Chapter 1
# Special Considerations of Fish Eggs and Larvae

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1.1   Introduction

Fishery science attempts to understand the dynamics of fish populations with the goal of optimizing some human benefit or value, such as the yield to a commercial fishery, hours of pleasurable angling, or conservation of a species, population, or ecological community. Virtually all management goals center on adult fishes and so the traditional tools of fishery science were forged in an understanding of the biology and ecology of adult fishes. The critical role that early life stages play in the dynamics of fish populations is easily recognized when we consider that every fish taken by commercial trawlers and long-liners, each trophy fish landed by the patient and skilled angler, and all of the spawners in the relic population of an endangered species were, at one time, inconspicuous embryos and larvae, and that only a tiny fraction of their cohort survived the first few months of life. With this realization it becomes clear that fishery science demands a broader understanding of fishes, one that encompasses the early life stages.

This chapter highlights some of the important differences between early life stages of fishes and the more familiar juveniles and adults. It provides a general introduction to the developmental changes that take place during early life and some of the ways in which early life-history traits are interrelated. A comprehensive description of all developmental changes or the breadth of variation among species is beyond the scope of this chapter. Rather, the intent is to impart an appreciation that morphology cannot be considered static during this period of life. With this dynamic morphology comes continually changing behavioral and physiological capabilities which alter the nature of a young fish's ecological interactions. Recognizing the fundamental differences between the life of an embryo or larva and that of an adult is a first step toward appreciating the unique contributions of early life stages to fishery science.

## 1.2   The life cycle and the nature of early life

The life history of a fish can be divided into five primary periods: embryo, larva, juvenile, adult, and senescent. The first four of these form a cycle and only those individuals that are especially adept at survival, or just lucky, become senescent (Figure 1.1). Each of these life-history periods can be characterized by one or two dominant physiological processes that
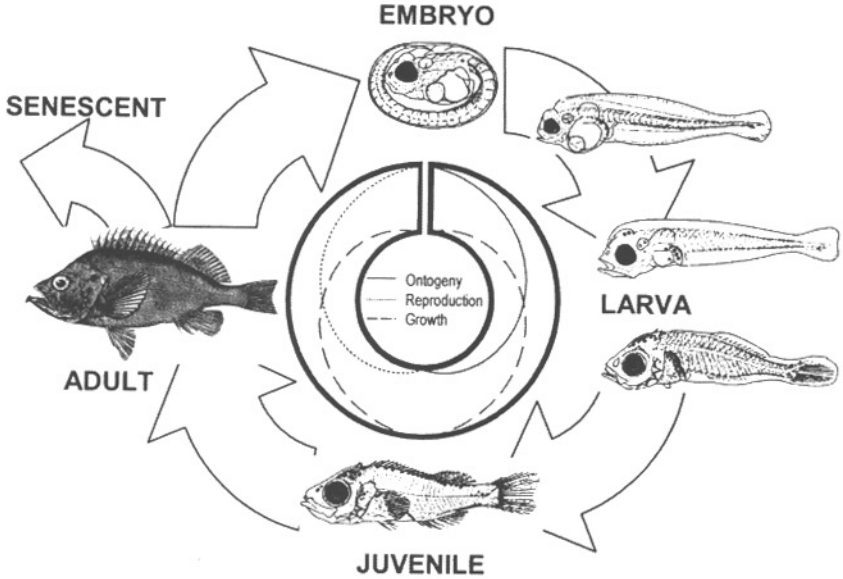
Figure 1.1   Generalized life cycle of a fish, using *Sebastes marinus* as an example. Major periods and the corresponding dominant intrinsic processes are shown. The circular chart at the center shows that ontogenetic changes (solid line) begin at fertilization of the egg and gradually diminish toward the juvenile period. Growth (dashed line) also begins at fertilization and diminishes toward adulthood. Reproduction (dotted line) begins when gonads differentiate and diminishes in senescence. Drawings from Bigelow & Welsh (1925).

largely determine the changes in morphological structure, physiological capabilities, behavioral motivation, and ecological role of an individual at that time of life. The embryonic period is a time of ontogeny, a complex set of changes that include rapid proliferation of cells, differentiation of new tissues, and reorganization or loss of existing ones. Since the embryo receives all of its energy from the maternal investment of yolk, the total weight of the embryo does not increase (it may actually decrease). This apparent lack of growth, as measured by total weight, disguises the conversion of yolk into new metabolically active biomass. In contrast, growth is the dominant process during the juvenile period. At the onset of the juvenile period, nearly all organs are present and the fish has the appearance of a small adult. Growth during the juvenile period can increase a fish's dry weight 1000–1 000 000 times, while differentiation is mostly confined to the reproductive organs. Between the embryonic and juvenile periods is the larval period, an especially dynamic interval when ontogeny continues and biomass begins to increase, sometimes by a factor of 10–1000 (Figure 1.2). Together, growth and ontogeny bring about major changes in structure and function over a brief span of time. Reproduction is the dominant process of the adult period. Growth continues at a reduced rate or ceases altogether. The post-reproductive senescent period is characterized by degeneration, which takes the form of reduced growth rate and spawning frequency, changes in external appearance, and endocrine dysfunction.

The embryonic and larval periods have important ecological and evolutionary functions. For many species, they represent an effective means of dispersal that can extend the range of a population and mix the gene pool. This is accomplished passively in species that have
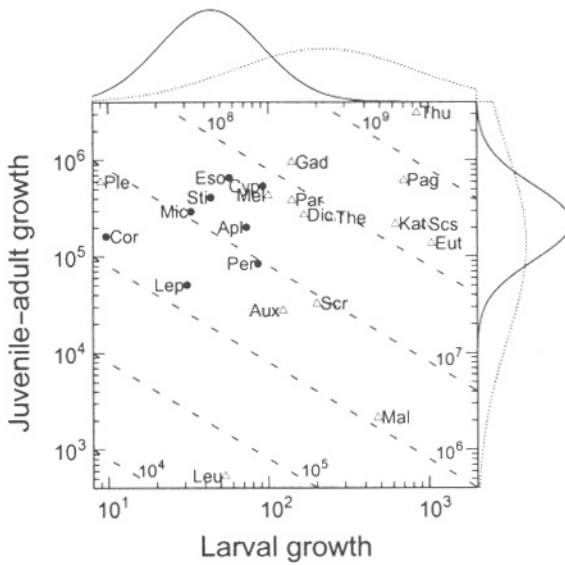
Figure 1.2 Biomass increase during major periods of the life cycle. The dry weight of larvae increases by one to three orders of magnitude before metamorphosis and three to six orders of magnitude after metamorphosis. Dashed lines show lifetime growth, expressed as a multiple of egg dry weight. Data points identify means for genera, based on 38 species in 23 genera from 14 families. Filled symbols represent freshwater species; open symbols are marine species. Abbreviations for genera are: Apl, *Aplodinotus*; Aux, *Auxis*; Cor, *Coregonus*; Cyp, *Cyprinus*; Dic, *Dicentrarchus*; Eso, *Esox*; Eut, *Euthynnus*; Gad, *Gadus*; Kat, *Katsuwonus*; Lep, *Lepomis*; Leu, *Leuresthes*; Mal, *Mallotus*; Mel, *Melanogrammus*; Mic, *Micropterus*; Pag, *Pagrus*; Par, *Paralichthys*; Per, *Perca*; Ple, *Pleuronectes*; Scr, *Scomber*; Scs, *Scomberomorus*; Sti, *Stizostedion*; The, *Theragra*; Thu, *Thunnus*.

nearly neutrally buoyant, planktonic eggs and early larvae, such as most marine fishes. Even the more robust larvae of freshwater species are feeble swimmers in comparison to the water movements of streams and rivers. This is not to say that dispersal is entirely passive. There are many examples of embryos or larvae timing their exposure to dispersing currents, such as using light intensity to initiate hatching from eggs in a nest, synchronous emergence of larvae from the gravel of a stream bed, or swimming vertically to achieve tidal stream transport. Lacustrine fish larvae often migrate actively from incubation sites along the shore out to the limnetic zone, and the later larval stages of coral reef fishes can swim across currents toward reef habitats.

The early life stages of fishes are sometimes referred to as ichthyoplankton and are typically considered inert particles. While this approach is convenient for examining large scale physical processes, such as oceanographic currents, it is a mistake to dismiss fish larvae as passive animals or to consider their ecology simple or unimportant. They are interactive components of the ecosystem. They can, for example, temporarily reduce local zooplankton populations so that the potential for competition for food is heightened (see Chapter 8). With the exception of reproduction, they face the same challenges that adult fishes experience. These challenges are made more severe by the larva's small size, incomplete state of development, and the fact that their size, structure, and behavioral and physiological capabilities are changing rapidly as they attempt to survive. It is no wonder that mortality to the

juvenile period usually exceeds 95%. In Chapter 3, we will see that high mortality during early life combined with high fecundity has an important consequence for understanding fish populations. Specifically, very small changes in survivorship of larvae can translate into very large variations in adult population size. Much of the research on early life stages of fishes has been motivated by this recognition that year-class strength may be determined during early life. A history of this thinking is presented in Chapter 4.

1.3   Developmental traits and patterns

1.3.1   Do fishes really have larvae?

The *Oxford English Dictionary* defines *larva* (plural: *larvae*) as:

> *"an insect in the grub state, that is, from the time of its leaving the egg till its transformation into a pupa; applied to the early immature form of animals of other classes, when the development to maturity involves some sort of metamorphosis."*

Our question now involves metamorphosis, which is defined as:

> *"change of form in animals and plants, or their parts, during life … ; especially in entomology, a change or one of a series of changes which a metabolous insect undergoes, resulting in complete alteration of form and habit."*

Whether fishes have larvae hinges upon the presence of a "complete alteration of form and habit." There are no known fishes that have a post-hatching stage analogous to the insect pupa, during which both form and habit change so dramatically and apparently abruptly. Rather, metamorphosis in fishes is more like that of amphibians, a gradual change in form. When changes in habit occur at metamorphosis, they are more subtle than the transition from an aquatic to a terrestrial existence in amphibians. Figure 1.3 shows clearly that fish larvae are quite different from their adult counterparts.

In practice, the completion of metamorphosis defines the boundary between the larval and juvenile periods and is determined on the basis of outward appearance (but see Box 1.1). Many species with pelagic larvae undergo a relatively subtle change in habit or habitat as metamorphosis finishes, such as leaving the plankton to become associated with a substrate (coral, rock, or bivalve reefs or vegetation). Settlement is sometimes used as a synonym for metamorphosis, even though these two terms refer to different changes, one a change in habit, the other a change in form. Despite these more common habitat shifts, there are splendid examples of fishes with changes in form or habit that approach those of amphibians and even insects. One of the most familiar and impressive is the metamorphosis of flatfishes. Flatfish larvae are similar to other fish larvae in most ways (Figure 1.3t) until the end of the larval period when one eye migrates over the top of the head to the other side. At the same time, body pigmentation becomes asymmetrical, they begin to swim with a noticeable tilt, and finally take up a benthic habit. This transition is not abrupt, it takes many days to a few weeks. Other dramatic metamorphoses include the transformation of sea lampreys (*Petromyzon marinus*) from a benthic, filter-feeding ammocoetes larva to an adult ectoparasite of other fishes, and the transparent, ribbon-like leptocephalus larva

Freshwater larvae
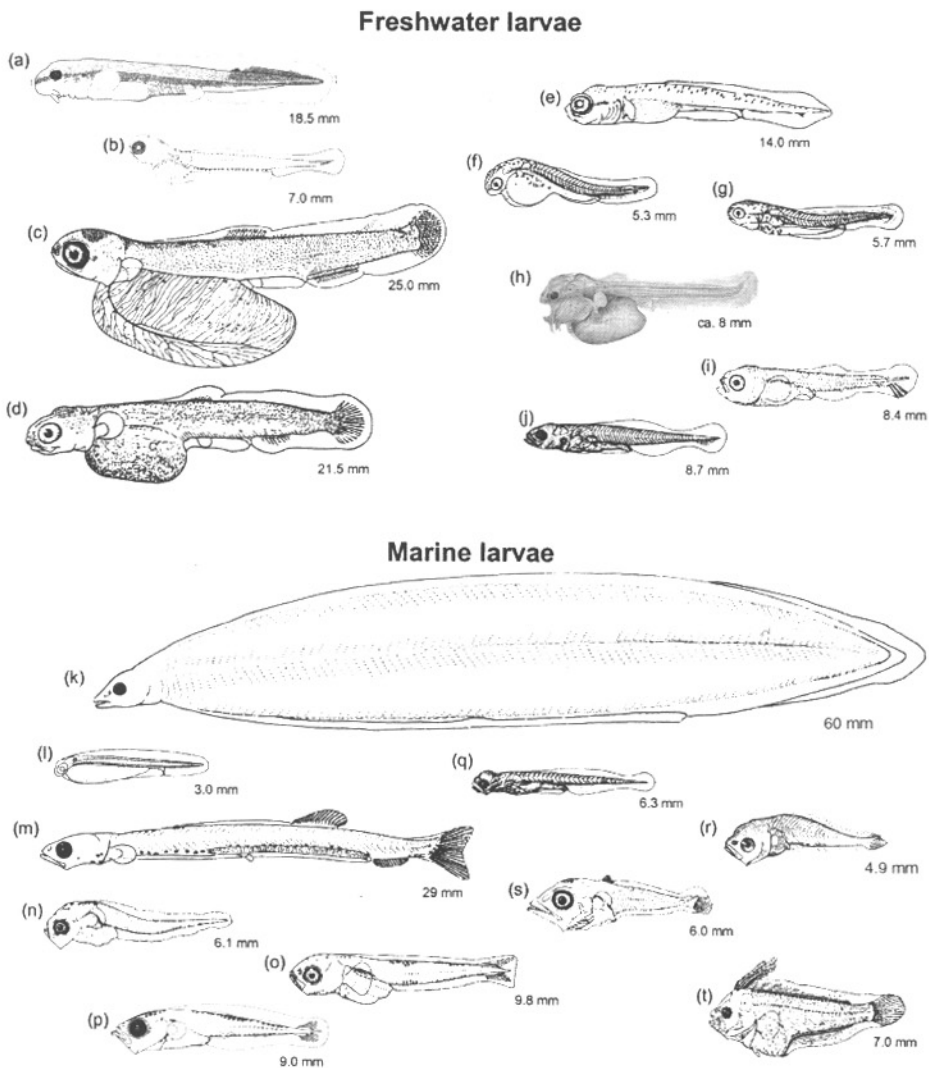
Marine larvae

Figure 1.3 Representative stages of larvae for selected species of freshwater and marine fishes. Sources are given in parentheses: (a) lake sturgeon, *Acipenser fulvescens* (Jude 1982); (b) bloater, *Coregonus hoyi* (Auer 1982); (c) chinook salmon, *Oncorhynchus tshawytscha* (Kendall & Behnke 1984); (d) lake trout, *Salvelinus namaycush* (Fish 1932); (e) northern pike, *Esox lucius* (Gihr 1957); (f, g) common carp, *Cyprinus carpio* (Nakamura 1969); (h) brown bullhead, *Ameiurus nebulosus* (Armstrong & Child 1962); (i) largemouth bass, *Micropterus salmoides* (Conner 1979); (j) yellow perch, *Perca flavescens* (Mansueti 1964); (k) American eel, *Anguilla rostrata* (Schmidt 1916); (l) Japanese anchovy, *Engraulis japonicus* (Mito 1961); (m) Atlantic herring, *Clupea harengus* (Ehrenbaum 1909); (n) haddock, *Melanogrammus aeglefinus* (Dunn & Matarese 1984); (o) walleye pollock, *Theragra chalcogramma* (Matarese *et al.* 1981); (p) Atlantic cod, *Gadus morhua* (Schmidt 1905); (q) striped bass, *Morone saxatilis* (Mansueti 1958); (r) Atlantic croaker, *Micropogonias undulatus* (Hildebrand & Cable 1930); (s) bluefin tuna, *Thunnus thynnus* (Collette *et al.* 1984); (t) California halibut, *Paralichthys californicus* (Ahlstrom *et al.* 1984). Drawings reproduced with permission of Great Lakes Fishery Commission (a, b), American Society of Ichthyologists and Herpetologists (c, n, s, t), Muséum d'Histoire Naturelle Genève (e), National Science Museum Tokyo (f, g), Syracuse University Press (h), Kyushu University (l), Estuarine Research Federation (q).

Box 1.1   Two metamorphoses?

The metamorphosis of fish larvae is considered a true vertebrate metamorphosis, like that of frogs and toads. There is, however, another type of metamorphosis that occurs in some fishes, such as lampreys, trouts, and freshwater eels. This so-called second metamorphosis takes place during the juvenile period. The changes brought about by the second metamorphosis are often associated with a diadromous migration. One of the most familiar examples of a second meta-morphosis is smoltification in salmonids, which prepares the freshwater parr for life at sea. Anguillid eels undergo a metamorphosis as they migrate into estuaries before undertaking their migration to oceanic spawning grounds. For the eels, the changes resulting from the second metamorphosis are much less dramatic than those that occur in the earlier transition from a leptocephalus larva to an elver.

  The presence of a larval period in a species implies a first metamorphosis because this is the process of changing from a larva to a juvenile. Species that lack a larva, those with direct development, have no first metamorphosis. Second metamorphosis is independent of first metamorphosis and, as such, is a second type of metamorphosis rather than the second in sequence. John Youson (1988) provided a thoughtful summary of fish metamorphoses.

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of eels (Figure 1.3k), tarpon, and bonefishes, which actually decrease in length by 10% or more during metamorphosis. So distinct are these larvae from their adult forms that the name *Leptocephalus* was originally used as the genus for these species.

  The presence of specialized structures that exist only during early life also supports the idea that fishes have larvae. Young larvae of some freshwater species (for example, pikes [Figure 1.3e], cyprinids [Figure 1.3f, g], characins) have adhesive organs on the head by which they attach to vegetation and other substrates. Marine larvae exhibit a particularly diverse array of temporary larval structures. Greatly elongated fin spines and rays are rela-tively common (for example, some flatfishes [see Figure 1.3t], sea basses, and goosefishes). Temporary head spines and plates can be so elaborate as to form a helmet (tilefishes, squirrelfishes, butterflyfishes) or a suit of armor (ocean sunfish). Some species have large, fluid-filled subdermal spaces that give the larva an inflated appearance (goosefishes). Especially fantastic are deep sea fish larvae that have trailing intestines or their eyes on stalks.

  These larval forms that have striking metamorphoses or ephemeral structures represent one extreme in a broad spectrum of developmental programs in fishes. At the other extreme are species with direct development, where the larval stage is greatly reduced or missing and most of their development occurs before they become free-living individuals. In these species, including such evolutionarily diverse groups as sharks and surfperches (Embiotocidae), most of the developmental changes take place inside large eggs or the par-ent, and the offspring is nourished through its period of ontogeny by a large yolk supply, some sort of maternal–fetal connection, or even siblicide. Although technically very differ-ent, mouthbrooding fishes, such as some catfishes and cichlids, are ecologically equivalent in that their embryos hatch into larvae but the larvae are retained in a parent's mouth often into the juvenile period. The vast majority of species have a developmental program some-where between these extremes, in which eggs incubate in the water and free-living larvae, which appear different from juveniles to varying degrees, change form, habit, or both as they grow.

1.3.2   Basic anatomy and development

Eggs

It is convenient in fishery science to refer to embryos as eggs. Because the actions of embryos are limited, most fishery-based investigations need not be directly concerned with the changes to the embryo that take place within the confines of the chorion. Substituting "egg" for "embryo," however, can lead to some confusion for those concerned with the production of eggs and the measurement of fecundity. A useful distinction can be made between ova or oocytes – internal, unfertilized cells in any stage of oogenesis – and eggs – ovulated cells after being expelled from the body and/or fertilized. These definitions do not cover all possibilities, but will suffice for many purposes of fishery science.

Fish eggs have a relatively small suite of permanent and distinctive features that can be used for identification. The most useful traits include: habit (for example, demersal, planktonic, encased in gelatinous material, in a nest, attached to vegetation or other substrate); overall size and shape; sculpturing or ornamentation of the chorion; width of the perivitelline space; amount, texture, and color of yolk; presence, number, and size of oil globules or droplets; and pigmentation on the body, yolk, or oil globules. These traits usually vary little within species or over the course of the incubation period. As ontogeny progresses, additional and more specific features appear that aid identification.

Most eggs are spherical with an apparently smooth chorion lacking ornamentation (Figure 1.4). Non-spherical eggs occur in diverse groups and may be ovoid (for example, anchovies, parrotfishes) to pear-shaped (gobies). The chorion of some species has obvious sculpturing but in others patterns can only be seen with the aid of scanning electron microscopy. Some species have threads, spikes, stalks, or other projections on the chorion that are used for attachment or to reduce their sinking rate. Eggs of bony fishes are generally between 0.7 and 7 mm in diameter. Oviparous sharks and rays have much larger eggs, each with a tough, leathery case and often with tendrils for attachment to the substrate. Within species of bony fishes, egg diameters vary by only a few tenths of a millimeter, some of which is due to maternal influences and some is due to environmental conditions, such as water hardness or salinity. Variations due to maternal investment are directly related to the size of the embryo and newly hatched larva, which can have important implications for survival as the larvae grow (see Chapters 3 and 4). Salinity and water hardness are inversely related to egg diameter by their influence on the width of the perivitelline space. The size of the embryo is not affected. Among species, the embryo (including yolk) may fill the chorion, leaving a negligible perivitelline space (Figure 1.4), or it may occupy as little as 50–60% of the egg diameter. Yolk commonly ranges from transparent and colorless to various degrees of translucent yellow, although greenish and reddish hues are known. Oil globules may be absent, numerous and small, or few and larger. They provide a final source of energy during the larval period, although they also provide a small degree of buoyancy. These characteristics of embryos do not vary much within a species.

Ontogeny begins with activation of the oocyte when sperm penetrates the chorion through the micropyle. Activation triggers delamination of the membrane that encloses the egg, dehiscence of cortical alveoli around the periphery of the yolk, and rapid uptake of water from the surrounding environment, resulting in the formation of the fluid-filled perivitelline space and a reduction in specific gravity of the egg (Figure 1.4). At the same
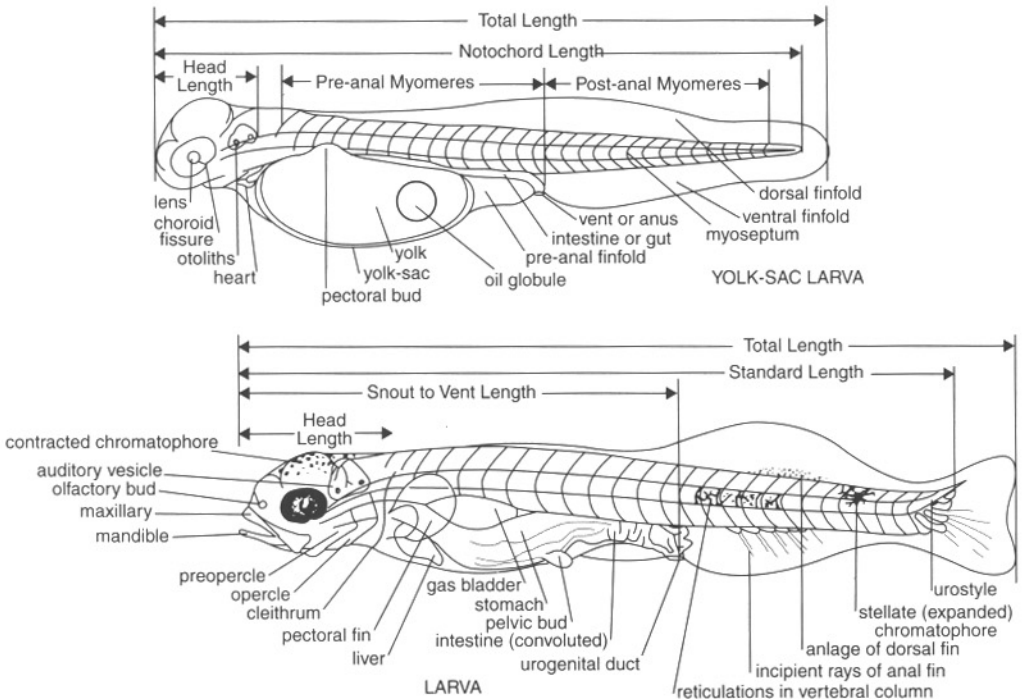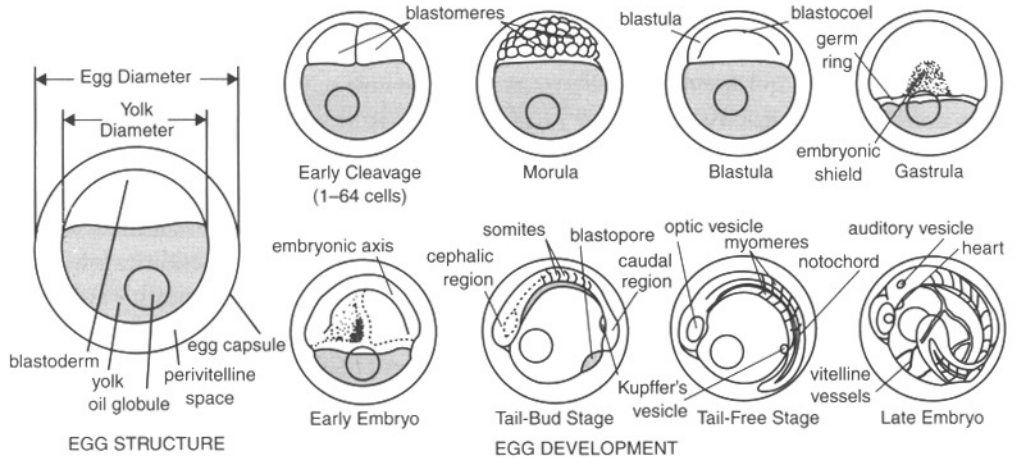
Figure 1.4 Anatomy of teleost embryos and larvae (from Hardy *et al.* 1978).

time, the micropyle closes to prevent polyspermy. These changes, which are sometimes referred to as "water-hardening," may take place even if fertilization fails to occur. Indeed, even some initial cleavages can occur in the absence of fertilization, making it difficult to distinguish fertilized and unfertilized eggs early in their development. The perivitelline space and hardened chorion provide a barrier for the embryo against some degree of mechanical and chemical damage.

Fertilization is the merging of nuclei from the egg and sperm and is required for full, normal development. The sequence of events follows the general scheme of vertebrate embryology: cleavage, morula, blastula, gastrula, neural crest, and so forth (Figure 1.4).

As the end of the embryonic period approaches, the fin folds, somites, heart, optic and auditory vesicles with otoliths, and chromatophores become apparent. The embryo increases in length to the point that it entirely surrounds the yolk, with its tail meeting or slightly overlapping its head.

Hatching results from the combined action of hatching enzymes (chorionase) that degrade the inner layer of the chorion and physical forces produced by the embryo's vigorous movements. Hatching enzymes are produced by clusters of unicellular hatching glands usually located on the head, anterior portion of the yolk sac, or pharyngeal region. Therefore, the embryonic or incubation period* ends only after these glands become functional and the appropriate trigger stimulates their secretions. Under normal conditions, hatching may be triggered when the embryo reaches a size where its metabolic demand for oxygen exceeds the rate at which oxygen diffuses across the chorion and perivitelline space. Indeed, hypoxia is one of the best-known triggers for hatching, whether it is brought about experimentally by reducing the oxygen concentration of the surrounding water, chemically inhibiting oxygen uptake of the embryo, or elevating the metabolic demand for oxygen. The reverse response has also been observed; hatching is delayed in hyperoxic conditions. Demersal eggs deposited in areas of reduced water flow may be at risk of suffocation, so accelerated hatching is adaptive because it frees the embryo to seek a more oxygen-rich environment. Interestingly, this response to reduced oxygen can be observed in species that are never likely to experience reduced oxygen levels, such as coral reef fishes that produce planktonic eggs.

Temperature, light, and pH also affect production and activity of hatching enzymes. In the few species studied experimentally, more hatching enzyme was produced, and it degraded the chorion faster, at warmer temperatures. Likewise, more eggs hatched during the light phase of a diel cycle than the dark phase, and hatching success was reduced under conditions of constant darkness. This response may require that a photoreceptive organ, such as the eye or pineal gland, be functional before hatching can occur unless the hatching gland cells respond directly to light or through a dermal light sense. In contrast, there are many species in which hatching naturally takes place in hours of darkness. This does not rule out the possibility that light, or lack of it, regulates production of hatching enzyme in those species as well. Finally, mechanical disturbance can accelerate hatching. This happens under laboratory conditions when a container of eggs at an advanced stage of development is transported. The cause of this response has not been examined, but it may be some degree of stress, like the other external agents that promote early hatching.

Delayed hatching is another adaptive response to environmental conditions. Several species deposit eggs out of the water and therefore out of reach of aquatic predators. For example, grunion (*Leuresthes tenuis*) and capelin (*Mallotus villosus*) deposit eggs at the high tide line so that the eggs spend much of the incubation period in moist sand or gravel. Other species, such as inanga (*Galaxias maculatus*) and the splashing tetra (*Copeina arnoldi*) attach eggs high on vegetation and other substrates that become exposed to air periodically. The chorion and perivitelline fluid protect the embryos from desiccation and collapse

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* The term "hatching period" is sometimes incorrectly used to refer to the incubation period. The hatching period is the span of time over which a batch of eggs hatches, from the first to the last. The incubation period extends from fertilization until hatching.

under their own weight in air, but hatched larvae have no such protection. The high oxygen tension while the eggs are in air probably reduces the production of hatching enzyme which would destroy the protective chorion. Such eggs do, however, hatch soon after they are reimmersed. Extremes of pH, both high and low, can also increase the incubation period by inhibiting the activity of hatching enzymes. This can have important consequences in poorly buffered freshwater systems (see Chapter 7).

Environmental conditions also regulate the rate of embryonic development and, therefore, the time it takes for hatching glands (and everything else) to appear. This has a more substantial impact on the incubation period than the minor adjustments caused by variations in the production or activity of hatching enzymes. Temperature, the most potent environmental regulator of fish physiology, follows a strong, negative relationship with incubation period. The precise relationship is species-specific and only roughly linear within the natural range of temperatures. Therefore, the product of temperature and the duration of incubation, usually expressed in units of day-degrees or degree-days, is roughly constant within a species and is a convenient tool for first approximations of the time from fertilization to hatching. The temperature term in the day-degree formulation sometimes incorporates a non-zero baseline or "biological zero," which is extrapolated from empirical data and usually assumes values less than 0°C. Over a broad range of temperatures, the relationship between incubation period (I) and temperature (T) is not linear (Figure 1.5). Several mathematical models have been applied, including the simple power function

$$I = \alpha \cdot T^{\beta} \tag{1.1}$$

where α and β are empirical constants.

Other environmental variables, including salinity, oxygen, and light, may also influence development rate. This is usually concluded from observations of effects on the incubation period, but in most cases the size and state of development at hatching are also affected.
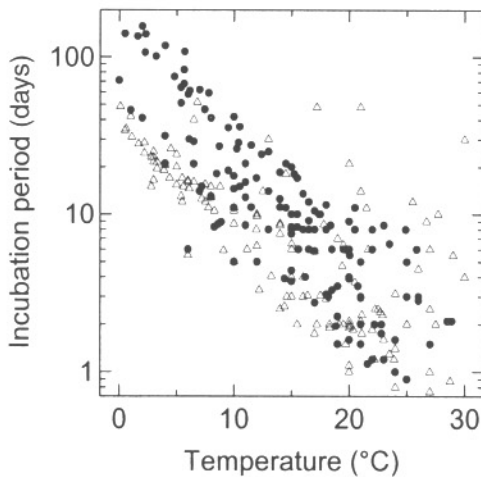
Figure 1.5   The effect of temperature on the duration of the incubation period of fish embryos. The relationship appears linear because the ordinate is logarithmic. Eggs deposited in freshwater (filled symbols) have longer incubation periods for a given temperature because they are larger. Data points represent 16 freshwater and 22 marine species.

For example, low salinity, low ambient oxygen, or high light intensity can result in a shorter incubation period and smaller, less developed larvae at hatching. It is possible that some portion of this response is due to the environmental effects on the activity of hatching glands, as described above, rather than the rate of development. Because environmental conditions can cause embryos to hatch at different stages of development, the duration of the incubation period is not a good measure of development rate. Regardless of the mechanism, the magnitude of the effects of salinity, oxygen, and light on incubation period is small in comparison to the effect of temperature.

There is a strong, species-specific component to the duration of the incubation period. Even at a fixed temperature, incubation periods vary greatly among species, sometimes more than they do within a species over the entire range of tolerable temperatures. For example, at 14°C, the incubation period for brook trout (*Salvelinus fontinalis*) is 30 days, for plaice (*Pleuronectes platessa*) it is 10 days, and for striped mullet (*Mugil cephalus*) it is 3–4 days. This interspecific variation in incubation period is highly correlated with egg size. Larger eggs have longer embryonic periods than smaller eggs. In the above example, the trout has the largest egg (4 mm diameter), followed by the plaice (2 mm) and mullet (1 mm). Although a species' egg size does vary among populations and individuals, the amount of intraspecific variation does not seem to have a large impact on the duration of the incubation period.

Larvae

Variation in the stage of development at hatching among species and in response to environmental conditions within species highlights an important, but unappreciated point: hatching is not strictly a developmental event; it is a physiologically regulated process that marks a major transition in the ecology of a fish. A larva emerging from an egg is able, for the first time, to move in space, to interact with biotic and abiotic components of the environment, and to actively influence its survival in varied ways. The ontogenetic changes that begin in the embryo continue after hatching so that additional physiological and behavioral capabilities accrue for some time. In addition to ontogenetic changes, the larva's size increases rapidly, with concomitant improvements in performance. Together, ontogeny and growth allow a larva's ecological interactions to become increasingly sophisticated and diverse.

The very small size and apparently featureless form of most fish larvae (Figure 1.3) is probably responsible for them being largely ignored by fishery scientists for so long. Identification of species or even genera is a difficult challenge that relies on taxonomic characters that are very different from those used on adult fishes. Newly hatched larvae can range in morphological complexity from very poorly developed animals that look scarcely fish-like, to nearly complete miniatures of the adult ("precocial" larvae; for example, in direct development). Identification becomes easier as development progresses and more distinctive features appear.

Larvae that are poorly developed at hatching, so-called "altricial" larvae, are usually only a few millimeters long and transparent (for example, Figure 1.3f, l). The large yolk sac, which still contains oil globules that were present in the embryo (although some may have coalesced), protrudes below the anterior half of the body. The larva's head may be bent

downward over the front of the yolk sac and attached to it. The eyes are formed but they lack pigment and therefore are not functional. Jaws are absent and there may not even be an oral opening. Gills may be absent, so the larva relies on cutaneous respiration facilitated by a circulatory plexus at one or more locations on the body surface, such as the yolk syncitium and bases of the future dorsal and anal fins. Bones, including vertebrae, are not ossified. Nearly all myomeres are formed; the few that may appear after hatching develop at the caudal end. A median fin fold fringes the body from a point on the mid-dorsal surface behind the head, around the urostyle, and anteriorly to the anus. A preanal fin fold extends forward from the anus. No fin rays are present and the caudal region of the median fin fold bears a superficial resemblance to the isocercal tail of some adult gadoid fishes because the urostyle is aligned with the rest of the notochord and the fin fold is symmetrical around it. Paired fins (pectoral and pelvic) are absent. Few, if any, chromatophores are present. Given this simple structure, identification is often based on general shape (length relative to depth), size at a given stage, position of the anus, numbers of myomeres, character of the yolk, and circumstantial data (location and date of collection, local fauna).

The preceding paragraph describes hatching at a very early stage of development. Many species progress somewhat beyond this point by the time they emerge from the egg and some will pass many of the subsequent stages as embryos. As ontogeny proceeds, the head separates from the yolk sac and aligns with the body axis. An opening forms at the mouth before the jaws appear. Gills begin to develop and paddle-shaped pectoral buds appear, although they lack fin rays. The yolk sac gradually diminishes but oil globules remain until all yolk has been absorbed when they, too, are metabolized. It is important to realize that larvae normally begin feeding before all yolk is absorbed. This is the period of mixed feeding. The stage of development when gas first appears in the swim bladder varies greatly among species. Once gas appears, the bladder remains inflated, although there may be a diel cycle in the volume of gas present.

Development of many ecologically important features, including fins, sense organs, skeleton, and external pigmentation, occurs gradually and over a large portion of the larval period. The caudal fin is often the first fin to show signs of differentiation when the urostyle, the final segment of the vertebral column, turns upward (shown in Figures 1.3r, s and 1.4). The term "flexion" is frequently used to refer to this stage of development. Soon afterward, hypural bones begin to form immediately below the upturned urostyle, and primordial fin rays appear as striations in the adjacent median fin fold. A slight constriction of the median fin fold develops in the region of the caudal peduncle as the outline of the median fins begins to take shape. Bony elements appear at the junction of the median fin fold and the body where the future dorsal and anal fins will be located, followed closely by their primordial fin rays. Rays are added to the fins sequentially, so that species that ultimately have a large number of rays in one or more fins take a long time to complete fin development. As the rays develop, sections of the median fin fold that lie between the final fins disappear and the margins of the median fins are refined. Meanwhile, the pectoral bud enlarges and begins to develop fin rays. Pelvic buds appear late as small outgrowths at the base of the preanal fin fold. This is a common sequence of fin development, but the sequence varies from species to species. Scales are among the last external features to be completed. They typically appear first on the sides of the caudal peduncle very late in the larval period and spread forward. Complete formation of fin rays is commonly used

to designate the end of the larval period and the beginning of the juvenile period (complete metamorphosis), however, complete squamation (coverage of scales) may be a more accurate endpoint. The late appearance of scales means that they cannot be used to age larvae as they are for adults (see Chapter 2) and it may account for the non-zero intercept observed in plots of scale radius on body length for juvenile and adult fishes.

Because of their critical role in survival, it is surprising that the sensory systems have such a prolonged period of development after hatching. A great many species hatch with poorly developed eyes. The eyeball and lens are formed but the retina lacks pigment to intercept light. Before all yolk and oil is absorbed, melanin forms in the eyes, making them very conspicuous black spots. When eyes reach this stage prior to hatching, as in some freshwater and anadromous species such as salmonids, the embryos are sometimes referred to as "eyed eggs." With very few known exceptions, the first photoreceptors to appear in the retina are cones. Their number increases rapidly, resulting in an increase in the number of cones per degree of visual angle. There is some evidence that a few rods may be present soon after hatching, but when present, their number remains low for most of the larval period. Rods typically begin rapid proliferation toward the end of the larval period. Developmental changes in visual system function will be described more thoroughly in Section 1.4.1. The lateral line system begins with a few neuromasts on the body surface in embryos. The number of these free or superficial neuromasts gradually increases throughout the larval period in specific patterns on the head and trunk. Lateral line canals begin to form very late. Development of the chemosensory system is not as well known. In the few species that have been studied, chemoreceptor cells in the nares appear to develop quickly. By the time of settlement in some reef fishes, the density of chemoreceptor cells is as high as in adults of many species.

Ossification of the skeleton progresses slowly. The outlines of some bones, such as the pectoral girdle and jaws, become visible relatively soon after hatching. Differential staining of cartilage and bone shows that most skeletal elements are cartilaginous when they first appear and that they become ossified later. Bones of the pectoral girdle, jaws, and gill arches calcify relatively early. Vertebral centra ossify later and more gradually, sometimes finishing after the fish has assumed a juvenile external appearance.

Pigmentation on the head and body surface generally increases during development. Melanophores are most obvious because they persist after fixation and storage in common preservatives. Chromatophores bearing more colorful pigments have been described, but only occasionally. Melanophores often spread over upward facing surfaces, such as the dorsal surface of the cranium and trunk. One can speculate that this arrangement may provide some degree of countershading while maintaining transparency along a horizontal line of sight, or it may shield sensitive tissues from ultraviolet radiation. By the time a larva approaches metamorphosis, its size has increased greatly making its body more opaque. Transparency is no longer an option for avoiding predators. Pigment extends onto the lateral body surfaces in species-specific patterns.

Differences in structure are not the only features that set larvae apart from juveniles and adults. Larvae have a different shape, which is often quantified in terms of body proportions. Eyes of larvae are relatively large, as they are in young of many other vertebrates. The head and tail are generally smaller proportions of total length than they are in adults. Species that are deep bodied as adults often have slender larvae. To reach adult proportions from these

initial sizes, various body parts must grow at different rates. This allometric growth is a distinctive feature of the larval period. Since juveniles have the adult appearance (shape), their growth is more or less isometric. Isometric growth maintains constant body proportions as all parts increase in size at the same rate. The transition to isometric growth is one criterion that has been used to signify completion of metamorphosis, although a careful analysis is required to determine when this transition occurs. Analyses of the pattern of relative growth (allometric and isometric) along the body of larvae show that there may be smooth growth gradients that are responsible for the orderly changes in shape that lead to metamorphosis.

1.3.3   Variety and patterns in early life history

Surveying the variety of egg and larval traits displayed by fishes brings to light some interesting and complicated relationships that tie early life-history traits to environmental characteristics, reproductive strategies, and population dynamics. These relationships are intertwined in such complex ways that cause and effect are difficult to distinguish. In addition, the trends are "noisy" and based on interspecific comparisons so that exceptions are not difficult to find. Nevertheless, these general relationships provide a useful context for understanding the diversity of early life-history traits and the ways in which early life stages are important to the practice of fishery science.

Egg size

The size and number of eggs produced, the duration of their incubation period, and their location in the environment vary tremendously among species and all of these traits have important consequences for survival. Egg size – principally weight and, secondarily, diameter (because of variations in the width of the perivitelline space) – is positively related to the duration of the incubation period and the size of the larva. The greater amount of yolk in large eggs provides more total energy for growth and ontogeny before the larva requires exogenous nutrition, resulting in larger larvae at hatching and at first feeding. This yields several vital benefits:

(1)   larvae emerge with a better repertoire of behavioral and physiological capabilities than less developed larvae from smaller eggs;
(2)   they are more resistant to starvation because weight-specific metabolic rates are lower and bodily energy stores are greater; and
(3)   the larval period is shorter.

One disadvantage of large eggs is that the embryonic period, during which they are unable to fend for themselves, is prolonged. Trade-offs involving egg size are discussed below (see *Patterns and strategies*) and the importance of larval stage duration to mortality and recruitment will be discussed more thoroughly in Chapters 3 and 4.

Planktonic vs. demersal

The broadest distinction between classes of fish eggs is whether they are planktonic or demersal, that is, where they occur in the environment. Demersal eggs that are not attached

to a substrate sink to the bottom because their low water content, which is generally between 55% and 85% of their wet weight, increases their specific gravity. By comparison, planktonic eggs have a very high water content (>90% of their wet weight), which makes them buoyant, or nearly so. The difference in water content can be seen in the high transparency and sometimes wide perivitelline space of planktonic eggs. The yolk of demersal eggs is optically more dense and the chorion may be thicker than that of planktonic eggs. Demersal eggs have a larger diameter than planktonic eggs, sometimes in excess of 15 mm. Planktonic eggs range from about 0.5 to 5.5 mm in diameter, but usually are 0.7–2.0 mm. This difference in size between planktonic and demersal eggs is amplified when the comparison is based on dry weight because the larger, fluid-filled perivitelline space of planktonic eggs is neglected.

Species that produce small eggs do not have the advantage of large, well-developed larvae at hatching. Rather, they improve their chances of having offspring survive by producing more eggs. Fecundity generally is inversely related to egg size, although it is constrained by adult body size and influenced by other factors, including age and diet of the female. As a result, fecundity in species with planktonic eggs can be $10^5–10^6$ eggs, whereas species with demersal eggs generally produce less than 10^5 eggs (one exception is large sturgeon, with a fecundity of almost 10^6 demersal eggs that average about 3.2–3.5 mm in diameter).

Species that produce planktonic eggs release them somewhere in the water column, rarely close to the substrate. This separates the eggs from benthic predators and facilitates their dispersion. Conversely, species with demersal eggs often spawn very close to a substrate so that their eggs are all in relatively close proximity to one another throughout the incubation period. Even species that scatter demersal eggs do so over a restricted area. Most demersal eggs receive some degree of protection from predators during the vulnerable embryonic period. This protection ranges from falling into interstices of a gravel bottom or being attached to vegetation to being deposited in a nest then abandoned or being guarded or carried by a parent. Planktonic eggs rely on transparency and perhaps dispersion itself for protection from predators.

Freshwater vs. marine

The distinction between demersal and planktonic eggs has an ecosystem component: planktonic eggs are almost exclusively found in the marine environment and freshwater fishes generally spawn demersal eggs. Accordingly, differences between freshwater and marine eggs and larvae (Table 1.1) parallel the differences between demersal and planktonic eggs. Marine fish eggs generally are smaller than freshwater eggs. Although the difference in modal diameter is not great, the distribution of egg diameters for freshwater species is strongly skewed toward larger eggs. Most freshwater species have eggs from 1.3 to 2.8 mm in diameter, and some are much larger. Eggs of most marine species are between 0.9 and 1.4 mm in diameter. The size difference is greater when expressed as dry weight because planktonic eggs, which have a higher water content, dominate in the marine environment. This difference in egg size accounts for the longer incubation periods of freshwater species at similar temperatures (Figure 1.5). Since embryos do not gain weight, the difference in egg weight can be seen in the 10-fold difference in the mean dry weight of larvae at hatching (Table 1.1). The larger freshwater larvae generally are at a more advanced state at

Table 1.1 Comparison of traits of freshwater and marine teleost fish eggs and larvae.

Early life-history trait	Freshwater	Marine
Egg diameter (median, mm)	1.70[a]	1.02[a]
Egg buoyancy	Mostly negative[a]	Mostly positive[a]
Incubation period (days)	10.9 ± 0.27[a]	7.0 ± 0.33[a]
Hatching length (median, mm)	5.40[a]	2.87[a]
Hatching dry weight (μg)	359.7 ± 72.8	37.6 ± 6.4
Metamorphic dry weight (mg)	9.3 ± 1.6	10.8 ± 0.95
Larval duration (days)	20.7 ± 1.1	36.1 ± 1.1
Metabolic rate ($\mu l\, O_2\, mg^{-1} h^{-1}$)	2.8 ± 0.4	5.9 ± 0.4
Ingestion rate ($\mu g\, \mu g^{-1} day^{-1}$)	0.46 ± 0.09	0.57 ± 0.07
Growth rate ($\mu g\, \mu g^{-1}\, day^{-1}$)	0.18 ± 0.02	0.20 ± 0.01
Growth efficiency	0.32 ± 0.03	0.29 ± 0.3
Instantaneous mortality (day^{-1})	0.16 ± 0.04	0.24 ± 0.02
Expected larval mortality (%)	94.7	99.9
Starvation risk	Lower	Higher
Larval mortality	Density-independent	Density-dependent
Stage for recruitment regulation	Juvenile period	Larval period
Recruitment variability	Lower	Higher

Values (means $\pm$ 1 SE, unless stated otherwise) are adjusted for differences in temperature, where appropriate. Data are from Houde (1994), except where indicated by superscript "a". Houde omitted salmonids, sturgeons, and ictalurid catfishes from calculations for freshwater fishes because of their unusually large, demersal eggs. Other calculations (with superscript "a") are based on data for 42 freshwater species from 21 families and 42 marine species from 34 families, derived from various published sources.

hatching. Metamorphosis is complete at about the same size in both environments. Therefore, the amount of growth and ontogeny that takes place between hatching and metamorphosis and the duration of the larval period are considerably greater for marine fishes. Calculations based on a sample of 22 species in 15 genera from six families show that marine larvae increase in dry weight between 130- and 660-fold during the larval period, whereas freshwater larvae (16 species, eight genera, six families) increase only by a factor of 30–80 (Figure 1.2). The average duration of the larval period in marine fishes (calculated from the increase in dry weight and temperature-adjusted growth rates) is 36 days compared to 21 days for freshwater fishes. These developmental differences are complemented by differences in the relative importance of density-dependent and density-independent mechanisms of mortality during the larval period, the time of life when recruitment is most strongly regulated and the potential for recruitment variability is greatest (Table 1.1, Chapter 3).

Parental care vs. independent offspring

Parental care of early life stages has obvious effects on the relationships outlined so far for demersal eggs. Fecundity is reduced and egg size is usually larger in species that provide a moderate or high degree of care for their eggs and larvae. The magnitude of these differences is directly related to the degree or duration of parental care. The majority of caregiving species produce large, yolky eggs that have all of the characteristics described for

such eggs: a long incubation period, large and precocial larvae at hatching, and a brief larval period. Some nest guarders, however, have small, highly transparent eggs that are attached to a substrate, and the eggs may even appear to be buoyant if not for their hold-fast. Although they are demersal, these are essentially attached planktonic eggs. They have a shorter incubation period and hatch as small, altricial larvae. Their parental care ceases at hatching and the larvae disperse from the nest into a long, planktonic phase before they settle and undergo metamorphosis. Examples are found among the damselfishes, gobies, blennies, and darters.

Patterns and strategies

One of the early attempts to understand this diversity in early life-history traits was formulated in the 1940s by Sergei Kryzhanovskii (also Kryzhanovsky) at the Research Institute of Morphogenesis at Moscow University. Kryzhanovskii recognized the importance of the embryonic and larval periods to adult populations and believed that two factors, predation mortality and oxygen availability, are of overriding importance to survival. He reasoned that the habitat in which eggs are released defines the respiratory conditions and predation potential for the early life stages and explains the diversity of eggs, larvae, and reproductive styles found in fishes. With extensive knowledge of the reproductive habits of many species, especially those in freshwaters, and the morphology and physiology of their eggs and larvae, he devised an ecological classification based on the spawning habitat and the degree of parental care provided. This system was expanded and renamed as a classification of reproductive guilds by Eugene Balon in 1975. Such ecological classifications are particularly useful for understanding the habitat requirements of early life stages, a matter we will discuss more thoroughly in Chapter 7.

Many early life-history traits vary in parallel with well known relationships among reproductive and demographic parameters, such as age at maturity, spawning frequency, fecundity, and survivorship, which have been interpreted in the context of evolutionary ecology. The traditional paradigm of *r*- and *K*-selection defines a two-sided continuum of strategies. On one side are species that are able to discover and quickly exploit resources that are unpredictable or ephemeral in space or time. Ideally, these so-called *r*-strategists are characterized by effective dispersal and a high rate of population increase (*r*). Most of the commercially important species of the oceans, with their high fecundities, small planktonic eggs, and altricial larvae, are nearer this end of the continuum. The food supply for their offspring is scattered in patches and the large number of propagules improves the chances of at least some offspring locating these patches. At the other extreme are *K*-strategists, species that are adept at competing for spatially and temporally stable resources. *K*-strategists typically have small batches of large eggs, precocial young, and are often provided parental care. Some fish species that tend toward this strategy are important to sport or subsistence fisheries and aquaculture, such as sharks, some catfishes (for example, *Clarias gariepinus, Ictalurus punctatus*) and tilapias (species of *Oreochromis, Sarotherodon, Tilapia*).

Analyses by Kirk Winemiller and his colleagues have expanded the traditional paradigm in a way that distinguishes three life-history strategies, rather than two. These strategies are defined by the relative magnitudes of fecundity, survivorship from fertilization until first reproduction, and age at maturity (Figure 1.6). The periodic strategy maximizes batch
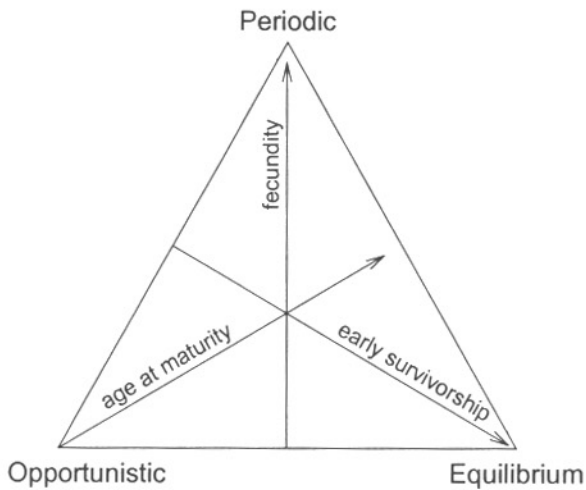
Figure 1.6 Adaptive surface of fish life-history strategies based on trade-offs among reproductive and demographic traits (after Winemiller & Rose 1992). The opportunistic strategy is typified by early maturity, which results in a shorter generation time but a smaller body size. This constrains fecundity and egg size, and reduces adult survivorship. The equilibrium strategy is marked by the high early survivorship achieved through large eggs and parental care. Larger eggs produce stronger, precocial larvae with a shorter larval stage duration. The high fecundity of the periodic strategy results in small eggs, poorly developed larvae, and a long larval stage, which reduces early survivorship.

fecundity but with costs in terms of delayed maturation and low and variable early survivorship. The reduced survivorship is a result of smaller, more altricial eggs and larvae that receive no parental care. This tactic functions well when resources, such as larval food supply, vary regularly (perhaps seasonally) or are distributed in large scale patches. The abundance of eggs or larvae is a poor predictor of future year-class strength for these species, and early life mortality plays a pivotal role in population dynamics. This is the dominant strategy among commercial fish stocks as well as some large tropical freshwater species, such as pacu (*Colossoma* sp.) and tigerfish (*Hydrocynus* sp.). The opportunistic strategy maximizes the rate of population increase by emphasizing early maturity and frequent spawning (that is, high reproductive effort). As a result of the smaller body size at maturity, fecundity is low, eggs are small (reflecting low early survivorship), and adult survivorship is also low. This strategy is favored when resources vary unpredictably on small temporal or spatial scales. These species, exemplified by anchovies, silversides, and a variety of small tropical freshwater species, can repopulate quickly after major disturbance to the environment. The third strategy, the equilibrium strategy, is much like the *K*-strategy of the traditional paradigm. It optimizes early survivorship through the production of a small number of large eggs, precocial offspring, and parental care. These species, including viviparous fishes and mouthbrooding cichlids, thrive in the presence of suitable habitat and stable environmental conditions.

1.3.4   Developmental progress and intervals

Early stages of several species appear so different from their familiar adult forms that upon their discovery they were assigned to their own genus. Some of these names are still used

Table 1.2 Modern intervals (roman text) for early stages of fishes and the criteria (italic text) used to separate them.

Balon (1975b)	Ahlstrom *et al.* (1976)	Snyder (1976)	Hardy (1978)
Eleutheroembryo *Yolk absorption*	Yolk-sac larva *Yolk absorption*	Protolarva *First median fin ray*	Yolk-sac larva *Yolk absorption*
Protopterygiolarva *First median fin rays*	Preflexion larva *Urostyle flexion*	Mesolarva *Adult median fin ray complement and pelvic buds or fins*	Larva *Adult fin ray complement*
Pterygiolarva	Flexion larva *Adult caudal fin ray complement* Postflexion larva	Metalarva	Prejuvenile

informally when referring to these distinctive forms (acronurus, ammocoetes, kasidoron, leptocephalus, querimana, tholichthys, vexillifer). Perhaps this is why there have been many attempts to divide the developmental period into discrete, named intervals. Or, maybe it is an extension of the practice of classical embryology to identify "normal stages." Regardless of its origins, the topic of terminologies for intervals of fish development continues to be controversial and there exists no single, widely accepted classification system. The principal value of these classification systems is to divide the range of ontogenetic variation into smaller, more tractable pieces for constructing taxonomic keys and other tools for identifying specimens. It is common to use one set of characters for distinguishing larvae during an early interval of development, then switch to a different set of characters to identify the same species later. One of the first widely used terminologies was developed for salmonids and included: egg, alevin, fry, fingerling, parr, smolt, adult, and kelt. These terms are still in use but are only applied to trouts and salmons. There are at least four modern terminologies for intervals of development (Table 1.2). Their popularity varies with geographic region of the investigator and ecological realm of the fish. A particularly ambiguous term that should be avoided at all costs is "postlarva."
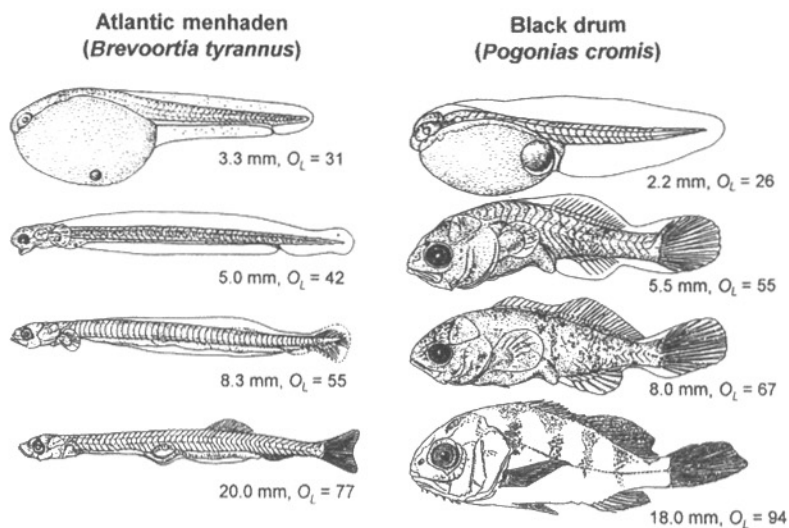
Outlining the fish life cycle at the start of this chapter (Figure 1.1) automatically created intervals: embryo, larva, juvenile, adult, and senescent. These are based on changes in the dominant physiological processes that define a fish's changing capabilities and requirements. The criteria dividing these categories – hatching, metamorphosis, maturation, and senescence – are significant life-history transitions. To be of importance to fishery science – as opposed to, say, embryology or developmental biology – further subdivision must reflect natural intervals in which ecological interactions take a new course. Most terminologies devised for fish development are based on morphological changes that were presumed to reflect changes in a fish's ecological role. The most common developmental milestones used in developmental classifications are hatching, yolk absorption, and fin development. There is no doubt that hatching is a major transition. It frees the larva to make effective behavioral responses to environmental stimuli. Yolk absorption, or more accurately the transition from endogenous to exogenous nutrition, is also a critical developmental and ecological transition

for a fish larva. Thus, the period between hatching and yolk absorption is ecologically distinct and the term "yolk-sac larva" is often applied (Table 1.2). Terminologies born out of classical embryology use yolk absorption as the criterion to separate the embryonic and larval periods, so that the term "embryo" applies long after hatching. This can cause some confusion for those unfamiliar with the differences among terminologies.

The fin-development criteria used in various systems include upward flexion of the urostyle, the first appearance of caudal fin rays, completion of median fins, and other traits. These milestones were selected with the expectation that they mark a new level of swimming performance. While this seems reasonable, subsequent studies of swimming performance in larvae have not shown distinct changes when these structures appear. This does not mean that the intervals defined by fin development are not useful, only that their contribution to understanding the ecological processes relevant to fishery science is limited. It can be argued that subdividing the larval period beyond recognizing yolk absorption is not necessary for a useful understanding of the role of eggs and larvae in population-level processes. The fact that developmental intervals more refined than egg, larva, and juvenile are rarely mentioned in subsequent chapters in this book supports this contention.

There are two schools of thought on the fundamental model for the time course of fish development. One view is that development is gradual, that changes accumulate continually, but not necessarily at a constant rate. The alternative view is that development is accomplished by periods of dramatic change in body structure and physiology, followed by longer intervals of little or no change. While the latter idea, proposed as "saltatory ontogeny" by Eugene Balon, is interesting, direct evidence is equivocal. Since fishery science is an especially quantitative endeavor, incorporating developmental trends into population models is easier if a larva's ontogenetic progress is expressed numerically on a continuous scale of measurement, rather than representing it as discrete, qualitative steps. Models that imply gradual development seem to produce reasonable results for purposes of fishery science.

Experimental studies and observations of field-caught larvae show that the appearance of specific structures and levels of performance during the development of a species are more closely tied to the size of a larva than its age or other convenient measures of "biological time." The importance of this observation cannot be overstated. Experimentalists, working with larval fishes under controlled environmental conditions, often use age as a means of identifying a larva's developmental progress. Comparisons based on age are only valid under identical environmental conditions. Size, on the other hand, integrates a larva's environmental experience, whether constant or fluctuating, and it is much easier to measure on field-caught larvae than age. Thus, size is a useful measure of developmental state, but what about the progress of development? Development follows a logarithmic progression with respect to body size. The rate of developmental change is most rapid early and continually slows toward metamorphosis. For example, a 2-mm difference in length of larvae soon after hatching represents a greater change in form and function than a 2-mm difference in length near metamorphosis. Therefore, a logarithmic scale of length appears to be an appropriate, if not convenient, scale for development within a species. Because species differ in the size of their larvae at comparable stages of development, it is necessary to adjust the logarithmic scale accordingly when it is desirable to compare species. This can be done simply by scaling a species' developmental period to one logarithmic cycle

Atlantic menhaden
(Brevoortia tyrannus)

3.3 mm, O_L = 31

5.0 mm, O_L = 42

8.3 mm, O_L = 55

20.0 mm, O_L = 77

Black drum
(Pogonias cromis)

2.2 mm, O_L = 26

5.5 mm, O_L = 55

8.0 mm, O_L = 67

18.0 mm, O_L = 94

Figure 1.7 Selected larval stages of a clupeid and a sciaenid demonstrating a two-fold difference in length at comparable stages of development. The ontogenetic index, O_L, adjusts for these differences (from Fuiman & Higgs 1997, drawings from Joseph *et al.* 1964 and Mansueti & Hardy 1967, reproduced with permission of Kluwer Academic Publishers, American Society of Ichthyologists and Herpetologists, and University of Maryland).

so that metamorphosis always assumes a value of 1.0 or 100%. Mathematically, this is accomplished by selecting a logarithm base equal to the species' size at metamorphosis, or equivalently:

$$O_L = \frac{\log L}{\log L_{\text{juv}}} \tag{1.2}$$

where O_L is the ontogenetic index, a numerical representation of the ontogenetic state of a larva of length L, and L_{juv} is the length at which that species completes metamorphosis. This results in a continuous measurement scale that assigns similar numerical values to individuals of different species but similar developmental state. For example, Atlantic menhaden (*Brevoortia tyrannus*) are roughly twice as long as black drum (*Pogonias cromis*) at comparable stages of development. This includes metamorphosis (complete squamation) at lengths of approximately 45 and 22 mm, respectively. Using the ontogenetic index, their similar poorly developed state at hatching takes on values of 31% and 26%, respectively. Their median fins are complete at about 79% and 71%, respectively (Figure 1.7). This quantitative scale for ontogeny is new and has proven useful when it has been applied.

1.4   Development and performance

Survival of individuals at any stage of life requires adequate levels of performance against a variety of ecological challenges, such as obtaining food, evading predators, and locating and

remaining in a suitable habitat. Meeting these challenges is especially difficult during early life because eggs and larvae are so small and incompletely developed, and body size and structure determine performance levels. Ontogeny and growth, the defining processes during early life, make this an especially dynamic period during which new capabilities arise and performance levels improve rapidly.

The effects of size on performance are more familiar, well documented, and quantitatively modeled than the effects of ontogeny. Diverse studies of animal physiology and functional morphology in many groups of organisms show that size is related to most measures of performance in a common way, according to the scaling relationship

$$\text{Performance} = \alpha \cdot \text{Size}^{\beta} \tag{1.3}$$

a power function in which size may be length, weight, area, or some other measure, and α and β are empirical constants. The scaling relationship depicts different rates of change in performance for smaller, younger individuals than for larger and older ones. Only in the unusual situation where $b = 1$ does performance change in direct proportion to a change in size. One familiar scaling relationship is that for standard metabolism in fishes. The exponent of body weight (b) for juvenile and adult carp (*Cyprinus carpio*, 25 g to 3.5 kg wet weight) is 0.85. This describes adult carp as having a higher standard metabolic rate than juveniles but a lower weight-specific metabolic rate. Generally, exponents of a scaling relationship vary little among species during the juvenile and adult periods. The consistency of exponent values underscores how fundamental and general the effects of size are for a given measure of performance.

Strictly speaking, scaling relationships apply to individuals that differ only in size and not structure or shape. Embryos and larvae are characterized by intense structural and shape change as a result of ontogeny and allometric growth, so we cannot expect early life stages to fit even the strongest scaling relationships derived for older fishes. Returning to the carp example, the weight exponent (b) for larvae (Figure 1.3f, g) ranging from 2 mg to 3.8 g is 0.98, much higher than the value of 0.85 for larger carp. The exponent of approximately 1.0 indicates that the weight-specific metabolic rate of larvae is independent of body size (weight), an observation that has been confirmed for several other species. The empirical relationship between standard metabolic rate and weight for larvae is not really a scaling relationship. Developmental relationship is a better term because the data include the combined effects of scaling (changes in size), ontogenetic changes in structure, and allometric growth. The differences between scaling and developmental relationships mean that we cannot extrapolate our knowledge of juveniles and adults to earlier stages or vice versa. For now, developmental relationships must be derived empirically. Despite the more complex processes that produce them, developmental relationships are just as useful as scaling relationships for understanding the mechanisms responsible for changes in performance and for modeling those changes. The following examples demonstrate the nature and magnitude of effects of ontogeny and growth on selected, ecologically important measures.

1.4.1   Sensory systems

Visual acuity is a measure of performance that determines the distance at which a visually feeding fish can see its prey, all other conditions being equal. Acuity is defined by the
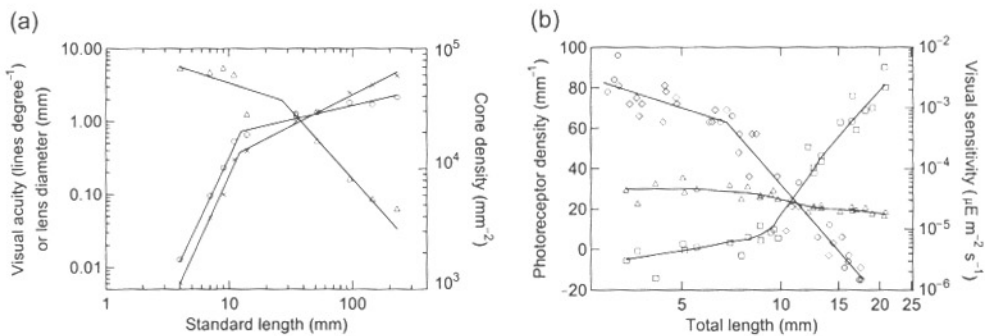
Figure 1.8 The effect of changes in eye morphology on visual performance. (a) Lens diameter (○) increases and cone cell areal density (△) decreases from the beginning of the larval period, resulting in rapidly increasing visual acuity (×) in the roach (*Rutilus rutilus*). (b) Cone cell lineal density (△) decreases slightly but rod cell lineal density (□) increases rapidly late in the larval period of red drum (*Sciaenops ocellatus*), to improve visual sensitivity (◇). Redrawn from data of Zaunreiter *et al.* 1991 and Fuiman & Delbos 1998.

diameter of the lens and the density of cone photoreceptors in the retina and can be calculated from measurements made on histological sections. Acuity of the cyprinid fish known as the roach (*Rutilus rutilus*) improves rapidly in the earlier stages of retinal development but the rate of improvement declines in later stages (Figure 1.8a). The driving force for the improvement is the rapid growth of the eye, and in particular the lens, which is more positively allometric (steeper slope) in larvae than in juveniles. At the same time and in opposition, the areal density of cones decreases because the expanding retinal area outpaces the differentiation of new cones, although the difference is less for larvae because cone differentiation is quicker than in juveniles. Such changes in acuity may constrain a larva's ability to find food.

Visual sensitivity, the minimum light intensity necessary for a particular visual task, is another measure of visual performance that improves in two phases. In red drum (*Sciaenops ocellatus*, similar in appearance to Figure 1.3r), improvement during the first phase is slower and not until rod photoreceptors begin to differentiate does the second phase begin, which brings a much more rapid improvement in sensitivity (Figure 1.8b). Ontogenetic improvements in sensitivity, such as this, may be an important determinant of vertical distribution patterns of larvae (see Section 1.5.3).

Successfully evading a predator's attack requires a larva to detect the predator and to initiate a well-timed response of suitable magnitude and in the appropriate direction. The gradual development of sensory systems after hatching has a direct impact on the ability of a larva to perceive the threat, to initiate its evasive response, and to do so at the appropriate moment. There is a general trend for increasing responsiveness to attacks as larvae develop. For most species studied to date, responsiveness increases in proportion to developmental progress. That is, there is a linear relationship between responsiveness and the logarithm of body size. This improvement coincides with increases in the peripheral end organs of the visual and lateral line systems, although reliance on a particular sensory system varies from species to species. Atlantic herring (*Clupea harengus*, Figure 1.3m) larvae provide an excellent example of a developmental bottleneck for sensory systems.

(a) (b)
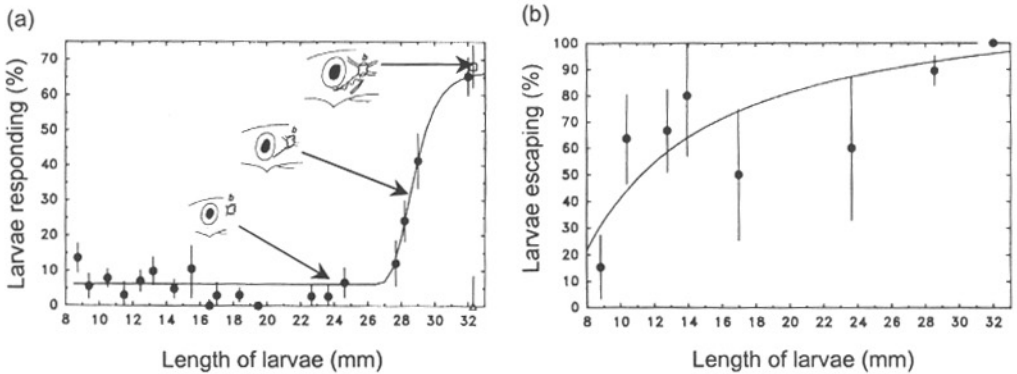
Figure 1.9 Ontogenetic changes in (a) responsiveness and (b) effectiveness of responses of Atlantic herring larvae to attacks by a predatory fish. Drawings of the developmental stage of the auditory bulla (*b*, posterior to the eye) and lateral line canal system show the role of these structures in initiating escape responses. Data from Fuiman (1989), drawings from Blaxter & Batty (1985).

This species and its close relatives rely on an air sac adjacent to the ear, called the auditory bulla, and its connection to the lateral line canal system on the head to provide them with an acute sense of underwater sounds and water movements. The bulla does not become functional until it fills with gas when herring larvae reach a length of about 25 mm. In laboratory experiments, only 6% of herring larvae less than 24 mm long (no gas in bulla) responded to attacks by larger herring. In contrast, 65% of 32-mm larvae (complete canals) responded. In addition, larger larvae initiated responses earlier in the attack sequence than younger stages, indicating improving sensitivity to predatory attacks. This sensory bottleneck is especially curious because the ability of herring larvae to escape successfully improves substantially during this period (Figure 1.9). Behavioral information such as this provides a more thorough understanding of the mechanisms of predation mortality, which is arguably the most important source of mortality during early life (Chapter 3).

1.4.2   Swimming performance

Changing size and structure have strong and varied influences on swimming performance. The gradual appearance of fin rays and reduction in the median fin fold are obvious changes to a larva's swimming apparatus. In many species, the caudal fin displays an exceptionally high degree of positive allometry during the larval period which results in a rapidly increasing propulsive surface area. Highly allometric growth also occurs in the region of the caudal peduncle, signaling disproportionate growth of locomotor muscle mass. The muscles themselves undergo important changes, starting with a single dominant fiber type and only later developing the two-gear system of red and white muscle. These ontogenetic changes, together with actual scaling effects, result in gradually improving swimming performance as larvae develop.

The routine swimming speeds of larval fishes, as well as their burst speeds, increase approximately linearly with body length among species (Figures 1.10 and 11.31). Generally, routine speeds increase by a factor of four to five or more from a length of 5 mm to a length of 20 mm. Therefore, length-specific speeds of larvae are about one to three body lengths
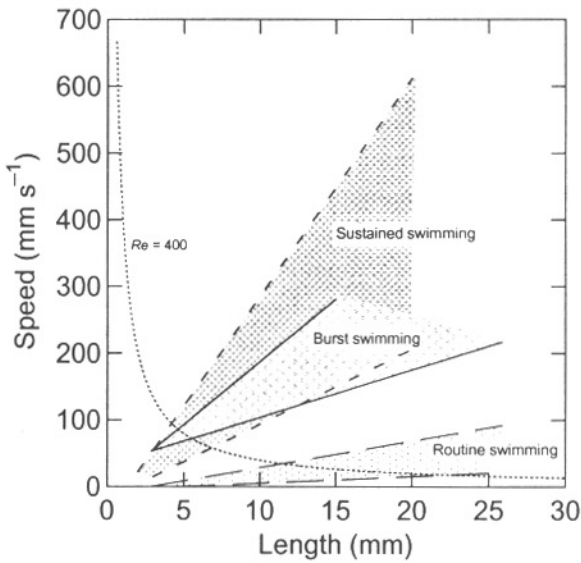
Figure 1.10   Ranges of swimming speeds of fish larvae relative to their length in different types of swimming. The dotted line represents the range of conditions for which the Reynolds number (*Re*) is equal to 400. Water viscosity and its natural variations can have a measurable effect on swimming when *Re* is less than 300–450. Data for routine and burst swimming are from freshwater and marine species (from summaries by Fuiman & Webb [1988], Miller *et al.* [1988] and Williams *et al.* [1996]). Data for sustained swimming are from coral reef fishes (Stobutzki & Bellwood [1994] and Fisher *et al.* [2000]).

per second ($BL\,s^{-1}$). Burst speeds increase by a factor of two to three over the same range. On a length-specific basis, burst speeds are highest for small larvae, commonly 15–20 $BL\,s^{-1}$ at 5 mm, with individual values recorded as high as 66 $BL\,s^{-1}$. This far surpasses the traditional rule of thumb of 10 $BL\,s^{-1}$ for maximum speed that is accepted for adult fishes. Recent work on young reef fishes shows that larvae have surprisingly high endurance at relatively high sustained swimming speeds. Just prior to settlement, some species are capable of sustained speeds of 20–60 $BL\,s^{-1}$. All of these general trends contain a good deal of variation, part of which can be attributed to differences in morphology at a given size. As swimming performance improves during development, larvae are able to forage over larger areas and they become better able to escape from predators, as well as plankton nets.

A less familiar, but very important, influence on swimming in larvae is the interplay between body size, swimming speed, and hydrodynamics. Small, slowly moving larvae experience hydrodynamic conditions in which water viscosity has a major impact on their motion, and inertia has little effect. For larger or faster fishes, inertial forces dominate and viscous effects are minor. The small size and large amount of growth that larvae exhibit take them from a viscosity-dominated regime to an inertia-dominated one in a short span of time. The effects of viscosity on small fish larvae can be seen in their routine swimming movements. Very small larvae come to rest immediately after they stop beating their tail. So, in order to travel appreciable distances, they swim continuously and vigorously. Larger larvae, juveniles, and adults, are able to save energy by incorporating glides into their swimming. Although definitive experiments have not been done, this hydrodynamic transition must have important consequences for a larva's energy budget. Experiments suggest

that larvae escape these effects of viscosity when the Reynolds number (a hydrodynamic parameter that is approximately the product of total length, in mm, and speed, in $mm\,s^{-1}$) exceeds 300–450. A quick calculation (Figure 1.10) will confirm that viscosity is a unique consideration for larval fishes, at least when they are traveling at low speeds, as they do when cruising for food using routine swimming. Another consideration is that viscosity is inversely related to temperature, changing by as much as 30% under temperature changes a larva might naturally experience. This compounds the well known physiological (Q_{10}) effects of temperature on swimming performance. At higher speeds, such as when fleeing predators, Reynolds numbers are much higher and viscous forces play a minor role.

1.5   Ecological consequences of development

A great many of the ecological performance measures that are critical to the survival and growth of early life stages vary according to a developmental relationship. That is, performance varies with size, but not because of size alone. This is true at many levels, from the performance of an individual organ, to the performance of an organism alone or in its interactions with other organisms. The following examples illustrate the ways in which ontogeny and growth (development) can influence the abilities of a fish in various ecological contexts.

1.5.1   Food and feeding

The great importance to fishery science of a larva's transition from endogenous nutrition to foraging in the environment was recognized a century ago by fishery scientists in Norway, among whom Johan Hjort is generally credited because of his pioneering publication of 1914, *Fluctuations in the Great Fisheries of Northern Europe*. One of Hjort's ideas, later called the Critical Period Hypothesis, recognized that larvae can survive for only a brief period without food after their supply of yolk and oil globules is gone, and that natural abundances of their food vary greatly in time and space. Therefore, starvation could be an important source of mortality during the larval period and this could translate into large variations in year-class strength. Hjort's ideas have given rise to several important hypotheses, which will be outlined in Chapter 4.

   Starvation is a more serious risk for larval fishes than juveniles or adults because of their high weight-specific metabolic energy demand (see Section 1.4). The length of time a fish can survive without food, its starvation resistance, is governed by the rate of energy expenditure (metabolic rate) and the amount of energy stored in the tissues. Recall that the metabolic rate of larvae is directly proportional to their weight ($W^{1.0}$), and that the weight exponent for juveniles and adults is lower (for example, $W^{0.85}$). Assuming relative constancy of body composition, a fish's energy stores are directly proportional to its weight. Therefore, larvae have smaller reserves on which to draw when food is scarce but the ability to withstand starvation improves with growth (Figure 1.11). When food is withheld from larvae, they reach a point of no return at which starvation is irreversible. The point of no return varies among species and, as expected, is related to body size and temperature. At temperatures of 5–10°C, larvae may reach irreversible starvation after 20–35 days, but at 25–30°C it may only take 4 or 5 days.
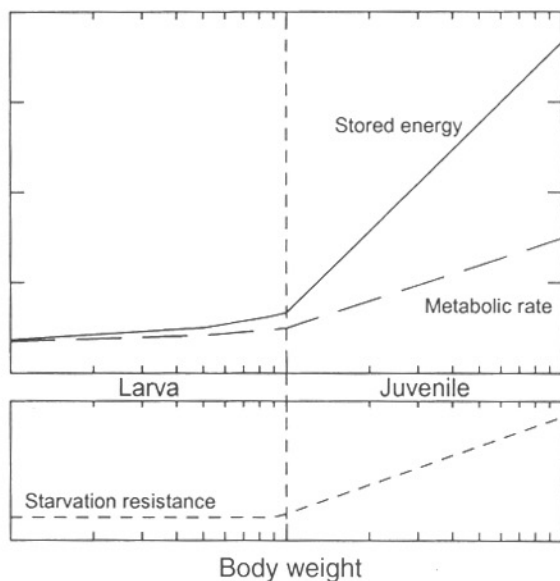
Figure 1.11 Changes in stored energy and metabolic rate with growth during the larval and juvenile periods. Stored energy is directly proportional to body weight through both periods (although the logarithmic abscissa distorts this trend). Metabolic rate is proportional to body weight for larvae (that is, weight-specific metabolic rate is constant), whereas weight-specific metabolic rate decreases in the juvenile period. The diverging trends result in increasing starvation resistance, the ratio of stored energy to metabolic rate in units of time.

The risk of starvation diminishes through the course of development not only because of lower weight-specific metabolism and increasing energy reserves, but also because of improvements in sensory and swimming performance. Older larvae are better equipped to locate more distant food supplies. Growth also allows larvae to select larger, more energy-rich prey while retaining the ability to feed on the smaller, more abundant prey. This increasing diet breadth may be critical to their ability to continue growing. The highly allometric growth of fish larvae leads to a particularly rapid increase in gape size, so much so that some species can cannibalize members of their own cohort that are 70–90% of their own length. By comparison, the maximum size of prey for piscivorous adults is generally 30–50% of their length.

1.5.2   *Predator detection and escape*

As mentioned above, burst swimming performance improves with development and this translates into increasingly effective escape responses (Figure 1.9b). Many investigations have measured the predator's capture success and arrived at a common negative trend relating capture success to larva size. These results on different species and sizes of larval prey attacked by various juvenile or adult predators can be summarized by a single curve according to which capture success decreases rapidly as prey become larger relative to the predator, implying that the sole or primary cause of the change in capture success is a matter of scaling (Figure 4.7).
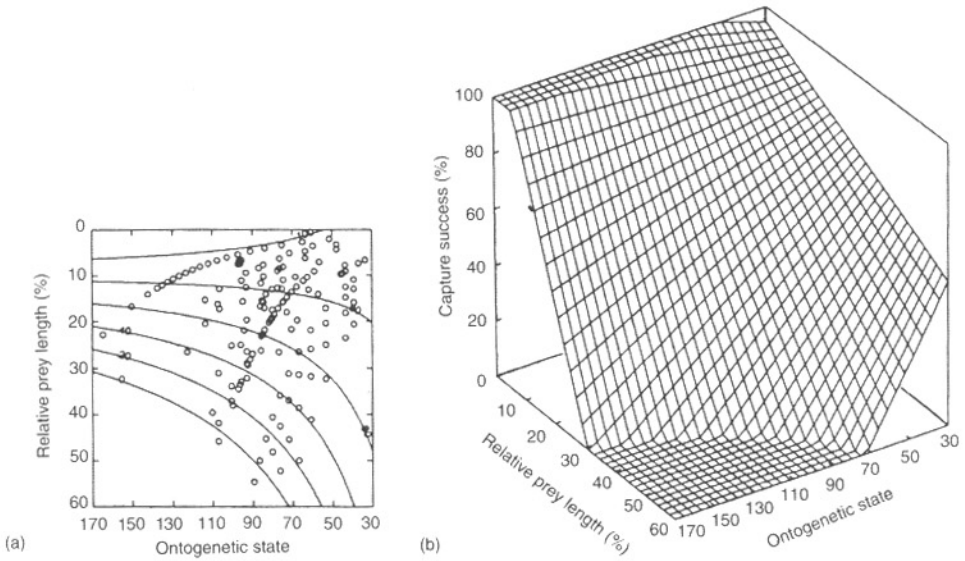
Figure 1.12 Capture success of predators attacking various species of fish larvae as a function of ontogenetic state and relative prey size (larva length divided by predator length) (from Fuiman 1994).

This final example of a developmental relationship (between capture success and relative prey size) assumes that developmental differences among species at a common size are trivial, a point that is often forgotten when the empirical results follow such obvious trends. Recall that body size is a suitable measure of developmental state within a species, but also that species differ in their size at a given developmental stage. An 8-mm Atlantic menhaden is still early in its developmental program, while a black drum at the same size is quite well developed (Figure 1.7). Therefore, in the capture-success relationship (Figure 4.7), prey:predator length accounts for scaling effects but the ontogenetic effects are confounded with size in this multi-species data set. The fact that the data appear to follow the curve so closely suggests that scaling is the principal determinant of capture success, but it may also reflect a limited or biased selection of larva types in the data set. Since we know that ontogenetic changes have important effects on aspects of performance that ultimately determine capture success, such as sensory and locomotor performance, the general model for capture success can be improved by adding a variable that describes ontogenetic state, such as O_L. Doing so results in a biologically more complete model that yields better insight into the mechanisms of change in capture success for larvae and improved quantitative predictions (Figure 1.12). Nevertheless, body size alone does tell us a great deal about how a larva will be affected by many of the mechanisms that influence its survival.

1.5.3 *Habitat shifts vs. sensory development*

Physical separation of life-history stages is a common strategy that is usually mentioned in regard to spawning migrations, which place the eggs and larvae in a different habitat from

the adults. Diadromous fishes provide an extreme example. Benefits generally attributed to this strategy include: a better match with life-stage-specific habitat requirements, reduced competition among age classes, and reduced cannibalism. Migrations or habitat shifts are also common within the early life of many species. As we will see in Chapter 7, these movements may serve the same ecological functions as in other periods of life. Their timing may be determined by one or more developmental events that provide the skills necessary to locate or succeed in a new habitat.

Atlantic herring hatch from demersal eggs and spend their larval period in offshore waters. They move into coastal waters around the time of metamorphosis. Their prolonged, low responsiveness to attacks by larger fishes (Section 1.4.1) poses interesting questions, especially in light of the fact that their evasive responses improve early, long before responsiveness increases (Figure 1.9). Why does responsiveness remain so low for so long, given that surviving an attack depends on responding? Why has there not been natural selection for earlier functionality of the auditory bulla or another sensory system to initiate a response? One possibility is that herring larvae may not experience much predation pressure from other fishes. The abundance of planktivorous fishes offshore is probably considerably lower than it is in coastal habitats. Thus, the timing of the movement of herring into coastal waters coincides with, and may be constrained by, the development of a specific sensory system that is needed for their survival in that environment. This does not mean that predation is not an important source of mortality for herring larvae. Invertebrate predators, principally medusae, are abundant and voracious consumers of fish larvae offshore. Herring larvae do not require functional auditory bullae to respond to these predators; they respond by touch or by sensing nearby water movements.

Various ontogenetic events have been implicated in habitat shifts of several other species. Like its relative, herring, Atlantic menhaden larvae (Figure 1.7) also move inshore after the auditory bullae and other sense organs reach a high level of functionality. Movements in the vertical direction have also been associated with ontogenetic changes. Young rockfish (*Sebastes diploproa*) and red sea bream (*Pagrus major*) larvae live in shallow seas until differentiation of the retina improves their visual sensitivity, when they move to depths of 500 and 150 m, respectively. At a finer level, vertical distribution patterns may be a result of ontogenetic constraints on vision and feeding performance in larval fishes, as evidenced by concordance between light sensitivity and field observations on the vertical distributions of reef fish larvae. Vertical distribution is also influenced by swim bladder inflation and resulting changes in buoyancy. Transition from pelagic larvae to epibenthic juveniles coincides with, or is preceded by, major changes in the lateral line system in flatfishes and dentition in a grouper.

This leads us to the complex matter of settlement in coral reef fishes, which involves both long distance horizontal movement and transition from a pelagic to a bottom-associated lifestyle. Ninety-five percent of the families of coral reef fishes have pelagic larvae and the duration of this phase can range from about 1 week to more than 3 months. Eggs and larvae are dispersed from the reef occupied by their parents, often far from any reefs, and weeks later must find a reef on which to settle and complete metamorphosis. Settlement takes place over a very narrow range of sizes for a given species, indicating that competency to settle is determined by their developmental state. Intriguingly, at least some species are able to delay settlement and metamorphosis, perhaps when there is no suitable habitat

nearby. During this delay their growth rate slows significantly, otherwise metamorphosis would probably begin and they would lose their pelagic body form. It is not clear which developmental events are critical for settlement. Those related to locating a reef over a distance of kilometers to tens of kilometers (sensory performance) and swimming to it seem paramount. Recent investigations have demonstrated the extraordinary swimming capabilities of pre-settlement-stage reef fishes. They are clearly not at the mercy of prevailing currents and we must hesitate applying the term ichthyoplankton. In addition, they seem to be able to orient their swimming in a consistent direction. Research attention is now turning to the cues that guide them to a reef. The most promising candidates appear to be chemical and acoustical signals. Settlement, or recruitment to a reef, is considered an important regulator of local species abundance and community structure under the Recruitment Limitation Hypothesis (Chapter 4).

Despite the relatively strong swimming performance of later larvae, few larval stages are able to swim against the strong flows of tidal currents. This challenge is faced by many species that enter estuaries from offshore and coastal spawning areas, as well as those spawned within the estuary but advected out of the system as eggs or young larvae, only to return later. Some species that enter estuaries from the sea appear to use selective tidal stream transport. In a tidal environment, where currents reverse once or twice each day, the velocity of the current is always very low in the boundary layer immediately adjacent to the bottom. Larvae can progress into the estuary by entering the water column on flood tide then sheltering in the boundary layer when the flow reverses. This requires a sense of the direction of flow, landward or seaward, or at least a circatidal rhythm in activity. Early observations of tidal stream transport were made on young eels (*Anguilla anguilla*) entering a Dutch estuary. The elvers were distributed throughout the water column on flood tides and near or on the bottom during ebb tides. Similar observations have been made since that time on other species, including flatfishes and sciaenids. Laboratory experiments indicate that the change in vertical position and behavior may involve detection of one or more stimuli, possibly olfactory cues in dissolved or particulate organic matter, that are associated with seaward flow of estuarine water. This may prevent younger larvae, with less developed sensory systems, from orienting with respect to certain stimuli.

1.6 Summary

The early life of fishes is distinct from the more familiar juvenile and adult periods because of two intrinsic processes, ontogeny and growth, that give rise to profound changes in body structure and size. Not only are embryos and larvae different from their later forms, but the degree of difference changes continually. These changes influence the behavioral and physiological performance of early life stages, which in turn alter the nature of ecological interactions. This chapter has examined a few representative performance measures and their associated morphologies to demonstrate the ways in which developmental changes work their way from morphology to ecology. In practice, it is better to avoid examining one organ system or one performance measure in isolation. A more comprehensive approach, when possible (Figure 1.13), will provide a better basis for understanding a species' requirements and limitations during early life.

Figure 1.13 Composite of developmental changes in body form, function, and ecology in red drum (*Sciaenops ocellatus*). Data from numerous sources. Drawings from Holt *et al.* (1981) and Pearson (1929).

Additional reading

Balon, E.K. (1975) Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Research Board of Canada* **32**, 821–864.

Balon, E.K. (1981) Saltatory processes and altricial to precocial forms in the ontogeny of fishes. *American Zoologist* **21**, 573–596.

Boehlert, G.W. & Mundy, B.C. (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3**, 51–67.

Chambers, R.C. (1997) Environmental influences on egg and propagule sizes in marine fishes. In: *Early Life History and Recruitment in Fish Populations*. (Ed. by R.C. Chambers & E.A. Trippel), pp. 63–102. Chapman and Hall, London.

Copp, G.H., Kovác, V. & Hensel, K. (Eds) (1999) When do fishes become juveniles? *Environmental Biology of Fishes* **56**, 1–280.

Cowen, R.K. & Sponaugle, S. (1997) Relationships between early life history traits and recruitment among coral reef fishes. In: *Early Life History and Recruitment in Fish Populations*. (Ed. by R.C. Chambers and E.A. Trippel), pp. 423–449. Chapman and Hall, London.

Fuiman, L.A. (1994) The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. *Journal of Fish Biology* **45**(suppl. A), 55–79.

Fuiman, L.A. & Higgs, D.M. (1997) Ontogeny, growth, and the recruitment process. In: *Early Life History and Recruitment in Fish Populations*. (Ed. by R.C. Chambers & E.A. Trippel), pp. 225–249. Chapman and Hall, London.

Fuiman, L.A. & Magurran A.E. (1994) Development of predator defences in fishes. *Reviews in Fish Biology and Fisheries* **4**, 145–183.

Fuiman, L.A., Poling, K.R. & Higgs, D.M. (1998) Quantifying developmental progress for comparative studies of larval fishes. *Copeia* **1998**, 602–611.

Hoar, W.S. & Randall, D.J. (Eds) (1988) *Fish Physiology, Volume 11. The Physiology of Developing Fish. Part A. Eggs and Larvae*. Academic Press, San Diego.

Hoar, W.S. & Randall, D.J. (Eds) (1988) *Fish Physiology. Volume 11. The Physiology of Developing Fish. Part B. Viviparity and Posthatching Juveniles*. Academic Press, San Diego.

Houde, E.D. (1994) Differences between marine and freshwater fish larvae: implications for recruitment. *ICES Journal of Marine Science* **51**, 91–97.

Houde, E. D. & Zastrow, C.E. (1993) Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. *Bulletin of Marine Science* **53**, 290–335.

Kamler, E. (1992) *Early Life History of Fish: An Energetics Approach*, Fish and Fisheries Series 4. Chapman and Hall, London.

Kryzhanovskii, S.G. (1949) Eco-morphological principles and patterns of development among minnows, loaches and catfishes (Cyprinoidei and Siluroidei). Part II. Ecological groups of fishes and patterns of their distribution. Academy of Sciences of the USSR. Trudy of the Institute of Animal Morphology, Volume 1, pp. 237–331. *Fisheries Research Board of Canada Translation Series No. 2945. 1974.*

Miller, T.J., Crowder, L.B., Rice, J.A. & Marschall, E.A. (1988) Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1657–1670.

Moser, H.G., Cohen, D.M., Fahay, M.P., Kendall, Jr., A.W., Richards, W.J. & Richardson, S.L. (Eds) *Ontogeny and Systematics of Fishes*. Special Publication No. 1, American Society of Ichthyologists and Herpetologists. Lawrence, Kansas.

Webb, J.F. (1999) Larvae in fish development and evolution. In: *The Origin and Evolution of Larval Forms*. (Ed. by B.K. Hall & M.H. Wake), pp. 109–158. Academic Press, San Diego.