa, A.C.A. & Ceccaldi, H.J. 1990. Changes in free amino acid concentration during larval development of *Penaeus japonicus* Bate (Crustacea, Decapoda, Penaeidae). *Arch. Int. Physiol. Bio.* 98 (1): 41-51.

March, J.G., Benstead, J.P., Pringle, C.M. & Scatena, F.N. 1998. Migratory drift of larval freshwater shrimps in two tropical streams, Puerto Rico. *Freshwater Biol.* 40 (2): 261-273.

Marino-Balsa, J.C., Poza, E., Vazquez, E. & Beiras, R. 2000. Comparative toxicity of dissolved metals to early larval stages of *Palaemon serratus*, *Maja squinado*, and *Homarus gammarus* (Crustacea: Decapoda). *Arch. Environ. Con. Tox.* 39 (3): 345-351.

Marinovic, B., Lemmens, J.W.T.J. & Knott, B. 1994. Larval development of *Ibacus peronii* Leach (Decapoda: Scyllaridae) under laboratory conditions. *J. Crust. Biol.* 14 (1): 80-96.

Markl, J. 1986. Evolution and function of structurally diverse subunits in the respiratory protein hemocyanin from arthropods. *Biol. Bull.* 171: 90-115.

Marliave, J.B. & Mills, C.E. 1993. Piggyback riding by pandalid shrimp larvae on hydromedusae. *Can. J. Zool.* 71: 257-263.

Marrec, M. 1944. L'organe lymphocytogène des Crustacés Decapodés. Son activité cyclique. *Bull. Inst. Oceanogr. Monaco* 867: 1-4.

Marshall, S.M. & Orr, A.P. 1960. Feeding and growth. In: Waterman, T.H. (ed), *The Physiology of Crustacea 1*; *Metabolism and growth*: 227-258. New York: Acad. Press.

Martin, G.G. & Hose, J.E. 1992. Vascular elements and blood (hemolymph). In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates 10*; *Decapod Crustacea*: 117-146. New York: Wiley-Liss.

Martin, J.W. 1988. Phylogenetic significance of the brachyuran megalopa: evidence from the Xanthidae. In: Fincham, A.A. & Rainbow, P.S. (eds), *Symposia of the Zoological Society of London 59; Aspects of Decapod Crustacean Biology*: 69-102. Oxford: Clarendon Press.

Martinez, R. 1992. Respiration and respiratory electron transport activity in marine phytoplankton: growth rate dependence and light enhancement. *J. Plankton Res.* 14: 789-797.

Mashiko, K. 1985. Comparison of survival and development between large and small neonates of a freshwater prawn under starvation conditions. *Zool. Sci.* 2: 397-403.

Mashiko, K. 1987. Relationships between egg size and incubation time among populations of two freshwater prawns. *Ecol. Res.* 2: 97-99.

Mashiko, K. 1990. Diversified and clutch sizes among local populations of the fresh-water prawn *Macrobrachium nipponense* (De Haan). *J. Crust. Biol.* 10: 306-314.

Mashiko, K. 1992. Effects of salinity on larval oxygen consumption rates in etuarine and riverine populations of *Macrobrachium nipponense* (De Haan). *Res. Crust.* 21: 15-20.

Mashiko, K. 1999. Polypatric evolution of egg size among local populations of the Palaemonid prawn *Macrobrachium nipponense* (de Haan, 1849) during colonization of inland waters. In: Schram, F.R. & von Vaupel Klein, J.C. (eds), *Crustaceans and the Biodiversity Crisis 1*: 527-532. Leiden, The Netherlands: Koninklijke Brill NV.

Mashiko, K. & Numachi, K.-I. 1993. Genetic evidence for the presence of distinct fresh-water prawn (*Macrobrachium nipponense*) populations in a single river system. *Zool. Sci.* 10: 161-167.

Mashiko, K. & Numachi, K.-I. 2000. Derivation of populations with different-sized eggs in the palaemonid prawn *Macrobrachium nippoense*. *J. Crust. Biol.* 20 (1): 118-127.

Mataliotaki, I. 1991. Experimentelle Untersuchungen zum Lebenszyklus der chinesischen Wollhandkrabbe (*Eriocheir sinensis*). M. Sc. Thesis, Universität Göttingen, Germany, 101 pp.

Mathers, E.M., Houlihan, D.F. & Burren, L.J. 1994. RNA, DNA and protein concentrations in fed and starved herring *Clupea harengus* larvae. *Mar. Ecol. Prog. Ser.* 107: 223-231.

Matsuda, H. & Yamakawa, T. 1997. Effects of temperature on growth of the Japanese spiny lobster, *Panulirus japonicus* (V. Siebold) phyllosomas under laboratory conditions. *Mar. Freshwater. Res.* 48: 791-796.

Matsumoto, K. 1958. Morphological studies on the neurosecretion in crabs. *Biol. J. Okayama Univ. (Jpn.)* 4: 103-176.

Matsumoto, K. 1962. Experimental studies of the neurosecretory activities of the thoracic ganglion of a crab, *Hemigrapsus*. *Gen. Comp. Endokrinol.* 2: 4-11.

Mauchline, J. 1976. The Hiatt growth diagram for Crustacea. *Mar. Biol.* 35: 79-84.

May, B.A. & Golding, D.W. 1983. Aspects of secretory phenomena within the sinus gland of *Carcinus maenas* (L.). *Cell Tiss. Res.* 228: 245-254.

Mayfield, S., Lopata, A.L. & Cockroft, A.C. 2000. Limitation and failure of immunological technique (ELISA) in resolving the diet of the South African rock lobster *Jasus Ialandii*. *Mar. Biol.* 137 (4): 595-604.

Mayzaud, P. 1976. Respiration and nitrogen excretion of Zooplankton. IV. The influence of starvation on the metabolism and the biochemical composition of some species. *Mar. Biol.* 37 (1): 47-58.

Mayzaud, P. & Conover, R.J. 1988. O:N atomic ratio as a tool to describe zooplankton metabolism. *Mar. Ecol. Prog. Ser.*45 (3): 289-302.

Mayzaud, P. & Martin, J.L.M. 1975. Some aspects of the biochemical and mineral composition of marine plankton. *J. Exp. Mar. Biol. Ecol.* 17 (3): 297-310.

McConaugha, J.R. 1979. The effects of 20-hydroxyecdysone on survival and development of first and third stage *Cancer anthonyi* larvae. *General and Comparative Endocrinology* 37 (4): 421-427.

McConaugha, J.R. 1980. Identification of the Y-organ in the larval stages of the crab, *Cancer anthonyi* Rathbun. *J. Morphol.* 164 (1): 83-88.

McConaugha, J.R. 1985. Nutrition and larval growth. In: Wenner, A.M. (ed), *Crustacean Issues 2*; *Larval Growth*: 127-154. Rotterdam: Balkema.

McConaugha, J.R. 1992. Decapod larvae: dispersal, mortality, and ecology. A working hypothesis. *Am. Zool.* 32 (3): 512-523.

McConaugha, J.R. & Costlow, J.D. 1980. Regeneration in larvae and juveniles of the mud crab, *Rhithropanopeus harrisii*. *J. Exp. Zool.* 213 (2): 247-256.

McConaugha, J.R. & Costlow, J.D. 1981. Ecdysone regulation of larval crustacean molting. *Comp. Biochem. Phys. A.* 68A(1): 91-93.

McConaugha, J.R., Tester, P.A. & McConaugha, C.S. 1991. Feeding and growth in meroplanktonic larvae of *Callinectes sapidus* (Crustacea: Portunidae). *Mem. Queensland Mus.* 31: 320.

McConnaughey, R.A. & Sulkin, S.D. 1984. Measuring the effect of thermoclines on the vertical migration of larvae of *Callinectes sapidus* (Brachyura: Portunidae) in the laboratory. *Mar. Biol.* 81 (2): 139-145.

McCormick, M.I. 1999. Delayed metamorphosis of a tropical reef fish (*Acanthurus triostegus*): a field experiment. *Mar. Ecol. Prog. Ser.* 176: 25-38.

McEdward, L.R. (ed) 1995. *Ecology of Marine Invertebrate Larvae.* Boca Raton, FL: CRC Press.

McKenney, C.L. & Celestial, D.M. 1993. Variations in larval growth and metabolism of an estuarine shrimp *Palaemonetes pugio* during toxicosis by an insect growth regulator. *Comp. Biochem. Phys. A.* 105C(2): 239-245.

McKenney, C.L. & Hamaker, D.B. 1984. Effects of fenvalerate on larval development of *Palaemonetes pugio* (Holthuis) and on larval metabolism during osmotic stress. *Aquat. Toxicol.* 5 (4): 343-355.

McKenney, C.L. & Neff, J.M. 1981. The ontogeny of resistance adaptation and metabolic compensation to salinity and temperature by the caridean shrimp, *Palaemonetes pugio,* and modifications by sublethal zinc exposure. In: Vernberg, F.J., Calabrese, A., Thurberg, F.P. & Vernberg, W.B. (eds), *Biological monitoring of marine pollutants*: 205-240. New York: Academic Press.

McKenney, C.L., Weber, D.E., Celestial, D.M. & MacGregor, M.A. 1998. Altered growth and metabolism of an estuarine shrimp (*Palaemonetes pugio*) during and after metamorphosis onto fenvalerate laden sediment. *Arch. Environ. Con. Tox.* 35 (3): 464-471.

McLaren, I.A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. *J. Fish. Res. Bd. Canada* 20: 685-727.

McLaughlin, P.A. 1983. Internal anatomy. In: Mantel, L.H. (ed), *The Biology of Crustacea 5*; *Internal Anatomy and Physiological Regulation*: 1-52. New York: Academic Press.

McLaughlin, P.A. & Holthuis, L.B. 1985. Anomura versus Anomala. *Crustaceana* 49: 204-209.

McMahon, B.R. 2001. Control of cardiovascular function and its evolution in Crustacea. *J. Exp. Biol.* 204 (5): 923-932.

McMahon, B.R. & Wilkens, J.L. 1983. Ventilation, perfusion, and oxygen uptake. In: Mantel, L.H. (ed), *The Biology of Crustacea 5*; *Internal Anatomy and Physiological Regulation*: 289-372. New York: Academic Press.

McNab, B.K. 1999. On the comparative ecological and evolutionary significance of total and mass-specific rates of metabolism. *Physiol. Biochem. Zool.* 72 (5): 642-644.

McNamara, J.C., Moreira, G.S. & Moreira, P.S. 1980. Respiratory metabolism of *Macrobrachium olfersii* (Wiegmann) zoea during the moulting cycle from eclosion to first ecdysis. *Biol. Bull.* 159 (3): 692-699.

McNamara, J.C., Moreira, G.S. & Moreira, P.S. 1982. The effect of salinity on the respiratory metabolism and duration of intermoult cycle in larval and adult *Macrobrachium olfersii* (Wiegmann) (Decapoda, Palaemonidae). *Bolm Fisiol. Animal. Univ. S. Paulo* 6: 117-125.

McNamara, J.C., Moreira, G.S. & Moreira, P.S. 1983. The effect of salinity on respiratory metabolism, survival and moulting in the first zoea of *Macrobrachium amazonicum* (Heller) (Crustacea, Palaemonidae). *Hydrobiologia* 101 (3): 239-242.

McNamara, J.C., Moreira, G.S. & Moreira, P.S. 1985. Thermal effects on metabolism in selected ontogenetic stages of the freshwater shrimps *Macrobrachium olfersii* and *Macrobrachium heterochirus* (Decapoda, Palaemonidae). *Comp. Biochem. Phys. A.* 80A(2): 187-190.

McNamara, J.C., Moreira, G.S. & Souza, S.C.R. 1986. The effect of salinity on respiratory metabolism in selected ontogenetic stages of the freshwater shrimp *Macrobrachium olfersii* (Decapoda, Palaemonidae). *Comp. Biochem. Phys. A.* 83A(2): 359-363.

McNamara, J.C., Salomão, L.C. & Ribeiro, E.A. 1991. Neuroendocrine regulation of osmotic and ionic concentrations in the hemolymph of the freshwater shrimp *Macrobrachium olfersii* (Wiegmann) (Crustacea, Decapoda). *General and Comparative Endocrinology* 84 (1): 16-26.

McNamara, J.C. & Torres, A.H. 1999. Ultracytochemical location of Na^+/K^+-ATPase activity and effect of high salinity acclimation in gill and renal epithelia of the freshwater shrimp *Macrobrachium olfersii* (Crustacea, Decapoda). *J. Exp. Zool.* 284 (6): 617-628.

McTigue, T.A. & Zommerman, R.J. 1991. Carnivory *vs.* herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives). *J. Exp. Mar. Biol. Ecol.* 151: 1-16.

McVey, J.P. (ed) 1983. *Handbook of Mariculture. Vol. I. Crustacean Aquaculture.* Boca Raton, Florida, USA: CRC Press.

McWilliam, P.S. 1995. Evolution in the phyllosoma and puerulus phases of the spiny lobster genus *Panulirus* White. *J. Crust. Biol.* 15 (3): 542-557.

McWilliam, P.S. & Phillips, B.F. 1997. Metamorphosis of the final phyllosoma and secondary lecithotrophy in the puerulus of *Panulirus cygnus* George: a review. *Mar. Freshwater. Res.* 48 (8): 783-790.

McWilliam, P.S., Phillips, B.F. & Kelly, S. 1995. Phyllosoma larvae of *Scyllarus* species (Decapoda, Scyllaridae) from the shelf waters of Australia. *Crustaceana* 68: 537-566.

Medakovic, D., Popovic, S., Grzeta, B., Plazonic, M. & Hrs-Brenko, M. 1997. X-ray diffraction study of calcification processes in embryos and larvae of the brooding oyster *Ostrea edulis*. *Mar. Biol.* 129: 615-623.

Meier, T. & Reichert, H. 1990. Neuronal development in the crustacean nervous system studied by neuron-specific antibody labelling. In: Wiese, K., Krenz, W.D., Tautz, J., Reichert, H. & Mulloney, B. (edseds), *Frontiers in Crustacean Neurobiology, Advances in Life Sciences*: 523-529. Basel: Birkhäuser.

Mellon, D.F. 1992. Connective tissue and supporting structures. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates 10*; *Decapod Crustacea*: 77-116. New York: Wiley –Liss.

Melo, S.G. & Brossi-Garcia, A.L. 1999. Postembryonic development of *Macrobrachium petronioni* (Caridea: Palaemonidae) in the laboratory. *J. Crust. Biol.* 19 (3): 622-642.

Merchie, G., Lavens, P. & Sorgeloos, P. 1997. Optimization of dietary vitamin C in fish and crustacean larvae: a review. *Aquaculture* 155: 169-185.

Messick, G.A. 1998. Diseases, parasites, and symbionts of blue crabs (*Callinectes sapidus*) dredged from Chesapeake Bay. *J. Crust. Biol.* 18: 533-548.

Metaxas, A. 2001. Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Can. J. Fish. Aquat. Sci.*58 (1): 86-98.

Metaxas, A. & Young, C.M. 1998. Responses of echinoid larvae to food patches of different algal densities. *Mar. Biol.* 130 (3): 433-445.

Metcalf, K.S. & Lipcius, R.N. 1992. Relationship of habitat and spatial scale with physiological state and settlement of blue crab postlarvae in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 82: 143-150.

Meyer, B. 1992. Freilanduntersuchungen zur Ernährung von Dekapoden-Larven. M.Sc. Thesis, Universität Kiel, Germany, 82 pp.

Meyer-Harms, B. & Harms, J. 1993. Detection of phytoplankton pigments by HPLC in *Hyas araneus* larvae (Crustacea, Decapoda): Comparison of field and laboratory samples. *Neth. J. Sea Res.* 31: 153-161.

Meyer-Rochow, V.B. 1975. Larval and adult eye of the western rock lobster (*Panulirus longipes*). *Cell Tissue Res.* 162: 439-457.

Meyers, T.R., Morado, J.F., Sparks, A.K., Bishop, G.H., Pearson, T., Urban, D. & Jackson, D. 1996. Distribution of bitter crab syndrome in tanner crabs (*Chionoecetes bairdi*, *C. opilio*) from the Gulf of Alaska and the Bering Sea. *Dis. Aquat. Org.* 26: 221-227.

Middaugh, D.P. & G. Floyd 1978. The effect of prehatch and posthatch exposure to cadmium on salinity tolerance of larval grass shrimp, *Palaemonetes pugio*. *Estuaries* 1: 123-125.

Mikami, S. & Greenwood, J.G. 1997a. Complete development and comparative morphology of larval *Thenus orientalis* and *Thenus* sp. (Decapoda: Scyllaridae) reared in the laboratory. *J. Crust. Biol.* 17 (2): 289-308.

Mikami, S. & Greenwood, J.G. 1997b. Influence of light regimes on phyllosomal growth and timing of moulting in *Thenus orientalis* (Lund) (Decapoda: Scyllaridae). *Mar. Freshwater. Res.* 48 (8): 777-782.

Mikami, S., Greenwood, J.G. & Gillespie, N.C. 1995. The effect of starvation and feeding regimes on survival, intermoult period and growth of cultured *Panulirus japonicus* and *Thenus* sp. Phyllosomas (Decapoda, Palinuridae and Scyllaridae). *Crustaceana* 68: 160-169.

Mikami, S., Greenwood, J.G. & Takashima, F. 1994. Functional morphology and cytology of the phyllosomal digestive system of *Ibacus ciliatus* and *Panulirus japonicus* (Decapoda, Scyllaridae and Palinuridae). *Crustaceana* 67: 212-225.

Mikami, S. & Takashima, F. 1993a. Development of the proventriculus in larvae of the slipper lobster, *Ibacus ciliatus* (Decapoda: Scyllaridae). *Aquaculture* 116 (2-3): 199-217.

Mikami, S. & Takashima, F. 1993b. Effects of starvation upon survival, growth and molting interval of the larvae of the spiny lobster *Panulirus japonicus* (Decapoda, Palinuridea). *Crustaceana* 64: 137-142.

Miller, C.B., Johnson, J.K. & Heinle, D.R. 1977. Growth rules in the marine copepod genus *Acartia*. *Limnol. Oceanogr.* 22: 326-335.

Miller, S.E. & Hadfield, M.G. 1990. Developmental arrest during larval life and life-span extension in a marine mollusc. *Science* 248: 356-358.

Milne Edwards, H. 1834. *Histoire naturelle des Crustacés, comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux.* Libraire Encyclopédique de Roret 1. Paris.

Milne Edwards, H. 1837. *Histoire naturelle des Crustacés, comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux.* Libraire Encyclopédique de Roret 2. Paris.

Milne Edwards, H. 1840. *Histoire naturelle des Crustacés, comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux.* Libraire Encyclopédique de Roret 3. Paris.

Milne Edwards, H. & Lucas, H. 1843. Crustacés. In: A. D. d'Orbigny *Voyage dans l'Amerique Meridionale (Le Brésil, la République crientale de l'Urugauy, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833*. Paris: Bertranad.

Minagawa, M. 1990a. Complete larval development of the red frog crab *Ranina ranina* (Crustacea, Decapoda, Raninidae) reared in the laboratory. *Nippon Suisan Gakk.* 56: 577-589.

Minagawa, M. 1990b. Influence of temperature on survival, feeding and development of larvae of the red frog crab, *Ranina ranina* (Crustacea, Decapoda, Raninidae). *Nippon Suisan Gakk.* 56 (5): 755-760.

Minagawa, M. 1992. Effects of salinity on survival, feeding, and development of larvae of the red frog crab *Ranina ranina*. *Nippon Suisan Gakk.* 58 (10): 1855-1860.

Minagawa, M. 1994. Effects of photoperiod on survival, feeding and development of larvae of the red frog crab, *Ranina ranina*. *Aquaculture* 120 (1-2): 105-114.

Minagawa, M., Chiu, J.R. & Murano, M. 1993. Developmental changes in body weight and elemental composition of laboratory-reared larvae of the red frog crab, *Ranina ranina* (Decapoda: Brachyura). *Mar. Biol.* 116 (3): 399-406.

Minagawa, M. & Murano, M. 1993a. Effects of prey density on survival, feeding rate and development of zoeas of the red frog crab *Ranina ranina* (Crustacea, Decapoda, Raninidae). *Aquaculture* 113 (1-2): 91-100.

Minagawa, M. & Murano, M. 1993b. Larval feeding rhythms and food consumption by the red frog crab *Ranina ranina* (Decapoda, Raninidae) under laboratory conditions. *Aquaculture* 113 (3): 251-260.

Minagawa, M. & Takashima, F. 1994. Developmental changes in larval mouthparts and foregut in the red frog crab, *Ranina ranina* (Decapoda: Raninidae). *Aquaculture* 126 (1-2): 61-71.

Miner, B.G., Morgan, S.G. & Hoffman. J.R. 2000. Postlarval chromatophores as an adaptation to ultraviolet radiation. *J. Exp. Mar. Biol. Ecol.* 249 (2): 235-248.

Miron, G., Walters, L.J., Tremblay, R. & Bourget, E. 2000. Physiological condition and barnacle larval behavior: a preliminary look at the relationship between TAG/DNA ratio and larval substratum exploration in *Balanus amphitrite*. *Mar. Ecol. Prog. Ser.*198: 303-310.

Miyawaki, M. & Taketomi, Y. 1971. Changes of Y gland cell structure of the crayfish, *Procambarus clarkii,* during the molt cycle and in some experimental conditions. *Kumamoto J. Sci. Biol.* 10: 55-67.

Mohammadian, M.A., Hansson, S. & De Stasio, B.T. 1997. Are marine planktonic invertebrates food limited? The functional response of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 150: 113-119.

Moksnes, P.-O., Lipcius, R.N., Pihl, L. & Montfrans, v.J. 1997. Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *J. Exp. Mar. Biol. Ecol.* 215: 157-187.

Moksnes, P.-O., Pihl, L. & van Montfrans, J. 1998. Predation on postlarvae and juveniles of the shore crab *Carcinus maenas:* importance of shelter, size and cannibalism. *Mar. Ecol. Prog. Ser* 166: 211-225.

Moksnes, P.-O. & Wennhage, H. 2001. Methods for estimating decapod larval supply and settlement: importance of larval behavior and development stage. *Mar. Ecol. Prog. Ser.*209: 257-273.

Moller, T.H. 1978. Feeding behaviour of larvae and postlarvae of *Macrobrachium rosenbergii* (de Man) (Crustacea: Palaemonidae). *J. Exp. Mar. Biol. Ecol.* 35: 251-258.

Moloney, C.L., Botsford, L.W. & Largier, J.L. 1994. Development, survival and timing of metamorphosis of planktonic larvae in a variable environment: the Dungeness crab as an example. *Mar. Ecol. Prog. Ser.*113: 61-79.

Momoyama, K. & Sano, T. 1996. Infectivity of baculoviral mid-gut gland necrosis virus (BMNV) to larvae of five crustacean species. *Fish Pathol.* 31 (2): 81-85.

Montu, M., Anger, K. & Bakker, C.d. 1990. Variability in the larval development of *Metasesarma rubripes* (Decapoda, Grapsidae) reared in the laboratory. *Nerítica, Pontal Do Sul (Brazil)* 5: 113-118.

Montu, M., Anger, K. & Bakker, S.d. 1996. Larval development of the Chinese mitten crab *Eriocheir sinensis* H. Milne-Edwards (Decapoda: Grapsidae) reared in the laboratory. *Helgoländer Meeresunters.* 50: 223-252.

Moore, S.F. & Dwyer, R.L. 1974. Effects of oil on marine organisms: a critical assessment of published data. *Wat. Res.* 8: 819-827.

Mootz, C.A. & Epifanio, C.E. 1974. An energy budget for *Menippe mercenaria* larvae fed *Artemia* nauplii. *Biol. Bull.* 146 (1): 44-55.

Moreira, G.S. & McNamara, J.C. 1980. Influence of salinity on the respiratory rate of the crustacean *Macrobrachium holthuisi* larvae. *Acta Physiol. Lat. Am.* 30 (1): 68-69.

Moreira, G.S., McNamara, J.C., Hiroki, K. & Moreira, P.S. 1981. The effect of temperature on the respiratory metabolism of selected developmental stages of *Emerita brasiliensis* Schmitt (Anomura, Hippidae). *Comp. Biochem. Phys. A.* 70A(4): 627-629.

Moreira, G.S., McNamara, J.C. & Moreira, P.S. 1986. The effect of salinity on the upper thermal limits of survival and metamorphosis during larval development in *Macrobrachium amazonicum* (Heller) (Decapoda, Palaemonidae). *Crustaceana* 50: 231-238.

Moreira, L.C. & Odinetz Collart, O. 1993. Migrção vertical nictemeral das larvas de *Macrobrachium amazonicum* num lago de várzea na Amazônia Central, Ilha do Careiro, Brasil. *Amazoniana* 12: 385-398.

Moreno, V.J., de Moreno, J.E.A. & Brenner, R.R. 1979. Fatty acid metabolism in the calanoid copepod *Paracalanus parvus*. I. Polyunsaturated fatty acids. *Lipids* 14: 313-317.

Morgan, G.J. 1987a. Abbreviated development in *Paguristes frontalis* (Milne Edwards, 1836) (Anomura: Diogenidae) from southern Australia. *J. Crust. Biol.* 7: 536-540.

Morgan, G.J. 1987b. Brooding of juveniles and observations on dispersal of young in the spider crab *Paranaxia serpulifera* (Guérin) (Decapoda, Brachyura, Majidae) from Western Australia. *Rec. West. Austr. Mus.* 13: 337-343.

Morgan, S.G. 1987. Morphological and behavioral antipredatory adaptations of decapod zoeae. *Oecologia* 73 (3): 393-400.

Morgan, S.G. 1989. Adaptive significance of spination in estuarine crab zoeae. *Ecology* 70 (2): 464-482.

Morgan, S.G. 1990. Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. *Ecology* 71 (5): 1639-1652.

Morgan, S.G. 1992. Predation by plankonic and benthic invertebrates on larvae of estuarine crabs. *J. Exp. Mar. Biol. Ecol.* 163 (1): 91-110.

Morgan, S.G. 1995a. Life and death in the plankton: larval mortality and adaptation. In: McEdward, L.R. (ed), *Ecology of Marine Invertebrate Larvae*: 279-321. Boca Raton, FL: CRC Press.

Morgan, S.G. 1995b. The timing of larval release. In: McEdward, L.R. (ed), *Ecology of Marine Invertebrate Larvae*: 157-191. Boca Raton, Florida: CRC Press.

Morgan, S.G. & Christy, J.H. 1996. Survival of marine larvae under the countervailing selective pressures of photodamage and predation. *Limnol. Oceanogr.* 41: 498-504.

Morgan, S.G. & Christy, J.H. 1997. Planktivorous fishes as selective agents for reproductive synchrony. *J. Exp. Mar. Biol. Ecol.* 209: 89-101.

Morgan, S.G., Zimmer-Faust, R.K., Heck, K.L. & Coen, L.D. 1996. Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply. *Mar. Ecol. Prog. Ser* 133: 73-88.

Morris, M.J. & Hopkins, T.L. 1983. Biochemical composition of crustacean zooplankton from the eastern Gulf of Mexico. *J. Exp. Mar. Biol. Ecol.* 69: 1-19.

Morris, S. 2001. Neuroendocrine regulation of osmoregulation and the evolution of air-breathing in decapod crustaceans. *J. Exp. Biol.* 204 (5): 979-989.

Mortimer, M.R. & Miller, G.J. 1994. Susceptibility of larval and juvenile instars of the sand crab, *Portunus pelagicus* (L.), to sea water contaminated by chromium, nickel or copper. *Aust. J. Mar. Freshwater Res.* 45: 1107-1121.

Moss, G.A., Tong, L.J. & Illingworth, J. 1999. Effects of light intensity and food density on the growth and survival of early-stage phyllosoma larvae of the rock lobster *Jasus edwardsii*. *Mar. Freshwater. Res.* 50: 129-134.

Mourente, G. & Rodríguez, A. 1997. Effects of salinity and dietary DHA (22:6*n*-3) content on lipid composition and performance of *Penaeus kerathurus* postlarvae. *Mar. Biol.* 128: 289-298.

Müller, F. 1864. *Für Darwin.* Leipzig: Engelmann.

Müller, K.J. 1983. Crustacea with preserved soft parts from the Upper Cambrian of Sweden. *Lethaia* 16: 93-109.

Mykles, D.L. 1979. Ultrastructure of alimentary epithelia of lobsters *Homarus americanus* and *H. gammarus* and crab, *Cancer magister*. *Zoomorphology* 92: 201-215.

Nagaraj, M. 1992. Combined effects of temperature and salinity on the zoeal development of the crab *Liocarcinus puber* (Decapoda: Portunidae). *Mar. Ecol. - Mar. Ecol.-P. S. Z. N. I.* 13: 233-241.

Nagaraj, M. 1993. Combined effects of temperature and salinity on the zoeal development of the green crab, *Carcinus maenas* (Linnaeus, 1758) (Decapoda: Portunidae). *Sci. Mar.* 57: 1-8.

Nakai, K. 1955. The chemical composition, volume, weight and size of the important marine plankton. *Spec. Publ. Tokai Fish. Res. Lab.* 5: 12-24.

Nakamura, K. 1974. A model of the functional response of a predator to prey density involving the hunger effect. *Oecologia* 16: 265-278.

Nakanishi, T. 1987. Rearing condition of eggs, larvae and post-larvae of king crab. *Bull. Jap. Sea Reg. Fish. Res. Lab.* 37: 57-161.

Nates, S.F., Felder, D.L. & Lemaitre, R. 1997. Comparative larval development in two species of the burrowing ghost shrimp genus *Lepidophthalmus* (Decapoda: Callianassidae). *J. Crust. Biol.* 17: 497-519.

Nates, S.F. & McKenney, C.L. 2000a. Growth and variations in lipid class and fatty acid composition during larval development of the stone crab, *Menippe adina* Williams and Felder, 1986. *Int. J. Inver. Rep. Dev.* 37 (2): 157-165.

Nates, S.F. & McKenney, C.L. 2000b. Growth, lipid class and fatty acid composition in juvenile mud crabs (*Rhithropanopeus harrisii*) following larval exposure to Fenoxycarb®, insect juvenile hormone analog. *Comp. Biochem. Phys. A.* 127C(3): 317-325.

Nates, S.F. & McKenney, C.L. 2000c. Ontogenetic changes in biochemical composition during larval and early postlarval development of *Lepidophthalmus louisianensis*, a ghost shrimp with abbreviated development. *Comp. Biochem. Phys. A.* 127B(4): 459-468.

Naviner, M., Bergé, J.P., Durand, P. & Le Bris, H. 1999. Antibacterial activity of the marine diatom *Skeletonema costatum* against aquacultural pathogens. *Aquaculture* 174 (15-24)

Neil, D.M., MacMillan, D.L., Robberson, R.M. & Laverack, M.S. 1976. The structure and function of thoracic expodites in the larvae of the lobster *Homarus gammarus* (L.). *Philos. T. Roy. Soc. B.*274 (929): 53-68.

Nelson, S.G. & Kropp, R.K. 1985. Ammonia excretion and nitrogen assimilation by the tropical freshwater prawn *Macrobrachium lar* (Crustacea, Palaemonidae). *Comp. Biochem. Physiol.* 81: 699-704.

Nelson, S.G., Li, H.W. & Knight, A.W. 1977. Calorie, carbon and nitrogen metabolism of juvenile *Macrobrachium rosenbergii* (De Man) (Crustacea, Palaemonidae) with regard to trophic position. *Comp. Biochem. Physiol.* 58: 319-327.

Nelson, S.G., Simmons, M.A. & Knight, A.W. 1985. Calorigenic effect of diet on the grass shrimp *Crangon franciscorum* (Crustacea: Crangonidae). *Comp. Biochem. Physiol.* 82: 373-376.

Neville, A.C. (ed) 1975. *Biology of the arthropod cuticle.* Berlin: Springer.

New, M.B. 1980. A bibliography of shrimp and prawn nutrition. *Aquaculture* 21: 101-128.

New, M.B. 1990. Freshwater prawn culture: a review. *Aquaculture* 88: 99-143.

Newell, G.E. & Newell, R.C. 1977. *Marine Plankton - a Practical Guide.* London, UK: Hutchinson.

Newell, R.C. 1979. *Biology of intertidal animals.* Faversham, Kent: Marine Ecological Surveys.

Newell, R.I.E. 1982. An evaluation of the wet oxidation technique for use in determining the energy content of seston samples. *Can. J. Fish. Aquat. Sci.* 39: 1383-1388.

Newton, C. & Potts, W.T.W. 1993. Ionic regulation and buoyancy in some planktonic organisms. *J. Mar. Biol. Assoc. Uk.* 73 (1): 15-23.

Ng, P.K.L. 1988. *The freshwater crabs of Peninsular Malaysia and Singapore.* Singapore: National University of Singapore.

Ng, P.K.L. 1992. The freshwater crabs and palaemonid prawns (Crustacea, Decapoda) of Batam Island, Riau-Archipelago, Indonesia, including descriptions of two new species. *P. Biol. Soc. Wash.* 105 (4): 788-794.

Nichols, J.H. & Lawton, P. 1979. The occurrence of the larval stages of the lobster *Homarus gammarus,* (Linnaeus, 1758) off the northeast coast of England in 1976. *J. Cons. Int. Explor. Mer.* 38: 234-243.

Nichols, J.H., Thompson, B.M. & Cryer, M. 1982. Production, drift and mortality of the planktonic larvae of the edible crab (*Cancer pagurus*) off the north-east coast of England. *Neth. J. Sea Res.* 16: 173-184.

Nicol, S., Stolp, M. & Nordstrom, O. 1992. Change in the gross biochemistry and mineral content accompanying the moult cycle in the Antarctic krill *Euphausia superba*. *Mar. Biol.* 113: 201-209.

Nielsen, C. 1995. *Animal evolution - interrelationships of the living phyla.* Oxford, U.K.: Oxford University Press.

Nijhout, H.F. 1975. A threshold size for metamorphosis in the tobacco hornworm, *Manduca sexta* (L.). *Biol. Bull. Mar. Biol. Lab. Woods Hole* 149: 214-225.

Nilsson, D.E. 1983. Evolutionary links beteen apposition and superposition optics in crustacean eyes. *Nature* 302: 818-820.

Nilsson, D.E. 1989. Optics and evolution of the compound eye. In: Stavenga, D.G. & Hardie, R.C. (eds), *Facets of Vision*: 30-73. Berlin: Springer.

Nilsson, D.E., Hallberg, E. & Elofsson, R. 1986. The ontogenetic development of refracting superposition eyes in crustaceans: transformation of optical design. *Tissue Cell* 18: 509-519.

Nishida, S. & Kittaka, J. 1992. Integumental organs of the phyllosoma larva of the rock lobster *Jasus edwardsii* (Hutton). *J. Plankton Res.* 14: 563-573.

Nishida, S., Quigley, B.D., Booth, J.D., Nemoto, T. & Kittaka, J. 1990. Comparative morphology of the mouthparts and foregut of the final-stage phyllosoma, puerulus, and postpuerulus of the rock lobster *Jasus edwardsii* (Decapoda: Palinuridae). *J. Crust. Biol.* 10: 293-305.

O'Connor, N.J. 1991. Flexibility in timing of the metamorphic molt by fiddler crab megalopae *Uca pugilator*. *Mar. Ecol. Prog. Ser.* 68: 243-247.

O'Connor, N.J. & Gregg, A.S. 1998. Influence of potential habitat cues on duration of the megalopal stage of the fiddler crab *Uca pugnax*. *J. Crust. Biol.* 18 (4): 700-709.

O'Connor, N.J. & Judge, M.L. 1997. Flexibility in timing of molting of fiddler crab megalopae: evidence from *in situ* manipulation of cues. *Mar. Ecol. Prog. Ser.*146: 55-60.

Obrebski, S. 1979. Larval colonizing strategies in marine benthic invertebrates. *Mar. Ecol. Prog. Ser.* 1: 293-300.

Ogawa, Y., Hashimoto, H., Kakuda, S. & Gushima, K. 1991. On the growth and life span of the population of oriental river prawn, *Macrobrachium nipponense* (De Haan), in the Ashida River. *J. Fac. Appl. Biol. Sci. Hiroshima Univ.* 30: 43-53.

Olmi, E.J. 1994. Vertical migration of blue crab *Callinectes sapidus* megalopae: implications for transport in estuaries. *Mar. Ecol. Prog. Ser.* 113: 39-54.

Olmi, E.J. & Lipcius, R.N. 1991. Predation on postlarvae of the blue crab *Callinectes sapidus* Rathbun by sand shrimp *Crangon septemspinosa* Say and grass shrimp *Palaemonetes pugio* Holthuis. *J. Exp. Mar. Biol. Ecol.* 151: 169-183.

Olson, R.R. & Olson, M.H. 1989. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? *Ann. Rev. Ecol. Syst.* 20: 225-247.

Omori, M. 1974. The biology of pelagic shrimps in the ocean. *Adv. Mar. Biol.* 12: 233-324.

Omori, M. 1978. Some factors affecting on dry weight, organic weight and concentrations of carbon and nitrogen in freshly prepared and in preserved zooplankton. *Int. Revue Ges. Hydrobiol.* 63: 261-269.

Omori, M. 1979. Growth, feeding, and mortality of larval and early postlarval stages of the oceanic shrimp *Sergestes similis* Hansen. *Limnol. Oceanogr.* 24: 273-288.

Omori, M. & Hamner, W.M. 1982. Patchy distribution of zooplankton behaviour, population assessment and sampling problems. *Mar. Biol.* 72: 193-200.

Orlamünder, J. 1942. Zur Entwicklung und Formbildung des *Birgus latro* L. mit besonderer Berücksichtigung des X-Organs. *Z. Wiss. Zool.* 155: 280-316.

Oshel, P.E. 1985. Paraffin carving: a preparative technique for scanning electron microscopy of crustaceans. *J. Crust. Biol.* 5: 327-329.

Ostrensky, A., Pestana, D. & Sternheim, U.S. 1997. Effects of different diets on the larval development and ammonia excretion rates of the crab *Chasmagnathus granulata* Dana, 1851, under laboratory conditions. *Cienc. Cult. J. Braz. Ass. Adv. Sci.* 49: 205-210.

Ott, F.S. & Forward, R.B. 1976. The effect of temperature on phototaxis and geotaxis by larvae of the crab *Rhithropanopeus harrisii* (Gould). *J. Exp. Mar. Biol. Ecol.* 23: 97-107.

Ouellet, P., Taggart, C.T. & Frank, K.T. 1992. Lipid condition and survival in shrimp (*Pandalus borealis*) larvae. *Can. J. Fish. Aquat. Sci.*49 (2): 368-378.

Ouellet, P., Taggart, C.T. & Frank, K.T. 1995. Early growth, lipid composition, and survival expectations of shrimp *Pandalus borealis* larvae in the northern Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.*126 (1-3): 163-175.

Owens, L. 1987. A checklist of metazoan parasites from Natantia (excluding the crustacean parasites of the Caridea). *J. Shellfish Res.* 6: 117-124.

Owens, T.G. & King, F.D. 1975. The measurement of respiratory electron-transport-system activity in marine zooplankton. *Mar. Biol.* 30: 27-36.

Packard, G.C. & Boardman, T.J. 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? *Comp. Biochem. Physiol.* 123A: 37-44.

Packard, T.T. 1985. Measurements of electron transport activity of microplankton. In: Jannasch, H. & Williams, P.J.L. (eds), *Advances in aquatic microbiology 3*: 207-261. New York: Academic Press.

Packard, T.T. & Williams, P.J.L. 1981. Rates of respiratory oxygen consumption and electron transport in surface seawater from the northwest Atlantic. *Oceanol. Acta.* 4: 351-358.

Paffenhöfer, G.-A. & Knowles, S.C. 1978. Feeding of marine planktonic copepods on mixed phytoplankton. *Mar. Biol.* 48: 143-152.

Pahl, B.C. & Opitz, H.M. 1999. The effects of cypermethrin (Excis) and azamethiphos (Salmosan) on lobster *Homarus americanus* H-Milne Edwards larvae in a laboratory study. *Aquac. Res.* 30 (9): 655-665.

Paine, R.T. 1971. The measurement and application of the calorie to ecological problems. *Ann. Rev. Ecol. Syst.* 2: 145-164.

Painter, S.D., Clough, B., Garden, R.W., Sweedler, J.V. & Nagle, G.T. 1998. Characterization of *Aplysia* attractin, the first water-borne peptide pheromone in invertebrates. *Biol. Bull.* 194: 120-131.

Palacios, E., Ibarra, A.M. & Racotta, I.S. 2000. Tissue biochemical composition in relation to multiple spawning in wild and pond-reared *Penaeus vannamei* broodstock. *Aquaculture* 185 (3-4): 353-371.

Palacios, E., Ibarra, A.M., Ramirez, J.L., Portillo, G. & Racotta, I.S. 1998. Biochemical composition of eggs and nauplii in White Pacific Shrimp, *Penaeus vannamei* (Boone), in relation to the physiological condition of spawners in a commercial hatchery. *Aquac. Res.* 29: 183-189.

Palacios, E., Pérez Rostro, C.I., Ramírez, J.L., Ibarra, A.M. & Racotta, I.S. 1999. Reproductive exhaustion in shrimp (*Penaeus vannamei*) reflected in larval biochemical composition, survival and growth. *Aquaculture* 171: 309-321.

Panning, A. 1938. *The Chinese mitten crab.* Ann. Rep. Smithsonian Inst. 1938. Washington, DC: Smithsonian Institution.

Papathanassiou, E. 1983. Effects of cadmium and mercury ions on respiration and survival of the common prawn *Palaemon serratus* (Pennant). *Rev. Inst. Oceanogr. Med.* 70: 21-35.

Paradis, A.R., Pepin, P. & Brown, J.A. 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. *Can. J. Fish. Aquat. Sci.* 53: 1226-1235.

Parker, G.H. 1890. The histology and development of the eye of the lobster. *Bull. Mus. Comp. Zool.* 20: 1-60.

Parry, G. 1960. Excretion. In: Waterman, T.H. (ed), *The Physiology of Crustacea 1*; *Metabolism and growth*: 341-366. New York: Academic Press.

Parsons, T.R., Takahashi, M. & Hargrave, B. 1977. *Biological Oceanographic Processes.* 2 ed. Oxford: Pergamon Press.

Paschke, K. 1998. Untersuchungen zum Energiestoffwechsel während der Embryonalentwicklung der Nordsee-Garnele *Crangon crangon* (Linnaeus 1758) (Decapoda: Caridea). Dissertation, Universität Hamburg, Germany, 93 pp.

Pasharawipas, T. & Flegel, T.W. 1994. A specific DNA probe to identify the intermediate host of a common microsporidian parasite of *Penaeus merguiensis* and *P. monodon*. *Asian Fisheries Sci.* 7: 157-167.

Passano, L.M. 1960. Molting and its control. In: Waterman, T.H. (ed), *The physiology of Crustacea*: 473-536. New York: Academic Press.

Passano, L.M. 1961. The regulation of crustacean metamorphosis. *Am. Zool.* 1: 89-95.

Pasupathi, K. & Kannupandi, T. 1989. Effect of the heavy metal zinc on larval stages of the mangrove grapsid crab *Sesarma pictum* De Haan. *Ind. J. Inv. Zool. & Aquat. Biol.* 1: 53-57.

Patten, B.D. & Odum, E.P. 1981. A cybernetic nature of ecosystems. *Amer. Nat.* 118: 886-895.

Paul, A.J. & Nunes, P. 1983. Temperature modification of respiratory metabolism and caloric intake of *Pandalus borealis* (Krøyer) first zoeae. *J. Exp. Mar. Biol. Ecol.* 66: 163-168.

Paul, A.J. & Paul, J.M. 1980. The effect of early starvation on later feeding success of king crab zoeae. *J. Exp. Mar. Biol. Ecol.* 44: 247-251.

Paul, A.J., Paul, J.M. & Coyle, K.O. 1990. Growth of stage I king crab larvae of *Paralithodes camtschatica* (Tilesius) (Decapoda: Lithodidae) in natural communities. *J. Crust. Biol.* 10 (2): 175-183.

Paul, A.J., Paul, J.M., Shoemaker, P.A. & Feder, H.M. 1979. Prey concentrations and feeding response in laboratory-reared stage-one zoeae of king crab, snow crab, and pink shrimp. *T. Am. Fish. Soc.* 108: 440-443.

Paul, J.M. & Paul, A.J. 1989. Reproductive of sublegal size male red king crab with access to multiple mates. In: *Lowell Wakefield Fisheries Symposium, Proceedings of the International Symposium on King and Tanner Crabs*, *Anchorage, Alaska USA, Nov.1989*. Anchorage, Alaska USA:

Paula, J. 1987. Seasonal distribution of Crustacea Decapoda larvae in S. Torpes bay, South-western Portugal. *Inv. Pesq.* 51: 267-275.

Paula, J. 1989. Rhythms of larval release of decapod crustaceans in the Mira Estuary, Portugal. *Mar. Biol.* 100 (3): 309-312.

Paula, J. 1993. Ecologia da fase larvar e recrutamento de crustáceos decápodes no estuário do Rio Mira. Dissertation, Universidade de Lisboa, Portugal, 282 pp.

Paula, J. 1998. Larval retention and dynamics of the prawns *Palaemon longirostris* H. Milne Edwards and *Crangon crangon* Linnaeus (Decapoda, Caridea) in the Mira estuary, Portugal. *Int. J. Inver. Rep. Dev.* 33 (2-3): 221-228.

Paula, J., Pinto, I., Guambe, I., Monteiro, S., Gove, D. & Guerreiro, J. 1998. Seasonal cycle of planktonic communities at Inhaca Island, southern Mozambique. *J. Plankton Res.* 20 (11): 2165-2178.

Pautsch, F. 1961. The larval chromatophoral system of the crab, *Carcinus maenas* (L.). *Acta Biol. Med. Gdansk* 5: 105-119.

Pautsch, F. 1965. System of the chromatophores and their behaviour in the larva of the crab, *Geograpsus lividus* (Milne Edwards). *Acta Biol. Et Med. Soc. Sc. Gedan.* 9: 15-24.

Payen, G. 1974. Morphogenèse sexuelle de quelques Brachyoures (Cyclométopes) au cours du développement embryonnaire, larvaire et post-larvaire. *Bull. Mus. Nat. Sci. Nat. 209, Zool.* 139: 201-262.

Payen, G., Costlow, J.D. & Charniaux-Cotton, H. 1971. Étude comparative de l'ultrastructure des glandes androgènes de crabes normaux et pédonculectomisés pendent la vie larvaire ou après la puberté chez les espèces: *Rhithropanopeus harrisii* (Gould) et *Callinectes sapidus* Rathbun. *Gen. Comp. Endocrinol.* 17: 526-542.

Pechenik, J.A. 1979. Leakage of ingested carbon by gastropod larvae, and its effect on the calculation of assimilation efficiency. *Estuaries* 2 (1): 45-49.

Pechenik, J.A. 1987. Environmental influences on larval survival and development. In: Giese, A.C., Pearse, J.S. & Pearse, V.B. (eds), *Reproduction of Marine Invertebrates 9*: 551-608. Palo Alto, CA: Blackwell.

Pechenik, J.A. 1990. Delayed metamorphosis by larvae of benthic marine invertebrates: Does it occur? Is there a price to pay? *Ophelia* 32 (1-2): 63-94.

Pechenik, J.A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar. Ecol. Prog. Ser.*177: 269-297.

Pechenik, J.A. & Cerulli, T.R. 1991. Influence of delayed metamorphosis on survival, growth, and reproduduction of the marine polychaete *Capitella* sp. I. *J. Exp. Mar. Biol. Ecol.* 151 (1): 17-27.

Pechenik, J.A. & Eyster, L.S. 1989. Influence of delayed metamorphosis on the growth and metabolism of young *Crepidula fornicata* (Gastropoda) juveniles. *Biol. Bull.* 176 (1): 14-24.

Pechenik, J.A., Rittschof, D. & Schmidt, A.R. 1993. Influence of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite*. *Mar. Biol.* 115 (2): 287-294.

Peñaflorida, V.D. 1989. An evaluation of indigenous protein sources as potential component in the diet formulation for tiger prawn, *Penaeus monodon,* using essential amino acid index (EAAI). *Aquaculture* 83: 319-330.

Peñaflorida, V.D. 1999. Interaction between dietary levels of calcium and phosphorus on growth of juvenile shrimp, *Penaeus monodon*. *Aquaculture* 172 (3-4): 281-289.

Penkoff, S.J. & Thurberg, F.P. 1982. Changes in oxygen consumption of the American lobster, *Homarus americanus* during the molt cycle. *Comp. Biochem. Physiol.* 72: 621-622.

Pennington, J.T., Rumril, S.S. & Chia, F.S. 1986. Stage-specific predation upon embryos and larvae of the Pacific sand dollar, *Dendraster excentricus*, by 11 species of common zooplankton predators. *Bull. Mar. Sci.* 39: 234-240.

Péqueux, A. 1995. Osmotic regulation in crustaceans. *J. Crust. Biol.* 15: 1-60.

Pereira, F., Pereira, R. & Queiroga, H. 2000. Flux of decapod larvae and juveniles at a station in the lower Canal de Mira (Ria de Aveiro, Portugal) during one lunar month. *Inv. Reprod. Devel.* 38: 183-206.

Pereira, G.A. & García D., J.V. 1995. Larval development of *Macrobrachium reyesi* Pereira (Decapoda: Palaemonidae), with a discussion on the origin of abbreviated development in Palaemonids. *J. Crust. Biol.* 15: 117-133.

Perez Farfante I. & Kensley B. 1997. Penaeoid and Sergestoid Shrimps and Prawns of the World. Keys and Diagnoses for the Families and Genera. *Memoirés Du Museum National D'Histoire Naturelle, Zoologie* 175: 1-223.

Perissinotto, R., Mayzaud, P., Labat, J.-P. & Razouls, S. 2001. Grazing dynamics of *Euphausia spinifera* in the region of the Subtropical Convergence and the Agulhas Front. *Can. J. Fish. Aquat. Sci.* 58: 273-281.

Perry, H.M., Johnson, D., Trigg, C., Eleuterius, C. & Warren, J. 1998. Application of remote sensing to settlement of *Callinectes sapidus* megalopae in the Mississippi bight. *J. Shellfish Res.* 17: 1439-1442.

Pestana, D. & Ostrensky, A. 1995. Occurrence of an alternative pathway in the larval development of the crab *Chasmagnathus granulata* Dana, 1851 under laboratory conditions. *Hydrobiologia* 306: 33-40.

Peters, F. & Marrasé, C. 2000. Effects of turbulence on plankton: an overview of experimental evidence and some theoretical considerations. *Mar. Ecol. Prog. Ser.*205: 291-306.

Peters, G., Saborowski, R., Buchholz, F. & Mentlein, R. 1999. Two distinct forms of the chitin-degrading enzyme N-acetyl-ß-D-glucosaminidase in the Antarctic krill: specialists in digestion and moult. *Mar. Biol.* 134: 697-703.

Petersen, S. 1995. The embryonic development of *Hyas araneus* L. (Decapoda, Majidae): Effects of temperature. *Sarsia* 80: 193-198.

Petersen, S. & Anger, K. 1997. Chemical and physiological changes during the embryonic development of the spider crab, *Hyas araneus* L. (Decapoda: Majidae). *Comp. Biochem. Physiol.* 117B: 299-306.

Pettis, R.J., Erickson, B.W., Forward, R.B. & Rittschof, D. 1993. Superpotent synthetic tripeptide mimics of the mud crab pumping pheromone. *Int. J. Pept. Prot. Res.* 42 (4): 312-319.

Pfaff, K. 1997. Einfluß der Salinität auf den Stoffbestand der Larvenstadien einer marinen Dekapodenart. M. Sc. Thesis, Technische Universität Darmstadt, Germany, 96 pp.

Pfannschmidt, S. 1995. Temporärer Salinitätsstreß beeinflußt die Larvalentwicklung von *Hyas araneus* (Linneus, 1758) (Decapoda, Brachyura, Majidae). M. Sc. Thesis, Universität Regensburg, Germany, 64 pp.

Philippi, T.E. & Seger, J. 1989. Hedging on's evolutionary bets, revisited. *Trend Ecol. Evol.* 4: 41-44.

Phillips, B.F. & Pearce, A.F. 1997. Spiny lobster recruitment off western Australia. *B. Mar. Sci.* 61 (1): 21-41.

Phillips, B.F. & Sastry, A.N. 1980. Larval ecology. In: Cobb, J.S. & Phillips, B.F. (eds), *The biology and management of lobsters. Vol. 2*: 11-57. New York: Acad. Press.

Pijanowska, J. 1997. Alarm signals in *Daphnia? Oecologia* 112: 12-16.

Pile, A.J., Lipcius, R.N., Vanmontfrans, J. & Orth, R.J. 1996. Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecol. Monogr.* 66 (3): 277-300.

Plath, K. 1998. Adaptive feeding behavior of *Daphnia magna* in response to short-term starvation. *Limnol. Oceanogr.* 43: 593-599.

Platt, T., Brawn, V.M. & Irwin, B. 1969. Caloric and carbon equivalents of zooplankton biomass. *J. Fish. Res. Bd. Can.* 26: 2345-2349.

Pohle, G.W. 1991. Larval development of Canadian Atlantic oregoniid crabs (Brachyura: Majidae), with emphasis on *Hyas coarctatus alutaceus* Brandt, 1851, and a comparison with Atlantic and Pacific conspecifics. *Can. J. Zool* 69 (11): 2717-2737.

Pohle, G.W. & Marques, F. 2000. Larval stages of *Paradasygyius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae. *Proc. Biol. Society Wash.* 113: 739-760.

Pollero, R.J., González Baró, M. & Irazú, C.E. 1991. Lipid classes' consumption related to fasting and thermal stress in the shrimp *Macrobrachium borellii*. *Comp. Biochem. Physiol.* 99B: 233-238.

Pollock, D.E. 1993. Speciation in spiny lobsters - clues to climatically induced changes in ocean circulation patterns. *Bull. Mar. Sci.* 53: 937-944.

Polovina, J.J., Kleiber, P. & Kobayashi, D.R. 1999. Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the northwestern Hawaiian Islands, 1993-1996. *Fish. Bull.* 97 (1): 132-143.

Polz, H. 1996. Eine Form-C-Krebslarve mit erhaltenem Kopfschild (Crustacea, Decapoda, Palinuroidea) aus den Solnhofener Plattenkalken. *Archaeopteryx* 14: 43-50.

Pond, D., Dixon, D. & Sargent, J. 1997. Wax-ester reserves facilitate dispersal of hydrothermal vent shrimps. *Mar. Ecol. Prog. Ser.* 146: 289-290.

Poulet, S.A. & Marsot, P. 1978. Chemosensory grazing by marine calanoid copepods (Arthropoda: Crustacea). *Science* 200: 1403-1405.

Poulin, E., v. Boletzky, S. & Féral, J.-P. 2001. Combined ecological factors permit classification of developmental patterns in benthic marine invertebrates: a discussion. *J. Exp. Mar. Biol. Ecol.* 257 (1): 109-115.

Prager, M.H. 1996. A simple model of the blue crab, *Callinectes sapidus,* spawning migration in Chesapeake Bay. *B. Mar. Sci.* 58: 421-428.

Precht, H., Christopherson, J., Hensel, H. & Larcher, W. 1973. *Temperature and life.* Berlin: Springer.

Preston, N.P., Burford, M.A., Coman, F.E. & Rothlisberg, P.C. 1992. Natural diet of larval *Penaues merguiensis* (Decapoda: Penaeidae) and its effect on survival. *Mar. Biol.* 113 (2): 181-191.

Prosser, C.L. 1986. *Adaptational Biology. Molecules to Organisms.* New York: Wiley.

Provasoli, L. & Shiraishi, K. 1959. Axenic culture of the brine shrimp *Artemia salina*. *Biol. Bull.* 117: 347-355.

Provenzano, A.J. 1968. *Lithopagurus yucatanicus,* a new genus and species of hermit crab with a distinctive larva. *Bull. Mar. Sci.* 18: 627-644.

Provenzano, A.J. (ed) 1983. *Pathobiology. The Biology of Crustacea 6.* New York: Academic Press.

Provenzano, A.J. 1985. Economic Aspects: Fisheries and Culture. In: Provenzano, A.J. (ed), *The Biology of Crustacea 10; Economic Aspects: Fisheries and Culture*. New York: Academic Press.

Provenzano, A.J. & Brownell, W.N. 1977. Larval and early post-larval stages of the West Indian spider crab, *Mithrax spinosissimus* (Lamarck) (Decapoda: Majidae). *Proc. Biol. Soc. Wash.* 90: 735-752.

Pütz, K. & Bucholz, F. 1991. Comparative ultrastructure of the cuticle of some pelagic, nektobenthic and benthic malacostracan crustaceans. *Mar. Biol.* 110 (1): 49-58.

Pyle, R.W. 1943. The histogenesis and cyclic phenomena of the sinus gland and X-organ in Crustacea. *Biol. Bull. Mar. Biol. Lab. Woods Hole* 85: 87-102.

Qian, P.Y., McEdward, L.R. & Chia, F.S. 1990. Effects of delayed settlement on survival, growth, and reproduction in the spionid polychaete, *Polydora ligni*. *Int. J. Inver. Rep. Dev.* 18 (3): 147-152.

Qiu, J.-W., Gosselin, L.A. & Qian, P.-Y. 1997. Effects of short term variation in food availability on larval development in the barnacle *Balanus amphitrite amphitrite*. *Mar. Ecol. Prog. Ser.*161: 83-91.

Quackenbush, L.S. 1986. Crustacean endocrinology, a review. *Can. J. Fish. Aquat. Sci.*43 (11): 2271-2282.

Queiroga, H. 1996. Distribution and drift of the crab *Carcinus maenas* (L.) (Decapoda, Portunidae) larvae over the continental shelf off northern Portugal in April 1991. *J. Plankton Res.* 18 (11): 1981-2000.

Queiroga, H. 1998. Vertical migration and selective tidal stream transport in the megalopa of the crab *Carcinus maenas*. *Hydrobiologia* 376: 137-149.

Queiroga, H., Costlow, J.D. & Moreira, M.H. 1994. Larval abundance patterns of *Carcinus maenas* (Decapoda, Brachyura) in Canal de Mira (Ria de Aveiro, Portugal). *Mar. Ecol. Prog. Ser.*111 (1-2): 63-72.

Queiroga, H., Costlow, J.D. & Moreira, M.H. 1997. Vertical migration of the crab *Carcinus maenas* first zoea in an estuary: implications for tidal stream transport. *Mar. Ecol. Prog. Ser.*149 (1-3): 121-132.

Rabalais, N.N. & Cameron, J.N. 1983. Abbreviated development of *Uca subcylindrica* (Stimpson, 1859) (Crustacea, Decapoda, Ocypodidae) reared in the laboratory. *J. Crust. Biol.* 3: 519-541.

Rabalais, N.N. & Cameron, J.N. 1985. The effects of factors important in semi-arid environments on the early development of *Uca subcylindrica*. *Biol. Bull.* 168: 147-160.

Rabalais, N.N. & Gore, R.H. 1985. Abbreviated development in Decapods. In: Wenner, A.M. (ed), *Crustacean Issues 2*; *Larval Growth*: 67-126. Rotterdam: Balkema.

Raje, P.C. & Ranade, M.R. 1975. Early life history of a stenopodid shrimp *Microprosthema semilaeve* (Decapoda: Macrura). *J. Mar. Biol. Ass. India:* 213-222.

Rao, K.R. 1967. Responses of crustacean larval chromatophores to light and endocrines. *Experientia* 231: 1-4.

Rao, K.R. 1985. Pigmentary effectors. In: Bliss, D.E. & Mantel, L.H. (eds), *The Biology of Crustacea 9*; *Integument, Pigments, and Hormonal Processes* 9: 395-462. New York: Academic Press.

Rao, K.R., Fingerman, S.W. & Fingerman, M. 1973. Effects of exogenous ecdysones on the molt cycles of fourth and fifth stage American lobsters, *Homarus americanus*. *Comp. Biochem. Physiol.* 44: 1105-1120.

Rathbun, M.J. 1897. Synopsis of the American *Sesarma*e, with description of a new species. *Proc. Biol. Soc. Wash.* 11: 89-92.

Rathbun, M.J. 1914. Stalk-eyed Crustaceans collected on the Monte Bello Islands. *Proc. Zool. Soc. Lond.1914:* 653-664.

Read, G.H.L. 1984. Intraspecific variation in the osmoregulatory capacity of larval, post-larval, juvenile and adult *Macrobrachium petersi* (Hilgendorf). *Comp. Biochem. Physiol.* 78: 501-506.

Rebelo, M.F., Rodriguez, E.M., Santos, E.A. & Ansaldo, M. 2000. Histopathological changes in gills of the estuarine crab *Chasmagnathus granulata* (Crustacea-Decapoda) following acute exposure to ammonia. *Comp. Biochem. Phys. A.* 125C(2): 157-164.

Reddy, H.R.V., Naik, M.G. & Annappaswamy, T.S. 1999b. Evaluation of the dietary essentiality of vitamins for *Penaeus monodon*. *Aquacult. Nutr.* 5 (4): 267-275.

Reddy, H.R.V., Rai, A. & Annappaswamy, T.S. 1999a. Essentiality of vitamins for juvenile white shrimp, *Penaeus indicus*. *Isr. J. Aquacult.-Bamid.* 51 (3): 122-132.

Reed, P.H. 1969. Studies of diet and diet concentration effects on dungeness crab zoeae. *Proc. Nat. Shellfisheries Ass.* 59: 1.

Reese, W. 1992. Experimentelle Untersuchungen zur sekundären Lecithotrophie in der Larvalentwicklung von *Pagurus bernhardus* L. (Decapoda: Paguridae). M. Sc. Thesis, Universität Hamburg, Germany, 88 pp.

Reeve, M.R. 1969. Growth, metamorphosis and energy conversion in the larvae of the prawn, *Palaemon serratus*. *J. Mar. Biol. Ass. U.K.* 49: 77-96.

Regnault, M. 1969a. Etude expérimentale de la nutrition d'*Hippolyte inermis* Leach (Décapode, Natantia) au cours de son développement larvaire, au laboratoire. *Int. Revue Ges. Hydrobiol.* 54: 749-764.

Regnault, M. 1969b. Influence de la température et de l'origine de l'eau de mer sur le développement larvaire au laboratoire d'*Hippolyte inermis* leach (Décapode-Natantia). *Vie Milieu A* 20: 137-152.

Regnault, M. 1971. Acides aminés libres chez les larves de *Crangon septemspinosa* (Caridea). Variation de leur taux de l'éclosion à la metamorphose. Leur role au cours du développement et leur importance dans la nutrition. *Mar. Biol.* 11: 35-44.

Regnault, M. 1972. Développement de l'estomac chez les larvaes de *Crangon septemspinosa* Say (Crustacea: Decapoda: Crangonidae); son influence sur le mode de nutrition. *Bull. Mus. Natl. Hist. Nat. Zool.* 67: 841-856.

Regnault, M. 1979. Ammonia excretion of the sand-shrimp *Crangon crangon* (L.) during the moult cycle. *J. Comp. Physiol.* 133: 199-204.

Regnault, M. 1987. Nitrogen excretion in marine and fresh-water crustacea. *Biol. Rev.* 62: 1-24.

Regnault, M. & Luquet, P. 1974. Study by evolution of nucleic acid content of prepuberal growth in the shrimp *Crangon crangon*. *Mar. Biol.* 25: 291-298.

Regnault, M. & Luquet, P. 1976. Influence du régime alimentaire sur les modalités de la croissance, estimèes par l'évolution des acides nucléiques, chez la crevette grise *Crangon crangon* L. *J. Physiol. Paris* 72: 959-970.

Remane, A. & Schlieper, C. 1971. *Biology of Brackish Water*. 2 ed. New York: Wiley.

Reyns, N. & Sponaugle, S. 1999. Patterns and processes of brachyuran crab settlement to Caribbean coral reefs. *Mar. Ecol. Prog. Ser.*185: 155-170.

Rice, A.L. 1966. The orientation of the pressure responses of some marine Crustacea. In: *Proceedings of the Symposium on Crustacea. Mar. biol. Ass, India, Part III*

Rice, A.L. 1968. Growth "rules" and the larvae of decapod crustaceans. *J. Nat. Hist.* 2: 525-530.

Rice, A.L. 1979. Plea for improved standards in descriptions of crab zoeae. *Crustaceana* 37: 214-218.

Rice, A.L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Trans. Zool. Soc. Lond.* 35: 271-424.

Rice, A.L. 1983. Zoeal evidence for brachyuran phylogeny. In: Schram, F.R. (ed), *Crustacean Issues 1*; *Crustacean phylogeny*: 313-329. Rotterdam: Balkema.

Rice, A.L. 1993. Two centuries of larval crab papers: a preliminary analysis. In: Truesdale, F. (ed), *Crustacean Issues 8*; *History of Carcinology*: 285-292. Rotterdam: Balkema.

Rice, A.L. & Ingle, R.W. 1975a. The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bull. Brit. Mus. Nat. Hist. (Zool.)* 28: 103-119.

Rice, A.L. & Ingle, R.W. 1975b. A comparative study of the larval morphology of the British portunid crabs *Macropipus puber* (L.) and *M. holsatus* (Fabricius), with a discussion of generic and sub-familial larval characters within the Portunidae. *Bull. Br. Mus. Nat. Hist. (Zool.)* 28: 123-151.

Rice, A.L. & Williamson, D.I. 1970. Methods for rearing larval decapod Crustacea. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 20 (1-4): 417-434.

Richard, P. 1978. Influence de la température sur la croissance et la mue de *Palaemon serratus* en function de leur taille. *Aquaculture* 14: 13-22.

Richard, P. & Ceccaldi, H.J. 1977. Variations des caractéristiques pondérales et des compositions amino-acide et protéique pendant le développement embryonnaire de *Palaemon serratus*. *Actes Colloq. CNEXO* 4: 203-212.

Rieger, R.M. 1994. The biphasic life cycle - a central theme of metazoan evolution. *Amer. Zool.* 34: 484-491.

Rigler, F.H. 1971. Methods for the measurement of assimilation of food by zooplankton. In: Edmondson, E.J. (ed), *IBP Handbook 17*; *A manual on methods for the assessment of secondary productivity in fresh waters*: 264-269. Oxford: Blackwell Scientific Publications.

Ringelberg, J. 2000. The role of infochemicals in lake plankton crustacean behavior and predator-prey relations. In: von Vaupel Klein, J.C. & Schram, F.R. (eds), *Crustacean Issues 12*; *The Biodiversity Crisis and Crustacea*: 161-175. Rotterdam: A.A. Balkema.

Rittschof, D. 1992. Chemosensation in the daily life of crabs. *Am. Zool.* 32 (3): 363-369.

Rittschof, D. 1993. Body odors and neutral-basic peptide mimics: a review of responses by marine organisms. *Am. Zool.* 33 (6): 487-493.

Rittschof, D. & Bonaventura, J. 1986. Macromolecular cues in marine systems. *J. Chem. Ecol.* 12: 1013-1023.

Rittschof, D., Forward, R.B., Cannon, G., Welch, J.M., McClary, M., Holm, E.R., Clare, A.S., Conova, S., McKelvey, L.M., Bryan, P., van-Dover, C.L., Clare, A.S., Fusetani, N. & Jones, M.B. 1998. Cues and context: larval responses to physical and chemical cues. *Biofouling* 12 (1-3): 31-44.

Rittschof, D., Forward, R.B. & Erickson, B.W. 1990. Larval release in brachyuran crustaceans: functional similarity of the peptide receptor and the catalytic site of trypsin. *J. Chem. Ecol.* 16: 1359-1370.

Roberts, M.H. 1974. Larval development of *Pagurus longicarpus* Say reared in the laboratory. V. Effect of diet on survival and molting. *Biol. Bull. Mar. Biol. Lab. Woods Hole* 146: 67-77.

Robertson, D.N., Butler, M.J. & Dobbs, F.C. 2000. An evaluation of lipid- and morphometric-based indices of nutritional condition for early benthic stage spiny lobsters, *Panulirus argus*. *Mar. Freshw. Behav. Physiol.* 33: 161-171.

Robertson, P.A.W., Calderon, J., Carrera, L., Stark, J.R., Zherdmant, M. & Austin, B. 1998. Experimental *Vibrio harveyi* infections in *Penaeus vannamei* larvae. *Dis. Aquat. Org.* 32: 151-155.

Robinson, M. & Tully, O. 2000. Seasonal variation in community structure and recruitment of benthic decapods in a sub-tidal cobble habitat. *Mar. Ecol. Prog. Ser.*206: 181-191.

Roch, P. 1999. Defense mechanisms and disease prevention in farmed marine invertebrates. *Aquaculture* 172: 125-145.

Rodríguez, A., Le Vay, L., Mourente, G. & Jones, D.A. 1994. Biochemical composition and digestive enzyme activity in larvae and postlarvae of *Penaeus japonicus* during herbivorous and carnivorous feeding. *Mar. Biol.* 118 (1): 45-51.

Rodriguez, C.A., Browman, H.I. & St-Pierre, J.-F. 2000. High survival of neustonic zoea I larvae of American lobster *Homarus americanus* following short-term exposure to ultraviolet radiation (280 to 400 nm). *Mar. Ecol. Prog. Ser.* 193: 305-309.

Rodríguez, E.M. & Amin, O.A. 1991. Acute toxicity of parathion and 2,4-d to larval and juvenile stages of *Chasmagnathus granulata* (Decapoda, Brachyura). *B. Environ. Contam. Tox.* 47 (4): 634-640.

Rodríguez, E.M. & Medesani, D. 1994. Pathological lesions in larvae hatched from ovigerous females of *Chasmagnathus granulata* (Decapoda, Brachyura) exposed to cadmium. *Experientia* 50 (10): 975-977.

Rodríguez, E.M. & Pisanó, A. 1993. Effects of parathion and 2,4-D to eggs incubation and larvae hatching in *Chasmagnathus granulata* (Decapoda, Brachyura). *Comp. Biochem. Phys. A.* 104C: 71-78.

Roman, M.R. & Boicourt, W.C. 1999. Dispersion and recruitment of crab larvae in the Chesapeake bay plume: Physical and biological controls. *Estuaries* 22 (3A): 563-574.

Román, R., Ortega, A.L. & Mejía, L.M. 2000. *Macrobrachium vicconi*, new species, a fresh-water shrimp from a rain forest in southeast Mexico, and comparison with congenors (Decapoda: Palaemonidae). *J. Crust. Biol.* 20 (1): 186-194.

Romano, J.-C. & Daumas, R. 1981. Adenosine nucleotide "Energy charge" ratios as an ecophysiolgical index for microplankton communities. *Mar. Biol.* 62: 281-296.

Ronquillo, J.D. & Saisho, T. 1997. Larval development of *Metapenaeopsis barbata* (de Haan, 1844) (Crustacea: Decapoda: Penaeidae). *Mar. Freshwater. Res.* 48: 401-414.

Rooney, P. & Cobb, J.S. 1991. Effects of time of day, water temperature, and water velocity on swimming by postlarvae of the American lobster, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.*48 (10): 1944-1950.

Roque, A., Mazari, A. & Gómez Gil, B. 2000. Oral challenge of postlarvae of *Litopenaeus vannamei* through bioencapsulation of *Vibrio parahaemolyticus* in *Artemia franciscana*. *Ciencias Marinas* 26 (1): 65-77.

Rosas, C., Martínez, E., Gaxiola, G., Brito, R., Díaz-Iglesia, E. & Soto, L.A. 1998. Effect of dissolved oxygen on the energy balance and survival of *Penaeus setiferus* juveniles. *Mar. Ecol. Prog. Ser.*174: 67-75.

Rosas, C., Ocampo, L., Gaxiola, G., Sánchez, A. & Soto, L.A. 1999. Effect of salinity on survival growth, and oxygen consumption of postlarvae (PL 10-PL 21) of *Litopenaeus setiferus*. *J. Crust. Biol.* 19 (2): 244-251.

Rosas, C., Sánchez, A., Dáaz, E., Soto, L.A., Gaxiola, G. & Brito, R. 1996. Effect of dietary protein level on apparent heat increment and post-prandial nitrogen excretion of *Penaeus setiferus, P. schmitti, P. duorarum,* and *P. notialis* postlarvae. *J. World Aquacult. Soc.* 27 (1): 92-102.

Rosas, C., Sánchez, A., Gallardo, P., Quiroz, J., Gaxiola, G., Díaz-Iglesia, E. & Soto, L.A. 1995. Oxygen consumption and ingestion rate of *Penaeus setiferus* larvae fed *Chaetoceros ceratosporum*, *Tetraselmis chuii* and *Artemia* nauplii. *Aquacult. Nutr.* 1 (1): 13-20.

Rothlisberg, P.C. 1979. Combined effects of temperature and salinity on the survival and growth of the larvae of *Pandalus jordani* (Decapoda: Pandalidae). *Mar. Biol.* 54: 125-134.

Rothlisberg, P.C. & Church, J.A. 1994. Processes controlling the larval dispersal and postlarval recruitment of penaeid prawns. In: Sammarco, P.W. & Heron, M.L. (eds), *Coastal and Estuarine Studies 45*; *The Bio-Physics of Marine Larval Dispersal*: 235-252. Washington, DC: American Geophysical Union.

Rothlisberg, P.C., Craig, P.D. & Andrewartha, J.R. 1996. Modelling penaeid prawn larval advection in Albatross Bay, Australia: defining the effects spawning population. *Mar. Freshwater Res.* 47: 157-168.

Rothlisberg, P.C., Jackson, C.J., Phillips, B.F. & Mcwilliam, P.S. 1994. Distribution and abundance of scyllarid and palinurid lobster larvae in the Golf of Carpentaria, Australia. *Aust. J. Mar. Fresh. Res.*45 (3): 337-349.

Rotllant, G., Charmantier-Daures, M., Charmantier, G., Anger, K. & Sardà, F. 2001. Effects of diet on *Nephrops norvegicus* (L.) larval and postlarval development, growth and elemental composition. *J. Shellfish Res.* 20 (1): in press.

Rotllant, G., Charmantier-Daures, M., De Kleijn, D., Charmantier, G. & Van Herp, F. 1995. Ontogeny of neuroendocrine centers in the eyestalk of *Homarus gammarus* embryos: an anatomical and hormonal approach. *Int. J. Inver. Rep. Dev.* 27: 233-245.

Rotllant, G., Charmantier-Daures, M., Trilles, J.P. & Charmantier, G. 1994. Ontogeny of the sinus gland and of the organ of bellonci in larvae and postlarvae of the European lobster *Homarus gammarus*. *Int. J. Inver. Rep. Dev.* 26 (1): 13-22.

Rotllant, G., de Kleijn, D., Charmantier-Daures, M., Charmantier, G. & Van Herp, F. 1993. Localization of crustacean hyperglycemic hormone (CHH) and gonad inhibiting hormone (GIH) in the eyestalk of *Homarus gammarus* larvae by immunocytochemistry and *in situ* hybridization. *Cell Tissue Res.* 271: 507-512.

Roustaian, P., Kamarudin, M.S., Omar, H., Saad, C.R. & Ahmad, M.H. 1999. Changes in fatty acid profile during larval development of freshwater prawn *Macrobrachium rosenbergii* (De Man). *Aquac. Res.* 30 (11-12): 815-824.

Roustaian, P., Kamarudin, M.S., Omar, H.B., Saad, C.R. & Ahmad, M.H. 2000. Amino acid composition of developing larval freshwater prawn *Macrobrachium rosenbergii*. *J. World Aquacult. Soc.* 31 (1): 130-136.

Rumrill, S.S. 1990. Natural mortality of marine invertebrate larvae. *Ophelia* 32: 163-198.

Rumrill, S.S., Pennington, J.T. & Chia, F.-S. 1985. Differential susceptibility of marine invertebrate larvae: Laboratory predation of sand dollar, *Dendraster excentricus* (Eschscholtz), embryos and larvae by zoeae of the red crab, *Cancer productus* Randall. *J. Exp. Mar. Biol. Ecol.* 90: 193-208.

Saiah, H. & Perrin, N. 1990. Autumnal *vs* spring hatching in the fairy shrimp *Siphonophanes grubii* (Dybowski) (Crustacea, Anostraca): Diversified bet-hedging strategy? *Funct. Ecol.* 4 (6): 769-775.

Saigusa, M. 1996. Two kinds of active factor in crab hatch water: ovigerous-hair stripping substance (OHSS) and a proteinase. *Biol. Bull.* 191 (2): 234-240.

Saigusa, M. & Iwasaki, H. 1999. Ovigerous-hair stripping substance (OHSS) in an estuarine crab: purification, preliminary characterization, and appearance of the activity in the developing embryos. *Biol. Bull.* 197: 174-187.

Saigusa, M. & Kawagoye, O. 1997. Circatidal rhythm of an intertidal crab, *Hemigrapsus sanguineus:* synchrony with unequal tide height and involvement of a light-response mechanism. *Mar. Biol.* 129 (1): 87-96.

Saigusa, M. & Terajima, M. 2000. Hatching of an estuarine crab, *Sesarma haematocheir*: From disappearance of the inner (E3) layer to rupture of the egg case. *J. Exp. Zool.* 287: 510-523.

Saito, T. & Konishi, K. 1999. Direct development in the sponge-associated deep-sea shrimp *Spongicola japonica* (Decapoda: Spongicolidae). *J. Crust. Biol.* 19: 46-52.

Saiz, E., Tiselius, P., Jonsson, P.R., Verity, P. & Paffenhöfer, G.-A. 1993. Experimental records of the effects of food patchiness and predation on egg production of *Acartia tonsa*. *Limnol. Oceanogr.* 38: 280-289.

Salman, S.D. & Ali, M.H. 1996. Larval development of *Elamenopsis kempi* (Chopra and Das) (Brachyura, Hymenosomatidae) reared in the laboratory. *Sci. Mar.* 60 (2-3): 407-416.

Salonen, K., Sarvala, J., Hakala, I. & Viljanen, M.-L. 1976. The relation of energy and organic carbon in aquatic invertebrates. *Limnol. Oceanogr.* 21: 724-730.

Sandeman, D.C. 1982. Organization of the central nervous system. In: Atwood, H.L. & Sandeman, D.C. (eds), *The Biology of Crustacea 3*; *Neurobiology: Structure and Function*: 1-61. New York: Academic Press.

Sandeman, D.C., Sandeman, R., Derby, C. & Schmidt, M. 1992. Morphology of the brain of crayfish, crabs, and spiny lobsters: a common nomenclature for homologous structures. *Biol. Bull.* 183: 304-326.

Sandeman, D.C., Scholtz, G. & Sandeman, R.E. 1993. Brain evolution in decapod Crustacea. *J. Exp. Zool.* 265: 112-133.

Sanders, B.M. & Costlow, J.D. 1981. Regulation of growth in larvae of the crab *Rhithropanopeus harrisii*. The effect of cyclic temperatures. *J. Therm. Biol.* 6: 357-363.

Sanders, B.M., Laughlin, R.B. & Costlow, J.D. 1985. Growth regulation in larvae of the mud crab *Rhithropanopeus harrisii*. In: Wenner, A.M. (ed), *Crustacean Issues 2*; *Larval growth*: 155-161. Rotterdam: Balkema.

Sandifer, P.A. 1972. Effects of diet on larval development of *Thor floridianus* (Decapoda, Caridea) in the laboratory. *Virginia J. Sci.* 23: 5-8.

Sandifer, P.A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Cheaspeake Bay, Virginia, 1968-1969. *Chesapeake Sci.* 14: 235-257.

Saotome, K. & Ikeda, T. 1990. Body composition and metabolism of the larvae of the pink shrimp (*Pandalus borealis* Krøyer) reared in the laboratory. *Bull. Japan Sea Natl. Fish. Res. Inst.* 40: 76-77.

Sasaki, G.C. 1984. Biochemical changes associated with embryonic and larval development in the American lobster *Homarus americanus* Milne Edwards. Dissertation, Woods Hole Oceanographic Institution, Woods Hole, MA, and Massachusetts Institute of Technology, 458 pp.

Sasaki, G.C., Capuzzo, J.M. & Biesiot, P. 1986. Nutritional and bioenergetic considerations in the development of the American lobster *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 43: 2311-2319.

Sastry, A.N. 1983a. Ecological aspects of reproduction. In: Vernberg, F.J. & Vernberg, W.B. (eds), *The Biology of Crustacea 8*; *Environmental adaptations*: 179-270. New York: Academic Press.

Sastry, A.N. 1983b. Pelagic larval ecology and development. In: Vernberg, F.J. & Vernberg, W.B. (eds), *The Biology of Crustacea 7*; *Behavior and Ecology*: 213-282. New York: Academic Press.

Sastry, A.N. & McCarthy, J.F. 1973. Diversity in metabolic adaptation of pelagic larval stages of two sympatric species of brachyuran crabs. *Neth. J. Sea Res.* 7: 434-446.

Savenkoff, C., Saint-Amand, L., Ouellet, P. & Packard, T.T. 1995. An index of respiratory efficiency in the shrimp *Pandalus borealis* (Krøyer) larvae. *Can. Tech. Rep. Fish. Aquat. Sci.* 2072: 1-26.

Scarratt, D.J. & Raine, G.E. 1967. Avoidance of low salinity by newly hatched lobster larvae. *J. Fish. Res. Bd. Can.* 24: 1403-1406.

Schatzlein, F.C. & Costlow, J.D. 1978. Oxygen consumption of the larvae of the decapod crustaceans, *Emerita talpoida* (Say) and *Libinia emarginata* Leach. *Comp. Biochem. Physiol.* 61A: 441-450.

Scheltema, R.S. 1971. The dispersal of the larvae of shoalwater benthic invertebrate species over long distances by ocean currents. In: Crisp, D.J. (ed), *Fourth European Mar. Biol. Symposium*: 7-28. Oxford, U.K.: Cambridge University Press.

Scheltema, R.S. 1975. Relationship of larval dispersal, gene-flow and natural selection to geographic variation of benthic invertebrates in estuaries and along coastal regions. *Estuarine Research* 1: 372-391.

Schembri, P.J. 1982. Locomotion, feeding, grooming and the behavioural responses to gravity, light and hydrostatic pressure in the stage I zoea larvae of *Ebalia tuberosa* (Crustacea: Decapoda: Leucosiidae). *Mar. Biol.* 72: 125-134.

Schiller, H., Spittler, P. & Heerkloss, R. 1977. Bestimmung von Freß-, Assimilations- und Abgaberaten planktischer Crustaceen mit Hilfe von Radiokohlenstoff. *Wiss. Z. Wilh.-Pieck-Univ. Rostock, Math.-Naturwiss. Reihe* 2: 223-229.

Schirf, V.R., Turner, P., Selby, L., Hannapel, C., de la Cruz, P. & Dehn, P.F. 1987. Nutritional status and energy metabolism of crayfish (*Procambarus clarkii*, Girard) muscle and hepatopancreas. *Comp. Biochem. Physiol.* 88A: 383-386.

Schoffeniels, E. & Dandrifosse, G. 1994. Osmorégulation; aspects morphologiques et biochimiques. In: Forest, J. (ed), *Systématique. Traité De Zoologie, Grassé, P.-P. (Ed) 6*; *Crustacés. Vol. 1. Morphologie, Physiologie, Reproduction*: 529-594.

Scholtz, G. 2000. Evolution of the nauplius stage in malacostracan crustaceans. *J. Zool. Syst. Evol. Research* 38: 175-187.

Scholtz, G. & Richter, S. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zool. J. Linnean Soc.* 113: 289-328.

Schram, F.R. 1982. The fossil record and evolution of Crustacea. In: Abele, L.G. (ed), *The Biology of Crustacea 2*; *Embryology, Morphology and Genetics*: 93-147. New York: Academic Press.

Schram, F.R. (ed) 1983. *Crustacean phylogeny.* Crustacean Issues 1. Rotterdam: Balkema.

Schram, F.R. 1986. *Crustacea.* New York, Oxford: Oxford University Press.

Schram, F.R., Feldman, R.M. & Copeland, M.J. 1978. The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. *J. Palaeontol.* 52: 1375-1387.

Schram, F.R., Yanbin, S., Vonk, R. & Taylor, R.S. 2000. The first fossil Stenopodidean. *Crustaceana* 73 (2): 235-242.

Schubart, C.D., Cuesta, J.A., Diesel, R. & Felder, D.L. 2000. Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Mol. Phylogenet. Evol.* 15 (2): 179-190.

Schubart, C.D. & Diesel, R. 1998. Osmoregulatory capacities and penetration into terrestrial habitats: a comparative study of Jamaican crabs of the genus *Armases* Abele, 1992 (Brachyura: Grapsidae: Sesarminae). *B. Mar. Sci.* 63: 743-752.

Schubart, C.D., Diesel, R. & Hedges, S.B. 1998. Rapid evolution to terrestrial life in Jamaican crabs. *Nature* 393: 363-365.

Schuh, M. & Diesel, R. 1995a. Breeding in a rock pool: larvae of the semiterrestrial crab *Armases* (=*Sesarma*) *miersii* (Decapoda: Grapsidae) develop in a highly variable environment. *J. Exp. Mar. Biol. Ecol.* 185: 109-129.

Schuh, M. & Diesel, R. 1995b. Effects of salinity, temperature, and starvation on the larval development of *Armases* (=*Sesarma*) *miersii* (Rathbun, 1897), a semterrestrial crab with abbreviated development (Decapoda: Grapsidae). *J. Crust. Biol.* 15: 205-213.

Schuh, M. & Diesel, R. 1995c. Effects of salinity and starvation on the larval development of *Sesarma curacaoense* De Man, 1892, a mangrove crab with abbreviated development (Decapoda: Grapsidae). *J. Crust. Biol.* 15: 645-654.

Schultze, K. 1993. Experimentelle Untersuchungen zur Larvalentwicklung von *Pandalus montagui* (Leach, 1814) (Crustacea, Decapoda, Natantia). Dissertation, Universität Hannover, Germany, 312 pp.

Schultze, K. & Anger, K. 1997. Larval growth patterns of the Aesop shrimp *Pandalus montagui*. *J. Crust. Biol.* 17: 472-479.

Schulz, H. 1888. Über Hefegifte. *Pflügers Arch. Gesamte Physiol. d. Menschen u. Tiere* 42: 517-541.

Schwamborn, R. 1997. Influence of mangroves on community structure and nutrition of macrozooplankton in Northeast Brazil. Dissertation, Universität Bremen, Germany, 77 pp.

Schwamborn, R. & Bonecker, A.C.T. 1996. Seasonal changes in the transport and distribution of meroplankton into a Brazilian estuary with emphasis on the importance of floating mangrove leaves. *Arquivos De Biologia e Tecnologia* 39: 451-462.

Schwamborn, R. & Criales, M.M. 2000. Feeding strategy and daily ration of juvenile pink shrimp (*Farfantepenaeus duorarum*) in a South Florida seagrass bed. *Mar. Biol.* 137 (1): 139-147.

Schwamborn, R., Voss, M., Ekau, W. & Saint-Paul, U. 1999. Stable isotope composition of particulate organic matter and zooplankton in north-east Brazilian shelf waters. *Archive of Fishery and Marine Research* 47 (2-3): 201-210.

Schwartz, S.S. & Jenkins, D.G. 2000. Temporary aquatic habitats: constraints and opportunities. *Aquatic Ecology* 34 (1): 3-8.

Sedgwick, R.W. 1980. The requirements of *Penaeus merguiensis* for vitamin and mineral supplements in diets based on freeze-dried *Mytilus edulis* meal. *Aquaculture* 19: 127-137.

Sehnal, F. 1985. Growth and life cycles. In: Kerkut, G.A. & Gilbert, L.I. (eds), *Comprehensive Insect Physiology, Biochemistry and Pharmacology*: 1-86. Oxford: Pergamon Press.

Seidler, D. 1993. Einfluß konstanter Hyposalinität auf die Respiration und das Wachstum in der Larvenentwicklung von *Pagurus bernhardus* L. (Decapoda, Paguridae). M. Sc. Thesis, Freie Universität Berlin, Germany, 106 pp.

Selvakumar, S. & Haridasan, T.M. 2000. Toxic effects of heavy metals copper, zinc, cadmium and mercury on the zoeal development of Sesarminid crab *Nanosesarma* (*Beanium*) *batavicum*. *J. Environ. Biol.* 21 (2): 101-104.

Selzer, J.A. 1992. Die Lipide von Krebslarven in Abhängigkeit von Nahrung und Temperatur. Dissertation, Universität Hamburg, Germany, 197 pp.

Sèrene, R. & Soh, C.L. 1970. New Indo-Pacific genera allied to *Sesarma* Say 1817 (Brachyura, Decapoda, Crustacea). *Treubia* 27: 387-416.

Seridji, R. 1990. Description of some panktonic larval stages of *Stenopus spinosus* Risso, 1826: notes on the genus and the systematic position of the Stenopodidea as revealed by larval characters. *Sci. Mar.* 54: 293-303.

Shanks, A.L. 1995a. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward, L.R. (ed), *Ecology of Marine Invertebrate Larvae*: 323-367. Boca Raton: CRC Press.

Shanks, A.L. 1995b. Orientated swimming by megalopa of several eastern North Pacific crab species and its potential role in their onshore migration. *J. Exp. Mar. Biol. Ecol.* 186 (1): 1-16.

Shanks, A.L. & Walters, K. 1997. Holoplankton, meroplankton, and meiofauna associated with marine snow. *Mar. Ecol. Prog. Ser.*156: 75-86.

Shaojing, L., Guizhong, W., Hong, T. & Qiongwu, L. 1995. Comparative studies on the hydrolytic enzyme activities for the mud crab, *Scylla serrata* (Forskal) during embryonic development. *J. Xiamen Univ. (Nat. Sci.)* 39: 970-974.

Shaw, S.R. & Stowe, S. 1982. Photoreception. In: Atwood, H.L. & Sandeman, D.C. (eds), *The Biology of Crustacea 3*; *Neurobiology: Structure and Function*: 291-367. New York: Academic Press.

Shealy, M.H. & Sandifer, P.A. 1975. Effects of mercury on survival and development of the larval grass shrimp *Palaemonetes vulgaris*. *Mar. Biol.* 33 (1): 7-16.

Sheehy, M.R.J. 1990. Individual variation in, and the effect of rearing temperature and body size on, the concentration of fluorescent morphological lipofuscin in the brains of freshwater crayfish, *Cherax cuspidatus* (Crustacea: Parastacidae). *Comp. Biochem. Physiol.* 96A: 281-286.

Sheehy, M.R.J. 1996. Quantitative comparison of in situ lipofuscin concentration with soluble autofluorescence intensity in the crustacean brain. *Exp. Gerontol.* 31 (3): 421-432.

Sheehy, M.R.J. 2000. Ageing crabs. *New Scientist* 165 (2227): 58.

Sheehy, M.R.J., Cameron, E., Marsden, G. & McGrath, J. 1995. Age structure of female giant tiger prawns *Penaeus monodon* as indicated by neuronal lipofuscin concentration. *Mar. Ecol. Prog. Ser.*117 (1-3): 59-63.

Sheehy, M.R.J., Caputi, N., Chubb, C. & Belchier, M. 1998. Use of lipofuscin for resolving cohorts of western rock lobster (*Panulirus cygnus*). *Can. J. Fish. Aquat. Sci.*55 (4): 925-936.

Sheehy, M.R.J. & Ettershank, G. 1988. Extractable age pigment-like autofluorescence and its relationship to growth and age in the water flea *Daphnia carinata* King (Crustacea, Cladocera). *Aust. J. Zool.* 36 (6): 611-625.

Sheehy, M.R.J. & Roberts, B.E. 1991. An alternative explanation for anomalies in soluble lipofuscin fluorescence data from insects, crustaceans, and other aquatic species. *Exp. Gerontol.* 26 (5): 495-509.

Sheehy, M.R.J., Shelton, P.M.J., Wickins, J.F., Belchier, M. & Gaten, E. 1996. Ageing the european lobster *Homarus gammarus* by the lipofuscin in its eyestalk ganglia. *Mar. Ecol. Prog. Ser.*143 (1-3): 99-111.

Sheen, S.S. & Huang, H.T. 1998. The effects of different protein sources on the survival of grass shrimp, *Penaeus monodon* (Fabricius, 1798) larvae from the zoea to postlarva (Decapoda, Natantia). *Crustaceana* 71: 909-924.

Shen, J., Boon, J.D. & Kuo, A.Y. 1999. A modeling study of a tidal intrusion front and its impact on larval dispersion in the James River estuary, Virginia. *Estuaries* 22 (3A): 681-692.

Shiau, S.Y. & Chen, Y. 2000. Estimation of the dietary vitamin A requirement of juvenile grass shrimp, *Penaeus monodon*. *J. Nutr.* 130 (1): 90-94.

Shiau, S.-Y. & Lung, C.-Q. 1993. Estimation of the vitamin B_{12} requirement of the grass shrimp, *Penaeus monodon*. *Aquaculture* 117: 157-163.

Shields, J.D. & Wood, F.E.I. 1993. Impact of parasites on the reproduction and fecundity of the blue sand crab *Portunus pelagicus* from Moreton Bay, Australia. *Mar. Ecol. Prog. Ser.* 92: 159-170.

Shigueno, K. & Itoh, S. 1988. Use of Mg-L-ascorbyl-2-phosphate as a vitamin C source in shrimp diets. *J. Wld. Aquacul. Soc.* 19: 168-174.

Shin, Y.K. & Chin, P. 1994. Physiological changes in related to molt cycle of *Macrobrachium nipponense* (De Haan). *Bulletin of the Korean Fisheries Society* 27 (4): 380-389.

Shin, Y.K. & Chin, P. 1995. Carbon budget during the molt cycle of *Macrobrachium nipponense* (De Haan) larvae. *Journal of the Korean Fisheries Society* 28 (3): 237-246.

Shirley, S.M. & Shirley, T.C. 1989. Interannual variability in density, timing and survival of Alaskan red king crab *Paralithodes camtschatica* larvae. *Mar. Ecol. Prog. Ser.*54 (1-2): 51-59.

Shirley, S.M., Shirley, T.C. & Rice, S.D. 1987. Latitudinal variation in the dungeness crab, *Cancer magister:* zoeal morphology explained by incubation temperature. *Mar. Biol.* 95 (3): 371-376.

Shirley, T.C. & Zhou, S. 1997. Lecithotrophic development of the golden king crab *Lithodes aequispinus* (Anomura: Lithodidae). *J. Crust. Biol.* 17 (2): 207-216.

Shojima, Y. 1963. Scyllarid phyllosomas habit of accompanying the jelly-fish (preliminary report). *Bull. Japan. Soc. Sci. Fish.* 29: 349-353.

Shumway, S.E., Perkins, H.C., Schick, D.F. & Stickney, A.P. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838. *FAO Fisheries Synopsis* 144: 57.

Sick, L.V. 1976. Selected studies of protein and amino acid requirements for *Macrobrachium rosenbergii* larvae fed neutral density formula diets. In: Price, K.S., Shaw, N.W. & Danberg, K.S. (eds), *Proceedings of the First International Conference on Aquacult. Nutr.*. Newark, Del.: Univ. Delaware.

Sick, L.V. & Millikin, M.R. 1983. Dietary and nutrient requirements for culture of the Asian prawn, *Macrobrachium rosenbergii*. In: McVey, J.P. (ed), *Handbook of Mariculture 1*; *Crustacean Aquaculture*: 381-389. Boca Raton, Florida: CRC Press.

Signoret, G.P.B., Ortega, A.L. & Brailovsky, D.S. 2000. Partially abbreviated larval development in an undescribed freshwater palaemonid prawn of the genus *Macrobrachium* from Chiapas, Mexico. *Crustaceana* 73 (3): 273-282.

Silas, E.G. & Mathew, K.J. 1977. A critique to the study of larval development in Euphausiacea. In: *Proc. Symp. Warm Water Zooplankton*. Dona Paula, Goa, India: Natl. Inst. Oceanography.

Simione, F.P. & Hoffman, D.L. 1975. Some effects of eyestalk removal on the Y-organs of *Cancer irroratus* Say. *Biol. Bull.* 148: 400-447.

Sims, H.W. & Brown, C.L. 1968. A giant scyllarid phyllosoma larva taken north of Bermuda (Palinuridea). *Crustaceana Suppl.* 2: 80-82.

Sindermann, C.J. 1991. Shell disease in marine crustaceans - a conceptual approach. *J. Shellfish Res.* 10: 491-494.

Skinner, D.M. 1962. The structure and metabolism of a crustacean integumentary tissue during a molt cycle. *Biol. Bull.* 123: 635-647.

Skinner, D.M. 1985a. Interacting factors in the control of the Crustacean molt cycle. *Amer. Zool.* 25: 275-284.

Skinner, D.M. 1985b. Molting and regeneration. In: Bliss, D.E. & Mantel, L.H. (eds), *The Biology of the Crustacea 9*; *Integument, Pigments, and Hormonal Processes*: 43-146. New York: Academic Press.

Skjermo, J. & Vadstein, O. 1999. Techniques for microbial control in the intensive rearing of marine larvae. *Aquaculture* 177: 333-343.

Slabber, M. 1778. *Naturkundige Verlustigingen, behelzende microscopise waarneemingen van in-en uitlandse Water-en Land-Dieren.* Haarlem.

Smith, D.M. & Dall, W. 1985. Moult staging the tiger prawn *Penaeus esculentus*. In: Rothlisberg, P.C., Hill, B.J. & Staples, D.J. (eds), *Second Australian National Prawn Seminar*: 85-93. Cleveland, Australia: NPS2.

Smith Derby, J.G. & Capuzzo, J.M. 1984. Lethal and sublethal toxicity of drilling fluids to larvae of the American lobster, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 41: 1334-1340.

Smith, G. 1974. The ultrastructure of the organ of Bellonci of *Carcinus maenas* (Crustacea: Decapoda). *Cell Tiss. Res.* 155: 127-134.

Smith, N.P. & Stoner, A.W. 1993. Computer-simulation of larval transport through tidal channels - Role of vertical migration. *Est. Coast. Shelf Sci.* 37: 43-58.

Snodgrass, R.E. 1956. Crustacean metamorphoses. *Smithson Misc. Collns.* 131: 1-78.

Snyder, M.J. & Chang, E.S. 1986a. Effects of eyestalk ablation on larval molting rates and morphological development of the American lobster, *Homarus americanus*. *Biol. Bull.* 170: 232-243.

Snyder, M.J. & Chang, E.S. 1986b. Effects of sinus gland extracts on larval molting and ecdysteroid titers of the American lobster, *Homarus americanus*. *Biol. Bull. Mar. Biol. Lab. Woods Hole* 170: 244-254.

Sochansky, J.B., Aiken, D.E. & Watson, N.H.F. 1972. Y-organ, molting gland, and mandibular organ: a problem in Decapod Crustacea. *Can. J. Zool.* 50: 993-997.

Souheil, H., Vey, A., Thuet, P. & Trilles, J.-P. 1999. Pathogenic and toxic effects of *Fusarium oxysporum* (Schlecht.) on survival and osmoregulatory capacity of *Penaeus japonicus* (Bate). *Aquaculture* 178: 209-224.

Southam, C.M. & Ehrlich, J. 1943. Effects of extract of western red cedar heartwood on certain wood decaying fungi in culture. *Phytopathology* 33: 517-524.

Spaargaren, D.H. 1996. Diseases in cultures of tiger prawns, *Penaeus monodon* Fabricius, 1798 (Decapoda, Natantia). *Crustaceana* 69: 1018-1024.

Spaziani, E. 1990. Morphology, histolog and ultrastructure of the ecdysial gland (Y-organ) in Crustacea. In: Gupta, A.P. (ed), *Morphogenetic hormones of arthropods 1, Part 2*: 233-267. New Brunswick, New Jersey: Rutgers University Press.

Speck, U. & Urich, K. 1969. Der Abbau körpereigener Substanzen in dem Flußkrebs *Orconectes limosus* während des Hungerns. *Z. Vergl. Physiologie* 63: 410-414.

Speck, U. & Urich, K. 1971. Quantitative Bedeutung der Reservestoffe für Chitinsynthese, Energiestoffwechsel und osmotische Vorgänge während der Häutung des Flußkrebses *Orconectes limosus*. *Z. Vergl. Physiologie* 71: 286-294.

Speck, U. & Urich, K. 1972. Resorption des alten Panzers vor der Häutung bei dem Flußkrebs *Orconectes limosus.* Schicksal des freigesetzten N-Acetylglucosamins. *J. Comp. Physiol.* 78: 210-220.

Spindler-Barth, M. 1976. Changes in the chemical composition of the common shore crab, *Carcinus maenas*, during the molting cycle. *J. Comp. Physiol.* B105: 197-205.

Spindler-Barth, M., Junger, E., Baumeister, R. & Spindler, K.-D. 1995. The epithelila cell line from *Chironomus tentans:* hormonal regulation of tissue differentiation and cuticle-formation. *Actes De Colloques* 18: 87-93.

Spindler-Barth, M. & Spindler, K.-D. 1998. Morphogenetic actions and mode of action of ecdysteroids in a dipteran cell line. *Current Topics in Steroid Research* 1: 73-81.

Spindler-Barth, M., Van Wormhoudt, A. & Spindler, K.-D. 1990. Chitinolytic enzymes in the integument and midgut-gland of the shrimp *Palaemon serratus* during the moulting cycle. *Mar. Biol.* 106: 49-52.

Spindler, K.-D. & Anger, K. 1986. Ecdysteroid levels during the larval development of the spider crab *Hyas araneus*. *Gen. Comp. Endocrinol.* 64: 122-128.

Spindler, K.-D., Van Wormhoudt, A., Sellos, D. & Spindler-Barth, M. 1987. Ecdysteroid levels during embryogenesis in the shrimp, *Palaemon serratus* (Crustacea Decapoda): Quantitative and qualitative changes. *Gen. Comp. Endocrinol.* 66: 116-122.

Spivak, E.D. 1997. Life history of a brackish-water population of *Palaemonetes argentinus* (Decapoda: Caridea) in Argentina. *Annls. Limnol.* 33: 179-190.

Spivak, E.D., Anger, K., Luppi, T., Bas, C. & Ismael, D. 1994. Distribution and habitat preferences of tow grapsid crab species in Mar Chiquita Lagoon (Province of Buenos Aires, Argentina). *Helgoländer Meeresunters.* 48: 59-78.

Sprung, M. & Widdows, J. 1986. Rate of heat dissipation by gametes and larval stages of *Mytilus edulis*. *Mar. Biol.* 91: 41-45.

St-Amand, L., Gagnon, R., Packard, T.T. & Savenkoff, C. 1999. Effects of inorganic mercury on the respiration and the swimming activity of shrimp larvae, *Pandalus borealis*. *Comp. Biochem. Physiol.* 122C: 33-43.

Starr, M., Himmelman, J.H. & Therriault, J.-C. 1991. Coupling of nauplii release in barnacles with phytoplankton blooms: a parallel strategy to that of spawning in urchins and mussels. *J. Plank. Res.* 13: 561-571.

Starr, M., Therriault, J.-C., Conan, G.Y., Comeau, M. & Robichaud, G. 1994. Larval release in a sub-euphotic zone invertebrate triggered by sinking phytoplankton particles. *J. Plankton Res.* 16: 1137-1147.

Staton, J.L. & Sulkin, S.D. 1991. Nutritional requirements and starvation resistance in larvae of the brachyuran crabs *Sesarma cinereum* (Bosc) and *S. reticulatum* (Say). *J. Exp. Mar. Biol. Ecol.* 152 (2): 271-284.

Stebbing, A.R.D. 1981a. Hormesis - stimulation of colony growth in *Campanularia flexuosa* (Hydrozoa) by copper, cadmium and other toxicants. *Aquat. Toxicology* 1: 227-238.

Stebbing, A.R.D. 1981b. The kinetics of growth control in a colonial hydroid. *J. Mar. Biol. Ass. U.K.* 61: 35-63.

Stentiford, G.D., Chang, E.S., Chang, S.A. & Neil, D.M. 2001. Carbohydrate dynamics and the crustacean hyperglycemic hormone (CHH): effects of parasitic infection in Norway lobsters (*Nephrops norvegicus*). *Gen. Comp. Endocrinol.* 121 (1): 13-22.

Stephenson, M.J. & Knight, A.W. 1980. Growth, respiration and caloric content of larvae of the prawn *Macrobrachium rosenbergii*. *Comp. Biochem. Physiol.* 66A: 385-391.

Stevenson, J.R. 1985. Dynamics of the integument. In: Bliss, D.E. & Mantel, L.H. (eds), *The Biology of Crustacea 9*; *Integument, Pigments, and Hormonal Processes*: 1-42. New York: Acad. Press.

Stewart, J.E. 1984. Lobster diseases. *Helgol. Meeresunters.* 37: 243-254.

Stickney, A.P. & Perkins, H.C. 1979. Environmental physiology of northern shrimp, *Pandalus borealis*. *Completion Report, Dep. Mar. Resour., W. Boothbay Harbor, Maine, Project 3-277-R:* 1-66.

Stickney, A.P. & Perkins, H.C. 1981. Observations on the food of the larvae of the northern shrimp, *Pandalus borealis* Kröyer (Decapoda, Caridea). *Crustaceana* 40: 36-49.

Storch, V. 1985. Die Zelle als Spiegel der Umwelt. *Umschau* 1: 21-23.

Storch, V. & Anger, K. 1983. Influence of starvation and feeding on the hepatopancreas of larval *Hyas araneus* (Decapoda, Majidae). *Helgoländer Meeresunters.* 36: 67-75.

Storch, V., Janssen, H.H. & Cases, E. 1982. The effects of starvation on the hepatopancreas of the coconut crab, *Birgus latro* (L.) (Crustacea, Decapoda). *Zool. Anz. Jena* 208: 115-123.

Stowe, M.K., Tumlinson, J.H. & Heath, R.R. 1987. Chemical mimicry: bolas spiders emit components of moth prey species sex pheromones. *Science* 236: 964-968.

Strasser, K.M. & Felder, D.L. 1998. Settlement cues in successive developmental stages of the ghost shrimps *Callichirus major* and *C. islagrande* (Crustacea: Decapoda: Thalassinidea). *Mar. Biol.* 132: 599-610.

Strasser, K.M. & Felder, D.L. 1999a. Sand as a stimulus for settlement in the ghost shrimp *Callichirus major* (Say) and *C. islagrande* (Schmitt) (Crustacea: Decapoda: Thalassinidea). *J. Exp. Mar. Biol. Ecol.* 239: 211-222.

Strasser, K.M. & Felder, D.L. 1999b. Settlement cues in an Atlantic coast population of the ghost shrimp *Callichirus major* (Crustacea: Decapoda: Thalassinidea). *Mar. Ecol. Prog. Ser.*183: 217-225.

Strasser, K.M. & Felder, D.L. 2000. Larval development of the ghost shrimp *Callichirus islagrande* (Decapoda: Thalassinidea: Callianassidae) under laboratory conditions. *J. Crust. Biol.* 20 (1): 100-117.

Strathmann, R.R. 1977. Egg size, larval development, and juvenile size in benthic marine invertebrates. *Am. Nat.* 111 (978): 373-376.

Strathmann, R.R. 1978. The evolution and loss of feeding larval stages of marine invertebrates. *Evolution* 32 (4): 894-906.

Strathmann, R.R. 1982. Selection for retention or export of larvae in estuaries. In: Kennedy, V.S. (ed), *Estuarine Comparisons*: 521-535. Academic Press.

Strathmann, R.R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annu. Rev. Ecol. Syst.* 16: 339-361.

Strathmann, R.R. 1986. What controls the type of larval development? Summary statement for the evolution session. *B. Mar. Sci.* 39 (2): 616-622.

Strathmann, R.R. 1987. Larval feeding. In: Giese, A.C., Pearse, J.S. & Pearse, V.B. (eds), *Reproduction of Marine Invertebrates 9*; *General Aspects: Seeking Unity in Diversity*: 465-550. California: Blackwell Scientific Publications & The Boxwood Press.

Strathmann, R.R. 1993. Hypotheses on the origins of marine larvae. *Annu. Rev. Ecol. Syst.* 24: 89-117.

Strathmann, R.R. 1996. Are planktonic larvae of marine benthic invertebrates too scarce to compete within species? *Oceanol. Acta.* 19 (3-4): 399-407.

Strenth, N.E. 1976. A review of the systematics and zoogeography of the freshwater species of *Palaemonetes* Heller of North America (Crustacea: Decapoda). *Smithson. Contr. Zool.* 228: 1-27.

Strom, S.L., Benner, R., Ziegler, S. & Dagg, M.J. 1997. Planktonic grazers are a potentially important source of marine dissolved organic carbon. *Limnol. Oceanogr.* 42: 1364-1374.

Stuck, K.C., Stuck, L.M., Overstreet, R.M. & Wang, S.Y. 1996. Relationship between BP (*Baculovirus penaei*) and energy reserves in larval and postlarval Pacific white shrimp *Penaeus vannamei*. *Dis. Aquat. Org.* 24: 191-198.

Styrishave, B. & Andersen, O. 2000. Seasonal variations in hepatopancreas fatty acid profiles of two colour forms of shore crabs, *Carcinus maenas*. *Mar. Biol.* 137 (3): 415-422.

Subramoniam, T. 2000. Crustacean ecdysteriods in reproduction and embryogenesis. *Comp. Biochem. Phys. A.* 125C(2): 135-156.

Suh, H.-L., Toda, T. & Terazaki, M. 1991. Diet of calyptodes of the euphausiid *Euphausia pacifica* in the Yellow Sea. *Mar. Biol.* 111: 45-48.

Sulkin, S.D. 1973. Depth regulation of crab larvae in the absence of light. *J. Exp. Mar. Biol. Ecol.* 13: 73-82.

Sulkin, S.D. 1975. The significance of diet in growth and development of larvae of the blue crab, *Callinectes sapidus* Rathbun, under laboratory conditions. *J. Exp. Mar. Biol. Ecol.* 20 (2): 119-135.

Sulkin, S.D. 1978. Nutrional requirements during larval development of the Portunid crab, *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol.* 34 (1): 29-41.

Sulkin, S.D. 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Mar. Ecol. Prog. Ser.*15 (1-2): 181-205.

Sulkin, S.D. 1990. Larval orientation mechanisms: the power of controlled experiments. *Ophelia* 32 (1-2): 49-62.

Sulkin, S.D., Blanco, A., Chan, J. & Bryant, M. 1998b. Effects of limiting access to prey on development of first zoeal stage of the brachyuran crabs *Cancer magister* and *Hemigrapsus oregonensis*. *Mar. Biol.* 131: 515-521.

Sulkin, S.D., Lehto, J., Strom, S. & Hutchinson, D. 1998a. Nutritional role of protists in the diet of first stage larvae of the dungeness crab *Cancer magister*. *Mar. Ecol. Prog. Ser.*169: 237-242.

Sulkin, S.D. & McKeen, G. 1994. Influence of temperature on larval development of four co-occurring species of the brachyuran genus *Cancer*. *Mar. Biol.* 118 (4): 593-600.

Sulkin, S.D. & McKeen, G.L. 1996. Larval development of the crab *Cancer magister* in temperature regimes simulating outer-coast and inland-water habitats. *Mar. Biol.* 127 (2): 235-240.

Sulkin, S.D. & McKeen, G.L. 1999. The significance of feeding history on the value of heterotrophic microzooplankton as prey for larval crabs. *Mar. Ecol. Prog. Ser.*186: 219-225.

Sulkin, S.D., Mojica, E. & McKeen, G.L. 1996. Elevated summer temperature effects on megalopa and early juvenile development in the dungeness crab, *Cancer magister*. *Can. J. Fish. Aquat. Sci.*53 (9): 2076-2079.

Sulkin, S.D., Morgan, R.P. & Minasian, L.L. 1975. Biochemical changes during larval development of the xanthid crab *Rhithropanopeus harrisii*. II. Nucleic acids. *Mar. Biol.* 32 (2): 113-117.

Sulkin, S.D. & van Heukelem, W. 1982. Larval recruitment in the crab *Callinectes sapidus* Rathbun: an amendment to the concept of larval retention in estuaries. In: Kennedy, V.S. (ed), *Estuarine comparisons*: 459-475. New York: Academic Press.

Sulkin, S.D. & van Heukelem, W.F. 1980. Ecological and evolutionary significance of nutritional flexibility in planktotrophic larvae of the deep sea red crab *Geryon quinquedens* and the stone crab *Menippe mercenaria*. *Mar. Ecol. Prog. Ser.*2 (2): 91-95.

Suthers, I.M. 1998. Bigger? Fatter? Or is faster growth better? Considerations on condition in larval coral-reef fish. *Aust. J. Ecol.* 23: 265-273.

Suthers, I.M. 2000. Significance of larval condition: comment on laboratory experiments. *Can. J. Fish. Aquat. Sci.* 57 (7): 1534-1536.

Takahashi, M. & Saisho, T. 1978. The complete larval development of the scyllarid lobster *Ibacus ciliatus* (von Siebold) and *Ibacus novemdentatus* Gibbes in the laboratory. *Mem. Fac. Fish. Kagoshima Univ.* 27: 305-353.

Takahashi, Y., Nishida, S. & Kittaka, J. 1994. Histological characteristics of fat bodies in the puerulus of the rock lobster *Jasus edwardsii* (Hutton, 1875) (Decapoda, Palinuridae. *Crustaceana* 66: 317-325.

Taketomi, Y. & Hyodo, M. 1986. The Y-organ in the crab *Portunus trituberculatus*: effects of ecdysone on the ultrastructure. *Cell Biology International Reports* 10: 367-374.

Takeuchi, T., Nakamoto, Y., Hamasaki, K., Sekiya, S. & Watanabe, T. 1999a. Requirement of n-3 highly unsaturated fatty acids for larval swimming crab *Portunus trituberculatus*. *Nippon Suisan Gakk.* 65 (5): 797-803.

Takeuchi, T., Satoh, N., Sekiya, S., Shimizu, T. & Watanabe, T. 1999b. Influence of the different feeding schedule of food organisms for larval swimming crab *Portunus trituberculatus*. *Nippon Suisan Gakk.* 65 (5): 804-809.

Takeuchi, T., Satoh, N., Sekiya, S., Shimizu, T. & Watanabe, T. 1999c. The effect of dietary EPA and DHA on the molting rate of larval swimming crab *Portunus trituberculatus*. *Nippon Suisan Gakk.* 65 (6): 998-1004.

Talbot, P., Clark, W.-H. & Lawrence, A.L. 1972a. Light and electron microscopic studies on osmoregulatory tissue in the developing brown shrimp, *Penaeus aztecus*. *Tissue Cell* 4: 271-286.

Talbot, P., Clark, W.-H. & Lawrence, A.L. 1972b. Ultrastructural observations of the muscle insertion and modified branchiostegite epidermis in the larval brown shrimp, *Penaeus aztecus*. *Tissue Cell* 4: 613-628.

Talbot, P., Clark, W.-H. & Lawrence, A.L. 1972c. Fine structure of the midgut epithelium in the developing brown shrimp, *Penaeus aztecus*. *J. Morphol.* 138: 467-486.

Talbot, P. & Demers, D. 1993. Tegumental glands of crustacea. In: Horst, M.N. & Freeman, J.A. (eds), *The crustacean integument. Morphology and biochemistry*: 151-191. Boca Raton, FL: CRC Press.

Talbot, P. & Zao, P. 1991. Secretion at molting by the pleopod tegumental glands of the lobster *Homarus americanus* (Milne Edwards). *J. Crust. Biol.* 11: 1-9.

Tamburri, M.N. & Zimmer-Faust, R.K. 1996. Suspension feeding: basic mechanisms controlling recognition and ingestion of larvae. *Limnol. Oceanogr.* 41: 1188-1197.

Tamone, S.L. & Chang, E.S. 1993. Methyl farnesoate stimulates ecdystoid secretion from crab Y-organs *in vitro*. *Gen. Comp. Endocrinol.* 89: 425-432.

Tang, C.H., Lu, W.Q., Wainwright, G., Webster, S.G., Rees, H.H. & Turner, P.C. 1999. Molecular characterization and expression of mandibular organ-inhibiting hormone, a recently discovered neuropeptide involved in the regulation of growth and reproduction in the crab *Cancer pagurus*. *Biochemical Journal* 343: 355-360.

Tankersley, R.A., McKelvey, L.M. & Forward, R.B. 1995. Responses of estuarine crab megalopae to pressure, salinity and light: implications for food-tide transport. *Mar. Biol.* 122: 391-400.

Tankersley, R.A. & Wieber, M.G. 2000. Physiological responses of postlarval and juvenile blue crabs *Callinectes sapidus* to hypoxia and anoxia. *Mar. Ecol. Prog. Ser.* 194: 179-191.

Tankersley, R.A., Wieber, M.G., Sigala, M.A. & Kachurak, K.A. 1998. Migratory behavior of ovigerous blue crabs *Callinectes sapidus:* evidence for selective tidal-stream transport. *Biol. Bull.* 195: 168-173.

Taylor, D.M., Hooper, R.G. & Ennis, G.P. 1985. Biological aspects of the spring breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, Newfoundland (Canada). *Fish. B-Noaa* 83 (4): 707-711.

Taylor, H.H. & Greenaway, P. 1994. The partitioning of water and solutes during evaporative water loss in three terrestrial crabs. *Physiological Zoology* 67: 539-565.

Taylor, H.H. & Taylor, E.W. 1992. Gills and lungs: the exchange of gases and ions. In: Harrison, F.W. & Humes, A.G. (eds), *Microscopic Anatomy of Invertebrates 10*; *Decapod Crustacea*: 203-293. New York: Wiley-Liss.

Tchernigovtzeff, C. 1965. Multiplication cellulaire et régénération au cours du cycle d'intermue des crustacés décapodes. *Arch. Zool. Exp. Gén.* 106: 377-529.

Tchernigovtzeff, C. 1976. Sur l'organisation des matrices sétigères chez deux Crustacés Malacostracés, étudiée au microscope électronique. *C.R. Acad. Sc. Paris, Ser. D* 282: 727-729.

Templeman, W. 1936. The influence of temperature, salinity, light and food on the survival and growth of the larvae of the lobster (*Homarus americanus*). *J. Biol. Bd. Can.* 2: 485-497.

Tenore, K.R., Boyer, L.F., Cal, R.M., Corral, J., Garcia-Fernandez, C., Gonzalez, N., Gonzalez-Gurriaran, E., Hanson, R.B., Iglesias, J., Krom, M., Lopez-Jamar, E., McClain, J., Pamatmat, M.M., Perez, A.R.D.C., de Santiago, G., Tietjen, J., Westrich, J. & Windom, H.L. 1982. Coastal upwelling in the Rias Bajas, N.W. Spain: contrasting the benthic regimes of the Rias de Arosa and de Muros. *J. Mar. Res.* 40: 701-772.

Terwilliger, N.B. 1991. Hemocyanins in crustacean oocytes and embryos. In: Wenner, A. & Kuris, A. (eds), *Crustacean Issues 7*; *Crustacean Egg Production*: 31-39. Rotterdam: Balkema.

Terwilliger, N.B. & Dumler, K. 2001. Ontogeny of decapod crustacean hemocyanin: effects of temperature and nutrition. *J. Exp. Biol.* 204 (5): 1013-1020.

Terwilliger, N.B. & Terwilliger, R.C. 1983. Changes in crustacean hemocyanin structure during development. In: Wood, E. (ed), *Life Chem. Reports Suppl. Structure and Function of Invertebrate Respiratory Proteins*: 357-360. Harwood Acad. Publ.

Teshima, S. 1972. Studies on the sterol metabolism in marine crustaceans. *Mem. Fac. Fish., Kagoshima Univ.* 21: 69-147.

Teshima, S. & Kanazawa, A. 1980. Lipid transport in crustaceans. *Min. Rev. Data File Fish. Res.* 1: 1-25.

Teshima, S. & Kanazawa, A. 1982. Variation in lipid compositions during the larval development of the prawn (*Penaeus japonicus*). *Mem. Fac. Fish., Kagoshima Univ.* 31: 205-212.

Teshima, S. & Kanazawa, A. 1983a. Effects of several factors on growth and survival of the prawn larvae reared with microparticulate diets. *Bull. Jap. Soc. Sci. Fish.* 49: 1893-1896.

Teshima, S. & Kanazawa, A. 1983b. Variation in lipid compositions during the ovarian maturation of the prawn. *Bull. Jap. Soc. Sci. Fish.* 49: 957-962.

Teshima, S. & Kanazawa, A. 1986. Nutritive value of sterols for the juvenile prawn. *Bull. Jpn. Soc. Sci. Fish.* 52: 1417-1422.

Teshima, S., Kanazawa, A. & Kakuta, Y. 1986b. Growth, survival, and body lipid composition of the prawn larvae receiving several dietary phospholipids. *Mem. Fac. Fish. Kagoshima Univ.* 35: 17-27.

Teshima, S., Kanazawa, A. & Koshio, S. 1992. Ability for bioconversion of n-3 fatty acids in fish and crustaceans. *Océanis* 18: 67-75.

Teshima, S., Kanazawa, A. & Koshio, S. 1993. Recent developments in nutrition and microparticulare diets of larval prawns. *Israeli J. Aquacult. Bamidgeh* 45: 175-184.

Teshima, S., Kanazawa, A. & Yamashita, M. 1986a. Dietary value of several proteins and supplemental amino acids for larvae of the prawn *Penaeus japonicus*. *Aquaculture* 51: 225-235.

Tetzlaff, K. 1995. Der Einfluß der Temperatur auf den Stoffwechsel der Larven von *Pagurus bernhardus* (Crustacea, Decapoda). M.Sc. Thesis, Universität Gießen, Germany, 79 pp.

Thatje, S. & Bacardit, R. 2000. Morphological variability in larval stages of *Nauticaris magellanica* (A. Milne Edwards, 1891) (Decapoda: Caridea: Hippolytidae) from South American waters. *B. Mar. Sci.* 66 (2): 375-398.

Thessalou-Legaki, M., Peppa, A. & Zacharaki, M. 1999. Facultative lecithotrophy during larval development of the burrowing shrimp *Callianassa tyrrhena* (Decapoda: Callianassidae). *Mar. Biol.* 133 (4): 635-642.

Thiel, M. & Dernedde, T. 1994. Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. *Helgoländer Meeresunters.* 48: 321-332.

Thomas, L.R. 1963. Phyllosoma larvae associated with medusae. *Nature* 198: 208.

Thompson, F.L., Abreu, P.C. & Cavalli, R. 1999. The use of microorganisms as food source for *Penaeus paulensis* larvae. *Aquaculture* 174: 139-153.

Thompson, J.V. 1828. On the metamorphoses of the Crustacea, and on the zoea, exposing their singular structure, and demonstrating that they are not, as has been supposed, a peculiar genus, but the larva of Crustacea. In: *Zoological Researches; or Natural History of nondiscript or imperfectly known animals, in a series of memoirs. Memoir I 1*: 1-11. Cork, Ireland:

Thompson, J.V. 1836. Metamorphosis in *Porcellana* and *Portunus*. *Entomological Magazine* 3: 275-280.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Reviews* 25 (1): 1-45.

Thorson, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. *Publs. Am. Ass. Advmt. Sci.* 67: 455-474.

Thorson, G. 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. *Ophelia* 1: 167-208.

Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* 3: 267-293.

Thuet, P., Charmantier-Daures, M. & Charmantier, G. 1988. Relation entre osmorégulation et activités d'ATPase Na^+- K^+ et d'anhydrase carbonique chez larves et postlarves de *Homarus gammarus* (L.) (Crustacea: Decapoda). *J. Exp. Mar. Biol. Ecol.* 115: 249-261.

Tiews, K. 1970. Synopsis of biological data on the common shrimp *Crangon crangon* (Linnaeus, 1758). *FAO Fisheries Synopsis* 91: 1167-1224.

Tiews, K. 1987. Zur Frage des Geschlechtswechsels bei der Nordseegarnele (*Crangon crangon* (L.)). *Informationen Für Die Fischwirtschaft* 3: 109-112.

Tirmizi, N.M. & Kazmi, Q.B. 1987. Larval development of two spider crabs reared in the laboratory, families Hymenosomatidae and Majidae. *Crustaceana* 53: 281-291.

Tong, L.J., Moss, G.A., Paewai, M.P. & Pickering, T.D. 2000. Effect of temperature and feeding rate on the growth and survival of early and mid-stage phyllosomas of the spiny lobster *Jasus edwardsii*. *Mar. Freshwater. Res.* 51 (3): 235-241.

Trask, T. 1974. Laboratory-reared larvae of *Cancer anthonyi* (Decapoda: Brachyura) with a brief description of the internal anatomy of the megalopa. *Mar. Biol.* 27: 63-74.

Trimble, W.C. & Sandifer, P.A. 1977. Bibliography. The biology and culture of the freshwater prawn (genus *Macrobrachium*). In: Hanson, J.A. & Goodwin, H.L. (eds), *Shrimp and Prawn Farming in the Western Hemisphere*: 385-439. Stroudsburg: Dowden, Hutchinson & Ross.

Trussell, R.P. 1972. The percent un-ionized ammonia in aqueous ammonia solutions at different pH levels and temperatures. *J. Fish. Res. Bd. Can.* 29: 1505-1507.

Tsai, M.F., Kou, G.H., Liu. H.C., Liu. K.F., Chang. C.F., Peng. S.E., Hsu. H.C., Wang C.H. & Lo. C.F. 1999. Long-term presence of white spot syndrome virus (WSSV) in a cultivated shrimp population without disease outbreaks. *Dis. Aquat. Org.* 38: 107-114.

Tucker, R.K. 1978. Free amino acids in developing larvae of the stone crab, *Menippe mercenaria*. *Comp. Biochem. Physiol.* 60: 169-172.

Tucker, R.K. & Costlow, J.D. 1975. Free amino acid changes in normal and eyestalkless megalopa larvae of the blue crab, *Callinectes sapidus*, during the molt cycle. *Comp. Biochem. Physiol.* 51: 75-78.

Tudge, C.C. 2000. *The Variety of Life.* Oxford: Oxford University Press.

Tunberg, B.G. & Creswell, R.L. 1991. Development, growth, and survival in the juvenile Caribbean king crab *Mithrax spinosissimus* (Lamarck) reared in the laboratory. *J. Crust. Biol.* 11 (1): 138-149.

Tyler, P.A. & Dixon, D.R. 2000. Temperature/pressure tolerance of the first larval stage of *Mirocaris fortunata* from Lucky Strike hydrothermal vent field. *J. Mar. Biol. Ass. UK* 80: 739-740.

Ueda, R., Sugita, H. & Deguchi, Y. 1999. Effect of transportation on the serum bactericidal activity of *Penaeus japonicus* and *Ovalipes punctatus*. *Aquaculture* 171: 221-225.

Uno, Y. & Kwon, C.S. 1969. Larval development of *Macrobrachium rosenbergii* (de Man) reared in the laboratory. *Jour. Tokyo Univ. Fish.* 52: 179-190.

van Dover, C.L., Factor, J.R. & Gore, R.H. 1982. Developmental patterns of larval scaphognathites: an aid to the classification of Anomuran and Brachyuran Crustacea. *J. Crust. Biol.* 2: 48-53.

van Dover, C.L., Factor, J.R., Williams, A.B. & Berg, C.J. 1985. Reproductive patterns of decapod crustaceans from hydrothermal vents. *Bulletin of the Biological Society of Washington* 6: 223-227.

van Dover, C.L., Williams, A.B. & Factor, J.R. 1984. The first zoeal stage of a hydrothermal vent crab (Decapoda: Brachyura: Bythograeidae). *P. Biol. Soc. Wash.* 97: 413-428.

van Herp, F. & Bellon-Humbert, C. 1978. Setal development and molt prediction in the larvae and adults of the crayfish, *Astacus leptodactylus* (Nordmann, 1842). *Aquaculture* 14: 289-301.

van Lenteren, J.C. 1999. Fundamental knowledge about insect reproduction: essential to develop sustainable pest management. *Inv. Repr. Devel.* 36: 1-15.

van Montfrans, J., Epifanio, C.E., Knott, D.M., Lipcius, R.N., Mense, D.J., Metcalf, K.S., Olmi, E.J., Orth, R.J., Poey, M.H., Wenner, E.L. & West, T.L. 1995. Settlement of blue crab postlarvae in western North Atlantic estuaries. *B. Mar. Sci.* 57 (3): 834-854.

van Wormhoudt, A. 1973. Variation des protéases, des amylases et des protéines solubles au cours du développement larvaire chez *Palaemon serratus*. *Mar. Biol.* 19: 245-248.

Vandenberghe, J., Verdonck, L., Roblesarozarena, R., Rivera, G., Bolland, A., Balladares, M., Gomezgil, B., Calderon, J., Sorgeloos, P. & Swings, J. 1999. Vibrios associated with *Litopenaeus vannamei* larvae, postlarvae, broodstock, and hatchery probionts. *Appl. Environ. Microbiol.* 65: 2592-2597.

Venegas, C.A., Nonaka, L., Mushiake, K., Shimizu, K., Nishizawa, T. & Muroga, K. 1999. Pathogenicity of penaeid rod-shaped DNA virus (PRDV) to kuruma prawn in different developmental stages. *Fish Pathol* 34: 19-23.

Vereshchaka, A.L., Vinogradov, G.M., Yu. Lein, A., Dalton, S. & Dehairs, F. 2000. Carbon and nitrogen isotopic composition of the fauna from the Broken Spur hydrothermal vent field. *Mar. Biol.* 136 (1): 11-17.

Verity, P.G. & Smetacek, V. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.* 130: 277-293.

Vernberg, F.J. 1969. Acclimation of intertidal crabs. *Amer. Zool.* 9: 333-341.

Vernberg, F.J. 1983. Respiratory adaptation. In: Vernberg, F.J. & Vernberg, W.B. (eds), *The Biology of Crustacea 8*; *Environmental Adaptations*: 1-42. New York: Academic Press.

Vernberg, F.J. & Costlow, J.D. 1966. Studies on the physiological variation between tropical and temperate-zone fiddler crabs of the genus *Uca.* IV. Oxygen consumption of larvae and young crabs reared in the laboratory. *Physiol. Zool.* 39: 36-52.

Vernberg, F.J. & Silverthorn, S.U. 1979. Temperature and osmoregulation in aquatic species. In: Gilles, R. (ed), *Mechanisms of osmoregulation in animals. Maintenance of cell volume*: 537-562. Chichester: Wiley.

Vernberg, F.J. & Vernberg, W.B. (eds) 1974. *Pollution and physiology of marine organisms.* New York: Academic Press.

Vernberg, W.B., DeCoursey, P.J. & Padgett, W.J. 1973. Synergistic effects of environmental variables on larvae of *Uca pugilator*. *Mar. Biol.* 22: 307-312.

Vernberg, W.B., Moreira, G.S. & McNamara, J.C. 1981. The effect of temperature on the respiratory metabolism of the developmental stages of *Pagurus criniticornis* (Dana) (Anomura: Paguridae). *Mar. Biol. Lett.* 2: 1-9.

Via, S.E. & Forward, R.B. 1975. The ontogeny and spectral sensitivity of polarotaxis in larvae of the crab *Rhithropanopeus harrisii* (Gould). *Biol. Bull.* 149: 251-266.

Victor, B.C. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fisch (*Thalassoma bifasciatum*). *Can. J. Fish. Aquat. Sci.* 43: 1208-1213.

Viitasalo, M. & Rautio, M. 1998. Zooplanktivory by *Praunus flexuosus* (Crustacea: Mysidacea): functional responses and prey selection in relation to prey escape responses. *Mar. Ecol. Prog. Ser.* 174: 77-87.

Villalobos, J.L. & Álvarez, F. 1999. A new species of *Macrobrachium* (Crustacea: Decapoda: Palaemonidae), with abbreviated development, from Veracruz, Mexico. *P. Biol. Soc. Wash.* 112 (4): 746-753.

Villamar, D.F. & Brusca, G.J. 1987. Survival and growth of *Crangon nigricauda* larvae (Decapoda, Caridea) raised on experimental diets. *J. World Aquacult. Soc.* 18: 11-25.

Villamar, D.F. & Langdon, C.J. 1993. Delivery of dietary components to larval shrimp *(Penaeus vannamei)* by means of complex microcapsules. *Mar. Biol.* 115: 635-642.

Vinogradov, A.P. 1953. *The elementary chemical composition of marine organisms.* Memoirs Sears Foundation for Marine Research 2. New Haven: Sears Foundation for Marine Research, Yale University.

Virtue, P., Mayzaud, P., Albessard, E. & Nichols, P. 2000. Use of fatty acids as dietary indicators in northern krill, *Meganyctiphanes norvegica*, from northeastern Atlantic, Kattegat, and Mediterranean waters. *Can. J. Fish. Aquat. Sci.* 57: 104-114.

Vitale, A.M., Monserrat, J.M., Castilho, P. & Rodriguez, E.M. 1999. Inhibitory effects of cadmium on carbonic anhydrase activity and ionic regulation of the estuarine crab *Chasmagnathus granulata* (Decapoda, Grapsidae). *Comp. Biochem. Phys. A.* 122C(1): 121-129.

Vogt, G. 1990. Pathology of midgut gland-cells of *Penaeus monodon* postlarvae after *Leucaena leucocephala* feeding. Dis. aquat. Org. 9: 45-61.

Vogt, G. 1992a. Enclosure of bacteria by the rough endoplasmic reticulum of shrimp hepatopancreas cells. *Protoplasma* 171: 89-96.

Vogt, G. 1992b. Palaemon B-cell reo-like virus: a new virus from the hepatopancreas of the shrimp *Palaemon elegans*. *J. Invert., Pathology* 59: 218-220.

Vogt, G. 1993. Differentiation of B-cells in the hepatopancreas of the prawn *Penaeus monodon*. *Acta Zool.* 74: 51-60.

Vogt, G., Stöcker, W., Storch, V. & Zwilling, R. 1989. Biosynthesis of *Astacus* protease, a digestive enzyme from crayfish. *Histochemistry* 91: 373-381.

Vogt, G., Storch, V., Quinitio, E.T. & Pascual, F.P. 1985. Midgut gland as monitor organ for the nutritional value of diets in *Penaeus monodon* (Decapoda). *Aquaculture* 48: 1-12.

Vollenweider, R.A. 1985. Elemental and biochemical composition of plankton biomass; some comments and explorations. *Arch. Hydrobiol.* 105: 11-29.

Vonk, H.J. 1960. Digestion and metabolism. In: Waterman, T.H. (ed), *The Physiology of Crustacea 1*; *Metabolism and growth*: 291-316. New York: Acad. Press.

Wache, S., Terwilliger, N.B. & Terwilliger, R.C. 1988. Hemocyanin structure changes during early development of the crab *Cancer productus*. *J. Exp. Zool.* 247: 23-32.

Waddy, S.L. & Aiken, D.E. 1999. Timing of the metamorphic molt of the American lobster (*Homarus americanus*) is governed by a population-based, photoperiodically entrained daily rhythm. *Can. J. Fish. Aquat. Sci.*56 (12): 2324-2330.

Wahle, R.A. & Incze, L.S. 1997. Pre- and post-settlement processes in recruitment of the American lobster. *J. Exp. Mar. Biol. Ecol.* 217: 179-207.

Wainwright, G., Prescott, M.C., Rees, H.H. & Webster, S.G. 1996a. Mass spectrometric determination of methyl farnesoate profiles and correlation with ovarian development in the edible crab, *Cancer pagurus*. *J. Mass. Spectrom.* 31: 1338-1344.

Wainwright, G., Webster, S.G. & Rees, H.H. 1998. Neuropeptide regulation of biosynthesis of the juvenoid, methyl farnesoate, in the edible crab, *Cancer pagurus*. *Biochem. J.* 334: 651-657.

Wainwright, G., Webster, S.G., Wilkinson, M.C., Chung, J.S. & Rees, H.H. 1996b. Structure and significance of mandibular organ-inhibiting hormone in the crab, *Cancer pagurus*. *J. Biol. Chem.* 271: 12749-12754.

Walossek, D. 1999. On the cambrian diversity of Crustacea. In: Schram, F.R. & von Vaupel Klein, J.C. (eds), *Crustaceans and the Biodiversity Crisis 1*: 3-27. Leiden: Brill.

Walsh, C.J. 1993. Larval development of *Paratya australiensis* Kemp, 1917 (Decapoda: Caridea: Atyidae), reared in the laboratory, with comparisons of fecundity and egg and larval size between estuarine and riverine environments. *J. Crust. Biol.* 13: 456-480.

Walter, I. 1993. Experimentelle Untersuchungen zur Verzögerung der Metamorphose bei dekapoden Krebsen. M. Sc. Thesis, Technische Universität München, Germany, 152 pp.

Walters, L.J., Miron, G. & Bourget, E. 1999. Endoscopic observations of invertebrate larval substratum exploration and settlement. *Mar. Ecol. Prog. Ser* 182: 95-108.

Wang, Y.-G. & Thomas, M.R. 1995. Accounting for individual variability in the von Bertalanffy growth model. *Can. J. Fish. Aquat. Sci.* 52: 1368-1375.

Warren, C.E. & Davis, G.E. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. In: Gerking, S.D. (ed), *The biological basis of freshwater fish production*: 175-214. New York: Wiley.

Watanabe, K., Yoshimizu, M., Obana, H., Kamata, K., Sugisawa, T., Sawabe, T. & Ezura, Y. 1999. Bacteriological study on the mass mortality of cultured Hanasaki crab larvae - causative bacterial characteristics and infection trial. *Bull. Fac. Fish. Hokkaido Univ.* 50: 19-32.

Wear, R.G. 1967. Life-history studies on New Zealand Brachyura. 1. Embryonic and post-embryonic development of *Pilumnus novaezealandiae* Filhol, 1886, and of *P. lumpinus* Bennnett, 1964 (Xanthidae, Pilumninae). *New Zealand J. Mar. Freshwat. Res.* 1: 482-535.

Wear, R.G. & Fielder, D.R. 1985. The marine fauna of New Zealand: larvae of the Brachyura (Crustacea, Decapoda). *N.Z. Oceanographic Institute Memoir* 92: 1-90.

Weber, A. 2001. Interactions between predator kairomone and food level complicate the ecological interpretation of *Daphnia* laboratory results. *J. Plankton Res.* 23: 41-46.

Weber, J.C. & Epifanio, C.E. 1996. Response of mud crab (*Panopeus herbstii*) megalopae to cues from adult habitat. *Mar. Biol.* 126 (4): 655-661.

Webster, S.G. 1991. Amino acid sequence of putative moult-inhibiting homone from the crab *Carcinus maenas*. *Proc. R. Soc. Lond.* B 244: 247-252.

Webster, S.G. & Dircksen, H. 1991. Putative molt-inhibiting hormone in larvae of the shore crab *Carcinus maenas* L.: an immunocytochemical approach. *Biol. Bull.* 180: 65-71.

Webster, S.G. & Keller, R. 1986. Purification, characterization and amino acid composition of the putative moult-inhibiting hormone (MIH) of *Carcinus maenas*. *J. Comp. Physiol.* B 156: 617-624.

Wehrtmann, I.S. 1989. Seasonal occurrence and abundance of caridean shrimp larvae at Helgoland, German Bight. *Helgoländer Meeresunters* 43: 87-112.

Wehrtmann, I.S. 1991. How important are starvation periods in early larval development for survival of *Crangon septemspinosa* larvae? *Mar. Ecol. Prog. Ser.* 73: 183-190.

Wehrtmann, I.S. & Albornoz, L. 1998. Larval development of *Nauticaris magellanica* (A. Milne Edwards, 1891) (Decapoda: Caridea: Hippolytidae), reared under laboratory conditions. *B. Mar. Sci.* 62: 45-72.

Wehrtmann, I.S. & Dittel, A.I. 1990. Utilization of floating mangrove leaves as a transport mechanism of estuarine organisms, with emphasis on decapod Crustacea. *Mar. Ecol. Prog. Ser.* 60: 67-73.

Welch, H.E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. *Ecology* 49: 755-759.

Welch, J.M. & Epifanio, C.E. 1995. Effect of variations in prey abundance on growth and development of crab larvae reared in the laboratory and in large field-deployed enclosures. *Mar. Ecol. Prog. Ser.*116 (1-3): 55-64.

Wendt, D.E. 1996. Effect of larval swimming duration on success of metamorphosis and size of the ancestrular lophophore in *Bugula neritina* (Bryozoa). *Biol. Bull.* 191: 224-233.

Wenner, E., Knott, D., Blanton, J., Barans, C. & Amft, J. 1998. Roles of tidal and wind-generated currents in transporting white shrimp (*Penaeus setiferus*) postlarvae through a South Carolina (USA) inlet. *J. Plankton Res.* 20: 2333-2356.

West, T.L. & Costlow, J.D. 1988. Determinants of the larval molting pattern of the crustacean *Balanus eburneus* Gould (Cirripedia: Thoracica). *J. Exp. Zool.* 248: 33-44.

Westwood, J.O. 1835. On the supposed existence of metamorphosis in the Crustacea. *Phil. Trans. R. Soc.* 125: 311-328.

Whitney, J.C. 1970. Absence of sterol biosynthesis in the blue crab *Callinectes sapidus* Rathbun and the barnacle *Balanus nubilus* Darwin. *J. Exp. Mar. Biol. Ecol.* 4: 229-237.

Wickham, D.E. 1979. The relationship between megalopae of the Dungeness crab, *Cancer magister,* and hydroid, *Velella velella,* and its influence on abundance estimates of *C. magister* megalopae. *Calif. Fish Game* 65: 184-186.

Wienberg, R. 1982. Studies on the influence of temperature, salinity, light, and feeding rate on laboratory reared larvae of deep sea shrimp, *Pandalus borealis* Krøyer 1838. *Meeresforschung* 29: 136-153.

Wiese, K., Krenz, W.D., Tautz, J., Reichert, H. & Mulloney, B. (eds) 1990. *Frontiers in Crustacean Neurobiology, Advances in Life Sciences.* Basel: Birkhäuser.

Wieser, W. 1986. *Bioenergetik. Energietransformationen bei Organismen.* Stuttgart: Georg Thieme.

Wieser, W. 1994. Cost of growth in cells and organisms: general rules and comparative aspects. *Biol. Rev.* 68: 1-33.

Wilhelm, G. & Mialhe, E. 1996. Dinoflagellate infection associated with the decline of *Necora puber* crab populations in France. *Dis. Aquat. Org.* 26: 213-219.

Willführ-Nast, J., Rosenthal, H., Udo, P.J. & Nast, F. 1993. Laboratory cultivation and experimental studies of salinity effects on larval development in the African river prawn *Macrobrachium vollenhovenii* (Decapoda, Palaemonidae). *Aquat. Living Resour.* 6: 115-137.

Williams, A.B. 1993. Reflections on crab research in North America since 1758. In: Truesdale, F. (ed), *Crustacean Issues 8*; *History of Carcinology*: 259-273. Rotterdam: Balkema.

Williams, A.J. & Lutz, P.L. 1975. Blood cell types in *Carcinus maenas* and their physiological role. *J. Mar. Biol. Ass. U.K.* 55: 671-674.

Williams, B.G. 1968. Laboratory rearing of the larval stages of *Carcinus maenas* (L.) (Crustacea: Decapoda). *J. Nat. Hist.* 2: 121-126.

Williams, B.G. 1980. The pelagic and benthic phases of post-metamorphic *Munida gregaria* (Fabricius) (Decapoda, Anomura). *J. Exp. Mar. Biol. Ecol.* 42: 125-141.

Williams, R. & Collins, N.R. 1986. Seasonal composition of meroplankton and holoplankton in the Bristol Channel. *Mar. Biol.* 92: 93-101.

Williamson, D.I. 1960. Crustacea Decapoda: Larvae. VII. Caridea, Family Crangonidae. Stenopodidea. *Fich. Ident. Zooplankton* 90: 1-5.

Williamson, D.I. 1969. Names of larvae in the Decapoda and Euphausiacea. *Crustaceana* 16: 210-213.

Williamson, D.I. 1974. Larval characters and the origin of crabs (Crustacea, Decapoda, Brachyura). *Thalassia Jugoslavica* 10: 401-414.

Williamson, D.I. 1976. Larvae of Stenopodidea (Crustacea, Decapoda) from the Indian Ocean. *J. Nat. Hist.* 10 (5): 497-509.

Williamson, D.I. 1982. Larval morphology and diversity. In: Abele, L.G. (ed), *The Biology of Crustacea 2*; *Embryology, Morphology and Genetics*: 43-110. New York: Academic Press.

Williamson, D.I. 1988. Evolutionary trends in larval form. In: Fincham, A.A. & Rainbow, P.S. (eds), *Aspects of Decapod Crustacean Biology, Symp. Zool. Soc. Lond. 59*: 11-25. Oxford: Clarendon Press.

Williamson, D.I. 1998. Larval transfer in evolution. In: Syvanen, M. & Kado, C.I. (eds), *Horizontal Gene Transfer*: 436-453. London: Chapman & Hall.

Williamson, D.I. & Rice, A.L. 1996. Larval evolution in the Crustacea. *Crustaceana* 69: 267-287.

Williamson, H.C. 1915. Crustacea Decapoda. Larven. *Nordisches Plankton* 18: 315-588.

Willig, A. & Keller, R. 1973. Molting hormone content, cuticle growth and gastrolith growth in the molt cycle of the crayfish *Orconectes limosus*. *J. Comp. Physiol.* 86: 377-388.

Wilson, E.O. 1975. *Sociobiology.* Cambridge, Mass.: Belnap Press of Harvard University Press.

Winberg, G.G. 1971. *Methods for the estimation of production of aquatic animals.* London: Academic Press.

Winemiller, K.O. & Rose, K.A. 1993. Why do most fish produce so many tiny offspring? *Am. Nat.* 142: 585-603.

Wolcott, D.L. & de Vries, M.C. 1994. Offshore megalopae of *Callinectes sapidus:* depth of collection, molt stage and response to estuarine cues. *Mar. Ecol. Prog. Ser.*109: 157-163.

Wollebaek, A. 1906. Le développement du genre *Sclerocrangon*, G.O. Sars. *Bergens Mus. Aarb.* 11: 1-9.

Wolvekamp, H.P. & Waterman, T.H. 1960. Respiration. In: Waterman, T.H. (ed), *The Physiology of Crustacea 1*; *Metabolism and growth*: 35-100. New York: Academic Press.

Wong, C.K., Chu, K.H., Tang, K.W., Tam, T.W. & Wong, L.J. 1993. Effects of chromium, copper and nickel on survival and feeding behaviour of *Metapenaeus ensis* larvae and postlarvae (Decapoda: Penaeidae). *Mar. Environ. Res.* 36: 63-78.

Wong, C.K., Yuen, Y.P. & Chu, K.H. 1989. Feeding rate during the larval development of the shrimp *Metapenaeus ensis*. *Mar. Behav. Physiol.* 15: 243-253.

Wong, J.T.Y. 1989. Abbreviated larval development of *Macrobrachium hainanense* (Parisi, 1919) reared in the laboratory (Decapoda, Caridea, Palaemonidae). *Crustaceana* 56: 18-30.

Woollacott, R.M., Pechenik, J.A. & Imbalzano, K.M. 1989. Effects of duration of larval swimming period on early colony development in *Bugula stolonifera* (Bryozoa, Cheilostomata). *Mar. Biol.* 102 (1): 57-63.

Wouters, R., Gómez, L., Lavens, P. & Calderón, J. 1999. Feeding enriched *Artemia* biomass to *Penaeus vannamei* broodstock: Its effect on reproductive performance and larval quality. *J. Shellfish Res.* 18 (2): 651-656.

Wübben, D.L. 2000. UV-induced mortality of zoea I larvae of brown shrimp *Crangon crangon* (Linnaeus, 1758). *J. Plankton Res.* 22: 2095-2104.

Wyllie, A.H., Kerr, J.F.R. & Currie, A.R. 1980. Cell death: the significance of apoptosis. *Int. Rev. Cytol.* 68: 251-306.

Xie, L. & Eggleston, D.B. 1999. Computer simulations of wind-induced estuarine circulation patterns and estuary-shelf exchange processes: the potential role of wind forcing on larval transport. *Est. Coast. Shelf Sci.* 49: 221-234.

Yagi, H., Ceccaldi, H.J. & Gaudy, R. 1990. Combined influence of temperature and salinity on oxygen consumption of the larvae of the pink shrimp, *Palaemon serratus* (Pennant) (Crustacea, Decapoda, Palaemonidae). *Aquaculture* 86: 77-92.

Yamamoto, H., Okino, T., Yoshimura, E., Tachibana, A., Shimizu, K. & Fusetani, N. 1997. Methyl farnesoate induces larval metamorphosis of the barnacle, *Balanus amphitrite* via protein kinase C activation. *J. Exp. Zool.* 278: 349-355.

Yamamoto, H., Shimizu, K., Tachibana, A. & Fusetani, N. 1999. Roles of dopamine and serotonin in larval attachment of the barnacle, *Balanus amphitrite*. *J. Exp. Zool.* 284 (7): 746-758.

Yamaoka, L.H. & Scheer, B.T. 1970. Chemistry of growth in crustaceans. In: Florkin, M.J. & Scheer, B.T. (eds), *Chemical Zoology 5*; *Arthropoda*: 321-341.

Yasunobu, H., Nagayama, H., Nakamura, K. & Hatai, K. 1997. Prevention of a fungal infection in the swimming crab *Portunus trituberculatus* larvae by high pH of rearing water. *Nippon Suisan Gakk.* 63 (1): 56-63.

Young, C.M. 1990. Larval ecology of marine invertebrates: a sesquicentennial history. *Ophelia* 32 (1-2): 1-48.

Young, C.M. 1995. Behavior and locomotion during the dispersal phase of larval life. In: McEdward, L.R.; *Ecology of Marine Invertebrate Larvae*: 249-277. Boca Raton: CRC Press.

Young, C.M. & Chia, F.S. 1981. Laboratory evidence for delay of larval settlement in response to a dominant competitor. *Int. J. Inver. Rep. Dev.* 3 (4): 221-226.

Young, C.M. & Chia, F.S. 1985. An experimental test of shadow response function in ascidian tadpoles. *J. Exp. Mar. Biol. Ecol.* 85 (2): 165-175.

Youngbluth, M.J. 1982. Utilization of a fecal mass as food by the pelagic mysis larva of the penaeid shrimp *Solenocera atlantidis*. *Mar. Biol.* 66: 47-51.

Yudin, A.I., Diener, R.A., Clark, W.H. & Chang, E.S. 1980. Mandibular gland of the blue crab, *Callinectes sapidus*. *Biol. Bull.* 159: 760-772.

Yufera, M. & Rodriguez, A. 1985a. Feeding rates and growth of *Palaemonetes varians* (Crustacea, Palaemonidae) during the larval development. *Investigación Pesquera* 49 (4): 597-606.

Yúfera, M. & Rodríguez, A. 1985b. Effect of prey density on feeding rates during larval rearing of *Palaemon serratus* Pennant (Crustacea: Palaemonidae). *Aquaculture* 50: 31-38.

Yúfera, M., Rodríguez, A. & Lubián, L.M. 1984. Zooplankton ingestion and feeding behaviour of *Penaeus kerathurus* larvae reared in the laboratory. *Aquaculture* 42: 217-224.

Zafran, J.F., Roza, D., Koesharyani, I. & Hatai, K. 1998. Increased survival of *Penaeus monodon* larvae treated with *Vibrio harveyi* bacterin. *Fish. Pathol.* 33: 449-450.

Zanders, I.P. & Rodríguez, J.M. 1992. Effects of temperature and salinity stress on osmoionic regulation in adults and on oxygen consumption in larvae and adults of *Macrobrachium amazonicum* (Decapoda, Palaemonidae). *Comp. Biochem. Phys. A.* 101A: 505-509.

Zang, W., Dai, X., Zhang, J. & Zhu, Z. 1995. Effects of Mg^{2+}, Ca^{2+}, and Mg^{2+}/Ca^{2+}, contents on survival rates of *Macrobrachium rosenbergii* larvae reared in mixed water. *Oceanologia Et Limnologia Sinica* 26 (5): 552-557.

Zeleny, C. 1905. Compensatory regulation. *J. Exp. Zool.* 2: 1-102.

Zeng, C.S. & Naylor, E. 1996a. Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas*: implications for ebb tide offshore dispersal. *Mar. Ecol. Prog. Ser.*132: 71-82.

Zeng, C.S. & Naylor, E. 1996b. Heritability of circatidal vertical migration rhythms in zoea larvae of the crab *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.* 202: 239-257.

Zeng, C.S. & Naylor, E. 1996c. Occurrence in coastal waters and endogenous tidal swimming rhythms of late megalopae of the shore crab *Carcinus maenas:* implications for onshore recruitment. *Mar. Ecol. Prog. Ser.*136: 69-79.

Zeng, C.S. & Naylor, E. 1996d. Synchronization of endogenous tidal vertical migration rhythms in laboratory-hatched larvae of the crab *Carcinus maenas*. *J. Exp. Mar. Biol. Ecol.* 198: 269-289.

Zeng, C.S. & Naylor, E. 1997. Rhythms of larval release in the shore crab *Carcinus maenas* (Decapoda: Brachyura). *J. Mar. Biol. Assoc. Uk.* 77: 451-461.

Zeng, C.S., Naylor, E. & Abelló, P. 1997. Endogenous control of timing of metamorphosis in megalopae of the shore crab *Carcinus maenas*. *Mar. Biol.* 128 (2): 299-305.

Zeuthen, E. 1953. Oxygen uptake as related to body size in organisms. *Q. Rev. Biol.* 28: 1-12.

Zhang, D., Lin, J.D. & Creswell, R.L. 1998a. Effects of food and temperature on survival and development in the peppermint shrimp *Lysmata wurdemanni*. *J. World Aquacult. Soc.* 29: 471-476.

Zhang, D., Lin, J.D. & Creswell, R.L. 1998b. Ingestion rate and feeding behavior of the peppermint shrimp *Lysmata wurdemanni* on *Artemia* nauplii. *J. World Aquacult. Soc.* 29: 97-103.

Zhao, J.-H., Guo, J.Y. & Lam, T.J. 1998. Lethal doses of ammonia on the late stage larvae of Chinese mitten-handed crab, *Eriocheir sinensis* (H.Milne Edwards), (Decapoda: Grapsidae) reared in the laboratory. *Aquac. Res.* 29: 635-642.

Zimmer-Faust, R.K. & Tamburri, M.N. 1994. Chemical identity and ecological implications of a waterborne, larval settlement cue. *Limnol. Oceanogr.* 93: 1075-1087.

Zimmermann-Ruf, C. 1997. Larvalentwicklung von *Armases miersii* (Rathbun 1897). Eine morphologische Betrachtung. M. Sc. Thesis, Universität Heidelberg, Germany, 70 pp.

INDEX