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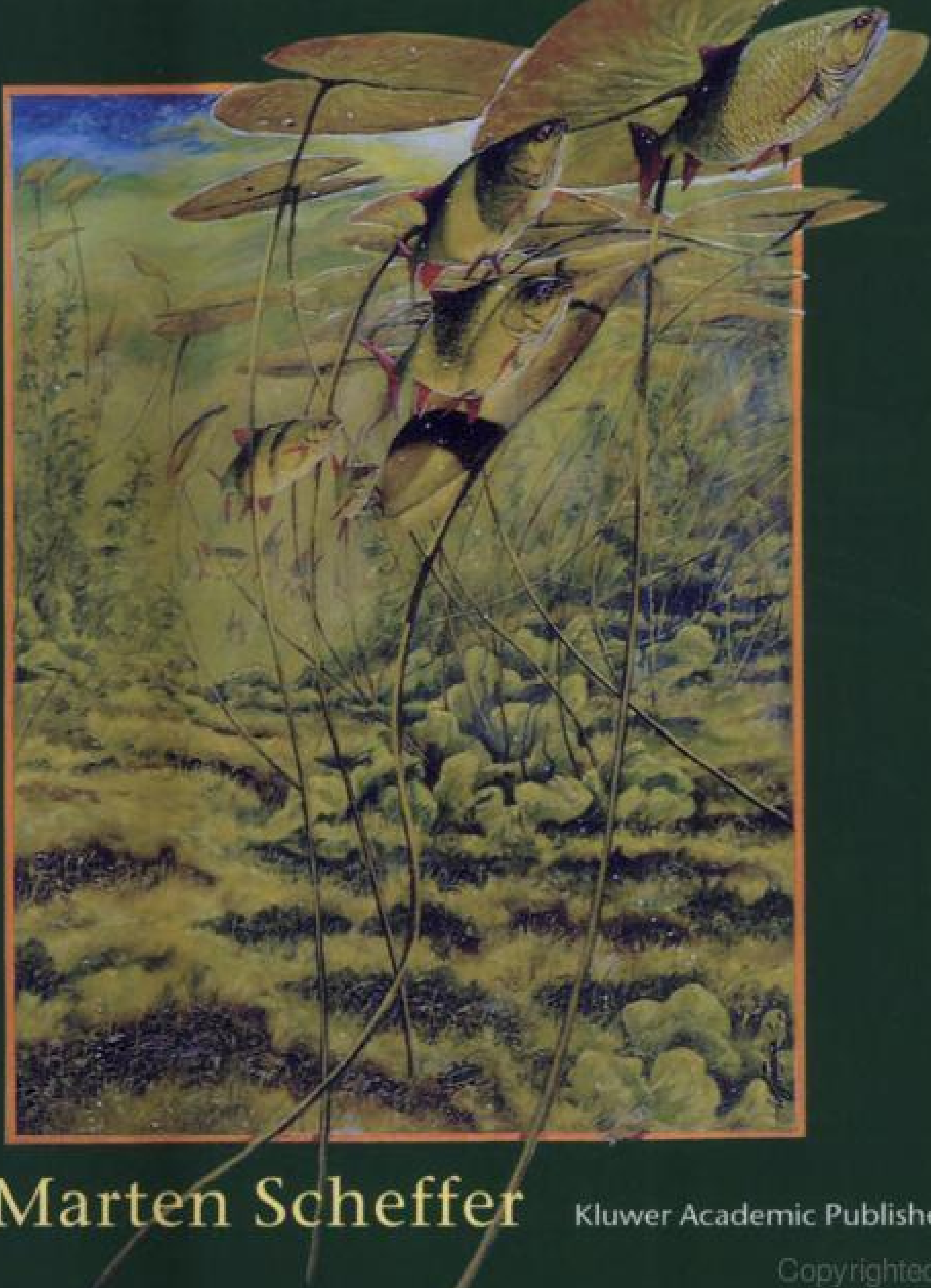
Ecology of Shallow Lakes



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ECOLOGY OF SHALLOW LAKES

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Preface

Looking into the water of a shallow lake or pond one might have a crystal clear view of gently waving submerged plants, fishes darting off and small animals moving busily around. More likely, however, the water is murky, troubled by blooming algae and suspended sediment particles hiding whatever is going on below. Remarkably, intermediate situations between these two extremes seem relatively rare. This impression may result from our persistent tendency to dichotomize in an attempt to simplify the world, but research suggests that in this case there is some truth in the dichotomy.

The two situations represent strongly contrasting community states, both of which have stabilizing feedback mechanisms. In the turbid state, the development of submerged vegetation is prevented by low underwater light levels. The unprotected sediment is frequently resuspended by wave action and by fish searching for food causing a further decrease of transparency. Since there are no plants that could serve as refuges, zooplankton is grazed down by fish to densities insufficient to control algal blooms. In contrast, the clear state in eutrophic shallow lakes is dominated by aquatic macrophytes. The weed beds prevent sediment resuspension, take up nutrients from the water, and provide a refuge for zooplankton against fish predation.

In view of these feedback mechanisms it is not surprising that shallow lakes refuse to obey simple rules such as the classical relationships between algal biomass and nutrient loading. The response of shallow lakes to eutrophication is often catastrophic rather than smooth, and several lakes are known to have switched back and forth between a clear and a turbid state repeatedly without obvious external forcing. In view of the relative neglect of shallow lakes in limnological literature, this disparate behaviour has apparently discouraged rather than tempted researchers for a long time. Even in countries where almost all the lakes are shallow, like Denmark and The Netherlands, limnological research has traditionally been focused entirely on the few deep lakes that were available. Over the last decade, however, this situation has changed.

Many of the shallow lakes have become turbid during this century because of eutrophication, and efforts to restore the clear state by means of reduction of the nutrient loading are often unsuccessful. This has invoked experiments with additional methods such as temporary reduction of the fish stock. The potential impact of such disturbances on shallow lake ecosystems appears to be huge, and several lakes have switched to a stable clear state in response. The careful monitoring of these changes has catalysed the development of insights into the mechanisms that govern the dynamics of shallow lake communities.

Writing this book has been an (unfinished) journey towards the goal of constructing a coherent picture of 'how shallow lakes work'. Unravelling the origin of main ideas is probably as difficult as unravelling the functioning of lake ecosystems, but some things can be said about the intellectual roots of the views presented in this book. The feeling that there was something like alternative stable states in our lakes, and ideas about the roles of fish and vegetation have been fermenting for at least a decade in a group of English, Danish and Dutch limnologists. Surely, Brian Moss and Erik Jeppesen were very important inspiring thinkers in this group. At our institute Andre Breukelaar, Harry Hosper and Marie-Louise Meijer were my partners in discussing these exciting views.

Erik Jeppesen was the one who after reading the first draft encouraged me, explaining that it was going to be great, but pointing out kindly that I needed to do quite a bit of extra homework. The book ripened during the subsequent phase when I tried to understand the often conflicting results from countless descriptive and experimental studies, a process that definitely helped the theoretician in me to become more modest. Sergio Rinaldi was my guide in the fascinating and dazzling world of dynamical systems theory with its attractors, bifurcations and other abstract structures. Together we looked for parallels to the even more dazzling world of aquatic food webs. Rob de Boer and Yuri Kuznetsov developed wonderful software for analysing models and guided me in using it.

Don DeAngelis, who suggested me to write this book, invited me over at the Oak Ridge National Laboratory to work, and gave many useful advices and comments. Eric Marteijn and the rest of the staff at RIZA have been very supportive and flexible, allowing excursions into research topics that go beyond a directly applied context, and giving me the time to write this book. It was a great pleasure to write a large portion of it in the beautiful Tennessean country house of Bob and Dorothy Jolley.

With Adriaan Achterberg I shared an unforgettable time doing our first work in aquatic ecology trying to figure out what happens in ditches. He made a number of pen drawings especially for this book (Figs. 4.3, 4.42, 1.4, 4.49, 3.13, 5.1, 2.15, 4.46). The cover illustrations are made by Ad Swier. Bert Jansen prepared most of the technical drawings and kindly tolerated my numerous changes of mind. Rita van Leeuwen did an invaluable job localizing relevant literature. Egbert van Nes has been a crucial help all the way, solving problems with software packages, writing better ones, helping organizing and finding literature, discussing countless important and unimportant ideas during our lunch-walks and quietly pointing out crucial problems in seemingly brilliant reasonings.

The complete draft of the book has been read by Irmgand Blindow, Steve Carpenter, Hugo Coops, Milena Holmgren, Harry Hosper, Mark Hoyer, Bas Ibelings, Erik Jeppesen, Eddy Lammens, Marie-Louise Meijer, Stuart

Mitchell, Brian Moss, Egbert van Nes, Ruurd Noordhuis, Marcel van der Berg and Diederik van der Molen, while portions were reviewed by Herman Gons and Hendrik Buiteveld. Without their extensive comments the book would have been much harder to read.

Symbols

The main symbols used in the book. Figures are produced using the listed default values unless indicated otherwise. Symbols that used only once, are explained in the text and can not be found in this list.

Symbol	Units	Default value	Definition
Γ	$g\ m^{-2}\ day^{-1}$		sediment resuspension rate
α			fraction of lake bottom where resuspension occurs
ε			intensity of seasonal variation in light and temperature
τ_r	year		hydraulic retention time
a	m^{-1}		absorption coefficient of light
A	$mg\ l^{-1}$		concentration of phytoplankton
b	m^{-1}		scattering coefficient of light
B	$mg\ l^{-1}$		concentration of cyanobacteria
Chl	$\mu g\ l^{-1}$		concentration of chlorophyll-a
D	m		average lake depth
d	day^{-1}		fraction of lake volume exchanged between parts with and without zooplankton
E	m^{-1}		vertical attenuation coefficient of light under water ('turbidity')
E_0	m^{-1}		turbidity in the absence of vegetation
e_a	$m^2\ g^{-1}$	0.1	specific light attenuation coefficient of phytoplankton
E_b	m^{-1}		turbidity due to other factors than phytoplankton
e_z	$g\ g^{-1}$		efficiency of conversion of food into growth of zooplankton
F	km		fetch, distance from the shore in the direction where the wind comes from
f	day^{-1}		wash-out losses of phytoplankton due to flushing of the lake.
G	$mg\ l^{-1}$		concentration of green algae
G_f	$mg\ l^{-1}\ day^{-1}$		maximum zooplankton consumption of entire fish community

Symbol	Units	Default value	Definition
g_z	$g\ g^{-1}\ day^{-1}$	0.4	maximum grazing rate of zooplankton
h_a	$mg\ l^{-1}$	0.6	halfsaturation concentration of algae for zooplankton functional response
h_E	m^{-1}		turbidity allowing 50% of the lake to be covered by vegetation
h_p	$mg\ l^{-1}$	0.003	halfsaturation concentration of soluble reactive phosphorus for algal growth
h_s	–	1	shade (EZ) leading to a reduction of algal growth of 50%
h_V			vegetation cover needed for a 50% reduction in turbidity
h_z	$mg\ l^{-1}$	1	halfsaturation concentration of zooplankton for fish functional response
i	$g\ g^{-1}\ day^{-1}$	0.01	inflow of phytoplankton from ungrazed parts
K	$mg\ l^{-1}$	10	carrying capacity for phytoplankton
l	day^{-1}	0.1	loss rate of phytoplankton
m_z	day^{-1}	0.15	mortality rate of zooplankton
N	$mg\ l^{-1}$		total nitrogen concentration of the lake water
P	$mg\ l^{-1}$		total phosphorus concentration in the lake water
p_a	$g\ g^{-1}$	0.01	phosphorus concentration in algae
q	–		fraction of total lake volume occupied by zooplankton concentrations
r	day^{-1}	0.5	maximum growth rate of phytoplankton
s	$m\ day^{-1}$		sinking rate of a particle
S	$mg\ l^{-1}$		concentration of suspended solids
S_d	m		secchi-depth
SRP	$mg\ l^{-1}$		soluble reactive phosphorus
V			fraction of lake area covered by submerged vegetation
W	$m\ s^{-1}$		wind velocity
z	m		vertical distance from a point under water to the water surface
Z	$mg\ l^{-1}$		concentration of large herbivorous zooplankton
z_{eu}	m		depth of the euphotic zone (where >1% of the surface light penetrates)
z_{max}	m		depth limit of submerged macrophyte growth
z_{mix}	m		depth of mixed water layer

Introduction

WHAT IS A SHALLOW LAKE?

Traditionally, limnology is mostly concerned with lakes that stratify in summer. Thermal stratification largely isolates the upper water layers (epilimnion) from the colder deep water (hypolimnion) and from interaction with the sediment during the summer. The impact of macrophytes on the community is relatively small in such lakes, as plant growth is restricted to a relatively narrow marginal zone. This book is about the functioning of lakes that can be largely colonized by macrophytes and that do not stratify for long periods in summer. This type of lake, where the entire water column is frequently mixed, is also referred to as polymictic. The average depth of most of the lakes addressed in this book is less than 3 m, but their surface area ranges from less than a hectare to over 100 km^2. The intense sediment–water interaction and the potentially large impact of aquatic vegetation makes the functioning of shallow lakes different from that of their deep counterparts in many aspects.

In several regions shallow lakes are more abundant than deep ones. Numerous shallow lakes, for instance, are found at the edge of the ice cover during the Weichselian glaciation period. Also, human activities such as digging for peat, sand, gravel or clay have produced considerable numbers of shallow lakes and ponds. The term wetlands is often used to refer to shallow lakes and adjacent marshy land. Such habitats are notoriously rich in wildlife. In densely populated areas even small lakes can be very important from a recreational point of view. Fishing, swimming, boating and bird watching attract a large public.

Over the last century, the quality as well as the quantity of wetlands has declined dramatically. Drainage for agricultural purposes has reduced the amount of wetlands worldwide, while eutrophication has radically altered the nature of many wetland communities.

MANAGEMENT PROBLEMS

The pristine state of the majority of shallow lakes is probably one of clear water and a rich aquatic vegetation. Nutrient loading has changed this situation in many cases. The lakes have shifted from clear to turbid, and with the increase in turbidity, submerged plants have largely disappeared. The sequence of changes during eutrophication is rarely documented well, but some elements are agreed upon by most workers in the field (Moss, 1988).

Shallow lakes with a low nutrient content usually have a vegetation dominated by relatively small plants. With increased nutrient loading the biomass of aquatic macrophytes increases and plants that fill the entire water column or concentrate much of their biomass in the upper water layer become dominant. Such dense weedbeds are often experienced as a nuisance by the fishing and boating public. When weed control programmes eradicate the vegetation, turbidity in shallow lakes tends to increase strongly due to algal blooms and wind resuspension of the sediment. Also, when vegetation is not controlled explicitly, further eutrophication of vegetated lakes can lead to a gradual increase of phytoplankton biomass and of the periphyton layer that covers the plants. Shading by these organisms ultimately leads to a collapse of the vegetation due to light limitation.

Restoration of non-vegetated turbid shallow lakes to the clear vegetated state is notoriously difficult. Reduction of the nutrient loading may have little effect, as during the period of eutrophication a large amount of phosphorus has often been adsorbed by the sediment. When the loading is reduced and its concentration in the water drops, phosphorus release from the sediment becomes an important nutrient source for phytoplankton. Thus a reduction of the external loading is often compensated by 'internal loading', delaying the response of the lake water concentration to the reduction of external loading.

However, internal loading is not the only reason why restoration of turbid shallow lakes is difficult. With the disappearance of aquatic vegetation the structure of the shallow lake community changes dramatically (Fig. 1).

Invertebrates that are associated with vegetation disappear and with these animals the birds and fishes that feed on them or on the plants. Also, vegetation provides an important refuge against predation for many animals, and hence its disappearance causes crucial shifts in many predator–prey relationships. Large zooplankton use vegetation as a day-time refuge against fish predation. In vegetated lakes they can contribute significantly to the control of phytoplankton biomass. In the absence of vegetation their numbers are strongly reduced. This, and the increased nutrient availability, allows phytoplankton biomass to be higher in the absence of vegetation. In addition, wave resuspension of the unprotected sediment can cause a considerable additional turbidity once the vegetation has vanished. The fish community of unvegetated lakes becomes dominated by species that forage on benthic invertebrates. Their activity promotes the nutrient flux from the sediment into the water and causes an extra resuspension of sediment particles, contributing to the already high turbidity.

Return of submerged plants in this situation is unlikely, in part because their absence has allowed a further increase in turbidity, but also because the frequent disturbance of sediment by wind and benthivorous fish hampers resettlement. Ecological feedback mechanisms are thus an important

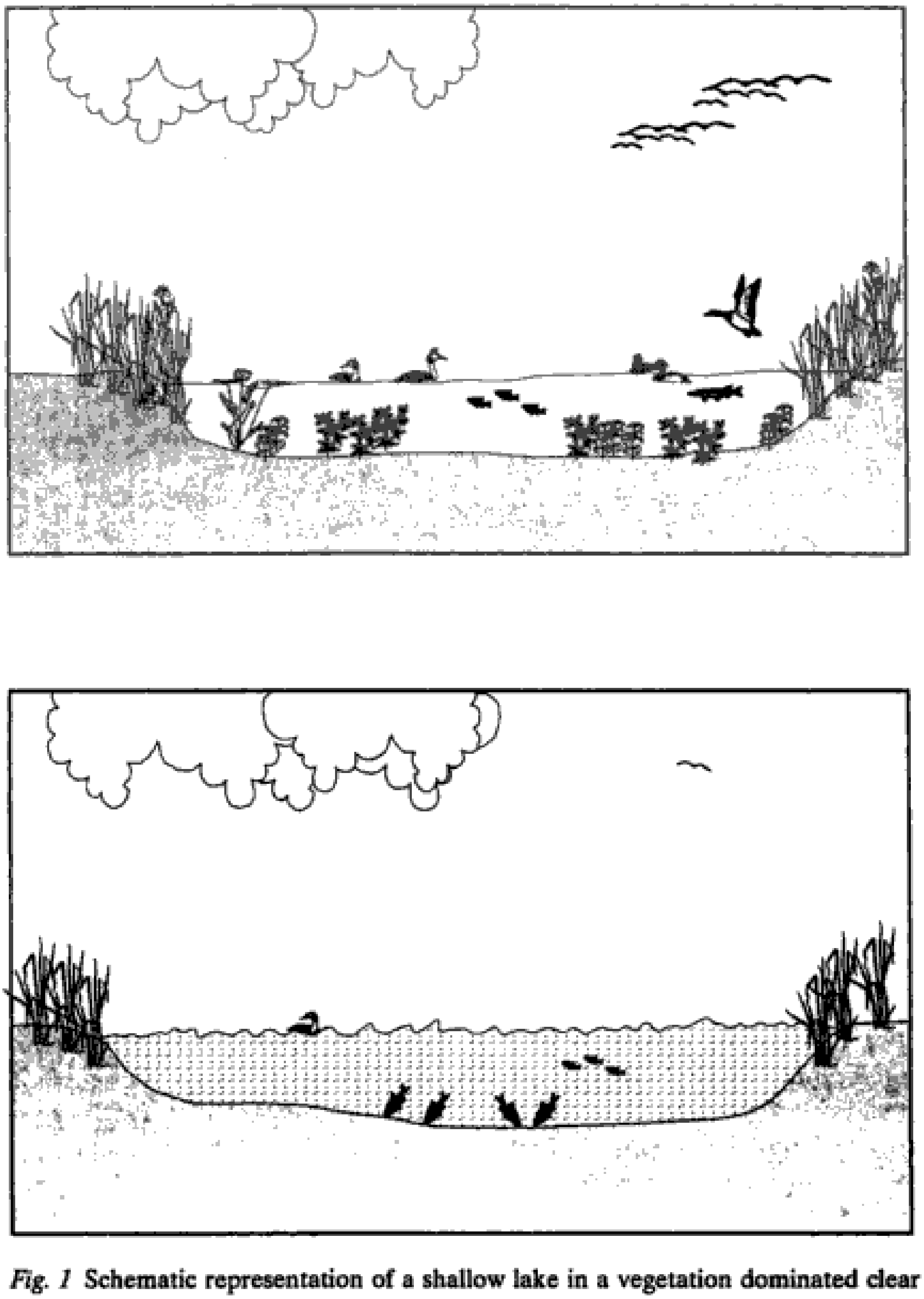

Fig. 1 Schematic representation of a shallow lake in a vegetation dominated clear state (upper panel) and in a turbid phytoplankton dominated state in which submerged plants are largely absent and benthivorous fish and waves stir up the sediments.

reason why restoration of the vegetated clear water state is difficult. In many cases, nutrient reduction alone may be insufficient to restore the clear state in shallow lakes. Additional measures, however, such as removal of part of the fish stock and changes in the water level, have been successfully used as a way to break the feedback that keeps such lakes turbid.

THEORY VERSUS NATURE

Many of the current ideas about the functioning of shallow lakes have emerged from comparison of the state of different lakes, observation of their dynamics, and the interpretation of laboratory and exclosure experiments that reveal the autecology of key-species and the nature of their interactions. However, the driving regulatory mechanisms and feedbacks are not easily revealed without experimenting with the system as a whole. Efforts to restore shallow lakes by means of manipulating the fish stock have provided such experiments and helped reveal the dominant regulating mechanisms. The ecosystem response to fish stock manipulations has provided new insights, not only into the functioning of the food web, but also into the regulation of aquatic vegetation dynamics and into the crucial role of submerged plants in keeping shallow lakes clear.

The array of sometimes conflicting and puzzling patterns emerging from these descriptive and experimental studies of shallow lake communities is impressive. In this book I often use simple models as a framework for discussing the empirical results. Models can be helpful in situations where feedbacks cause unexpected patterns. Such mechanisms are usually not easily grasped intuitively. However, models are just hypotheses about the cause of observed patterns, and the development of theory for explaining patterns in nature has some serious caveats that are worth highlighting (Scheffer and Beets, 1994c).

First of all, theory is tentative by definition and as Chamberlin (1897) remarked a century ago we should be alert to 'the imminent danger of an unconscious selection and of a magnifying of phenomena that fall into harmony with the theory and support it and an unconscious neglect of phenomena that fail of coincidence'. While keeping an open eye for alternative explanations is important in all science, it is especially essential in ecology. In fact, even the classic ideas about hypothesis testing are of rather limited use in ecology. A small excursion to the history of the discussion of the ideas on this topic may clarify this.

The classical method of scientific study is the hypothetico-deductive approach. The main ideas were advocated as early as 1620 by Francis Bacon in his *Novum Organum*, and elaborated later by the influential science philosopher Karl Popper. In the early 1960s, Platt (1964) argued once more that this systematic method of scientific thinking which he calls 'strong inference' clearly produces much more rapid progress than anything else, and hence should be closely adhered to. The steps of strong inference as formulated by

Platt are:

1. Devising alternative hypotheses;
2. Devising a crucial experiment (or several of them), with alternative possible outcomes, each of which will, as nearly as possible, exclude one or more of the hypotheses;
3. Carrying out the experiment so as to get a clean result;

1' Recycling the procedure making subhypotheses or sequential hypotheses to refine the possibilities that remain; and so on.

According to Platt, the superiority of this approach is overwhelming. As he phrases it: 'The difference between the average scientist's informal methods and the methods of the strong-inference users is somewhat like the difference between a gasoline engine that fires occasionally and one that fires in steady sequence. If our motorboat engines were as erratic as our deliberate intellectual efforts, most of us would not get home for supper.' Platt's compelling plea inspired many ecologists. It was felt that unsystematic working methods could indeed be the reason that ecology was not proceeding at the pace of sciences like molecular biology and high-energy physics put forward as examples by Platt. It was argued that hard to crack problems such as understanding the effect of competition on natural communities could only be solved by following the path of null-hypothesis formulation and testing (Connor and Simberloff, 1979; Strong, Jr. 1983).

In 1983, however, two essays appeared in the *American Naturalist* (Quinn and Dunham, 1983; Roughgarden, 1983) pointing out that there are some fundamental reasons why rigid strong inference is of very limited use in ecology. The most basic argument is that strong inference assumes that the competing hypotheses to explain observed phenomena are general and mutually exclusive, whereas in ecosystems several independent mechanisms do often contribute to an observed phenomenon that could also in theory be explained from each mechanism alone. One of the mechanisms will often dominate, but dominance will differ from case to case and may even shift in time.

With respect to the interpretation of simple models the problem of multiple causality implies that some modesty is appropriate. Even if the model is based on reasonable assumptions and its behaviour mimics the patterns in the real system very well, it might be that these patterns are caused by something else in reality. The fact that the modelled mechanisms can be shown to operate in the field is not a sufficient basis either for concluding that it offers the appropriate explanation in that specific case as the modelled mechanism may well be acting in concert with other, possibly more important ones.

In summary, the simple models or theories used to bring some order into the bewildering diversity of field patterns necessarily capture only part of the mechanisms involved in causing these patterns. If we are fortunate, the incorporated mechanisms are the dominant ones in nature, but the relative importance of different mechanisms is likely to differ from case to case. Obviously, it would be naive to assume that ecological models or hypotheses can simply be proven to be right or wrong.

SET-UP OF THE BOOK

Throughout the book I have attempted to present a mix of models and hypotheses with empirical results that may fall into harmony or highlight additional aspects. Thus the models serve as a framework, representing a number of dominant mechanisms against which the diverse collections of empirical observations are presented. I realize that mathematical formulae and the abstract terminology used in dynamical systems theory could cause some readers to drop out. Therefore, mathematics are kept very simple, and most model analyses are presented in graphs* rather than formulae. Furthermore, some relatively technical text sections are printed in a smaller font. The take-home message of these sections is repeated in the main text, so that readers who find this material indigestible can skip it without missing too much.

The discussion of most of the topics has three components. A description of the major patterns observed in the field is followed by a more theoretical part that seeks to explain the governing mechanisms. The final section presents more empirical results that often indicate additional mechanisms that can be important. The book as a whole also has this structure.

The first chapter merely brings the story of a number of widely different shallow lakes in which conspicuous changes have been documented. Often the observations are fragmentary. Nonetheless, from this material a picture emerges of the variety of states that shallow lakes can be in, and the factors that can induce the often swift changes observed in such lakes. The next chapters focus on the specific mechanisms involved. The peculiarities of the physical and chemical environment are discussed in Chapter 2. It treats the underwater light climate as it is experienced by macrophytes and algae, the resuspension of sediment by waves and benthivorous fish, and the role of sediment, animals and plants in nutrient cycling. In Chapter 3 the regulation of phytoplankton dynamics is discussed. Some simple models that help in the understanding of algal growth are introduced, and the mechanisms that cause cyanobacterial dominance in shallow lakes are analysed. The top-down regulation of phytoplankton and periphyton by zooplankton and other invertebrates and the major role of predation by fish are the topics of Chapter 4. Chapter 5 is a turning point in the book. The effects of vegetation on the animal community and turbidity of lakes are discussed, as well as the

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*For the graphical model analyses I used the software packages GRIND (isoclines and simulations) and LOCBIF (bifurcation analysis). GRIND is public domain software that requires a FORTRAN compiler. It can be obtained from the author, Dr. Rob J. de Boer, email address: RDB@ALIVE.RUU.NL. The program LOCBIF can be ordered at CAN diensten, email address: INFO@CAN.NL.

factors that regulate vegetation abundance. It is shown how several feedbacks cause the vegetation dominated clear state and the non-vegetated turbid state to be alternative equilibria in many shallow lakes. Chapter 6 gives an overall synthesis of the presented material from the practical viewpoint of lake management. The possibilities and caveats of several restoration methods are discussed. The final chapter evaluates the limitations of our mechanistic understanding of shallow lake ecosystems, and the prospects for improving our ability to predict the response of such systems to management measures.

1 The story of some shallow lakes

This chapter tells the history of a number of shallow lakes in which conspicuous changes in community structure have been observed (Table 1.1).

The lakes range in area from 1 to 18200 hectares and in geographic position from New Zealand to Sweden. Although some of the lakes have been studied in detail for several years, the information remains fragmentary in most cases. Nonetheless, when viewed in combination, clear patterns emerge. Together, these histories give an idea of the large and often rapid shifts that can occur in shallow lake ecosystems, but also of the internal mechanisms and external forces involved in causing such changes. While the next chapters zoom in on specific regulatory mechanisms, the series of short stories in this chapter sets the stage by depicting the main phenomena that the work described in the rest of the book is ultimately aimed at understanding.

1.1 NUTRIENT INDUCED CHANGES

Veluwemeer

Veluwemeer is an artificially isolated part of a large body of water in the centre of The Netherlands that used to be a brackish bay called Zuiderzee. In 1932 a dam was constructed to isolate the bay from the North Sea. Tides disappeared and salinity gradually declined over the following years. The resulting lake was called IJsselmeer. In 1952 construction of dams started in the south-eastern part of the lake around areas that were subsequently turned into polders by pumping the water out. (In one of these polders, 4 m below sea level, this book has been written.) To prevent the groundwater levels at the farmlands on the old coast from dropping too much, an area of about 100 km^2 with water at the original level was left between the new polders and the old land. This water body, divided into six hydrological units by dams, is now called randmeren ('border-lakes'). Veluwemeer and the adjacent Drontermeer were the first units to become isolated. Since then a sequence of pronounced changes has occurred in the aquatic community (Fig. 1.1).

Before its isolation the area that would become Veluwemeer had a vegetation dominated by Sago pondweed (*Potamogeton pectinatus*), a species with long narrow leafs that flourishes in many brackish lakes. In addi-

Table 1.1 Details of some lakes discussed in the text

Lake	*Size (ha)*	*Mean depth (m)*	*Country*	*Probable cause of change*
Veluwemeer	3300	1.4	The Netherlands	nutrients
Alderfen Broad	5	0.8	England	nutrients
Lake Apopka	12800	1.7	Florida, USA	storm
Ellesmere	18200	2.7	New Zealand	storm
Lake Tämnaren	3500	1.5	Sweden	water level
Rice Lake	52	0.8	Wisconsin, USA	water level
Lake Zwemlust	1.5	1.5	The Netherlands	biomanipulation
Linford Lakes	17	1.5	England	biomanipulation
Krankesjön	290	1.5	Sweden	unclear (water level)
Lake Tåkern	3130	1.0	Sweden	unclear (water level)
Lagoon of the Islands	867	2.0	Tasmania	unclear (water level, nutrients)
Lake Christina	1620	1.5	Minnesota, USA	unclear (biomanipulation)
Tomahawk Lagoon	10	0.9	New Zealand	unclear

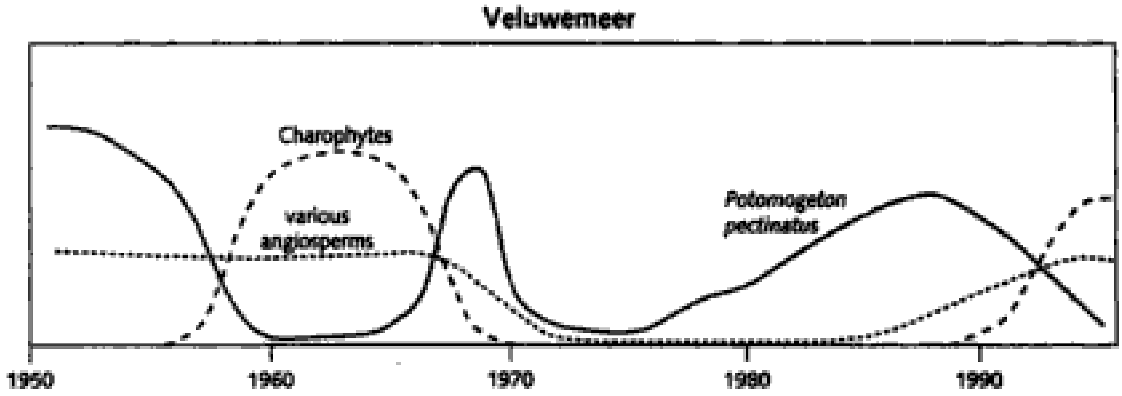


Fig. 1.1 Schematic representation of the changes in the vegetation of Lake Veluwemeer over half a century.

tion, the broad-leafed *Potamogeton perfoliatus* and some charophytes (*Chara* sp. and *Nitellopsis* sp.) were commonly found. In winter large numbers of Bewick's swans (*Cygnus columbianus*) came to forage on the overwintering tubers of these plants.

Soon after the dams were finished the situation changed dramatically. In 1961 the flora and fauna of Veluwemeer was surveyed. The lake was remarkably clear. Sago pondweed had disappeared completely. Instead, a rich vegetation was found dominated by extensive dense mats of charophytes. On the deeper sites a lush and diverse vegetation of angiosperms occurred, while closer to the shores some areas with macro-algae were found. In late summer blooms of a cyanobacteria (*Microcystis aeruginosa*) occurred, but in general algal densities were low. The charophyte stands were rich in water fleas, snails and larvae of the zebra mussel. The swans kept visiting the lake, but were now accompanied by numerous ducks and coots (*Fulica atra*). The fish community in this period is not known well, but pike (*Esox lucius*) and perch (*Perca fluviatilis*) used to be caught by the fisherman. In the adjacent Drontermeer the situation was the same at first glance, but a closer examination revealed that the plants were covered by a conspicuous layer of attached algae (periphyton). Also, the vegetation disappeared much earlier at the end of the year than in Veluwemeer. These and other differences were attributed to the inflow of nutrient rich water from the river IJssel in Drontermeer.

In 1965 the situation in Veluwemeer was still the same, but the vegetation in Drontermeer had started to decline. By 1969 the situation had deteriorated also in Veluwemeer. The water had become turbid, the charophyte beds had disappeared and the vegetation was dominated once again by sago pondweed, with some stands of *Potamogeton perfoliatus*, the same species that occurred during the years before the isolation. Over the following five years summer transparency decreased further to a Secchi-depth of only 0.2–0.3 m. The pondweed beds still covering almost half the lake area in 1969 declined to a few sparse stands of *Potamogeton pectinatus* covering only 10% of the lake in 1975. The algal community was dominated by filamentous blue-green algae (*Planktothrix agardhii*), and wave resuspension of detritus and inorganic sediment particles was an important additional source of turbidity. The formerly diverse fish community now consisted largely of bream (*Abramis brama*), a carp-like species that forages on benthic invertebrates.

Around 1979 the nutrient loading of the lake was reduced, leading to a substantial drop in phosphorus concentration. In addition, the lake was flushed with water pumped out of the new polders, in an attempt to break the year-round blue-green algal blooms. The flushing led to a strong reduction of phosphorus release from the sediment probably due to buffering of the pH by high concentrations of calcium and carbonate in the used polder water. Although the measures led to a reduction in algal biomass of more than 50%, turbidity remained high, in part due to the continuous resuspension of sediment. Over the subsequent decade, transparency increased slowly and the pondweed stands gradually expanded. *Potamogeton perfoliatus* recovered and some other species were seen again.

In the early 1990s charophytes started to recover. They first occurred in small isolated stands, but since 1993 large dense *Chara* beds have been observed, and by 1996 most of the pondweed beds have been replaced by *Chara*. Remarkably, the water in the *Chara* stands had become crystal clear, resembling the situation of 30 years before, whereas the transparency in the rest of the lake was still only a few decimetres in summer. In the following year transparency also increased in the deeper unvegetated parts.

Interestingly, the recent succession of plant species is more or less comparable to the changes that occurred when the lake became isolated in the

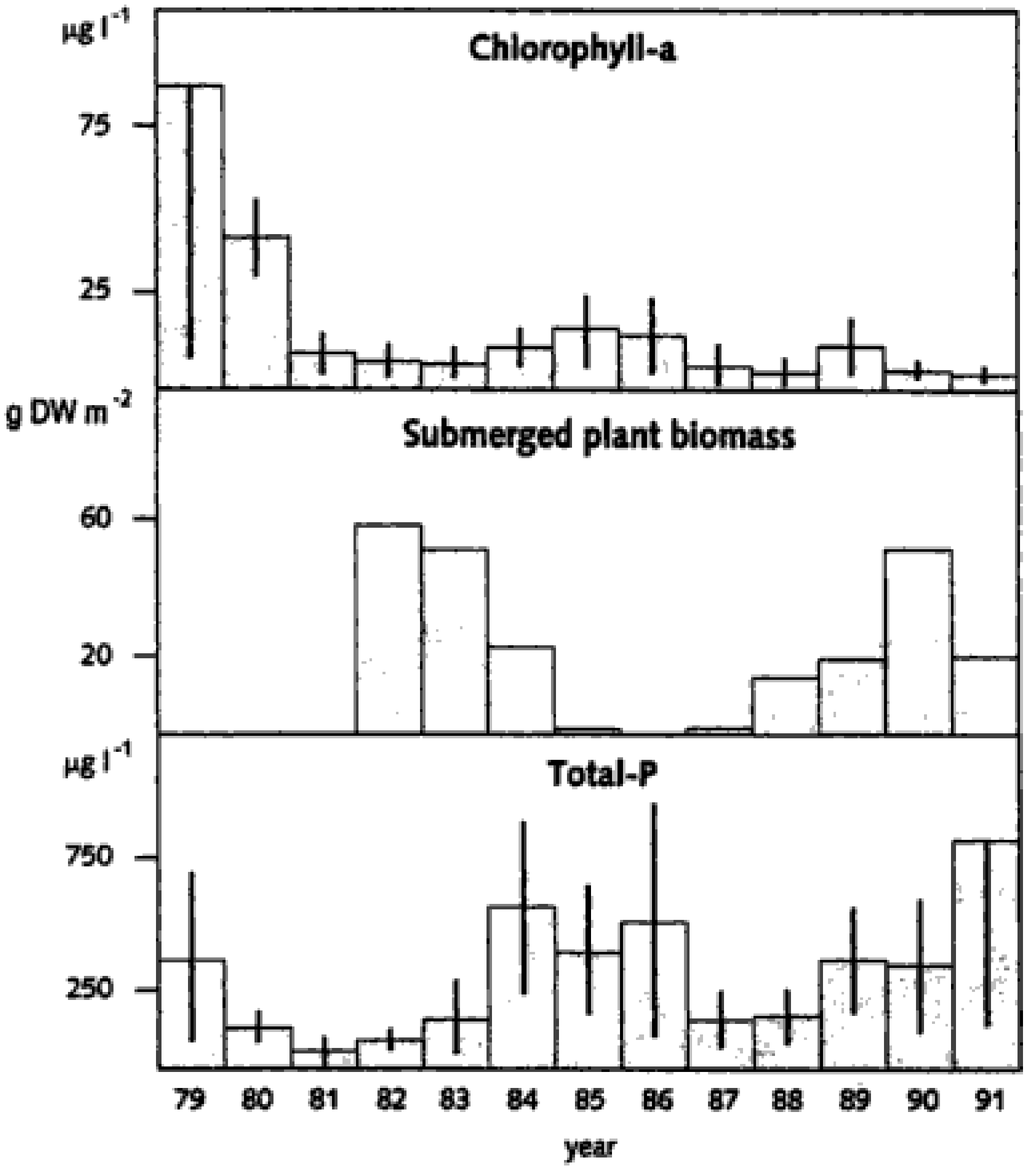


Fig. 1.2 Changes in the mean summer concentrations of chlorophyll-a and total-P and in the biomass of submerged plants in Alderfen Broad, UK, following disconnection of the lake from a nutrient rich inflow stream. Redrawn from Perrow *et al.* (1994).

1950s, while the decline with eutrophication in the late 1960s is the mirror image of these changes (Fig. 1.1).

(Brouwer and Tinbergen, 1939; Leentvaar, 1961; Leentvaar, 1966; Hosper, 1985; Scheffer *et al.*, 1992; Scheffer *et al.*, 1994a; Scheffer *et al.*, 1994b; Noordhuis, 1997; Van den Berg *et al.*, 1997)

Alderfen Broad

Alderfen Broad is one of the fifty or so small lakes in the peaty Norfolk Broadland (UK). These so-called Broads are connected by rivers that also serve to transport the sewage of about 400000 people to the nearby North

Sea. This and the draining of farmland has caused a strong eutrophication of the Broads. Once low in both phosphorus and nitrogen compounds, the lakes now have 10 times their former concentration of these nutrients. The water that according to the locals used to be 'gin-clear' is now turbid and the once famous fields of submerged plants are largely gone.

Alderfen Broad is surrounded by a wetland dominated by alder (*Alnus glutinosa*). It had clear water and a dense submerged vegetation (mainly *Ceratophyllum demersum*) until at least the late 1960s, but in the next decade it lost its aquatic plants completely and became turbid due to high algal biomass. This was linked with discharge of sewage effluent to the inflow stream. In 1979, the inflow stream was diverted into existing ditches from where the water rejoined the outflow stream below the lake. This isolation led to a sequence of conspicuous changes in the lake over the next 12 years (Fig. 1.2).

The total phosphorus concentration as well as the release of phosphorus from the sediments declined considerably over the first three years, and this led to a substantial decrease of algal biomass. During 1982 and 1983 a dense vegetation of *Ceratophyllum* was found and the phytoplankton populations remained low. In 1984, however, vegetation was less abundant and the phosphorus level in the lake water had become high again. Very few plants were found over the next three years. Some blooms of blue-green algae (*Anabaena spiroides*) developed in 1985 and 1986, but on average phytoplankton biomass remained relatively low during these years, probably because of nitrogen limitation. From 1987 onwards vegetation expanded again and algal biomass dropped to lower levels. With the increase in vegetation, phosphorus concentrations also rose again to reach a peak value in 1991 when vegetation biomass was once again declining.

The observed pattern (Fig. 1.2) suggests a cycle with a period of about 8 years. It is not clear what drives the decline of the vegetation. It seems unlikely that turbidity prevented plant growth in the 1985–1987 period. Conspicuous absence of plants has been observed in several other clear Broads, suggesting that another factor is at work.

(Moss *et al.*, 1986; Moss *et al.*, 1990; Perrow *et al.*, 1994.)

1.2 STORM EFFECTS

Lake Apopka

The large and shallow Lake Apopka (128 km^2; mean depth 1.65 m) is situated in Florida. The lake was well known as an outstanding sport fishing lake with exceptionally clear water and dense beds of aquatic plants until the autumn of 1947 when a hurricane wiped out the vegetation. Soon after this catastrophic event the first phytoplankton bloom was observed. Over the following 4 years the total fish stock was estimated to have increased 10-fold, and game fish populations had greatly expanded. By 1957, however, the omnivorous shad had become the dominant fish species in the lake and the abundance of game fish had strongly decreased. Rotenone applications killed an estimated total of 9 million kg of shad during the late 1950s in an unsuccessful attempt to restore the game fish dominance. Today the lake is still turbid and vegetation has not recovered since the hurricane of 1947. A thick layer (1.5 m) of unstable sediment is involved in frequent resuspension, and turbidity of the water increases strongly during windy periods.

(Schelske and Brezonik, 1992; Schelske *et al.*, 1995; Schelske *et al.*, 1997.)

Lake Ellesmere

The story of the New Zealand Lake Ellesmere is comparable to that of Lake Apopka. During the 1950s and 1960s the lake was known to harbour a population of up to 80000 black swans (*Chenopsis atrata*) living on the abundant aquatic vegetation. In 1968, however, a violent storm killed 5000 swans. Probably more importantly, the storm annihilated the extensive weedbeds in this huge unprotected lake. Vegetation has not recovered since then, and waves stir up the sediments most of the time. Together with high concentrations of phytoplankton this suspended sediment causes the lake to be very turbid. By 1986 only 4000 swans resided in the lake, a mere 5% of the original population.

(Mitchell *et al.*, 1988; McKinnon and Mitchell, 1994; Hamilton and Mitchell, 1996.)

1.3 WATER LEVEL CHANGES

Tämnaren

The large ($35\,km^2$) and shallow (now 1 m mean depth) Lake Tämnaren is situated 120 km northwest of Stockholm in a flat part of Sweden dominated by forests and farmlands. It used to be common in these areas to reduce the lake levels to minimize flooding of farm areas. Farming also increased the nutrient loading of the originally oligotrophic lakes, and caused the sparse plant stands to be replaced by a lush aquatic vegetation in many cases.

The water level of Lake Tämnaren was intentionally lowered twice. The first time, in 1870, by 1 m, and the second time, in 1950–54, by another 0.5 m. After the last draw-down, aquatic macrophytes expanded strongly, and the lake became famous for its waterfowl. In the spring and autumn many migratory birds flocked in great numbers in the lake and in summer about 500 mute swans (*Cygnus olor*) used to live there. The water was clear enough to see the bottom anywhere in the lake. The lush vegetation, mapped in 1973, was dominated by *Elodea canadensis* and by floating leafed species (*Nuphar lutea* and *Potamogeton natans*).

In the spring of 1977 the water level rose 0.3 m leading to dramatic changes in the community. The swans as well as many other birds disappeared from the lake and the submerged and floating leafed vegetation as well as a large part of the emergent vegetation vanished. Aerial photographs taken in 1973 and 1983 revealed that the total vegetation coverage, including reed, was reduced from 80% to 14% of the lake area. The water had become turbid with a Secchi-depth of only 0.6 m. This turbidity was partly due to an increased phytoplankton density (up to 70 µg l^{-1}), but resuspended sediments contributed strongly as well.

(Wallsten and Forsgren, 1989; Bengtsson and Hellström, 1992.)

Rice Lake

Rice Lake is a medium-sized shallow lake in Wisconsin (USA), named for the extensive beds of wild rice (*Zizania*) that used to grow along the shores together with cattails (*Typha*) and bulrushes (*Scirpus*). Pollen analysis shows that quillwort (*Isoetes*) used to grow in the lake, a species that requires very clear water. Aerial photographs since 1938 and testimony from local residents suggest that the lake stayed clear until the 1970s when high water flooded the wild rice. The high water, promoted by a newly constructed beaver dam in the outlet creek allowed summer winds to sweep across the lake unabated by the flooded vegetation. Waves eroded the bottom, tearing away chunks of marsh that subsequently disintegrated, producing a soft sediment. The erosion of the marsh vegetation was further promoted by a peculiar interplay of freezing and water level dynamics. Water levels rose in March when the lake was still frozen. This lifted the ice cover within the marsh border, pulling up mats of rhizomes and roots. Wind and wave action in early spring pulled out the frozen mats to form floating islands. Many islands drifted downstream and grounded in the outlet creek. This caused the water levels to rise even higher, making the situation worse.

A decade later the water levels fell, but the wild rice never recovered and the lake has stayed turbid. Secchi-depth in summer is now only 0.3 m on average. This is only partly caused by phytoplankton, reaching a maximum of only 40 µg Chl l^{-1} during blooms of green algae. Probably, resuspension of sediment by waves and fish is a more important source of turbidity. The sediment of Rice Lake is now so loose and flocculent that a steel pipe shoved into the lake bottom hits firm bottom only after penetrating 6 m of this soft sediment. The role of wave resuspension is illustrated by the large difference in suspended solid concentration during ice cover (<2 mg l^{-1}) and during ice free periods (59 mg l^{-1}). The present submerged vegetation is very sparse, 90% of which is sago pondweed (*Potamogeton pectinatus*). Cattail dominates the shore vegetation, and some stands of water lilies and floating leaf pondweed are found along the shores.

(Engel and Nichols, 1994.)

1.4 FISH STOCK MANAGEMENT

Zwemlust

Zwemlust is a very small shallow lake in the centre of The Netherlands. In summer it is used as a swimming pool. The lake receives water through seepage from the polluted River Vecht running closely along the lake. As a result the nutrient loading of the lake is high. The chlorophyll-a concentration in the lake was as high as 250 mg l^{-1} and blooms of blue-green algae (*Microcystis*) frequently turned the lake bright green. After several unsuccessful attempts to improve the water quality it was decided to manipulate the fish stock. This measure had spectacular results (Fig. 1.3).

In March 1987 the water was pumped out of the lake to facilitate complete removal of the fish. It appeared that 1000 kg ha^{-1} of fish had been present, 75% of which was bream. Seepage refilled the lake in three days, and a small fish stock of pike and rudd (*Scardinius erythrophtalmus*) was introduced together with water fleas and some charophytes and yellow waterlilies. Shortly after the refill there was an algal bloom, but soon large water fleas became abundant and grazed down algal biomass to a mere 2% of the pre-manipulation values and the water became crystal clear. Some filamentous green algae (*Hydrodictyon*; *Enteromorpha*) developed in the shallower parts, but only a small part of the lake bottom became covered by macrophytes in the first summer.

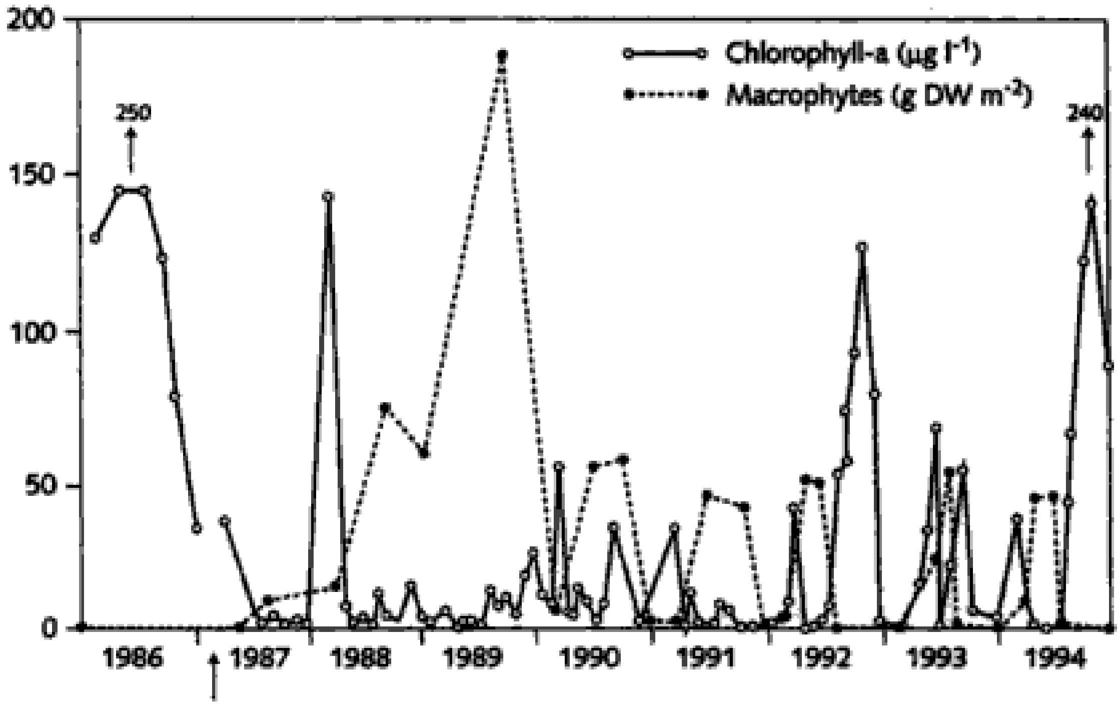


Fig. 1.3 Seasonal variation in chlorophyll-a concentrations and vegetation biomass in Lake Zwemlust, The Netherlands, in the years following a strong reduction of the fish stock in the winter of 1986–87. Redrawn from Van Donk and Gulati (1995).

In 1988 a spring bloom of phytoplankton occurred, but by the end of April the algae were grazed down by a rapidly expanding zooplankton population again. That summer the submerged vegetation expanded strongly, covering more than 50% of the lake bottom. Probably as a result of this, ammonium and nitrate levels in the lake water dropped to below detection levels and the phytoplankton became nitrogen-limited. Zooplankton declined due to low food concentration and quality, but the water remained clear. That summer a very large population of snails (*Lymnaea peregra*) developed. This snail is an intermediate host of a bird-parasitizing trematode which can cause an itching when penetrating human skin. In July 40% of the bathers complained about this so-called swimmer's itch (*Schistosome dermatitis*).

The next year, *Daphnia* populations that had persisted during the winter had already risen strongly by March. Despite the high nutrient levels, no spring bloom of algae occurred and chlorophyll concentrations remained around detection level. The submerged vegetation covered around 80% of the lake bottom that summer, causing phytoplankton to be nitrogen-limited again. After the decline of water fleas in early summer other small crustaceans that live in close association to the aquatic plants became the dominant phytoplankton grazers. Because macrophytes were a nuisance for the swimmers, plants were removed from the swimming area in June and September. Snail density decreased by an order of magnitude in that area, and complaints about swimmer's itch stopped.

From 1990 to 1995 the situation changed only gradually. The fish stock increased in the first 3 years after the initial manipulation to a biomass of about 400 kg ha^{-1}, but the species composition became strongly different from that in the turbid pre-manipulation state. Also, the species composition of the vegetation shifted. *Ceratophyllum demersum*, a species with hard unpalatable leaves, became the dominant submerged plant in 1990 and 1991. Exclosure studies suggest that this shift in dominance was caused by selective grazing by coots (Fig. 1.4) and rudd on *Elodea*.

In 1993 and 1994, however, *Potamogeton berchtoldii*, one of the first colonizers, dominated the vegetation again. This plant was overgrown by epiphytic algae more than other species in the lake, and its biomass declined relatively early in the season. A moderate spring peak of phytoplankton occurred each year, but summer algal biomass was invariably low over the entire period. The main change in phytoplankton dynamics has been that from 1992 onward the decline of vegetation at the end of summer is followed by blooms of blue-green algae (*Microcystis*).

(Van Donk *et al.*, 1990; Van Donk *et al.*, 1993; Van Donk *et al.*, 1994a; Van Donk and Gulati, 1995.)

Linford lakes

The Great Linford sand and gravel-pit complex covers an area of about 300 ha in the flood plain of a river near Newport Pagnell (UK). The site

Fig. 1.4 Coot (*Fulica atra*) are largely herbivorous. In the breeding season birds are territorial and population densities are usually not very high. However, in the autumn and winter large numbers of animals may concentrate in lakes and reduce the biomass of aquatic vegetation.

encompasses 14 lakes which have been excavated over the past four decades. Two distinct ways of gravel extraction were used in this area: wet-digging and dry-digging. When a new quarry is opened, groundwater enters. The wet-digging method proceeds by sucking the gravel from the bottom with a suction dredger and depositing it in a floating barge. The gravel rapidly settles out and the silt laden water flows directly back into the newly forming lake. There the fine silt forms a thick layer of loose sediment. During the process of dry-digging the entering groundwater is continuously pumped out of the quarry. The excavated material is transported to a washing and grading plant where the washings are run off into special silt settlement lagoons. When pumping ceases the dry-dug lakes fill up with water.

These different digging methods have resulted in two different lake types in the area. Wet-dug lakes have typically remained turbid, even though most of them have been left undisturbed for over 20 years. They have very little submerged vegetation and the sediment is flocculent and easily resuspended by waves. During storms the lakes turn chocolate brown, with suspended solid concentrations of up to $0.2\,g\,l^{-1}$. The dry-dug lakes, on the other hand, are clear and densely vegetated. They also have many more birds than the wet-dug lakes. This led workers of the Game Conservancy research station to try to determine why the turbid lakes are a poor habitat for ducks and other waterfowl, and find out ways of changing this.

One of the wet-dug lakes that has been studied in some detail is Main Lake. The lake was very turbid during a survey in 1982 and less than 1% of its area was found to be vegetated. Sago pondweed was the only recorded species. In the winter of 1987–88 the lake was pumped down and almost the entire fish stock was removed with seine nets. It appeared that about $356\,kg\,ha^{-1}$ of fish, mainly bream and roach (*Rutilis rutilis*), had been present. The following years vegetation expanded spectacularly (Fig. 1.5) to reach a coverage of 93% in 1989 when *Elodea canadensis* had become the dominant species.

At the same time, the density of midge larvae and snails increased markedly (Fig. 1.5). These changes were followed by a sharp increase in the number of overwintering coots, ducks and swans. Also, the nesting success of ducks increased, as early survival of ducklings improved, presumably because of a better food situation. Transparency of the lake water increased strongly after the fish removal. This was in part due to an increase in large water fleas (*Daphnia* spp.) that graze on phytoplankton, but after the development of vegetation the resuspension of sediment by waves has also decreased.

In 1990 a bay was isolated from the rest of the lake by nets and stocked with the original fish community. This led to a reversal of the changes observed after the fish removal. Vegetation development was strongly suppressed again in the bay and the densities of midge larvae and snails dropped to their original values (Fig. 1.5). In the main lake, however, the clear and vegetated state has persisted (Traill-Stevenson pers. comm.).

(Giles, 1987; Hill *et al.*, 1987; Wright and Shapiro, 1990; Giles, 1992.)

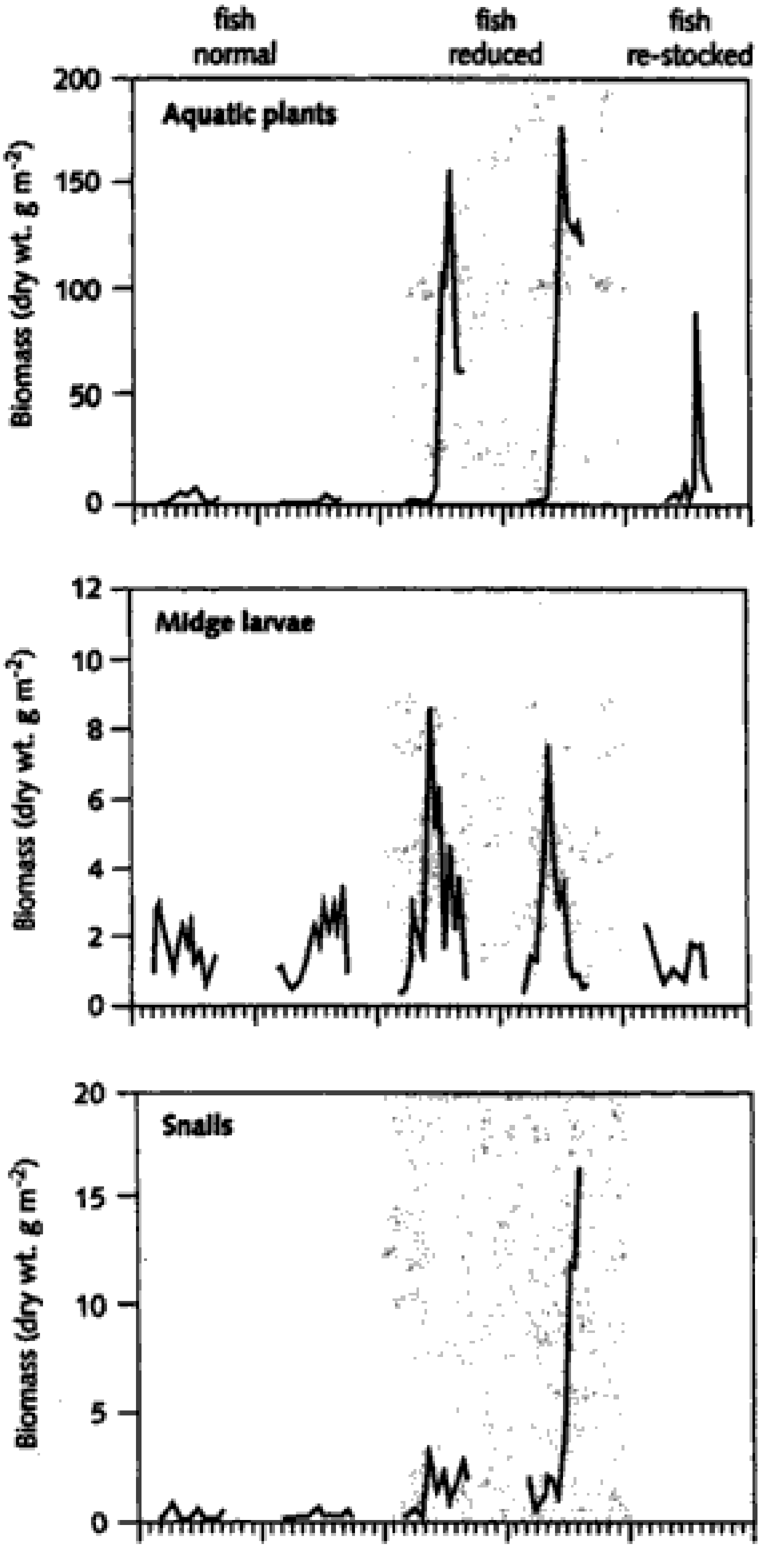


Fig. 1.5 Effect of a removal of fish and subsequent restocking on the biomass of aquatic vegetation, midge larvae and snails in Main Lake, Great Linford, UK. Redrawn from Giles (1992).

1.5 MISCELLANEOUS CASES

Lakes Tåkern and Krankesjön

The southern Swedish lakes Tåkern and Krankesjön have changed repeatedly from a clear state with abundant vegetation to a turbid state with few submerged plants and vice versa over the last century (Fig. 1.6).

Early data on the vegetation are sparse, but waterfowl that are associated with plants have been continuously recorded, and these data were used as an indirect indicator of vegetation abundance. In neither of the lakes are changes in the external nutrient loading thought to have occurred. Instead, variations in the water level seem to be involved in causing the switches from one state to the other.

Lake Tåkern was largely covered by a dense vegetation dominated by charophytes at the beginning of the century. In 1914 after a dry period, the vegetation disappeared from the lake, but rapidly recovered again. In the early 1930s, large parts of the lake dried out. This desiccation and subsequent freezing of the bottom in winter are thought to have caused the complete disappearance of submerged plants during these years. Within a few years, however, a dense vegetation had returned. In the early 1950s submerged plants disappeared completely again and the water became turbid. This time there was no obvious cause of the changes. At the beginning of the 1960s the vegetation recovered starting with stands of angiosperms and some charophytes. In 1969 the charophytes had expanded into dense mats covering large parts of the lake again. The lake has stayed clear and vegetated until 1995 when summer transparency decreased and the condition of the vegetation deteriorated. The next year this downward trend continued, leaving the lake in a turbid and poorly vegetated state once again.

Like Lake Tåkern, Lake Krankesjön was covered by a charophyte dominated vegetation at the beginning of the century. In the 1940s, vegetation disappeared for some years, presumably due to low water levels in winter that allowed the bottom to freeze, eliminating the plants. However, vegetation recovered soon, and the lake stayed clear and densely vegetated till the early 1970s. Inspection in 1975 revealed that submerged macrophytes had disappeared entirely. Exceptionally high water levels during the growing

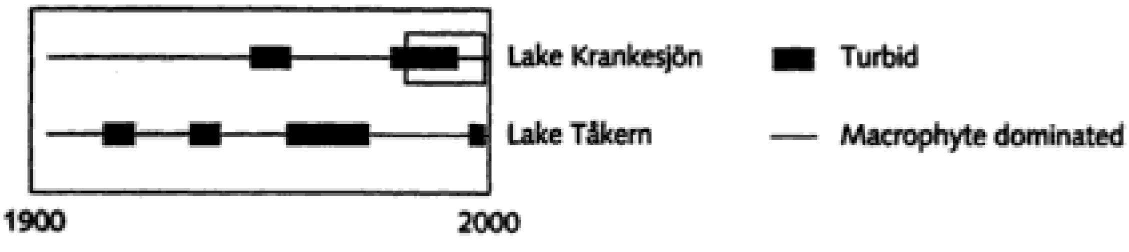


Fig. 1.6 Repeated shifts between a turbid state (thick line) and a clear vegetation dominated state (thin line) in the Swedish lakes Krankesjön and Tåkern. The window marks the period represented in Fig. 1.7. Modified from Blindow *et al.* (1993).

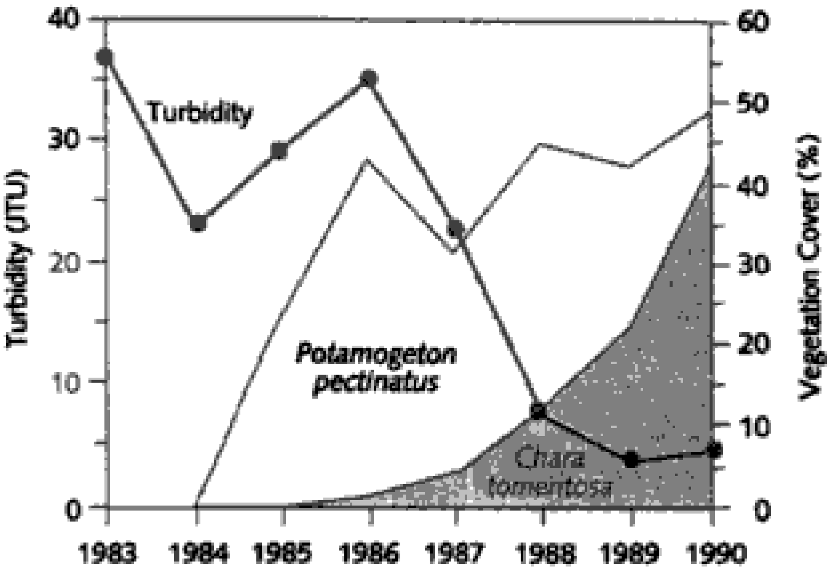


Fig. 1.7 Shift from a turbid state to a vegetation dominated clear situation in Lake Krankesjön. Redrawn from Hargeby *et al.* (1994).

season may have shaded out the vegetation, although the absence of ice cover during mild winters resulting in strong wave erosion is another possible explanation.

From 1983 onward the lake has been monitored more closely revealing the scenario of a subsequent vegetation recovery episode in some detail. It is unclear what initiated the recovery, but low summer water level allowing more light to penetrate to the bottom, and a disease causing a reduction of the bream population are mentioned as possible causes. Despite the fact that the sediment contained very high densities of oospores of charophytes the first macrophyte to expand was sago pondweed (*Potamogeton pectinatus*) (Fig. 1.7).

Only after some years, the relatively sparse stands of pondweed were replaced by exponentially increasing dense mats of charophytes, leaving angiosperms to play a minor role. Turbidity decreased only slightly during the expansion of pondweed, but subsequently dropped almost an order of magnitude during the expansion of charophytes. A decrease was also observed in the chlorophyll-a and total phosphorus levels and in the density of large herbivorous zooplankton. Conspicuous changes occurred in the bird community. During the turbid years, only some fish-eating birds resided in the lake. With the increase of vegetation biomass, however, the number of coots and swans (Fig. 1.8) and the populations of dabbling ducks increased steeply.

(Blindow, 1992b; Blindow *et al.*, 1993; Hargeby *et al.*, 1994.)

Lagoon of the Islands

Lagoon of the Islands on Tasmania (Australia) used to be a natural swamp known for its islands of floating reed mats supporting terrestrial plants. In

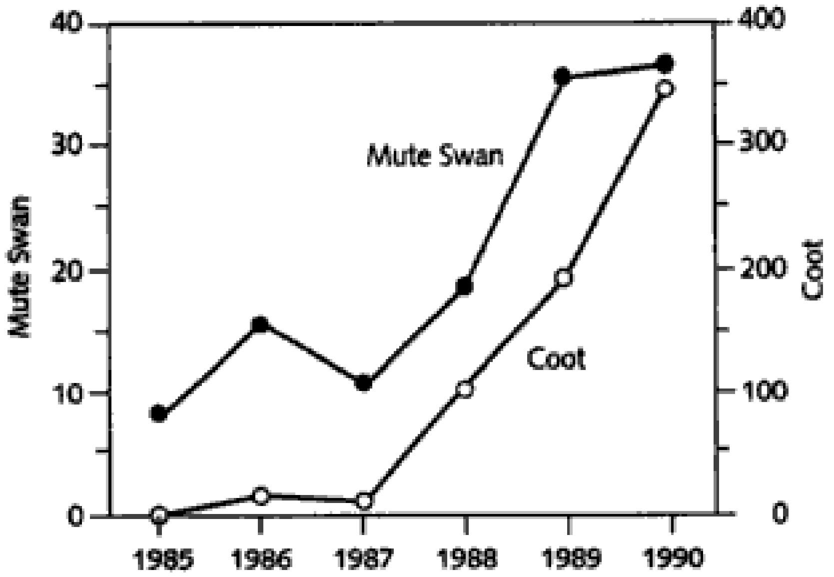


Fig. 1.8 Increase in swan and coot numbers following vegetation recovery in Lake Krankesjön. Redrawn from Hargeby *et al.* (1994).

1964 a dam was constructed turning the swamp into a shallow (2.5 m mean depth) reservoir, intended to create a storage of irrigation water, and a place for trout fishery. The majority of the original macrophytes died as a result of the flooding, but other submersed vegetation colonized the lake bottom. Over the following two decades, trout fishery flourished, but due to its small storage capacity the lake was found to be an unreliable source of irrigation water. In 1984, a canal was constructed to divert water into the storage from a nearby creek. Subsequently, high water levels were maintained at the lagoon for several years. In the summer of 1987–88 the water quality declined and so did the condition of the trout. The problems which persisted during the next year were thought to be due to a suppression of macrophyte growth caused by the increased water levels and elevated nutrient loading. These factors caused a switch from a diverse macrophyte dominated community, to a simpler one dominated by phytoplankton, and apparently unfavourable for the production of trout. It was therefore decided to switch to a management regime of lower water levels. This has led to a recovery of the macrophytes, water quality and trout fisheries.

(Sanger, 1992; Sanger, 1994.)

Lake Christina

Lake Christina is a large and shallow prairie lake in Minnesota (USA). The lake freezes in winter, and ice is out usually by the beginning of April. In the autumn, it is heavily used by migrating waterbirds. The lake was one of the most important feeding and staging areas for migrating diving ducks in the so-called Mississippi flyway during the first half of the century. The lake supported lush beds of aquatic plants in this period, and the water was clear. By 1959, however, transparency had rather suddenly declined to <25 cm,

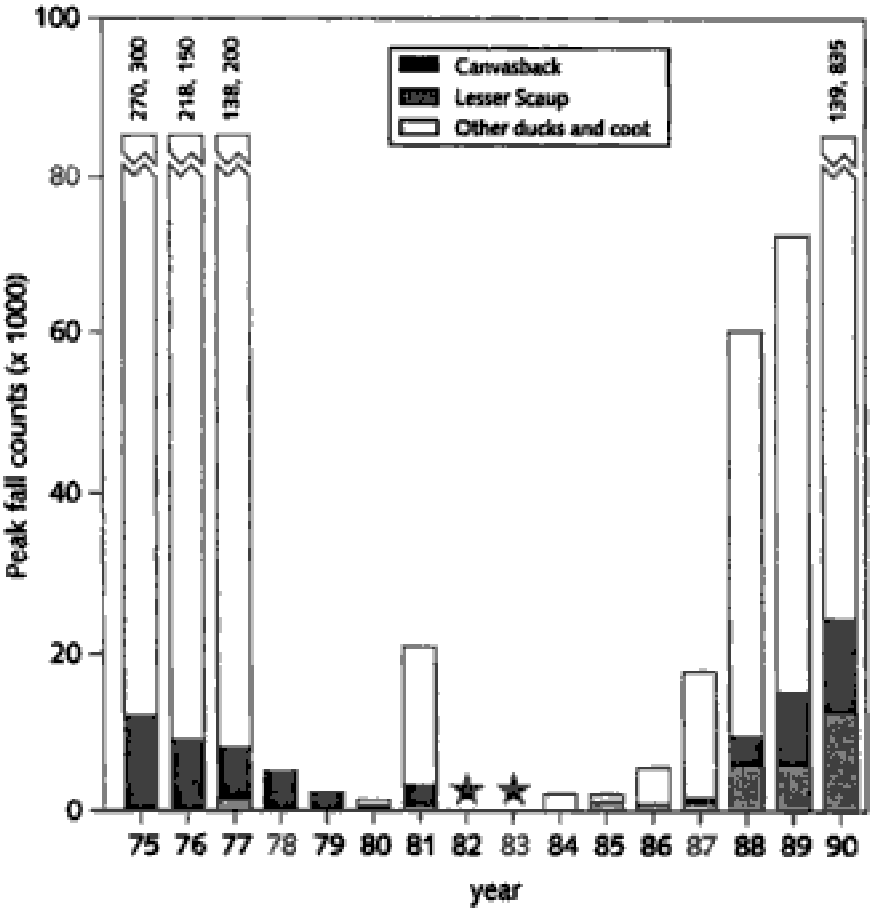


Fig. 1.9 Trends in peak autumn waterfowl counts in Lake Christina, Minnesota, USA. The period of low waterfowl numbers from 1978 till 1987 corresponds to a period with little vegetation and turbid water. Redrawn from Hanson and Butler (1994b).

vegetation had become very sparse and bird numbers had dropped about 2 orders of magnitude. These changes were probably associated with higher water levels and much larger fish populations. The latter may result in part from the high water, as winter-kills of fish during periods of ice-cover are less likely in deeper water. In 1965, state biologists eliminated part of the fish using toxaphene, and water clarity, macrophytes and duck numbers increased. In the mid 1970s, however, water transparency and vegetation abundance declined again. Peak autumn counts of waterfowl dropped spectacularly from more than 130000 in 1977 to less than 5000 in the following years (Fig. 1.9).

In the autumn of 1987 all fish in the lake were killed by spraying 62700 l of rotenone from the air. Most of the original species reinvaded the lake relatively quickly, but predatory fish (largemouth bass and walleye) was stocked regularly in an attempt to slow down the recovery of the fish biomass. During May and June of the following year transparency of the water increased to about 90 cm in contrast with the 30–40 cm in the years before the fish manipulations (Fig. 1.10).

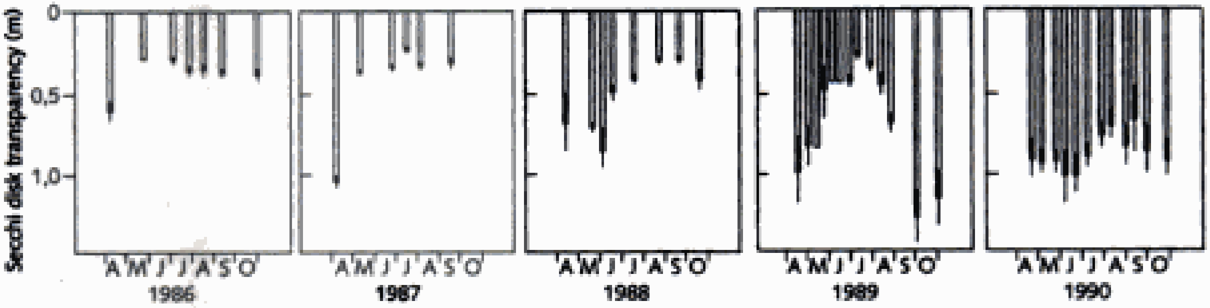


Fig. 1.10 Seasonal dynamics of Secchi-depth transparency during a period of vegetation recovery (Fig. 1.2) in Lake Christina, Minnesota, USA. The fish stock has been reduced in the autumn of 1987. Redrawn from Hanson and Butler (1994a).

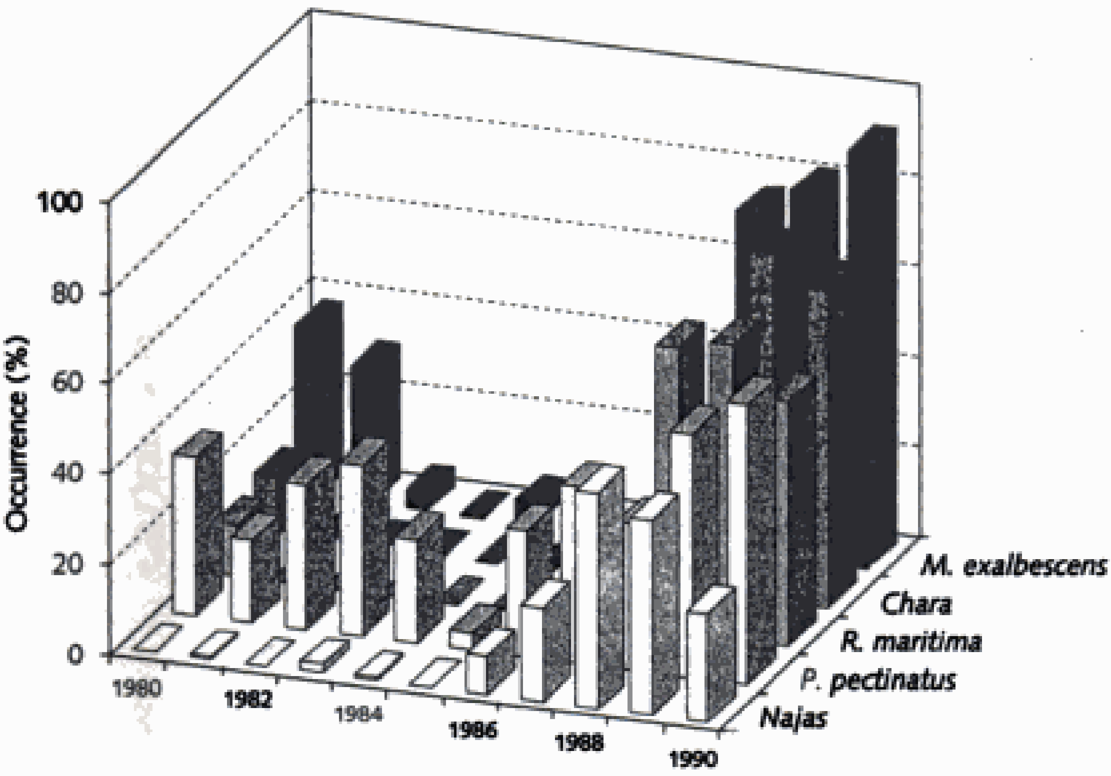


Fig. 1.11 Recovery of the aquatic vegetation between 1980 and 1990 in Lake Christina, Minnesota, USA. Redrawn from Hanson and Butler (1994a).

This spring clear water phase was caused by an increase of large bodied herbivorous water fleas (*Daphnia*) that were estimated to have a filtration potential of 100–200% of the lake volume per day, as opposed to <10% during the years before the fish kill. In summer *Daphnia* populations decreased, filtration rates dropped and turbidity increased. Nonetheless, vegetation expanded that year and became more diverse (Fig. 1.11), including the originally common sago pondweed and *Ruppia maritima*, but also large stands of charophytes, *Myriophyllum exalbescens* and *Najas flexis*.

The same pattern of plankton dynamics occurred in the second year but, unlike before, the water became clear again in September. Remarkably, it

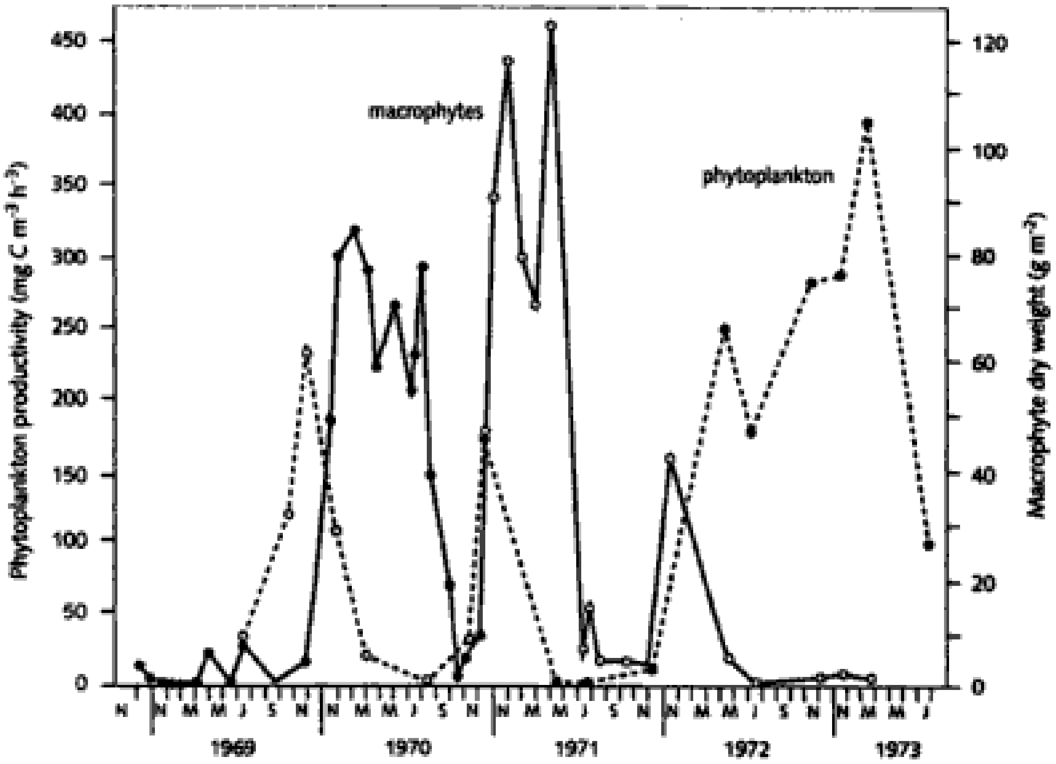


Fig. 1.12 A shift from phytoplankton dominance to vegetation dominance in Tomahawk Lagoon, New Zealand. Note that at the southern hemisphere the summer is in December–February. Redrawn from Mitchell *et al.* (1988).

stayed clear throughout the next year. With the return of the vegetation, waterfowl numbers recovered as well (Fig. 1.9). The following years, the lake stayed vegetated and rich in waterfowl. Since 1995 transparency has gradually declined again although vegetation has remained quite abundant.

(Hanson and Butler, 1990; Hanson *et al.*, 1990; Hanson and Butler, 1994a; Hanson and Butler, 1994b, Hanson pers.comm.).

Tomahawk Lagoon

Tomahawk Lagoon is a small and very shallow lake on South Island, New Zealand. The lake is fed by a stream draining mainly pastures. Due to the oceanic climate the lake rarely freezes for more than a few hours, and summer temperatures are usually below 20°C. During 1963 when studies started and the following year, the lake was turbid with high phytoplankton densities and few macrophytes. In 1965, however, it became clear with abundant macrophyte growth, until 1970 when it became turbid again for two years, switching back to a clear and vegetated state in 1972. During periods when vegetation dominated the lake, phytoplankton density was as much as two orders of magnitude lower than in the years when vegetation was sparse. In years with abundant vegetation large numbers of black swans foraged on the plants in the lake. This herbivory contributed to the decline of vegetation in some periods, but the more dramatic vegetation declines must have been due largely to other factors, storms being a possible candidate.

From 1969 to 1973 the seasonal dynamics of plankton and macrophytes were studied more closely (Fig. 1.12).

These studies revealed the details of a switch from a turbid to a vegetation dominated state. In the spring, both macrophyte biomass and phytoplankton productivity usually increase. During the first two years of the study the macrophyte development was short lived and a dense phytoplankton bloom developed over the summer. In the third year, however, the spring bloom of algae collapsed and vegetation became abundant for the rest of the summer. In the autumn of that year charophytes started to become dominant. Vegetation biomass remained high over the winter and expanded further in the subsequent year, when no phytoplankton peak occurred. Vegetation was thought to suppress the phytoplankton development. No single clear mechanism could be revealed, but during some periods nitrogen-limitation of the algae could be demonstrated, while at other times the grazing pressure by zooplankton living between the plants was shown to be important.

It is not quite clear what causes the switches from phytoplankton dominance and vice versa. Herbivory by black swans and storms are thought to be involved in vegetation decline, while collapse of phytoplankton blooms may be related to zooplankton grazing and to pulses of highly turbid inflow during rainy periods.

(Mitchell *et al.*, 1988; Mitchell, 1989; McKinnon and Mitchell, 1994.)

2 The abiotic environment

2.1 LIGHT UNDER WATER

Turbidity of the water is a central topic in the discussions throughout this book. Lack of clarity caused by algal blooms and suspended sediment strongly affects the general appearance of a lake. Importantly, it also affects many biological mechanisms. Therefore, understanding the functioning of shallow lake communities requires a basic understanding of under-water optics. Only the main points are treated here. A good comprehensive treatment can be found in Kirk (1994).

Absorption and scattering

Only two things can happen to a photon under water; it can be absorbed or it can be scattered into a different direction. Absorption can be characterized by the absorption coefficient a (m^{-1}), while scattering is characterized by the scattering coefficient b (m^{-1}) and the angular distribution of the scattering (Kirk, 1994). These are the so-called inherent optical properties. They are defined for a thin layer of water illuminated by a narrow beam of monochromatic light as: the fraction (a) that is absorbed divided by the width of the layer, the fraction (b) that is scattered out of the beam divided by the width, and the angular distribution of the scattered light. The fraction removed from the incoming beam by absorption and scattering together is called the beam attenuation coefficient ($c = a + b$).

Although water itself contributes to the absorption and scattering of light, the optical properties of turbid lakes depend largely on suspended particles and dissolved substances. Absorption is due to all coloured material. In some lakes, notably with peaty sediments, dissolved organic substances ('gilvin', 'gelbstoff') can play an important role, giving a dark brownish colour to the water, but in many shallow lakes, light is predominantly absorbed by particulate matter such as phytoplankton cells, detritus and suspended sediment particles. Since the absorbing material is coloured, absorption is not the same for all wavelengths, and some colours will always penetrate deeper than others (Fig. 2.1).

Scattering in lakes hardly depends on the colour of the light (Kirk, 1994). Materials differ strongly in their relative contribution to scattering and absorption. Suspended clay particles, for instance, predominantly cause scattering, while dissolved organic substances only cause absorption and phytoplankton contributes to both scattering and absorption. The total scattering and absorption coefficients at a given wavelength are simply the sums of the individual contributions of water, gilvin, phytoplankton, suspended sediment, etc. (Prieur and Sathyendranath, 1981).

Absorption and scattering are well defined and measurable but unfortunately of little interest per se. In practice, limnologists are more interested in so-called 'apparent' optical properties such as the attenuation of light with depth and the visual transparency. Although these apparent optical properties can in principle be understood as the result of absorption and scattering, the relationship between inherent and apparent properties is rather intricate.

Light attenuation with depth

The intensity of light diminishes with depth in an approximately exponential way (Fig. 2.1):

$$I_z = I_0\, e^{-Ez} \tag{1}$$

where I_z and I_0 are the intensities of light at depth z and just below the surface respectively, and E is the vertical attenuation coefficient for downward irradiance.

Usually light intensities are measured only over the range of wavelengths that can be used by plants for photosynthesis. This portion of the light is

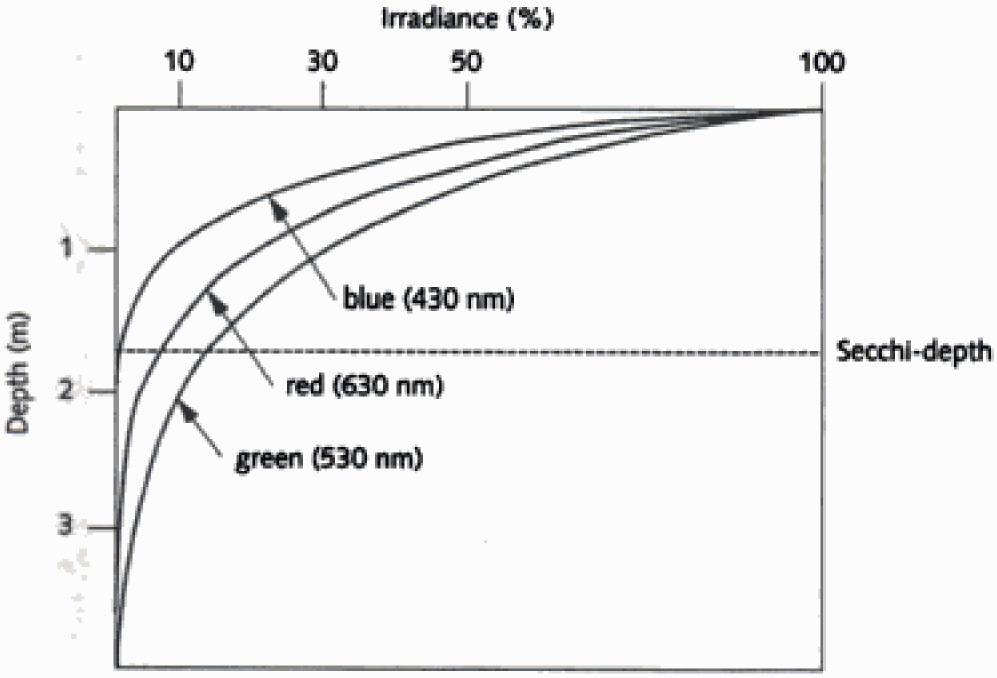


Fig. 2.1 Attenuation of irradiance with depth in each of three spectral blocks in Crose Mere, UK. Irradiance in each spectral block is expressed as percentage of the irradiance in the corresponding spectral block just beneath the water surface. Redrawn from Reynolds (1984).

called the Photosynthetic Active Radiation (PAR). The vertical attenuation coefficient is often denoted as K_d. However, since K is reserved in this book for the carrying capacity in logistic growth equation, E is used throughout the text to prevent confusion. A problem with the use of E for characterizing light attenuation is that its value is different for light of different colours (Fig. 2.1). Green light usually penetrates the water column deeper than other colours that can be used for photosynthesis. As a result of this differential light attenuation, the attenuation coefficient measured over the PAR spectrum as a whole is not constant over depth. The colours that are absorbed the most attenuate first, and, consequently, the remaining light penetrates the water better. As a result, E diminishes with depth. Fortunately, this effect appears to be relatively small in turbid waters (Kirk, 1994). Therefore, the vertical attenuation coefficient (E) of PAR is, as Kirk states (Kirk, 1986): 'the best single parameter in terms of which to compare the light-attenuating properties of one water-body with another'. It follows that E can be roughly characterized from a simultaneous measurement of the irradiance at depth z and just under the water surface:

$$E = \frac{In \frac{I_0}{I_Z}}{Z} \tag{2}$$

The attenuation of radiation with depth depends on scattering as well as absorption, but is not simply the sum of the two (called the beam attenuation, c). Scattering does not remove light as absorption does; it merely changes its direction. Because of this, scattering increases the average path-length travelled by an incoming photon to reach a given depth, and therefore the chance of being absorbed. In addition, a small proportion is scattered in a backward direction, and the fraction of this back-scattered light that is not reflected downward again by the surface leaves the water.

For monochromatic light there is a simple empirical relationship between E and the coefficients of absorption (a) and scattering (b):

$$E = \frac{1}{\mu_0}\sqrt{a^2 + (0.425\mu_0 - 0.19)ab} \tag{3}$$

where μ_0 is the cosine of the angle of the underwater light to the vertical (Kirk, 1994). To obtain an impression of what this implies for an average condition in the temperate climate zone we can substitute the value of 0.8 for μ_0, giving:

$$E = 1.25\sqrt{a^2 + 0.15ab} \tag{4}$$

Thus light attenuation depends largely on the absorption coefficient but also increases with the product of scattering and absorption. It can be seen from this formula that scattering only affects vertical light attenuation through the interaction with absorption. If absorption is nil, scattering does not cause an attenuation of light. This is because, as explained earlier, scattering merely increases the path-length of photons under water. Absorption along the way is needed to let this affect the vertical light attenuation.

Secchi-depth

The simplest way to characterize the optical properties of lake water is by means of a so-called Secchi-disc. This approach, systematically studied more than a century ago by the Italian physicist Angelo Secchi, is still widely used. A black-and-white disc is lowered into the water, and the depth at which it just disappears from view is noted as the Secchi-depth. A problem of the use of Secchi-depth is that in clear shallow lakes, the bottom can be visible throughout the lake. In that case Secchi-depth is not measurable. However, the method is simple and relatively robust, and, not surprisingly, data on the Secchi-depth of waters are abundant.

Unfortunately Secchi-depth (S_d) is not a very good indicator of light penetration into the water. On the basis of measurements in marine waters, Poole and Atkins (1929) noted an inverse relationship between E and S_d:

$$S_d = \frac{c_p}{E} \tag{5}$$

However, the Poole Atkins coefficient, c_p, appears to vary strongly (roughly around 2) from case to case. Later workers showed that the relationship between Secchi-depth and light attenuation can be more accurately described if the beam attenuation coefficient ($c = a + b$) is taken into account (Tyler, 1968):

$$S_d = \frac{9}{c+E} \tag{6}$$

In view of this empirical relationship, the simple inverse proportionality proposed by Poole and Atkins would hold only if c varies proportionally to E in the data set, which is of course unlikely (see Eq. 3). Basically, the reason why the simple Pool–Atkins relationship does not work well, is that scattering has a stronger effect on (inverse) Secchi-depth than on the vertical light attenuation (Fig. 2.2).

Therefore, two waters can have the same Secchi-depth, but differ markedly in light attenuation if the relative importance of scattering differs. For instance, a lake in which turbidity is mainly caused by suspended clay particles (which scatter rather than absorb), will have a lower light attenuation than a lake with the same Secchi-depth in which the turbidity is mainly due to phytoplankton.

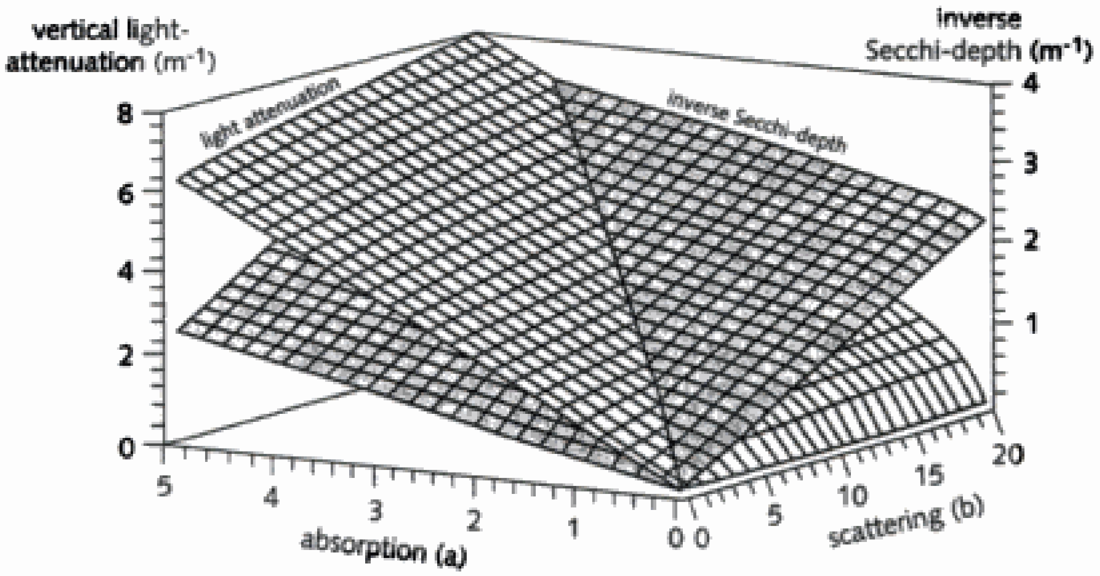


Fig. 2.2 Vertical attenuation coefficient (E) and the inverse Secchi-depth ($1/S_d$), both plotted as a function of the scattering coefficient (*b*) and the absorption coefficient (*a*) of lake water. Note that Secchi-depth is strongly affected by scattering, whereas the effect of scattering on vertical light attenuation is minor.

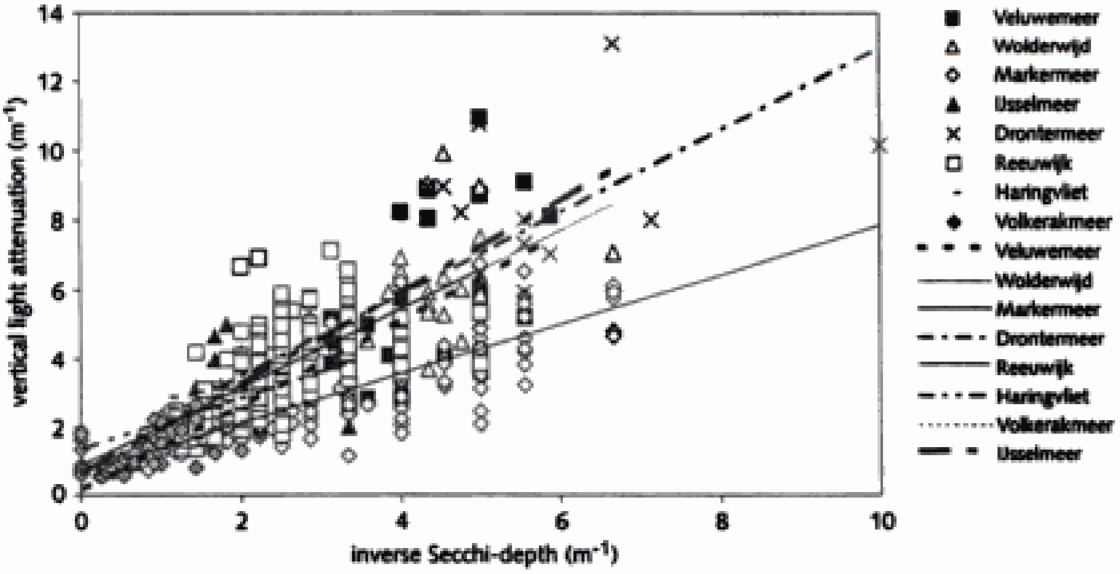


Fig. 2.3 Poor relationship between inverse Secchi-depth ($1/S_d$) and the vertical light attenuation (*E*) illustrated by data sets from eight Dutch lakes. The deviating position of Markermeer is explained by the high concentration of suspended clay particles in this lake. These particles contribute relatively much to scattering of the light which affects Secchi-depth stronger than it affects vertical light attenuation.

A plot of inverse Secchi-depth against light attenuation coefficients for data from a diverse set of shallow lakes (Fig. 2.3) demonstrates the poor relationship between visual transparency and actual light attenuation in practice.

Especially illustrative with respect to the presented theoretical relationships (Fig. 2.2) is the deviating position of the data from Markermeer. In this lake, suspended clay particles contribute strongly to turbidity, resulting in lower light attenuation than would be expected on the basis of the general relationship between E and the inverse Secchi-depth.

Although visual transparency can not easily be translated into light attenuation, this does not mean that Secchi-depth does not provide useful information. The impression of clarity itself is obviously more important to recreants than the penetration of PAR. Also transparency may be relevant to visually hunting fish and piscivorous birds. Thus Secchi-depth is a useful characteristic in itself.

Nephelometric turbidity

In this book the word turbidity is used in a loose sense to indicate the lack of clarity of lake water. There are, however, also laboratory devices that measure so-called nephelometric turbidity. In such turbidimeters a light beam is sent through a cylindrical glass container that holds the lake water to be studied. A light cell on the side of this container measures the light that is scattered out of the beam in an angle perpendicular to the beam. The stronger this scattering, the higher the turbidity which is expressed in nephelometric turbidity units (NTU). This is an essentially arbitrary unit determined relative to that of artificial standard suspensions made up in a prescribed manner. In practice, nephelometric turbidity corresponds closely to the scattering coefficient, b (Kirk, 1994). Since Secchi-depth and vertical light attenuation also depend on absorption, it follows that these apparent optical properties can not simply be derived from nephelometric turbidity measurements.

Euphotic depth

Sometimes the light climate of a lake is characterized in terms of its 'euphotic depth'. This is the depth beyond which the light level falls below 1% of the surface irradiation which is considered too low for algae to maintain a positive net photosynthesis. Obviously, this is a rough approximation, as the absolute light at that level depends on the surface irradiation, and different algal species will require different amounts of light.

Substituting the ratio 100:1 of I_0 to I_z in Eq. 2, it can be seen that there is a fixed inverse proportionality between euphotic depth (z_{eu}) and the vertical attenuation coefficient:

$$Z_{eu} \approx \frac{4.6}{E} \tag{7}$$

However, the most penetrating colours that can be used for photosynthesis have an attenuation coefficient (E_{min}) of about 75% of that measured over the whole PAR spectrum. Therefore, E_{min} is often used instead of E, and in that case the relationship becomes:

$$Z_{eu} \approx \frac{3.5}{E_{min}} \tag{8}$$

Note that because of the roughly inverse proportionality to the vertical attenuation coefficient E, Secchi-depth is more or less linearly related to the euphotic depth. In fact, when E is not known, euphotic depth is sometimes estimated as 1.7 times the Secchi-depth (Reynolds, 1984). However, as argued, the relationship between Secchi-depth and light attenuation is highly variable in shallow lakes. Therefore, Secchi-depth is really an unreliable basis for estimating euphotic depth in such lakes.

Since algal cells are dispersed throughout the mixed layer, the light they experience depends not only on the vertical light attenuation but also on the depth of the mixed layer water (which in most shallow lakes is the entire water column). The ratio of the mixed depth to the euphotic depth (z_{mix}/z_{eu}) is often used to characterize the light climate for phytoplankton. However, since z_{eu} is a rather arbitrary measure, it is more straightforward to use E directly. Thus instead of z_{mix}/z_{eu} the product $z_{mix} * E$ can be used as an indicator of shade experienced by the phytoplankton. In shallow lakes where z_{mix} equals the lake depth D, shade can be characterized simply using the product of light attenuation and lake depth (ED).

Finding the causes of turbidity

Most of the present theory on underwater optics is devoted to the understanding of relationships between absorption, scattering, light attenuation and Secchi-depth. However, in order to be able to determine the causes of turbidity in a lake, it is also necessary to know how these optical properties are related to the concentrations of algae, suspended sediment particles and detritus. This problem has been addressed less frequently, and appears relatively hard to resolve.

First of all, it is not possible to derive simple relationships between the concentrations of different fractions of suspended material and the resulting Secchi-depth or light attenuation from the established theory. The total absorption (a) and scattering (b) coefficients of lake water can be computed as the sum of the absorption and scattering coefficients of the constituent fractions (viz. phytoplankton, inorganic suspended matter, detritus, gilvin) for monochromatic light. However, the light attenuation coefficient (E) is not simply a linear combination of a and b (Eq. 3). Therefore, although we can write E as a function of the concentrations of suspended and dissolved material by substituting a and b by linear combinations of these concentrations, the resulting equation is a bit awkward. Furthermore, it needs to be extended to cover the variation of absorption and scattering coefficients of the fractions with wavelength over the PAR band. Buiteveld (1995) used the theory to construct a relatively complex set of formulae relating *E* and *1/S* to the concentrations of suspended and dissolved substances. The parameter values need to be fitted to field data using an optimization algorithm. After such tuning, the resulting model can predict Secchi-depth and vertical light attenuation quite well from the concentrations of chlorophyll, detritus and inorganic suspended solids. Surprisingly, however, regression analysis of the outputs versus the inputs of the model shows that the predicted light attenuation coefficients and inverse Secchi-depths are related to the input concentrations of phytoplankton, detritus and inorganic suspended solids in an almost perfectly linear way. Also, direct regression analyses on field data show that *E* and the inverse Secchi-depth are roughly linear combinations of the concentrations of algal chlorophyll-a (*Chl*), detritus (*Det*) and inorganic suspended solids (*Iss*) (Kirk, 1994):

$$E = \tau_C\, Chl + \tau_D\, Det + \tau_I\, Iss + \tau_0 \tag{9}$$

$$\frac{1}{S_d} = \sigma_C\, Chl + \sigma_D\, Det + \sigma_I\, Iss + \sigma_0 \tag{10}$$

The intercepts (τ_0 and σ_0) represent the light attenuation, and inverse Secchi-depth that are due to gilvin and other factors that are not in the equation. The parameter values obtained by regression through the values predicted by Buiteveld's model and values obtained from regression through field data are presented in Table 2.1 and 2.2.

Table 2.1 Parameter values for the regression model $E = \tau_0 + \tau_C Chl + \tau_D Det + \tau_I Iss$ relating the vertical light attenuation coefficient, E (m^{-1}) to the concentrations of chlorophyll-a, *Chl* ($\mu g\, l^{-1}$). Detritus *Det* ($mg\, l^{-1}$) and inorganic suspended solids ($mg\, l^{-1}$). 'Model Buiteveld' refers to a set of data generated by Buitevelds (1995) light-model. Stars (***) denote that the model is fitted without the corresponding term. For the models fitted without intercept R^2 is computed as ($1-SS_{residual}/SS_{total}$). The parameter-sets printed in bold produces little systematic deviation in clear water. The set marked by the #-symbol is used to produce Fig. 2.4

	τ_0	τ_C	τ_D	τ_I	R^2	*n*
model Buiteveld	0.81	0.020	0.043	0.028	1.00	521
combined field data	0.70	0.022	0.029	0.030	0.77	521#
combined field data	****	0.028	*****	0.046	0.76	521
combined field data	0.76	0.024	*****	0.035	0.82	521
Veluwemeer	0.61	0.024	*****	0.052	0.90	53
Wolderwijd	1.17	0.021	*****	0.078	0.72	38
Markermeer	0.83	0.024	*****	0.034	0.72	314
IJsselmeer	1.29	0.017	*****	0.002	0.62	39
Volkerak	0.68	0.009	*****	0.077	0.55	77

Table 2.2 Parameter values for the regression model $1/S = \sigma_0 + \sigma_C Chl + \sigma_D Det + \sigma_I Iss$ relating Secchi-depth S (m^{-1}) to the concentrations of chlorophyll-a, Chl ($\mu g\ l^{-1}$), Detritus Det ($mg\ l^{-1}$) and inorganic suspended solids ($mg\ l^{-1}$). Stars (***) denote that the model is fitted without the corresponding term. For the models fitted without intercept R^2 is computed as $(1\text{-}SS_{residual}/SS_{total})$. Parameter-sets that produce little systematic deviations are printed in bold. The set marked by the #-symbol is used to produce Fig. 2.4

	σ_0	σ_C	σ_D	σ_I	R^2	n
model Buiteveld	0.13	0.010	0.068	0.070	1.00	761
combined field data	0.79	0.011	0.044	0.041	0.70	761
combined field data	****	0.014	0.068	0.044	0.65	761#
combined field data	****	0.019	*****	0.056	0.61	761
combined field data	0.88	0.013	*****	0.048	0.69	521
Veluwemeer	1.84	0.010	*****	0.028	0.50	83
Wolderwijd	2.03	0.011	*****	0.012	0.42	62
Markermeer	1.26	0.011	*****	0.048	0.71	404
IJsselmeer	0.70	0.010	*****	0.019	0.66	85
Volkerak	0.25	0.009	*****	0.068	0.73	127

Note that the concentration of detritus is not measured directly in practice. Instead, the ash free dry-weight of suspended solids minus the dry-weight of algae is considered to be due to detritus. Algal biomass in turn is estimated from the chlorophyll-a concentration assuming a dry-weight/chlorophyll ratio of 70 as a rule of thumb.

Although one would at first sight expect the regression coefficients (τ and σ) to represent more or less universal optical properties of the fractions (A, D and I), they can actually differ considerably between lakes (Tables 2.1 and 2.2). Since the algal community, the nature of the detritus, and the type of sediment differ between lakes, the variation in the coefficients is not really surprising. In view of this variation it is always best to fit these regression equations to series of data from the lake in which one wishes to unravel the causes of turbidity.

Another conspicuous problem of the regression approach is that most analyses yield unrealistically high intercepts (τ_0 and σ_0). As a result, these models can not predict low values for the attenuation coefficient or inverse Secchi-depth. The high intercepts may be explained in part from the fact that the increase of light attenuation with scattering and adsorption is not really linear (Eq. 3 and Fig. 2.2). However, a probably more important reason is that the optical properties of one or more seston fractions change systematically with turbidity. In turbid lakes, for instance, different algae dominate.

Despite these inaccuracies, the simple empirical relations can be useful to obtain an indication of the contribution of algae, detritus and resuspended

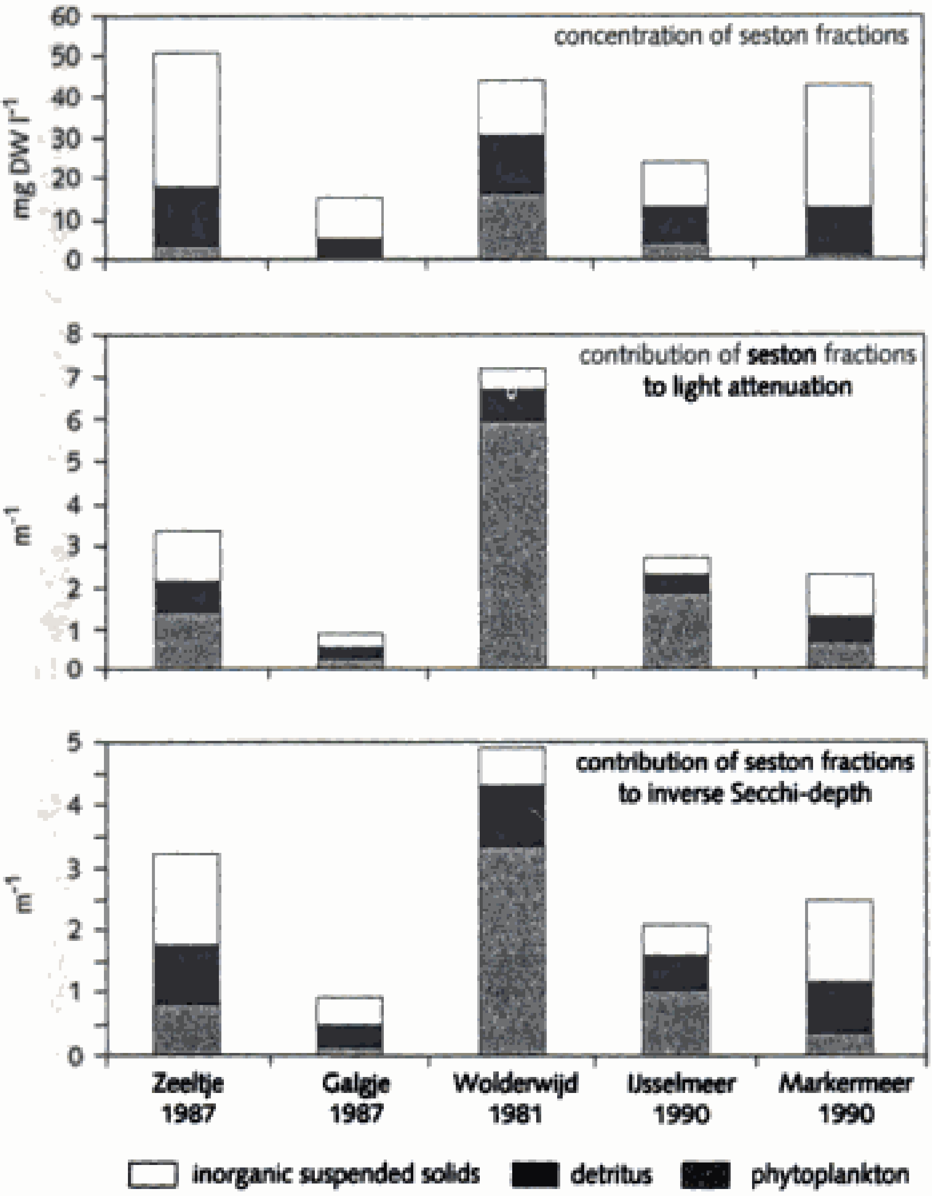


Fig. 2.4 The average summer concentrations of different seston fractions in five Dutch lakes and the contribution of these fractions to the vertical light attenuation (E) and to the inverse Secchi-depth ($1/S$) in the lakes estimated using the regression equations presented in Tables 2.1 and 2.2.

inorganic sediment particles to turbidity in a specific lake if the concentrations of these substances are known. Figure 2.4 gives an example of such a diagnosis of sources of turbidity for some contrasting lakes.

The contribution of inorganic suspended solids to light attenuation is always smaller than would be expected at first sight from their often dominant role in terms of dry-weight. A comparison of the adjacent lakes IJsselmeer and Markermeer illustrates the fact that suspended sediments have a stronger effect on Secchi-depth than on light attenuation. The sediment of the large, wind-exposed Markermeer consists mainly of easily resuspendable clay. Consequently, the concentration of inorganic suspended solids is much higher than in IJsselmeer which has a more sandy sediment. The figure demonstrates that the high algal biomass in IJsselmeer is responsible for much of the light attenuation under water, whereas the suspended inorganic sediment in Markermeer strongly affects visual transparency.

Pragmatic solutions to estimate light attenuation

Since the distribution and abundance of algae and submerged vegetation depends strongly on light availability, light attenuation is among the most important physical aspects of a lake from an ecological point of view. Unfortunately, measuring light attenuation with depth is a bit tedious, and requires relatively expensive equipment. As a consequence, measurements of the attenuation coefficient are rare, especially in historical data sets. As shown, Secchi-depth is a poor indicator of actual light penetration under water. The empirical relations presented in the previous section potentially allow a better estimation of *E* if the concentrations of detritus, inorganic suspended solids and chlorophyll are measured, but often only the latter is available. Clearly chlorophyll alone is also a rather incomplete basis for estimating light penetration, as detritus and suspended sediment particles contribute significantly to turbidity in most shallow lakes (Fig. 2.4).

Since Secchi-depth and chlorophyll concentration contain information about the light climate that is, at least in part, complementary, it is to be expected that vertical light attenuation can be estimated more accurately from the combination of these two measures than from either of them alone. Indeed, reanalysis of the data set represented in Fig. 2.3 reveals that *E* can be predicted quite well as:

$$E = 0.81 + 0.016\, Chl + \frac{0.46}{S_d} \qquad (11)$$

or

$$E = 0.016\, Chl + \frac{1.3}{\sqrt{S_d}} \qquad (12)$$

Both models explain 80% of the variance in *E* in the data set, as opposed to 57% for a Poole Atkins model (Eq. 5) in which only Secchi-depth is used as an explanatory variable. The second model (Eq. 12) has the advantage that it can also predict low values of *E*, which is prevented by the rather high intercept in the first model. Regressions of the observed vertical light attenuation coefficients against the values predicted by Eq. 11 for the separate lakes (Fig. 2.5) show that it does not only predict the value of *E* reasonably well, but also accounts for most of the systematic differences between lakes

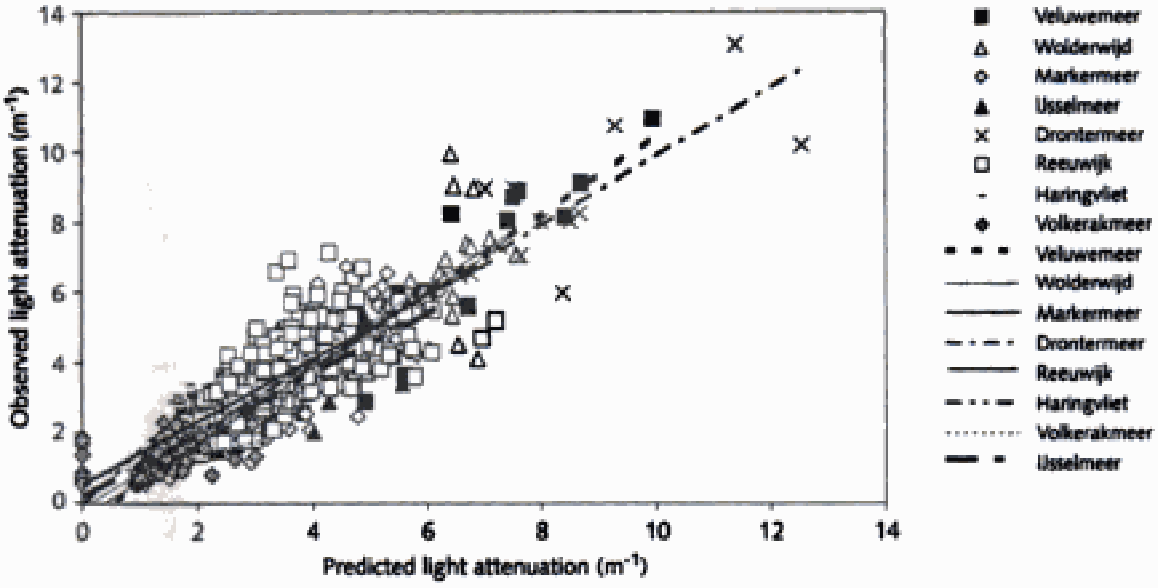


Fig. 2.5 Correspondence of observed vertical attenuation coefficients (E) to the values predicted from Secchi-depth and chlorophyll concentrations using Eq. 11.

that were apparent in the relationships between light attenuation and Secchi-depth.

Thus in the absence of direct measurements of vertical light attenuation, these simple empirical models may serve to provide an estimate on the basis of usually available measurements of Secchi-depth and the concentration of chlorophyll-a.

It is important to note that since the optical properties of algae, detritus and inorganic suspended solids differ from case to case, this model and the other empirical relationships between light climate and suspended solids presented in the previous sections can not be expected to describe the relationship equally well in all lakes. If sufficient data are available, it will always be preferable to fit the models especially for application to a specific lake or set of lakes.

2.2 SEDIMENTATION AND RESUSPENSION

In many shallow lakes, inorganic sediment particles, but also algal cells, go through a rapid cycle of sedimentation and resuspension. Often, resuspension is mainly due to wave action, but also fish searching for food in the bottom can stir up considerable amounts of sediment in some situations. In this section the laws that govern resuspension and sedimentation are outlined, and the role of waves and fish in resuspension is explained.

The balance of resuspension and sedimentation

As illustrated by the analyses of the light climate in different lakes (Fig. 2.4), algal cells and other suspended particles are the main cause of turbidity in most shallow lakes. With the exception of some algae that can swim or regulate their buoyancy, all of these suspended particles continuously tend to sink to the bottom. In deep lakes, particles can not return to the turbulently mixed top layer (epilimnion) once they sink through the thermocline into the cold hypolimnion. In shallow lakes, thermal stratification may occur on sunny days. However, during the night such micro-stratifications are usually broken and a stable stratification never occurs for long periods. Consequently, there is usually no thermocline in shallow lakes to act as a point of no return for sinking particles. However, water movement declines strongly in the small boundary layer at the sediment surface. As a result, the lake bottom can trap sinking particles, more or less as a thermocline does. The difference is that particles on the sediment can return to the water column when the water movement at the sediment–water interface is strong enough to pass a critical threshold beyond which the sediment is whirled up again.

In shallow water, the concentration of suspended particles in lake water depends strongly on these continuous processes of sedimentation and resuspension. Obviously, there are other ways for suspended particles to appear or disappear from the seston. Algal cells, for instance, are produced in the water column by cell division, and most particles can be removed by filter feeding invertebrates. These mechanisms are treated extensively in the following chapters. To understand the dynamic interplay of sedimentation and resuspension it is useful to write it in a simple mathematical form. The loss rate of particles from a water column due to sedimentation is equal to the ratio of the sinking velocity s ($\mathrm{m\,day^{-1}}$) to the depth of the column D (m) in still water. The rate of change in concentration of suspended particles, dS/dt ($\mathrm{g\,m^{-3}\,day^{-1}}$) can be written as a function of this loss rate and the rate of return through resuspension, Γ ($\mathrm{g\,m^{-2}\,day^{-1}}$):

$$\frac{dS}{dt}=\frac{\Gamma}{D}-\frac{s}{D}S \qquad (13)$$

Note that the depth of the water column occurs in both terms: in the gain term because the suspended material becomes more diluted if the water is deeper, in the loss term because a sinking particle reaches the bottom sooner in shallower water. As a result of this inverse proportionality to depth, the rates of these processes can become very high in shallow water. The sinking rate of a particle depends on its specific weight but also on its size and shape. Light particles with irregular shapes sink relatively slowly. Since seston usually consists of a large variety of particles, some fractions will settle much slower than others. Typically, however, sinking velocities of suspended solids are more than a few decimetres per day. As a result the water column of many shallow lakes could potentially clear out in a few days if all resuspension through wave action and fish activity was excluded ($\Gamma \approx$

0). Indeed, when shallow lakes freeze, the quiet water under the ice often becomes very clear. The rapid settling of material is also apparent when a bottle of turbid lake water is left to rest. In a day, the water usually becomes clear, and a layer of settled particles becomes visible at the bottom.

The equilibrium concentration of suspended solids in the water column (S^*) is reached when sedimentation equals resuspension. From the above equation it follows that:

$$S^* = \frac{\Gamma}{s} \tag{14}$$

If the effect of factors like wind velocity or fish activity on resuspension (Γ) is known, these simple equations allow a translation into effects on suspended matter concentrations in a lake.

When and where wave resuspension occurs

When wind blows over the water surface, waves are produced. Water motion in waves is very complex, but the horizontal water movement that they cause along the sediment surface is the main aspect needed to understand resuspension. A look under water with a diving mask at the shoreline of a rough sea or large lake shows that waves can cause strong water flows going back and forth along the bottom as waves come and go. How strong these horizontal 'shear' flows at the sediment surface are, depends on the size of the waves and the depth of the water. The maximum horizontal water velocity caused by waves decreases exponentially with depth (Fig. 2.6).

Whether or not this water movement along the sediment surface leads to resuspension of particles depends on the shear velocity and on the properties of the sediment. The response of a sediment layer to a gradual increase of water velocity along its surface is typically discontinuous. Erosion only occurs after a critical shear stress has been exceeded. The critical velocity needed for resuspension depends on the type of sediment. Fine silt or organic deposits are more easily suspended than sand. In addition, the critical shear increases with the time that the sediment is left undisturbed due to physical consolidation of the material and the development of a microbial community of benthic algae and bacteria that makes the sediment surface more resistant to resuspension (Delgado *et al.*, 1991).

One way to predict when resuspension will occur on a site is to use models to compute water velocity at the sediment surface as a function of wind velocity, water depth and the distance that the wind blows over the water ('fetch'), and subsequently relate this computed shear velocity to estimates of the critical shear velocity that leads to resuspension (Aalderink *et al.*, 1985; Bengtsson and Hellström, 1992; Blom *et al.*, 1994). This approach seems quite rigorous, although in practise there is still a very large

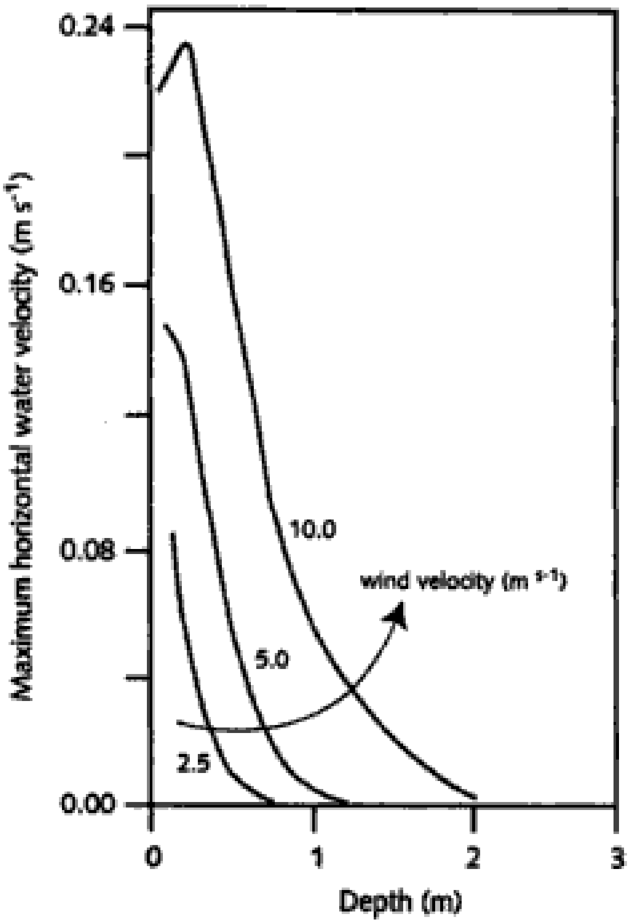


Fig. 2.6 Relationship between the maximum horizontal water velocity and water depth for a fixed fetch of 1000 m and wind velocities of 2.5, 5.0 and 10 m s^{-1} respectively. Redrawn from Aalderink *et al.* (1985).

variation in the relation between shear velocity and suspended solids (Hamilton and Mitchell, 1996).

Another, more pragmatic, approach is to use relatively simple empirical formulae that give wavelength as a function of wind velocity and fetch, and subsequently apply the rule of thumb that resuspension occurs if the waves 'touch the bottom' which is considered the case if the wavelength exceeds twice the water depth. Carper and Bachmann (1984) show that this simple approach, developed originally by engineers working with problems of beach erosion, actually works well to describe resuspension in the shallow prairie lake that they studied. Because the approach is relatively transparent, the formulations are used here to explore the effect of lake depth and size on susceptibility to resuspension.

As long as waves do not touch the bottom they are called 'deep water waves'. The size of such waves increases in a predictable way with wind velocity, W (m s^{-1}) and with the fetch, F (km) which is the distance to the shore measured in the direction from which the wind comes, i.e. the distance over which the waves have been allowed to build up. A relatively simple empirical formula gives wavelength (L_w) as a function of fetch and wind velocity:

$$L_w = 1.56\left[0.77\,W \tanh\left[0.077\left(\frac{9.8F}{W^2}\right)^{0.25}\right]\right]^2 \tag{15}$$

Wavelength increases almost linearly with wind velocity, while the increase with fetch is clearly non-linear (Fig. 2.7).

The latter can be observed in any pond if there is some breeze. At the sheltered shore the water is quiet, but the size of waves rapidly increases with the distance from the shore. Further from the sheltered shore waves keep growing but this increase with fetch is less steep than that observed over the initial few metres. The formula can be used to generate a map of wavelengths in a lake, given its contours and the wind speed. The area where sediment is predicted to become resuspended at given wind speeds can subsequently be found by overlaying the map of water depths, and applying the rule of thumb that resuspension occurs if the waves 'touch the ground', that is if the wavelength exceeds twice the depth ($L_w > 2D$). Obviously, the resuspended area increases with wind speed (Fig. 2.8), and sheltered areas are affected only at the highest wind velocities.

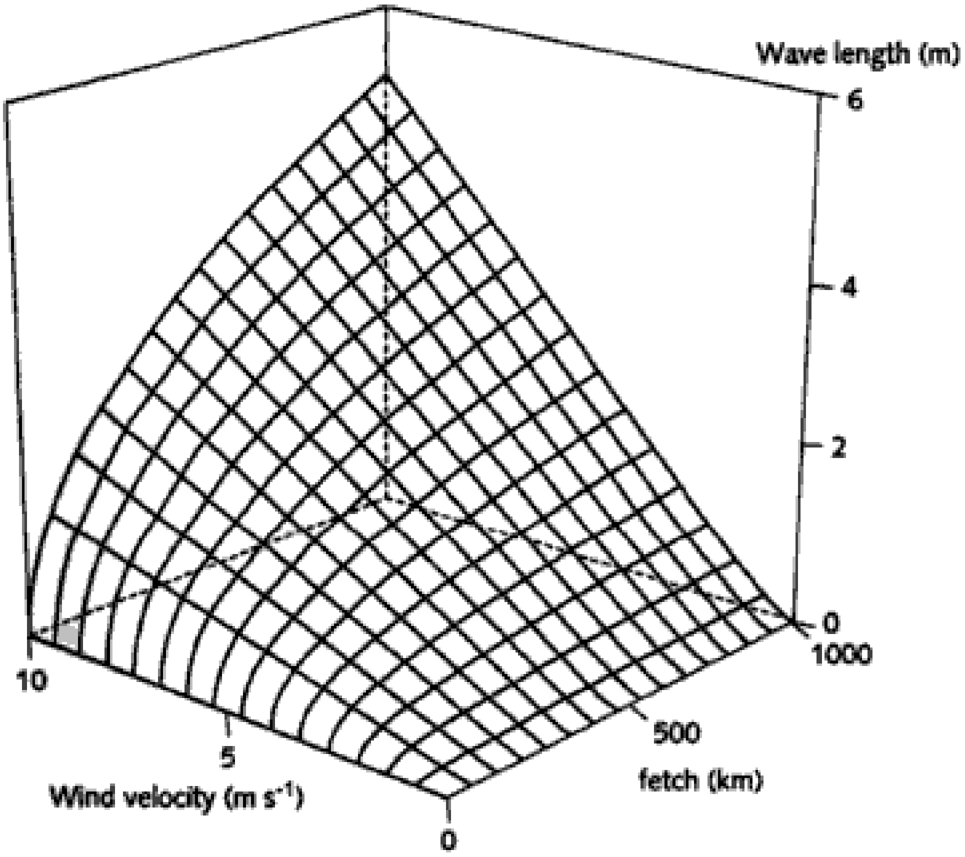


Fig. 2.7 Increase of wavelength (L_w) with fetch (F) and wind velocity (W) in deep water as described by Eq. 15.

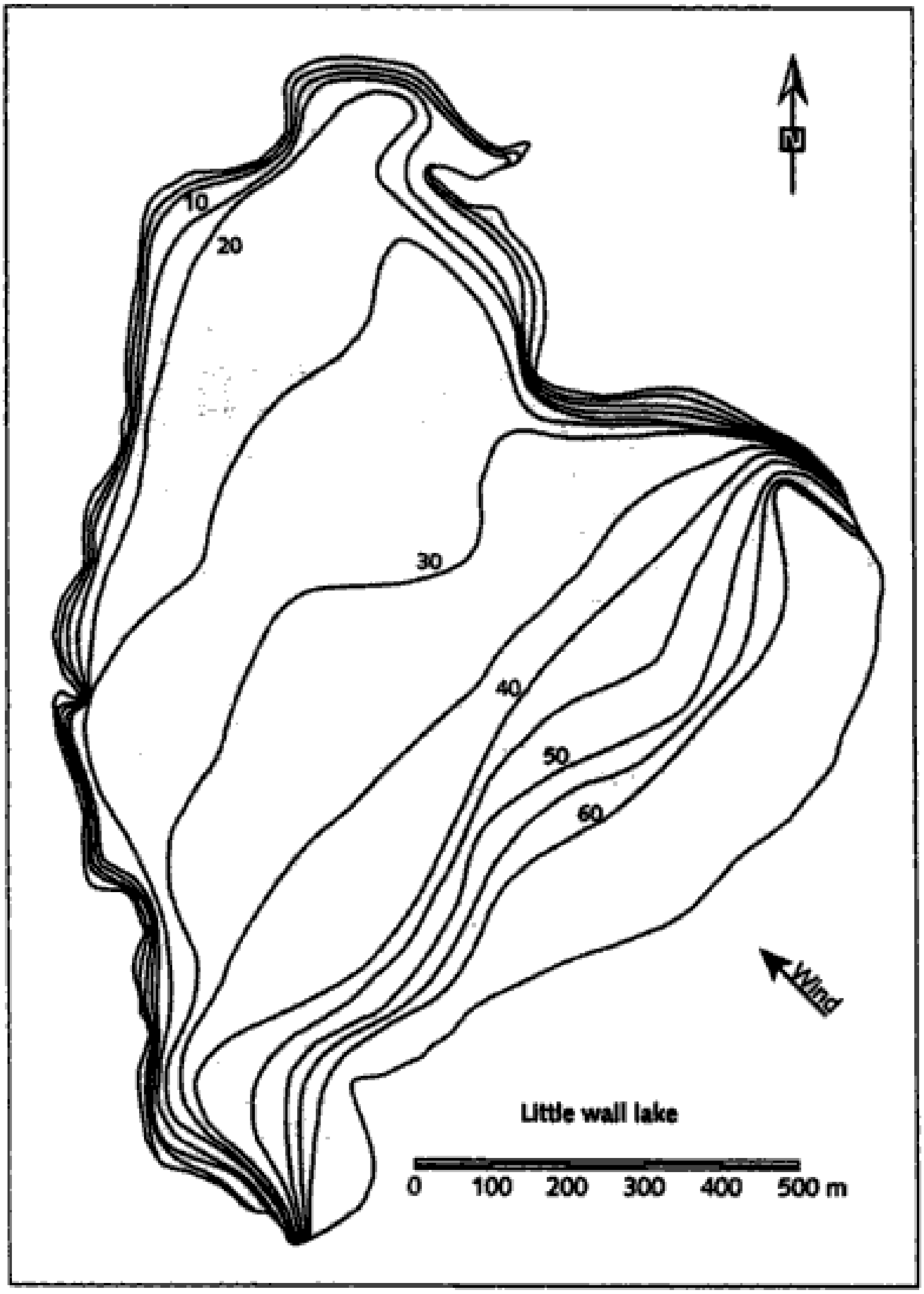


Fig. 2.8 Contours showing the wind velocities ($km\,h^{-1}$) necessary for resuspension to occur at a southeasterly wind in the shallow Little Wall Lake. Wave resuspension is predicted to occur in the area northwest of the contours. From Carper and Bachmann (1984).

Wave resuspension in relation to lake size and depth

The susceptibility to resuspension is different for each lake as it depends on the sediment type and on the shape and depth profile of a lake. To explore, nonetheless, some general tendencies, imagine a hypothetical square lake of

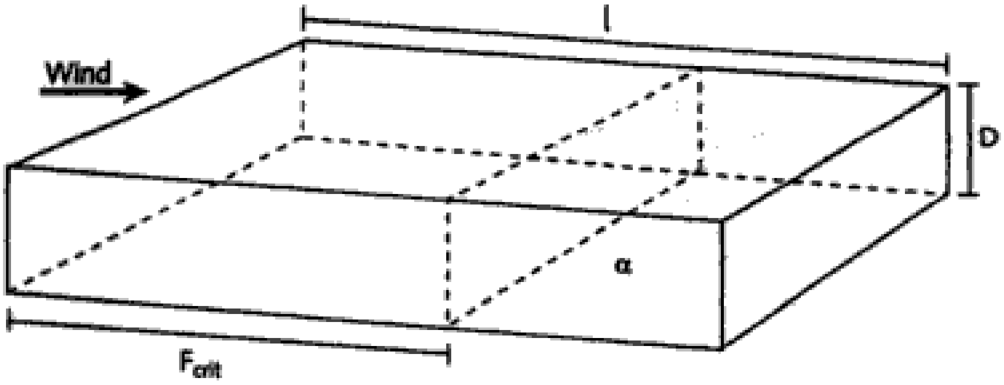


Fig. 2.9 The proportion (a) of a hypothetical square lake where wave resuspension occurs depends on the critical fetch (F_{crit}) at which the wavelength exceeds twice the depth (D), relative to the total length (l) of the lake measured in the direction of the wind.

homogeneous depth positioned perpendicular to the direction of the wind (Fig. 2.9).

In this case, the fraction α of the lake surface where resuspension occurs depends only on the ratio of the critical fetch for resuspension (F_{crit}) to the maximum fetch (F_{max}) in the lake:

$$\alpha = 1 - \frac{F_{crit}}{F_{max}} \Leftrightarrow F_{crit} = (1-\alpha)F_{max} \tag{16}$$

Substituting this and the critical condition for resuspension (at $D = 2\ L_w$) in Eq. 15, we obtain a single formula that relates the resuspended fraction (α) to the maximum fetch (F_{max}) and the depth (D m) of the lake and to the wind speed (W m s^{-1}):

$$D = 2 * 1.56\left[0.77W \tanh\left[0.077\left(\frac{9.8(1-\alpha)F_{max}}{W^2}\right)^{0.25}\right]\right]^2 \tag{17}$$

For a given (hypothetical) lake of fixed depth and size, this formula can be used to plot the increase of the resuspended area with wind speed (Fig. 2.10).

At low wind speeds no resuspension occurs as the critical fetch is larger than the maximum fetch in the lake. Above a critical wind speed, the resuspended fraction of the lake rises asymptotically to 1 with increasing wind.

To see better how the effects of fetch and depth interact, we change the viewpoint and ask the question which combination of lake depth and size leads to a 50% resuspension (α = *0.5*) at a given wind speed (Fig. 2.11).

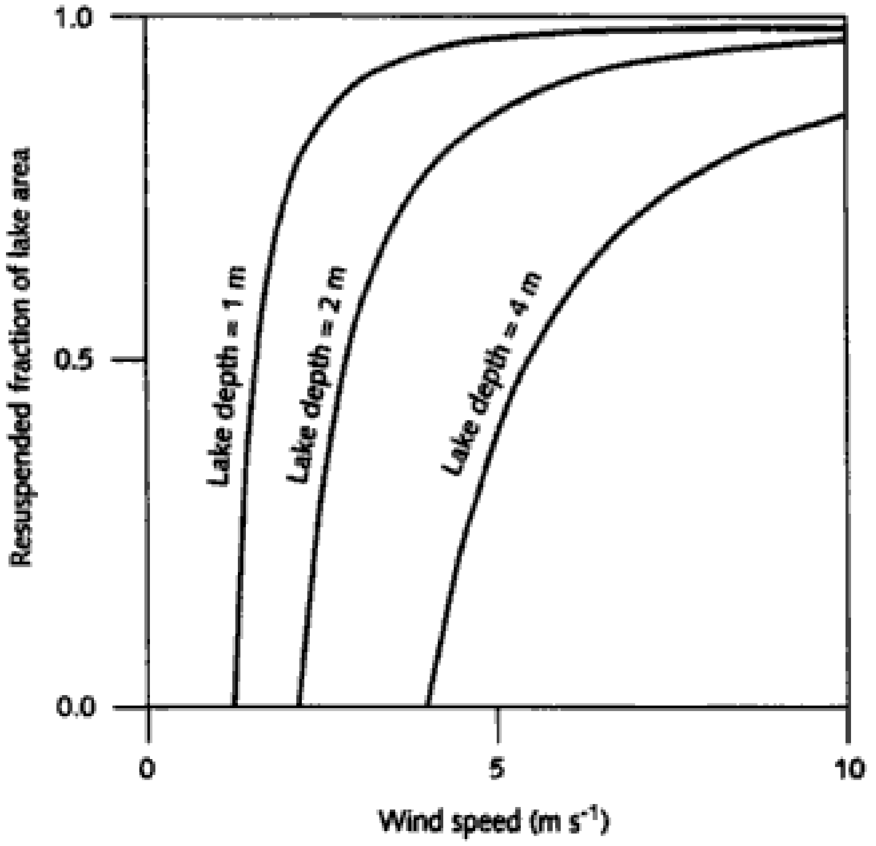


Fig. 2.10 Relationship between wind velocity (*W*) and the fraction (a) of the surface area of hypothetical lakes of 1 m 1 km (Fig. 2.9) where resuspension occurs as predicted for three different lake depths.

The resulting iso-resuspension lines are not straight lines, implying that it is not simply a fetch/depth ratio that counts. Therefore, scale models of lakes can not be used for studying resuspension. The sediment of a pond with a maximum fetch of 100 m and a depth of 0.5 m is more easily resuspended than a lake with a maximum fetch of 1 km and a depth of 5 m. A plot with the logarithm of the lake area shows more precisely how resuspension susceptibility depends on size and depth of lakes (Fig. 2.11b). All other things being equal, lakes that are on the same iso-resuspension line in this plot, should have a comparable sensitivity to wind resuspension according to our simple model. Thus, it can be seen, for instance, that a pond with a size of one hectare and a depth of 0.5 m is comparable to a lake of 100 ha and a depth of 1.3 m. Because of the sharp decrease of resuspension with water depth, a change in water level can affect wind resuspension in a lake rather strongly. This is illustrated, for instance, by the case of Lake Chapala in Mexico (Lind *et al.*, 1994). A drop in water level caused a considerable increase in clay resuspension and turbidity in this lake.

The amount of material that is brought into suspension when the waves touch the sediment depends on the situation. In general, the ongoing process of sedimentation and resuspension leads to a sorting of material in lakes. The sediment in exposed shallow areas with frequent resuspension is coarse, because lateral transport causes the fine material to concentrate in

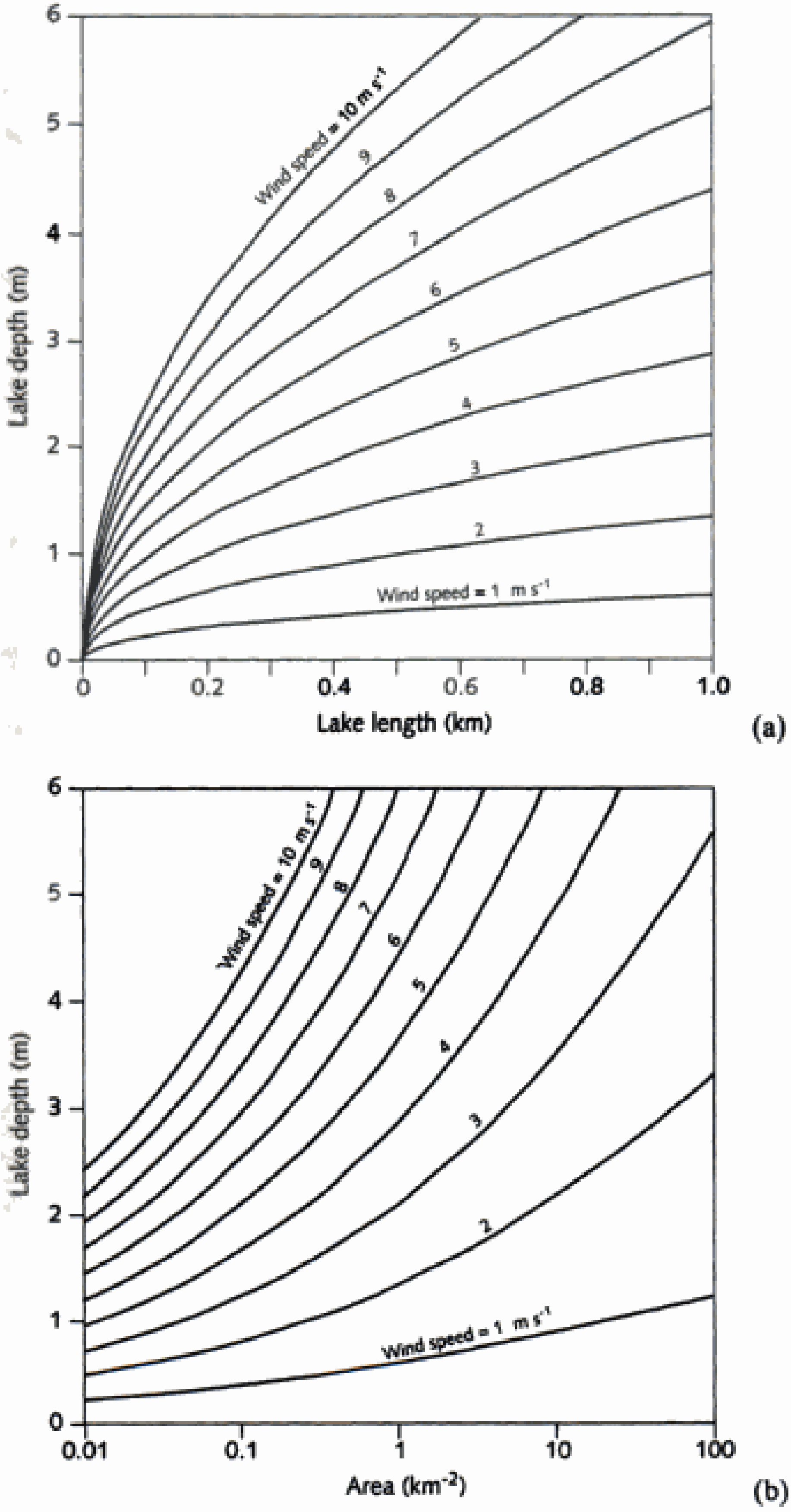


Fig. 2.11 Iso-resuspension lines indicating at which conditions 50% of the bottom of hypothetical lakes (Fig. 2.9) is subject to wave resuspension at different wind velocities (*W*). Lakes that are on the same iso-resuspension line are comparable in their susceptibility to wind resuspension. Note that susceptibility to resuspension decreases rapidly with lake depth. Size of the lake can be expressed as maximum fetch, i.e. the length of the lake measured in the direction of the wind (*a*), or as lake surface area (*b*).

deeper sheltered parts where resuspension occurs rarely (Evans, 1994). As pointed out by Carper and Bachmann (1984) this implies that the exposed 'erosion areas' are often not an important source of suspended solids. In such lakes, resuspension only becomes important in periods when winds are strong enough to affect areas in which resuspension occurs rarely, as easily resuspendable material is restricted to these areas. By definition, resuspension is thus relatively unimportant most of the time in lakes in which the exposed areas contain just coarse sediment due to horizontal sorting.

On the other hand, there are many lakes in which there is hardly any horizontal sorting because there are no deep parts where soft sediment can accumulate, and resuspension frequently occurs over most of the area. Such lakes often have a more or less discrete top layer of sediment consisting of fine material that is frequently resuspended (Luettich, Jr. *et al.*, 1990; Bengtsson and Hellström, 1992). Due to the frequent resuspension there is little consolidation of this layer and the material is resuspended easily. Obviously, if there is such a relatively discrete resuspendable layer, the amount of suspended sediment should simply increase linearly with the area over which resuspension occurs. This is indeed found, for instance, by Bengtsson and Hellström (1992) in their studies of Lake Tämnaren (Fig. 2.12).

In principle, a linear increase of suspended solids with the resuspended

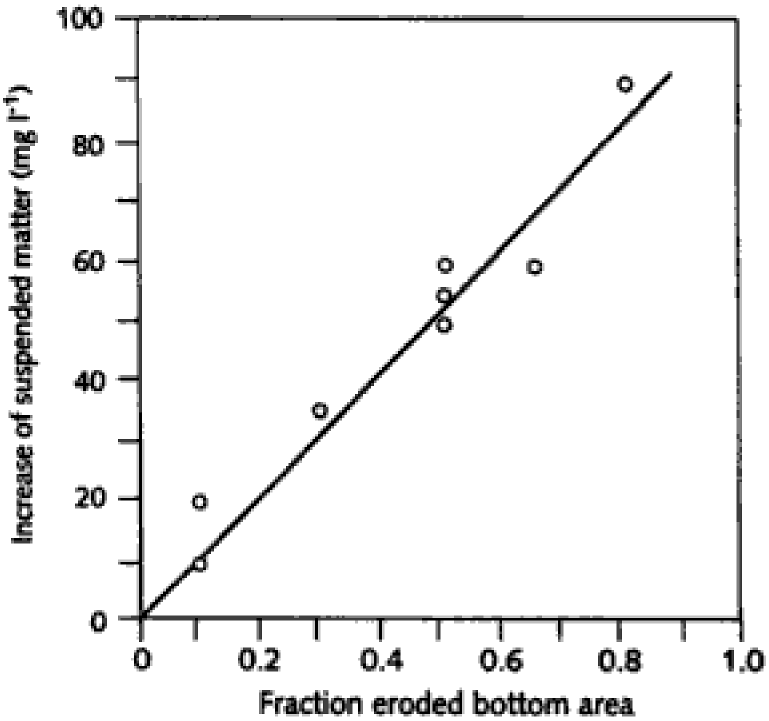


Fig. 2.12 Measured concentration of suspended matter versus the computed fraction of the lake area where wave resuspension occurred at the time of measurements in the Swedish Lake Tämnaren. From Bengtsson and Hellström (1992).

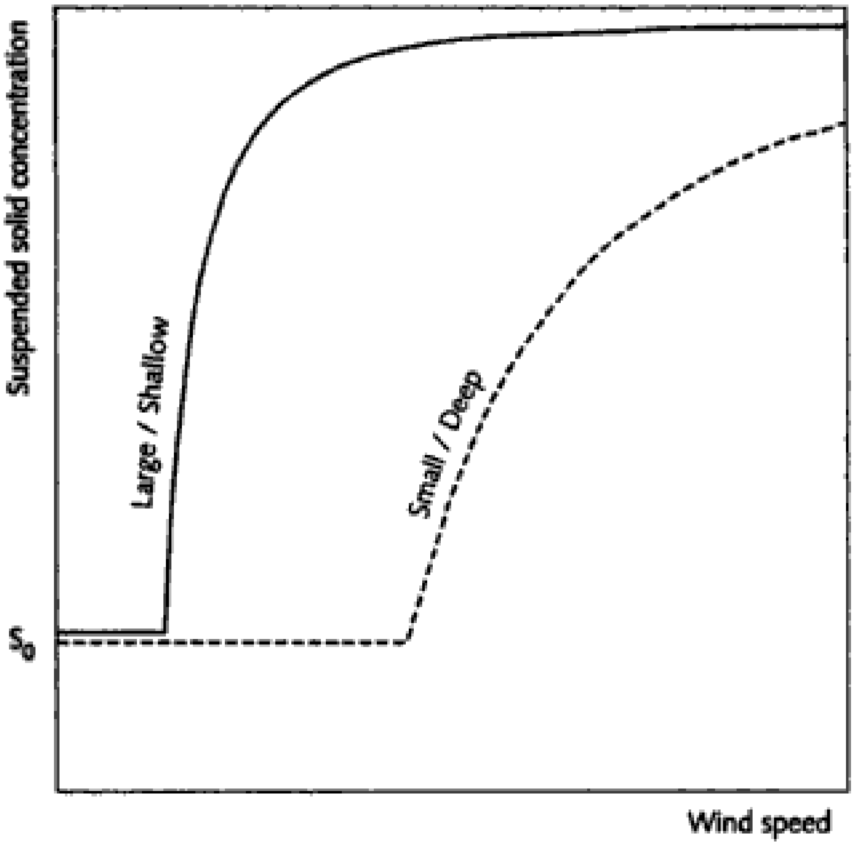


Fig. 2.13 Predicted increase in suspended solid concentration (S) with wind velocity for a large shallow versus a smaller or deeper hypothetical lake (Fig. 2.9) (see text).

area implies that the theoretically derived relationships between resuspended area and wind speed (Fig. 2.10) can be simply translated to give the concentration of suspended solids (S) as a function of wind speed and a background concentration (S_0) that does not depend on wind resuspension (Fig. 2.13).

Note that this idealized picture assumes the hypothetical situation of a rectangular lake with a homogeneously distributed resuspendable top layer. In real lakes the increase of suspended solids with wind will look different. Nonetheless, a sigmoidal shape may be expected in general. Low wind speeds have little effect, but as soon as waves start 'touching' resuspendable sediment the concentration in the water increases asymptotically towards a level where all suspendible matter is in the water column.

Lake specific empirical models

How much sediment is resuspended at a given wind velocity differs strongly between lakes, depending among other things upon the shape and depth profile of the lake and on the distribution and nature of suspendible sediment. As shown, describing wind resuspension mechanistically on a whole lake scale is surprisingly difficult. For a given lake, however, one can also simply fit an empirical relationship between suspended solids and wind speed if sufficient data are available. A reasonable description is usually obtained with the balance equations presented in the first part of this section (Eqs. 13 and 14) if an exponential function of wind velocity, *W*, is substituted for resuspension (Γ), and a fixed background concentration S_b is added that stays in the water column even in the absence of any wind:

$$\frac{dS}{dt} = \frac{a_s W^{b_s}}{D} - \frac{s}{D}\left(S - S_b\right) \tag{18}$$

The steady state version gives the equilibrium concentration of suspended solids (S*):

$$S^* = S_b + \frac{a_s W^{b_s}}{S} \tag{19}$$

The background concentration (S_b), sinking rate *s* and the parameters a_s and b_s are simply tuned in such a way that the model results fit to time-series of wind speeds and suspended solid concentrations in the lake. This approach has been used to describe the situation in Lakes Balaton (Somlyody, 1982; Somlyody and Stanbury, 1986), Arresø (Kristensen *et al.*, 1992) and Veluwemeer (Aalderink *et al.*, 1985). The increase of resuspension in the fitted model can be either concave ($b_s = 0.4$ in Veluwemeer) or convex ($b_s = 1.45$ in Arresø) (Fig. 2.14).

Although this difference is surprising at first sight, a look at the theoretically derived relationship (Fig. 2.13) may explain the discrepancy. As ar-

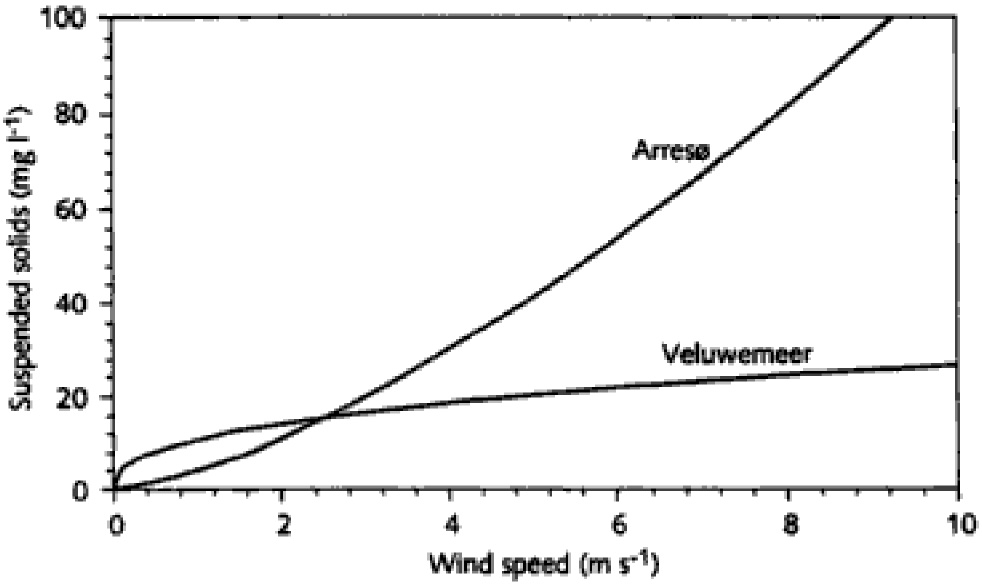


Fig. 2.14 Increase of suspended solid concentration (*S*) with wind velocity (*W*) according to Somlyody's empirical model fitted to data from two different lakes (see text).

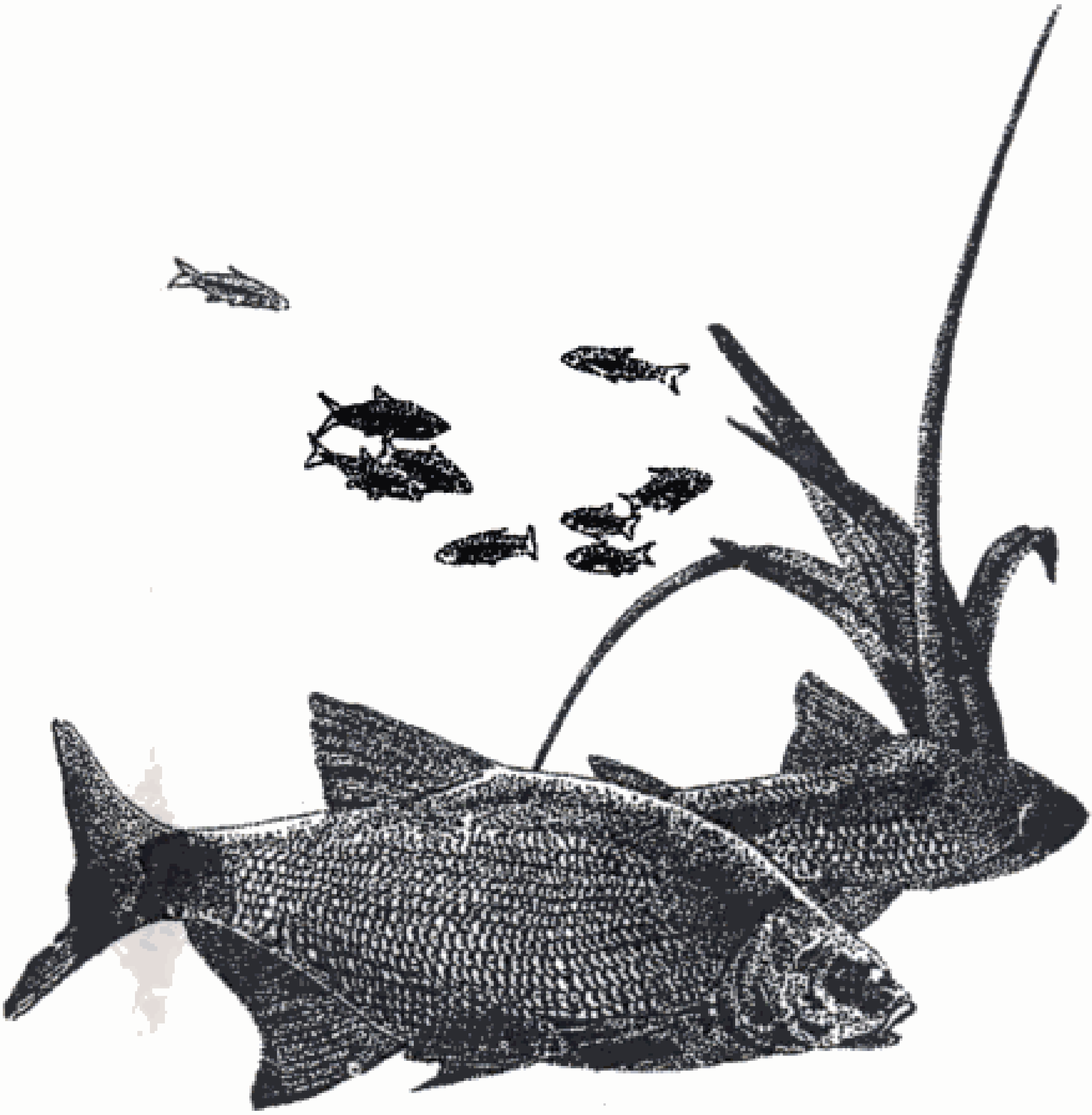


Fig. 2.15 Benthivorous fishes such as bream (*Abramis brama*) usually dominate the fish community of turbid shallow lakes. These animals can increase turbidity by whirling up the sediment in search for benthic food. They also stimulate algal blooms by enhancing the nutrient flow from the sediment to the water column and by consuming waterfleas that would otherwise graze on algae.

gued, the general relationship between resuspension and wind velocity should be roughly sigmoidal. A simple exponential function, as used in the above models, can not produce the complete sigmoid. With an exponent (b_r) larger than one, however, it can mimic the exponential increase in the left part of the sigmoid, while the saturating right part of the sigmoid can be described if the exponent is set smaller than one. Thus, the simple exponential model should give good results as long as the data points are restricted to either of the sides. The explanation for the difference in b_s between the two lakes may thus be that Veluwemeer is simply closer to the saturated side of the range than Arresø.

Sediment resuspension by fish

In shallow lakes a large part of the fish community usually feeds on invertebrates that live in the surface layer of the sediment, such as midge larvae, molluscs and worms. Bream (*Abramis brama*) is a notorious benthivore in European lakes (Fig. 2.15). It forages by sucking in sediment, from which the food particles are retained by filtering through the gill raker system (Lammens, 1991).

As a result, the non-retained fine sediment particles become suspended in the water, and a small pit (2–4 cm across) is left in the sediment surface from the feeding event. A look under water in lakes where benthivorous fish are abundant often shows the sediment surface almost entirely covered by such forageing craters. The effect of the continuous resuspension by benthivorous fish on turbidity can be pronounced. This is illustrated, for instance, by the effects of the experimental reduction of the fish stock in the shallow Lake Bleiswijkse Zoom (The Netherlands). The density of benthivorous fish was about 600 kg ha^{-1} in this small turbid lake. Reduction of the stock to about 200 kg ha resulted in an almost instantaneous increase

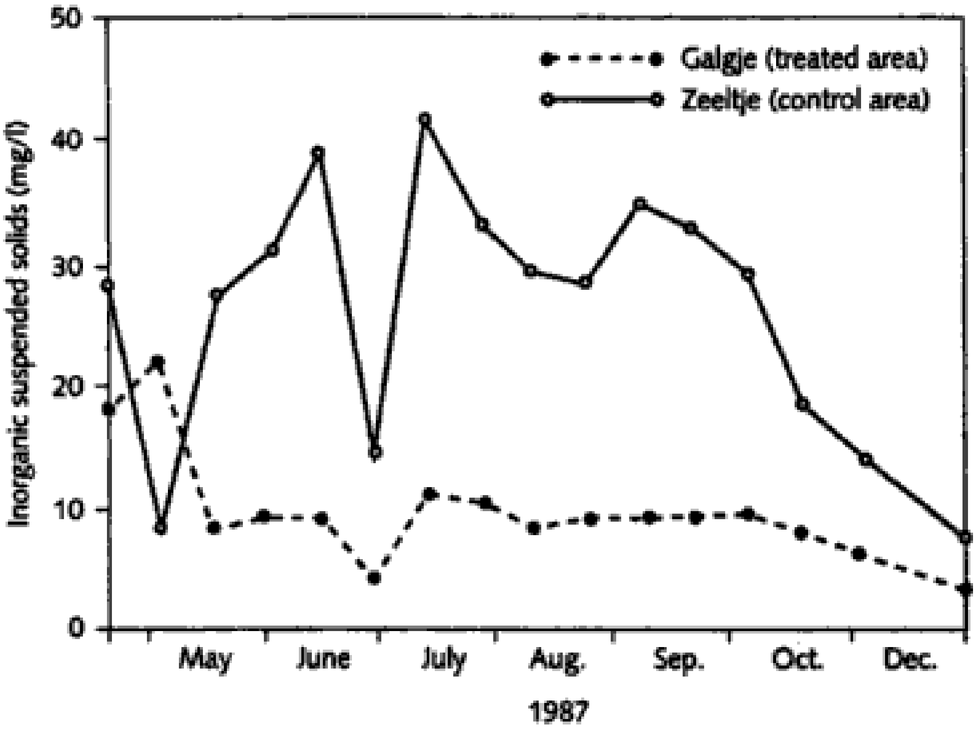


Fig. 2.16 Inorganic solids concentration in Lake Bleiswijkse Zoom following fish removal in April 1987. From Meijer *et al.* (1989).

in transparency which appeared to be largely due to a drop in the concentration of inorganic suspended solids (Fig. 2.16).

Theoretically, the effect of benthivores on suspended solids can be understood from the basic equations that describe the balance of resuspension and sedimentation in a similar way as wind resuspension (Eqs. 18 and 19). If the daily amount of material that is resuspended is assumed to be proportional to the biomass of benthivorous fish B_b the model can be written as:

$$\frac{dS}{dt}=\frac{q\,B_b}{D}-\frac{s}{D}\left(S-S_o\right) \tag{20}$$

and the equilibrium concentration in the water column (S^*)is predicted to increase linearly with the biomass of benthivorous fish:

$$S^*=S_o+\frac{q}{s}B_b \tag{21}$$

where q is the amount of sediment stirred up per unit of fish biomass each day.

This simple model is surprisingly well in line with observations. For instance, the concentration of inorganic suspended solids in several Dutch ponds and small lakes where wind resuspension is unimportant shows a linear increase with the biomass of benthivorous fish (Fig. 2.17).

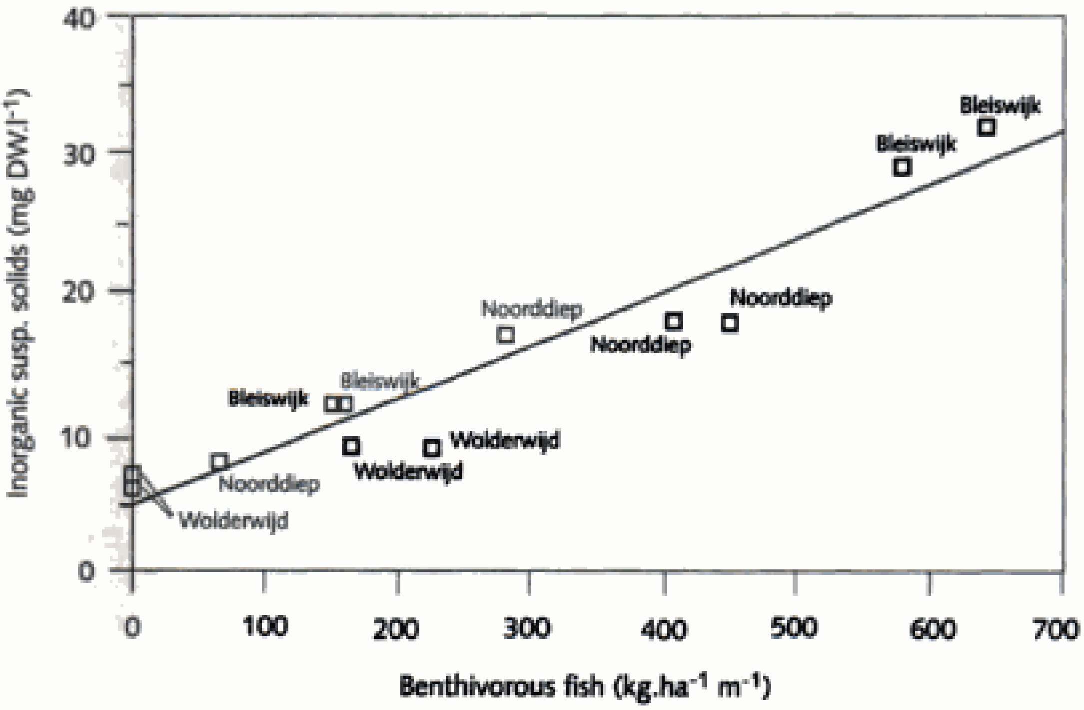


Fig. 2.17 Relationship between inorganic suspended solid concentrations and the biomass of benthivorous fish in several Dutch ponds. From Meijer *et al.* (1989).

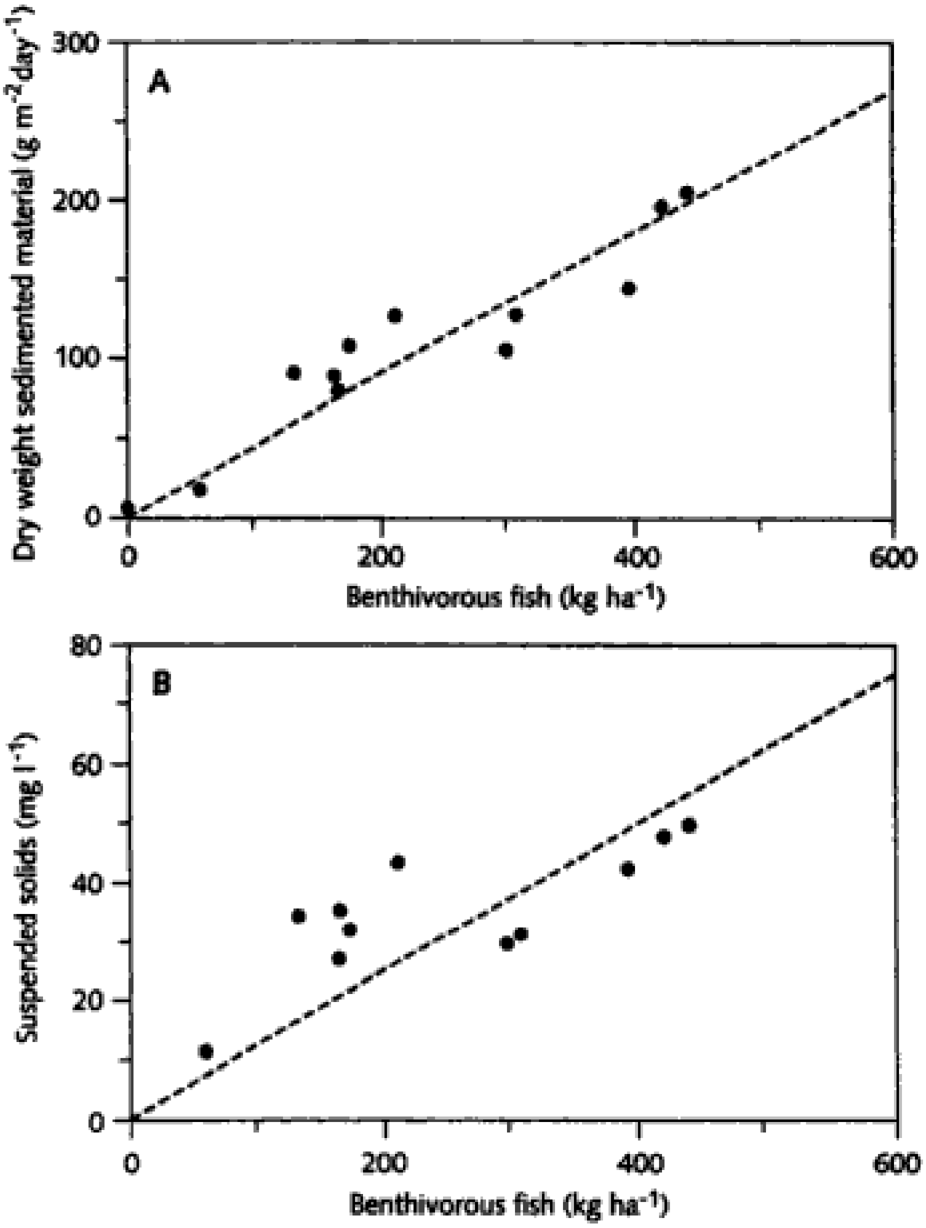


Fig. 2.18 Increase of the flux of sedimentating material (upper panel) and the concentration of suspended solids with the biomass of benthivorous bream in a series of experimental ponds. Modified from Breukelaar *et al.* (1994).

The effect of sediment resuspension by fish has also been studied experimentally in a series of ponds that were stocked with carp (*Cyprinus carpio*) and bream (*Abramis brama*) of different size classes and in different densities (Breukelaar *et al.*, 1994). As expected, both the sedimentation rate, measured with sediment traps, and the concentration of suspended solids in the water column increased approximately linearly with fish density (Fig. 2.18).

The impact of resuspension on turbidity in these ponds is considerable. Using regression models to separate the effect of changes in phytoplankton, Breukelaar *et al.* (1994) estimated that, roughly speaking, resuspension by a moderate benthivorous stock of $30\,\mathrm{kg\,ha^{-1}}$ suffices to reduce the Secchi-depth from crystal clear water to less than 1 m. This impact is not surprising in view of the activity of the fish. An average bream was computed to suspend five times its own body weight per day ($q = 5\,\mathrm{g\,g^{-1}\,day^{-1}}$) in these ponds.

Obviously, the obtained results can not be simply extrapolated to other situations. The activity of fish may vary from case to case, and the type of sediment will affect resuspension as well as the settling rate of particles. The sediment in the experimental ponds consisted mainly of clay. On sandy soils the effect will probably be less, while, on the other hand, certain soft organic sediments can have much lower settling rates, increasing the potential impact of benthivores on the concentration of suspended material.

As mentioned earlier, the sensitivity of sediment to resuspension by waves depends strongly on the state of the sediment surface layer. If the sediment is left undisturbed, the critical shear needed for resuspension increases over time due to consolidation. In view of this mechanism, benthivorous fish may be expected to increase the sensitivity of shallow lakes to wind. Their activity keeps the sediment from consolidating in periods with low wind. As a consequence, a smaller shear and therefore less wind is needed for resuspension. Obviously, this mechanism will not be important if the fetch to depth ratio of a lake is such that wind resuspension itself is very frequent, preventing consolidation altogether, as in Lake Arresø mentioned in Chapter 2. Nor will it be of any significance in cases where wind resuspension is very rare, as in the experimental ponds discussed above. In intermediate situations, however, this indirect effect of benthivorous fish on resuspension may be expected to contribute to turbidity.

The effect of vegetation on sedimentation and resuspension

The effect of vegetation on resuspension has been long since noted. Jackson and Starrett (1959), for instance, showed that in Lake Chatauqua (Illinois, USA) turbidity is much higher in winter when wind-induced waves stir up the unprotected sediments, than in summer when vegetation covers the lake bottom and wind has little or no effect upon turbidity (Fig. 2.19).

Also, the effect of vegetation is indicated by the fact that resuspension has become a major source of turbidity in several large shallow lakes that were clear until they lost their vegetation, such as Lakes Apopka and Tämnaren described in the previous chapter. Not surprisingly, it has been found that macrophyte abundance is an important source of error in models that attempt to relate predicted wave induced shear stress to actual suspended sediment concentrations (Hamilton and Mitchell, 1996).

Not only submerged plant beds, but also zones of emergent vegetation help to reduce wind resuspension in shallow lakes. This is shown, for instance, by Dieter (1990), who measured sediment resuspension in open and

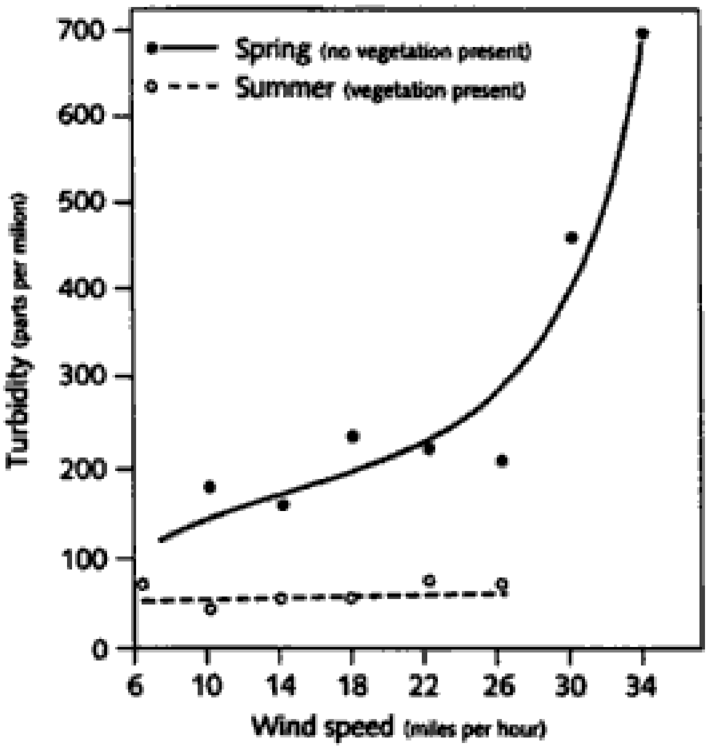


Fig. 2.19 Turbidities of Lake Chautauqua, Illinois, USA, occurring at various wind velocities in the spring when no vegetation is present and in the summer when vegetation has developed. Redrawn from Jackson and Starret (1959).

protected areas in a couple of shallow Dakota lakes. The amount of suspended matter collected in sediment traps appeared to be 2–4 times less in areas sheltered by emergent vegetation stands than in more open parts.

Obviously, the effect of submerged plants on resuspension will depend on vegetation density and structure. Especially strong effects have been noted in dense fields of charophytes. Indeed inoculation of new farmponds with charophytes has been suggested as a practical method to prevent them from becoming turbid with suspended sediment (Crawford, 1979). Charophyte vegetation can reach a high biomass and most species concentrate this biomass close to the sediment, covering it like a dense mat. Obviously, this strongly reduces the water movement at the sediment surface. Resuspension by waves within such vegetation will occur rarely if at all. Also, access of benthivorous fish to the sediment is hindered. These animals are generally not found in densely vegetated areas. Thus the resuspension part of the cycle is largely blocked. In addition, sedimentation may be speeded up in such vegetation due to a reduction of the effective mixing depth. If the vegetation is dense enough turbulent mixing will be prevented throughout the plant filled volume. This stagnation of vertical mixing may be enhanced by steep vertical temperature gradients that can build up on sunny days. The mechanism is the same as that operating at the thermocline that separates the epilimnion from the hypolimnion in stratified lakes. The warm upper layers tend not to mix with the colder lower ones because warm water 'floats' on the denser layers of cold water. Thus the gradient is stable. As a result, turbulent mixing is reduced to the often shallow layer of water above the vegetation. Since, as explained earlier, settling loss is inversely related to mixing depth, this situation may lead to high loss rates of algal cells and other suspended particles.

The effect of *Chara* vegetation on the sedimentation–resuspension cycle is illustrated nicely by a phenomenon that can sometimes be observed in Veluwemeer (see also Section 5.2). Large areas with clear water occur above dense mats of *Chara contraria*, contrasting sharply with the highly turbid water in the rest of the lake. Aerial photographs show that the transition from the clear to the turbid area is very sharp, occupying a zone of only about 10 m. Storms can induce horizontal currents that destroy the gradient, pushing turbid water over the vegetation fields. When the wind stops, however, the water clears up in the fields within a day. The lake depth in these areas is only between 0.3 and 0.8 m, at least 0.2 m of which is occupied by vegetation. Since the average sinking velocity of the seston particle is in the order of magnitude of 1 m per day, this clearing up can easily be accounted for by settling loss.

Obviously, weed beds may be expected to be net sinks of sediment as settling of matter from incoming water will usually exceed resuspension. A study of erosion and sedimentation in vegetated and nonvegetated areas in a Wisconsin reservoir confirms this idea (James and Barko, 1990). In the summer period when macrophytes were present, sediment accretion was found not only on deep sites but also in shallow plant dominated areas.

2.3 NUTRIENT DYNAMICS

The seasonal dynamics of nutrient availability in shallow lakes differ profoundly from the typical pattern observed in deep stratified lakes. In deep lakes there is a continuous loss of nutrients from the epilimnion to the hypolimnion during the summer. Despite the fact that recycling within the epilimnetic community is very efficient, there is always a fraction of the particulate matter that gets lost as it sinks irreversibly through the thermocline to the bottom. Due to this sinking loss the epilimnion of a stratified lake can lose up to half of its total phosphorus during the summer (Guy *et al.*, 1994). Nutrients from the material that is mineralized in the hypolimnion can only return to the epilimnion after the autumn turnover when the whole lake becomes mixed again.

In contrast, the pelagic system of shallow lakes does not show this systematic loss of nutrients during the summer. The intense sediment–water contact ensures a rapid return of most sedimentated material into the water column. In addition, the relatively high sediment temperatures in summer lead to an increase in mineralization rates, and consequently to an increased

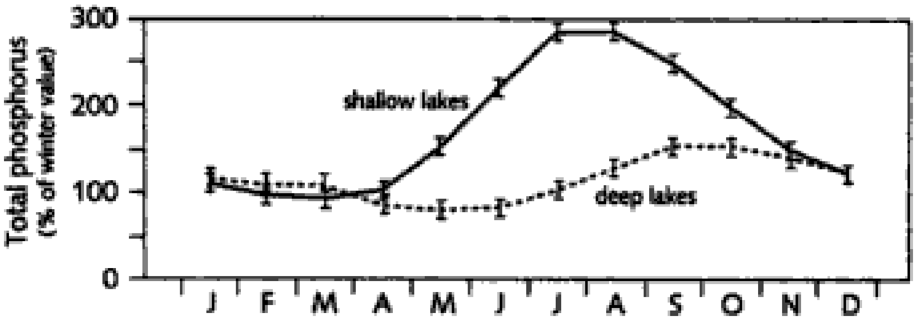


Fig. 2.20 Difference between the seasonal changes in total-P concentrations in the epilimnion of stratified lakes (upper panel) as opposed to total-P dynamics in shallow (well mixed) lakes (lower panel) in Denmark. Data are from a eutrophic set of lakes ($0.2 <$ total-P < 0.5 mg/l). Redrawn from Jeppesen (1996).

release of nutrients from the sediment (Jeppesen *et al.*, 1996). As a result the nutrient concentration in shallow lakes tends to follow the opposite seasonal pattern of what is generally observed in stratified lakes (Fig. 2.20).

Riley and Prepas (1985) found that, on average, the total phosphorus concentration in mixed lakes increased by 57% from the spring to summer while the summer values in the epilimnion of stratified lakes in their data set were 13% below the spring concentrations on average.

Phosphorus has probably received more attention than any other nutrient in limnology. In shallow lakes, the intense sediment–water contact gives an extra dimension to the eutrophication problem. Much of the phosphorus that has been absorbed by the sediment during eutrophication can be released to the water column later. This 'internal loading' can cause a delay of many years in the response of lake water concentrations to a reduction of the external loading. For nitrogen the sediment–buffer effect is less relevant (Jensen *et al.*, 1991). Instead, it has been shown that substantial amounts of nitrogen can disappear from shallow lakes as a result of denitrification. Although nitrogen limitation occurs frequently, its dynamics have been studied less extensively.

The availability of phosphorus

A major problem of analysing the role of phosphorus as a nutrient for algae in lakes, is that it is very difficult to determine how much is actually available to the algae. Phosphorus in the water column occurs in many different forms. It is common practice to split up this highly diverse total pool of phosphorus into a few fractions that can be distinguished by simple techniques (Fig. 2.21).

First, filtering over a membrane of 0.45 µm separates the particulate fraction (including the algae) from the total soluble phosphorus. The latter is further divided by chemical methods into soluble reactive phosphorus (SRP) and soluble unreactive phosphorus (SUP).

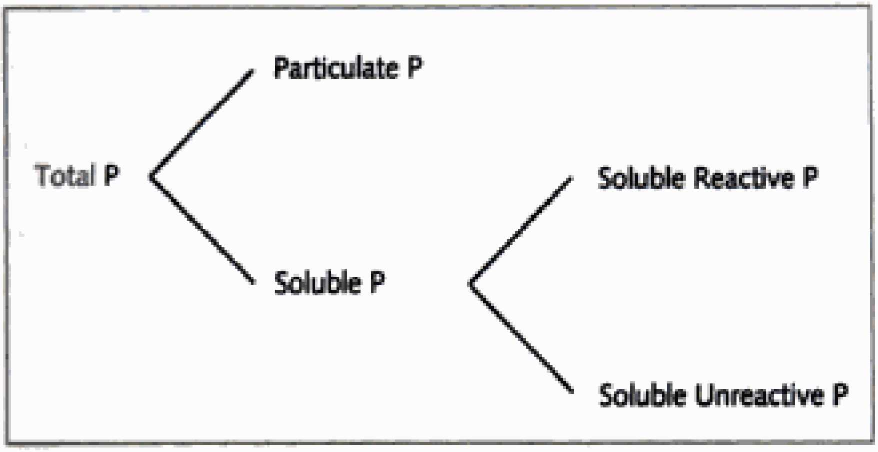


Fig. 2.21 The total pool of phosphorus in lake water is split up in fractions that can be distinguished by simple techniques. The particulate fraction is separated by filtration from the total soluble phosphorus. The latter is further divided by chemical methods into soluble reactive phosphorus (SRP) and soluble unreactive phosphorus (SUP).

Unfortunately, this subdivision does not give much insight into what is actually available for algal growth. First of all, it is important to distinguish between immediate availability, and long-term availability. Immediately available is what can be taken up by phosphorus starved test algae in the laboratory within a few hours (Boström *et al.*, 1988b). It was long assumed that SRP was a good estimate of the immediately available fraction. The idea was that SRP was largely equivalent to orthophosphate (HPO_4^{2-}, $H_2PO_4^-$), and that this orthophosphate was the sole form of phosphorus utilized by algae. It is now clear that neither of these assumptions is really correct and that there is not even a fixed proportionality between immediately bioavailable phosphorus and chemically assessed SRP (Boström *et al.*, 1988b). Nonetheless, laboratory experiments to estimate the immediately available pool are tedious, and SRP still gives the best estimate in practice.

With respect to understanding why some lakes have a higher algal biomass than others, immediately available phosphorus is not really the most relevant statistic. Many of the forms of phosphorus that are not directly available to algae can be transformed into available forms relatively quickly. Desorption and dissolution can make part of the inorganic particulate phosphorus available, and also the turnover of phosphorus that is present in algae can be extremely rapid (e.g. Rigler, 1956) . Obviously, it would be useful to have an indication of the total amount of phosphorus that is available to algae. In practically all eutrophication studies the total concentration in the water column ('total-P') is used as such. This pragmatic solution has two problems. First of all, part of the phosphorus fractions in the lake water can not be converted into available phosphorus. Secondly, and in our context more importantly, in shallow lakes there is an intensive exchange between phosphorus in the water column and phosphorus in the sediments. Thus, a substantial part of the relevant available phosphorus pool in shallow lakes is present in the sediment rather than the water column. Therefore, the traditionally used 'total-P' is in fact a far from perfect indicator for the nutrient status of shallow lakes. Release of SRP from the sediment into the water depends on the composition of the sediment and the SRP concentration in the lake water (Søndergaard *et al.*, 1992), but also varies strongly depending on the conditions at the sediment–water interface. Understanding this sediment–water interaction is therefore crucial for understanding the phosphorus dynamics of shallow lakes.

Sediment as a phosphorus buffer

In lakes that have received a more or less constant input of water and nutrients for many years, the phosphorus concentration in the lake water (P) is usually lower than the concentration of the inflowing water (P_i). This is because part of the nutrients are retained in the slowly accumulating sediment layer, a process that is mainly driven by a net sedimentation of dead organic material. Of course, this discrepancy between inflow and lake concentration depends on the time that water spends on average in the lake. If water passes quickly through the lake, the so-called hydraulic retention time (τ_r) is short, and the relative influence of processes in the lake becomes less. In that situation, the nutrient concentration in the lake water resembles the concentration of the inflowing water more closely. In the 1970s Vollenweider (1977) found that the effect of retention time and inflow concentration on the lake water concentration can be reasonably described by a simple equation:

$$P = c\frac{P_i}{1+\sqrt{\tau_r}} \qquad (22)$$

Later an exponent was added to the function to obtain a slightly better fit (Vollenweider and Kerekes, 1982), but the above formula has become well known as the Vollenweider model.

Since the empirical Vollenweider equation describes a generic relationship between input and the equilibrium concentration in the lake, it can in principle also be used to predict the effect of a reduction in nutrient loading on the concentration in the lake water. After a transient period the nutrient concentration in the lake should settle to a new equilibrium value depending on the new input concentration and hydraulic retention time in the way described by Vollenweider's equation. If the hydraulic situation (and hence τ_r) is unaltered by the restoration measures, a short-cut is sometimes made by estimating that the mean P concentration in the lake should decrease roughly in proportion to the change in P input (Sonzogni *et al.*, 1976). Jeppesen and co-workers (1991) used this approximation to study the set-

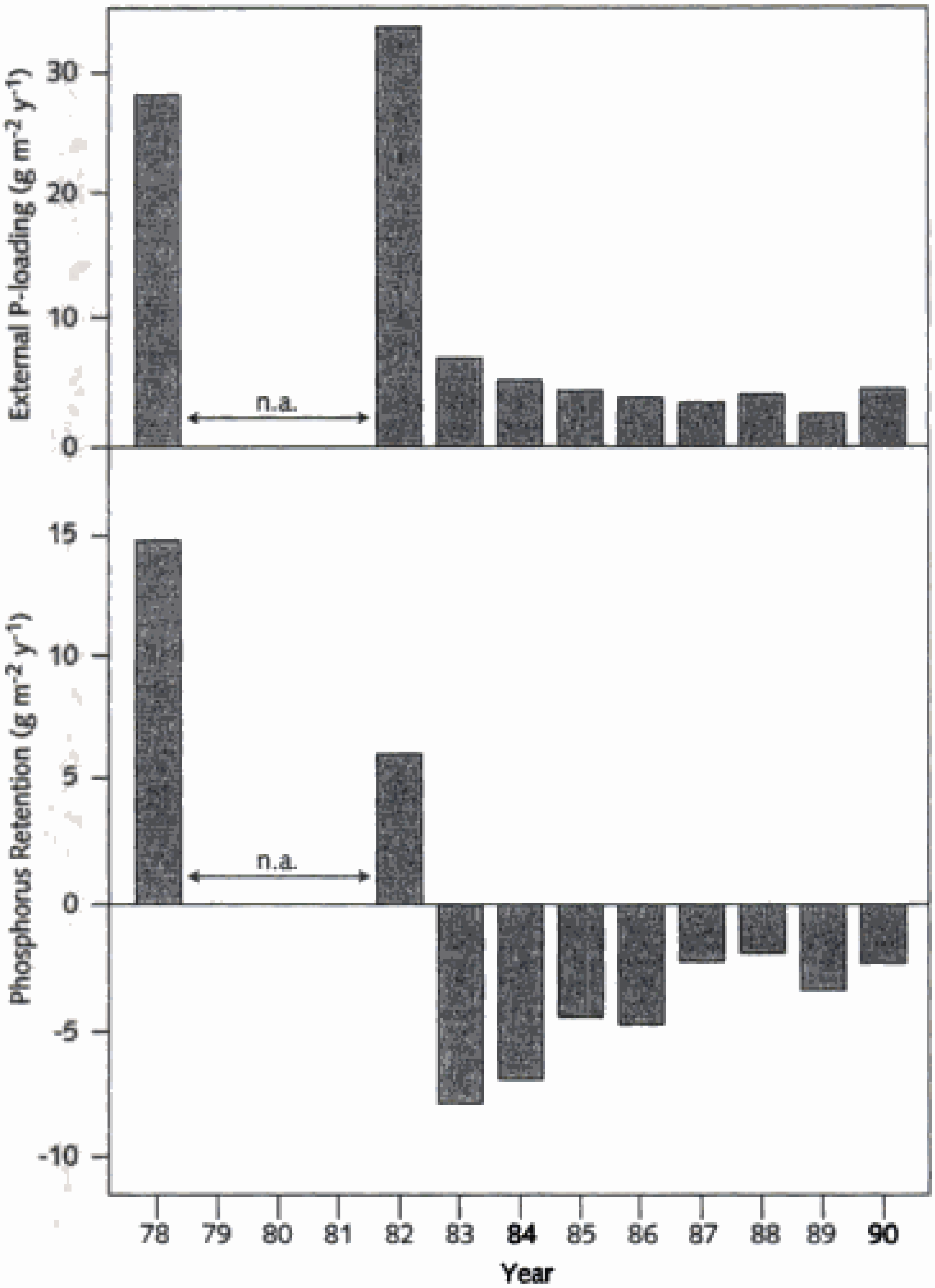


Fig. 2.22 External phosphorus loading (upper panel) and phosphorus retention (lower panel) in the Danish Lake Søbygaard from 1978 to 1990. Before 1983 the loading was high and the lake accumulated phosphorus. After a strong reduction in the external loading at the end of 1982 there is a net loss of phosphorus from the lake that continues for years, indicating that the sediment keeps releasing phosphorus to the lake water. From Søndergaard *et al.* (1993).

tling to the predicted new state for 27 Danish lakes that had received a substantial reduction in nutrient loading. It appeared that even 4–16 years after the reduction in loading, the decrease in concentration in most lakes was still far less than expected from the reduction in the input concentration.

Part of this delay can be explained from the time it takes to dilute the nutrient rich lake water with the cleaner inflowing water. Assuming a homogeneous well mixed system with no exchange between sediment and water, it can be derived that it takes about three times the hydraulic retention time to reduce the surplus pool of phosphorus in the lake water by 95% (Sas, 1989). In some cases the delay can indeed be largely explained by this dilution effect, but usually the response to a reduction of the inflow concentration takes much longer. The main reason for this is that the sediment starts acting as a source rather than a net sink of phosphorus (Marsden, 1989; Sas, 1989; Jeppesen *et al.*, 1991). This is illustrated, for instance, by the response of Lake Søbygård (Fig. 2.22) to a reduction of the external nutrient loading.

In the period prior to the restoration efforts the lake showed a net retention of phosphorus (as expected from the Vollenweider relation). After a strong reduction of the inflow concentration, however, the lake started showing a negative retention (that is a net release) of phosphorus. Although this 'internal phosphorus loading' decreased gradually over the eight years studied, the authors suggest that the sediment contains enough phosphorus to support a net release for another 10 years or so.

In view of these buffer effects it is not surprising that in the years following a reduction of the external loading, phosphorus concentrations in shallow lakes are correlated with release from the sediment rather than with inflow concentrations (Van der Molen and Boers, 1994). From a restoration point of view it is therefore useful to be able to predict the effect of internal loading on the lake water after an intended reduction of the inflow concentration. A reasonable guess would be that the phosphorus content of the sediment is indicative of the potential internal loading. Correlative studies, however, show that the concentration of phosphorus in the lake water is not (Jensen *et al.*, 1992) or only weakly (Van der Molen and Boers, 1994) related to the phosphorus concentration in the sediment. Instead, the concentrations in the water tend to correlate well with the ratio between phosphorus and iron concentrations (P:Fe) in the sediment (Jeppesen *et al.*, 1991; Jensen *et al.*, 1992; Van der Molen and Boers, 1994). This is presumably because iron is the most important agent binding phosphorus in the aerobic upper layer of the sediment in most lakes. Interestingly, for the subset of lakes where the P/Fe ratio (g/g) in the sediment is lower than 1/10, the correlation with lake water concentrations becomes weak (Jensen *et al.*, 1992; Van der Molen and Boers, 1994). This suggests the simple rule that iron in the sediments of these shallow lakes is able to bind more or less permanently an amount of phosphorus equivalent to about 10% of its own weight, and that it is basically only the surplus phosphorus that constitutes the pool from which there can be a release to the lake water.

This empirical 10% rule is also reflected in the vertical concentration gradient of iron and phosphorus in the sediment of Lake Søbygård (Søndergaard *et al.*, 1993). As mentioned earlier, eight years after reduction of the external loading, the sediment was still releasing phosphorus (Fig. 2.22). The depth profile of the Fe:P ratio (Fig. 2.23), however, shows that the Fe:P ratio in the upper sediment layers has already stabilized at a value of approximately 10, suggesting that the main source of released phosphorus is now the sediment at a depth of around 20 cm where the ratio is lower.

Besides being able to predict the effect of internal loading after a reduction of the external loading, it is also of practical interest to predict for how many years this phenomenon is likely to delay the recovery. Since the phosphorus released by the sediment has to be washed out somehow by the water flowing through the lake, it seems reasonable to expect that lakes with a higher throughflow ('flushing rate') recover faster. Danish data, however, indicate that this is not the case (Jeppesen *et al.*, 1991). Lakes with a high flushing rate are just as slow to approach the predicted new equilibrium as the rest. A possible explanation for this is that a high inflow generally also implies a high overall nutrient loading in the past, allowing a large accumulation of phosphorus in the sediment during the period before restoration. Indeed hydraulic retention time in the Danish lakes is strongly correlated with the yearly P-load and the P-pool in the upper 20 cm of the sediment. Thus, although lakes with high flushing rates may have a better potential to wash out their phosphorus, this advantage seems to be counterbalanced by the fact that they also tend to have accumulated more phosphorus in the past.

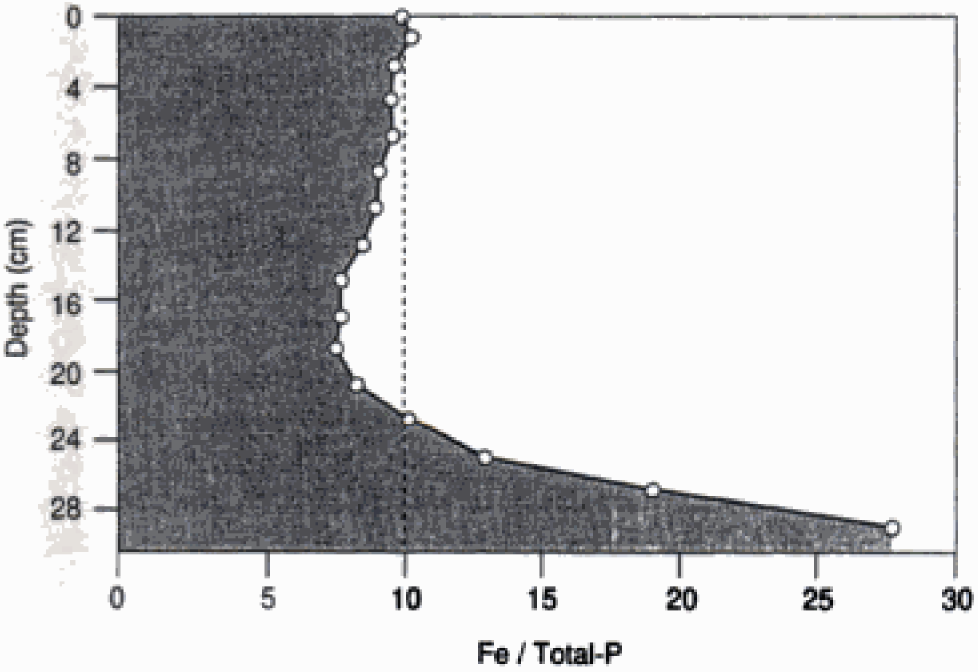


Fig. 2.23 Variation of the Fe:P ratio with depth in the sediment of Lake Søbygaard. In the top layer the ratio has decreased to about 10, suggesting that the remaining phosphorus in this layer can now be entirely immobilized by iron under aerobic conditions. Redrawn from Søndergaard *et al.* (1993).

The mechanisms that govern sediment phosphorus release

Although some empirical relationships between lake concentrations, external loading and sediment characteristics have been found, a large part of the variation remains unexplained. Several studies have shown that differences in, for instance, turbulence, animal activity and plant growth can cause large variations in the release of phosphorus from the sediment. To understand these effects, it is necessary to zoom in more closely on the mechanisms that govern phosphorus dynamics at the sediment surface.

The role of oxygen and iron

It has become evident over the past decade that what happens at the sediment–water interface is extremely complex (see the reviews by Boström *et al.*, 1988 and by Marsden 1989). The main point, however, was demonstrated more than half a century ago. Einsele (1936; 1938) and Mortimer (1941; 1942) showed that iron is very important in immobilizing phosphorus in sediments, but that this binding only works under aerobic conditions. Under reduced conditions iron-bound phosphorus is released. Insoluble Fe(III) is reduced to Fe(II) and both iron and phosphorus are brought in solution. Due to microbial respiration, oxygen is used up in sediments where decomposition of organic matter occurs. In deep stratified lakes where there is practically no oxygen supply to the sediment, sediments are therefore anoxic. In shallow lakes, however, mixing usually supplies enough oxygen to the sediment surface to maintain a superficial aerobic layer. It is in this narrow layer that Fe(II) is oxidized to Fe(III) and precipitates with phosphorus. Because of this immobilization the concentration of phosphorus that can diffuse from the sediment surface into the lake water drops sharply when the sediment surface becomes aerobic.

Although phosphorus immobilization is mainly an oxygen and iron story, some other factors are known to play a role as well. Importantly, high pH values reduce the capacity of iron to bind phosphorus (Lijklema, 1977). Elevated pH values in the water column arise when photosynthetic activity is very high, and this can affect the pH of the sediment surface, promoting the release of iron-bound phosphorus. Inlet of water that is rich in calcium and carbonate may buffer the pH in such situations leading to a decrease in phosphorus release from the sediment (Hosper, 1985; Hosper and Meijer, 1986). On the other hand in poorly buffered soft-water systems, inlet of HCO_3^--rich water may result in a pH rise causing an increased phosphorus release from the sediment (Smolders and Roelofs, 1995). A special situation can arise in highly organic sediments where sulphide is sometimes produced from sulfate reduction (Moss, 1988; Phillips *et al.*, 1994; Smolders and Roelofs, 1995). In that case part of the iron can become unavailable for phosphorus immobilization because Fe(II) is removed from the pore water due to precipitation with sulphide as insoluble FeS.

It has also been suggested that high concentrations of nitrate may sometimes buffer the redox potential of the sediment surface, preventing a release of iron-bound phosphorus in much the same way as oxygen supply does (Andersen, 1982). In addition, aluminum and calcium carbonate can play a role in immobilizing phosphorus in some lakes (see reviews by Boström *et al.* 1988; Marsden 1989 and Lijklema 1994). However, it seems that iron remains the dominant factor for phosphorus immobilization in virtually all cases. Even in the hard water Lake Balaton, for instance, where 65% of the sediment consists of carbonates and only 0.5% of iron, most of the sediment phosphorus is associated with the latter (Lijklema, 1994).

Turbulence and decomposition

Because of the overriding importance of iron as a precipitating agent, the aerobic surface layer plays a key role in the regulation of the internal phosphorus cycle of shallow lakes (Fig. 2.24) as it can prevent a major part of the sediment phosphorus pool from entering the lake water.

Turbulence in the water column and decomposition in the sediment are key factors in the internal phosphorus cycle of shallow lakes, not only because of their obvious roles in transport and production of SRP (soluble reactive phosphorus), but also because of their effect on the redox situation

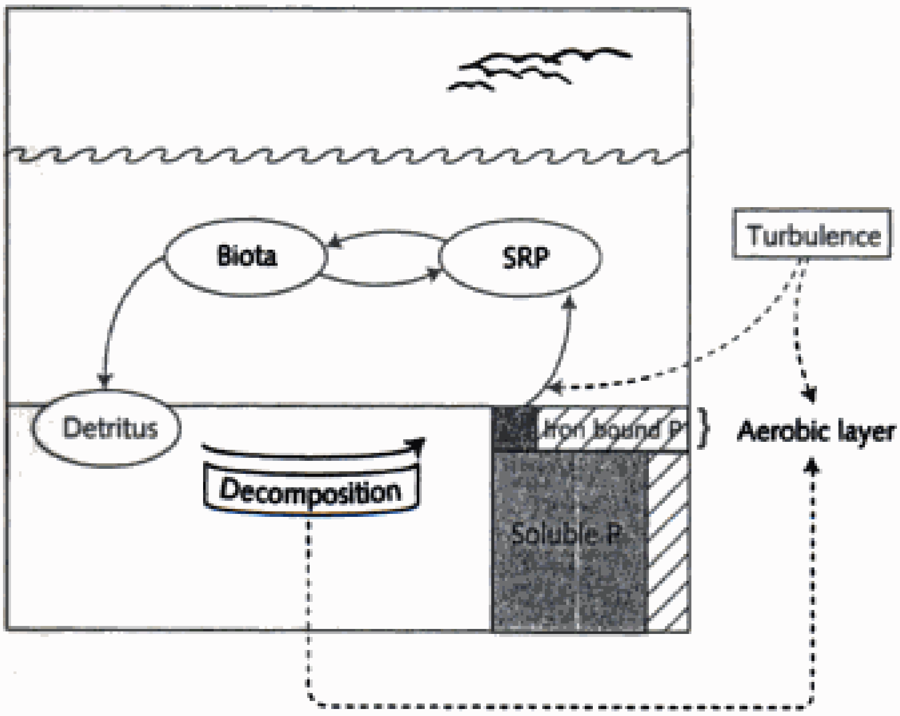


Fig. 2.24 Schematic representation of the main processes involved in the internal phosphorus cycle of a shallow lake. Turbulence promotes diffusion of phosphorus out of the sediment, but also helps maintaining the anaerobic surface layer where phosphorus is immobilized by iron. The decomposition process supplies mineral phosphorus, but also uses oxygen, thereby reducing the size of the aerobic layer.

at the sediment surface. The maintenance of an aerobic layer depends critically on the balance between microbial consumption of oxygen in the sediment and oxygen supply from the aerobic water layer. If oxygen supply from the water column is insufficient to counterbalance the microbial uptake, the sediment surface becomes anoxic and phosphorus can no longer be immobilized by iron.

The importance of turbulence for oxygenating the sediment surface is well illustrated by an incident that occurred during experiments in an *in situ* chamber in Gullmarsfjorden in Sweden (Sundby *et al.*, 1986). When stirring device in the chamber failed, black anaerobic patches soon developed on the sediment surface and the SRP concentration within the chamber increased fivefold, even though the water column had remained aerobic. Although animal activity can contribute significantly to mixing at the sediment surface, wind-induced turbulence may explain most of the differences between lakes. Since resuspension and oxygenation of the sediment are both driven by the turbulence at the sediment surface it is not surprising that iron controlled phosphorus release is in practice related to lake size and depth in much the same way as resuspension (Fig. 2.25).

Lakes that are on the borderline in this plot may stratify only during short periods of warm weather in summer. Such periods may suffice to cause anoxic conditions in the ephemeral hypolimnion that induce a shot of anaerobic phosphorus release from the sediment. Subsequent mixing of the lake may then bring about a significant increase of phosphorus concentration in the whole water column (Riley and Prepas, 1984; Kallio, 1994). Even

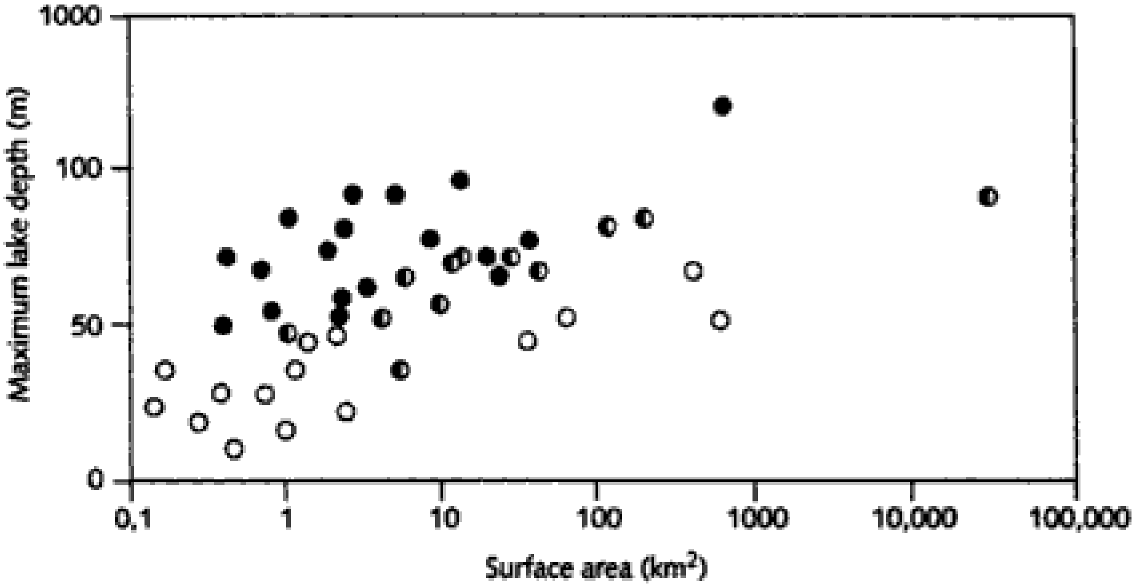


Fig. 2.25 The distribution of the reported form of sediment phosphorus release relative to the lake surface area and maximum depth. Closed circles represent anaerobic release, open circles aerobic release and partly open circles are lakes with both forms of release. Redrawn from Marsden (1989).

in the absence of distinct stratification, however, a reduced turbulence can lead to anoxic conditions at the sediment surface as shown by the experimental mixing problem in Gullmarsfjorden.

The overall relationship between turbulence and sediment phosphorus release is complicated by the fact that turbulence has two opposite effects (Fig. 2.24). It prevents excessive anaerobic phosphorus release by oxidizing the sediment surface, but it also promotes diffusion of phosphorus from the aerobic top sediment into the water. The subtle balance between these two effects is illustrated by a time-series analysis of phosphorus dynamics and wind velocity for the shallow (2.7m) Dutch Lake Westeinder (De Groot, 1981). In this lake the phosphorus release from the sediment peaks on windy days probably due to enhanced diffusion from the sediment. However, when longer periods (months) are considered the correlation between average wind and phosphorus release is reversed; The flux of phosphorus from the sediment into the water column being higher during calm periods than in periods with windy weather. Supposedly, diffusion of oxygen into the top sediment is insufficient in such periods of reduced turbulence to prevent anaerobic conditions at the sediment, resulting in an elevated phosphorus release.

Resuspension

At the most turbulent side of the range of mixing conditions, sediment is resuspended. Depending on the situation resuspended particles can either adsorb phosphorus from the surrounding water or release it (Serruya, 1977; Yousef *et al.*, 1980; Gunatilaka, 1982; Lennox, 1984), but in the P-loaded sediments of many eutrophic lakes release is likely to dominate in summer. The potential importance of resuspension in enhancing sediment P release is illustrated well by the work of Søndergaard and co-workers (1992). They measured how phosphorus release from sediment cores collected in Lake Arresø increased during experimental resuspension. Internal P-loading induced by resuspension appeared to be 20-30 times greater than release from the undisturbed sediment. This could not be explained simply from entrance of nutrient rich pore water into the water column. Also, the SRP release was not related to the amount of sediment that was brought into suspension. This suggests that SRP release during resuspension depends largely on the absorption-desorption kinetics. When the suspended particles are oversaturated, they release phosphorus. The net release becomes nil when the SRP concentration in the water has increased enough to be in equilibrium with the particle bound P-fraction. For sediment sampled in summer, an extra portion of SRP could be released when the sediment was resuspended again one day later, but such an extra release could not be obtained from sediment sampled in the spring. This indicates that it is largely the mineralization of fresh organic material present in the summer sediment that feeds the pool of exchangeable phosphorus in the top layer of Lake Arresø.

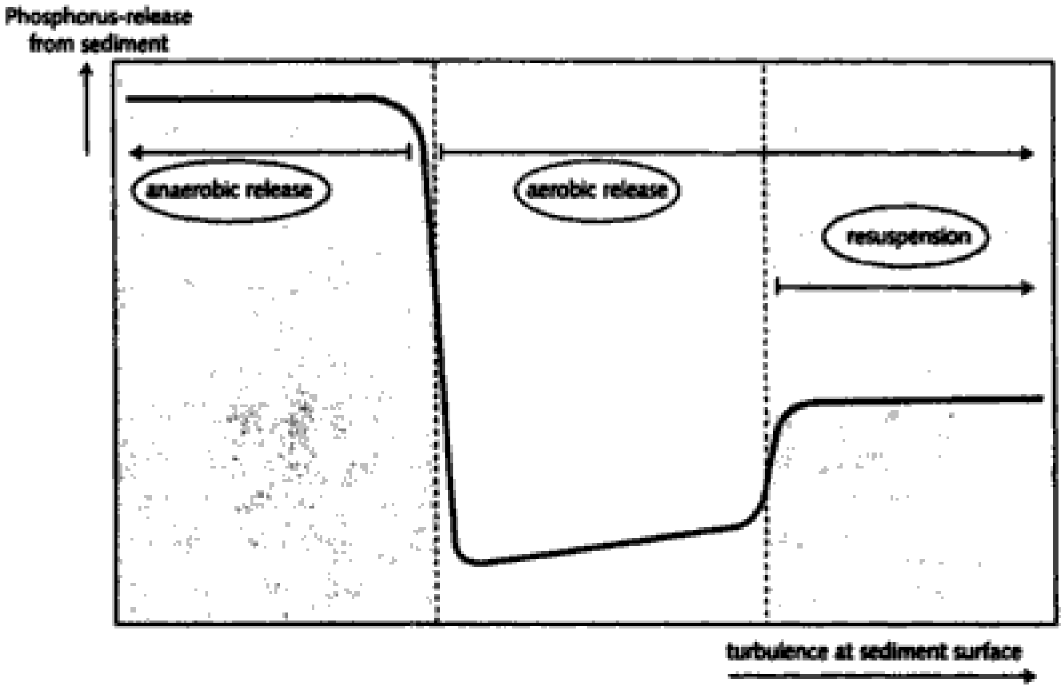


Fig. 2.26 Schematic representation of the effect of turbulence at the sediment surface on phosphorus release from the sediment (see text).

Summarizing the overall-effect of turbulence on sediment phosphorus release (Fig. 2.26): at low turbulence, oxygen supply to the sediment surface is insufficient to balance uptake by bacteria.

The resulting anaerobic conditions result in a high phosphorus release. At higher turbulence the sediment surface becomes oxygenated and phosphorus is immobilized by iron. A further increase in turbulence slightly enhances diffusion of phosphorus from the sediment, until a critical turbulence is exceeded and the top layer of the sediment is resuspended. At this point diffusion is no longer limiting and phosphorus release depends only on the SRP concentration in the water and the amount of phosphorus that is bound 'loosely' to the suspended sediment particles.

Mineralization of organic material in the top layers of the sediment is a main process affecting the shape of this hypothetical relationship. As argued, decomposition promotes phosphorus release from the sediment in two ways (Fig. 2.24). First, it enriches the pool of exchangeable phosphorus in the sediment. As shown in the Arresø experiments this enhances the potential release of phosphorus in repeated resuspension events (the right-hand saturation level in Fig. 2.26). Secondly, microbial decomposition uses up oxygen, and if oxygen supply from the water column is insufficient to counterbalance the microbial uptake, the aerobic surface layer becomes thinner and may eventually disappear entirely, allowing the iron-bound phosphorus to go into solution. Thus the critical turbulence needed to prevent anaerobic phosphorus release (Fig. 2.26) will increase with microbial activity. Obviously, mineralization activity increases with eutrophication. In addition, it shows a strong seasonal variation with a maximum in summer. This is because microbial activity increases with temperature, but also because the large amounts of settling algae provide a continuous input of fresh substratum for the bacteria. As argued, increased chances of temporal 'micro-stratification' are another reason why warm summer weather can boost sediment phosphorus release.

Nitrogen dynamics

Nitrogen is less often reported as a limiting nutrient in lakes than phosphorus. Also it does not show the strong resilience to reduction efforts described for phosphorus. Both factors probably contributed to the fact that its dynamics have received less attention than those of phosphorus. Although there are some similarities, the processes that govern nitrogen cycling differ widely from those implied in the phosphorus dynamics. Three major features set nitrogen aside from phosphorus: it does not accumulate in the sediment that strongly; it can disappear as gas into the atmosphere under certain conditions; and some cyanobacteria can use atmospheric nitrogen as a nutrient (Fig. 2.27).

Decomposition of organic material normally leads to the release of nitrogen as ammonium (NH_4^+). The ammonium produced by this so-called 'ammonification' of detritus can diffuse into the water column where it can be readily used as a nitrogen source by algae and macrophytes. In the aerobic top layer of the sediment, ammonium can be transformed microbially to nitrate (NO_3^-). This process is called nitrification. Although it can happen under the aerobic conditions in the water column as well, it

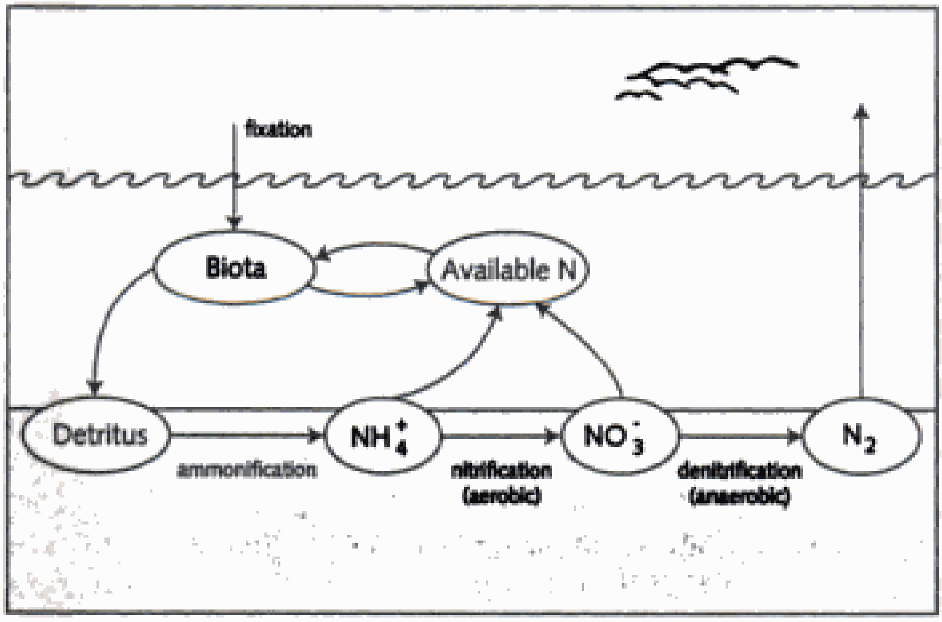


Fig. 2.27 Schematic representation of the main processes involved in the internal nitrogen cycle of a shallow lake (see text).

is reported to occur predominantly in the sediment where ammonium concentrations are normally high (Lijklema, 1994). Unlike phosphate, ammonium and nitrate are hardly adsorbed by sediment particles and do not normally precipitate to insoluble forms in the sediment either. Therefore, the strong accumulation in the sediment that is found for phosphorus in eutrophied lakes does not occur for nitrogen (Jensen *et al.*, 1991). This is probably the reason why lake water concentrations of nitrogen tend to respond more promptly to reduction of the external loading than phosphorus concentrations.

When nitrate ends up in an anaerobic situation, it can be microbially transformed into N_2 which can not be used as a nutrient by most algae, and largely disappears as gas to the atmosphere. This process, called denitrification, can constitute the major loss of nitrogen from lakes (Jensen *et al.*, 1991; Lijklema, 1994; Windolf *et al.*, 1996). Because denitrification itself requires anaerobic conditions, but its substrate (nitrate) is produced under aerobic conditions, denitrification works mainly where both conditions co-occur or alternate in time. Therefore, the sediment surface is a very important site for denitrification. Denitrification rates are difficult to measure in the field. An indirect way to estimate denitrification is through the mass balance. What goes into the lake and does not leave it is normally called retention. In the case of nitrogen this is obviously not a very adequate term, as part of it may be retained in the sediment, but another part is released into the atmosphere. Jensen and co-workers (1991) showed for a set of 69 shallow Danish lakes that burial in the sediment could only explain 23% of the total nitrogen loss. The remaining 77% is likely to disappear largely through denitrification, as the contribution of other loss processes are thought to be minor.

Empirical studies show that nitrogen loss is highest in shallow systems (Vollenweider and Kerekes, 1982; Lijklema *et al.*, 1989; Jensen *et al.*, 1991). This fits well with the idea that denitrification is the dominant process involved and that the sediment surface is the most important site for denitrification. As with phosphorus, the retention of nitrogen in a lake is larger when the water passes through the lake more slowly. In shallow lakes with a hydraulic retention time of more than a month it is not unusual to find that more than 50% of the nitrogen is 'retained' (Fig. 2.28), most of which has probably disappeared into the air. Because of this, shallow lakes can play an important role in reducing nitrogen concentrations in the passing water.

Obviously, the effect of nitrogen loss on the lake water concentration is also highest in lakes with a high hydraulic retention time, as the longer water stays in the lake, the stronger nitrogen concentrations can be reduced by denitrification and burial in the sediment. Windolf and co-workers (1996) analysed this effect statistically and found that 83% of the variation in annual mean lake water concentrations (*N*) in a set of well studied Danish

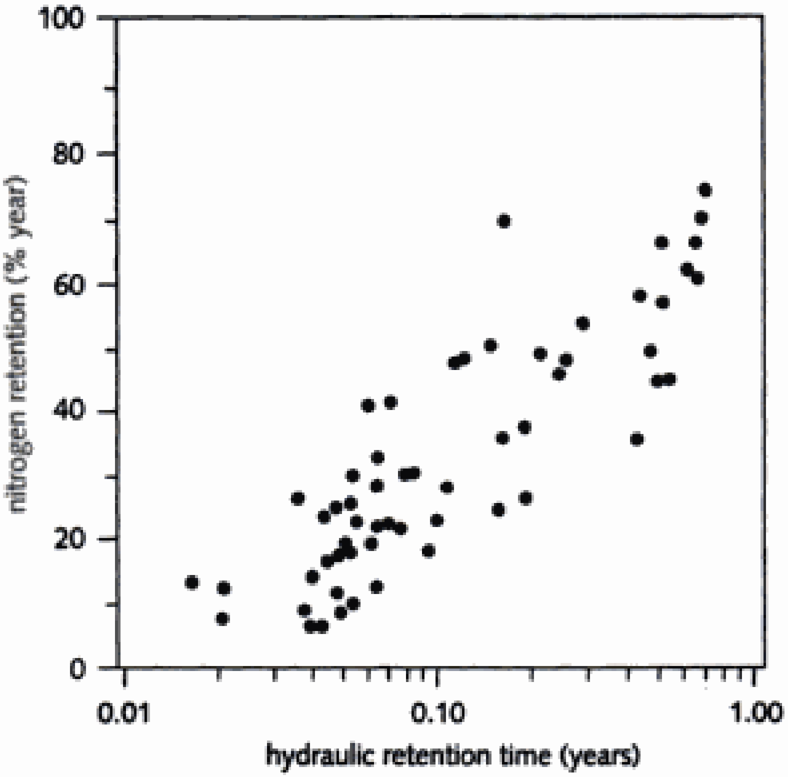


Fig. 2.28 Annual mean percentage retention of nitrogen (N_{m}) versus hydraulic retention time (τ_r) during four subsequent years in 16 Danish lakes. From Windolf *et al.* (1996).

shallow lakes from the inflow concentration (N_i) and hydraulic retention time (τ_r) by the following equation:

$$N = \frac{0.32 N_i}{\tau_r^{0.18}} \tag{23}$$

As explained in the next chapter, some cyanobacteria are able to use N_2 as a nitrogen source. Since this form of nitrogen is replenished by diffusion from the atmosphere into the lake water, N_2 fixation by cyanobacteria represents a net influx of nitrogen into the system. The contribution of nitrogen fixation to the total nitrogen balance of the lake has been studied in some detail for Naardermeer and Nieuwkoopse Plassen (DeNobel, unpublished results). In these Dutch lakes, nitrogen fixing cyanobacteria often bloom for a period of about three months in the summer. Nitrogen fixation during the blooms was estimated to represent about 20% of the total nitrogen – input to the lakes on an annual basis. This equals the losses estimated to result from denitrification in the lakes. However, most rates of N_2 fixation reported in the literature (Howarth *et al.*, 1988) are very low relative to the contribution of external loading found in shallow lakes (Windolf *et al.*, 1996).

Carbon as a limiting nutrient

The availability of carbon as a limiting nutrient has received relatively little attention. In a sense inorganic carbon is an inexhaustible resource as it can be continuously supplied from the atmosphere. However, the strong increase in pH observed in productive lakes indicates that the supply rate may often be outstripped by the demand. Nonetheless, phytoplankton growth is probably rarely limited by carbon (Harris, 1986). This is certainly not the case for the growth of submerged macrophytes (Vadstrup and Madsen, 1995). As explained later slow diffusion of carbon through the boundary layer around the leaves is a major problem preventing a high enough supply rate to keep up with the photosynthetic demand. Unlike in terrestrial environments not only CO_2 but also HCO_3^- can be an important source of carbon for many aquatic plants, even though the latter is usually assimilated less efficiently (Hutchinson, 1975). In addition to diffusion from the air, mineralization of organic material at the sediment surface may be an important source of carbon for the water column of shallow lakes. Nonetheless, carbon enrichment experiments also indicate that in shallow water supply rates may be insufficient to prevent carbon limitation in submerged vegetation (Vadstrup and Madsen, 1995).

The effect of algae and macrophytes on nutrient dynamics

Phytoplankton

There are several mechanisms through which phytoplankton tends to increase the total concentration of nutrients in the water column. As explained earlier, fixation of atmospheric nitrogen by cyanobacteria may contribute significantly to the influx of nitrogen into the lake under some conditions. But especially pronounced are the effects of phytoplankton on the release of phosphorus from the sediment into the water column. As argued, settling algae are rapidly mineralized at the sediment surface during the summer. Depending on the conditions, the phosphorus released in the mineralization process can be efficiently recycled into the water column. In addition to this, high algal productivity may stimulate the release of iron-bound phosphorus. This is due to three different mechanisms. First, the flux of settling algae stimulates the mineralization process increasing the probability of anoxic conditions at the sediment surface. Secondly, high photosynthetic activity causes the pH in the water column to rise. Since the capacity of iron to bind phosphorus decreases at high pH, this can promote the release of iron-bound phosphorus from the sediment surface. The third way in which algae stimulate release of phosphorus from the sediment is by depleting the orthophosphorus concentration in the water column. When phosphorus is limiting, algae can reduce SRP to very low values. As argued, the release of phosphorus from resuspended sediment depends largely on adsorption–desorption kinetics of SRP to the sediment particles. When

SRP is removed from the water column by algae, this will lead to a release of loosely bound phosphorus from the sediment until the adsorption–desorption equilibrium is restored.

Thus, phosphorus-limited algae mobilize phosphorus from the sediment through various mechanisms. This has an important consequence for the interpretation of 'total-P', the traditional indicator of the nutrient status of lakes, since it implies that the total-P concentration in the water column is really to a certain extent caused by the algae rather than vice versa. Obviously, this makes the interpretation of regression models explaining algal biomass from total-P in shallow lakes problematic. The true total available phosphorus pool for algal growth includes part of the phosphorus in the sediment. Since this is difficult to measure, water column total-P is used to indicate the nutrient status of the lake. When algae grow to reach a phosphorus-limited maximum, a large part of the total available phosphorus may be measurable as water column total-P. However, when algal biomass is kept low, for instance through zooplankton grazing, an increasing part of the total available phosphorus pool will be in the sediment and 'total-P' in the water column will be lower (Fig. 2.29).

It is important to note that this mechanism will lead to correlations between algal biomass and total-P, even when the total available phosphorus pool is constant and the variations in algal biomass are due solely to other factors. Thus statistical analysis will tend to overestimate the variation in algal biomass that can be explained from variation in phosphorus.

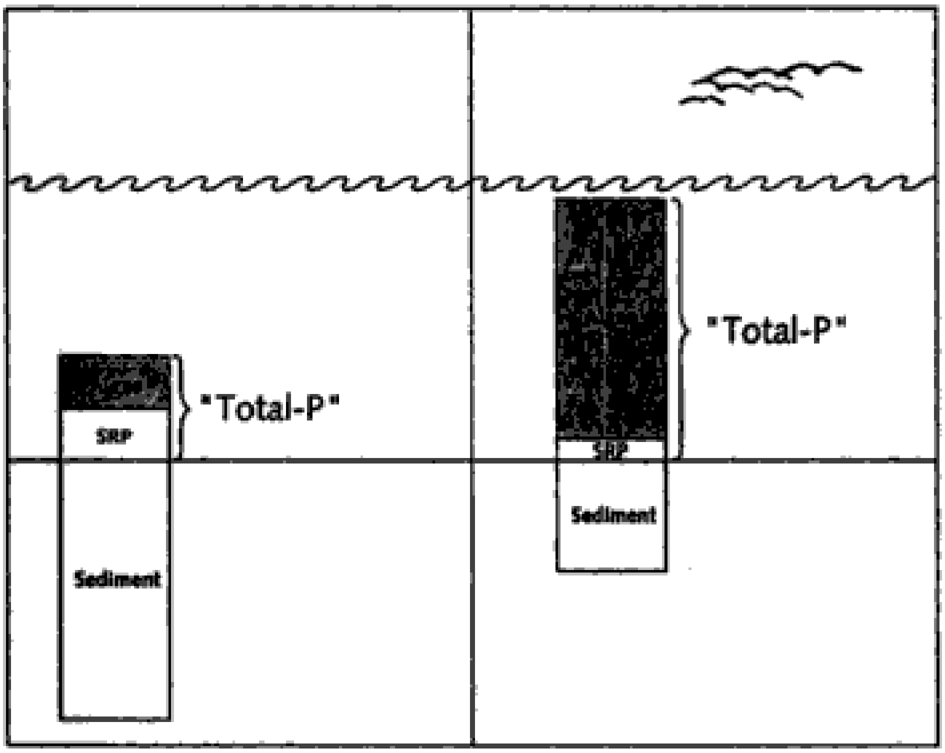


Fig. 2.29 Effect of algal biomass on the total-P concentration in the water column (see text).

Macrophytes

Aquatic vegetation affects nutrient dynamics in an even more intricate way than phytoplankton. Like algae, macrophytes produce detritus that is mineralized, leading to a release of phosphorus, and potentially to anoxic conditions inducing the release of iron-bound phosphorus. Also, high pH values can arise due to photosynthesis in macrophyte stands, again stimulating sediment phosphorus release. In other aspects, however, the effect of macrophytes on the phosphorus cycle is different from that of phytoplankton. Importantly, macrophytes reduce turbulence. As explained earlier, this works in two opposing ways. It enhances the probability that anaerobic conditions arise at the sediment surface, but at the same time it prohibits resuspension and limits diffusion of phosphorus out of the sediment.

Another important difference between vegetation and phytoplankton is that depending on the situation, macrophytes can obtain many of their nutrients from the sediment rather than from the water column (Hutchinson, 1975; Barko and Smart, 1980). This implies that nutrients released from living or decaying plants can potentially represent a net translocation from the sediment to the water column (Prentki *et al.*, 1979; Carpenter, 1980; Carpenter, 1981; Landers, 1982). On the other hand, a large part of the phosphorus in macrophyte detritus may return to the sediment (Van Donk *et al.*, 1993); hence macrophyte stands can also act as a net sink for phosphorus. The bottom line is that in theory, the effect of macrophytes on phosphorus in the lake water can work either way.

This ambiguity is also reflected by the published experimental results and field patterns. In the Polish Lake Luknajno, the entire annual phosphorus load of the lake is estimated to be stored in the dense mats of charophytes that cover the sediment (Kufel and Ozimek, 1994). In Veluwemeer, however, ortho-phosphorus concentrations are higher in the dense *Chara* fields than in adjacent unvegetated areas (Van den Berg *et al.*, 1997), and in Alderfen Broad periods of high biomass of submerged plants are characterized by a conspicuous increase in total-P concentrations (Fig. 1.2). An overview of the response of lakes where submerged macrophytes developed after biomanipulation (Meijer *et al.*, 1994a) shows that total-P concentrations increase in some cases but decrease in others (Fig. 2.30).

The same biomanipulation studies suggest that the effect of macrophytes on nitrogen dynamics is more consistent. Since many things change after reduction of the fish stock, causality is not readily unravelled in these experiments. Nonetheless, the year-to-year changes in total-N concentration in these lakes follow the changes in vegetation abundance remarkably closely, suggesting that macrophytes can cause a reduction of the nitrogen concentration in the water column (Fig. 2.31).

There is also a negative correlation between total-N concentration and macrophyte coverage in a set of 84 Dutch shallow lakes ($P = 0.04$, unpub-

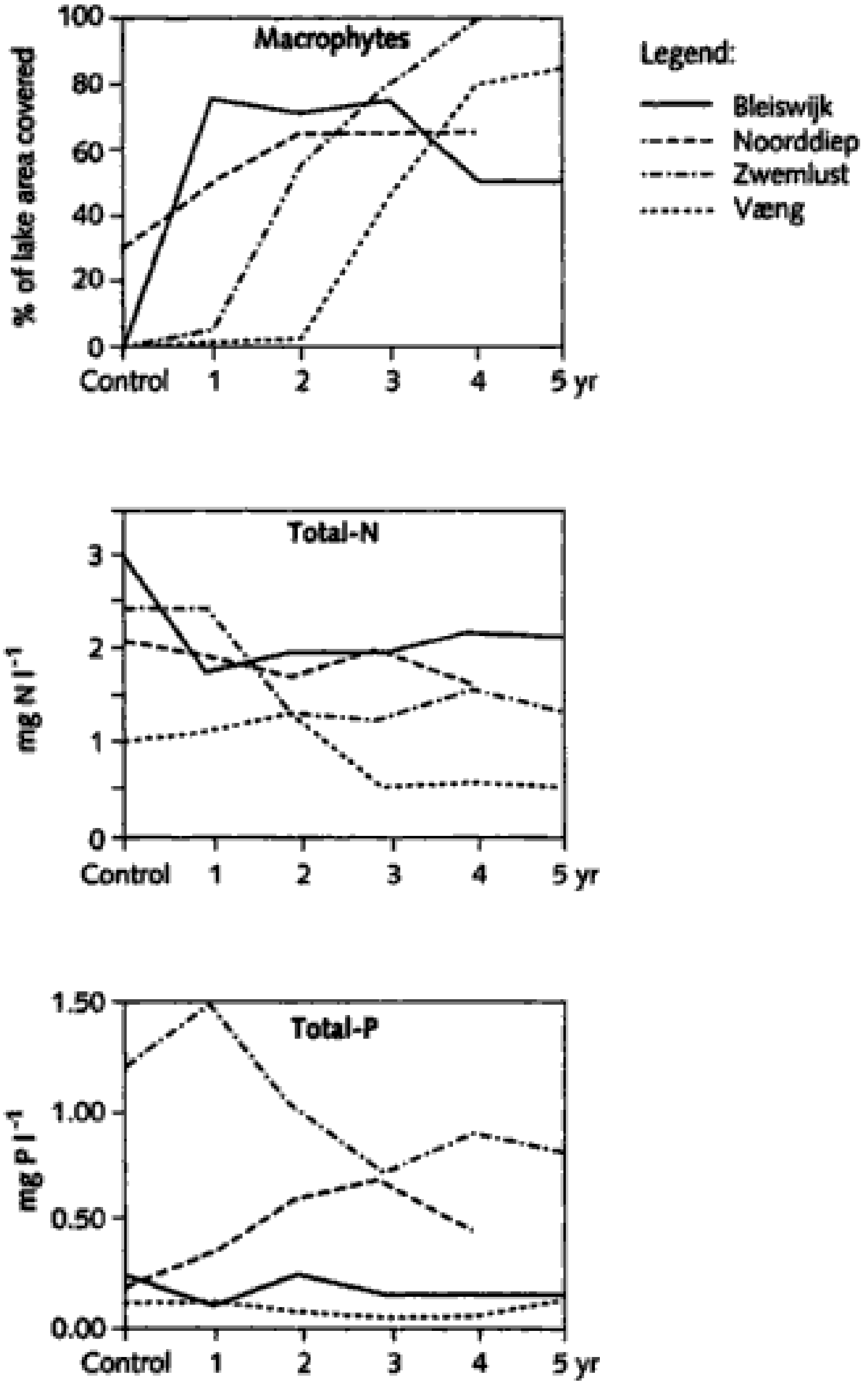


Fig. 2.30 Changes in total-N and total-P concentrations in the water of lakes where macrophytes have developed in response to a reduction of the fish stock. From Meijer *et al.* (1994a).

lished results). The slope of a regression through these data corresponds well to the magnitude of the effect observed in the biomanipulation experiments. Both analyses suggest that a colonization of 50% of the lake area by submerged plants results in a decrease of about 1 mg l^{-1} in the total-N concentration. In the same data set, no significant relationship exists between vegetation coverage and total-P concentrations.

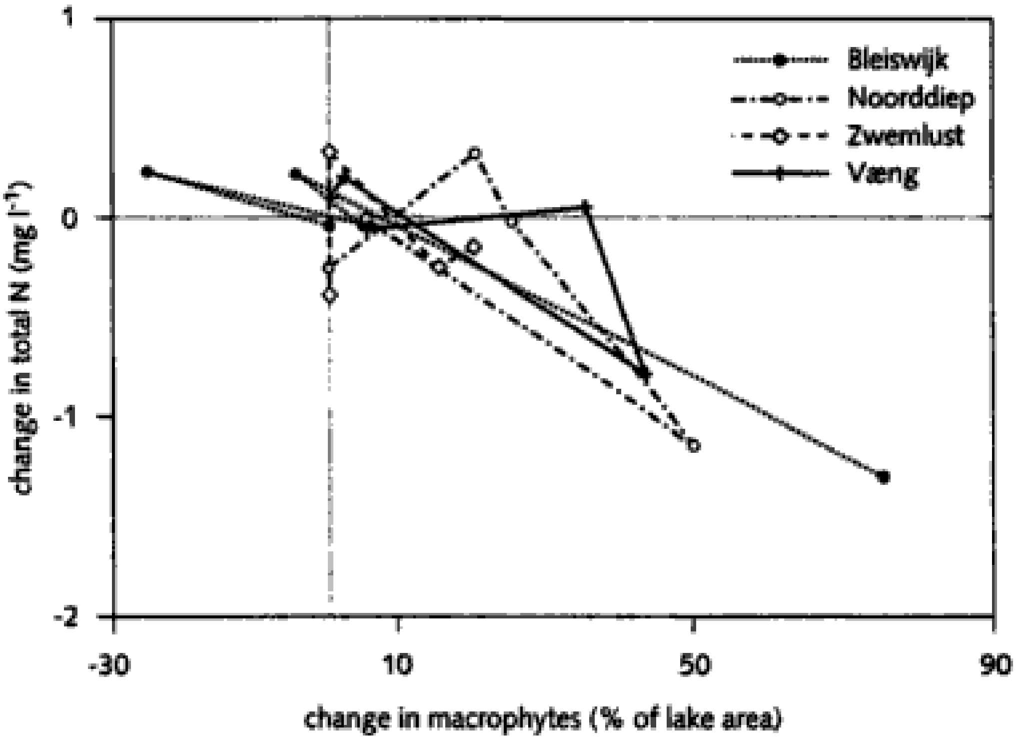


Fig. 2.31 Relationship between the year-to-year changes in the percentage of lake area covered by vegetation and change in the total-N concentrations for the biomanipulated lakes represented in Fig. 3.30.

The effect of macrophytes on nitrogen concentration may be explained in part as a result of uptake from the water column. Submerged plants can take up considerable amounts of nitrogen from the water, part of which is buried as detritus in the sediment at the end of the growing season. Probably another important way in which aquatic plants affect nitrogen dynamics is through their effect on denitrification. As explained, denitrification works mainly where aerobic and anaerobic conditions co-occur or alternate in time. Such conditions are likely to occur in plant beds. Oxygen production in dense vegetation stands is high during the day, but the levels of oxygen can drop dramatically at night due to respiration. This variation may cause patches of sediment surface that are aerobic during the day to become anoxic at night. Also, leakage of oxygen from the roots can cause local aeration of the anaerobic sediments.

The effects of submerged macrophytes on nutrient dynamics have been examined in some detail for Lake Zwemlust (Van Donk *et al.*, 1993) (Fig. 2.32).

A dense aquatic vegetation gradually developed in this small lake after biomanipulation (see Chapter 1). Despite the high external nitrogen loading ($9.6\,g\,N\,m^{-2}\,y^{-1}$) ammonium and nitrate concentrations became reduced below detection levels in the spring and summer in years with abundant vegetation. On the contrary, SRP concentrations were hardly reduced relative to the situation when vegetation was absent.

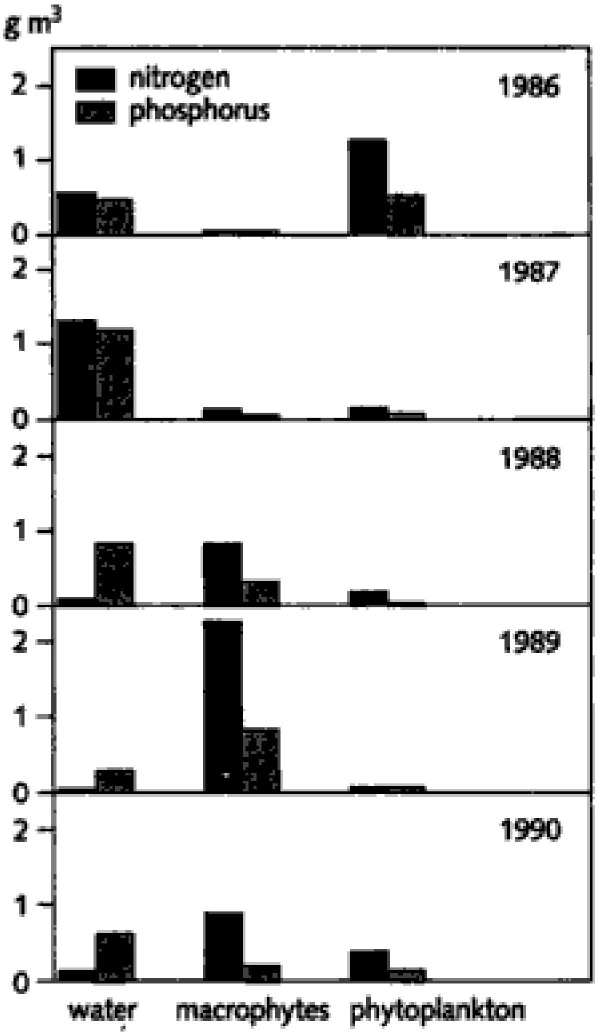


Fig. 2.32 The amount of N and P in water, macrophytes and phytoplankton before (1986) and development of aquatic vegetation in response to a reduction of the fish stock (N.B. water-N is NH_4-N and NO_3-N; water-P is SRP). Modified after van Donk *et al.* (1993).

In tempered lakes, vegetation usually becomes senescent in the autumn and largely disappears largely during the winter. Hence the effect on nutrient dynamics is seasonal. Uptake from the water column can be maximal during rapid growth in early summer, while release of nutrients by senescing plants in the autumn can lead to an increased phytoplankton production in this period (Goulder, 1969; Landers, 1982; Van Donk *et al.*, 1993; Van Donk and Hessen, 1995).

Benthic algae

The sediment surface is usually a place of high microbial activity. As decribed in this chapter the continuous supply of settling organic material and the aerobic conditions ensure optimal conditions for decomposing bacteria. However, if resuspension does not occur too frequently and some light penetrates to the bottom, the surface can also be quickly colonized by benthic algae. The resulting microbial community of algae and bacteria can form a soft crust that further reduces the probability of resuspension (Delgado *et al.*, 1991) and forms a barrier to diffusion between sediment and water. Obviously, the growing benthic algae benefit from the high nutrient concentrations at the sediment surface and may take up nutrients that would otherwise have been released to the water column. Also, they oxygenate the upper sediment layer, facilitating immobilization of phosphorus by iron. In addition, the increase of the aerobic surface layer tends to enhance the coupled denitrification–nitrification process as explained in the previous section. A set of laboratory experiments with undisturbed sediment cores from Lake Wolderwijd demonstrates the impact of benthic algae (mostly diatoms) on nutrient dynamics at the sediment surface (Van Luijn *et al.*, 1995). The overlying water of the cores was replaced by nutrient free water in a continuous flow set-up, and the temperature was kept at 20°C. Half of the cores were incubated in the dark, while the others were continuously illuminated, allowing development of benthic diatoms. After 10 days the upper 2cm of the illuminated cores had a markedly higher oxygen content than the dark cores. The release of mineral nitrogen and silicon from the sediment into the water column was reduced by a factor 6 in the illuminated cores relative to the dark ones where the benthic algae were unable to grow. Also, the flux of ortho-phosphorus was three times lower in the illuminated cores. In the field, temperature and light conditions are less favourable and algal productivity was estimated to be only 10–30% of what was realized in the lab. Nonetheless, the results indicate that benthic diatoms may markedly reduce nutrient release from the sediment.

In addition to the relatively modest development of benthic diatoms, a thick mat of filamentous algae can sometimes develop at the bottom of clear shallow water. Often these mats will be pulled up by trapped gas bells forming the so-called flab (from 'FLoating Algal Beds'). Strong increases in SRP can occur in water dominated by filamentous algae, presumably due to anaerobic phosphorus release from the sediment under the beds (Meijer *et al.*, 1994a).

The effect of animals on nutrient dynamics

Pelagic animals

The role of animals in regulating the nutrient cycling in lakes has been the topic of much research (see review by Andersson,1988). For pelagic feeding zooplankton and fish the effect on nutrient dynamics is rather straightforward. The main part of nutrients contained in the food is soon returned to the water column through excretion. These mineral nutrients are usually taken up quickly by phytoplankton again. Thus animals remove biomass and return a large part of the nutrients almost instantaneously to the water column. The fast nutrient recycling by herbivorous zooplankton in the pelagic zone has received particlar attention (Lehman, 1980). Since animals retain nutrients in a more or less fixed ratio, the excreted mix usually has a different N:P ratio than the surrounding water. This implies that animals can affect the N:P ratio in the water, which may in some cases tip the competitive balance between different groups of algae (see review by Carpenter *et al.*, 1992).

The part of the nutrient supply that is retained in the growing animal returns to the water only after the animal is eaten itself or dies in another way. Periods of high animal mortality may thus cause a peak in the nutrient supply to the water column. Sometimes, for instance, many fish die in a short period in the spring after spawning. Decomposition of dead animals after such mortality peaks can cause a significant nutrient input to the lake water (Kitchell *et al.*, 1975).

Benthic invertebrates

In the case of benthic invertebrates the effect on nutrient cycling is more complex (Andersson *et al.*, 1988). Not only do they excrete mineral nutrients, they also enhance mixing at the sediment surface. As argued above, the latter can work in two ways (Figs. 2.24 and 2.26), as it promotes diffusion of phosphorus across the sediment surface, but also reduces the chance of anaerobic phosphorus release because of enhanced aeration of the top sediment. The effect of tubificids and chironomid larvae on oxygen penetration in the sediment has been amply documented (e.g. Davis, 1974; Granéli, 1979). Nonetheless, the overall phosphorus release from the sediment tends to increase with the density of benthic invertebrates, as shown from comparisons between lakes (Wiśniewski and Planter, 1985). Obviously, such correlative studies do not allow the conclusion that the benthos is actually the cause of the elevated phosphorus release. Various laboratory experiments, however, have clearly demonstrated a causal link. Gallepp (1979), for instance, showed a linear increase of phosphorus release from the sediment with increasing densities of *Chironomus tentans* larvae, in a throughflow system (Fig. 2.33).

Benthivorous fish

Benthivorous fish eat benthic invertebrates. By reducing invertebrate biomass they can thus potentially reduce the positive effect of these animals on sediment phosphorus release. On the other hand, most benthivorous fish whirl up a lot of sediment while foraging. Also, they excrete much of the nutrients originating from the consumption of benthos, directly into the water column, thereby acting as a nutrient pump from the sediment to the water. The relative importance of these direct and indirect effects is hard to separate in practice, but many experiments have shown that, overall,

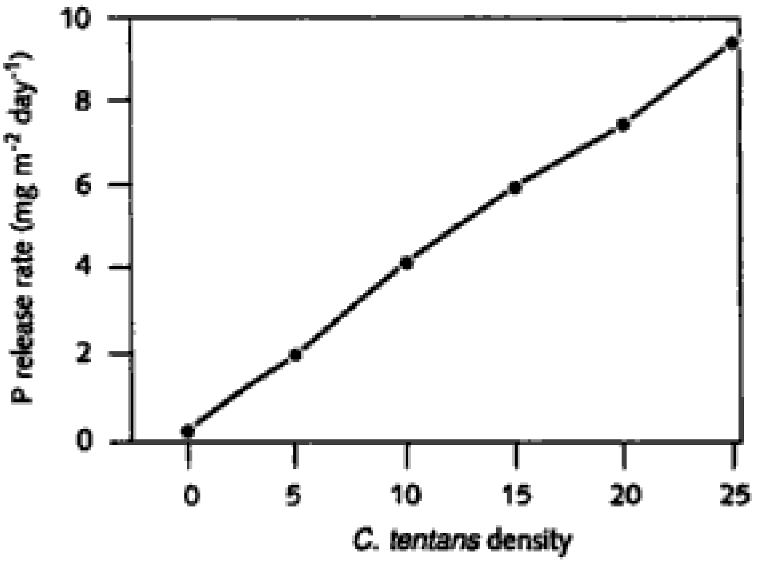


Fig. 2.33 The release rate of total-P as a function of the density of chironomid larval density (*Chironomus tentans*) per test tube (37.5 cm^2). Redrawn from Gallepp (1979).

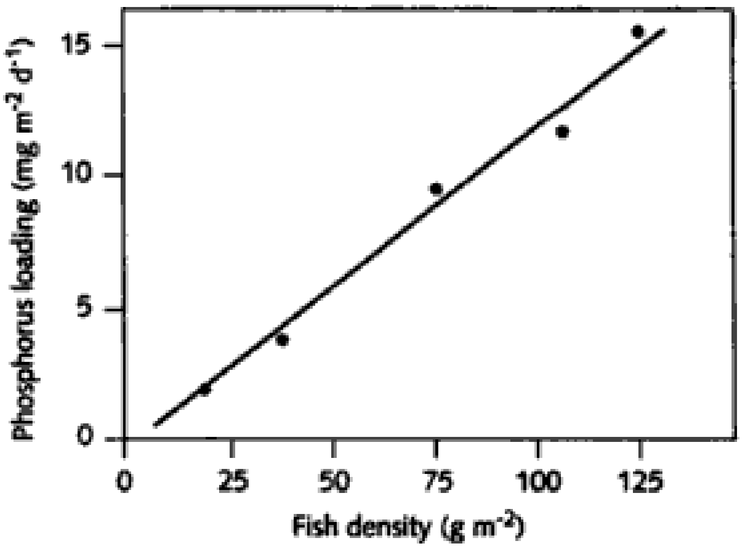


Fig. 2.34 Effect of carp density on phosphorus release into the water column 7–14 days after introduction of carp in enclosures. Redrawn from Lamarra (1974).

benthivorous fish have a positive effect on the concentration of total-P and algal biomass in the water column (Fig. 2.34) (Lamarra, 1974; Andersson *et al.*, 1988; Havens, 1993; Breukelaar *et al.*, 1994; Van Donk *et al.*, 1994b).

Havens, for instance, showed these effects in enclosures set up in a shallow isolated bay of Lake Erie (Ohio, USA) (Havens, 1991; Havens, 1993). Chlorophyll-a was higher in enclosures with fish than in those without fish, but the effect of fish was largely eliminated by installing a net just above the bottom to prevent fish from reaching the sediment (Fig. 2.35).

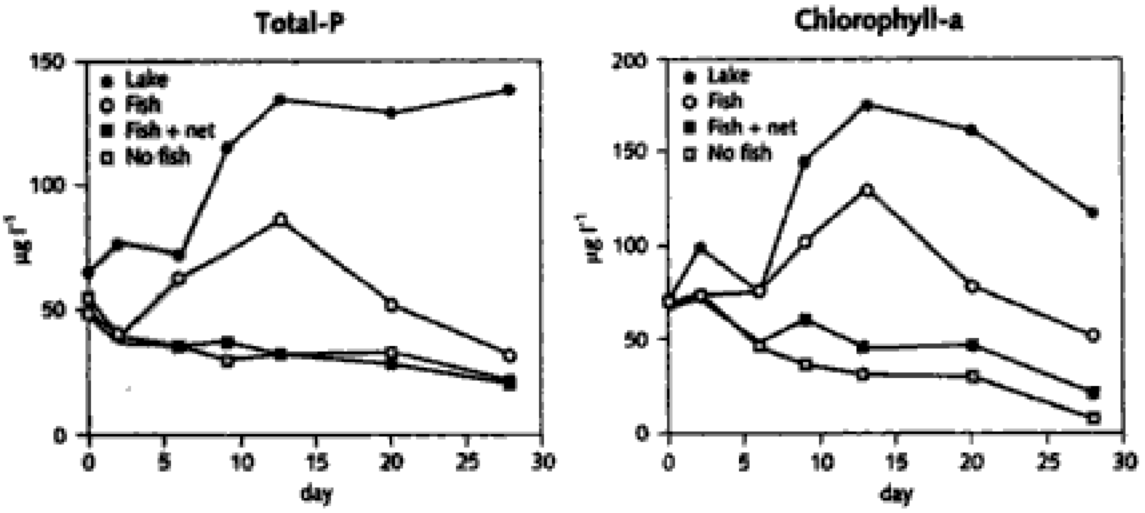


Fig. 2.35 Total-P and chlorophyll concentrations in lake water and in enclosures set up in a shallow isolated bay of Lake Erie (Ohio, USA). In enclosures where fish are prevented from reaching the sediment by installing a net just above the bottom fish effects on total-P and chlorophyll are reduced almost to no-fish levels. Modified from Havens (1993).

While these results indicate that the effect of fish on phytoplankton in this case was mainly due to the benthivorous behaviour, the exact mechanism is not clear. The most obvious causal link is through nutrient enrichment.

Indeed all published enclosure experiments show an elevated total-P concentration in response to the benthivorous behaviour of fish. Most of the total phosphorus content of the water column, however, is usually contained in algae and other suspended material rather than being present as dissolved ortho-phosphate. As argued this implies a chicken-and-egg problem. Other mechanisms may contribute to the elevated phytoplankton biomass, and a high algal biomass can be the cause rather than the effect of the high total-P content of the water, as explained earlier.

Therefore, to check whether the phosphorus pump mechanism can be responsible for the effect of benthivorous fish on phytoplankton biomass, ortho-phosphorus concentrations are more informative than the total-P content. The results of the experimental pond study discussed earlier in the section on resuspension by fish (Breukelaar *et al.*, 1994) show that at least in this case, enhanced phosphorus input into the water phase can not be the mechanism behind the increase of total-P and chlorophyll concentrations with fish biomass (Fig. 2.36).

Indeed, the chlorophyll-a concentrations are lowest in the ponds with low benthivorous fish densities, and this pattern is also recognizable in the total-P concentrations. However, the ortho-phosphate available for algal growth shows no consistent relation to benthivorous fish biomass, indicating that phosphorus-limitation is an unlikely explanation for the effect of fish on algae.

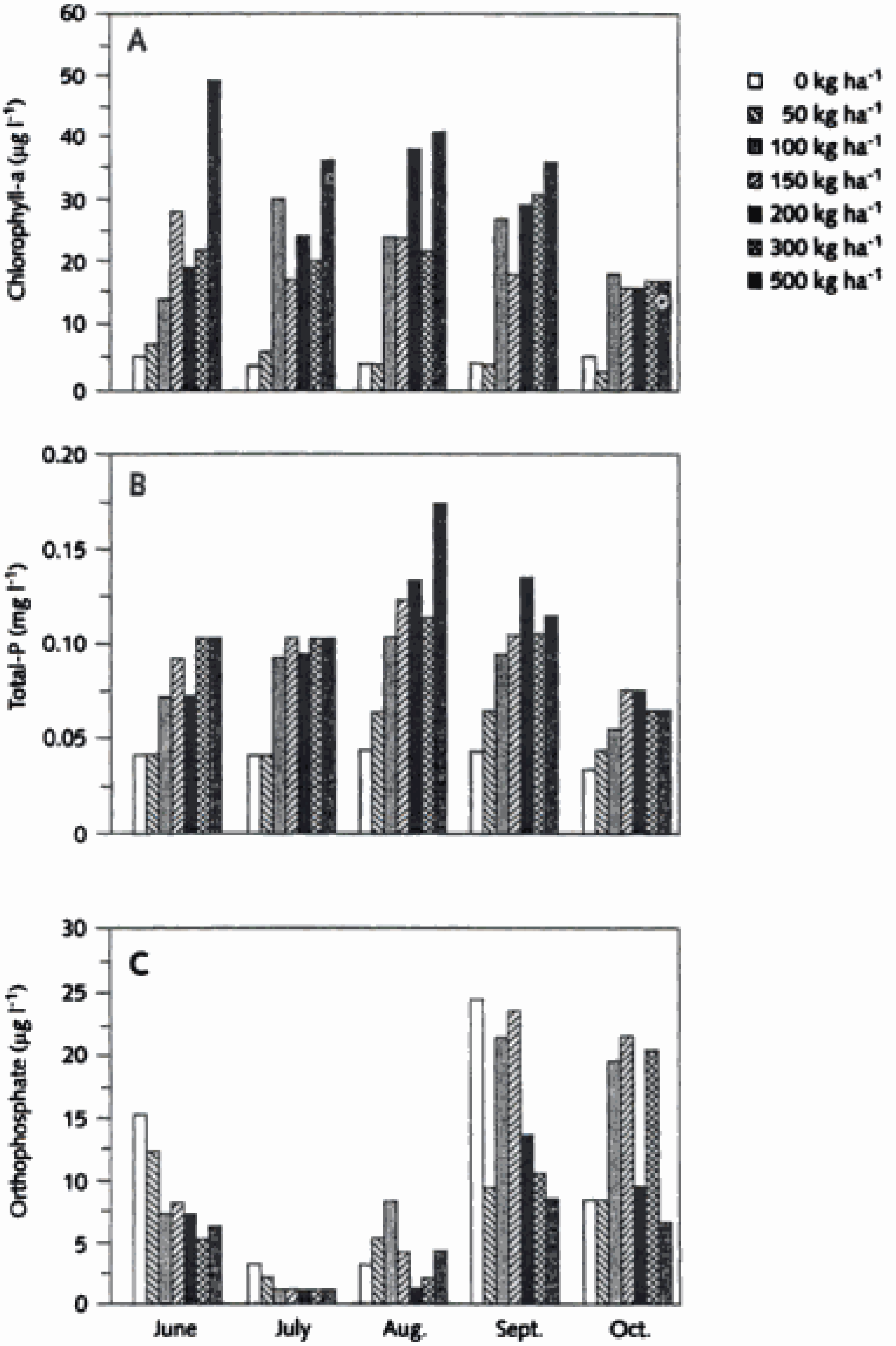


Fig. 2.36 Effect of different densities of benthivorous fish on the concentrations of chlorophyll, total-P and ortho-phosphate in experimental ponds. The high orthophosphate concentrations in some of the low-fish treatments suggest that phosphorus limitation is not the reason for the low chlorophyll concentrations in those ponds. From Breukelaar *et al.* (1994).

Daphnia numbers were kept low during this experiment by stocking with young-of-the-year planktivorous perch (*Perca fluviatilis*). Therefore, elevated *Daphnia* grazing is also unlikely to explain the reduction in phytoplankton in this experiment. An alternative explanation may be that benthivores resuspended settled phytoplankton. As explained in the section on resuspension, the loss rate of particles from the water column due to sedimentation is potentially very high in shallow water, and this holds also for phytoplankton cells and colonies. In most situations wind resuspension will keep the algae in circulation, but in very calm water this rehabilitation does not work and losses are high. Only motile, buoyant and slowly sinking species can potentially maintain their populations under such conditions. Obviously, wave impact is nil in enclosures and small ponds where mixing occurs only by convection. Therefore, resuspension of settled algae by fish may well be an important mechanism to sustain high phytoplankton densities under these conditions.

The idea that resuspension is important for maintaining a high algal biomass is further supported by the fact that algal biomass usually decreases in rigid enclosures where wave action is absent even when fish are present. This is exemplified by Haven's results (Fig. 2.33), but similar exclosure effects are observed in various other studies. In 25 × 25 m mesocosms in the shallow Lake Breukeleveen, for instance, reduction of resuspension caused a threefold decrease in chlorophyll-a concentration shortly after closure (Van Donk *et al.*, 1994b). The role of resuspension for sustaining algal populations is discussed more thoroughly in the next chapter.

3 Phytoplankton

Phytoplankton is a component of practically all the discussions and models that follow. This chapter focuses on the factors that control the biomass and composition of the algal community. The first section explores how the combined effects of nutrients, light, grazing and turbulence affect the total biomass of the algal community. The next section shows that at least cyanobacteria should be treated separately in order to explain the dynamics of phytoplankton in shallow lakes. This group, also called blue-green algae, often dominates the plankton in hypertrophic shallow lakes. It is shown that cyanobacterial dominance can be an alternative stable state of the algal community. The third section shows that at the species level, algal dynamics are very complex, and there is little hope of predictability.

3.1 THE REGULATION OF ALGAL BIOMASS

Empirical relationships between chlorophyll and nutrients

Traditionally, nutrients have received more attention than any other factor affecting algal biomass. Regression models describing the amount of phytoplankton as a function of the nutrient concentration in a lake have been widely used in applied limnology. The total amount of phytoplankton is usually characterized as the number of cells, total cell volume, the amount of chlorophyll-a or algal ashfree dry-weight per volume of lake water. Of these measures, chlorophyll-a concentration is used most often, probably because it can be measured relatively easily. Chlorophyll is also one of the most important compounds determining the light attenuation in water due to algae. However, chlorophyll concentration is not always the most relevant measure. Scattering of light, for instance, may be more related to algal volume, while the energy content for grazing zooplankton may correlate better with dry weight. It is possible to compute average ratios between chlorophyll and other characteristics and use these to estimate one from the other, although there is a large variation between species, and even within species depending on the conditions (Reynolds, 1984; Heyman and Lundgren, 1988). Most reported chlorophyll-a content of algae are in the range between 1 and 2% of their dry weight (Reynolds, 1984). The phosphorus content of the algae in eutrophic lakes usually varies between 0.4 and 1% of the dry weight (Ahlgren *et al.*, 1988), and their nitrogen content is usually about a factor 10 higher than that (Smith, 1982).

When nutrients become limiting both the nutrient content and the chlorophyll concentration in the algae tend to decrease. This phenomenon is exemplified, for instance, by the change in phytoplankton in Veluwemeer following a reduction of the phosphorus loading (Hosper, 1985). Expressed as chlorophyll-a, algal abundance showed a pronounced decrease. However, measured in biovolume algal density decreased much less. These observations suggest that the nutrient to chlorophyll ratio of phytoplankton may be more constant than the ratio of nutrient to biomass or biovolume.

In summer, a major part of the total amount of phosphorus in the water column is often contained in algae. It is therefore not surprising that total-P in the water column is usually well correlated with chlorophyll-a concentrations. As pointed out in the previous chapter, the interpretation of causality in such correlations is tricky in shallow lakes, as the algae stimulate release of the sediment phosphorus into the water column. Thus to a certain extent, algal biomass explains total-P rather than vice versa. Nonetheless, total-P is usually the best available indicator of the available nutrient pool and many regression models explaining algal biomass from total-P have been produced. Most studies find a linear relation or an accelerating increase of chlorophyll with total phosphorus. Obviously, such models can not be extrapolated to high phosphorus values, as at some point light or other factors should become limiting for algal growth. Indeed, several analyses have shown that the increase in chlorophyll levels off at high phosphorus concentrations. When high enough phosphorus levels occur in the data set,

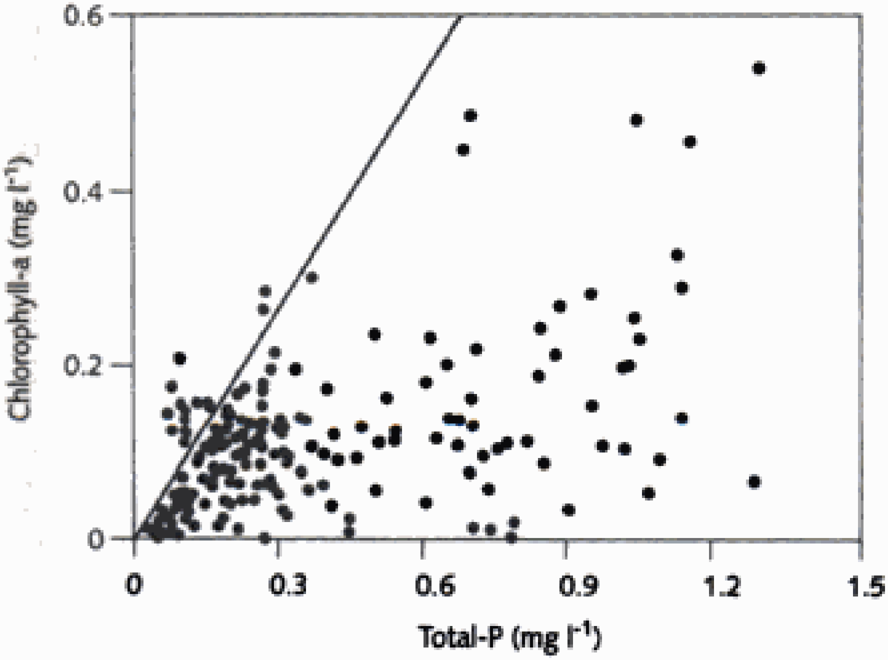


Fig. 3.1 Relationship between the summer average total-P concentration (P mg l^{-1}) and the summer average chlorophyll-a (*Chla* mg l^{-1}) concentration in a set of 88 Dutch shallow (2.1 m mean depth) lakes. The line ($Chla = 0.9P$) is fitted by eye to represent the upper limit of the cloud of 406 data points.

a sigmoidal increase is probably the general pattern (McCauley *et al.*, 1989; Prairie *et al.*, 1989; Watson *et al.*, 1992).

Although the correlations are usually significant, the unexplained variation in relationships between algal biomass and the phosphorus level is typically huge in shallow lakes. It has been noted that only the upper limit of the cloud of points in scatter plots is relatively well delineated (Fig. 3.1).

This suggests that it might be more appropriate to interpret the effect of nutrients as posing an upper limit to the summer chlorophyll concentration, than to fit a regression model through the points (Hosper, 1980). All points above the limiting line in this figure represent lakes dominated by filamentous cyanobacteria. This phytoplankton group is able to reach a higher biomass with the same amount of phosphorus than other algae. As explained later, this has important implications for the potential of cyanobacteria to dominate the plankton in turbid shallow lakes.

Since relatively few lakes have chlorophyll concentrations close to the upper limit, other factors apparently have a pronounced effect on algal biomass in most cases. One obvious possibility is nitrogen limitation. Phytoplankton cells contain approximately 10 times more nitrogen than phosphorus. Therefore, nitrogen is more likely to be limiting than phosphorus when the N:P ratio in the water column falls below a critical value of about 10 (see Smith 1982). In macrophyte dominated lakes in particular available nitrogen concentrations can be strongly reduced as explained in the previous chapter, and nitrogen is often found to be limiting algal growth in such cases (Van Donk *et al.*, 1993). Indeed, a plot of chlorophyll concentrations against total-N shows a sharp upper limit (Fig. 3.2) indicating that nitrogen availability limits algal biomass in many cases. Note that intersection of the limiting line with the horizontal axis suggests that at least about $0.7\,\mathrm{mg\,l^{-1}}$ of the total-N content of the water is unavailable for algal growth.

The approach of using such upper limits of scatter plots to predict the maximum algal biomass at a given nutrient concentration has been followed for many years in The Netherlands. The majority of the data points, however, are neither close to the P-limitation nor to the N-limitation line, suggesting that other factors are often limiting. Light is an important limiting factor in many turbid lakes. Also, on sheltered sites and between aquatic plants losses due to sinking can be large while in fast flushed lakes algal concentrations can be low because the inflowing water that is initially almost free of algae stays in the lake far too brief a time to allow the algae to reach the maximum biomass. Especially spectacular and important are the effects that zooplankton grazing can have on phytoplankton. To obtain an insight into how factors like lake depth, flushing, resuspension and grazing interact with the effect of nutrients in determining algal biomass it is useful to go beyond the empirical regression approach and analyse algal growth in a more mechanistic way. In the next sections some simple models of algal

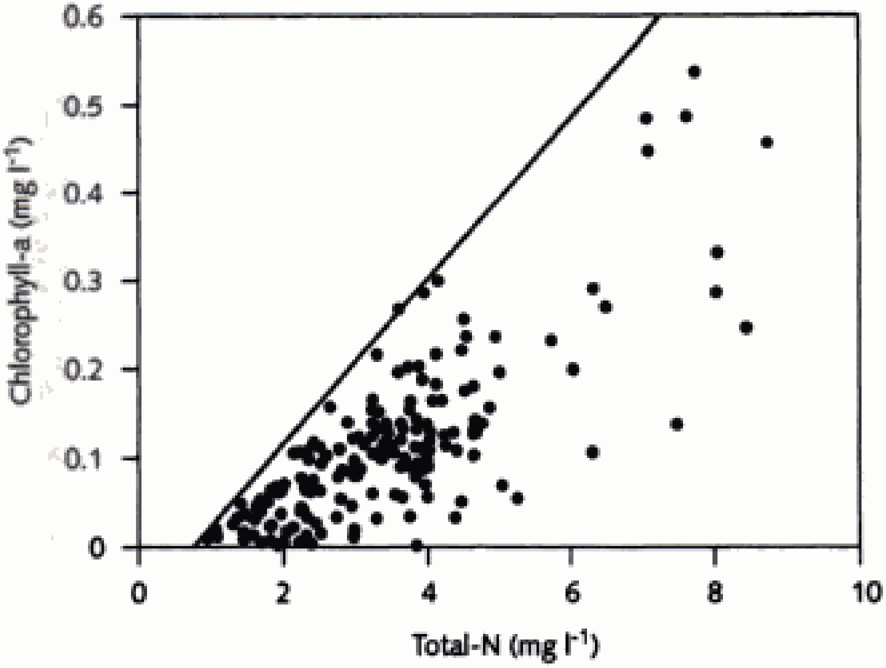


Fig. 3.2 Relationship between the summer average total-N concentration (N mg l^{-1}) and the summer average chlorophyll-a ($Chla$ mg l^{-1}) concentration in a set of 79 Dutch shallow (2.1 m mean depth) lakes. The line ($Chla = 0.09\ (N - 0.7)$) is fitted by eye to represent the upper limit of the cloud of 383 data points.

growth are presented for this purpose. The insights from these models serve as a framework to discuss the patterns observed in the field.

The logistic equation as a model of algal growth

Probably the best known growth model is the logistic equation. It describes population increase (dA/dt) as a function of population density (A) and two parameters:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) \tag{1}$$

The properties of this simple model are illustrated in Fig. 3.3.

The relative growth rate ($dA/dt/A$) is highest (r) when the population density (A) is very low relative to the carrying capacity of the environment (K). In that case the competition term ($1 - A/K$) is close to one. The logistic equation assumes competition to cause a linear decrease of the relative (‘*per capita*’) growth rate ($dA/dt/A$) with the population density (Fig. 3.3a). The result is that the overall productivity (dA/dt) has a maximum at half the carrying capacity (Fig. 3.3b). When the population density is too low the productivity is limited by the amount of reproducing algae (A), when the population approaches the carrying capacity ($A = K$) productivity tends to

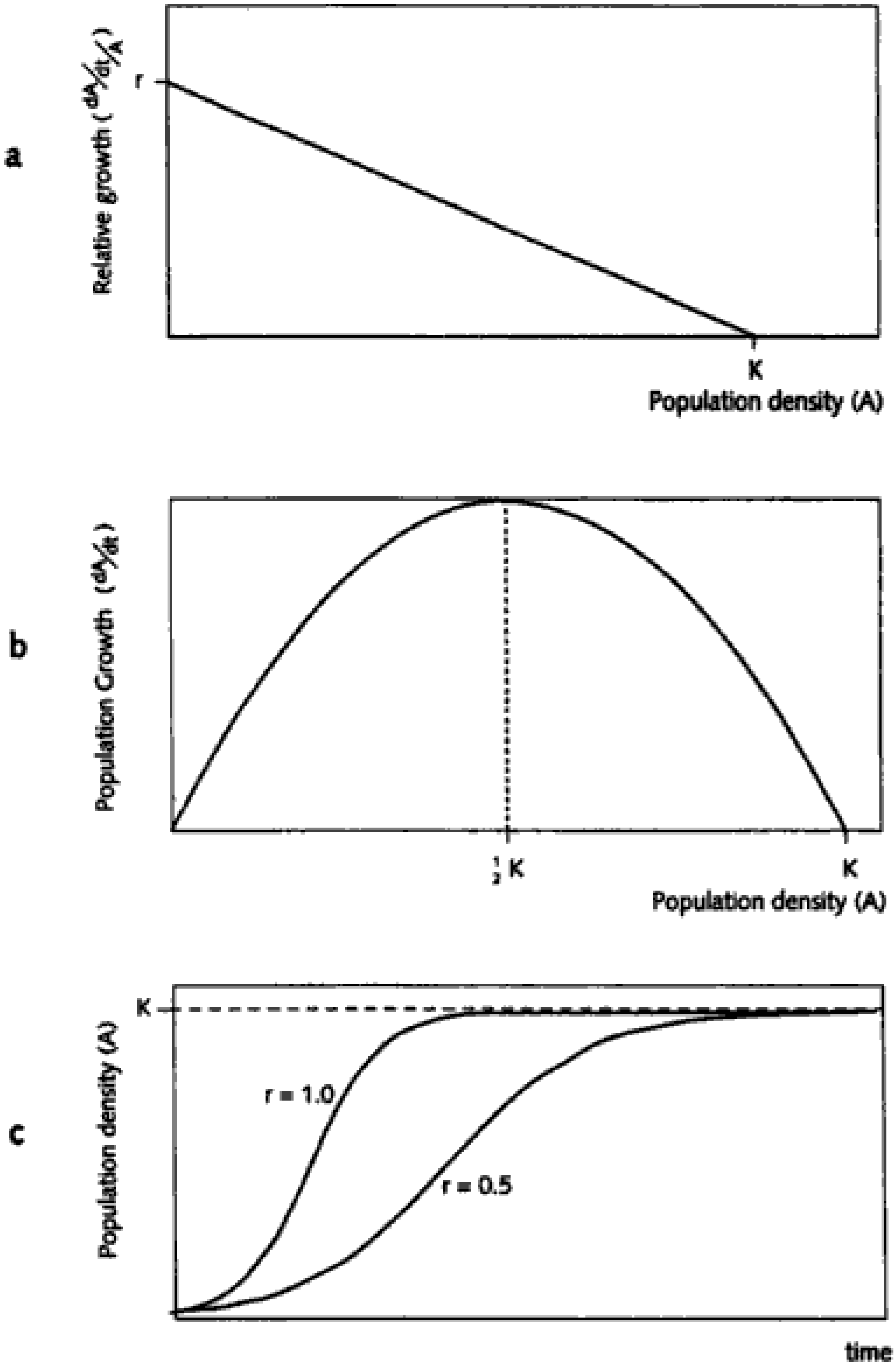


Fig. 3.3 Some properties of the logistic growth equation: (a) The relative ('per capita') growth rate (*dA/dt/A*) decreases linearly with the population density. (b) The growth rate (*dA/dt*) of the total population has a maximum at half the carrying capacity. (c) Population density of a growing population evolves in a sigmoidal way over time.

zero due to competition. Note that the logistic equation predicts that optimal harvest can be obtained by maintaining the population at a density of half its carrying capacity. Plotted against time the density of a logistically growing population follows a sigmoidal curve, with the steepest growth occurring at half the carrying capacity (Fig. 3.3c).

Its simplicity makes the logistic equation very attractive for use in simple models. Obviously, the model is a crude simplification. A strictly linear decrease of per capita growth with density seems unlikely to be found in any real-life situation, and it may seem even more unlikely that the dynamics of the total biomass of a complex algal community with many species can be described by such a naive model. Nonetheless, the development in time of natural algal communities in lakes appears to fit reasonably well to the logistic equation in practice (Heyman and Lundgren, 1988).

In a simple model like the logistic equation, many underlying regulatory mechanisms are not explicitly included. Clearly, factors that affect growth such as the nutrient status and the depth of a lake should affect the parameters, but *a priori* it is not obvious how. The maximum growth rate r is probably rather species specific. It varies with physical conditions such as incident light and temperature, but does not change too much with the nutrient level (Heyman and Lundgren, 1988), although a shift in species composition with enrichment may of course alter the r at the community level. The effects of different factors on K are somewhat easier to estimate from field data, as data on biomass are far more abundant than information on maximum growth rates. The empirical evidence shows that the maximum algal density in lakes increases with the nutrient content, and, indeed, increasing K is a usual way to mimic nutrient enrichment in the logistic model.

To explore in a more mechanistic way how the combined effects of lake depth and nutrients can be explained, it is necessary to elaborate the description of algal growth further as explained later. The simple logistic equation, however, serves as a useful basis to analyse the effects of losses due to sedimentation, lake flushing and grazing by herbivorous zooplankton and other filter feeders.

Losses due to sinking and flushing

As explained in the previous chapter, particles from the surface layer of the sediment often go through a fast cycle of sedimentation and resuspension in shallow lakes. Resuspension of sedimented material by waves can occur daily in exposed lakes, and even in the absence of any wave action benthivorous fish populations can resuspend the sediment surface intensively. On the other hand the loss rate of suspended particles from the water column in shallow water is also high. This is because the loss rate due to sedimentation (k_s) is proportional to the sinking velocity (s) and inversely related to the depth of the column (D) in still water:

$$k_s = \frac{s}{D} \tag{2}$$

In principle algal cells are prone to the same processes as sediment particles. Some species are able to swim actively or regulate their buoyancy. Most species, however, lack these abilities and may therefore suffer large losses due to sedimentation when there is little or no resuspension. Such a situation is most likely to arise on sheltered or vegetated sites and on days when wind speed is low and warm weather enhances the chance of thermal stratification. An important feature that sets algae aside from dead sediment particles is their ability to reproduce. Even for species that are unable to swim or float, reproduction can at least partially balance the settling loss. A basic idea of how this potentially affects the phytoplankton dynamics can be obtained using the logistic equation for algal growth, adding an extra term to represent the settling loss:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) - \frac{s}{D}A \tag{3}$$

The algal density in equilibrium A^*, when growth is zero by definition, can be found by solving the equation for $dA/dt = 0$:

$$A^* = K\left(1 - \frac{s}{rD}\right) \tag{4}$$

Thus settling loss brings the equilibrium density of phytoplankton down from the potential carrying capacity. The deviance from the carrying capacity in the absence of settling loss depends on the maximum per capita growth rate (r) and the ratio of sinking velocity (s) to depth of the water column (D) (Fig. 3.4).

The population can only survive if this equilibrium density is positive, requiring:

$$r > \frac{s}{D} \tag{5}$$

Phrased in biological terms this result is intuitively straightforward. At the border of extinction algal density is very low. In that situation competition is practically nil and the remaining algae reproduce at the maximum rate r. However, this high reproduction will only save the population if r exceeds the sinking loss s/D. This implies that settling should select for algal species with a low sinking velocity and a high growth rate. Both properties tend to go with small cell size. Even for small algae, however, s will be no less than about $0.25\,\mathrm{m\,d^{-1}}$ and r no more than about $0.5\,\mathrm{d^{-1}}$ in general, implying a required depth of at least 0.5 m to prevent extinction in completely still water.

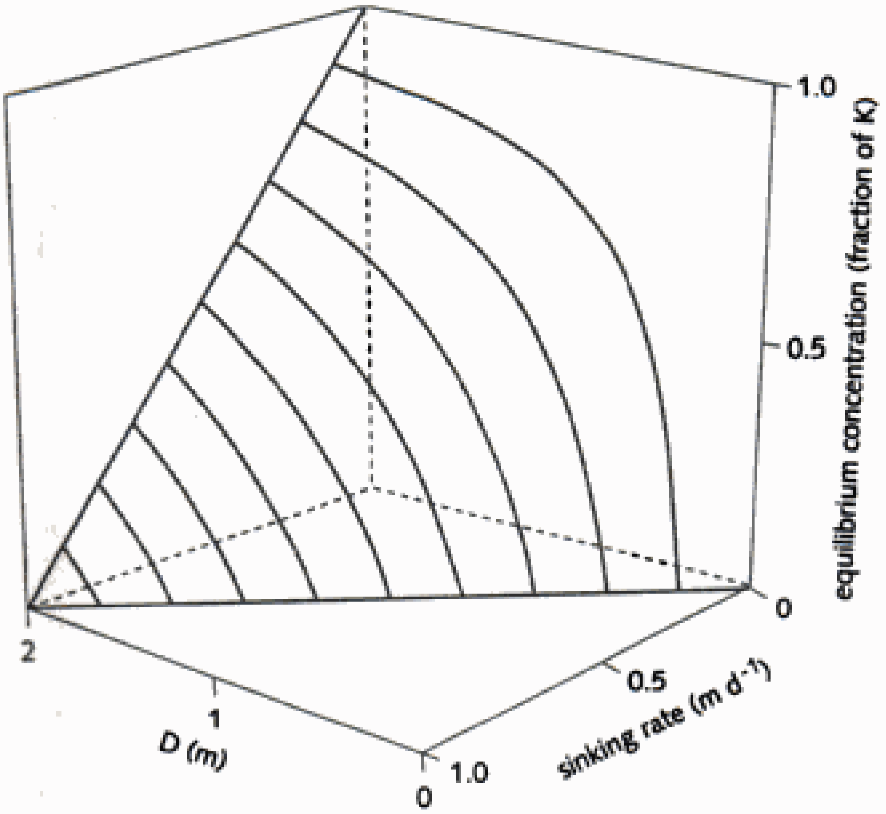


Fig. 3.4 Equilibrium concentration of a logistically growing phytoplankton population with sinking losses depending on the sinking rate of cells (s m d^{-1}) and the depth of the water column (D m)

Obviously, species that have high sinking rates and are unable to swim or float upwards thus depend on turbulence for survival in the water column of shallow lakes. As discussed in the previous chapter, the resuspension frequency depends mainly on the depth and size of a lake. Large exposed lakes should therefore be expected to support species with potentially high sinking losses better than smaller sheltered ones. Also windy periods should favour such species, and therefore variation in wind could influence the seasonal dynamics of algae.

The importance of resuspension for phytoplankton in shallow lakes is well illustrated by the close correlation between wind speed and the biomass and species composition of the algal community in the Florida Lake Apopka (Schelske *et al.*, 1995). In this large and shallow lake (128 km^2, 1.7 m mean depth) as much as 53% of the variation in chlorophyll contents of the water column is explained by wind (Fig. 3.5). During calm periods relatively large diatoms (20–200 μm) settle to the bottom and the surface water is dominated by small pico and nannoplankton (<20 μm).

Systematic seasonal variations in wind may also play a role in the seasonal succession of phytoplankton. Gons *et al.* (1991), for instance, showed that the seasonal pattern of diatom abundance in the shallow Loosdrecht lakes suggests a dependence on turbulence. He computed an estimation of sinking loss assuming that sinking loss in parts of the lake where no

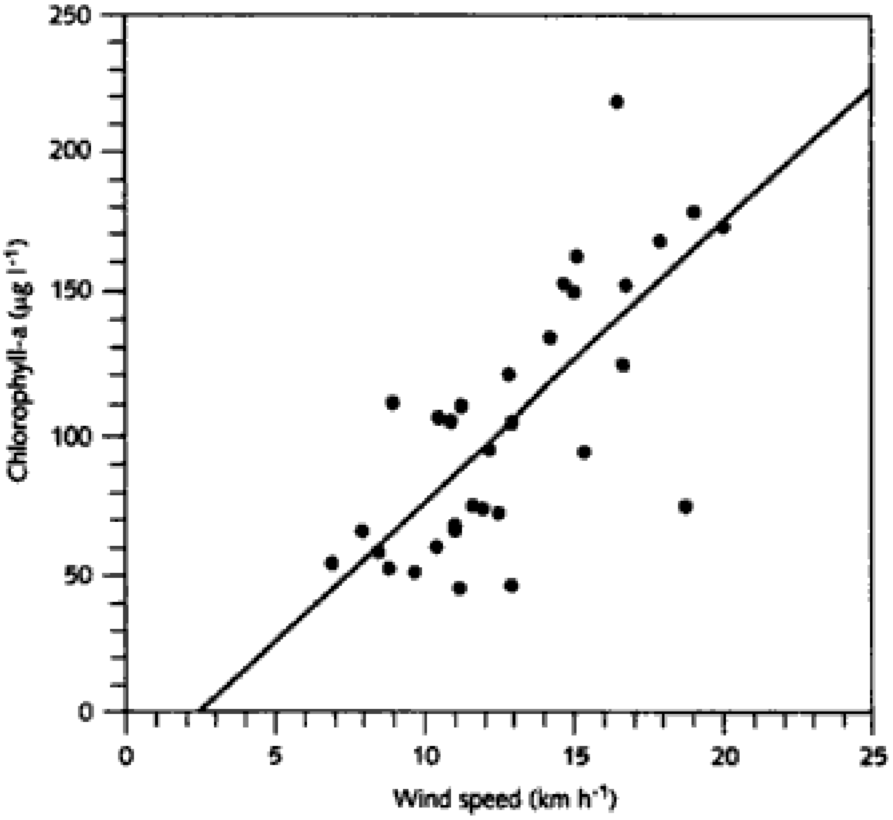


Fig. 3.5 Relationship between average daily wind speed and the chlorophyll-a concentration in surface water of Lake Apopka. Redrawn from Schelske *et al.* (1995).

resuspension occurs equals the ratio of settling velocity to lake depth (Eq. 2), while sinking loss was assumed to be nil in parts where waves stir up the sediment. The fraction of the lake area where resuspension occurred on any given day was estimated from wind speed data using a simple model (Gons *et al.*, 1986). Indeed, the spring peak of diatoms coincides with relatively windy periods, whereas the calm weather in summer leads to estimated sinking losses of 50% of the population per day, which is unlikely to be compensated by growth even under favourable conditions.

As explained later, the effect of settling on the algal community also explains part of the pronounced differences that often exist between the open water and dense weedbeds where turbulence is low. In the vegetation, algal biomass is usually lower and the community is dominated by small species that have high growth rates and low settling velocities and by flagellate species that can actively swim.

Resuspension will affect algal dynamics not only by bringing settled algae back into the water column but also indirectly through its impact on the light climate and the nutrient dynamics. These light and nutrient effects are treated in the next sections.

Settling causes a so-called density independent mortality. Unlike density dependent mechanisms such as predation, density independent processes kill a fixed proportion of the population independently of the population density. Flushing of a lake with water that is free of algae also causes a density independent loss, and in some aspects the effects of flushing and sinking are therefore comparable. When 10% of the lake water with algae is washed out every day, this implies a loss rate of 0.1 day^{-1} for the population. Such a flushing loss (f) can be added to the logistic equation in the same way as the sinking loss (s/D), and by analogy the equilibrium biomass drops linearly with f, while the requirement for survival is $r > f$. In Danish lakes algae disappear when f exceeds 0.3 day^{-1} (Jeppesen, pers. comm.). Assuming flushing to be the main loss factor in these situations, this can thus be directly interpreted as an indication of the maximum algal growth rate r in these lakes. In general, density independent losses affect slow growing species more, offering a competitive advantage to fast growing species. As explained later this explains why flushing may cause a switch from dominance by large, slowly growing cyanobacteria to other algae.

Lake depth and light limitation

Lake depth influences sinking loss and resuspension but also has very pronounced implications for the light climate experienced by algae, and thus for their growth rates and realized biomass. A simple approach to include the effect of depth in the empirical chlorophyll models is to fit separate regression lines to shallow and deep lakes. However, the effect of lake depth is really continuous rather than abrupt and a separation into two classes is therefore artificial. To clarify the way in which lake-depth can affect algal biomass it is useful to explore a slightly more elaborate description of algal growth than the logistic equation used in the previous sections.

The precise dependence of productivity upon the underwater light climate is rather complex. Photosynthetic responses of algae to light can be measured in the lab, but translating this to the growth resulting from the light climate in the field is less easy. In well mixed shallow lakes algae are distributed more or less homogeneously over the water column. Since light extinguishes exponentially with depth and varies with the time of the day, the average daily growth should thus be estimated by integrating the net photosynthesis over depth and time. This can be done, but produces rather lengthy formulae (Straškraba, 1980; Straškraba and Gnauck, 1985). Furthermore, the approach still neglects many aspects, preventing it from accurately describing the situation in any real lake. The depth of the water column, for instance, varies from site to site. Importantly, individual algal cells experience a fluctuating light climate in a lake, due to the turbulent mixing. Experiments have shown that the net photosynthesis of the algae depends on the frequency of these fluctuations, and can not be estimated simply by integrating the response over the experienced light gradient (Ibelings *et al.*, 1994).

Obviously, including these and other aspects explicitly would make the model too complex. The core of the problem, however, can also be captured in a simpler, more descriptive way. As explained in Section 2.1, shade experienced by phytoplankton can be characterized by the product of the vertical light attenuation coefficient (E) and the depth of the mixed water layer, which in shallow lakes equals the lake depth (D). To incorporate the shade indicator (ED) in a simple model, we need a function describing its effect on algal growth in the water column. A simple formulation that describes such a decline of photosynthesis with shade is:

$$\frac{h_s}{h_s + ED} \tag{6}$$

This shade-impact function is of a Monod type, declining from 1 to 0 when shade (ED) goes from 0 to infinity and reaching a value of 0.5 when ED equals h_s. The half saturation constant h_s thus represents shade tolerance of the algae. Note that since the function is formulated in terms of shading (ED) rather than absolute light (I_0e^{-ED}), the shade tolerance h_s is not a universal physiological property of the algae, as it depends on I_0 and thus on latitude and season. If the incoming radiation is higher, a higher turbidity can be tolerated. As explained in the previous chapter, E depends on the concentration of algae and their specific light attenuation coefficient (e_a), but also on background turbidity (E_b) due to resuspended sediment and other factors:

$$E = e_aA + E_b \tag{7}$$

If light is the only limiting factor, algal growth can now be described as the result of light dependent productivity and a fixed loss rate (l) resulting from respiration and mortality:

$$\frac{dA}{dt} = rA\frac{h_s}{h_s + D(e_aA + E_b)} - lA \tag{8}$$

Since an equilibrium is characterized by zero net growth, the algal biomass in equilibrium A^* can be found by solving this equation for $dA/dt = 0$. The solution is:

$$A^* = \frac{rh_s - lh_s - lDE_b}{le_aD} \tag{9}$$

It can be seen from this formula that algal density in equilibrium A^* is predicted to decrease with lake depth D (Fig. 3.6a).

This fits with the observations (Fig. 3.10) and with the intuitively straightforward explanation that shallow lakes can become more turbid than deep ones, simply because in a shallow water column higher turbidity is needed to cause enough shade

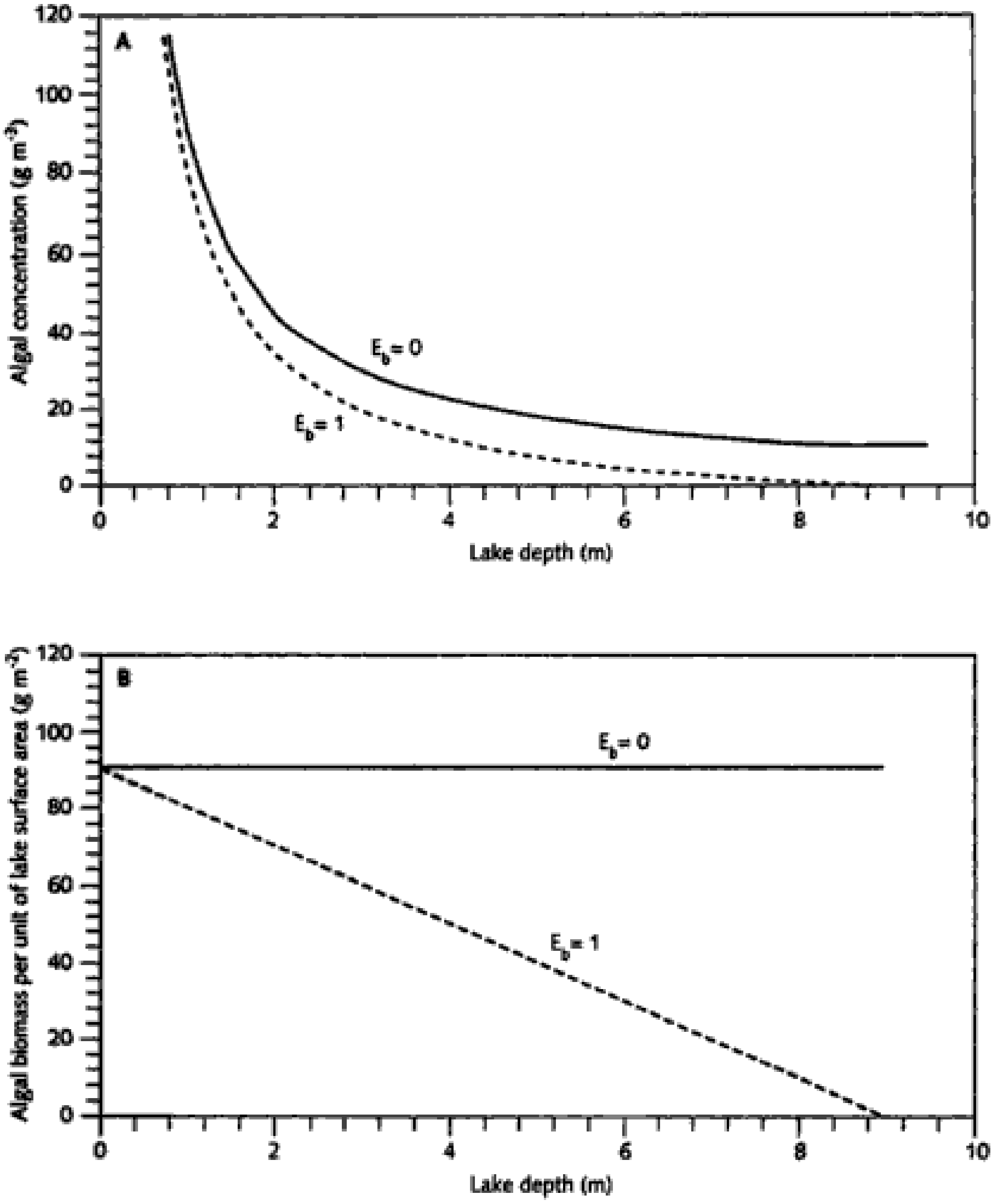


Fig. 3.6 Theoretically expected relationship between (mixed) lake depth and phytoplankton biomass expressed per unit of volume (a) and expressed per unit of lake surface area (b) with and without background turbidity.

to stop algal growth. The prediction can be made more specific if we consider algal biomass per unit area A^*_{area} (g m^{-2}). This can be done simply by multiplying the above formula for equilibrium algal concentration A^* (g m^{-3}) with the depth D (m):

$$A^*_{area} = \frac{rh_s - lh_s - lDE_b}{le_a} \tag{10}$$

This formulation shows that in the absence of background turbidity ($E_b = 0$) the equilibrium algal biomass per square metre is predicted to be independent of the depth of the water. If, on the other hand, there is some background turbidity, the algal biomass per unit area declines linearly with the (mixed) depth of the lake (Fig. 3.6b). Similar results have been obtained from elaborate models that use realistic photosynthetic responses to light and integrations over depth and time (Straškraba, 1980) indicating that these patterns are not an artifact arising from our very simple formulation of light limitation.

Another interesting suggestion can be derived with respect to the light on the bottom of the lake when algae are in equilibrium. Since light at any point under water is an exponential function of the product of depth and turbidity (Chapter 2, Eq. 1), light at the bottom when algae are in equilibrium is therefore a function of:

$$DE^* = D(E_b + e_a A^*) = D\left(E_b + e_a \frac{rh_s - lh_s - lDE_b}{le_a D} \right) \tag{11}$$

which after some algebra appears to boil down to:

$$DE^* = \frac{h_s(r - l)}{l} \tag{12}$$

Both background turbidity E_b and lake depth D have disappeared. Thus, the model suggests that light on the bottom of a lake with light-limited phytoplankton depends neither on the depth of the lake nor on the background turbidity of the water.

These theoretical results imply that when algae are light-limited, an increase in background turbidity caused, for instance, by resuspension, should not lead to a decrease of light at the bottom. It simply leads to less algae in such a way that the amount of light that reaches the lake bottom remains the same. Likewise, an increase of the water level in a light-limited situation should not affect the light reaching the bottom, as the concentration of algae will decrease in such a way that the light reaching the bottom remains the same. Since the light effect is treated quite naively in the model, these predictions could easily be an artifact caused by over simplification. It can be proven, however, that independently of the precise model formulation the 'fixed bottom light' prediction holds. If factors other than light are not limiting, algae tend to stabilize at such a density that the light level at the bottom of a well mixed lake reaches a characteristic value that depends on the shade tolerance of the algae, but not on the depth or on the incoming radiation (Huisman and Weissing, 1994).

As explained in Section 2.1, shade experienced by phytoplankton can be characterized by the product of the vertical light attenuation coefficient (E) and the depth of the mixed water layer, which in shallow lakes equals the

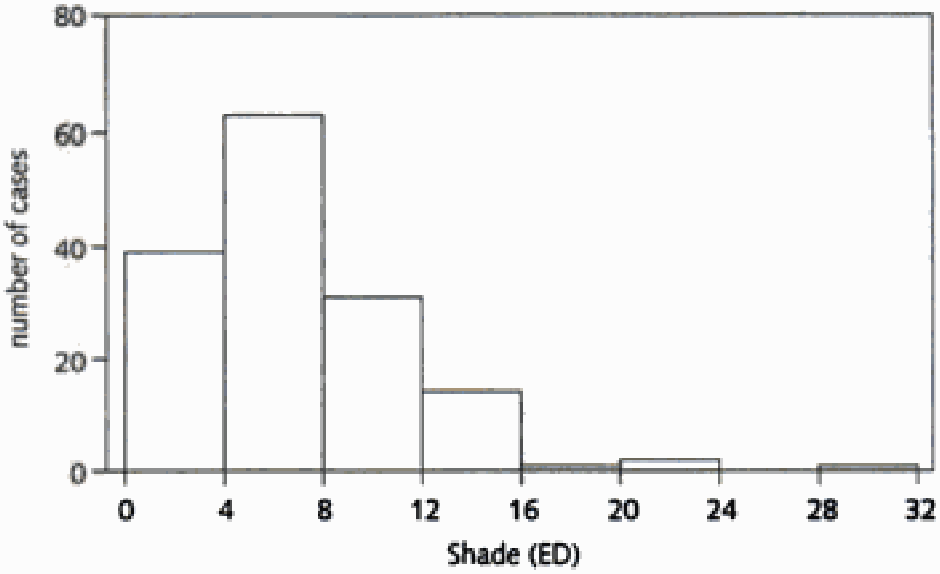


Fig. 3.7 Frequency distribution of 151 summer average (July–August) values of underwater shade (E D) in Dutch and Danish lakes. The vertical light attenuation coefficient (E) has been estimated from Secchi-depth and the chlorophyll concentrations using Eq. 11, p. 30.

lake depth (D). An indication of what the characteristic 'maximum shade' (ED) is in practice, can be obtained from the frequency distribution of shade in a large set of Dutch and Danish lakes (Fig. 3.7).

Less than 3% of these lakes have a shade level (ED) of more than 16, indicating that this is about the maximum shade tolerated by algal communities in northern temperate lakes. A plot of the vertical attenuation coefficient (E) against mean lake depth (D) shows that maximum turbidity does indeed decrease with depth in the theoretically expected way (Fig. 3.8).

The line $E = 16/D$ is a good delimiter of the cloud of points. Note that this information allows a judgement of whether phytoplankton is light-limited in a given lake (when ED is close to 16). Furthermore, if the turbidity due to other factors than phytoplankton can be estimated, it allows an indication of the maximum chlorophyll level of a lake in light-limited situations.

The combined effects of nutrients and light

To explore how nutrient limitation can interact with the discussed shade effects, we extend the minimal model with a nutrient term. For simplicity we focus only on phosphorus as a limiting nutrient, but an analogous approach could be used to analyse the role of nitrogen, which can also be limiting algal growth in many situations. As argued, phosphorus availability is difficult to characterize in practice. Most of the total phosphorus in the water column, but also part of the phosphorus in the sediment of shallow lakes, can be used to build up the summer algal biomass. In the following models P stands for this total available pool. In the short term, the growth of algae depends on

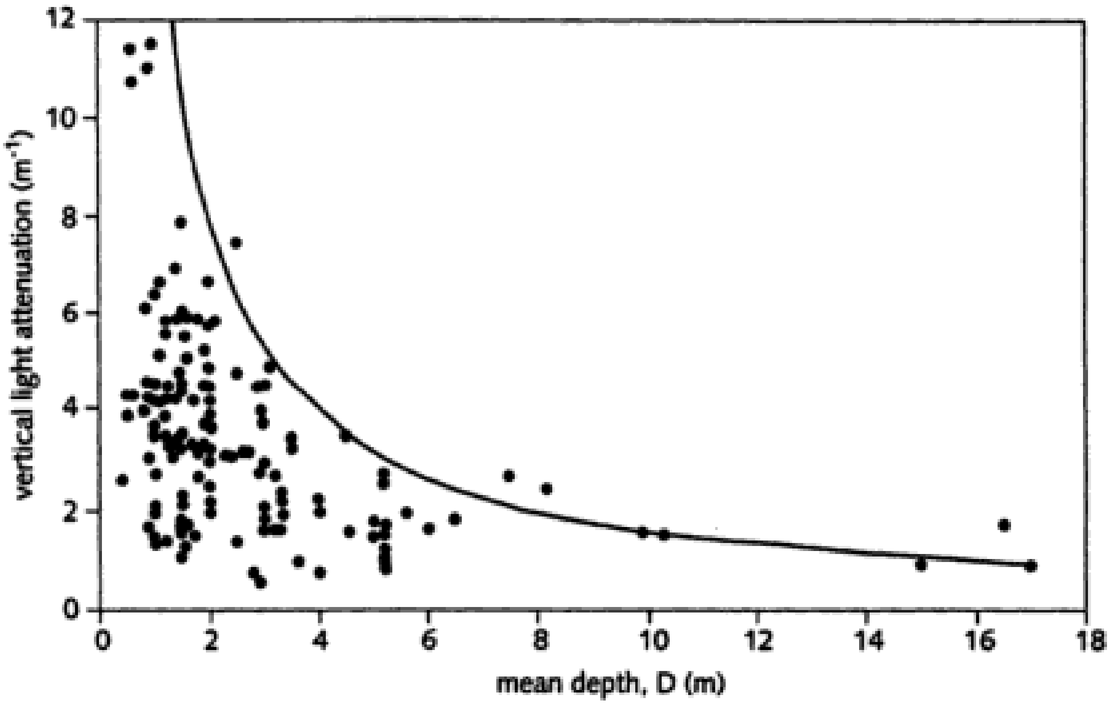


Fig. 3.8 Relationship between the vertical light attenuation coefficient (E) and the mean depth (D) of lakes in the data set used for Fig. 3.7. The line represents a shade level (ED) of 16.

the immediately available phosphorus, usually characterized as SRP or ortho-phosphate concentrations. For the dependence of growth upon the directly available 'free' nutrient concentration (P_f) we take the classical Monod form with a half-saturation concentration (h_p):

$$\frac{P_f}{h_p + P_f} \tag{13}$$

When P_f equals h_p this Monod function takes the value of 1/2, and will thus reduce the growth by 50%. Free nutrients are depleted in the course of population growth, and supplied again by processes like desorption from particle bound forms. To describe this properly, a separate set of differential equations for nutrient dynamics would be needed. A way to avoid that is to assume that free phosphorus (P_f) at any time is simply the total pool minus the phosphorus present in algae:

$$P_f = P - p_a A \tag{14}$$

where p_a is the phosphorus content of algae. Substituting this into the Monod formulation (Eq. 13), we obtain a function that describes nutrient limitation directly in terms of total nutrients and algal biomass:

$$\frac{P - p_a A}{h_p + P - p_a A} \tag{15}$$

Note that this short-cut necessarily implies an overestimation of the phosphorus concentration directly available to the algae, as it neglects the fact that part of the total available phosphorus that is not contained in the algae is bound to sediment particles. Therefore, this approach will tend to overestimate the immediately available concentration and thus the growth rate at which the equilibrium is approached. However, since algal growth becomes phosphorus-limited only at very low SRP concentrations (h_p is small) this problem is probably minor compared with the inaccuracies caused by other simplifications.

The easiest way to 'combine' light and nutrient limitation is to apply the so-called Liebig law of the minimum, stating that growth is only affected by one factor at a time, namely the factor that poses the strongest limitation. A more neutral assumption is that both nutrients and light affect productivity at any time. This means that we should simply multiply the growth rate by both limiting functions:

$$\frac{dA}{dt} = rA\frac{h_s}{h_s + D\left(e_a A + E_b\right)}\frac{P - p_a A}{h_p + P - p_a A} - lA \qquad (16)$$

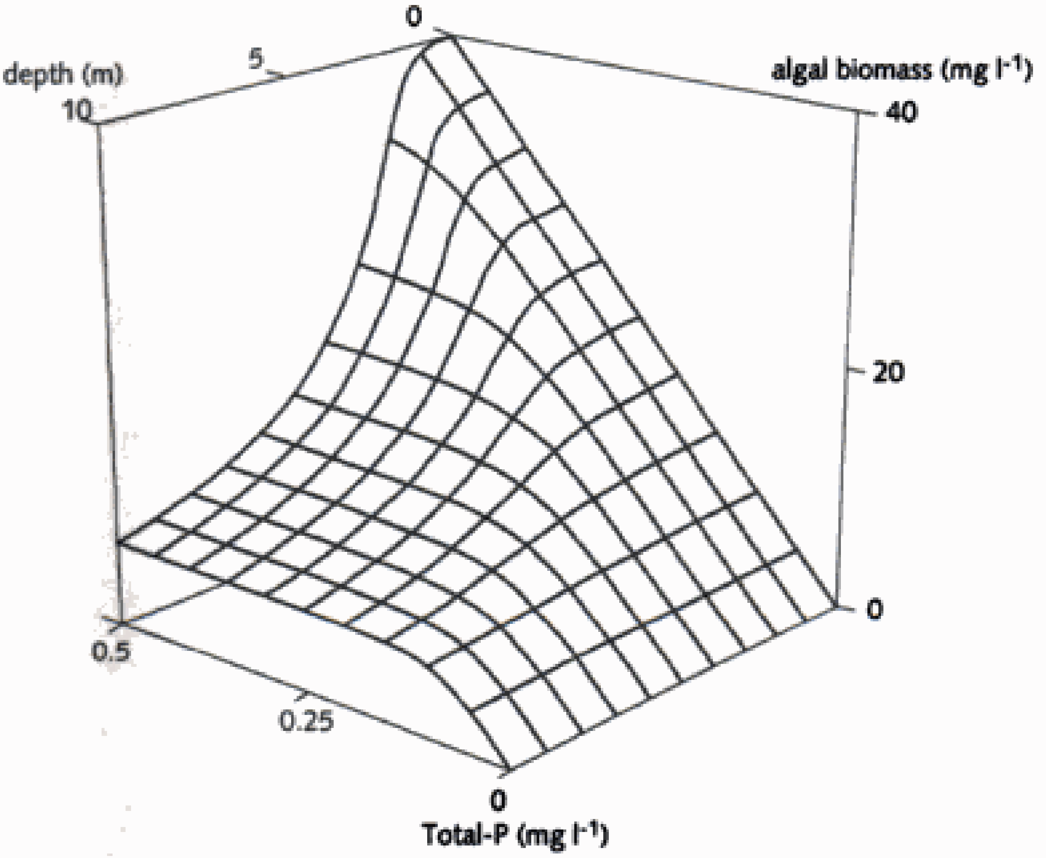
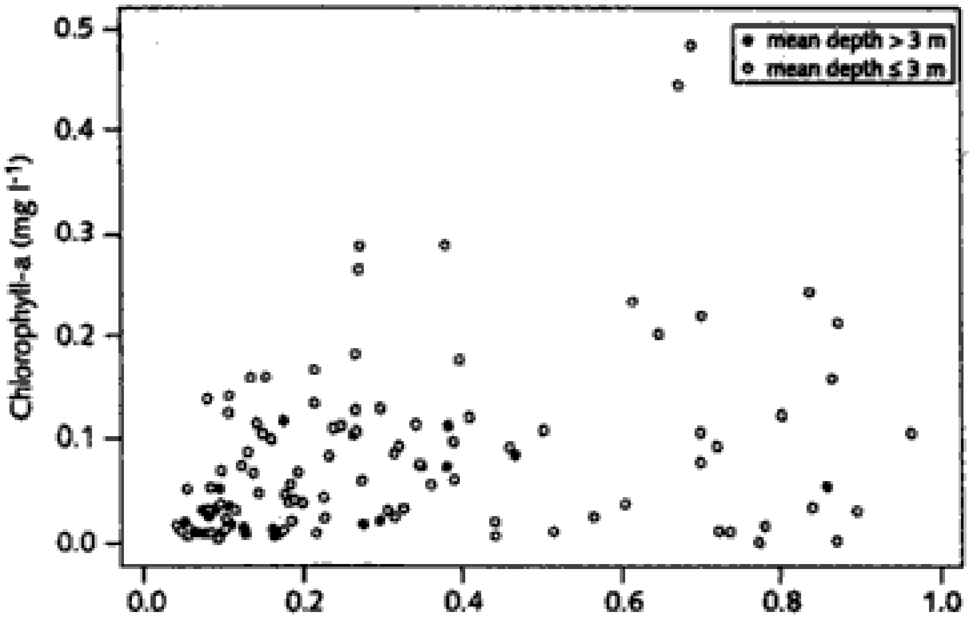
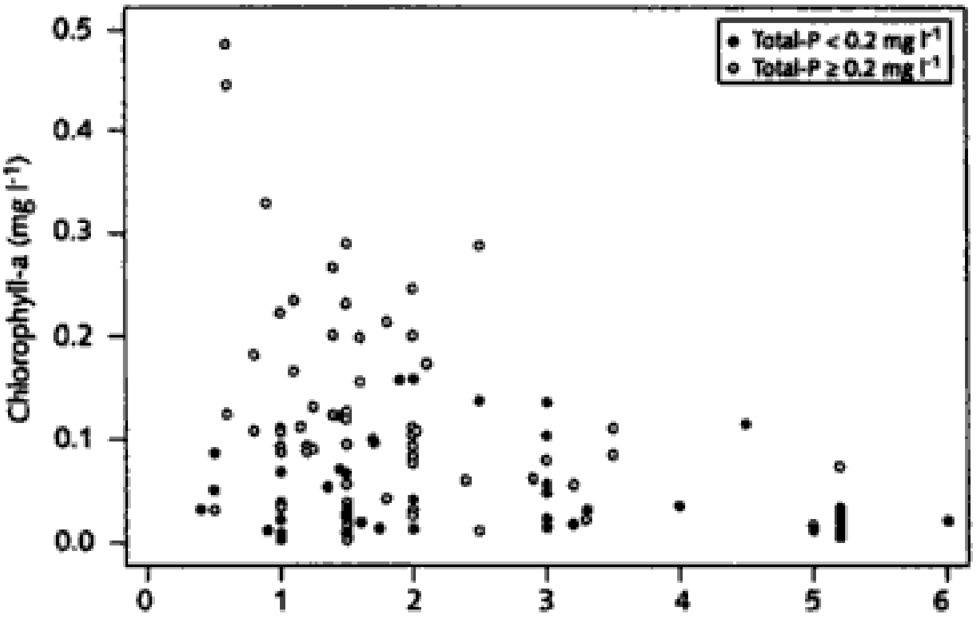


Fig. 3.9 Theoretically expected effect of total-P concentration (*P*) and (mixed) lake depth (*D*) on phytoplankton concentration (*A*). In deeper lakes light limitation occurs already at low total-P concentrations, whereas in shallow lakes phytoplankton concentration can reach very high levels.



(a)



(b)

Fig. 3.10 (a) Relationship between the summer (July–August) average concentration of total-P and chlorophyll-a in 142 Dutch lakes. In shallow lakes (open circles $D < 3\,\text{m}$) chlorophyll concentrations can become higher than in deeper lakes (closed circles $D > 3\,\text{m}$). (b) Relationship between the mean depth (D) and the summer (July–August) average concentration of chlorophyll-a in the same data set. The maximum chlorophyll concentration decreases with depth, but in lakes with a low total-P concentration (open circles $P < 0.2\,\text{mg}\,\text{l}^{-1}$) chlorophyll concentrations remains limited even in shallow lakes.

Solving this equation to find the equilibrium biomass can be done, but leads to a very lengthy formula.

Figure 3.9 shows the predicted effect of nutrients and lake depth on algal biomass graphically.

The model suggests that algal biomass should initially increase with the total-P level, until a light-limited maximum value is reached that depends on the depth of the lake. At low nutrient levels lake depth does not affect algal biomass. At high nutrient levels, however, the concentration of algae rises with decreasing lake depth until nutrient limitation poses a limit. Note that, although the minimum law is not applied, regions can be distinguished where either light or nutrients seem to be 'the' limiting factor. The transition between these regions is smooth rather than abrupt, but in large areas one limiting factor dominates completely. At high nutrient concentrations and in 'deep' water, for instance, algal biomass hardly increases with nutrients. Here, light is the dominant factor limiting algal growth.

As shown in previous sections, field data confirm that nutrients (Figs. 3.1 and 3.2) but also light (Fig. 3.8) can impose an upper limit to algal concentrations. A simple way to check the combined effects of nutrients and depth suggested by the model is to classify the points in such graphs (Fig. 3.10).

This confirms that the maximum chlorophyll level increases with phosphorus to very high values in the shallowest lakes, while in the deeper ones chlorophyll concentrations soon level off and become largely independent of the phosphorus concentration (Fig. 3.10a). Similarly, the maximum chlorophyll concentration increases with decreasing depth, but only when the phosphorus concentration is high enough (Fig. 3.10b). Thus, as predicted by the simple model, at low levels nutrients impose an upper limit on algal biomass that does not depend upon depth while in very eutrophic lakes, depth set an upper limit to algal biomass that does not vary with the phosphorus concentration. Another way to visualize the combined effects of phosphorus and lake depth on algal biomass is to fit a three-dimensional response surface through the data points using a local interpolation technique (Fig. 3.11).

Note that this bumpy surface shows how the *average* chlorophyll concentration changes with nutrients and lake depth and does not indicate an upper boundary as shown in the other figures. Nonetheless, it suggests roughly the same patterns. Note that the patterns in field data correspond quite well with the predictions from the model (Fig. 3.9), suggesting that the explored simple formulations and reasonings may still capture much of the essence of the complex mechanisms involved.

As shown in the previous chapter, the contribution of resuspended sediment particles to turbidity can be very high in shallow lakes. The expected effect of such background turbidity on the response of algal biomass to enrichment can also be explored using the model (Fig. 3.12).

Not surprisingly, algal biomass is predicted to be reduced at high background turbidity. An analysis of data from 96 reservoirs in the Midwest of

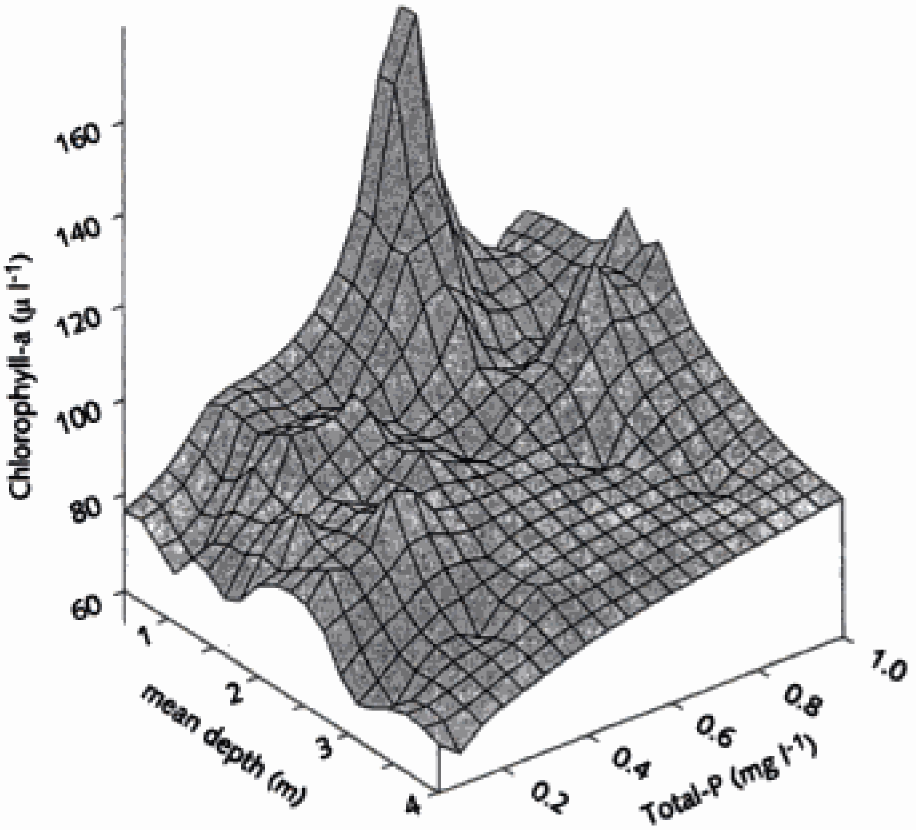


Fig. 3.11 Relationship between average summer (July–August) total-P concentration, chlorophyll concentration and mean lake depth in 142 Dutch lakes. The surface is interpolated through the data using inverse distance weighting.

the USA confirms that the chlorophyll concentration at a given nutrient status is systematically lower when the concentration of inorganic suspended solids is higher (Hoyer and Jones, 1983). This effect may be quite strong in wind-exposed shallow lakes. In Lake Tämnaren, for instance, where sediment resuspension is a major source of turbidity, algal productivity is estimated to be reduced to about 15% of what it would be in the absence of resuspension related background turbidity (Hellström, 1991).

Note that the effect of background turbidity on algal biomass is more pronounced at high nutrient levels (Fig. 3.12a) as light is the dominant limiting factor under such conditions. In contrast, the effect of E_b on total turbidity ($e_a{*}A + E_b$) is strongest at low nutrient levels (Fig. 3.12b). At high nutrient concentrations total turbidity becomes independent of the background turbidity. The latter is explained by the phenomenon discussed in the previous section that algae grow to reach a fixed maximum shade at the lake bottom when nutrients are not limiting. An important implication is that in lakes with high non-algal turbidity, reduction of nutrient concentration can be insufficient to cause a desired increase in transparency. When a large part of the 'background' turbidity is caused by relatively fresh algal detritus, the prognosis is better. In that case a

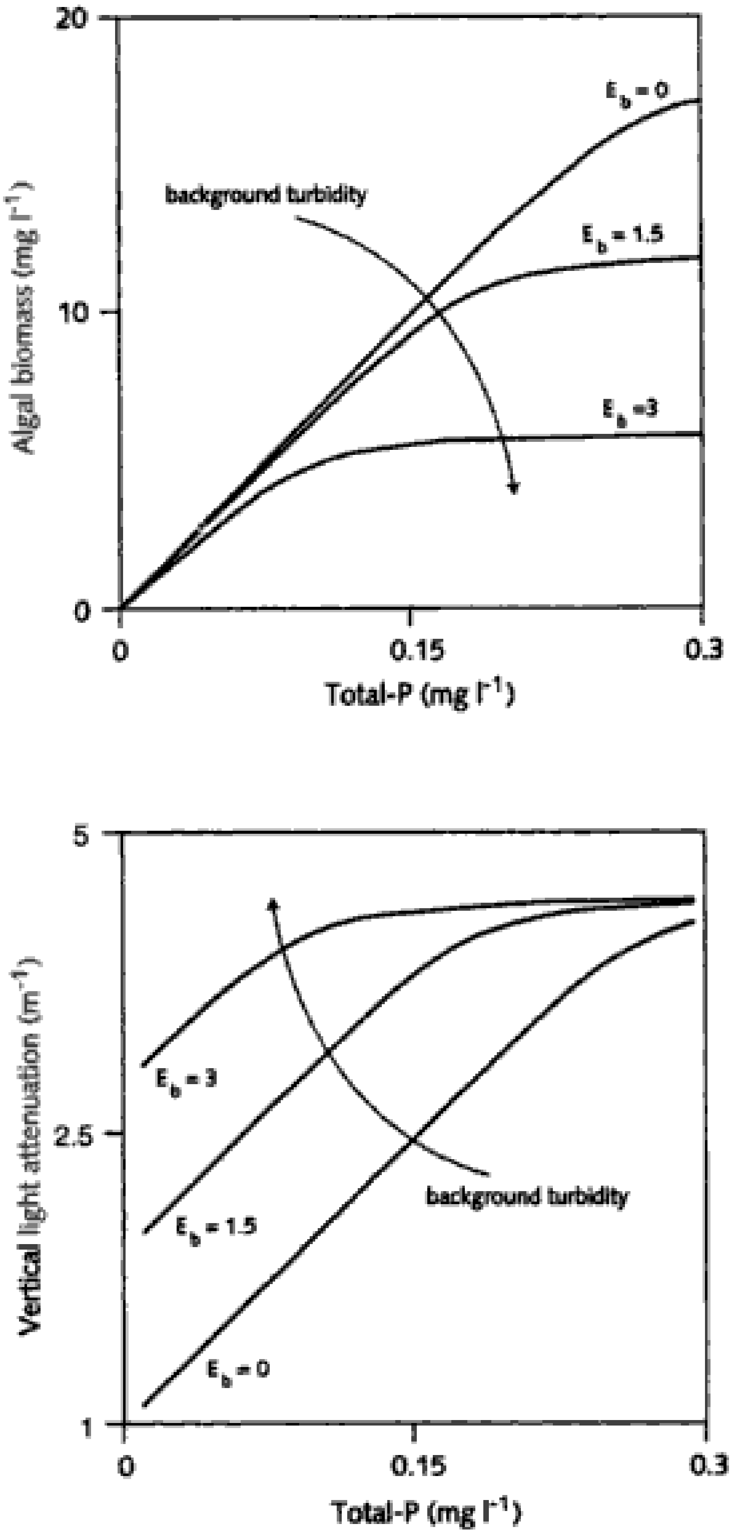


Fig. 3.12 Theoretically expected effect of background turbidity on the relationship between total-P concentration and the phytoplankton concentration (upper panel) and the vertical light attenuation coefficient (lower panel) of a hypothetical lake with a depth of 2 m.

reduction of algal productivity will be followed relatively soon by a decrease in detritus related background turbidity.

Phytoplankton control by grazers

Even when all other conditions are favourable for building up a high algal biomass, filter feeding grazers can often keep phytoplankton concentrations low. This topic is treated extensively in the next chapter. Details and references can be found there. Here, the most important groups and their potential impacts are merely mentioned as a preview.

In most freshwater systems, zooplankton is by far the most important consumer of phytoplankton. The potential impact of zooplankton grazing is illustrated in many lakes by the clear-water phase in the spring, an often spectacular dip in algal biomass caused by a peak in *Daphnia* populations around May or June. During this clear-water phase algal biomass can be reduced by an order of magnitude by zooplankton grazing. The resulting high irradiance can stimulate the spring growth of submerged macrophytes. In the summer the predation pressure by young-of-the-year fish is often too severe to allow substantial *Daphnia* densities, but in vegetated lakes high zooplankton numbers can survive throughout the summer using the weed beds as a refuge against fish predation in the daytime. These zooplankton populations can cause a high grazing pressure in the vegetation, but part of the animals also swims out at night to filter phytoplankton in the adjacent open water. Thus zooplankton grazing is one of the mechanisms responsible for the remarkable clarity of many vegetated shallow lakes. In addition to *Daphnia* and other pelagic zooplankton groups there are many, less conspicuous filter-feeders in submerged plant stands. Plant associated cladocerans such as *Sida crystallina* and *Simocephalus vetulus* and other filter feeding invertebrates can reach high densities in the vegetation. These animals could well play an important role in filtering the water in between the macrophytes.

Unlike in many estuarine systems, filter feeding bivalves are generally not abundant in freshwater lakes, but there are exceptions to this rule. The zebra mussel (*Dreissena polymorpha*, Fig. 3.13) is probably the most important bivalve with respect to algal consumption in European and American lakes. This species has only recently invaded the American continent. Its potential for grazing down algal biomass is illustrated by the remarkable drops in chlorophyll-a concentrations following *Dreissena* colonization of shallow lakes and bays in the United States. There are several cases in which Secchi-depth in shallow waters has been reported to increase by 100% following mussel colonization. In many turbid shallow lakes, however, zebra mussel densities remain low due to a lack of hard substratum for colonization. Soft, frequently-resuspended sediments are not a suitable habitat for these small sessile animals, and colonization in lakes with soft sediments is

Fig. 3.13 The zebra mussel, *Dreissena polymorpha* can massively colonize poles, rocks, boats and other hard substratum. Filtration by these animals has cleared up the water remarkably in some lakes in the USA where the species is a recent invader that spreads rapidly.

usually restricted to safe sites such as plants, rocks, boats and poles (Fig. 3.13).

Allelopathic effects

Aquatic macrophytes have long been suspected of suppressing phytoplankton through the excretion of chemical substances that inhibit phytoplankton growth (Hutchinson, 1975). Such chemical suppression, called allelopathy, is known to play an important role in some vegetations

(Rice, 1974), and seems an obvious candidate to explain the apparent conspicuous reduction of phytoplankton growth in densely vegetated lakes as well. Especially *Chara* has been subject of many investigations. Stands of this macrophyte are often surrounded by remarkably clear water. Also the plants have a pungent smell, suggesting that they might excrete something suspect.

Indeed, chemical compounds isolated from *Chara* and from some other plants have been shown to inhibit the photosynthesis of natural phytoplankton assemblages and of an epiphytic diatom in the laboratory. (Anthoni *et al.*, 1980; Wium-Andersen *et al.*, 1982; Wium-Andersen *et al.*, 1987). Whether or not these effects occur in the field has been a topic of much debate. Forsberg *et al.* (1990) found, for instance, that phytoplankton biomass in a set of *Chara* dominated lakes was not lower than expected from their total-P concentrations, and concluded that allelopathy apparently did not reduce algal growth in these lakes. Clearly, to have an effect on phytoplankton the allelopathic substances have to be released naturally in the surrounding water and be stable enough to stay there for some time. This appears less easy to demonstrate in practice.

More convincing than experiments with plant extracts are experiments with intact plants or water from natural weed beds. To exclude the possibility that depletion of nutrients by the macrophytes reduces algal growth, the water is artificially enriched in such experiments. Mostly, the observed effects on phytoplankton growth are not spectacular. Water from *Chara* dominated ponds, for instance, appeared to reduce the biomass of a culture of green algae (*Scenedesmus*) by only 10–15% compared with water from ponds with little or no vegetation (Hootsmans and Breukelaar, 1990), while experiments with intact *Ceratophyllum* plants showed little effects at all on total biomass of a natural phytoplankton assemblage (Jasser, 1995). Remarkably, bio-assays have even demonstrated positive effects on algal growth of (non-nutrient) exudates of early growth stages of *Myriophyllum spicatum* (Godmaire and Planas, 1983).

Although overall results of aquatic allelopathy research are rather equivocal, several studies indicate that cyanobacteria (or 'blue-green algae') are much more sensitive to allelopathic exudates from macrophytes than other algae. Turkmenistan workers, for instance, studying the effect of *Ceratophyllum* and *Myriophyllum* plants on cultures of the blue-green algae *Anabaena* and *Anabaenopsis* recorded drops in the algal density of almost 90% in the presence of the macrophytes (Kogan and Chinnova, 1972). Also, German work shows that the submerged plant *Myriophyllum spicatum* releases polyphenols into the surrounding water that can strongly suppress the growth of cyanobacteria, but have much smaller effects on green algae and diatoms (Gross and Sütfeld, 1994). This difference in sensitivity to allelopathic substances suggests that exudates from macrophytes may be important in tipping the competitive balance between cyanobacteria and other algae. Indeed, recent Polish experiments show this (Jasser, 1995).

Natural phytoplankton assemblages in which cyanobacteria were abundant were incubated in the field in bags together with intact plants of *Ceratophyllum demersum*. Although total algal biomass was not significantly affected, cyanobacterial abundance was greatly reduced and green algae became dominant. Extracts of four other plant species had largely the same effects.

Thus, although release of allelopathic substances by aquatic macrophytes has not been demonstrated to reduce total phytoplankton biomass markedly in natural situations, it may well be an important factor preventing cyanobacterial dominance in vegetated lakes. The mechanisms involved in the competition between cyanobacteria and other algae are treated further in the next section.

Allelopathic substances are not only produced by macrophytes. Cyanobacteria of the genus *Anabaena*, for instance, have been shown to release heat labile substances that repress the growth of diatoms (Keating, 1977; Keating, 1978). Also, filtrates from *Anabaena* cultures led to a reduction of oxygen production by the submersed plant *Zanichellia peltata* (Van Vierssen and Prins, 1985).

3.2 COMPETITION BETWEEN ALGAE AND CYANOBACTERIA

When asked for a priority list of properties that characterize the phytoplankton community of a shallow lake, the chlorophyll-a level is likely to be put first by most experts. The percentage of cyanobacteria, however, is probably second on the list. Cyanobacteria, often called blue-green algae, differ in many aspects from the rest of the phytoplankton. They resemble algae in the fact that they are photoautotrophes. However, they are prokaryotes and therefore more similar to eubacteria than to algae in many aspects. Cyanobacteria have, for instance, no defined nuclei, chloroplasts and organelles. Many species can form large inedible colonies which makes them less vulnerable to top-down control. In addition, some groups are shade tolerant and can therefore grow at a higher turbidity than other algae. Since they can also form green scums on the water surface and be toxic to animals and humans, cyanobacterial blooms are a considerable nuisance in many eutrophic lakes.

Within the group of cyanobacteria there is a large variety in physiological and morphological characteristics (for reviews see Fogg *et al.*, 1973; Carr and Whitton, 1982). Very small coccoid, ovoid and rod shaped species can be found in the plankton of most lakes. More conspicuous are the larger filamentous types (e.g. *Planktothrix*, *Limnothrix*, *Oscillatoria* and *Lyngbya*), and the groups that can form clumps (e.g. *Microcystis* and *Gomphosphaeria*) or filamentous aggregates (e.g. *Anabaena* and *Aphanizomenon*). Such colonies can consist of hundreds of cells and be discernible as small particles in the water with the naked eye. Since colony formation reduces the surface to volume ratio, it limits the uptake rate of nutrients from the water, and therefore the potential growth rate (Reynolds, 1988). However, it also offers some advantages. Vertical migration through buoyancy regulation, for instance, can be faster than in single cells of comparable density (Reynolds, 1975). Importantly, aggregation tends to reduce grazing losses, as colonies are inedible to most herbivorous zooplankters (Lampert, 1987b). This suggests that aggregation can be an adaptation to survive under high grazing pressure. In the tropics, however, colony formation simultaneously increases vulnerability to other grazers. Several cichlid fishes (*Tilapia*) feed on cyanobacterial colonies (Moriarty, 1973) and flamingos are known to depend largely on colonies of *Spirulina* and *Microcystis* for their protein supply (Fogg *et al.*, 1973).

A well known feature of several cyanobacteria is their ability to use atmospheric N_2 as a source of nitrogen. In many species N_2 fixation is achieved by metabolically specialized thick-walled cells termed heterocysts. Obviously, nitrogen fixation could represent an advantage in lakes where nitrogen is a limiting factor. Indeed some analyses have suggested that N_2-fixing cyanobacteria are more abundant at low N:P ratios (Schindler, 1977; Smith, 1983), but this pattern could not be found in shallow lakes (Jensen *et al.*, 1994).

Another aspect that sets many species apart from other algae is that they have gas vesicles providing them with the ability to regulate their buoyancy (Fogg *et al.*, 1973). When photosynthesizing they build up carbohydrates, which increases their density and makes them sink. In the darkness of the deeper layers, they lose carbohydrates due to respiration and become buoyant again. In lakes (or periods) with relatively low turbulence the buoyancy regulation can help algae like *Microcystis* to optimize their position in the water column. In situations with a thermal stratification they float up out of the non-turbulent hypolimnion to arrive in the mixed water layer (epilimnion) where light conditions are better. In calm warm weather, colonies can massively float up to the surface where they become trapped by the surface tension and form conspicuous scums (Ibelings *et al.*, 1991; Ibelings, 1992). When such floating algal masses accumulate at shores they can be notoriously bothersome to recreants. In shallow well mixed lakes, however, *Microcystis* blooms are not common.

Probably the most important nuisance algae in shallow lakes are filamentous blue-green algae. The most important genera are *Limnothix*, *Planktothrix* (formerly *Oscillatoria*), *Anabaena*, *Aphanizomenon* and at lower latitudes in high pH lakes, *Spirulina*. Especially *Planktothrix agardhii* (formerly *Oscillatoria agardhii*) can dominate the algal community completely during the summer. Although this group has gas vesicles too, their shape does not allow rapid adjustment of their position in the water column as found in spherical colonies of cyanobacteria in the *Microcystis* group (Ibelings, 1992). Other features, however, make this filamentous group extremely successful in many turbid shallow lakes. When winters are not too cold, many lakes can even be dominated all year round (Berger, 1975; Sas, 1989). The remaining part of this section focuses on the factors that explain dominance by filamentous blue-green algae. Taxonomy in this group is a bit confusing, because the important genus *Oscillatoria* has recently been split up and species of this group can now be found in the genus *Planktothrix* and the genus *Limnothrix*. The name *Oscillatoria*, however, is found throughout the literature, and in this book this name or the family name Oscillatoriaceae is used to indicate the group.

Empirical relationships with nutrients and turbidity

Dominance by filamentous cyanobacteria is typically associated with eutrophic conditions (Berger, 1975; Schindler, 1975; Sas, 1989). Many shallow lakes are known to have switched to a state dominated by such filamentous blue-green algae in response to nutrient enrichment, and in several cases a reduction of the phosphorus loading has resulted in a switch back to a community that is not dominated by cyanobacteria (Sas, 1989). In data sets combining information from different lakes, however, the percentage of cyanobacteria tends not to be correlated with the total-P concentration.

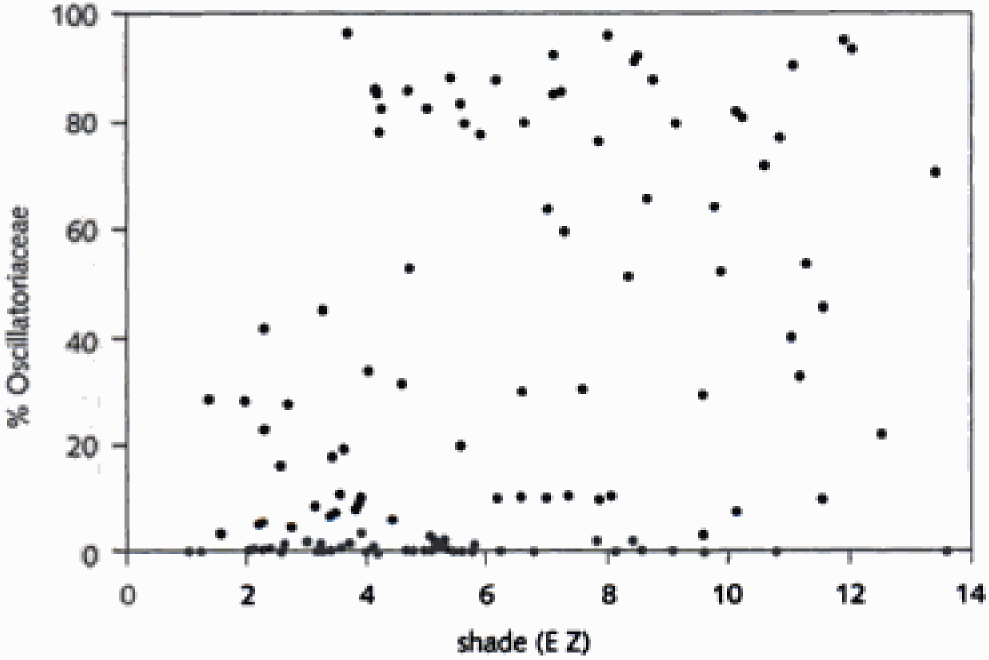


Fig. 3.14 Relative abundance (% biovolume) of Oscillatoriaceae plotted against an index of under water shade experienced by the algae (the product of mean lake depth and the vertical light attenuation coefficient, *EZ*), for 55 shallow (mean depth < 3 m) Dutch lakes averaged over the period July–August. For several lakes information from different years is included. The total data set encompasses 118 lake-years. From Scheffer *et al.* (1997a).

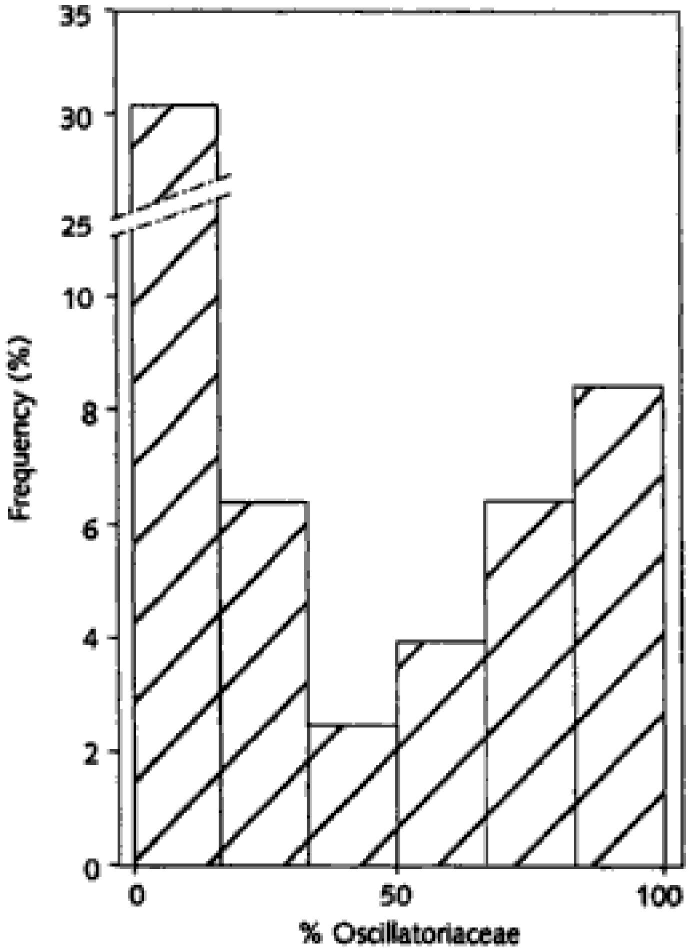


Fig. 3.15 Frequency distribution of the relative abundance of Oscillatoriaceae (% of total algal biovolume) in the shallow lakes data set described in the legend to Fig. 3.14. From Scheffer *et al.* (1997a).

Much better correlations are found when instead of phosphorus, an indicator of under-water light intensity is used (Fig. 3.14) (Scheffer *et al.*, 1997a).

Note that the points in Fig. 3.14 are found mainly at very high or very low *Oscillatoria* abundance. Indeed, the frequency distribution of the relative abundance of Oscillatoriaceae is bi-modal (Fig. 3.15). In the majority of the cases these cyanobacteria are either a minor component of the phytoplankton community or strongly dominant, and the probability of the latter rises steeply with shade.

These patterns suggest that it is the low light level rather than the high nutrient availability per se that leads to dominance by Oscillatoriaceae in eutrophic situations. If this is indeed the main causal link between *Oscillatoria* dominance and eutrophication, disappearance of these cyanobacteria in response to a reduction of the nutrient concentration should occur at comparable shade levels rather than at comparable nutrient levels in different lakes. Indeed this pattern has been described for a couple of well studied *Oscillatoria* dominated lakes (Mur *et al.*, 1993). Sharp drops

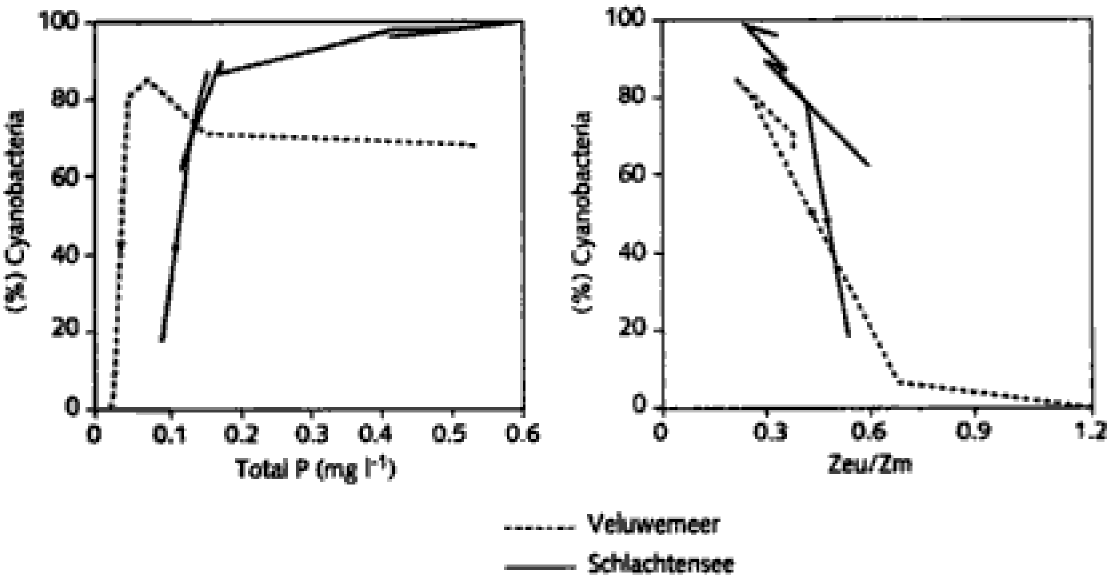


Fig. 3.16 The decline of cyanobacteria (dominated by *Planktothrix agardhii*) with a reduction of the nutrient level in the Lakes Schlachtensee and Veluwemeer. The collapse of *Planktothrix* occurs at a higher total-P level in the shallower Lake Veluwemeer (upper panel), but both lakes switch at roughly the same underwater light conditions expressed as the ratio of euphotic depth to mixed depth, Z_{eu}/Z_{mix} (lower panel) (redrawn from Mur *et al.* (1993).

in the percentage of cyanobacteria (*Planktothrix*) have occurred in the lakes Schlachtensee and Veluwemeer where phosphorus concentrations have gradually decreased due to a reduction in loading. In Veluwemeer, cyanobacteria disappeared at a considerably lower phosphorus level than in the approximately three times deeper Schlachtensee. However, the light climate (expressed as the ratio $Z_{eu}:Z_{mix}$) at which the cyanobacteria collapsed was practically the same in both lakes (Fig. 3.16).

The abrupt character of the changes in these lakes is typical for the transition between *Oscillatoria* dominance and other algal assemblages (Sas, 1989). Abrupt switches have also been described for tropical lakes. Here the species involved is *Spirulina platensis*, another representative of the *Oscillatoria* family. Accurate data are scarce, but some of these lakes are actually known to switch back and forth repeatedly. Melack (1980), who described these patterns, noted that the relatively stable states of the community between the switches persisted for more than 10 generations, indicating that they represent disjunct equilibrium states.

Further analysis of the Dutch data set shown in Figs. 3.14 and 3.15 reveals another important pattern. Lakes where Oscillatoriaceae dominate tend to be shady compared with lakes of the same nutrient level where these algae are rare (Fig. 3.17). The difference is especially marked for lakes with a total-P concentration of less than 0.3 mg l^{-1} (Fig. 3.17 lower panel). This suggests that Oscillatoriaceae dominance is not only favoured by shady conditions, but also promotes such conditions. Obviously, this sounds like a

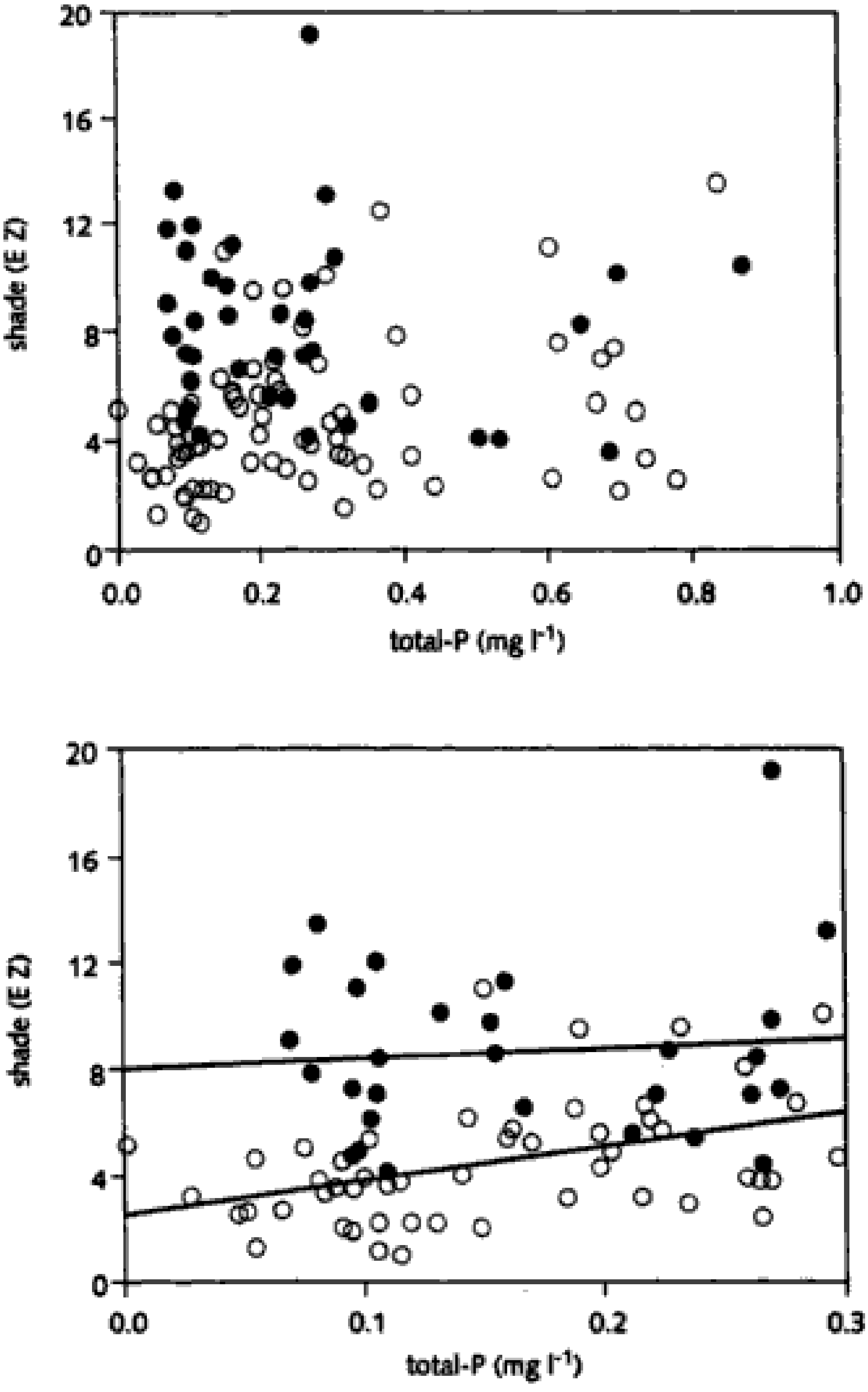


Fig. 3.17 Under water shade (*EZ*) as a function of the total phosphorus concentration. Solid dots refer to lakes where Oscillatoriaceae comprise more than 50% of the algal biovolume open dots are for lakes with less than 50% Oscillatoriaceae. The upper panel represents the entire data set described in the legend to Fig. 3.14. The lower panel represents the subset of lakes where the total phosphorus concentration is less than 0.3 mg l^{-1}. The regression lines are computed for the subset of data represented in the lower panel. The upper regression line is for the *Oscillatoria* dominated lakes (solid dots), the lower line for the other lakes. From Scheffer *et al.* (1997a).

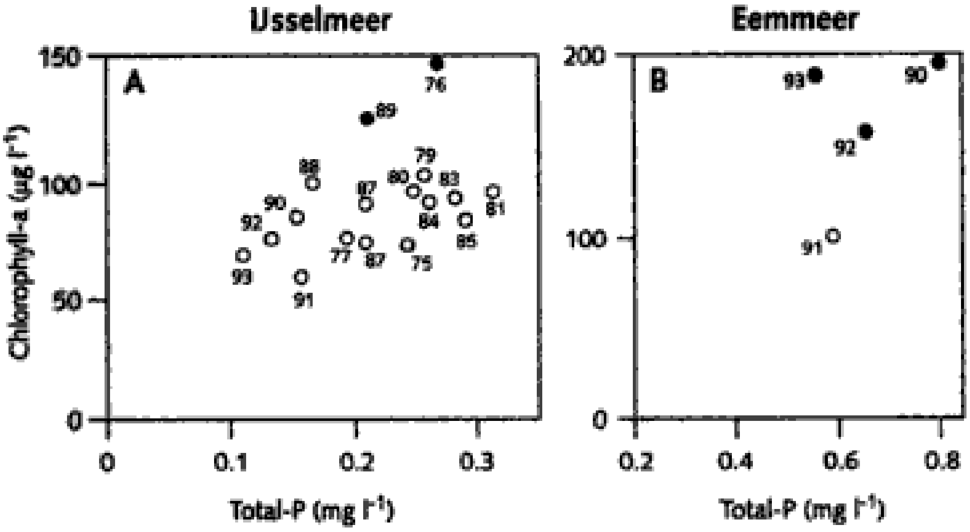


Fig. 3.18 Average summer chlorophyll-a concentrations plotted against the total-P concentration in different years for two eutrophic shallow lakes. Blue-green algae dominated years are marked as solid dots. chlorophyll is the main light attenuating seston component in these lakes, and shade will be higher in the years with higher chlorophyll levels. From Scheffer *et al.* (1997a).

chicken and egg problem and causality cannot be inferred from correlations alone. Other factors that vary between lakes may influence shade and cyanobacteria in such a way that the same pattern is produced. Therefore, it is informative to see that individual lakes that alternate between cyanobacterial dominance and another algal community tend to show the same pattern (Fig. 3.18).

In IJsselmeer, for instance, filamentous cyanobacteria have been rare over the past 20 years. However, during the summers of 1976 and 1989 the summer algal community was dominated by *Planktothrix agardhii*. In both summers chlorophyll-a was exceptionally high. Another Dutch lake, Eemmeer, is usually dominated by *Planktothrix*. In 1991, however, the cyanobacterial density was low for most of the summer. This coincided with a drop in chlorophyll-a.

Hysteresis as an implication

The patterns in the field data suggest that shade promotes *Oscillatoria* dominance (Fig. 3.14), but that Oscillatoriaceae also promote shady conditions (Fig. 3.17 and 3.18). This would imply an positive feedback in the development of blooms of Oscillatoriaceae. The consequences can be seen more clearly by setting up a simple *graphical model* (Fig. 3.19), based on the empirically derived patterns.

As argued before, shade experienced by the algae in a well mixed lake depends on the depth and the vertical light attenuation coefficient. The model, however, describes a given hypothetical lake in which depth is fixed

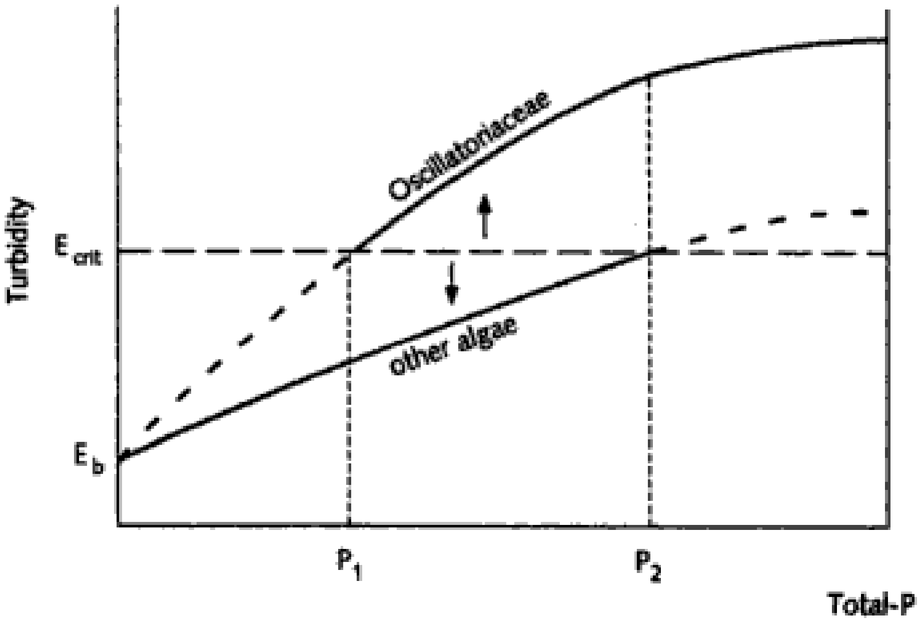


Fig. 3.19 Generalized diagram of the equilibrium states of the algal community of shallow lakes inferred from the patterns observed in the field (see text for explanation). From Scheffer *et al.* (1997a).

and shade therefore depends only on turbidity (E). Turbidity will increase with the phosphorus level, starting at a background value (E_b) and leveling off at high P concentrations when light becomes limiting (Fig. 3.19 lower curve). When cyanobacteria dominate, however, turbidity will be higher at the same nutrient concentration (cf. Fig. 3.17). Thus a separate turbidity-nutrient relationship should apply to *Oscillatoria* dominated situations (Fig. 3.19 upper curve).

The field patterns further suggest that the probability that Oscillatoriaceae will dominate the community depends strongly on the shade level. Since many other factors may have an effect on the probability of cyanobacterial dominance, it would be surprising if the response to shade would be identical in all situations. However, for a given well mixed lake, the simplest assumption is that there is a single critical shade level, which (because of the fixed depth) translates into a critical turbidity, E_{crit}, above which cyanobacteria will become dominant (Fig. 3.19 horizontal line). Above this critical shade level Oscillatoriaceae will become dominant, at lower turbidities other algae will dominate. This implies that below the horizontal line the cyanobacterial turbidity–nutrient relation is irrelevant, whereas above the critical level the turbidity–nutrient relation for other algae is irrelevant. Neglecting these irrelevant (dashed) parts, the two curves combine with the middle segment of the horizontal line to an S-shaped curve of steady states that is typical of so-called catastrophic systems. The figure suggests that at low total-P levels only the non-cyanobacterial state is possible, whereas at very high total-P levels only the cyanobacteria dominated state exists. However, over a range of intermediate nutrient levels ($P_1 < P < P_2$) both states are possible. Here, the community will tend to settle in either of the two states depending on whether the turbidity in the initial state is above or below the critical value (E_{crit}).

This graphical model implies that the response to changes in the nutrient level should be discontinuous ('catastrophic') rather than smooth. When starting from a low total-P level, the nutrient loading of the lake is slowly increased, turbidity will gradually increase too. This smooth response ends when the critical total-P value (P_2) is reached, since above this level only the blue-green algae dominated state exists. When this 'breakpoint' is passed the system will jump to a higher turbidity at the *Oscillatoria* dominated upper branch of the diagram. If from this point the total-P concentration is gradually reduced, the algal community will stay on the cyanobacteria dominated branch until the lower critical nutrient concentration (P_1) is reached, and then jump back to the lower branch. It can also be inferred that *Oscillatoria* will not easily disappear from lakes that have a high background turbidity (E_b).

The tendency of systems with alternative stable states to stay in the same state despite changes in external conditions is called hysteresis, and that term is also used in a broader sense to indicate that a system has alternative stable states over a range of conditions.

Competition as an explanation

The hysteresis inferred from the field patterns can be understood from the distinct differences in physiology between cyanobacteria and other algae. This can be shown by extending the model for algal growth presented in the previous section (Eq. 16). To make it a competition model we write an equation for each of the algal types, fitting one with parameter values measured in the laboratory for green algae (G) and the other one with values representing the physiology of *Planktothrix agardhii* as a typical representative of filamentous blue-green algae (B):

$$\frac{dG}{dt} = r_g G \frac{h_{s_g}}{h_{s_g} + DE} \frac{P_f}{h_{p_g} + P_f} - (l_g + f)G \qquad (17)$$

$$\frac{dB}{dt} = r_b B \frac{h_{s_b}}{h_{s_b} + DE} \frac{P_f}{h_{p_b} + P_f} - (l_b + f)B \qquad (18)$$

where turbidity (E) depends on the biomass of both groups and their specific light attenuation coefficients (e_g and e_b):

$$E = e_g G + e_b B \qquad (19)$$

and free available phosphorus (P_f) depends on the total available pool (P) and the concentrations of phosphorus in the two groups (p_g and p_b):

$$P_f = P - \left(p_g G + p_b B\right) \tag{20}$$

In addition to the specific loss rates due to respiration, settling losses and other mortality causes of both groups (l_g and l_b), this model has a loss rate f due to flushing of the lake, which is the same for both species. Note that background turbidity is not considered explicitly in this model. Its potential implications, however, can be easily inferred from the previous analyses as pointed out in the next section.

The model accounts for four important aspects in which cyanobacteria differ from other algae: they have a lower maximum gross productivity (r); a lower loss rate (l); a higher shade tolerance (h_s); and cause a higher turbidity per unit of biomass (e) than other algae. Thus:

$$r_b < r_g \qquad l_b < l_g \qquad h_{s_b} < h_{s_g} \qquad e_b < e_g \tag{21}$$

The exact parameter values used to produce the diagrams from this model are estimated from the results of laboratory studies (Table 3.1).

However, the conclusion that this system produces a hysteresis can already been drawn from the qualitative differences between the parameters (Scheffer *et al.*, 1997a).

The traditional way to study competition models is by plotting the lines of zero growth of either of the species ($dG/dt = 0$ and $dB/dt = 0$) (Fig. 3.20).

These so-called isoclines separate regions in the state space where a population increases from regions where it decreases. By definition intersections of the isoclines of the two species are equilibria, as the growth of both species is zero. Intersections of the isoclines with the axis on which the other species is zero (G^* and B^* in Fig. 3.20) are also equilibria because zero populations can not grow. Because this represents a somehow degenerate situation, these intersections are called trivial equilibria. If the isoclines do not intersect, that is, if one is entirely above the other, the species with the

Table 3.1 Parameter dimensions and the values used to produce Figs. 3.20–3.23 from the model of competition between filamentous cyanobacteria and other algae (Eqs. 17 and 18, p. 107). Derivation and sources of the values can be found in Scheffer *et al.* (1997a). (Note that in that paper algal abundance is expressed in grams of phosphorus rather than biomass, and sensitivity to turbidity, q, in a 3 m water column is used rather than shade tolerance h_s)

	Green algae	*Filamentous cyanobacteria*	*Dimensions*
Maximum gross production	$r_g = 1.2$	$r_b = 0.6$	d^{-1}
Loss rate	$l_g = 0.12$	$l_b = 0.06$	d^{-1}
Specific extinction	$e_g = 0.5$	$e_b = 1.0$	$m^2 mg^{-1}$
Shade tolerance	$h_{sg} = 1.5$	$h_{sb} = 3$	–

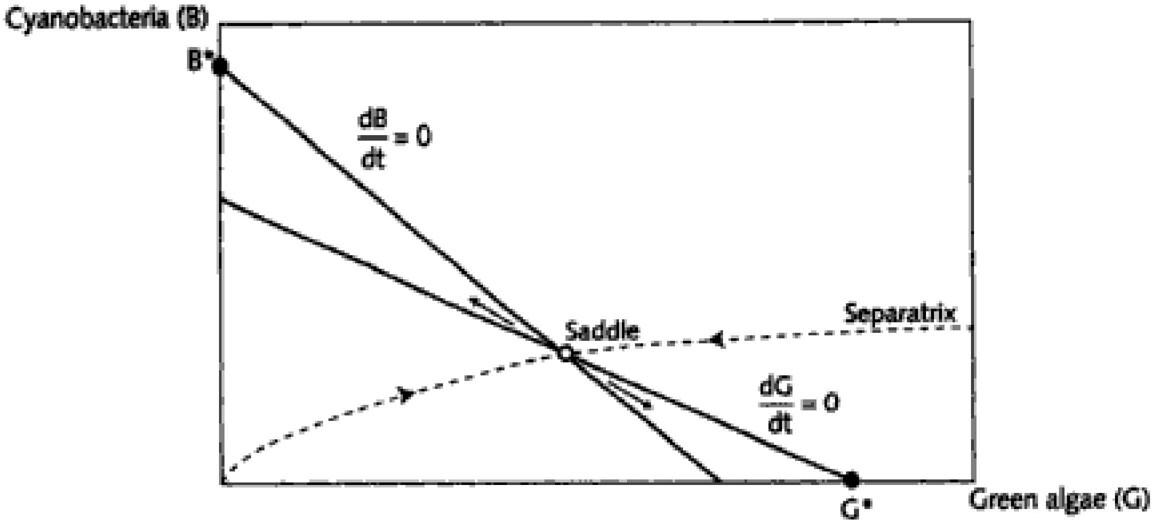


Fig. 3.20 Isoclines of cyanobacteria (dc/dt = 0) and other phytoplankton (da/dt = 0) (see text). Arrows indicate the direction of change in simulation runs at the corresponding points. Simulations starting above the dashed separatrix end in the stable cyanophyte dominated state (c*), whereas runs starting from below the separatrix end up in a state dominated by other algae (a*).

highest isocline wins and the system ends up in the trivial equilibrium at which its competitor is absent. If the isoclines intersect, the properties of the system depend on the stability of the equilibrium at the intersection. If it is stable, and there is no other intersection, the trivial equilibria are both unstable. Therefore, the intersection is the only stable equilibrium. Any simulation starting with both species will end up in this state of stable coexistence. In the case of our model (Fig. 3.20), the intersection is always an unstable equilibrium. This can be formally proven from the inequalities, as stated above. This specific type of unstable equilibrium is called a 'saddle' because of the pattern produced by the paths of trajectories in its vicinity. The saddle repels trajectories in the direction of the trivial equilibria but attracts them from the perpendicular directions. The saddle point lays on the 'separatrix', a line that starts from the origin and separates the attraction basins of the two trivial equilibria which are in this case stable. Simulations starting from an initial state above the separatrix always end up in a monoculture of cyanobacteria (B^*) whereas trajectories starting below the separatrix lead to the other trivial equilibrium (G^*).

Obviously, the positions of the isoclines and equilibria depend on the value of the control parameters. By playing with the nutrient level (P) and the flushing rate (f), either of the isoclines can be brought entirely above the other. As explained, these are situations in which only one stable (trivial) equilibrium exists. Changing the value of one of the control variables gradually makes the saddle move in the direction of either of these equilibria. Since the separatrix moves in the same direction the region of attraction of that equilibrium progressively declines, until the saddle collides with the

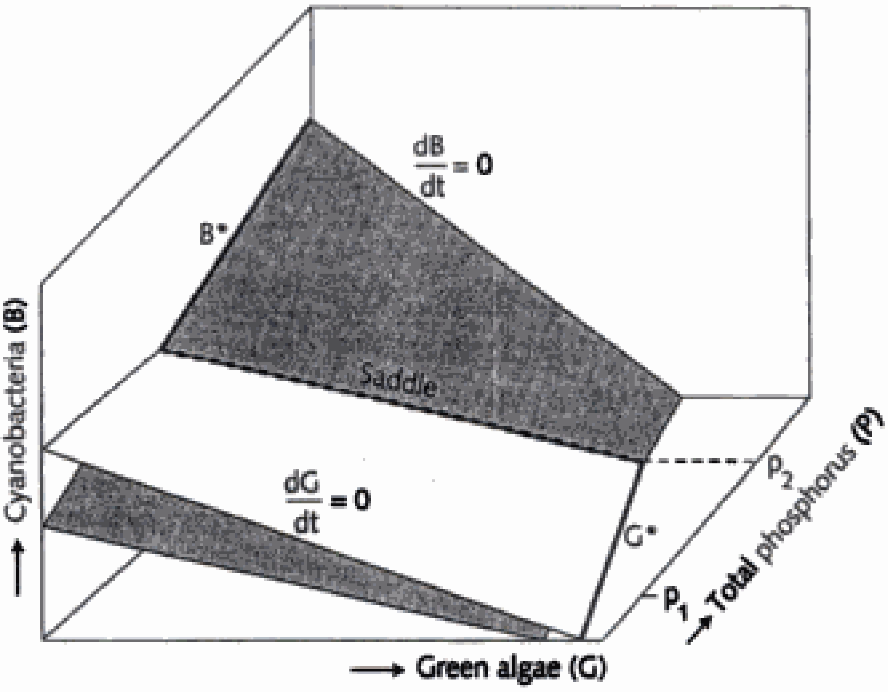


Fig. 3.21 Effect of the total-P concentration of the lake on the isoclines used to analyse the competition between cyanobacteria (*c*) and other phytoplankton (a) (Fig. 3.20) (see text). Two alternative stable states exist at phosphorus concentrations between P_1 and P_2.

equilibrium and makes it unstable. In fact, the saddle moves out of the positive quadrant to negative concentrations of cyanobacteria where it does not make biological sense any more. The collision of the saddle with the stable equilibrium is an example of a so-called bifurcation. Bifurcations happen when, due to change of a control variable, equilibria meet and change their nature. If, as in this case, one of the equilibria goes through the axis (driving a species extinct) the bifurcation is called transcritical. Bifurcations always mark a change in the qualitative properties of the system. Therefore, tracing the parameter values for which they occur can be a very useful technique for analysing the system's behaviour, as shown later.

The effect of a control variable on the isoclines and equilibria can be illustrated by adding the control variable as an extra dimension to the isocline picture (Fig. 3.21). Over the range of nutrient values for which the saddle exists ($P_1 < P < P_2$) the two trivial equilibria (G^* and B^*) occur as alternative stable states.

It is easier to grasp a two-dimensional plot in which both algal groups are combined in one variable, and the equilibria of the model are shown as a function of the control variable. In our case, an interesting state variable that combines the density of both algal groups is the total turbidity (E). Figure 3.22a shows the turbidity in equilibrium predicted by the competition model as a function of the total nutrient concentration (P). The two

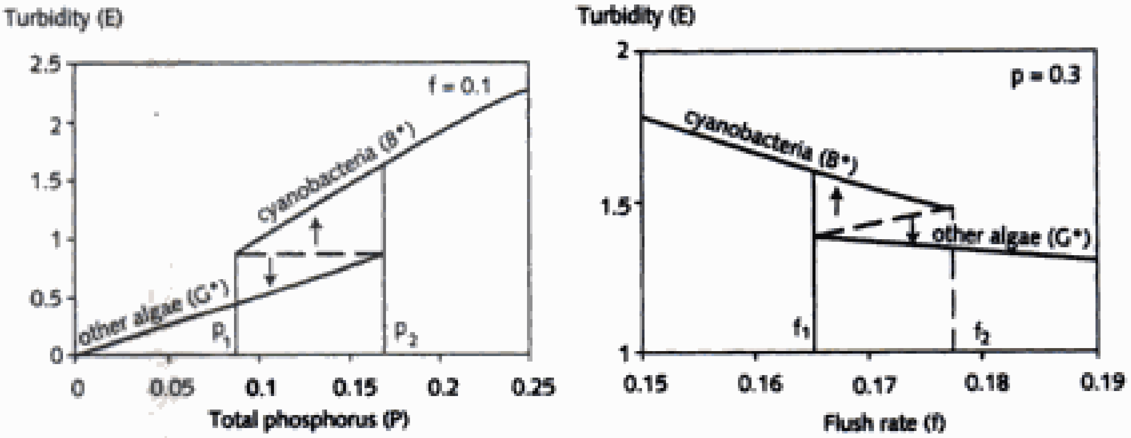


Fig. 3.22 Hysteresis shown as the response of the turbidity (E) with respect to the control parameters total-P (P) and flush rate (f). Modified from Scheffer *et al.* (1997a).

branches correspond to the stable (trivial) equilibria. The upper branch represents a monoculture of cyanobacteria (B^*), while the lower one represents the equilibrium without blue-green algae (G^*). The horizontal dotted line that connects the two branches is the unstable (saddle) equilibrium. It demarcates the border of the regions of attraction of the two stable branches over the range of nutrient values ($P_1 < P < P_2$) where they coexist. Obviously this figure, computed with the model from laboratory data on the physiology of the algal groups, corresponds closely to the tentative picture of hysteresis derived from the field data (Fig. 3.19).

The fact that the same result can be derived in different ways from independent sets of information (laboratory and field) is, of course, encouraging. As Levins (1966) phrased it, we are more likely to accept something as the truth when it emerges 'as the intersection of independent lies'. Although 'lies' may sound a bit too harsh, both approaches clearly have their shortcomings. Model results can be artifacts of over-simplification due to the representation of a complex mechanism in simple mathematics. Also, the model includes just a few mechanisms, whereas in the field other mechanisms may contribute to explain the observed patterns. On the other hand, the fact that field data show the effect of many more factors obscures the patterns and makes it difficult to infer the mechanisms that cause the observed behaviours. Also, variations in the weather, measurement errors and numerous differences between lakes make data noisy, and patterns are complicated by the fact that communities in the field are never really in equilibrium, due among other things to the continuous change of light, temperature and hydrological conditions over the year.

An important factor that may affect cyanobacterial dominance is the hydraulic retention time of the lake. Since the flushing rate is in the equations, the model also allows us to explore the response to this factor (Fig. 3.11b). Again a hysteresis occurs, but the picture is reversed as increasing

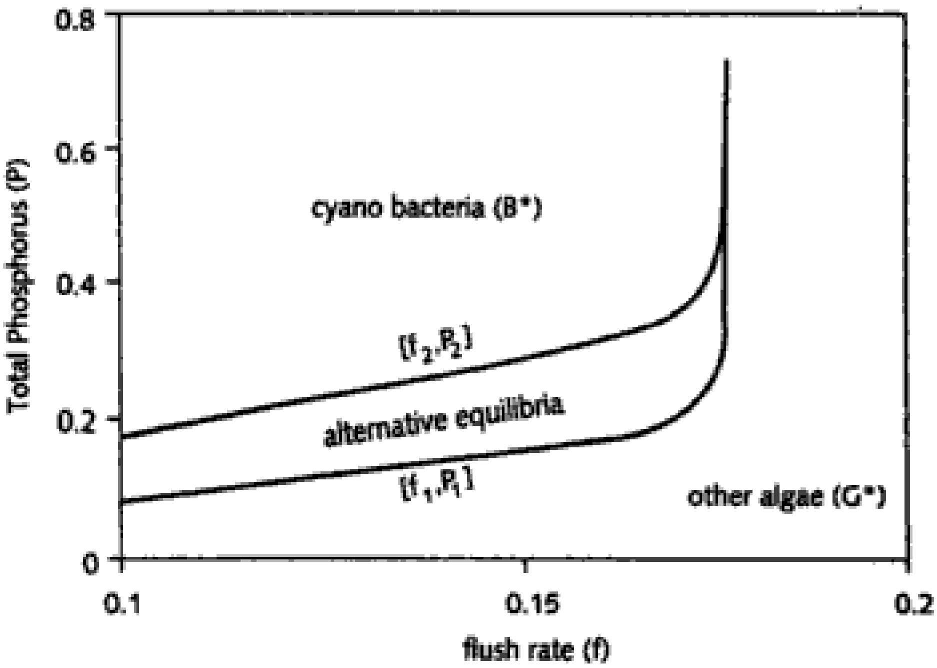


Fig. 3.23 Bifurcation diagram of the model showing for which combinations of flush rate (f) and total-P concentration (P) cyanobacteria [*c*] or other algae [*a*] will dominate, and for which combinations those states are alternative equilibria. From Scheffer *et al.* (1997a).

the control parameter, f, the situation now becomes less favourable for cyanobacteria. Interestingly, the catastrophic transitions between the two branches (at f_1 and f_2) do not occur at the same turbidity any more as was the case in the hysteresis with respect to P (Fig. 3.22a). This illustrates that the effect of flushing can not simply be explained as affecting the competitive balance through a reduction of turbidity. Instead, the clue to understanding the effect of flushing is that cyanobacteria have low rates of productivity ($r_b < r_g$) but usually compensate this by having low loss rates ($l_b < l_g$). Consequently, the relative impact of an extra loss due to flushing is much higher for the slow growing blue-green algae than for the other algae. In fact, the effect of flushing on the algal community is analogous to the much discussed effect of 'disturbance' on terrestrial vegetations. It keeps the slow-growing K-select species from outcompeting the fast growing r-select species.

Depicting the combined effects of flushing (Fig. 3.22a) and nutrients (Fig. 3.22b) on the turbidity would require a three-dimensional graph. It is easier to produce and read a projection of such a graph in the parameter plane (Fig. 3.23).

The two lines in this graph represent the edges of the hysteresis where the catastrophes occur ([f_1,P_1] and [f_2,P_2]). Because, as explained earlier, the corresponding connections of the stable (trivial) equilibria with the unstable saddle equilibrium are so-called 'bifurcations', this type of representation is known as a bifurcation graph. The cyanobacterial monoculture (B^*) is stable above the lower bifurcation line, whereas the equilibrium without cyanobacteria (G^*) is stable below the upper line. The area between the lines represents the conditions under which the two states are present as alternative equilibria. Note that Figs. 3.22 a and b correspond to a vertical and a horizontal transect through this bifurcation diagram respectively, and can be used to understand how turbidity varies with the two parameters in this graph. The bifurcation graph adds a lot of information to the separate hysteresis curves. It shows, for instance, that the hysteresis with respect to P is largest if there is some flushing, whereas the hysteresis with respect to flushing shrinks to almost nothing at high phosphorus levels.

Restoration strategies, manipulating nutrients and flushing rate can be interpreted in terms of this diagram. Obviously, they are not independent, as reduction of the nutrient content normally requires reduction of the concentration in the inflow. A dilemma occurs when water flows can be diverted to flush the lake but the nutrient concentration of the available water is high. Theory predicts that flushing with high nutrient water can still work (Fig. 3.23) if the flushing rate is sufficiently high. This view is supported by information from Danish lakes (Jeppesen, pers. comm.). Blue-green algal dominance is never observed in lakes where the hydraulic retention time is shorter than five days, even though such lakes can have very high nutrient concentrations. Importantly, flushing effects will be stronger in winter when algal growth rates are low. Indeed winter flushing with water from the nearby polder areas has probably helped to break cyanobacterial dominance in Veluwemeer (The Netherlands) (Hosper, 1985; Hosper and Meijer, 1986). Unfortunately, causality is complicated in this case because the flushing also caused a strong reduction in phosphorus concentration.

The above treatment of hysteresis is phrased in terms of dynamical systems theory. However, studying competition has a long tradition in ecology. A short note on the connection to existing theory and terminology is therefore appropriate. Importantly, our alternative equilibria or 'unstable coexistence' case is also one of the qualitative possibilities in standard Volterra competition models based on the logistic growth equation. In such models the mechanisms of competition are not specified. Instead, the intensity of inter- and intra-specific competition is defined directly. For alternative equilibria to occur, inter-specific competition needs to be stronger than intra-specific competition; loosely phrased; it should be better to have conspecifics around than individuals of the other species. Obviously, this is in line with the mechanism in our more specific model. Cyanobacteria have a competitive advantage in the turbid situation caused by their own dominance.

Our general result is also analogous to that obtained from the graphical models of competition for two resources elaborated by Tilman (Taylor and Williams, 1975; Tilman, 1977; Tilman, 1982; Tilman, 1985). Tilman's resource-ratio theory predicts that the coexistence between two competing species is unstable if each species consumes relatively more of the resource of which it also tolerates the lowest levels. In our case competition is for light and nutrients. Blue-green algae cause a higher turbidity at the same nutrient level. In resource-ratio terms, this means that they use relatively more light. Since they are also the most shade tolerant group, this fits with the resource-ratio requirement for unstable coexistence.

Other mechanisms involved

The simple model suggests that competition between blue-green and other algae is a plausible explanation for the hysteresis that can be observed in lakes. However, many other mechanisms than the ones included in this simple competition model will obviously operate in real situations.

An aspect that is not considered explicitly in the competition model is background turbidity. Background turbidity due to sediment resuspension can be high in shallow lakes. This allows a high turbidity to be reached at lower nutrient levels (Fig. 3.12). Thus lakes that are turbid due to a frequent resuspension of sediment particles are likely to be shady enough to allow dominance by filamentous blue-green algae even at a low nutrient level. In extreme cases one could even envision background turbidity to be high enough to make blue-green algae the superior competitors in any nutrient condition. Indeed, environments with uninterrupted mixing are very often dominated by *Oscillatoria* (Reynolds, 1993). Reynolds (1993) attributes this to the frequent 'disturbance' that eliminates all other species but the tolerant *Oscillatoria*, much like grasses are more likely to survive in a frequently cut pasture than trees. As outlined here, filamentous blue-green algae are in fact more comparable to trees that can be found in mature forests than to grasses. They are shade tolerant, slow growing and sensitive to losses due to flushing. They survive in many situations not because of fast regeneration, but because they are relatively immune to grazing and shade tolerant. The fact that shade tolerance is the main reason for their notorious dominance in wind mixed lakes is confirmed by an analysis of the factors that drive algal dynamics in the Loosdrecht Lakes (Gons *et al.*, 1991). High background turbidity caused by frequent resuspension is thought to be a major reason for the persistent dominance of cyanobacteria in these shallow turbid peat lakes.

A topic of much discussion with respect to cyanobacteria is their inedibility. Even large herbivorous zooplankters are unable effectively to consume filamentous cyanobacteria under most conditions (Arnold, 1971; Schindler, 1971; Gliwicz and Lampert, 1990). An obvious implication of the inedibility is that grazing mortality will in general be lower for filamentous blue-green than for edible algae. However, the interaction of filamentous cyanobacteria, herbivorous zooplankton and edible algae is rather intricate. Model analyses suggest that depending on the selectivity of grazers and the nutritious value, grazing may push the competitive balance either way and under some conditions it may also result in a stable coexistence of both groups (Gragnani *et al.*, 1997)

Indeed, an absolute monoculture of filamentous blue-green algae as predicted by the minimal model is never observed in real lakes (Fig. 3.14), and, obviously, the monoculture prediction is an artifact of simplification. Selective grazing is one possible explanation, but many studies have shown that spatial heterogeneity of the environment also helps to prevent competitive exclusion and it seems reasonable to assume that this factor plays a role in algal communities as well. Also temporal variation of the environment will tend to prevent competitive exclusion in algal communities (e.g. Padisák *et al.*, 1993). This factor is surely relevant to *Oscillatoria* dynamics. Although these algae can stay dominant throughout the year in eutrophic lakes (Sas, 1989) the seasonal pattern depends on the temperature conditions. In Denmark overwintering of filamentous blue-green algae occurs hardly at all (Jeppesen, pers comm.), while in the milder climate of The Netherlands, the dominant *Planktothrix agardhii* disappears from the eutrophic shallow lakes only in cold winters (Berger, 1975). Winter can apparently bring the system past the breakpoint below which blue-green algal dominance ends. The sensitivity of *Planktothrix agardhii* to cold winters fits with the observation that the growth of this species, like that of most large algae, drops relatively steeply with temperature (Reynolds, 1988). Obviously, seasonal alternation between blue-green and other algae implies 'coexistence' during the transitional phase, and especially averages over a period including a transition will suggest coexistence.

Although the field patterns as well as the model results indicate that nutrients, through their effect on shade, influence the competition between Oscillatoriaceae and other algae, it is clear that temperature and flushing rate are also important for the competitive balance. As mentioned in the previous section, allelopathy is another factor that may also affect cyanobacterial dominance. Various aquatic macrophytes have been shown to release substances that inhibit the growth of cyanobacteria while having a much smaller impact on the development of other algae (Gross and Sütfeld, 1994; Jasser, 1995), and bag experiments in the field demonstrated that plants tend to cause a switch from cyanobacterial dominance to a dominance by green algae even though total algal biomass is not significantly affected (Jasser, 1995). There are some indications that allelopathy among different phytoplankton groups may also play a role in competition. Experiments by Keating (1977; 1978) suggest that blue-green algae can release allelopathic substances that are toxic to diatoms.

The current information is insufficient to see exactly how nutrients (shade), flushing rate, temperature and allelopathic substances interact in their effect on competition. In general, however, a catastrophic system will show hysteresis in its response to all control variables. Also the 'threshold value' for one variable will normally depend on the value of the other variables. The latter is illustrated for the combination of flushing and nutrients by the model analysis (Fig. 3.23). At low nutrient levels, the sensitivity to flushing increases. An example of the combined effects of nutrients and temperature is provided by the history of eutrophication of Lake Albufera in Spain (Romo and Miracle, 1994). In the 1970s eutrophication had caused the phytoplankton community to be dominated by Oscillatoriaceae during summer and autumn, but in the spring chlorophytes and diatoms were still dominant. Ongoing enrichment in the 1980s, however, led *Oscillatoria* to become dominant throughout the year, suggesting that the cyanobacterial dominance is less sensitive to the low temperatures when nutrient levels are higher.

In conclusion, field patterns as well as the physiologically based competition model indicate that dominance by Oscillatoriaceae can be an alternative stable state of the algal community of shallow lakes because these shade tolerant cyanobacteria are able to cause an increase in turbidity that favours their competitive advantage. The model and field observations indicate that high flushing rates reduce the probability of blue-green algal dominance because of their relatively slow growth rates. In addition, there is evidence that low winter temperatures and allelopathic substances from aquatic macrophytes can affect the competitive balance in favour of other algae.

3.3 MULTI-SPECIES COMPETITION AND SUCCESSION

Throughout the former sections phytoplankton is treated simply as one homogeneous group or as two competing populations. Algal dynamics are mostly studied at such highly lumped levels. Although usually a distinction between the major taxonomical groups is made, neither eutrophication models nor descriptive studies of lake phytoplankton often go down to the species level, except when one species dominates, as in the cases described for cyanobacteria. The reason for lumping species is obvious. The algal community of the average lake consists of hundreds of different species, and dynamics at the species level are usually very erratic (Cottingham, 1996).

In a classical paper entitled 'The paradox of the plankton', Hutchinson (1961) drew attention to the fact that the high diversity of phytoplankton is really remarkable, as there seems not much room for niche specialization in this relatively homogeneous environment where everyone is competing for a few limiting nutrients and light. Indeed, simple competition models suggest that the number of species that can coexist in equilibrium can not be greater than the number of limiting resources unless additional mechanisms are involved. Hutchinson already offered an outline of potential explanations of his paradox. Importantly, he suggested that, in general, the plankton community might not be in equilibrium at all.

Causes of non-equilibrium dynamics

Although, with this non-equilibrium argument, the issue of Hutchinson's paradox may seem solved, the question remains what actually drives the non-equilibrium dynamics. The continuous variation in environmental conditions due to the seasonal cycle and less predictable factors like the change in weather and hydraulic conditions is the most obvious explanation (Padisák *et al.*, 1993).

As pointed out by Sommer (1991) and Reynolds (1993) the seasonal succession of algal species is comparable in many aspects to succession in terrestrial vegetations, although the time scales differ widely. The typical generation time of algae is about a thousand times shorter than that of terrestrial plants. Therefore, one summer in plankton dynamics is comparable to many centuries of terrestrial succession. In fact, Reynolds (1993) argues that what happens between two winters in plankton is comparable to what happened since the Weichselian glaciation period in temperate forests. Indeed, there are remarkable similarities between seasonal succession in algae and the successional patterns described for terrestrial plant communities. The 'colonizers' that start off the successional sequence are small rapidly growing species, while the species that dominate at the end of the succession in summer are large, shade-tolerant algae that grow slowly, but are well able to conserve biomass and nutrients. The sequence of algal groups that appear in the course of the seasonal successional depends on aspects like lake depth and nutrient status. Although there can be differences from year to year, the overall pattern of biomass and succession of dominant groups is more or less predictable in most lakes (Sommer *et al.*, 1986).

On top of the regular annual cycle driven by the gradual change of temperature and light during the year, there is a continuous weather related 'disturbance'. Meteorological events like heavy rainfall, hot weather periods and stormy days can have a pronounced impact on hydraulics, water temperature and nutrient supply. Such short-term variability can be thought of as setting back succession, and thus preventing one species from outcompeting the rest. Indeed a fluctuating nutrient supply suffices to prevent equilibrium conditions leading to competitive exclusion in the laboratory (Sommer, 1984; Sommer, 1985), and also in real lakes, weather related disturbances are thought to be important in keeping algal communities diverse and dynamic (Padisák *et al.*, 1993).

It is usually thought that in the absence of any externally imposed disturbance the algal succession should in one or two months lead to a stable state in which most species have been outcompeted by one or a few dominants: 'undisturbed successions should eventually approach competitive exclusion and ecological equilibrium' (Reynolds *et al.*, 1993). However, laboratory experiments show that even in the absence of any external variation, multi-species planktonic systems can show erratic fluctuations and stay diverse for years (Kersting, 1985). More than likely, these complex dynamics are the result of interactions between the species, and should therefore be classified as 'deterministic chaos' (Scheffer, 1991b). Consequently, what we see in real lakes may well be the behaviour of an intrinsically chaotic system in a fluctuating environment. It may be argued that in the end there is not much difference between intrinsic chaos or the effect of fluctuations in the environment, since for all practical purposes the result is just noise. Conceptually, however, the phenomenon of intrinsic chaos has important theoretical implications: first, the final state ('asymptotic regime') to which a chaotic system settles in the absence of any perturbation is a so-called strange attractor. Simulations with most dynamical systems that have been studied in the past tend to a stable equilibrium point ('point attractor') or a regular cycle ('cyclic attractor'). A chaotic system, however, tends to a state of continuous change in which the same pattern is never exactly repeated ('strange attractor'). A second important feature of a chaotic system is that small differences in initial state blow up exponentially with time. This implies that the long-term behaviour is fundamentally unpredictable. Even if we would exactly know the rules that govern the plankton community, the final result remains unpredictable, because we can never precisely determine the current state and, even if we could, the slightest perturbation has huge effects on the long term. Thus if planktonic systems are indeed chaotic, the discussed weather effects will tend to blow up with time, and predictability at the species level seems unlikely even under constant conditions.

Reasons to expect chaotic dynamics

The idea that the dynamics of natural communities are intrinsically chaotic stems mainly from the results of analyses of simple models. It has been shown that chaotic dynamics can arise from a variety of trophic interactions (Fig. 3.24).

Although all of these interactions are potentially seeds of chaos, models for each of them only produce chaotic behaviour for a restricted range of parameter settings. Therefore, we cannot infer much from these observations without further information on the specific conditions that lead these interactions to behave chaotically. Going into the details of this for any specific model appears not to be very illuminating, but there is a crucial generic rule to be learned from physics in this context: systems that contain interacting oscillators can easily show intrinsically chaotic dynamics (Rogers, 1981). As zooplankton species tend to show strong demographic cycles, oscillators may be considered abundant in plankton communities. Obviously, these zooplanktonic oscillators are coupled since there are large overlaps in food among the different species (Brooks and Dodson, 1965; Demott, 1982; Boersma, 1995). Hence, it seems reasonable to expect plankton dynamics to be intrinsically chaotic.

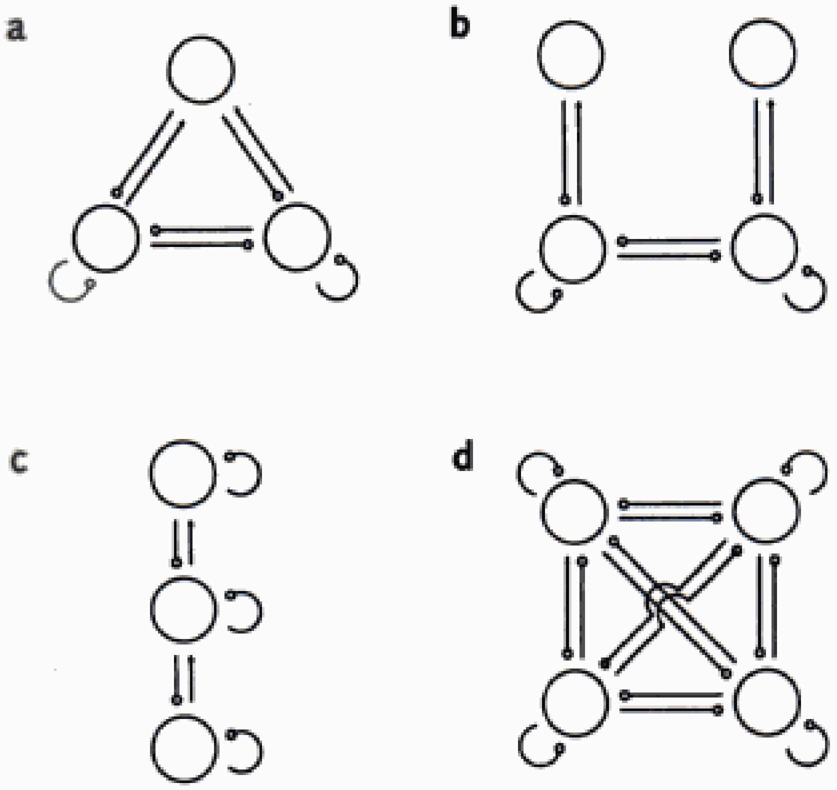


Fig. 3.24 Some interaction structures for which simple models have been demonstrated to produce chaotic behaviour: (a) a consumer exploiting two competing preys, (b) two consumers exploiting prey that compete, (c) a carnivore on top of a simple consumer–food system, (d) a network of at least four competing species. From Scheffer (1991b).

The last interaction scheme presented in Fig. 3.24 suggests an additional source of chaos. Even in the absence of consumers, a network of competing species can behave chaotically. The minimum number of interacting populations required in this case, if biologically reasonable parameter settings are to be used, is four (Arneodo *et al.*, 1982). Although a full fledged strange attractor can be produced for the four species case, the chaotic behaviour appears to be rather fragile (Scheffer, 1991b). The attraction basin of the strange attractor is limited so that a disturbance might easily kick the system out of its chaotic behaviour in which case it degenerates into a stable one-species case. Furthermore, the chaotic behaviour is easily lost if parameters are modified. Therefore, it does not seem very likely that a system like this will display chaotic behaviour in the real world. It has, however, been proved that competitive interactions of five and more species can lead to any type of behaviour including chaos, and that complex dynamics become more likely if many species are involved (Smale, 1976). Obviously, the number of algal species in an aquatic system is generally much larger, and it might therefore well be that even if there is no detectable impact of zooplankton, algal communities can behave chaotically.

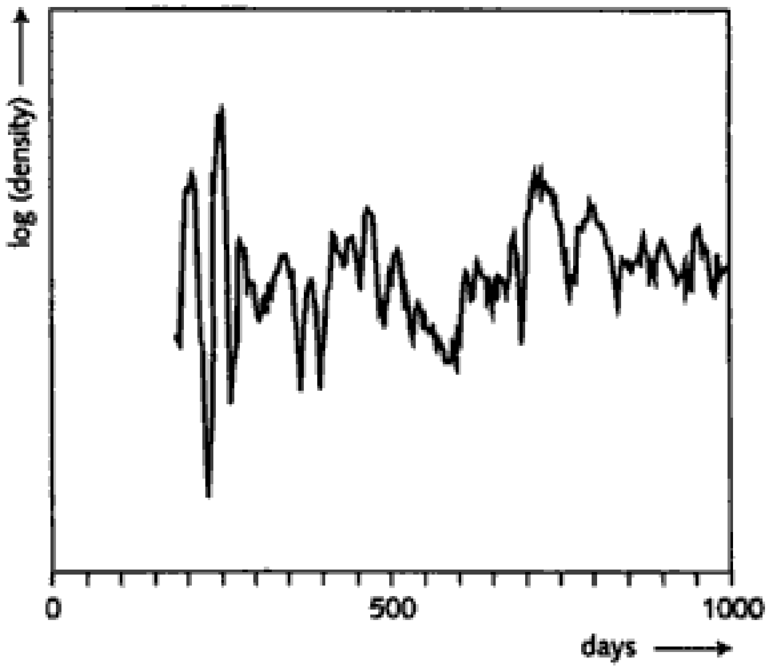


Fig. 3.25 Fluctuation of total particle density in the autotrophic compartment of a micro-ecosystem over a period of 100 days. Redrawn from Ringelberg (1977).

This hypothesis is supported by observations on small aquatic model ecosystems ('micro-ecosystems') that have been kept undisturbed in the laboratory for as long as 10 years (Kersting, 1985). Basically these micro-ecosystems consist of a phytoplankton compartment, a zooplankton compartment and a decomposition compartment, connected by a continuous circular water flow. Apart from a few perturbations which are unavoidable over such long time periods, temperature and light are kept constant and the systems remain closed. Nonetheless, these systems typically do not settle to a stable state, but instead keep exhibiting irregular dynamics throughout the whole observation period (Fig. 3.25).

There are strong indications that the oscillations measured in the algal compartment result only from interactions within this part of the system. The outflow is continuous, as is the phosphate concentration of the inflow (Ringelberg, 1977). Therefore, competition seems the most likely cause of the fluctuations in this small multi-species algal community. This view is supported by the observation that on rare occasions when such a system collapsed to a one species dominated state, the fluctuations disappeared (Kersting, pers. comm.). In such stable monocultures blue-green algae were invariably the winners. Note that this is remarkably well in line with the observation discussed in the former section that in real lakes, blue-green algae dominated states tend to be almost monocultures, and typically show very stable seasonal dynamics.

In summary, it seems likely that real world algal communities are intrinsically chaotic. In addition, they are subject to environmental stochasticity, and the effects of the latter may be expected to be magnified rather than damped by the interactions within the community due to the sensitivity to initial conditions characteristic of chaotic systems. It is therefore not surprising that algal dynamics are usually highly erratic at the species level (Cottingham, 1996), and predictability on this level of detail seems unlikely. Nonetheless, as explained in the previous sections, the effect of environmental factors on total algal biomass and dominance by cyanobacteria can be predicted relatively well.

4 Trophic cascades

A strong reduction of the fish stock usually leads to a marked increase in water fleas which graze down phytoplankton biomass to a low level (Shapiro and Wright, 1984; Van Donk *et al.*, 1990; Meijer *et al.*, 1994a). Also, an increase in piscivorous fish can reduce the planktivorous fish stock leading to an increase in water fleas and a decrease in algal biomass (Benndorf *et al.*, 1988; Hambright, 1994; Mittelbach *et al.*, 1995; Søndergaard *et al.*, 1997). This effect of fish through zooplankton on phytoplankton has been termed a cascading trophic interaction, as the impact cascades down the trophic levels in the food chain (Carpenter *et al.*, 1985). Since phytoplankton blooms are one of the main problems arising with eutrophication, using this trophic cascade seems an obvious way to enhance the effect of eutrophication control. The idea is appealingly simple: reduce the planktivorous fish and phytoplankton will be grazed by the increased *Daphnia* populations.

A generic black-and-white version of this cascade of trophic control has been worked out by Hairston, Smith and Slobodkin (HSS) (Hairston *et al.*, 1960) to produce a caricatural view of the world that was, nonetheless, an eye-opener in its early years: in the absence of consumers, plants are abundant and the world will be green. Introduction of uncontrolled herbivores would lead to a repression of plants, resulting in a desert-like world. Subsequent introduction of uncontrolled carnivores would, in turn, control the herbivores and make the world green again (Fig. 4.1).

This HSS hypothesis as well as the trophic cascade theory for lake communities have evoked considerable debate, as many ecologists felt that the potential for top-down control was greatly overestimated. The contrasting view was that the abundance of most organisms is determined by the availability of food rather than by predation. Interestingly, this controversy about the importance of top-down control was already a hot item more than a century ago. A good impression of the situation is given by the Italian scientist Lorenzo Camerano (1880). His description of the scientific controversies in those days and the theory he presents for explaining food-chain dynamics contain such striking similarities with more recent developments in the field that it is worthwhile to reflect on his work. About the top-down bottom-up controversy Camerano writes:

One of the most debated issues these days is that of animals which are useful and those harmful to crops [. . .] Naturalists are divided on this topic, as is

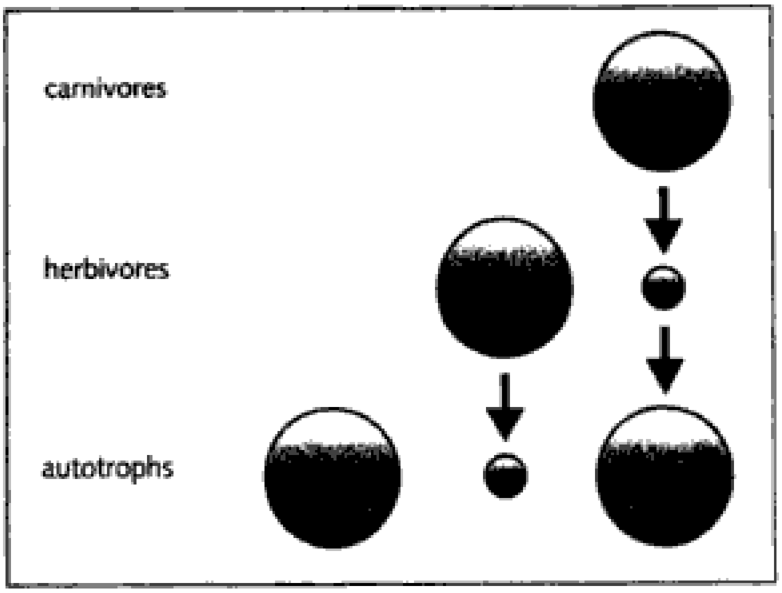


Fig. 4.1 Top-down control in food chains of different lengths as suggested by the HSS hypothesis, stating that top-down control of primary producers occurs only in food chains with an odd number of links (see text). From Scheffer (1997).

well known, in two categories. One category admits the usefulness of birds since these destroy insects which damage crops, and believes that by promoting increase of bird numbers the number of insects and the extent of the damage they do could be reduced. The other category, on the other hand, believes that the effect of birds is of little importance concerning the destruction of insects harmful to crops, and that the development of birds would not prevent the development of insects.

Naturalists belonging to the first category reason this way: the number of insects which cause damage to crops increases; that of birds, on the other hand, decreases. Now, birds feed to a great extent on insects; so if we increase the numbers of birds, the number of insects will decrease. The second category of naturalists think differently: the number of birds is high particularly in those places where insects are very abundant. When the number of insects decreases, so does the number of birds. Regions with low insect abundance also have few birds. The amount of insects in a region depends essentially on the amount of food found in it [. . .]. Hence, they conclude: birds play only a small effect in destroying insects which may damage crops. Well-known naturalists have argued in favor of either one of the theories mentioned. However, the number of naturalists who support the first theory is decreasing every day, while those in favor of the second one increase

Camerano also brings up several familiar sounding explanations for the fact that no clear insights on this topic had been obtained yet, such as the fact that applied science has been too sloppy ('an inclination to hasten to applications while disregarding data from pure science') and neglecting important feedbacks in the food web ('without taking into account the many and very important relations among different groups of animals'). He proceeds, presenting a theoretical framework for understanding food-chain dynamics that contains many of the key concepts of later ecological theory, for instance, the idea that consumer and food populations are in dynamic equilibrium: 'It is a well accepted fact by all that animals and plants develop in direct proportion to the available food. From this it follows that no species, be it carnivore or herbivore, can develop beyond a certain limit which, if surpassed, would destroy the source of its own nourishment. Equilibrium broken by the excessive growth of either kind of animal, would again be reestablished.' Camerano explains in detail how the effect of disturbances on one trophic level will cascade through the food chain, the same idea that would provoke so much debate almost a century later (Hairston *et al.*, 1960), and describes how equilibrium will tend to be re-established through damped oscillations.

Camerano's work has been rediscovered only recently (by Jacobi and Cohen, see Camerano's reference) and apparently his systems ecology *avant la lettre* has not been appealing enough to the scientists of his days to create a school that kept the ideas alive. Much more influential were the simple mathematical models of species interactions presented about half a century later by Alfred Lotka (1925) and by Vito Volterra (1926). Ever since their contribution, these and later, more realistic minimal models have catalysed the understanding of the dynamics resulting from trophic interactions. Indeed, the dynamic results of 'eating and being eaten' are often rather intricate and in many cases simple models have provided the little push needed to grasp the full implications of consumer – food interactions intuitively. In this chapter such minimal models are used to explain some basic features of the interactions between phytoplankton, zooplankton and fish. The resulting insights serve as a basis from which more complex aspects of trophic relations such as size selective predation and predator avoidance strategies are discussed.

4.1 TOP-DOWN CONTROL OF PHYTOPLANKTON

Grazing by mussels

In shallow marine systems, bivalves are often the dominant filter feeders. This is not the case in freshwater lakes, although there are exceptions. In the New Zealand Lake Tuakitoto, for instance, a local mussel species (*Hyridella menziesi*) was estimated to filter the lake water once every 32 hours and reduce the phytoplankton standing crop by as much as 90% (Ogilvie and Mitchell, 1995). Most examples of intensive bivalve filtration in lakes come from shallow waters in the United States that have been recently colonized by the zebra mussel *Dreissena polymorpha* (Fig. 3.13). Although other bivalve invaders such as the Asiatic clam *Corbicula fluminea* have had considerable impacts on the receiving communities, the vigour of the zebra mussel invasion of the American continent has been unsurpassed. An overview of the abiotic and biotic impacts of the invasion is presented by MacIsaac (1996). Soon after the first occurrence the species started to cause an extensive 'fouling' of hard substratum such as rocks, buoys and docks, and economically more importantly, water inlets, trash bars, steam condensers, gauges and other vital parts of power plants.

Massive populations of *Dreissena* can have a marked effect on algal biomass and the concentration of other suspended solids in shallow water. This is illustrated by conspicuous increases of transparency and drops in chlorophyll-a concentrations following the invasion of lakes or bays by zebra mussels. In the south part of the western basin of Lake Erie, for instance, phytoplankton concentrations dropped by almost an order of magnitude compared with the situation before the *Dreissena* invasion, and Secchi-depths increased by 100% (Holland, 1993). Secchi disk transparency in Lake St. Clair increased from 0.5–1.5 m before the zebra mussel invasion to 1.8–2.8 m in 1990 when mussels had become abundant (Griffiths, 1992). In Saginaw Bay, Lake Huron, mean Secchi-depth increased from 1.3 m when the first mussels were observed to 2.7 m the next year when maximum mussel density was five times higher already (MacIsaac, 1996).

The potential of *Dreissena* to clear up the water column has been tested experimentally in The Netherlands (Reeders *et al.*, 1992). Mussels ($540\,m^{-2}$) were added to one of two adjacent hypertrophic ponds. As a substratum, wire netting was added to the pond, as the soft muddy sediments were unsuitable for survival of the mussels. Before the manipulation mussels were not found in the ponds and severe cyanobacterial blooms usually developed in summer. During the subsequent year Secchi-depths in the mussel pond were consistently higher than those in the control pond (Fig. 4.2). Cyanobacterial blooms did not occur and algal biomass was reduced to approximately half of that in the control situation.

Zebra mussels are able to filter out particles of a large size range. Only part of the retained particles are really ingested. Unpreferred items such as large diatom cells and inorganic sediment particles are enveloped in mucus and expelled as pseudofecal pellets. The mussel induced changes in western Lake Erie suggest that all major phytoplankton taxa, including large colonial forms, are equally vulnerable to *Dreissena* filtering (Nicholls and Hopkins, 1993). Even small zooplankters (including *Dreissena* larvae) are ingested by the mussels (MacIsaac *et al.*, 1991). Indeed, the densities of rotifers and small copepods are often found to decline following a *Dreissena* invasion (MacIsaac, 1996). However, since mussels and zooplankton also compete for food, it is difficult to determine how much of the observed decline in zooplankton is due to ingestion by mussels.

All examples of strong *Dreissena* impact on plankton are from shallow relatively well mixed systems. In deeper water the effect of filtration seems

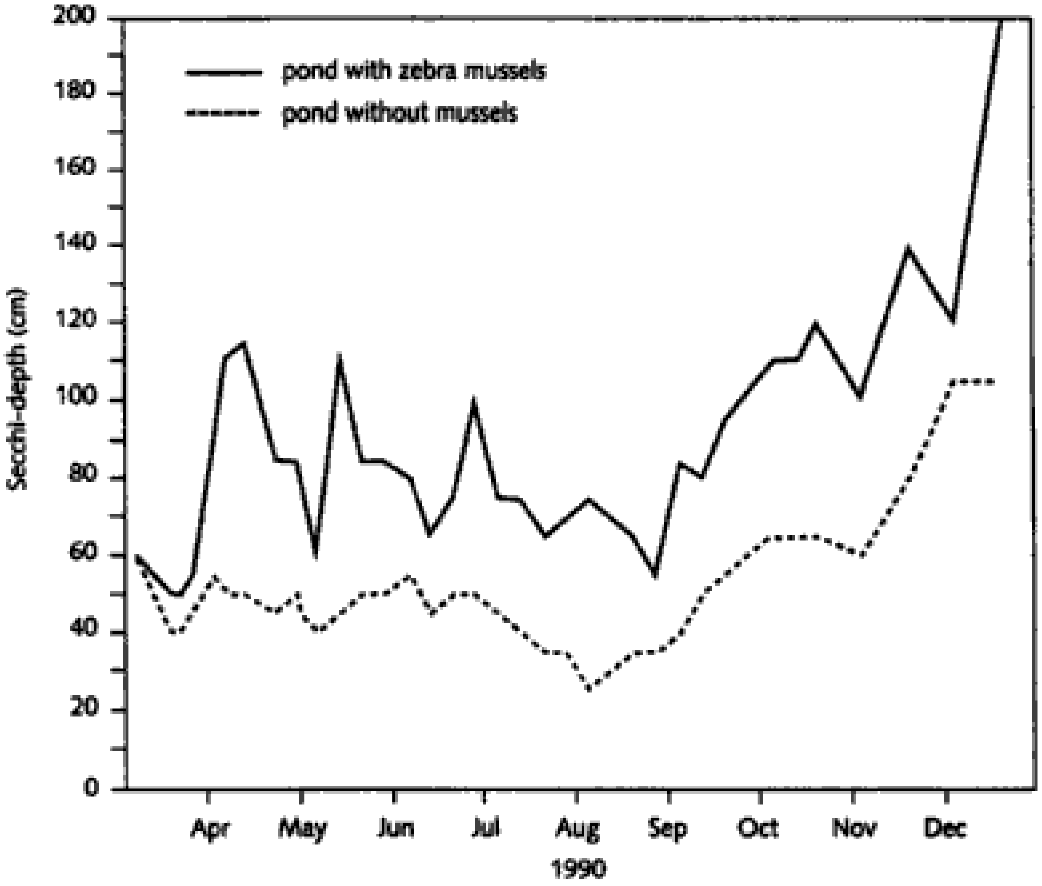


Fig. 4.2 Changes in Secchi-depth over a 1-year period in experimental ponds with (treated) and without (reference) zebra mussels. From Reeders *et al.* (1992)

less likely to affect transparency throughout the water column. The increase in Secchi-depth associated with massive *Dreissena* populations is about a factor 2 in the cited cases. Although zooplankton grazing can cause more spectacular increases in transparency, the effect of zebra mussel grazing is less ephemeral than that of the often short-lived outbreaks of *Daphnia*. Since, in addition, zebra mussels can filter out particles of a much larger size range than *Daphnia*, research has been done to find ways of stimulating zebra mussel populations as a possible aid in reducing turbidity of shallow lakes (Reeders and Bij de Vaate, 1990). In practice, it appears that lack of suitable hard substrate prevents the species from becoming abundant in many of the European turbid shallow lakes. The continuous resuspension and sedimentation in unvegetated shallow lakes buries the mussels except on safe sites like stones, poles, trunks or boats. When lakes clear up due to mussel grazing, aquatic vegetation can expand (Griffiths, 1992). Since macrophytes are a suitable substratum for settlement of juvenile mussels and help to prevent wave resuspension of sediments, this may further improve expansion possibilities for *Dreissena*. The resulting positive feedback may boost the changes observed after *Dreissena* invasions in shallow parts of American lakes (MacIsaac, 1996).

Several molluscivorous fish species can feed on zebra mussels (French, 1993) and when the water is not too deep, diving waterfowl are known to consume considerable quantities of mussels in some cases (Wormington and Leach, 1992; Hamilton *et al.*, 1994). Nonetheless, strong top-down control of *Dreissena* populations has not been reported. Lack of suitable substratum for settlement is probably a main restriction of *Dreissena* expansion in many shallow lakes.

The special position of *Daphnia*

Zooplankton is by far the most important group with respect to top-down control of algae in most lakes. It is a heterogeneous group of organisms. Expressed in individual numbers, small animals such as rotifers and copepods are usually the most important. They serve as food for fish larvae and carnivorous zooplankton like cyclopoid copepods, and feed on small algae and bacteria. Due to their restriction to small food particles, these animals cause a shift to larger phytoplankters rather than reducing total algal biomass. Although a reduction of total algal biomass by small zooplankters has occasionally been reported (Jeppesen *et al.*, 1990b), the only planktonic animals that can usually cause a significant decline in chlorophyll are large cladocerans (Brooks and Dodson, 1965; Pace, 1984). Species of the genus *Daphnia* (Fig. 4.3) are especially well known for their high potential grazing pressure. Their size allows them to feed on a wide array of algal species, excluding only the ones that form large colonies. Unlike many generalists in nature, they are also very efficient, reducing their food to levels that are too low to sustain most competitors (Brooks and Dodson, 1965). The densities of smaller species will, therefore, often drop when *Daphnia* populations are high. Due to this mechanism, possibly enhanced by mechanical interference, rotifer densities can sometimes be almost a mirror image of the fluctuations in *Daphnia* populations (Lampert and Rothhaupt, 1991).

Daphnia is thus an extremely successful competitor in the zooplanktonic community. Nonetheless, in many shallow lakes these animals are rare. Various factors may be involved in suppressing *Daphnia* populations. Several studies, for instance, indicate that suspended clay particles are detrimental for *Daphnia* feeding (Arruda *et al.*, 1983; Kirk and Gilbert, 1990; Kirk, 1991), that the animals do not grow and reproduce well when they forage on phosphorus-limited algae (Hessen, 1990; Sommer, 1992; Sterner, 1993), and that *Daphnia* hardly occurs in brackish water (Bales *et al.*, 1993; Jeppesen *et al.*, 1994). Also, large cyanobacterial colonies are usually not easily edible (Arnold, 1971; Schindler, 1971) and *Daphnia* growth can be severely reduced in their presence (Gliwicz, 1990; Gliwicz and Lampert, 1990), while toxic substances released by cyanobacteria have been shown to reduce filtering rates of daphnids by 50% or more (Haney *et al.*, 1994).

Fig. 4.3 Waterfleas (*Daphnia*) are small planktonic crustaceans that filter the water to obtain their algal food. They can reach densities of hundreds of animals per litre and reduce phytoplankton to low levels. However, waterfleas are also very vulnerable to fish predation and this explains their absence in many situations.

However, probably the most important weak point in the success formula of *Daphnia* is that they are very profitable food for planktivorous fish. This leads to their absence in many situations as explained further in the next section. Many studies illustrate the strong impact of *Daphnia* on algal biomass when they are released from fish predation. Sometimes long ice-cover in winter leads to massive fish-kills due to lack of oxygen. Such natural winter kills are typically followed by the occurrence of dense *Daphnia* populations that graze down algal biomass (Schindler and Comita, 1972; Haertel and Jongsma, 1982; Sarnelle, 1993). The same is observed after artificial strong reductions of the fish stock by means of fishing or rotenone treatments (Shapiro and Wright, 1984; Van Donk *et al.*, 1990; Meijer *et al.*, 1994a).

The potential of *Daphnia* to graze down algal biomass to very low levels is also illustrated by the spring clear-water phase that occurs in many lakes (Lampert *et al.*, 1986; Luecke *et al.*, 1990; Carpenter *et al.*, 1993; Rudstam *et al.*, 1993; Sarnelle, 1993; Hanson and Butler, 1994a; Townsend *et al.*, 1994; Jurgens and Stolpe, 1995). The details of this phenomenon are treated more thoroughly later, but the general scenario is easy to understand. The spring bloom of algae provides a wealth of food for *Daphnia*, allowing a high individual growth rate and reproduction. The population expands in a couple of weeks to a density at which its grazing capacity exceeds the algal production. As a result, the algal community collapses to a low level. During this phase the water can be spectacularly clear. This state of over-exploitation of algae does not last long. The condition of the *Daphnia* individuals deteriorates due to food shortage. The number of eggs per female decreases and reproduction practically stops. Finally the *Daphnia* population collapses and the algal community recovers. Obviously, this is a classic predator – prey cycle scenario, and indeed in laboratory populations such cycles tend to produce a steady oscillation (Pratt, 1943). Also, in the field a regular sequence of cycles is sometimes observed in the course of the summer, but often, young-of-the-year planktivorous fish will prohibit a next *Daphnia* outbreak after the spring peak.

In the following, a simple classic model of the *Daphnia* – algae relationship is presented and it is shown how its dynamics are affected by factors like the nutrient level and spatial heterogeneity. This minimal model will serve as a basis to explore the effects of fish and seasonality in later parts.

A minimal plankton model

Daphnia is not only a crucial organism for limnologists, it is also one of the most important test organisms in toxicology. Consequently, much is known about its biology and a large number of different models are available to describe its dynamics. At the simple end of the range are the modules used in classical eutrophication models (see Straškraba and Gnauck, 1985, for a review). Intermediate in complexity are the models that use size or age classes to take the demographic structure of the population into account (e.g. de Roos *et al.*, 1992). On the most elaborate side of the spectrum are the detailed models used in ecotoxicology that go down to the level of individual physiology (e.g. Kooijman 1986).

To explore some basic properties of the *Daphnia* – algae interaction we use a simple two-equation predator – prey model:

$$\frac{dA}{dt} = rA\left(1-\frac{A}{K}\right) - g_z Z \frac{A}{A+h_a} \qquad (1)$$

$$\frac{dZ}{dt} = e_z g_z Z \frac{A}{A + h_a} - m_z Z \quad (2)$$

The basic growth of algae (A) is logistic, but an extra term is added to account for the consumption by *Daphnia*. This consumption depends on the amount of *Daphnia* (Z) and its maximum consumption rate (g_z) and on the phytoplankton density. The latter dependence is formulated as a Monod function representing a simple saturating functional response with a fixed half-saturation value (h_a). The zooplankton population converts the ingested food into growth with a certain efficiency (e_z) and suffers losses due to respiration and mortality at a fixed rate (m_z).

This model or a similar one can be found in most ecological textbooks. Such simple predator–prey models have a long history of analysis and consequently much is known about their behaviour (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971; DeAngelis *et al.*, 1975; Murdoch and Oaten, 1975; Scheffer, 1991a). The traditional way to explore the properties of these minimal models is through analysis of the zero-isoclines. The formula of these isoclines is obtained simply by solving the above equations for zero growth ($dA/dt = 0$ and $dZ/dt = 0$).

The resulting formula for the algal isocline is:

$$Z^* = rA\left(1 - \frac{A}{K}\right)\frac{A + h_a}{g_z A} \quad (4)$$

The first part is really the productivity curve of the logistically growing algae while the second part is the inverse of the functional response of zooplankton. The height of the algal isocline ($dA/dt = 0$ in Fig. 4.4) at any point can be interpreted as the amount of zooplankton needed to consume exactly the production of the algae at that density, thus balancing their population growth to zero.

The logistic growth causes the isocline to be humped: at low algal densities the total productivity of the population is low and little grazing is needed to balance it, whereas at high algal densities productivity drops again because of competition and again little grazing is needed to keep it from growing further. The (inverse) functional response causes the isocline to be asymmetrical; the left-hand side is higher than the right-hand side. This is because more zooplankton can be tolerated at low algal densities when zooplankton can not gather food as effectively as at high algal densities.

The isocline of zooplankton ($dZ/dt = 0$ in Fig. 4.4) is simply vertical, as Z is eliminated from the equation:

$$A^* = \frac{h_a}{\frac{e_z g_z}{m_z} - 1} \quad (5)$$

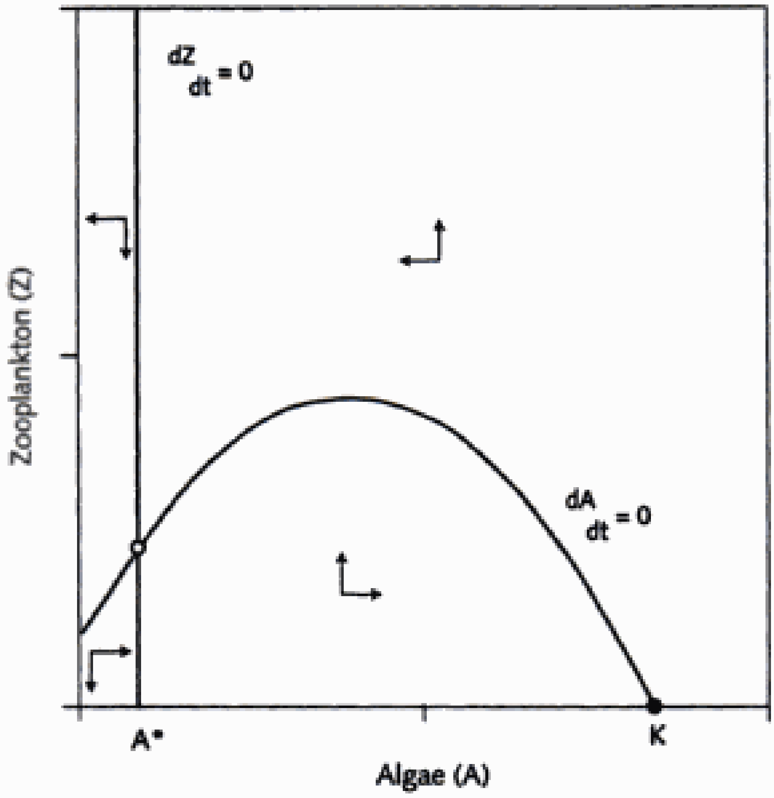


Fig. 4.4 Zero-growth isoclines of zooplankton (*dZ/dt* = 0) and algae (*dA/dt* = 0) derived from the model described in the text (Eqs. 49 and 50). These lines of zero growth divide the 'state space' into areas with positive and negative growth of the two populations (indicated by the arrows). Growth of the zooplankton population is positive only to the right-hand side of the vertical zooplankton isocline. Algal population growth is positive only in the area under the humped algal isocline. The intersection point of the isoclines represents an (unstable) equilibrium as growth of both populations is zero.

In biological terms, the reason for the vertical isocline is that there is no negative feedback of high population densities other than via the food in the model. Thus there is simply one fixed food density (A^*) at which the population gains just outbalance the losses.

The assumption that the consumers affect each other only through depleting food is probably quite realistic in the case of *Daphnia* (Slobodkin, 1954), but certainly not for all consumers. Consumer interference (mostly termed 'predator interference') can either be incorporated by modelling direct interactions between the animals (Rosenzweig, 1971; Gilpin, 1972) or by using a predator-dependent functional response (Beddington, 1975; DeAngelis *et al.*, 1975; Ruxton *et al.*, 1992; Abrams and Roth, 1994). A special case of predator dependence is the ratio dependent functional response (Arditi and Ginzburg, 1989). Although this formulation captures the essence of predator dependence in a simple way, its use has some serious theoretical problems (Abrams and Roth, 1994).

As explained in the previous chapter the isoclines of zero-growth divide the 'phase plane' (Fig. 4.4) into regions with positive and regions with negative growth of the populations. In this case algal growth is negative above the algal isocline and positive below it. Similarly, zooplankton growth is negative to the left of the vertical isocline and positive on the right-hand side. Intersections of isoclines are equilibria as growth of both populations is zero. Since on the axis the density of either of the populations is zero and thus its growth rate is zero, the axes are also (trivial) isoclines. Consequently, the origin and part of the intersections of isoclines with the axes are (trivial) equilibria.

In this case the intersection of the algal isocline with the x-axis is such a trivial equilibrium. Since zooplankton is absent, the logistic equation alone determines algal biomass and the algae equilibrate at carrying capacity (K). This trivial equilibrium is unstable. The system will not return to it if we add a little bit of zooplankton. Note that unlike in the competition model dis-

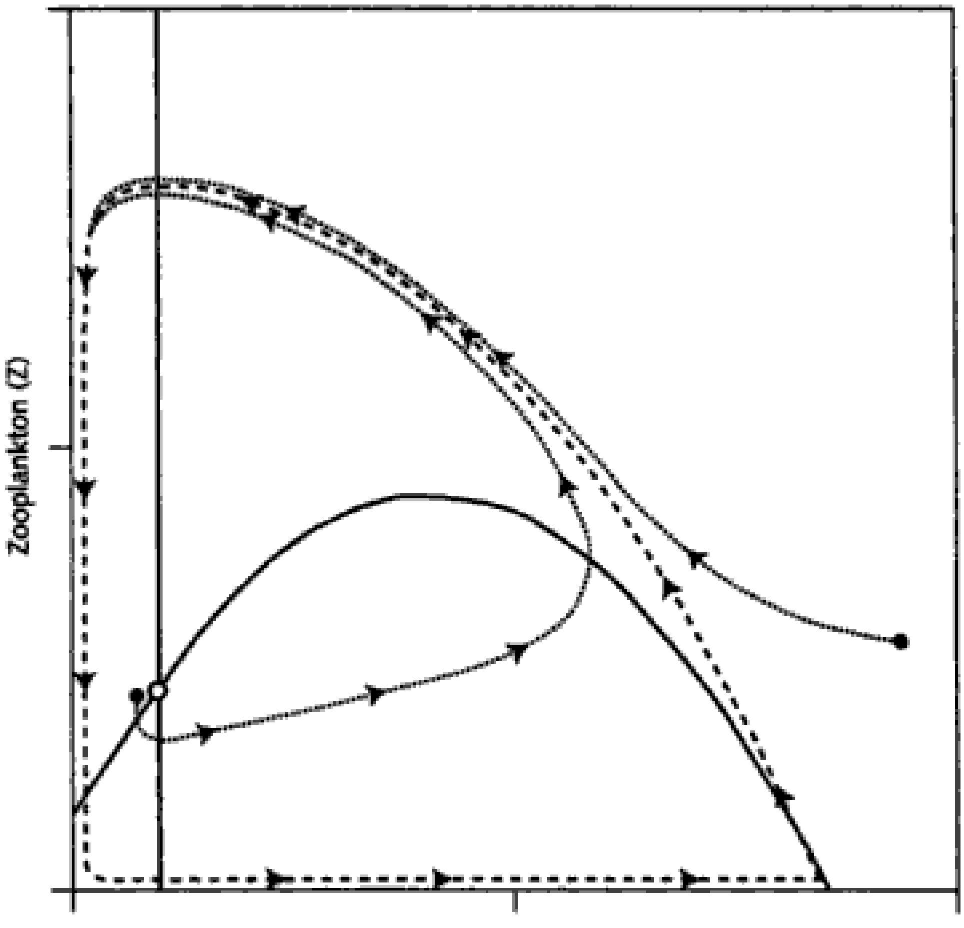


Fig. 4.5 Simulations (dotted) starting from any non-zero combination of zooplankton and algal density converge towards a cyclic path (dashed) around the unstable equilibrium point. This cycle is a stable attractor called a limit cycle. See text for further explanation.

cussed in the former chapter we have only one trivial equilibrium here. The zooplankton isocline does not intersect with the y-axis to produce a trivial equilibrium with only zooplankton present, for the obvious reason that they need food to sustain their population.

More interesting than the trivial equilibrium is the equilibrium at the intersection of the two isoclines. Like the one in the competition model, this intersection can be stable or unstable. In the depicted case the intersection point is an unstable equilibrium. It is, however, not a saddle as in the competition model. Instead, this equilibrium is a repelling point surrounded by a limit cycle. In a sense this limit cycle is now the 'equilibrium' of the system as it attracts all trajectories of simulation runs (Fig. 4.5).

Starting from a point close to the unstable focus the system spirals out until it reaches the limit cycle. Starting from any point outside the limit cycle the trajectory will spiral in towards the cycle. Once on the cycle, the system keeps moving along it. Because of the oscillations it is not correct to call the limit cycle an equilibrium. Instead, cycles and more complex attracting structures like torusses and strange attractors are called asymptotic regimes, as the system approaches them asymptotically if a simulation is continued for a sufficiently long time.

Biologically, the oscillations on the limit cycle can be understood as the result of overshoots due to a delayed response of the population density of zooplankton to the amount of available food. Starting at the part of the cycle close to the trivial equilibrium where algae are at carrying capacity, zooplankton grows and depletes its food to a level that is too low to support further growth and reproduction. As a result, the zooplankton population collapses to a level low enough to let the algal population expand to a high density again. The resulting good food condition allows a new expansion of zooplankton, and the cycle starts all over again. This is indeed what can happen in real populations, although there are of course many details such as competition between size classes and suppression of egg production that do not show up in this minimal model.

In the case of a vertical consumer isocline it can be proved that the intersection of the isoclines represents an unstable equilibrium surrounded by a limit cycle if the slope of the producer isocline at the intersection is positive (Rosenzweig and MacArthur, 1963). This rule implies that the equilibrium can be stabilized by changing the isoclines in such a way that the intersection moves to the right side of the hump. One way to do this is to make the consumer less efficient so that the food density needed to sustain its population (A^* in our case) increases, thus moving the consumers isocline to the right. The isocline equation (Eq. 5) shows that, in our model, this can be realized by decreasing the values of g_z or e_z, or increasing the values of h_a or d_z. The default values, however, represent the biology of *Daphnia* reasonably. It is, indeed, an efficient consumer that can deplete its food to low levels, and probably this is exactly the reason why these strong oscillations tend to occur. Therefore, we let the parameters characterizing

Daphnia as they are, and explore the remaining possibility of moving the intersection to the right side of the hump by means of changing the algal isocline.

The paradox of enrichment

The effect of nutrients on simple consumer – food systems are in some respects surprising. The first paper in which they were explored in detail was called 'paradox of enrichment' (Rosenzweig, 1971) and invoked strong reactions (McAllister *et al.*, 1972). It became a classic in ecological theory. To see the 'paradox' in our model, we mimic the effect of enrichment manipulating *K*. As argued in the previous chapter this is the suitable parameter to represent the nutrient content of the system in the logistic growth equation. Reducing *K*, the top of the hump moves to the left (Fig. 4.6).

When it passes to the left side of the zooplankton isocline the intersection becomes a stable equilibrium and the limit cycle disappears. If the nutrient level is low enough to let carrying capacity fall below the density

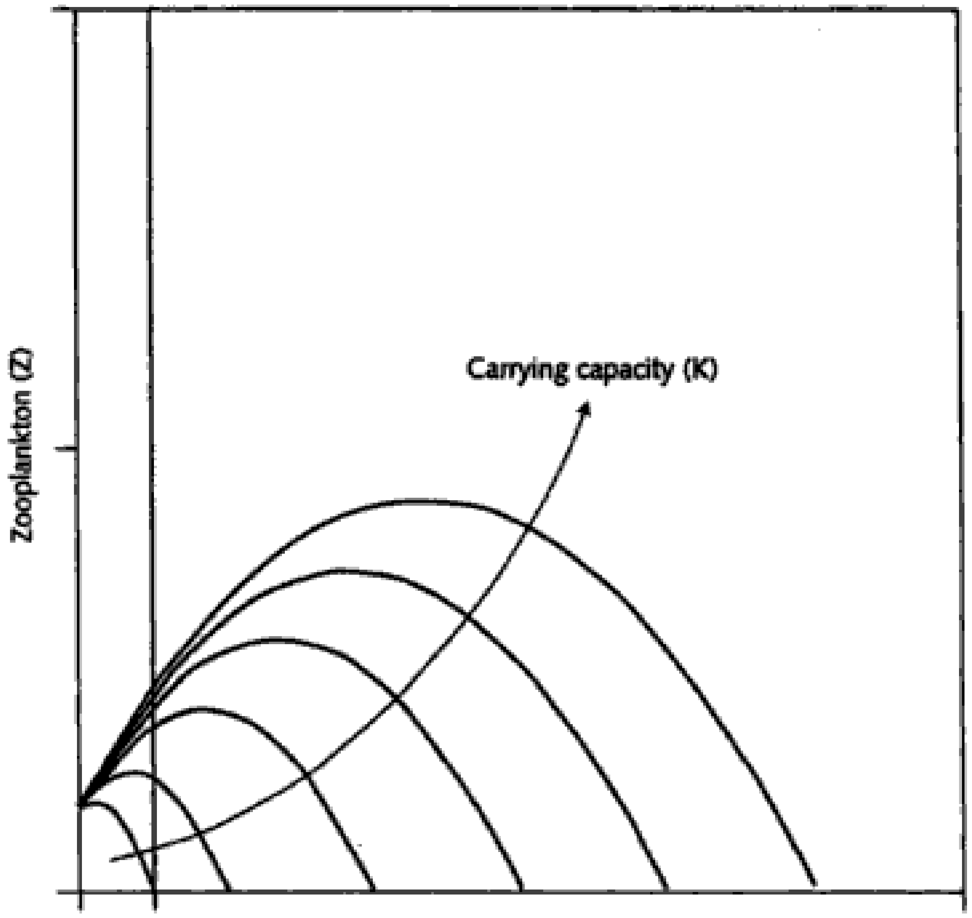


Fig. 4.6 The effect of nutrient enrichment (represented by an increase of algal carrying capacity, *K*) on the isoclines.

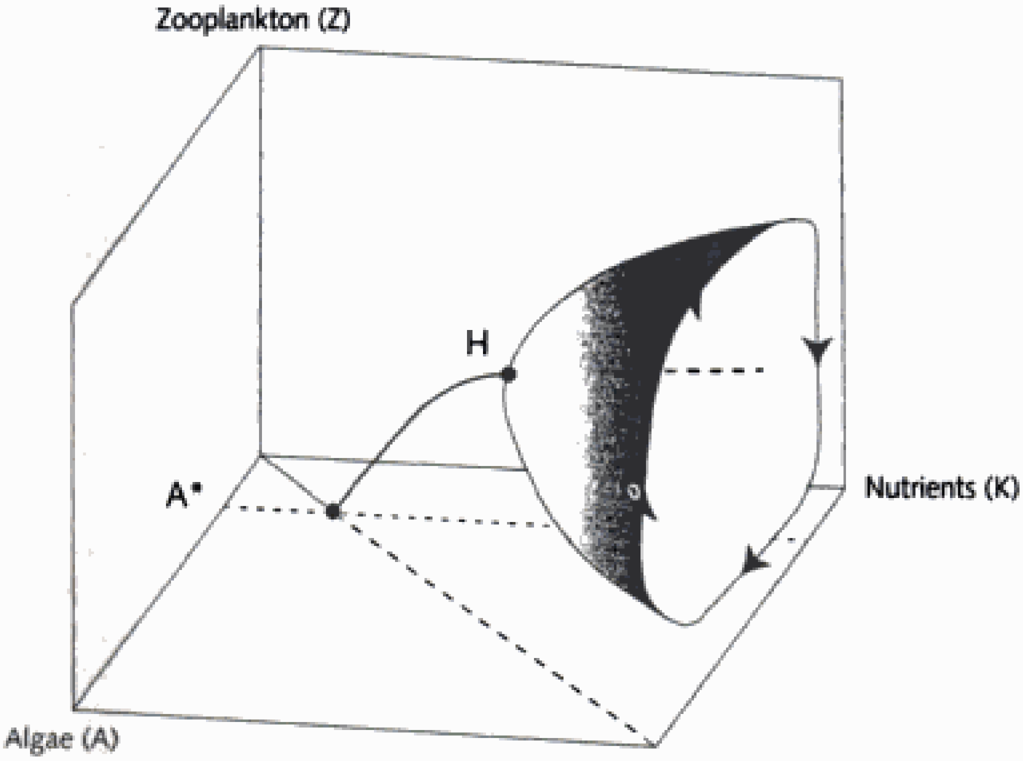


Fig. 4.7 Effect of enrichment (increasing *K*) on the equilibrium and limit cycle of the zooplankton–algae model. In the Hopf bifurcation point (*H*) the equilibrium point becomes unstable and the limit cycle evolves around it (see text for full explanation).

(A^*) needed to maintain zooplankton, the intersection disappears. Consequently, no equilibrium with zooplankton exists in such unproductive situations. Instead, the trivial equilibrium with only algae ($A = K$ and $Z = 0$) becomes stable. It has been argued that due to this effect food chains become shorter in unproductive environments in general, as the higher trophic levels are lost because of food shortage (Oksanen *et al.*, 1981). However, algal carrying capacity is usually far above the critical level to support *Daphnia*.

A remarkable consequence of the vertical isocline is that, as soon as zooplankton are present ($K > A^*$), the algal biomass does not increase with nutrients (mimicked by *K*) any more, until the point where the limit cycle occurs and things become more complex. Such a complete buffering of enrichment by zooplankton is usually not found in nature. In practice, both phytoplankton and zooplankton biomasses increase with nutrients (Sarnelle, 1992). As argued, a predator dependent functional response would make the zooplankton isocline non-vertical, and this would result in a more natural response to enrichment. Since in practice interference effects are not found at reasonable *Daphnia* densities, however, other factors should be responsible for this deviation between model predictions and field patterns. As pointed out later, spatial heterogeneity and predation by planktivorous fish are likely explanations.

Isoclines can be useful as a way of finding equilibria and, in some cases, like the one above, their shape can even indicate whether an equilibrium is stable or not. Nonetheless, the possibilities of isocline analysis are limited. The position of the cyclic equilibrium, for instance, can not be inferred from the isoclines. A more powerful and straightforward way to find out the effect of changing a parameter like *K*, is simply to look directly at what happens to the equilibria (Fig. 4.7).

Increasing the carrying capacity, starting from a very low level, algal density equals *K* as long as it is in its trivial equilibrium. As soon as the level needed to allow zooplankton growth is reached, the effect of increasing K is passed to this next trophic level. Zooplankton density increases while phytoplankton stays constant ($A = A^*$) until the limit cycle appears. More precisely, what happens in that point (*H*) is that the stable equilibrium 'bifurcates' into two other equilibria: a stable limit cycle and an unstable point equilibrium. Several types of such bifurcations are distinguished, depending on what kind of equilibria are involved. This particular type is called a 'Hopf bifurcation' despite the fact that authors other than Hopf had actually described it before him (Kuznetsov, 1995).

The destabilizing effect of increasing *K*, causing large cycles in which the population of both predator and prey pass through periods of low numbers, led Rosenzweig (1971) to infer the paradoxical prediction that enrichment might actually work adversely for some species as it increases the risk of extinction. McAllister and co-workers (1972), however, immediately responded that fertilization experiments conducted by them in lakes did not destabilize the plankton at all. Indeed, together with the curious fact that the algae do not respond to enrichment, the extremely large amplitude of the limit cycles is one of the most conspicuous deviations of the model behaviour from real plankton dynamics. For reasonable values of *K*, the

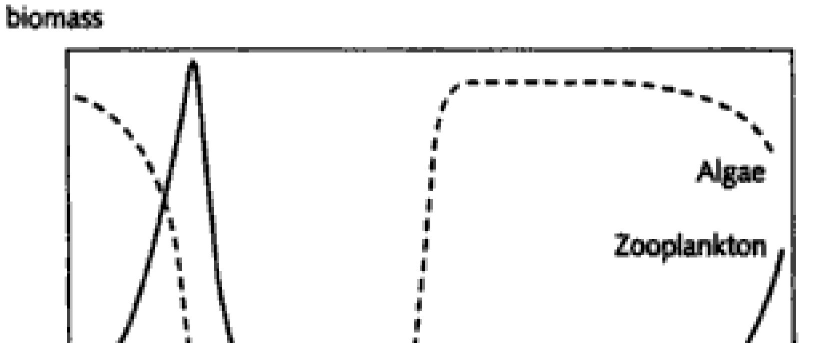


Fig. 4.8 On the limit cycle of the classical minimal model extreme oscillations of zooplankton and algal populations occur.

cycles pass very close along both axes of the phase plane (Fig. 4.5), corresponding to periods during which zooplankton or phytoplankton reach densities that are close to zero. Although, natural populations and laboratory populations of *Daphnia* do tend to oscillate, their cycles typically have a much smaller amplitude. Also, the period of the model oscillations produced by the model is unrealistically large, almost half a year as opposed to 20–45 days in real populations (McCauley and Murdoch, 1987). The problems of the large cycle and the low frequency are in fact closely related. The episodes in which either of the population densities becomes almost zero stretch the cycle period (Fig. 4.8) because recovery from the near extinctions is very slow. In the following sections it is shown how the presence of alternative food, inedible algae, spatial heterogeneity and fish modify the above patterns to produce a more realistic view of *Daphnia* dynamics.

Stabilizing mechanisms

In the ecological literature about the mechanisms that can stabilize predator – prey relations, spatial heterogeneity and prey switching are probably the two most abundant topics. In deep lakes *Daphnia* does not really have the option of switching to different food, as it has to rely solely on the seston in the epilimnion. In vegetated shallow lakes, however, there are indications that *Daphnia* feeds on detritus accumulated at the bottom when phytoplankton densities are low (Jeppesen *et al.*, 1996). Although this is probably a relatively low-quality food source it may keep the populations from collapsing completely, thus stabilizing the system. Unfortunately, little information is available on the diet selection of *Daphnia* in the field, but the idea that the presence of detritus as an alternative food source should stabilize *Daphnia* populations seems reasonable.

Another potentially stabilizing factor is the presence of inedible algae such as large cyanobacterial colonies. Obviously, unravelling the subtleties of the interaction of competing algal groups with grazers is rather complicated. However, put simply, there are two reasons why the presence of inedible algae may be stabilizing: (1) they compete for resources with the edible algae, thus lowering the ‘effective carrying capacity’, and (2) inedible species reduce the efficiency with which zooplankton can consume the edible algae (Gliwicz and Lampert, 1990). In terms of isoclines, as explained earlier (1) moves the top of the humped algal isocline to the left, while (2) moves the vertical zooplankton isocline to the right. Since the oscillations disappear when the top in the algal isocline is on the left side of the zooplankton isocline (1) and (2) should thus be expected to stabilize *Daphnia* dynamics. The potentially stabilizing effect of inedible algae has been demonstrated with simple models (Kretzschmar *et al.*, 1993; Gragnani, 1997), but has not been shown experimentally yet.

One of the most frequently mentioned topics in the literature about stabilization of predator – prey dynamics is spatial heterogeneity. Using models many authors have shown a stabilizing effect of partial isolation of habitat patches (Gurney and Nisbet, 1978; Nisbet *et al.*, 1989). Other models have been formulated to show that predator – prey oscillations are stabilized when the predators aggregate in patches with high prey density (Hassel and May, 1974). Stabilization can also be achieved by limiting the speed of movement of individuals in individual-based predator – prey models (De Roos *et al.*, 1991). All of these mechanisms are in fact closely related. The space outside the patches where the predator is concentrated can be considered a 'partial refuge' where part of the prey population can escape predation. As explained in the next section, spatial heterogeneity is likely to be an important reason why the extreme model oscillations with near extinctions of both algae and *Daphnia* are not found in the field.

Implications of spatial heterogeneity

The distribution of *Daphnia* in lakes is usually far from homogeneous. The animals are often concentrated in dense swarms (Kuenne, 1925; Colebrook, 1960; Klemetsen, 1970; Johnson and Chua, 1973; Malone and McQueen, 1983; Jakobsen and Johnsen, 1987). In addition, zooplankton in deep lakes usually exhibit diel vertical migration, concentrating in deep water layers during the day and at the surface during night (Gliwicz, 1986; Lampert, 1992; Brancelj and Blejec, 1994). In shallow lakes a similar diel migration is found. During the day the animals concentrate in vegetation stands, and at night they swim out to the adjacent open water (Timms and Moss, 1984; Lauridsen and Buenk, 1996).

With respect to food competition, such aggregation should be unfavourable. Indeed algal densities can be considerably reduced in zooplankton swarms (Tessier, 1983; Jakobsen and Johnsen, 1987). It has been shown that animals are able to swim actively away from low food concentrations (Cuddington and McCauley, 1994; Neary *et al.*, 1994). Therefore, one would expect a reason why daphnids nevertheless aggregate. Reduction of predation loss is generally considered the driving force. This has been discussed extensively with respect to swarm formation (Heller and Milinski, 1979; Jakobsen and Johnsen, 1987; Young *et al.*, 1994), and it has been demonstrated that the presence of planktivorous fish drives the diel migration to deep water (Gliwicz, 1986; Leibold, 1990; Loose and Dawidowicz, 1994) and vegetation stands (Lauridsen and Lodge, 1996).

To see the potential implications of this aggregation on safe sites for the dynamics of *Daphnia* and algae we depart from the same model. Obviously, including spatial dynamics in detail is rather complex. A way to simplify while preserving the essential feature of spatial aggregation is to consider *Daphnia* to be aggregated in one part of the lake that occupies a fraction

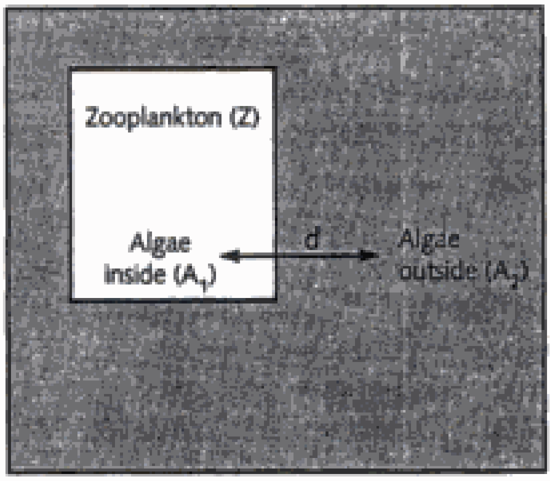


Fig. 4.9 Simple spatial structure assumed in the spatial version of the zooplankton algae model (Eqs. 5.3, 5.4 and 5.5). Zooplankton (Z) is confined to one part of the space. Their algal food grows both inside (A_1) and outside (A_2) the zooplankton compartment, and diffuses (d) between both parts of space. From Scheffer and De Boer (1995).

q of the total volume, while phytoplankton are present homogeneously throughout the lake. Thus we have two imaginary compartments (Fig. 4.9).

In the first one *Daphnia* grazes down the local subpopulation of algae (A_1), while in the second one the algae (A_2) are predation-free. Between the compartments we define an exchange of a fraction d of the lake volume per day. This can be thought of as water with algae moving through the areas where *Daphnia* is concentrated, but it could equally represent the effect of the movement of the aggregations of *Daphnia* through the lake. The resulting spatial model (Scheffer and De Boer, 1995) becomes:

$$\frac{dA_1}{dt} = rA_1\left(1-\frac{A_1}{K}\right) - g_z Z\frac{A_1}{A_1+h_a} + \frac{d}{q}\left(A_2 - A_1\right) \tag{6}$$

$$\frac{dA_2}{dt} = rA_2\left(1-\frac{A_2}{K}\right) - \frac{d}{1-q}\left(A_2 - A_1\right) \tag{7}$$

$$\frac{dZ}{dt} = e_z g_z Z\frac{A_1}{A_1+h_a} - m_z Z \tag{8}$$

The combined effect of the mixing rate (d) and the fraction of the lake occupied by *Daphnia* (q) on the dynamics of the model can be summarized in a bifurcation diagram (Fig. 4.10).

Since this does not show what the oscillations look like there is a separate plot displaying the corresponding dynamical patterns (Fig. 4.11).

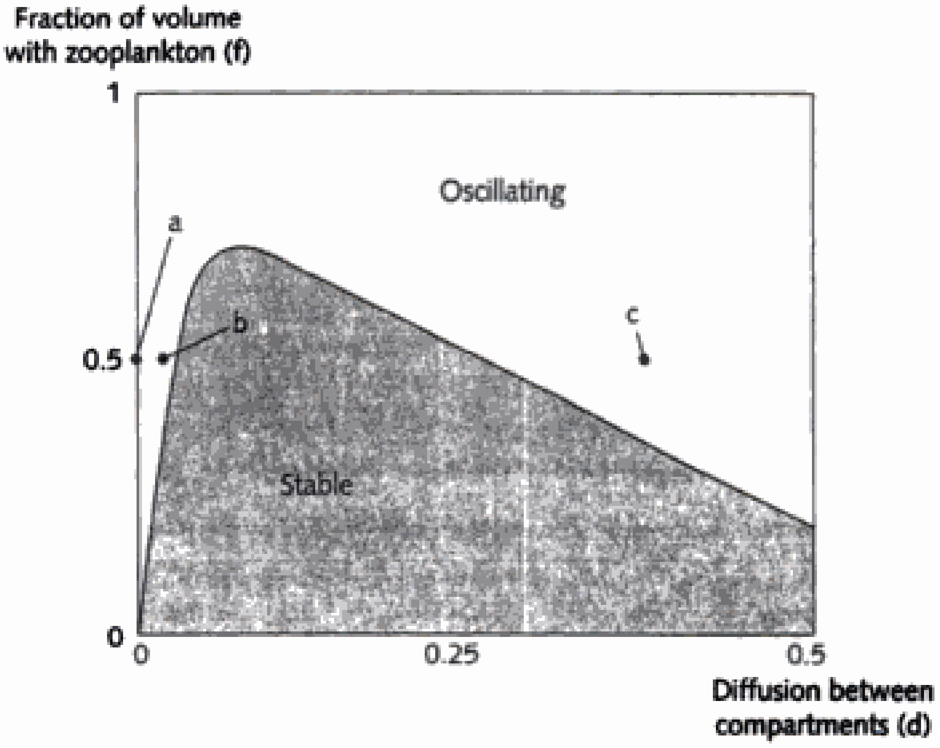


Fig. 4.10 Bifurcation graph of the spatial zooplankton algae model showing the effect of the fraction of the volume occupied by zooplankton (q) and the diffusion rate of algae between the two parts of space (d) on the behaviour of the model. The curve represents the Hopf bifurcations and defines the borderline in parameter space between oscillatory and stationary behaviour. A stable equilibrium state exists when the grazed fraction of the space (q) is sufficiently small and the exchange rate (d) is intermediate. Stabilization becomes increasingly difficult if zooplankton occupies a larger part of space. The parameter settings for which the behaviour is shown in Fig. 4.11 a, b and c is indicated. From Scheffer and De Boer (1995).

The result of no mixing at all (a) is trivial. We simply have the ungrazed algae at carrying capacity while the other population oscillates with *Daphnia* in exactly the same way as before. A slight mixing (b) is sufficient to change the dynamics in the grazed part completely. The system still oscillates, but the amplitude of the cycles is reduced, and the period falls nicely in the range reported from the field. The algae in the ungrazed part now show a mild oscillation too, driven by an exchange with the grazed part.

A further increase of mixing stabilizes the system completely. Recalling the bifurcation in the paradox of enrichment story (Fig. 4.7), the system now goes backward through a Hopf bifurcation, implying that the limit cycle collides with an unstable point to produce a stable point equilibrium.

Increasing the mixing rate further, the system passes through another Hopf bifurcation and becomes oscillatory again (c). Intuitively this can be easily understood, as we approach the limit case of a completely mixed volume again. The dynamics of both algal subpopulations become increas-

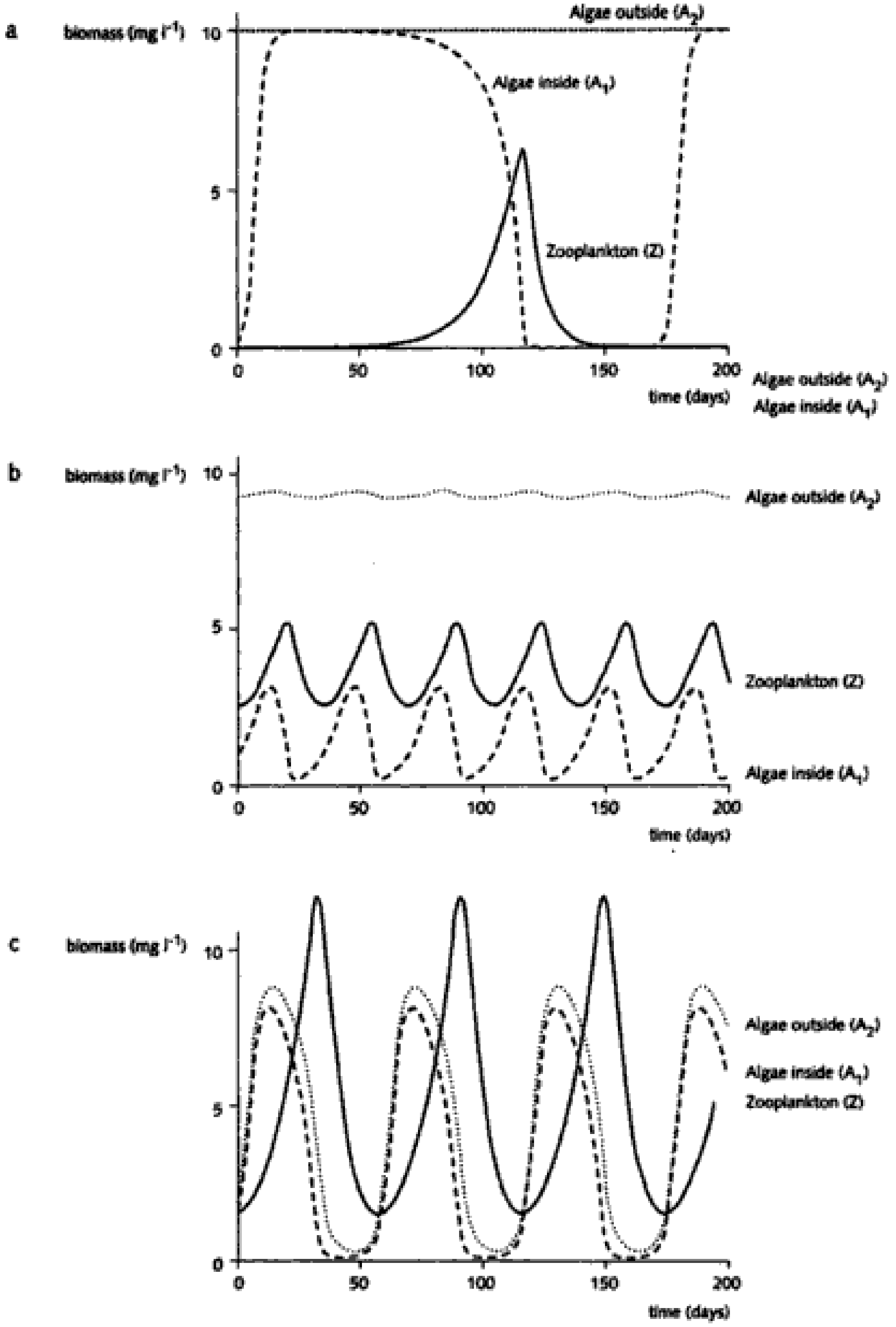


Fig. 4.11 Time plots showing the behaviour of the spatial plankton model for the parameter settings indicated in Fig. 4.10. Parameters: $q = 0.5$ and $d = 0.0$, 0.02, and 0.4 for panels a, b and c, respectively. From Scheffer and De Boer (1995).

ingly alike, and the density of *Daphnia* in its refuge becomes very high due to the inflow of food from the rest of the lake.

Biologists usually describe the dynamics of populations by sampling at various points at a lake, and averaging the samples. In the model we can do the same by averaging the densities of algae (A_T) and zooplankton (Z_T) over the total volume:

$$A_T = qA_1 + (1-q)A_2 \qquad Z_T = qZ \tag{9}$$

The dynamics of such spatially averaged population densities can be puzzling at first sight. The relative amplitude of *Daphnia* oscillations will remain the same: the overall concentration of *Daphnia* is reduced because we take the average with the empty part, but rescaling the axis there is no visible difference. The relative amplitude of the algal fluctuations, however, declines if we average with the ungrazed part. Especially if the ungrazed part is large and little affected, the oscillations in the *Daphnia* occupied area cause only a ripple in the overall average algal density (Fig. 4.12). As sampling errors can be far greater than this ripple, the field observations will show the illusory situation of an oscillating predator with a stable prey. Indeed this pattern is sometimes observed in *Daphnia* – algae dynamics and has puzzled aquatic ecologists. McCauley and Murdoch who published an extensive review of *Daphnia* dynamics in the field (1987) found this pattern 'sufficiently odd' to check it thoroughly, but had to conclude that it was not

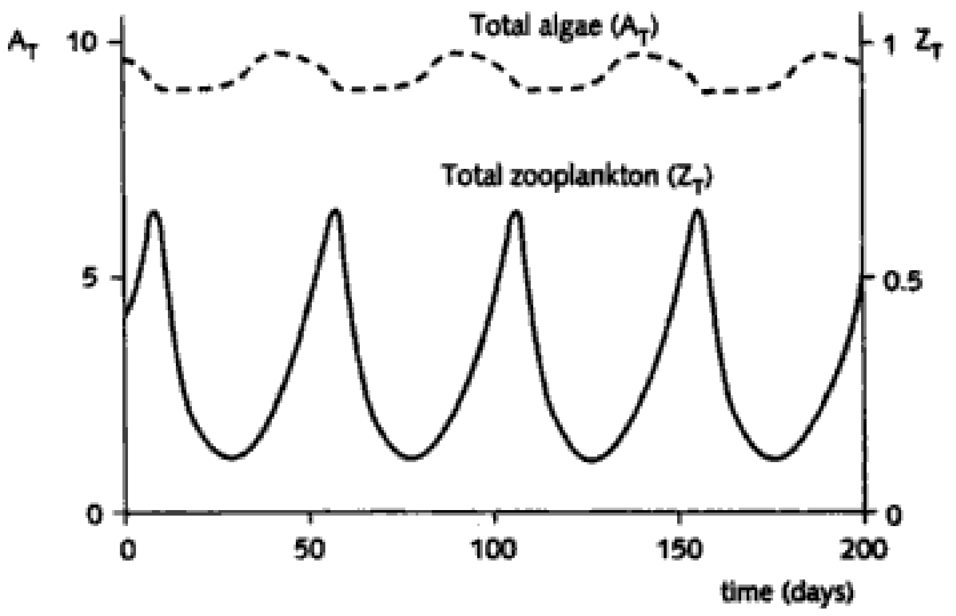


Fig. 4.12 Time plot showing the dynamics of the concentrations of zooplankton and algae averaged over the total volume (Z_T and A_T) generated by the spatial model for a small value of the exchange rate and the grazed fraction, i.e. $d = 0.001$ and $q = 0.1$. Zooplankton oscillates while their algal food stays practically constant. From Scheffer and De Boer (1995).

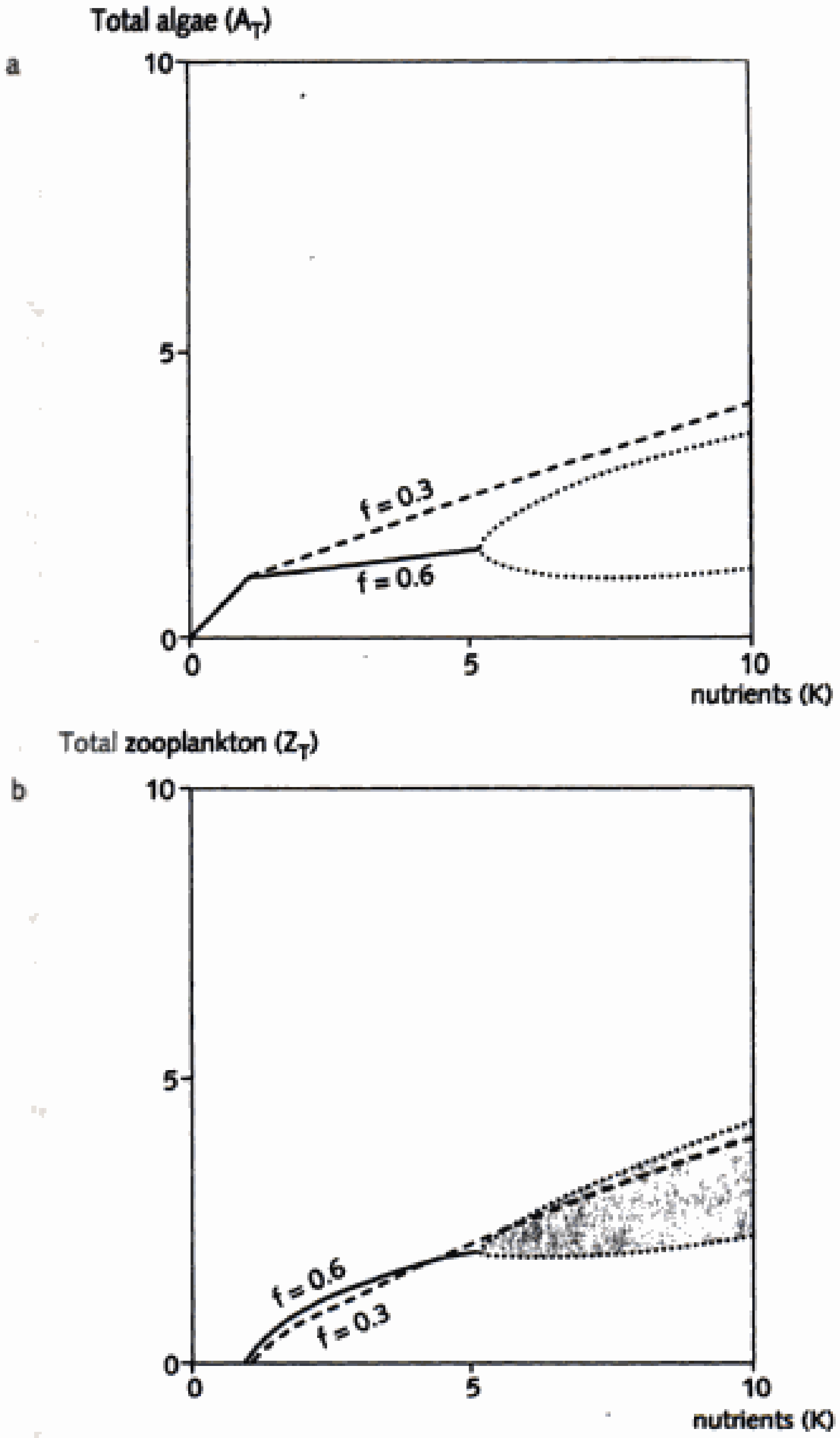


Fig. 4.13 Response to enrichment of the space-averaged equilibrium densities of algae A_T (first panel) and zooplankton Z_T (second panel) generated by the spatial plankton model. For all plots the value of d is fixed to 0.2 but the response is shown for a situation in which zooplankton occupies 30% and 60% of the volume respectively ($q = 0.3$ and $q = 0.6$). The shaded area represents the amplitude of limit cycles. From Scheffer and De Boer (1995).

an artifact. Indeed, the above explanation is supported by observations in experimental conditions. McCauley, working on *Daphnia* – algae interactions in stock tanks, reported population oscillations in a swarm of *Ceriodaphnia* that stayed aggregated on one side of the tank, while phytoplankton in the rest of the tank was little affected (McCauley, pers. comm.).

Importantly, the spatially averaged population densities of the model also show a much more natural response to enrichment than observed in the original minimal model that neglects spatial heterogeneity. This can be seen by plotting A_T and Z_T as a function of the carrying capacity K (Fig. 4.13).

For very low values of K the algal density is too low to sustain zooplankton, and algal density traces the carrying capacity as in the original model. However, in the presence of *Daphnia*, i.e. beyond the critical bifurcation, algal densities keep increasing modestly with enrichment rather than staying constant, as predicted by the classical model. Indeed such an 'intermediate control' of phytoplankton by *Daphnia* is what is observed in most experiments and field data (Sarnelle, 1992; Watson *et al.*, 1992).

Obviously, the very large oscillations produced by the classical model and its unnatural response to enrichment are a result of over-simplification. Although it helps to account for spatial heterogeneity explicitly, models easily become rather complex if we proceed by adding, for instance, fish. Also, spatial heterogeneity is not the only stabilizing force. It would, therefore, be good to have a more generic, simple but reasonable modification to the original model, that stabilizes the system without adding too much complexity to the formulation. This can be done in several ways that preserve the original dynamics to various extents (Scheffer and De Boer, 1995). A relatively simple solution is to assume that algal density in the zooplankton-free refuges is not affected by the exchange with the grazed parts. This implies that $A_2 = K$ thus we obtain a two-equation model where algal growth can be written as:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) - g_z Z \frac{A}{A + h_a} + i\left(K - A\right) \tag{10}$$

Note that to simplify further, the single parameter i now replaces the more explicit ratio d/q to represent the rate at which ungrazed algae enter the studied volume. Since the two-compartment model is a rather abstract representation of the situation in any real lake the value of the parameters d and q will be hard to characterize in practice. Thus, although these parameters were useful to clarify some general principles, their preservation is not of much importance for further analyses.

If the mixing rate is low the above formulation yields a reasonable approximation of the dynamics in the zooplankton occupied compartment of the spatial model. (Note that, because the model produces only these local dynamics, the average over a lake, including the parts without *Daphnia*, should be computed as explained earlier, assuming algae to be at carrying capacity in the remaining space.) The model can be simplified further by replacing the entire last term, $i(K-A)$, by a single constant inflow of algae (mg l^{-1} d^{-1}). This works quite well in most situations (Scheffer and De Boer, 1995). However, since in the following sections K is varied with enrichment and change of seasons, it is more appropriate to keep the full term, $i(K-A)$, to make it vary in concert with carrying capacity.

The isocline picture of the new model differs from the classical one in that the algal isocline rises sharply at low algal densities (Fig. 4.14).

A small inflow term (i) suffices to get rid of the unnaturally large limit cycles with near extinction periods. Increase of i causes the range over which the algal isocline has a positive slope to decrease until the complete isocline has a negative slope (Fig. 4.14). Since oscillations occur only when the algal isocline has a positive slope at the intersection, it can be seen from change in the algal isocline that increasing i tends to stabilize the model.

A very similar isocline picture arises if a sigmoidal functional response, or Holling type III, instead of a simple saturating one is used. Indeed the use of

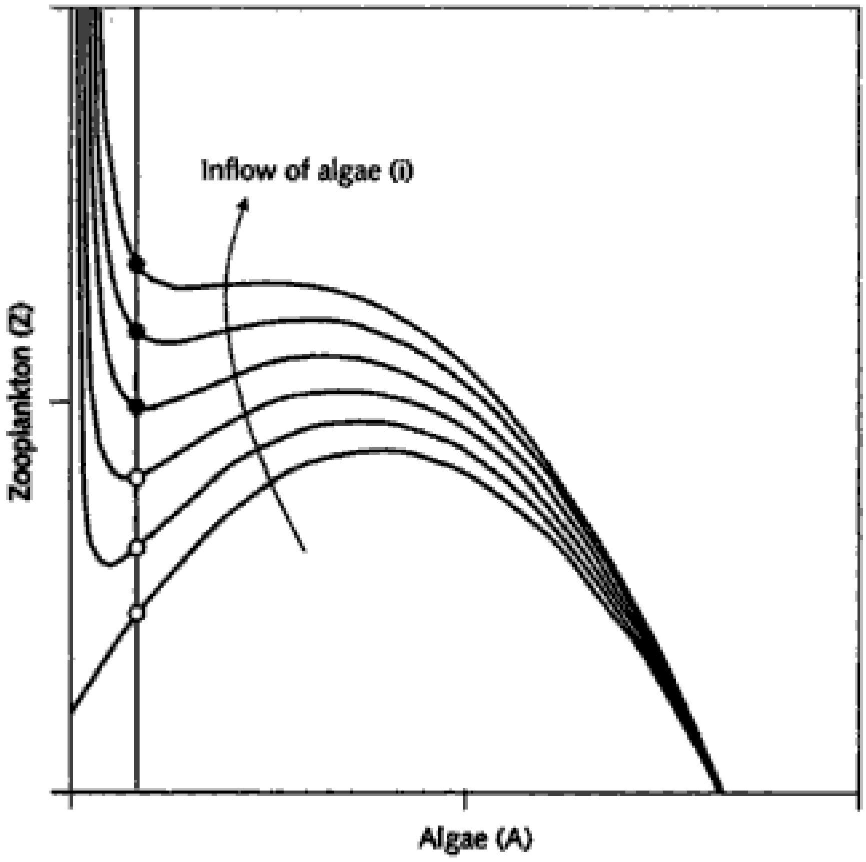


Fig. 4.14 Zero growth isoclines of zooplankton (vertical) and algae (curved) of a simplified version of the spatial model for increasing values of the parameter i which represents import of algae from an ungrazed part of space (Eq. 10, p. 144). Open circles denote unstable equilibria, closed circles represent stable equilibrium points.

a sigmoidal functional response is an effective way to stabilize predator – prey models. A problem with the use of sigmoidal functional responses for *Daphnia* is that they may be inferred from the presence of an alternative food source like bottom detritus, but are never really measured. Even if there is prey switching, though, there is a conceptual problem of modelling it through the use of a sigmoidal response, as in the above model. From the point of view of the prey it describes the situation well, but for the predator does not. Put simply, *Daphnia* stops eating the algae when they are rare, but does not get the alternative food to which it is supposed to switch.

4.2 THE EFFECT OF PLANKTIVOROUS FISH

Field observations and experimental results

The discussion about the effect of fish on plankton was triggered in the early 1960s by Hrbáček and his colleagues (1961) who drew attention to the large differences between the plankton of different ponds depending on the presence of fish. In ponds with fish the zooplankton consisted mainly of small bodied species, and algal biomass was high. In ponds without fish phytoplankton production was low and larger herbivores like *Daphnia* dominated the zooplankton.

Shortly after this, Brooks and Dodson (1965), who observed similar relationships between fish and plankton in New England lakes, developed the so-called 'size-efficiency hypothesis' to explain such shifts. The large bodied zooplankters are much more efficient at grazing down phytoplankton biomass than their smaller competitors which are, moreover, restricted to foraging only on the smallest particles. Since fish forages selectively on larger zooplankton, it causes a shift in the zooplankton community towards small bodied animals that have little impact on total algal biomass.

Later work largely confirms the suggestion of Brooks and Dodson that high densities of planktivorous fish lead to a zooplankton community dominated by small, relatively inefficient grazers (Shapiro and Wright, 1984; Hambright, 1994; Seďa and Duncan, 1994), although the mechanisms through which fish affects the zooplankton community appear to be more intricate than originally thought. Not only does selective predation of fish remove the larger individuals, some *Daphnia* clones also change their behaviour and life history strategy in response to chemical cues released by fish (Dodson, 1988; Demeester *et al.*, 1995; Stirling, 1995), leading amongst other things to a smaller average size of individuals (Weider and Pijanowska, 1993; Engelmayer, 1995). In addition, lakes with a high fish stock are frequently dominated by large filamentous blue-green algae which have been shown to inhibit the growth of large bodied *Daphnia* species under some conditions (Hawkins and Lampert, 1989; Gliwicz, 1990; Gliwicz and Lampert, 1990), suggesting an additional explanation for their absence in such lakes.

Clearly, we are still far from unravelling the complex interplay of mechanisms that leads to shifts in size distributions of zooplankton and algae in the presence of fish. The problem becomes much simpler if we focus merely on the explanation of strong top-down control of algal biomass. As argued in the previous section, large zooplankters of the genus *Daphnia* are practically always responsible for really clearing the water.

Although top-down control in the simplified 'trophic cascade' of fish, large *Daphnia*, and algae is clearly important, the details of the resulting patterns are not always straightforward. The difference between the effect of high fish densities and situations with no fish at all is usually clear-cut, and largely supports the black-and-white view of Hairston, Smith and Slobodkin (1960) that herbivores completely suppress the primary producers unless they are themselves suppressed by carnivores (Fig. 4.1). Levitan and co-workers (1984), for instance, showed that addition of nutrients to limnocorrals with fish resulted in an increase of phytoplankton biomass, indicating a bottom-up control of algae. In limnocorrals without fish, however, enrichment left the phytoplankton biomass unaffected. Instead the *Daphnia* population increased strongly after nutrient supplementation (Fig. 4.15). Also the effect of a complete fish die-off in real lakes tends to be spectacular.

More interesting than such all-or-none experiments, however, are the ones that explore how plankton dynamics are affected by gradual change in

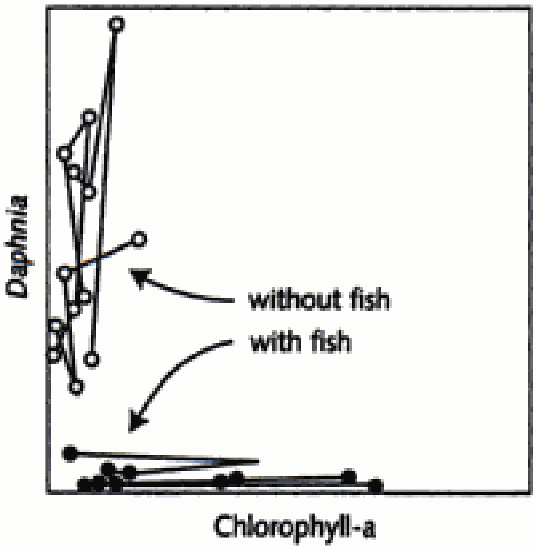


Fig. 4.15 Response of *Daphnia* numbers and chlorophyll-a concentrations to the addition of nutrients to enclosures with and without fish. From Levitan *et al.* (1984).

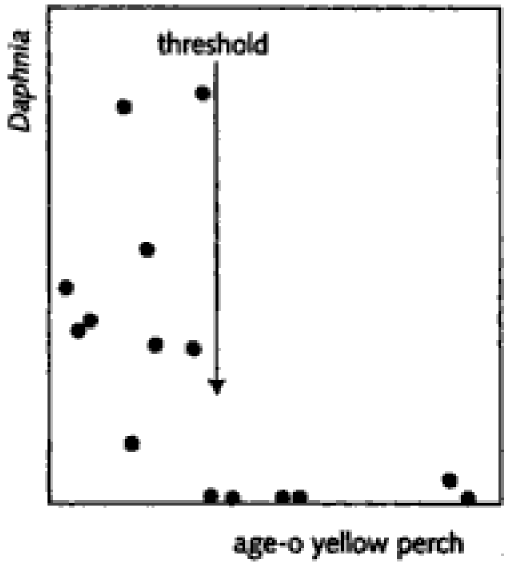


Fig. 4.16 Relationship between the density of *Daphnia pulex* and the number of age-0 yellow perch on the first of August in Oneida Lake over a period of 15 years. Redrawn from Mills *et al.* (1987)

fish predation pressure. In limnocorrals where fish biomass increased slowly due to individual growth, the zooplankton biomass has been shown to respond discontinuously (McQueen and Post, 1988). Above a critical fish biomass of around 50 kg ha^{-1} zooplankton was severely reduced. Long-term studies of the community dynamics of Lake Oneida also provide evidence that there is a threshold in predation pressure beyond which zooplankton collapses (Mills *et al.*, 1987). The most important planktivorous fish in this system is yellow perch (*Perca flavescens*) during the first year of life. The density of age-0 perch differs significantly from year to year. In years in which the density of age-0 yellow perch on the first of August exceeds a threshold of 14 000 individuals ha^{-1}, the late summer *Daphnia* pulex population of the lake appears to collapse completely (Fig. 4.16). In these years the abundance of smaller herbivorous zooplankton and of phytoplankton is elevated. The discontinuity in the response of zooplankton to fish predation can be understood with the help of a simple graphical model as explained in the next section.

The classical consumption catastrophe

In the consumer – food couple *Daphnia* – algae, the consumer population dynamics largely depend on the availability of this specific food. Considering the effect of *Daphnia* consumption by fish, the situation is different. Fish will benefit from the consumption of this profitable food but for most individuals it is just part of their diet. Overall fish density depends on the productivity of the whole system, but does not react as directly to *Daphnia* density as *Daphnia* dynamics respond to phytoplankton. Therefore, it is possible to study the impact of fish on *Daphnia* dynamics without directly considering the effect of *Daphnia* on the population dynamics of fish.

A well studied case in which the consumer density is also largely independent of its food is cattle grazing. The dynamics of the vegetation are driven by grazing but density of cattle is set by man. Noy-Meir (1975) used an illuminating simple graphical approach to analyse the risk of overgrazing in such systems. This approach is not only helpful for understanding the effect of cattle on grass, but also for explaining the effect of fish on zooplankton, of piscivores on fish and of herbivorous birds on aquatic vegetation.

The idea is to plot the production of the food population and the losses due to consumption in the same graph (Fig. 4.17).

The difference between the two can then be interpreted as the net growth of the food population. The production of the food population plotted against its density shows an optimum. This is a generic property as discussed in the section on logistic growth. At low population densities the per capita growth rate is high, but because there are just a few reproducing individuals; overall productivity is still low. At the highest population densities the productivity is low because the carrying capacity of the environment is reached. The consumption curve represents the functional response of the consumer multiplied by its population density. Consumption increases with food density because the gathering of food becomes increasingly efficient.

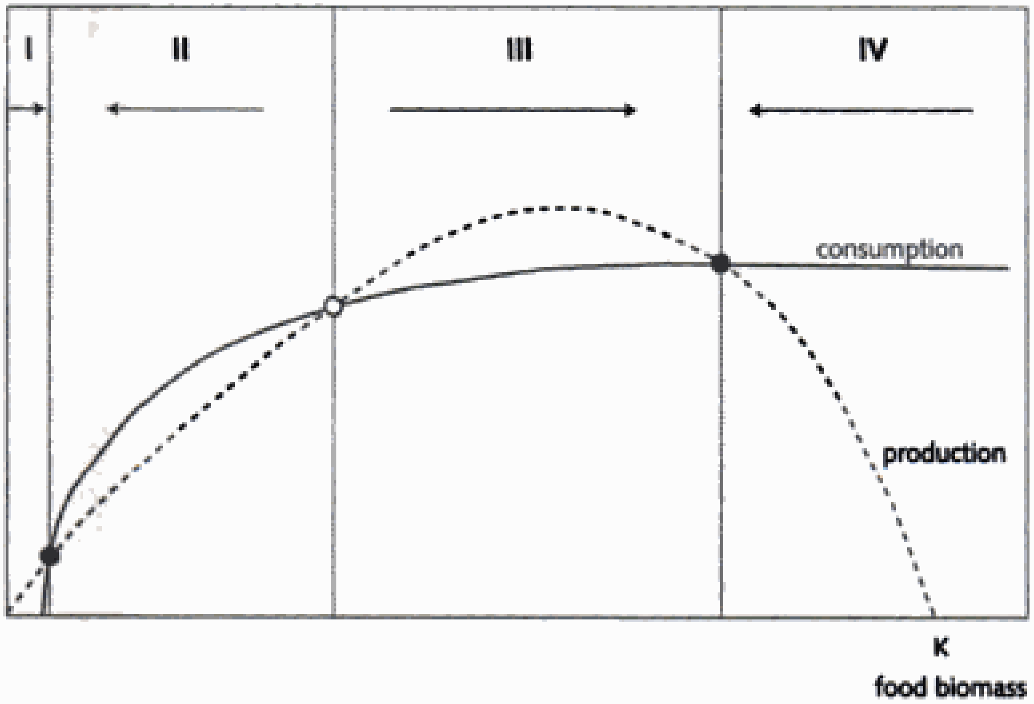


Fig. 4.17 Graphical analysis of the stability of an exploited food population. At the intersections of the two curves consumption equals production and the food population is in equilibrium. However the equilibrium on the intersection marked by an open circle is unstable (for further explanation see text).

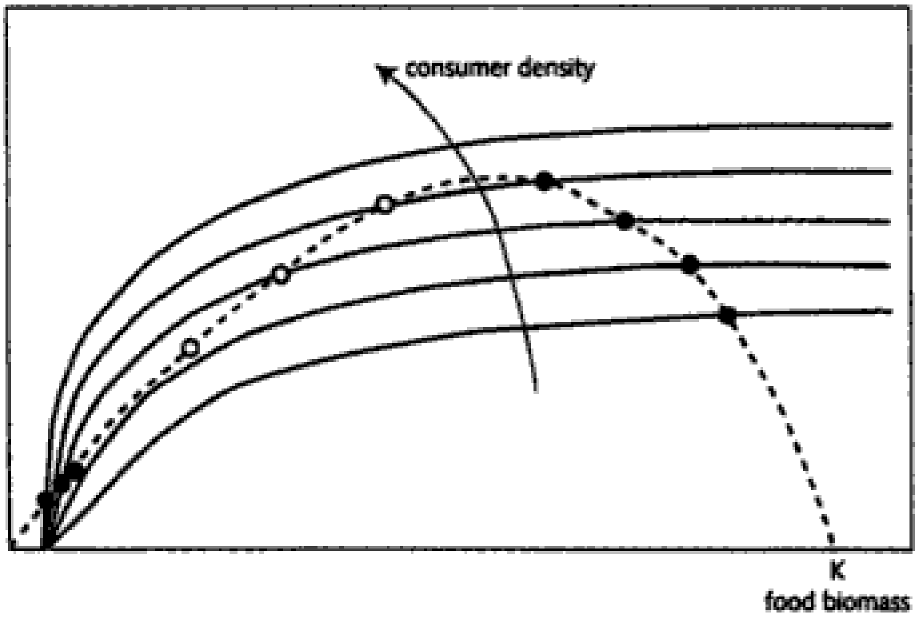


Fig. 4.18 Consumption increases with consumer density and this affects the position of the stable and unstable equilibrium points at the intersections of the production and the consumption curves (see also Fig. 4.17).

For high food densities it saturates as the maximum consumption rate of the consumer individuals is approached. Assuming that the food population can never be eaten completely because there is always a part unreachable for the consumers, the consumption starts at a food level slightly higher than zero.

If the functional response saturates at sufficiently low food densities the curves can intersect in three points as in the illustrated case. Obviously, the food population will increase if production is higher than the consumption losses (sections *I* and *III*) and decrease if consumption exceeds production (sections *II* and *IV*). All three intersections are equilibria, as consumption balances growth. The middle one, however, is unstable. This is because after a small disturbance, the system will move further away from it rather than returning as in the case of the other two intersection points. The unstable point represents the breakpoint food density below which the system collapses into an over-exploited state with low food biomass where production is very low.

Since the overall consumption increases with the amount of consumers present, the height of the consumption curve will increase in proportion to the consumer density (Fig. 4.18).

If one tracks the shift in the equilibria with changing consumer density, it can be seen that this configuration implies a hysteresis much like the one in the competition between cyanobacteria and other algae, but in this case due to a completely different mechanism. Starting from the lowest consumer density there is just one equilibrium. Increasing consumer density, this equilibrium moves to the left. Food density decreases but productivity increases until the consumption curve becomes too high to intersect with the

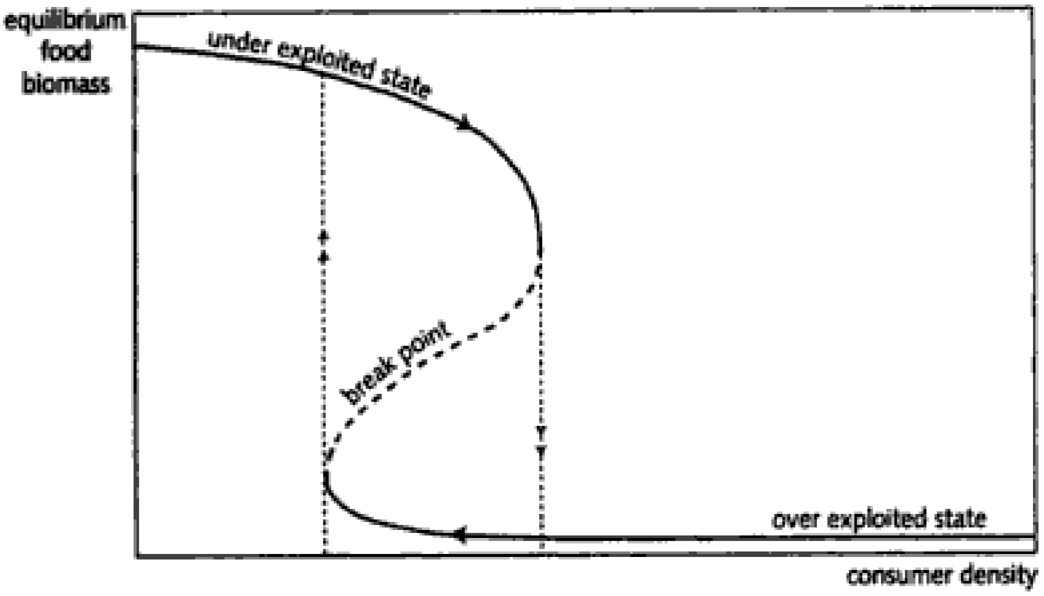


Fig. 4.19 Food density in equilibrium plotted as a function of consumer density. The dashed middle section of the curve corresponds to the unstable breakpoints of the system (open circles in Figs. 4.17 and 4.18). In the range of consumer densities over which this unstable equilibrium exists the system tends to either of the two alternative stable equilibria depending on the initial density of the food population relative to the breakpoint (see text for further discussion).

production curve. At that point the equilibrium hits the unstable breakpoint and disappears. As a result, the system collapses into the overexploited state. If after this collapse the consumer density is reduced in order to restore the productive state, the system shows hysteresis. It stays in the overexploited equilibrium with low food densities until the consumption curve has become low enough to let the intersections at the left side disappear. Again this happens when the breakpoint collides with the stable state. Plotting the position of the three equilibria against consumer density (Fig. 4.19) one obtains a hysteresis curve that is analogous in interpretation to the ones obtained from the cyanobacteria model (Figs. 3.19 and 3.22) although the processes involved are very different.

Noy-Meir used this model to explain the effect of overgrazing by cattle that is often observed in arid vegetations. There is, however, in principle no reason why it should not apply to the effect of increasing fish densities on *Daphnia* as well. Indeed, the response of *Daphnia* to fish seems to be nonlinear (e.g. Fig. 4.16) and, as explained later, a collapse into an overexploited state is likely to be the underlying reason. However, the situation is obviously more complex here because *Daphnia* dynamics depend also on their interaction with phytoplankton. In fact, the *Daphnia* – phytoplankton cycles themselves are oscillations between over-exploitation and under-exploitation of the algae. To understand better how the effect of fish cascades down to phytoplankton, we need to consider the dynamics of the planktonic system explicitly.

A minimal model of planktivory

To explore the potential impact of fish on the dynamical interaction of *Daphnia* and algae we slightly modify the zooplankton – algae model developed in the previous section. The algal equation remains the same, as fish generally do not eat phytoplankton. To account for the effect of predation by fish on *Daphnia* we simply add an extra loss term to their growth equation:

$$\frac{dA}{dt} = rA\left(1-\frac{A}{K}\right) - g_z Z\frac{A}{A+h_a} + i(K-A)$$

$$\frac{dZ}{dt} = e_z g_z Z\frac{A}{A+h_a} - m_z Z - G_f\frac{Z^2}{Z^2+h_z^2} \tag{12}$$

The new loss term in the zooplankton equation represents the impact of the fish community as a whole. In reality, different groups of fish forage on *Daphnia* with different functional responses. Therefore, this term is really just a pragmatic solution to mimic the effect of many different animals switching to forage on *Daphnia* at different moments with different efficiencies. Since most of the larger individuals usually switch to *Daphnia* only when it is not too scarce (Lammens, 1985; Lammens *et al.*, 1985), the predation pressure is likely to increase more than linearly with *Daphnia* density over part of the range. Therefore, the overall functional response is made sigmoidal by adding a square to the formulation. The maximum consumption rate (G_f) is set directly, rather than as the product of the fish biomass and their weight specific maximum intake. The latter is not easily defined for a whole community, since large animals consume less per gram of body weight than small ones.

Note that fish is not modelled dynamically. The effect of varying fish predation pressure over the year will be shown later, but even then, fish growth will not be modelled as a function of *Daphnia* consumption. This is reasonable, since, as argued, *Daphnia* represents only a small part of the diet of most fish. Therefore, overall fish density depends on the productivity of the lake, but does not react directly to *Daphnia* density.

Hysteresis in the response to fish

As a first step in the analyses of the impact of fish on the zooplankton – algae interaction we look at the effect of fish on the isoclines of zero-growth. The parameter (G_f) is used to mimic the effect of increasing fish density. Since the effect of fish occurs only in the zooplankton equation, the algal isocline remains unaffected. The zooplankton isocline, however, starts bending out if fish is increased (Fig. 4.20).

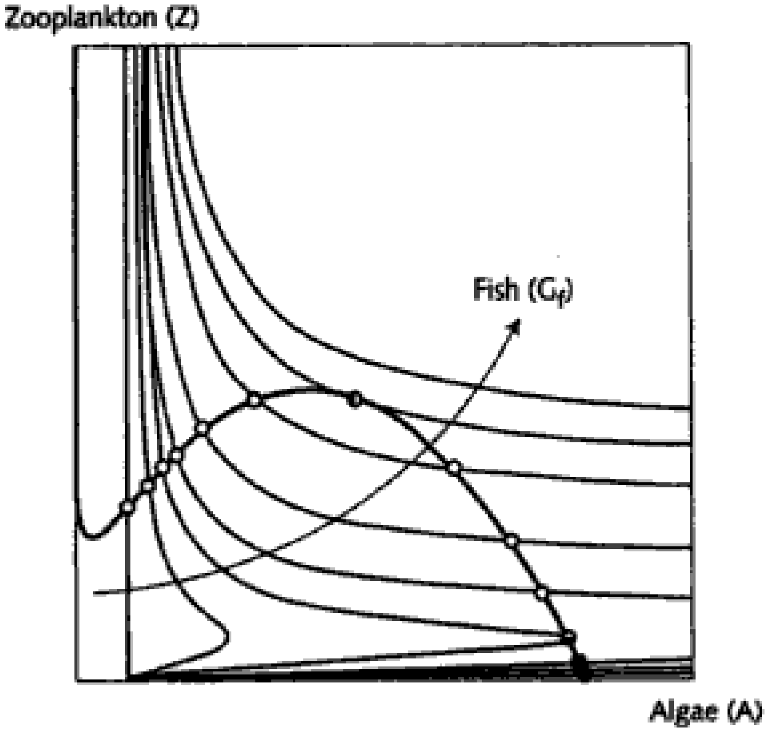


Fig. 4.20 Effect of increasing fish predation pressure (G_f) on the zero-growth isoclines of the plankton model. The zooplankton isocline bends out with increasing fish density while the algal isocline remains unaffected. Dots denote stable equilibria, open circles denote unstable ones. The half open circles and corresponding isoclines are associated with fold bifurcations. From Scheffer *et al.* (1997b).

This causes the intersection (that represents the unstable focus of the limit cycle) to move to the right. When it is pushed far enough to the right it can become stable, as discussed in the paradox of enrichment section. In this case the corresponding Hopf bifurcation is close to the top of the hump, but not exactly on it, as that conjunction is only valid for vertical predator isoclines. In addition to the shift in the existing equilibrium, new intersections, and thus new equilibria, with high algal biomass and very little zooplankton arise at the lower right-hand part of the graph for sufficiently high fish densities.

A more complete view is obtained by adding fish as an extra dimension to the isocline picture (Fig. 4.21). This shows how the position of the intersections changes smoothly with fish predation to form one continuous equilibrium curve. Projected in the fish – algae plane or the fish – zooplankton plane this curve shows an S-shape (Fig. 4.22) similar to the one indicating hysteresis in the simple Noy-Meir model (Fig. 4.19) and in the competition model of algae and cyanobacteria (Fig. 3.22).

At low fish predation, zooplankton density is high and algal density low, whereas at high fish predation, a single equilibrium with high algal biomass and very little zooplankton occurs. These contrasting states co-exist as alternative equilibria over a range of intermediate fish densities ($F_1 < G_f < F_2$).

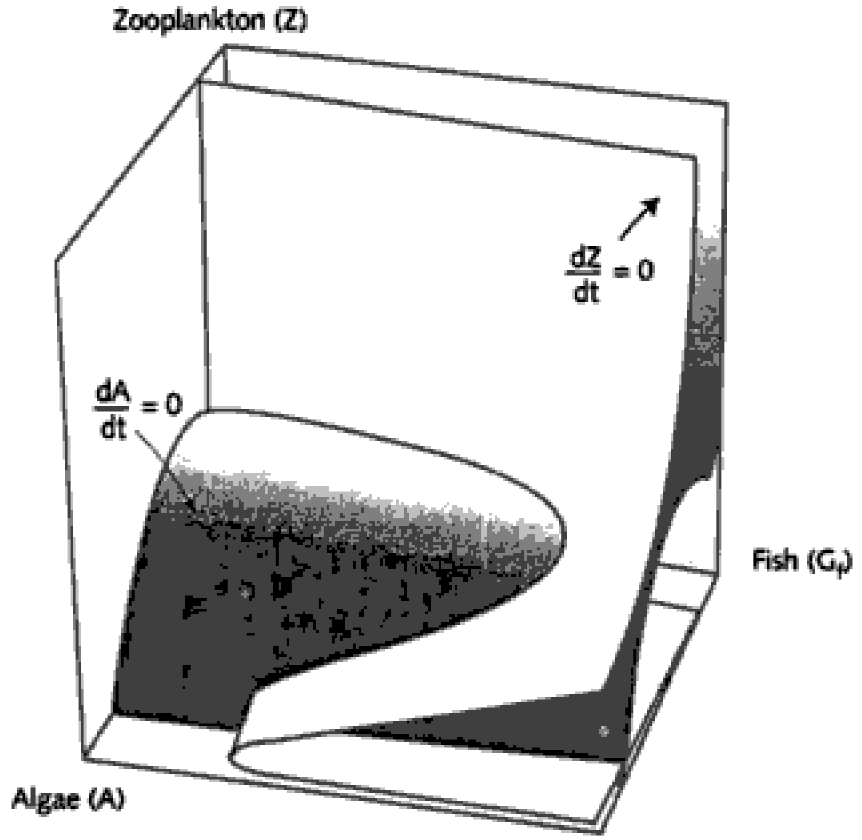


Fig. 4.21 Three dimensional representation of the effect of fish on the isoclines of the plankton model (see Fig. 4.20). The isoclines have now become zero-growth surfaces of zooplankton and algae. Note that the intersection representing the systems equilibria has a sigmoidal shape. From Scheffer *et al.* (1997b).

Analogous to the Noy-Meir model and the cyanobacteria model, the system will show hysteresis and catastrophic transitions between alternative stable states in response to changes in fish predation pressure. However, there is an important difference from the hysteresis in the previous models. In the competition model and the Noy-Meir model the upper and lower branches of the hysteresis were stable. Here, the branch with high zooplankton biomass and little algae is really the unstable focus of a limit cycle (except for a small part after the Hopf bifurcation where it can become stable ($H < G_f < F_2$)). The presence of this limit cycle has major implications for the qualitative behaviour: when the zooplankton – algae oscillations are large enough to pass the unstable breakpoint (the middle branch) they bring the system within the basin of attraction of the stable algal dominated equilibrium. Thus the oscillations promote a jump to an algal dominated situation where zooplankton is kept in an over-exploited state by fish. As explained later, this is probably what happens in many lakes after the collapse of the spring peak in zooplankton that causes the clear-water phase. The main reason for this collapse is food shortage due to the depletion of phytoplankton, but once the zooplankton populations are

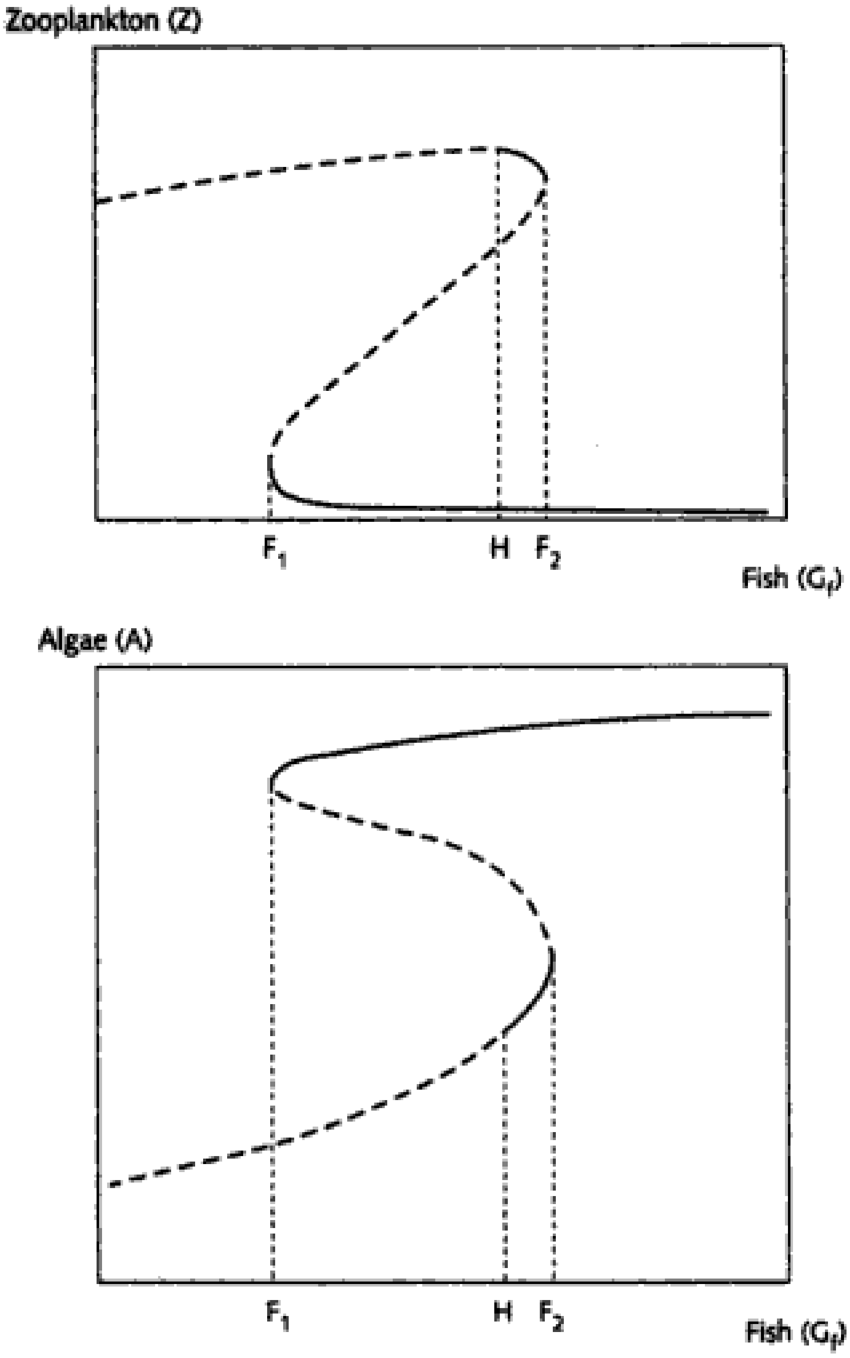


Fig. 4.22 Two-dimensional projections of the sigmoidal intersection of the surfaces in Fig. 4.21. The resulting hysteresis graphs show how the density of zooplankton and algae in equilibrium depends on the fish predation pressure. Between the twofold bifurcations ($F_1 < G_f < F_2$) the system has alternative equilibria. The dashed parts of the curves represent unstable equilibria. The zooplankton-dominated branch of the equilibrium curve is the unstable focus of a limit cycle except for a small part where it has gone through a Hopf bifurcation (*H*). From Scheffer *et al.* (1997b).

low they can be kept in an overexploited state even by relatively low densities of planktivorous fish. This mechanism where consumer – food oscillations make the system vulnerable to over-exploitation by a third trophic level (fish) corresponds to a so-called 'homoclinic bifurcation'. This phenomenon is explained further in the following two, slightly more technical, sections.

Implications of oscillations

Since isoclines do not tell much about the limit cycle, we look directly at the effect of fish on the equilibria to obtain an overview of the implications of the oscillatory equilibrium on the hysteresis (Fig. 4.23), using snapshots at fixed fish densities to clarify the link to the change in isoclines (Fig. 4.24). For zero fish, we simply have the original zooplankton – algae model and the limit cycle is the only stable equilibrium. Increasing fish, we first arrive at the lower left inflection point of the hysteresis curve. Because it occurs at the folding point of the hysteresis curve, this is called a fold bifurcation (F_1). If we look at the isoclines, we can see that two intersections arise after the curved zooplankton isocline hits the algal isocline (Fig. 4.24a). Because one is a stable 'node' equilibrium and the other one an unstable 'saddle', this bifurcation is sometimes called saddle-node bifurcation. The stable point is an equilibrium with almost no zooplankton and a high algal density, close to carrying capacity. Note that

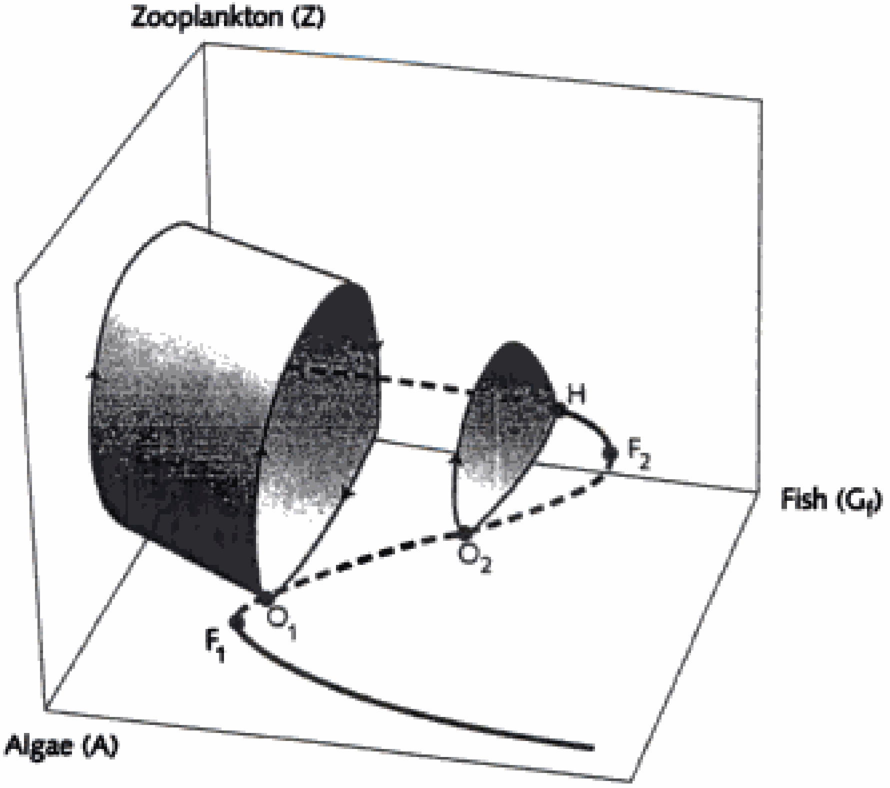


Fig. 4.23 Schematic representation of the effect of fish predation pressure on the equilibria and limit-cycles of the system. The limit cycle does not exist between the two homoclinic bifurcations (O_1 and O_2). In these bifurcations the stability of the limit cycle is destroyed due to the collision with the saddle that marks the border of the basin of attraction of the stable algal dominated equilibrium. From Scheffer *et al.* (1997b).

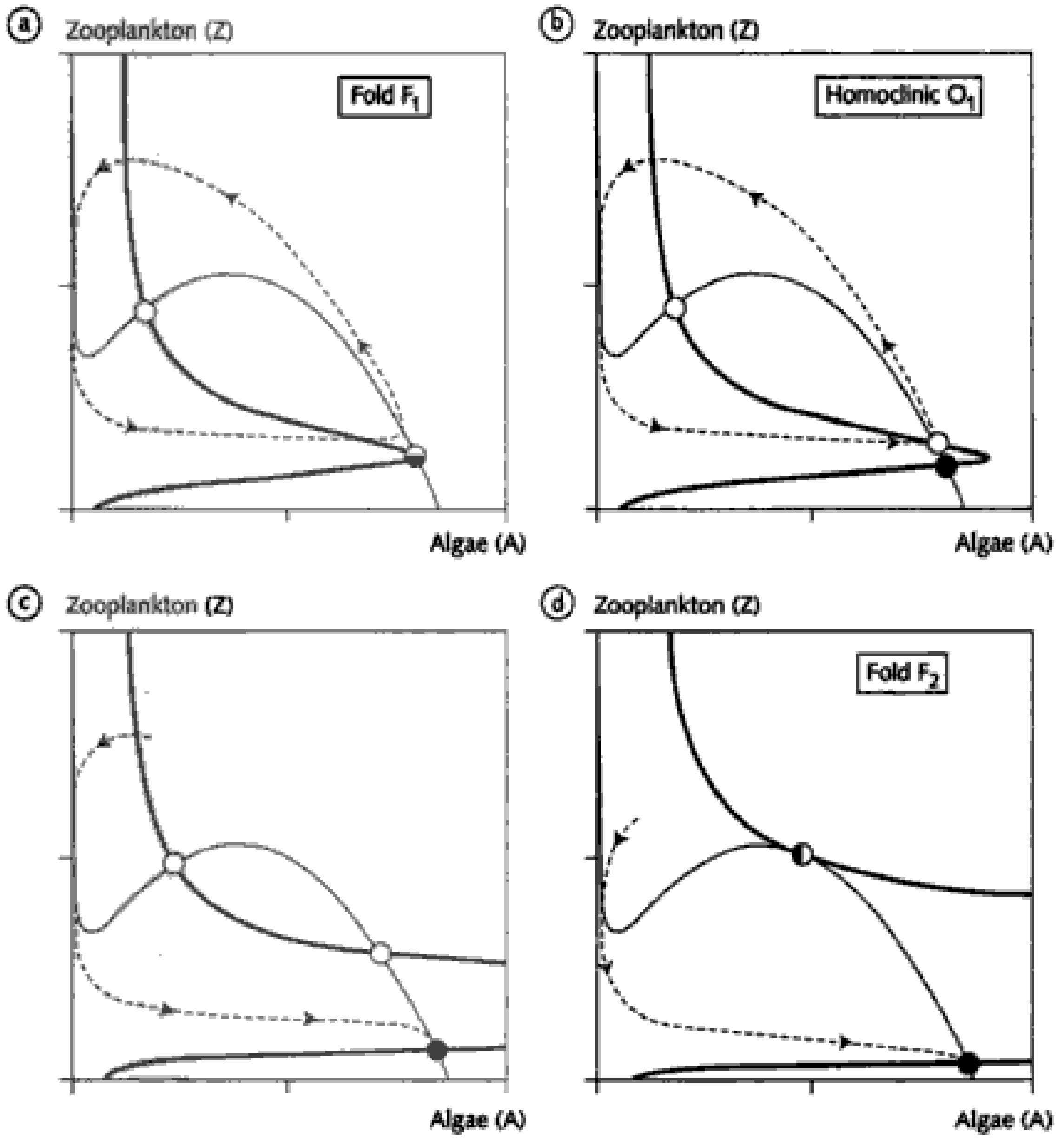


Fig. 4.24 Trajectories and isocline configurations corresponding to the first (a) and second (d) fold bifurcations, the first homoclinic (b) and a fish density in the range between the two homoclinics (c). From Scheffer *et al.* (1997b).

zooplankton does not go completely extinct. Therefore the equilibrium is not a 'trivial' one with only algae in carrying capacity. This is the reason that we have a fold rather than a 'transcritical' bifurcation as in the algal competition model. Obviously, trivial equilibria and the corresponding transcritical bifurcations are mostly due to over-simplification. In the current model, the sigmoidal functional response of fish prevents extinction of zooplankton. A simple saturating functional response would make the algal dominated equilibrium trivial and the bifurcation transcritical.

As in the competition model, the saddle is a point on the separatrix that marks the limit of the basin of attraction of the new stable equilibrium. Increasing fish further, the saddle and the node separate and the attraction area of the stable algal dominated equilibrium grows until the saddle collides with the limit cycle (O_1) (Fig. 4.24b). This is a so-called homoclinic bifurcation. Clearly, it means the end of the stable limit cycle, as beyond this bifurcation a trajectory on the former limit cycle ends up inevitably in the attraction area of the stable phytoplankton equilibrium (Fig. 4.24c).

Increasing fish further, the limit cycle can reappear through a second homoclinic bifurcation (O_2). This is because the limit cycle shrinks approaching the Hopf bifurcation (H) where it collides with its unstable focus to become a stable point attractor. The last qualitative change of equilibria with increasing fish density is a fold bifurcation (F_2) again (Fig. 4.24d). The stable point attractor that was formed through the Hopf bifurcation collides with the saddle in the point where the hysteresis curve is folded back.

Note that the part from the second homoclinic to the second fold, is mainly of theoretical interest, as the system will normally not arrive at these equilibria. A simulation with slowly increasing fish density, starting from zero fish, will show oscillations until the homoclinic (O_1) is reached. Here the system jumps to the only remaining stable equilibrium, namely the algal dominated lower branch of the hysteresis, where it will stay, no matter how much the fish predation is increased further. Lowering the amount of fish from this point will keep the system in the algal state until the fold bifurcation (F_1) is reached. At this point it will jump back to the oscillatory mode. Only a disturbance could potentially bring the system in the equilibria around the Hopf. However, since their basin of attraction is small this is unlikely to happen. For all practical purposes we can therefore forget about this part of the picture.

An inventory of theoretical possibilities

The above scenario with five bifurcations is one of the most complex ones that can arise from the effect of fish. The only bifurcation that may exist on top of it is an extra Hopf bifurcation for low fish densities (Fig. 4.25a). This can happen if the immigration term in the algal equation is such that it causes one of the stable situations depicted in Fig. 4.14. In that case, an increase in fish can initially destabilize the system, as it brings the intersection to the rising part of the algal isocline.

Most changes in conditions, however, will let the complex scenario degenerate into more simple cases. The second homoclinic (O_2), for instance, can be absent (Fig. 4.25b). Obviously, this does not make much difference in our case, since, as argued, these equilibria were already irrelevant in practice, because of their isolation and small basin of attraction.

Another simplification occurs when the fold F_1 and the homoclinic O_1 coincide (Fig. 4.25c). This is a so-called saddle-node homoclinic bifurcation (Kuznetsov, 1995). In this situation the zooplankton dominated clear-water regime and the algal dominated turbid regime are mutually exclusive. The limit cycle can also remain

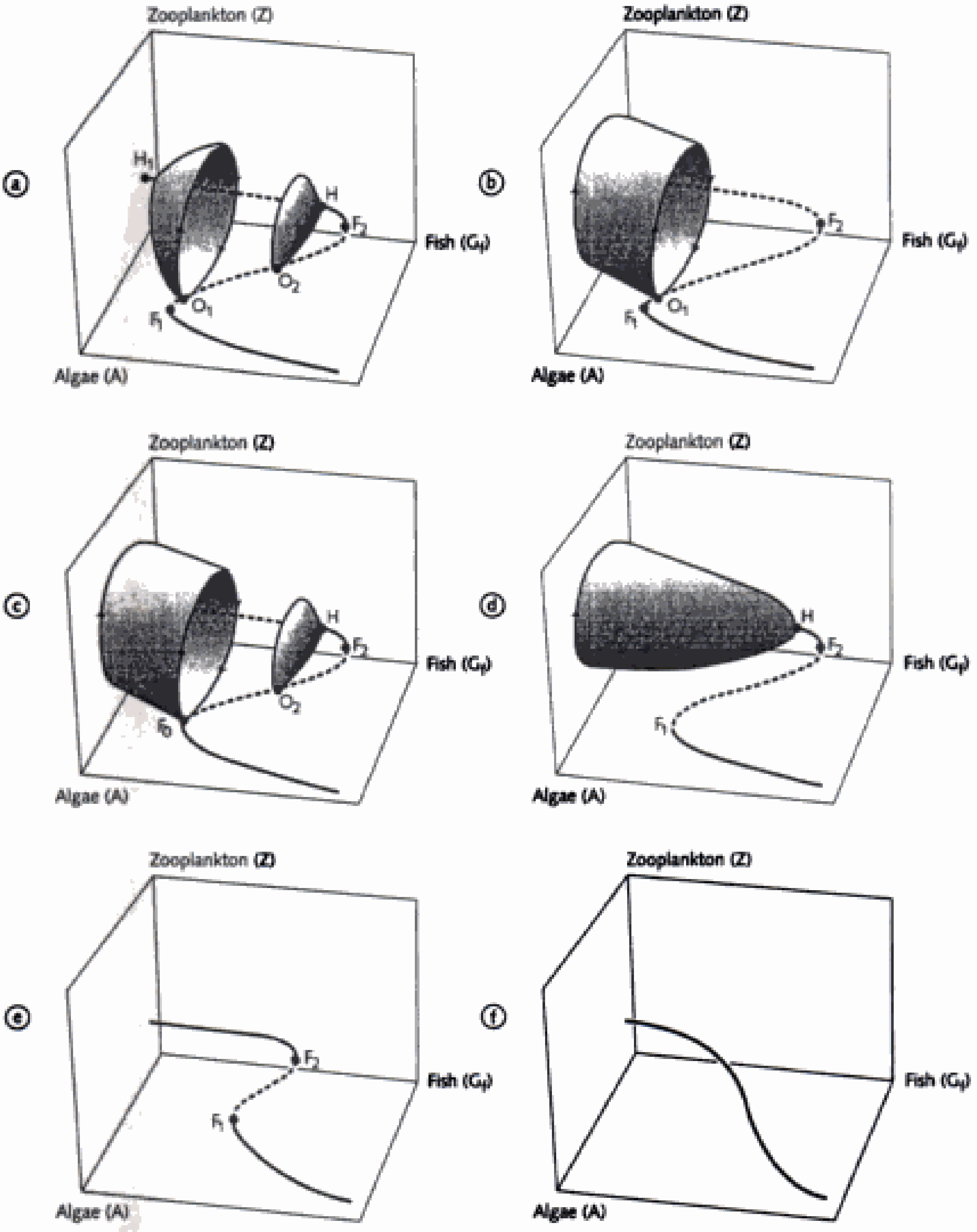
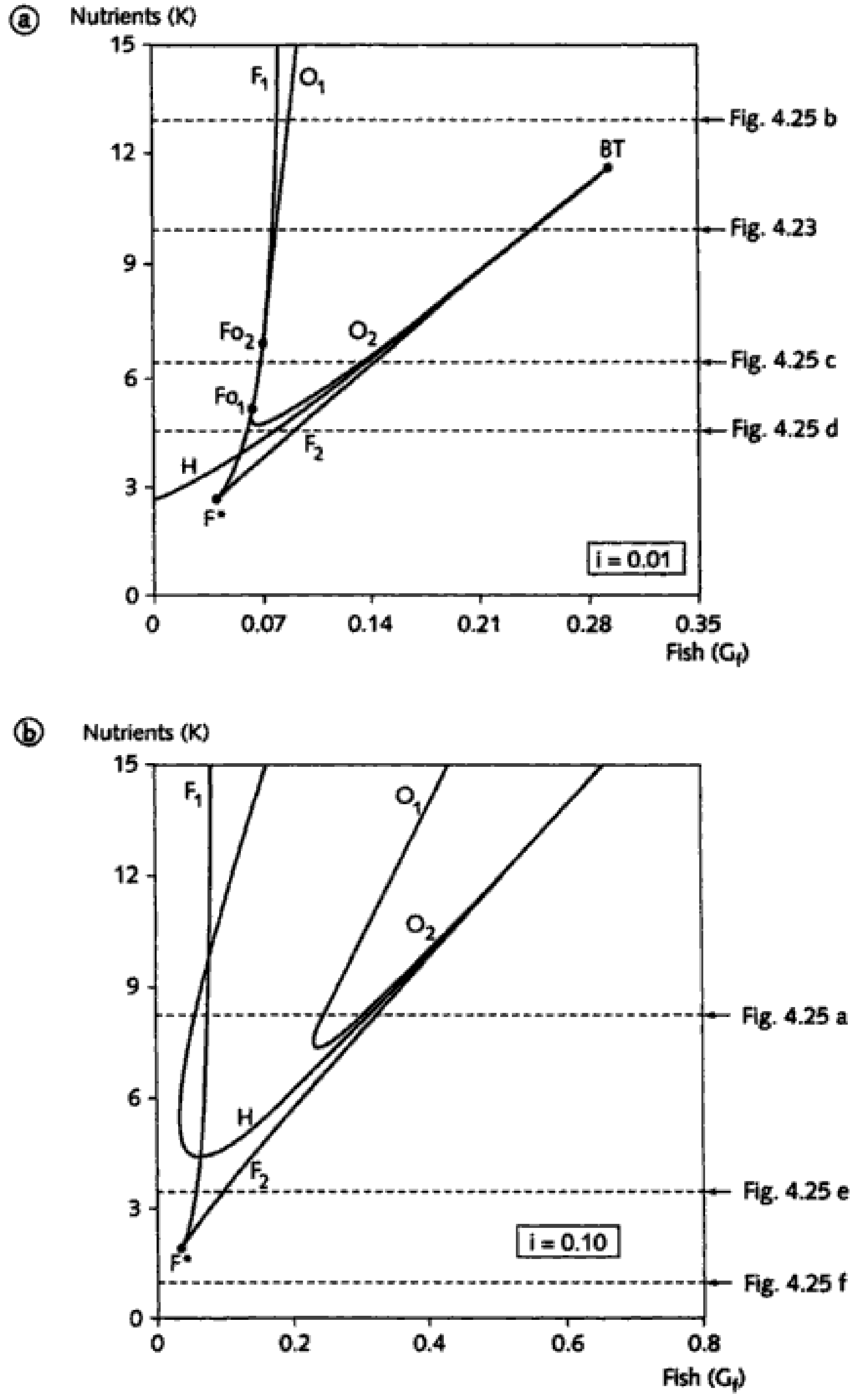


Fig. 4.25 Six qualitatively different diagrams showing the equilibria and cycles of the system that can be obtained by manipulating the carrying capacity for algae (K) and the stabilizing diffusive inflow of algae (i). From Scheffer *et al.* (1997b).

sufficiently small to avoid touching the saddle. In that case homoclinic bifurcations do not occur (Fig. 4.25d). The most simple situations arise if there are no oscillations (Fig. 4.25e) and eventually no folds (Fig. 4.25f). In the latter case there are no bifurcations at all, and the system responds smoothly to an increase in fish, shifting


ⓐ
Nutrients (K)
15
12
9
6
3
0
F₁
O₁
BT
Fo₂
O₂
Fo₁
H
F₂
F*
i = 0.01
Fig. 4.25 b
Fig. 4.23
Fig. 4.25 c
Fig. 4.25 d
0
0.07
0.14
0.21
0.28
0.35
Fish (G_f)
ⓑ
Nutrients (K)
15
12
9
6
3
0
F₁
O₁
O₂
H
F₂
F*
i = 0.10
Fig. 4.25 a
Fig. 4.25 e
Fig. 4.25 f
0
0.2
0.4
0.6
0.8
Fish (G_f)

from a stationary regime with predominantly *Daphnia* to a regime with mainly algae. These simple cases with no or small oscillations are obviously associated with relatively stable basic *Daphnia* – algae systems. As argued in the previous chapter, such stability may be promoted by aggregated spatial distributions of *Daphnia*, low nutrients, the availability of detritus as an alternative food source, and the presence of inedible algae.

Although this inventory gives an overview of what might happen if the conditions change, the discussion with respect to the parameters remains ad hoc. A more systematic image of the effect of various parameters on the system's mode of behaviour can be obtained by drawing the lines at which the bifurcations occur in a two-parameter plane. We have already used this bifurcation analysis technique to map the behaviour of the cyanobacteria competition model (Fig. 3.23) and the stabilizing effect of spatial aggregation of *Daphnia* (Fig. 4.10). Here we apply it to explore how change in the nutrient level (expressed through K) influences the effect of fish on the system (Fig. 4.26).

At zero fish predation the system reduces to the original *Daphnia* – phytoplankton model, which has only a Hopf bifurcation (H). This bifurcation stays present if fish is increased until it meets the second fold (F_2) and homoclinic (O_2) bifurcations in a so-called Bogdanov – Takens point (BT). Beyond this point the bifurcations are no longer relevant as they are not associated with attractors. Such points in parameter space where different bifurcations meet are called codimension-two points. Note that those represent a higher hierarchical level than the simple bifurcations of equilibria. Our model has three other codimension-two points: a cusp point for low values of K and G_f at which the hysteresis is born and two fold bifurcations emerge (F^*), and two points at which the fold and homoclinic curves merge (F_{O1} and F_{O2}). As indicated in the figure, the scenarios of change in equilibria and cycles with fish density (Fig. 4.25), represent horizontal sections through the bifurcation graph.

Obviously, the configuration of the bifurcation lines in the two parameter plane (Fig. 4.26a) depends on the values of the other parameters. A parameter that is really related to the environment rather than to the physiology of the species is i, used to

Fig. 4.26 **Bifurcation diagrams showing when the Hopf (H), fold (F) and homoclinic (O) bifurcations occur depending on the fish predation (G_f) and the carrying capacity for algae (K). The horizontal sections that are indicated correspond to the diagrams in Figs. 4.23 and 4.25 as indicated. *a*. The Hopf, homoclinic and fold are very close together before merging in the Bogdanov-Takens point, indicating that the part between O_2 and F_2 in Figs. 4.23 and 4.25 is very small in reality. Dots denote codimension-two bifurcation points. *b*. Diagram for a higher value of the stabilizing diffusive inflow parameter i. The Hopf bifurcation is no longer rooted in the vertical axis, implying that in the absence of fish, there are no plankton oscillations. From Scheffer *et al.* (1997b).**

mimic the stabilizing effect of a non-homogeneous spatial distribution of *Daphnia*. If i is increased a bit, the homoclinic no longer merges with the first fold (not shown). A further increase of the stabilizing factor i causes the Hopf bifurcation to be no longer rooted in the K-axis of the bifurcation graph (Fig. 4.26b). In this case the system does not oscillate in the absence of fish. Increasing fish can be destabilizing in this case, as it can bring the system through the Hopf. The horizontal cross-sections indicated in this bifurcation graph (Fig. 4.26b) correspond to the three left panels of Fig. 4.25.

Roughly speaking, all lines in the bifurcation graphs have a positive slope, indicating that in systems which are richer in nutrients (higher algal carrying capacity (K)) all bifurcations appear at higher fish levels. A biological interpretation is that more fish is needed to let *Daphnia* collapse if the system is more eutrophic. There is, however, an important complication on top of this. If K is low enough the system does not go through homoclinic bifurcations with increasing fish predation, and *Daphnia* does not collapse until the second fold is reached (F_2), whereas if K is larger *Daphnia* collapses much earlier due to the homoclinic bifurcation (O_1).

Put in biological terms, the oscillation in the *Daphnia* population makes it vulnerable to fish. This is because it periodically brings the density down to a level that is low enough to let a relatively small amount of fish prevent recovery of the population. If there is no such oscillation, a much higher fish predation is needed to let the *Daphnia* population collapse into the over-exploited state. Note that in general any factor that stabilizes *Daphnia* oscillations will help to prevent the homoclinic bifurcation that triggers the collapse of *Daphnia*.

These theoretical diagrams and the abstract terminology of dynamic systems theory may give the impression that we fly high in the sky far away from any down-to-earth biology. However, the next sections will show that this mathematical world does indeed reflect crucial mechanisms that govern plankton dynamics in the field.

4.3 SEASONAL DYNAMICS OF PLANKTON AND FISH

In this section the seasonal dynamics of the trophic cascade are discussed. The first part offers an overview of the patterns in *Daphnia* and algal biomass that are observed in the field. Subsequently, it is shown how the minimal plankton model presented in the previous sections can be used to help understanding the effect of seasonal dynamics of the fish community, but also how inclusion of the seasonal cycle in temperature and light should change the minimal view of food-chain dynamics. The section ends with a synthesis discussing how the results of the analysed trophic interactions are really intertwined with the effects of other mechanisms in practice.

The spring clear-water phase

One of the most distinctive events in the seasonal cycle of lake plankton communities is the clear-water phase that often occurs at the end of the spring. This dip in algal biomass can be partially caused by depletion of the available nutrients by the spring bloom of phytoplankton (Reynolds, 1984; Sommer *et al.*, 1986; Vyhnálek, 1989). However, usually, heavy grazing on algae by large zooplankton species that peak after the spring algal bloom is the main mechanism causing the clear-water phase (Lampert *et al.*, 1986; Luecke *et al.*, 1990; Carpenter *et al.*, 1993; Rudstam *et al.*, 1993; Sarnelle, 1993; Hanson and Butler, 1994a; Townsend *et al.*, 1994; Jurgens and Stolpe, 1995). The phenomenon can be especially spectacular in eutrophic lakes where this short clear period contrasts strongly with the turbid situation in the rest of the growing season.

As argued in the previous sections, the *Daphnia* outbreak and the subsequent clear-water phase can be seen as a predator – prey cycle. Unlike most predator – prey oscillations, however, the clear-water phase is just a single cycle that does not repeat. Usually, after the collapse of the spring peak *Daphnia* does not reoccur the rest of the year, except for an occasional extra peak in the autumn. The traditional explanation for the failure of *Daphnia* to recover from the spring collapse has been that the quality of the algal

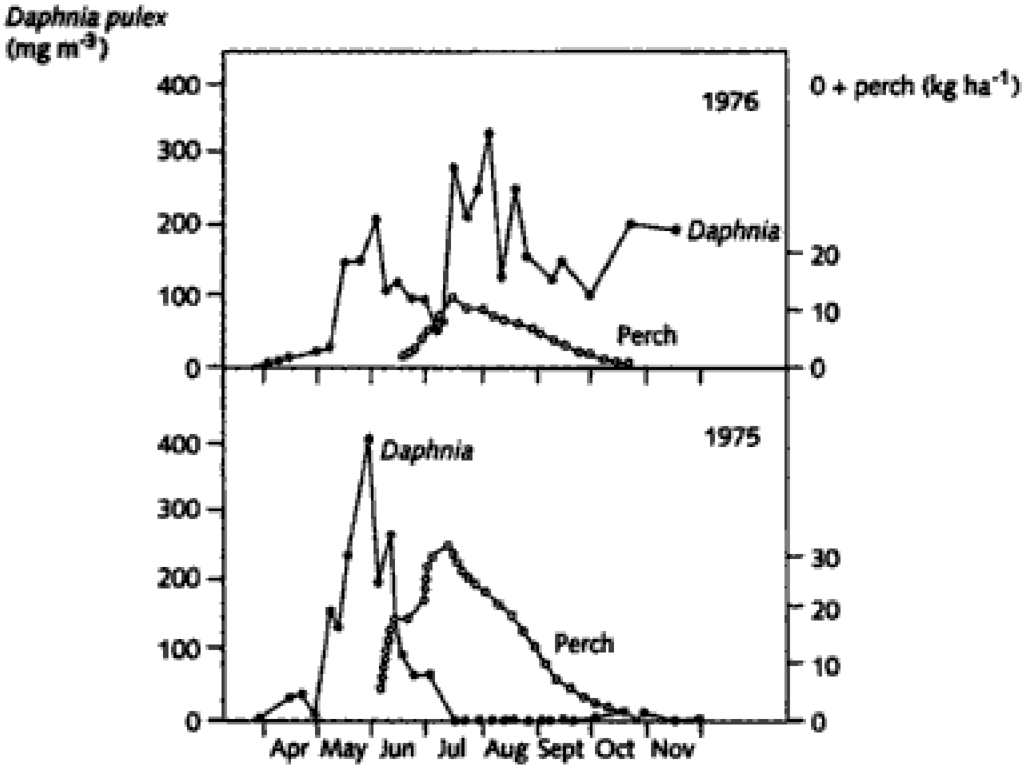


Fig. 4.27 **Comparison of biomass dynamics of age-0 yellow perch and *Daphnia pulex* in Oneida Lake for two contrasting years. *Daphnia* is able to recover after the spring collapse only when the density of young yellow perch is low. Redrawn from Mills and Forney (1983).**

food in summer is poor due to the increase in inedible colonies of blue-green algae (Threlkeld, 1985; Lampert *et al.*, 1986). With the rise in interest in the effect of planktivorous fish, however, evidence accumulated in favour of an alternative explanation. The early summer increase predation pressure due to the young-of-the-year fish development could be the main responsible mechanism of suppression of *Daphnia* in summer.

The long-term studies of the food-web dynamics in Lake Oneida show especially suggestive patterns in this respect (Mills and Forney, 1981; Mills and Forney, 1983). Young yellow perch are the most important planktivores in this lake. The biomass of a cohort of young-of-the-year perch increases sharply in early summer due to individual growth and this increase coincides with the collapse of *Daphnia* (Fig. 4.27).

In years with few perch, however, *Daphnia* usually recovers after the spring collapse, while in years with many perch *Daphnia* stays practically absent for the rest of the season. As mentioned earlier, analysis of data from many years suggests that there is a well defined critical perch density above which summer *Daphnia* populations are suppressed (Fig. 4.16).

The coincidence of the biomass increase of young-of-the-year fish with the collapse of *Daphnia* suggests that fish predation may actually be an important cause of this collapse. On the other hand, food shortage is likely to be a major problem for the zooplankters during the clear-water phase when algal biomass can be extremely low. A good example of how causality in these things can be unravelled is the analysis of the 1987 *Daphnia galeata* dynamics in Lake Mendota, Wisconsin, USA (Luecke *et al.*, 1990). The study shows that the number of eggs per adult female decreased dramatically in the course of the spring peak (Fig. 4.28a).

This number of eggs is an indication of the nutritional status, as starving individuals can not support the production of eggs. Thus the low egg numbers indicate a severe food shortage in the course of the clear-water phase. In July, the *Daphnia* density stays very low, but the numbers of eggs carried by the remaining animals are high again, suggesting that their nutritional status is not the problem. Using the egg numbers, one can estimate the potential reproductive rate of the population over the spring and summer. Comparison of this with the realized rate of increase gives an estimate of *Daphnia* mortality. Subsequently, the *Daphnia* consumption by the fish community was reconstructed over the same period, using fish censuses, stomach analysis and bioenergetic models. The results show that fish consumption could completely account for *Daphnia* mortality in summer, while contributing only 2% to the mortality at the collapse of the spring peak (Fig. 4.28b). Thus the emerging picture is that the spring peak of *Daphnia* collapses due to food shortage, while the populations are subsequently kept low by fish predation. A comparable analysis with similar outcome has been published for the Dutch lake Tjeukemeer (Boersma *et al.*, 1996).

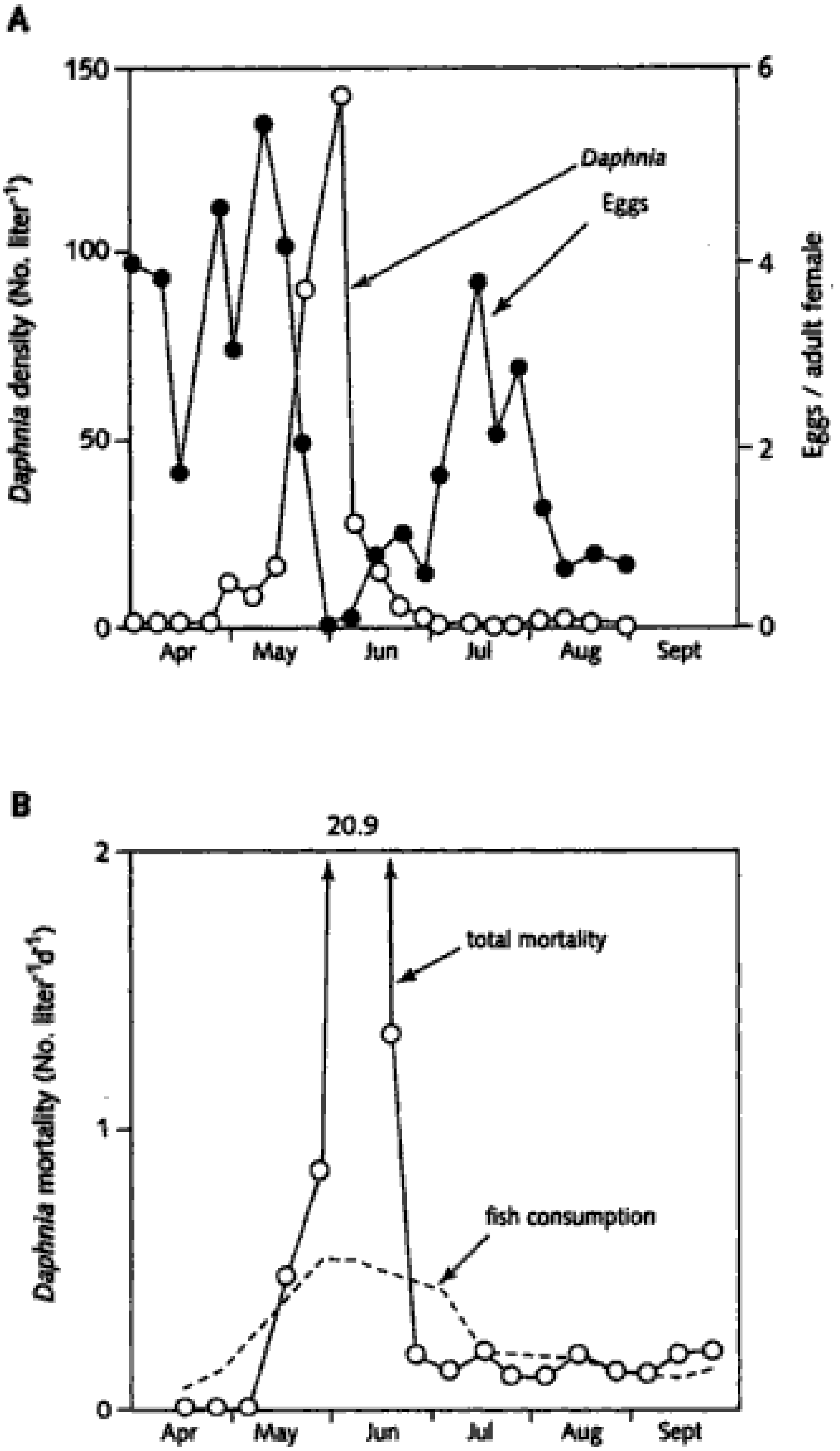


Fig. 4.28 (a) During the spring peak of *Daphnia galeata* in Lake Mendota, egg numbers per adult female drop dramatically, indicating food shortage. After the collapse egg numbers recover, suggesting that food shortage is not the reason that the population does not recover. (b) Estimated mortality of *Daphnia* during the spring collapse is much higher than can be explained from consumption by fish. In the summer, however, fish consumption can account for all *Daphnia* mortality. Redrawn from Luecke *et al.* (1990).

Other seasonal scenarios

Although the spring clear-water phase has received most attention, a single clear-water phase in the spring is just one of the possible scenarios of seasonal plankton dynamics. In particular, a repetition of the spring pattern in the autumn appears to be very common in lakes. Indeed, an international assemblage of lake plankton specialists (the Plankton Ecology Group, PEG) described the pattern with a spring and an autumn peak as the typical scenario for eutrophic lakes (Sommer *et al.*, 1986) (Fig. 4.29).

There are also several case studies that demonstrate that recurrent *Daphnia* peaks can cause several clear-water phases during the summer. Examples are the French Lake Aydat where three *Daphnia* peaks and corresponding clear-water phases were found in one year (Lair and Ayadi, 1989), and the German Lake Grosser Binnensee where four *Daphnia* peaks occurred in one season, three of which led to a conspicuous clear-water phase (Lampert and Rothhaupt, 1991).

It is likely that such repeated outbreaks of large *Daphnia* are only possible in lakes with few planktivorous fish in summer. An example that supports this idea is the development of the community dynamics in Bough Beech Reservoir, a newly created water reservoir in south-east England from which all coarse fish was removed in the first year (Munro and Bailey, 1980; Harper and Ferguson, 1982). Fish populations established slowly and

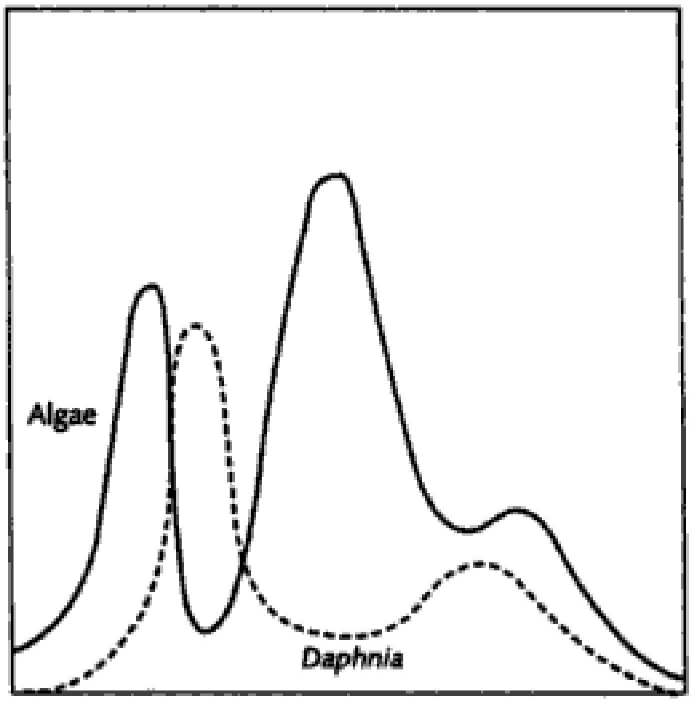


Fig. 4.29 A seasonal cycle with a spring and an autumn peak of large *Daphnia* and corresponding dips in algal biomass, considered the typical pattern for moderately eutrophic lakes. Redrawn from Sommer *et al.* (1986).

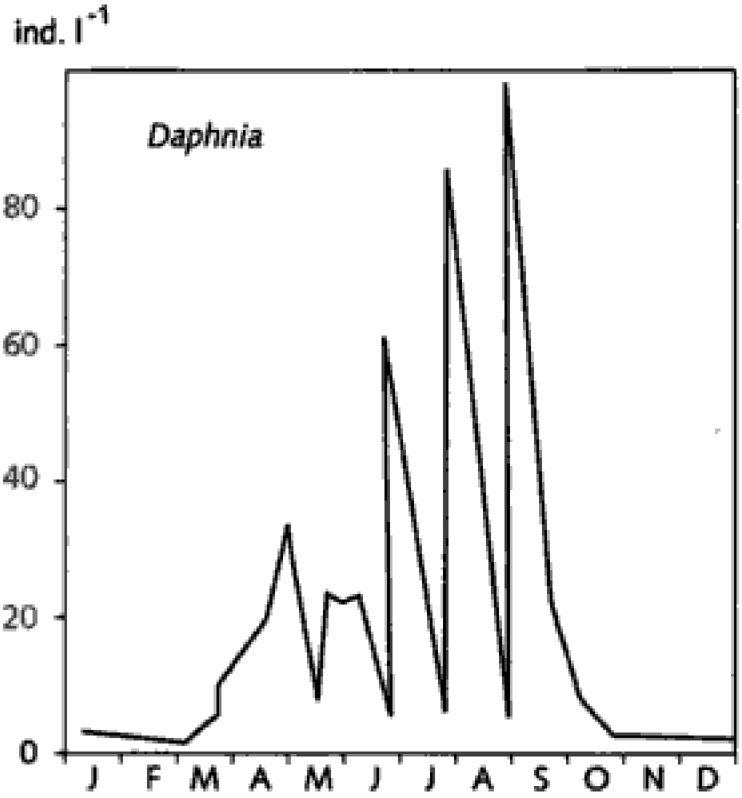


Fig. 4.30 A sequence of peaks in *Daphnia* numbers observed in the newly created Bough Beech Reservoir, UK, before the development of a significant fish stock. Redrawn from data of Harper and Ferguson (1982).

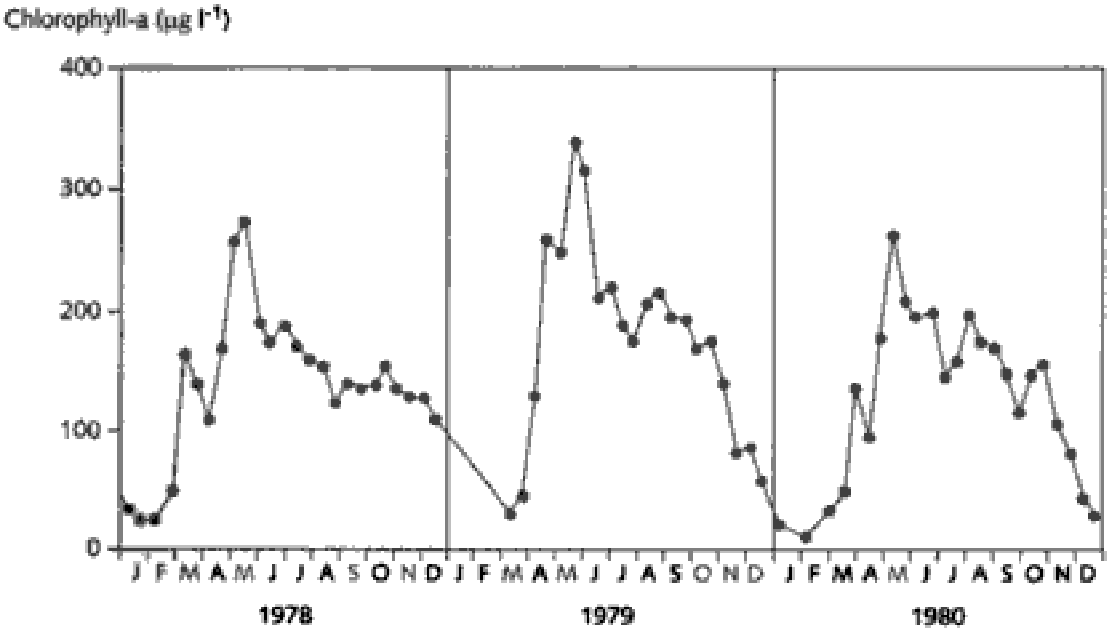


Fig. 4.31 Time-series of chlorophyll-a concentrations for three subsequent years in Lake Tjeukemeer, The Netherlands, illustrating the absence of pronounced clear-water phases in many hypertrophic lakes. From Scheffer *et al.* (1997c).

planktivorous young-of-the-year individuals became abundant only after several years. Recurring *Daphnia* peaks were among the most striking features of the plankton dynamics during the first years (Fig. 4.30), while in later years, when planktivorous fish established, *Daphnia* oscillations were greatly reduced.

Although *Daphnia* peaks and pronounced clear-water phases occur in many lakes, they can be entirely absent too. Hypertrophic lakes in particular are known to lack zooplankton induced clear-water phases (Gulati, 1983). Indeed, algal biomass follows a more or less smooth seasonal pattern in many of the relatively shallow and eutrophic Dutch lakes (Fig. 4.31).

Interestingly, isolated clear-water phases are sometimes observed in such hypertrophic lakes which do not necessarily occur in the spring, but take place even in the middle of the summer or in the autumn (Fig. 4.32).

In fact the timing of the spring clear-water phase can vary quite strongly in general. Obviously, annual differences in the weather will affect the timing of spring events. On the other hand fish predation is likely to play a role too. The spring clear-water phase has been reported to come relatively early in years when predation pressure from planktivorous fish on zooplankton is low (Temte *et al.*, 1988; Vanni *et al.*, 1990; Rudstam *et al.*, 1993).

Patterns across many lakes

The collection of cited case studies give a good impression of the large variety of seasonal dynamics that can be observed. Another way to characterize the timing and occurrence of clear-water phases is to analyse large

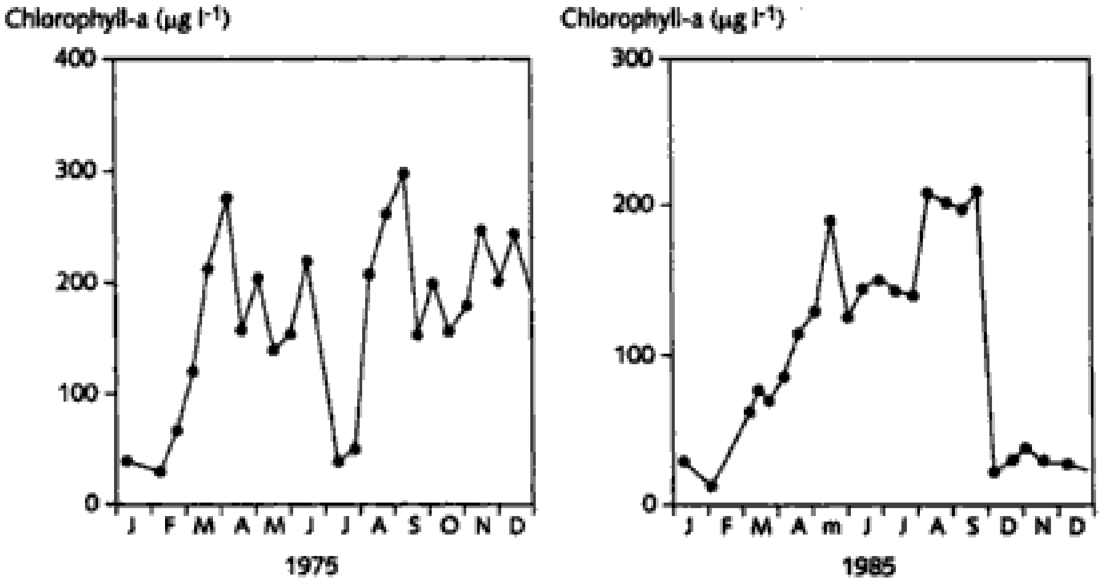


Fig. 4.32 Conspicuous clear-water phases in Lake Tjeukemeer some times occur in the summer (left panel) or autumn (right panel) rather than in the spring. From Scheffer *et al.* (1997c).

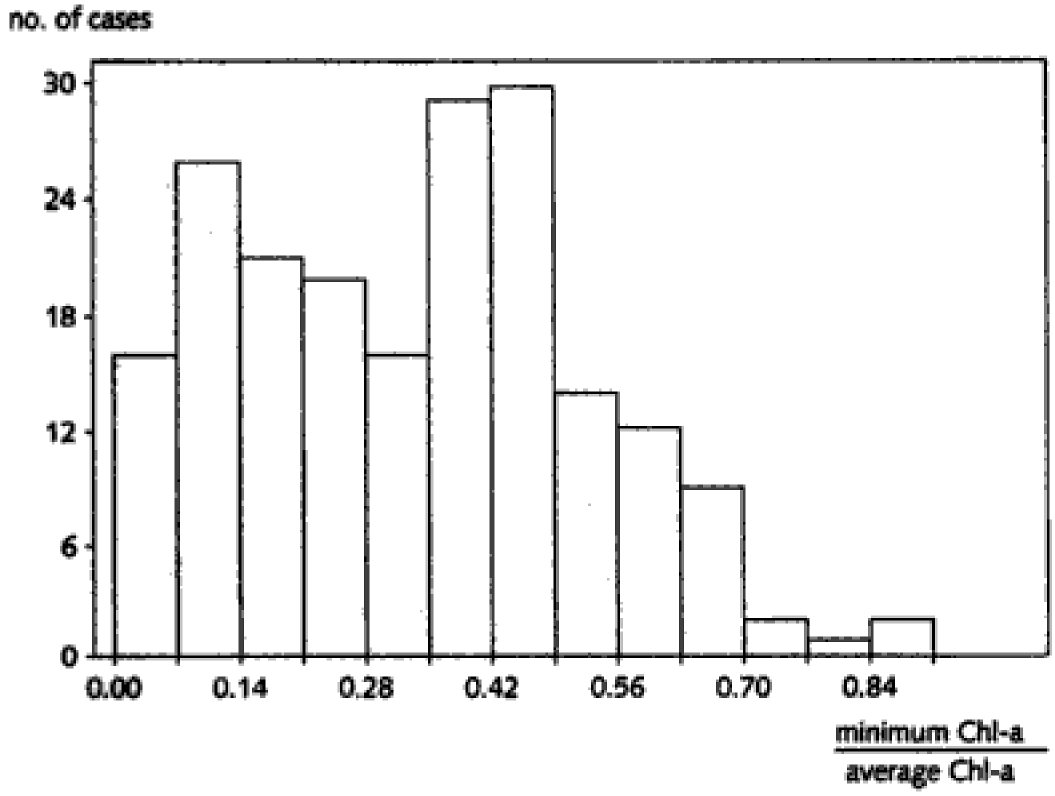


Fig. 4.33 Frequency distribution of the relative depth of the deepest dip (minimum/average of recorded values) in 257 time-series of chlorophyll-a from 71 Dutch lakes. Each time-series covers the period from 1st April to 1st November of a given year. From Scheffer *et al.* (1997c).

databases of time-series in a systematic way. As an example, consider the patterns found in a database with 257 seasonal series of chlorophyll-a concentrations from 71 shallow Dutch lakes that were sampled on a routine basis at least once every month in the period from April to October of the analysed years (Scheffer, 1997b). To check if clear-water phases can be distinguished from normal fluctuations in algal concentrations, the relative depth of the deepest dip in algal biomass was computed for each annual pattern (lowest Chl-a/average Chl-a over the April – October period). Indeed, this dip-depth has a distinct bi-modal distribution (Fig. 4.33).

The main peak in the figure shows that the minimum is often about 40% of the average chlorophyll level, but the hump on the left indicates that there is another set of cases in which a dip to about 10% of the average concentration occurs. The bi-modal pattern suggests that dips deeper than 25% of the average concentration represent a distinct phenomenon and can be classified as clear-water phases for further analysis. Such deep dips occur in 98 of the 257 analysed time-series.

A plot of the relative depth of the dip in chlorophyll against the average concentration (Fig. 4.34), reveals that clear water phases are almost absent in lakes with an average chlorophyll level higher than 150mg l^{-1} (Chi^2 P =

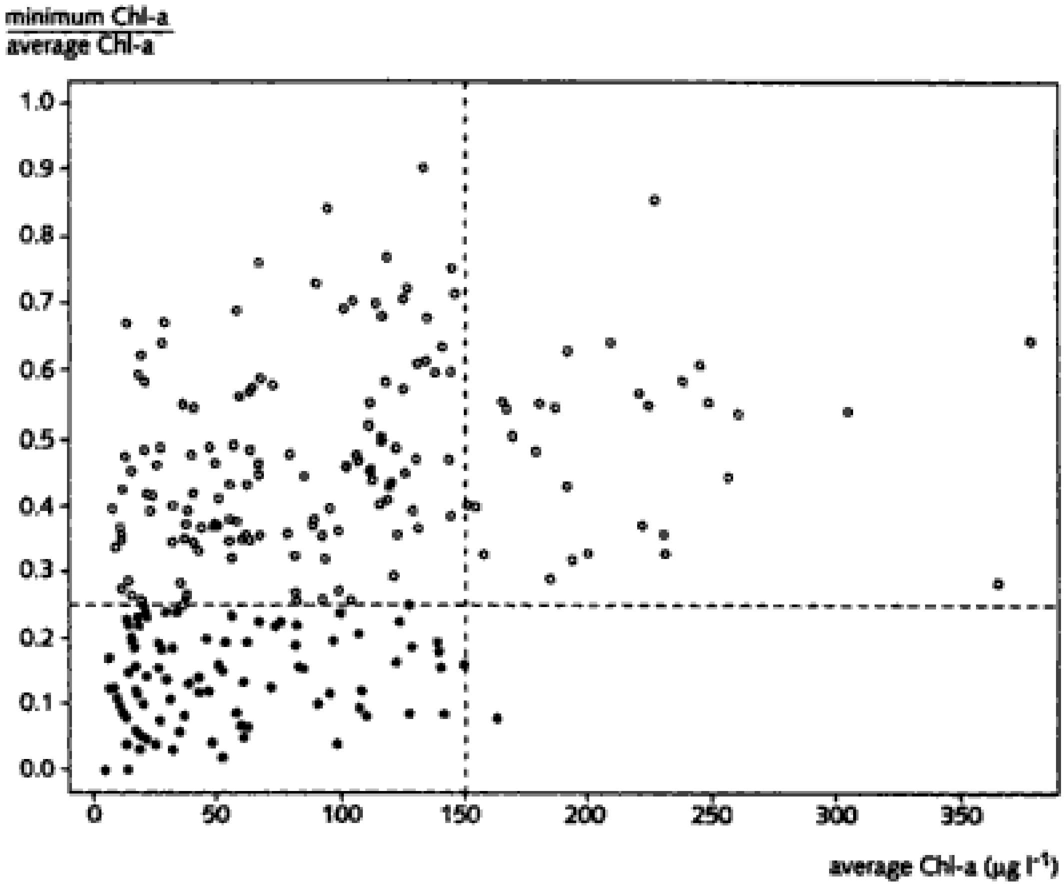


Fig. 4.34 Relative depth of the deepest dip in chlorophyll-a plotted against the average chlorophyll concentration in each of the analysed time-series (see Fig. 3.14). Drops in chlorophyll to less 25% of the average value of that time-series (heavy dots) are practically absent in lakes where the average level exceeds 150 mg l^{-1}. From Scheffer *et al.* (1997c).

0.0001). This result is in line with the earlier analyses by Gulati (1983) showing that strong peaks in zooplankton grazing and associated clear-water phases are rare in highly eutrophic situations.

To analyse the timing of clear-water phases, the date of occurrence of the dips deeper than 0.25 was checked. Deep dips in algal biomass appear to occur at any time of the studied period of the year, although the majority of the clear-water phases are found around May, with another peak of occurrences in the autumn (Fig. 4.35a). Obviously this fits well with reported bestuary of seasonal patterns described in more detailed case studies.

The analysed chlorophyll data set does not allow a check whether grazing is really the cause of the deep dips in algal biomass, as zooplankton densities are not available. However, Danish workers have systematically analysed time-series of zooplankton abundance from many lakes (Jeppesen *et al.*, 1996). To estimate the potential grazing pressure of zooplankton on the phytoplankton, they used the rule of thumb that cladocerans can consume a daily amount of algae equal to their own body weight, while copepods can consume only half their own weight per day. The results indicate that in

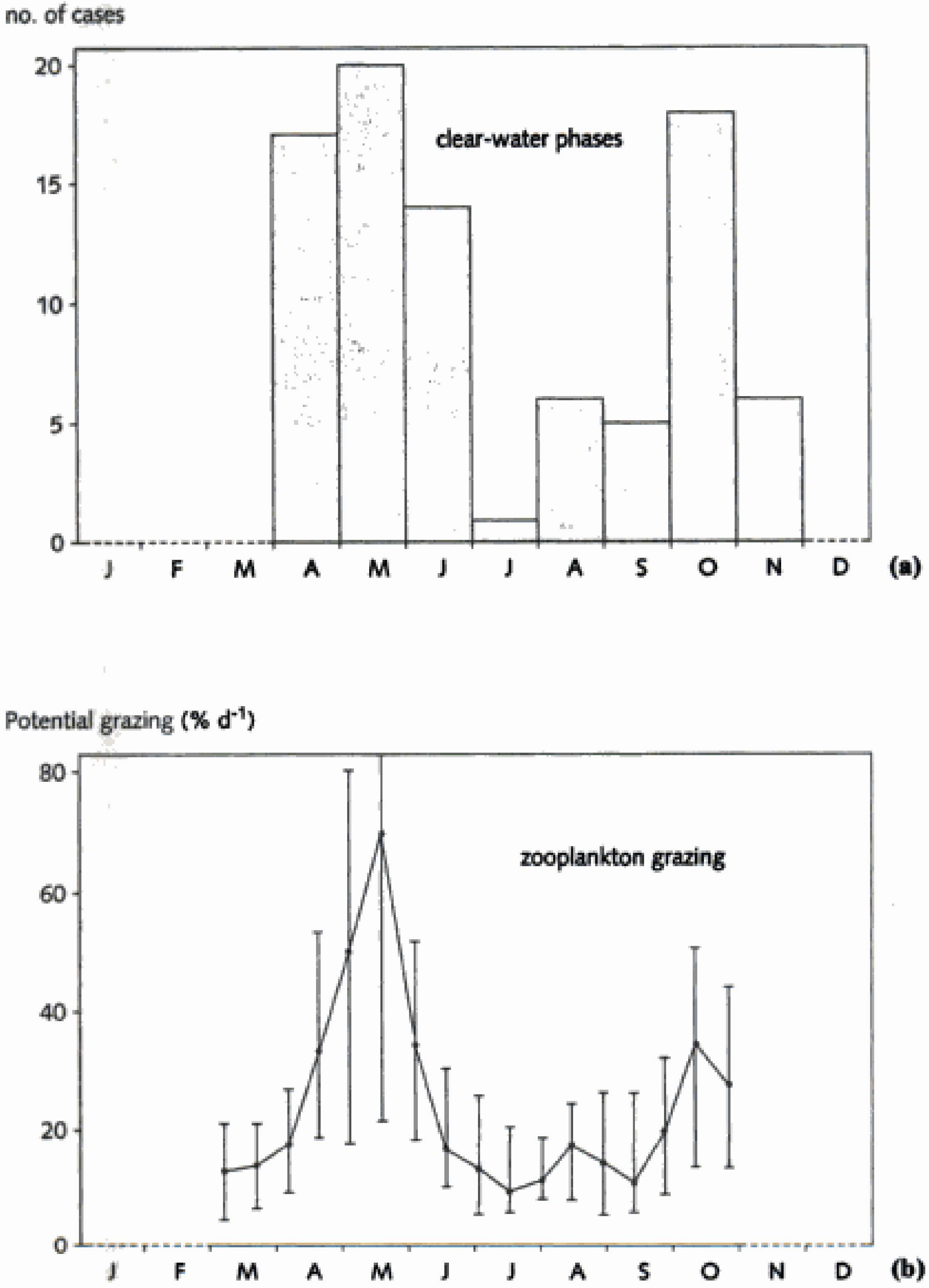


Fig. 4.35 (a) Frequency distribution of the moment of occurrence of drops in chlorophyll concentration below 25% of the average of a time-series (see Fig. 3.14) (heavy dots in Fig. 4.34). From Scheffer *et al.* (1997c). (b) Seasonal variation in the zooplankton grazing pressure on phytoplankton (% of the phytoplankton biomass ingested per day) for moderately eutrophic Danish lakes (TP 0.05–0.10 mg l^{-1}). The curve indicates the median, the bars represent the 25–75% percentiles. From Jeppesen *et al.* (1996).

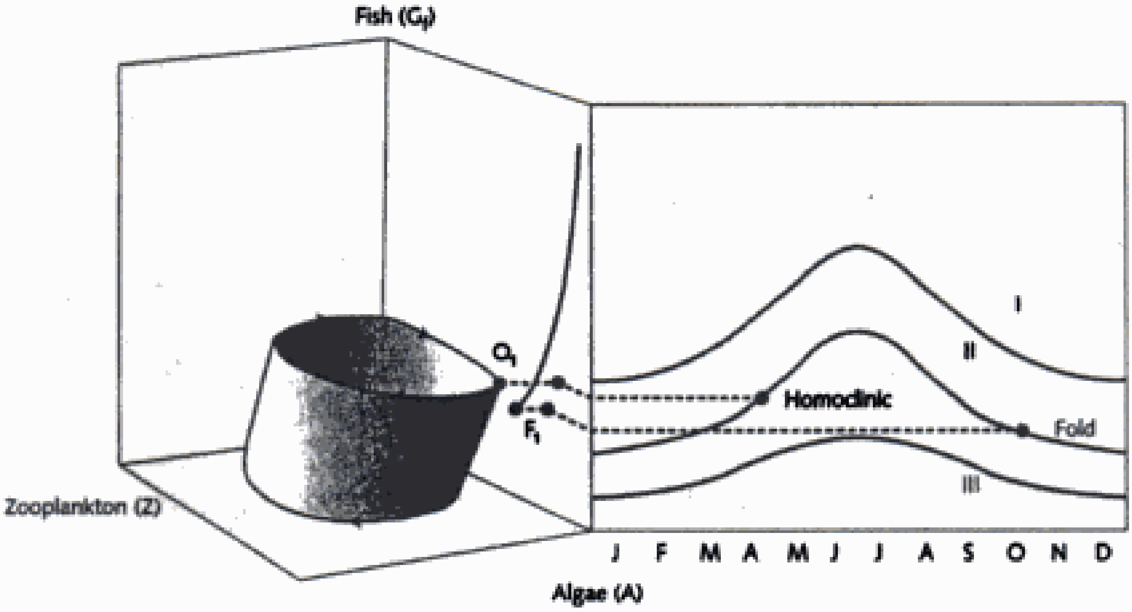


Fig. 4.36 Seasonal variation in biomass of planktivorous fish (right-hand panel) can cause the planktonic system (left-hand panel) to switch between cycles with periodic *Daphnia* peaks (cylinder in left-hand panel) and a stable algal dominated state (vertical equilibrium line in left-hand panel), depending on whether the two main bifurcations in the system are crossed. If planktivory is high (I) no *Daphnia* peaks will occur at all. When planktivorous fish stays low (III) *Daphnia* can remain abundant throughout the summer. However, intermediate scenarios cause *Daphnia* to collapse through a homoclinic bifurcation in the spring, leaving algae to dominate throughout the summer. From Scheffer *et al.* (1997c).

corresponding (technical) text sections. Here, the figure is tilted so that fish predation is on the vertical axis. At low fish predation there are zooplankton – algae oscillations (cylinder) whereas at higher fish predation there is a stable algal dominated equilibrium where zooplankton is overexploited by fish (curve rooted in F_1). These two modes of behaviour co-exist as alternative 'equilibria' for a small range of fish predation. Two 'bifurcation points' mark the transitions from the oscillatory regime to the stationary one (O_1, the 'homoclinic bifurcation') and vice versa (F_1, the 'fold bifurcation') .The exact development of planktivory over the year is hard to know, but if we assume that it can be mimicked in the model by a cycle in the consumptive capacity for plankton (G_f) with a maximum in summer (right-hand panel), three qualitatively different scenarios can be distinguished:

I Planktivory remains entirely above the threshold at which *Daphnia* can recover from over-exploitation (the fold bifurcation, F_1).

II The annual minimum in planktivory is below this threshold but the maximum is above the threshold at which the oscillating *Daphnia* state collapses due to the homoclinic bifurcation (O_1).

III Planktivory stays entirely below the homoclinic threshold (O_1) at which *Daphnia* would collapse.

The first scenario corresponds to lakes where large zooplankters are absent throughout the year and there is no clear-water phase. The second situation corresponds to the classical clear-water phase scenario, with a *Daphnia* peak in the spring but low *Daphnia* numbers and high algal biomass in summer. The third scenario represents a situation where *Daphnia* remains oscillating throughout the summer. Indeed, as mentioned earlier, all of these scenarios are observed in lakes, and model results suggest that differences in their fish communities could be a reasonable explanation.

As argued, scenario *I* is especially common in hypertrophic shallow lakes (Fig. 4.34), where, as explained in section 4.5, the fish stock can be very high due to the availability of benthic food. Since these benthivorous fish switch to feeding on zooplankton when it is available, the potential grazing pressure on *Daphnia* is high even in the absence of young-of-the-year fish (Jeppesen *et al.*, 1996).

The model suggests that the collapse of *Daphnia* at the end of the clear-water phase and their subsequent absence in summer (scenario *II*) corresponds to a 'homoclinic bifurcation'. The essence of this bifurcation in biological terms is that *Daphnia* collapses due to food shortage (the limit cycle), and that this brings the population down to a level that is low enough to let a relatively small amount of fish prevent recovery (the over-exploited state). Indeed, this corresponds precisely to the mechanism revealed by the analysis of the factors that drive the plankton dynamics in Lake Mendota (Fig. 4.28).

Note that it is the starvation collapse of the *Daphnia* population that makes it vulnerable to fish. If there is no such oscillation in *Daphnia*, a much higher fish predation is needed to let the *Daphnia* population arrive at the over-exploited state, as explained more thoroughly in the corresponding technical section (Fig. 4.26). This implies that, factors that stabilize *Daphnia* oscillation will help to prevent the collapse of *Daphnia*. As argued above, vegetation may help to stabilize *Daphnia* dynamics in shallow lakes by supplying refuges in which the animals aggregate and detritus that can be used as an alternative food source.

It is interesting to note that the mechanism that causes the famous snowshoe hare – lynx cycles is thought to be closely related to the emerging picture of the clear-water phase. The decline in the hare population that sets the cycle is initiated by a food limitation of the hares that have overgrazed the vegetation. When the hare population has collapsed to low numbers, the impact of the predator populations, whose numbers stay roughly constant, becomes increasingly important, keeping the hare population low for an extended period (Keith, 1983; Keith, 1990).

Modelling seasonality of plankton

Fish predation is not the only thing changing over the year. Light and temperature are probably the most i seasonal cycle in ecosystems and both factors affect the phytoplankton – zooplankton system directly. Therefore, the current approach (Fig. 4.36) of studying the effect of changing fish predation pressure in the spring and summer is really too simple to describe the complete annual pattern of plankton dynamics. The consequences of seasonality for the dynamics of the plankton can be analysed in a more realistic way by periodically varying all parameters of the model that should depend on light or temperature. The simplest way to do this is to impose a sinusoidal variation of the value of the relevant model parameters over the year (Scheffer *et al.*, 1997c).

In eutrophic lakes, light limitation tends to set an upper limit to algal biomass. We therefore assume the carrying capacity (K) to be a function of light. The parameters related to the metabolism of algae, zooplankton and fish (r, g, m, G_f) will depend upon temperature. The summer maximum in the temperature of a lake is usually delayed compared with the maximum in irradiation. For simplicity we neglect this phase shift and many other subtleties like the exact shapes of temperature and light dependence of the organisms and simply mimic the effect of seasons by multiplying each of those parameters by a seasonal impact, σ_t, which is a periodic function of time t (days):

$$\sigma_{(t)} = \frac{1-\varepsilon\cos\left(\dfrac{2\pi t}{365}\right)}{1+\varepsilon} \tag{14}$$

where $t=0$ stands for the first of January. In this formulation the minimum value of each parameter (i.e. the value in the middle of the winter) is equal to its maximum (in summer) multiplied by $(1-\varepsilon)/(1=\varepsilon)$. Thus, the summer maximum of a parameter corresponds to the default value and e determines the amplitude of seasonal change.

In addition to the temperature induced variation, fish predation pressure (G_f) should show a seasonal variation due to the reproductive cycle. Assuming this cycle to be sinusoidal and in phase with the variation in temperature and light we can include the effect simply by multiplying G_f with an extra seasonal impact (σ). Thus the complete seasonal model becomes:

$$\frac{dA}{dt} = \sigma_{(t)} r A\left(1-\frac{A}{\sigma_{(t)}K}\right) - Z\sigma_{(t)} g\frac{A}{A+h_A} + d\left(\sigma_{(t)}K - A\right) \tag{15}$$

$$\frac{dZ}{dt} = e\sigma_{(t)} g Z\frac{A}{A+h_A} - \sigma_{(t)} m Z - \sigma_{(t)}\sigma_{(t)} G_f\frac{Z^2}{Z^2+h_z^2} \tag{16}$$

A simple way to look at the consequences of such a seasonal variation is to compute the cycles and equilibria of the system for each day of the year with

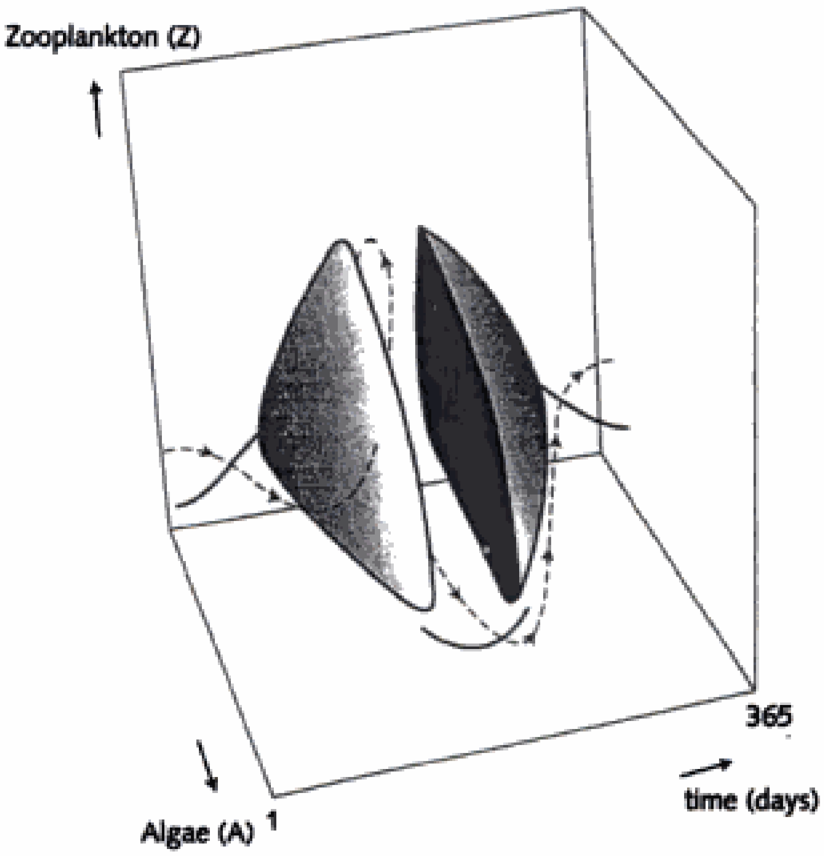


Fig. 4.37 The attractors (equilibria and cycles) of the seasonal plankton model constructed by computing the cycles and/or stable equilibria separately for each day *t* of the year using the appropriate value of σ_t. The dotted line represents the true asymptotic behaviour of the seasonally forced model. From Scheffer *et al.* (1997c).

the appropriate seasonal values of the parameters and assemble them into a picture that shows the entire year (Fig. 4.37).

This representation shows that plankton has the tendency to oscillate in the spring and autumn whereas it is stationary with high algal biomass in summer and stationary with low algal biomass in winter. The discontinuities show that the transitions to and from the turbid summer equilibrium are catastrophic (corresponding to the homoclinic and fold bifurcations). However, the dynamic behaviour of a periodically forced system can not really be inferred from such an assemblage of frozen asymptotic behaviours. This becomes apparent if real simulated dynamics are plotted in the same figure (dashed line in Fig. 4.37). The depicted simulated path shows the asymptotic behaviour to which the seasonal model always converges after many simulation years. Therefore, this seasonal cycle is a real attractor, comparable to the stable points and limit cycles of the non-seasonal model. This seasonal attractor follows the artificially constructed 'frozen attractor set' only approximately. The discrepancy is understandable. The populations never have time to reach the asymptotic behaviour corresponding to the conditions at a certain day of the year because the conditions change continu-

their stable and unstable manifolds, will smoothly change as parameter values are varied and incidentally collide at bifurcation points.

If, for example, fish predation (G_f) decreases, the turbid regime can disappear if the two cycles outside the torus collide. This is analogous to the fold bifurcation in the constant parameter case (F_1 in Fig. 4.23). Also the quasi-periodic clear-water regime can disappear. This happens when the saddle cycle 'collides' with the torus, thus giving rise to a bifurcation called *torus destruction*. This bifurcation corresponds to the homoclinic bifurcation of the constant parameter case (O_1 in Fig. 4.23).

Close to the torus destruction, the nature of the torus changes. Because the torus is very close to the saddle cycle, the trajectories on the torus remain very similar to this saddle cycle (the unstable equilibrium in the constant parameter case) from time to time for a long period. As a result the torus is actually composed of alternate episodes of regular clear-water occurrence with periods in which there are no zooplankton peaks. If one increases fish predation (G_f), the saddle cycle approaches the torus further and the phase of turbid water becomes longer and longer. This implies that the transition from a clear-water regime to a turbid regime is not characterized by gradually less pronounced clear-water episodes but, instead, by increasingly rare clear-water phases.

One more phenomenon, called *frequency locking* is important for understanding the seasonal model. When a periodically forced nonlinear system has a torus, it can happen that, for a particular value of the parameters, a cycle exists on that torus which attracts all other nearby trajectories. This implies that the behaviour of the system becomes periodic (on torus) and will show up as such on the Poincaré section. A simulation trajectory will no longer cover the torus densely, as it converges to the periodic cycle. (Nonetheless, the complete torus still exists as a so-called invariant set, which means that any trajectory starting on the torus will remain on it while approaching the cycle.) Remarkably, such periodic solutions on the torus persist when the values of parameters are varied slightly. This is because the external frequency tends to 'lock' the system, in the sense that the system is forced to behave periodically with the same period as the forcing function or with a period that is an integer multiple of it. In our case, seasons can force the algae – zooplankton communities to behave periodically with a period of 1,2,3, . . . years, even though the system would have the tendency to cycle at another frequency in the absence of seasons. In general, the regions of the parameter space in which the system is locked are larger if the amplitude of the season is larger. Like torus destruction and the tangent bifurcation of cycles, frequency locking is a bifurcation of the system and can be detected as such by the appropriate software.

The best overview of the behavioural repertoire of the seasonal model can be obtained from a bifurcation diagram (Fig. 4.39). On the vertical axis ($\varepsilon = 0$) there are two bifurcation points F_1 and O_1 corresponding to the fold and homoclinic bifurcations shown in Fig. 4.23. These points are the roots of the two bifurcation boundaries separating regions 1, 2 and 3 in which the model has qualitatively different asymptotic behaviours. The top boundary corresponds to torus destruction and, as pointed out, is actually not a curve but a very narrow band with complex structure. As this

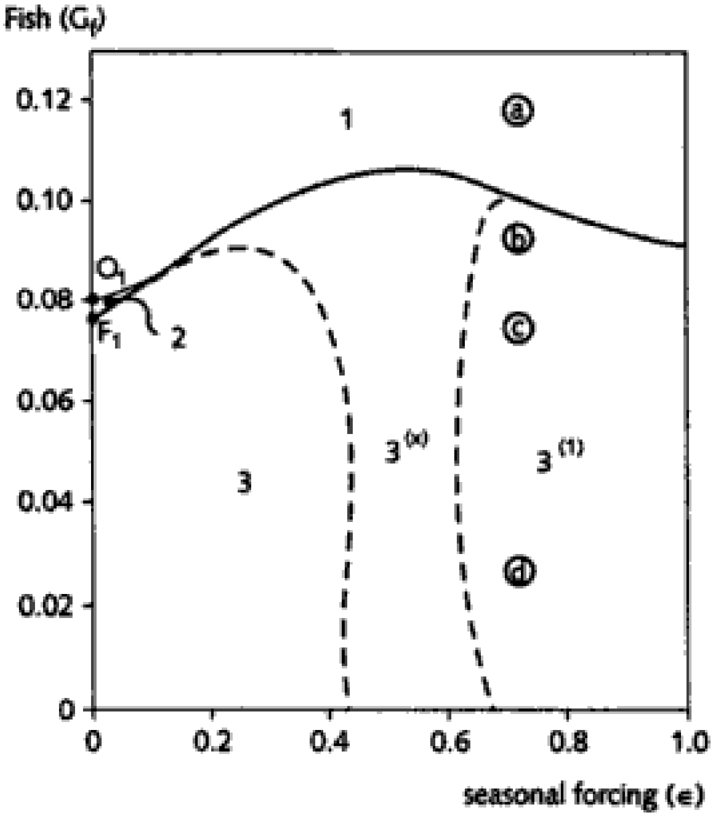


Fig. 4.39 Bifurcation diagram showing how seasonal forcing and planktivory affect the behaviour of the model. The bifurcation boundaries merging from points O_1 and F_1 divide the parameter space into three distinct regions where the asymptotic behaviour of the model is different (see text). In region (1), clear-water phases are absent, while in region (3) clear-water phases occur. In region (2) the asymptotic behavioural regimes of region (1) and (3) co-exist. On the left side of the dashed curves the dynamics in region ($3^{(1)}$) are not locked with the rhythm of the seasons (see text), on the right side of these curves (region $3^{(1)}$) the system behaves periodically with a period of one year. The dynamic behaviour at the parameter settings marked as a, b, c and d is illustrated in Fig. 4.40. From Scheffer *et al.* (1997c).

band is crossed from below, the torus disappears through homoclinic contacts. The boundary rooted at F_1 is a tangent bifurcation curve. As this curve is crossed from above, a stable cycle and a saddle cycle collide and disappear. Thus, region 1 contains a unique attractor, namely a stable seasonal cycle with high algal biomass (Fig. 4.40a) corresponding to the 'turbid equilibrium' of the constant parameter case. In the small region 2, this turbid regime coexists with a quasiperiodic regime characterized by clear-water episodes. Region 3 is characterized by the existence of a torus, although in many subregions ($3^{(i)}$) the regime is locked to be purely periodic with a period of *i* years (see below). In our case all of these subregions are small with the exception of region $3^{(1)}$ where the behaviour on the torus is locked to a period of one year. The bifurcation line demarcating the border of region $3^{(1)}$ corresponds to a tangent bifurcation of cycles on torus. Although numerical experiments have shown in which zone of the parameter space it occurs ($3^{(x)}$) the exact position could not be

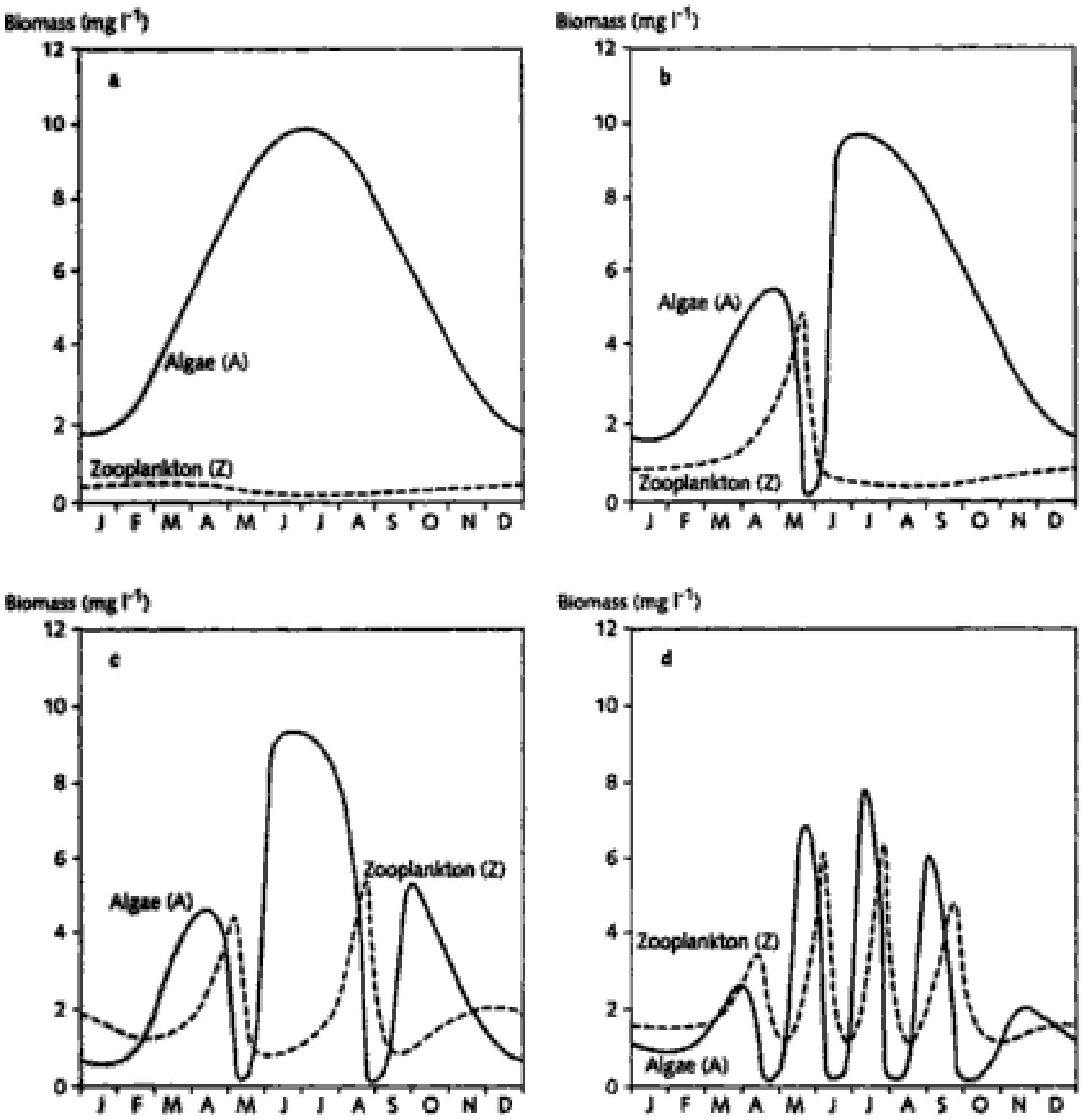


Fig. 4.40 Seasonal dynamics of the plankton model for parameter setting corresponding to points a, b, c and d in Fig. 4.39 ($\varepsilon = 0.7$; $G_f = 0.12, 0.09, 0.075$ and 0.025 respectively). From Scheffer *et al.* (1997c).

detected due to numerical problems. In this parameter zone ($3^{(x)}$) several small islands occur where cycles with a period of more than one year exist. At a seasonal forcing of $\varepsilon = 0.7$ which is probably reasonable for simulating temperate lakes (Scheffer *et al.*, 1997c) the frequency of oscillations in the plankton tends to be locked with that of the seasons, in such a way that the same pattern of plankton dynamics repeats each year (Fig. 4.40).

Behaviour of the seasonal plankton model

The simplest way to investigate the seasonal model is to simulate its behaviour for different parameter settings. The effect of fish (G_f) is shown in the simulations presented in Fig. 4.40. If fish predation on zooplankton is very high (region 1) the seasonal cycle is simple (Fig. 4.40a). *Daphnia* biomass remains low throughout the year and algal biomass develops smoothly with a minimum in winter and a maximum in summer. If the predation pressure from fish is less extreme, the spring bloom of algae is followed by a zooplankton peak which causes a clear-water episode with low algal density (Fig. 4.40b,c,d). What happens after this clear-water phase depends on the predation pressure by fish. At high fish density the spring dip is the only clear-water phase of the season (Fig. 4.40b). If planktivory is lower, a second *Daphnia* peak occurs at the end of the summer (Fig. 4.40c). At very low fish densities, the number of *Daphnia* peaks that occur over the summer can increase up to four (Fig. 4.40d). Note that the first clear-water phase occurs remarkably constantly around May, although there is a dependency on fish predation pressure (G_f). With increasing fish the spring clear-water phase tends to occur later (Fig. 4.40).

Increasing the fish biomass in the model gradually from the situation depicted in figure 4.40b to that shown in figure 4.40a, a remarkable kind of transition can be observed. In a narrow critical range of fish densities (around the border between regions 1 and 3 in figure 4.39) the clear-water phase disappears. However, it does not become gradually less pronounced but rather increasingly rare. In each individual year, the clear-water phase is either fully present or completely absent, but with increasing fish density we go gradually from a situation in which the clear-water occurs every year to a situation in which it never happens. In this narrow transition zone regular cycles with a length of more than one year are found. Clear-water phases may occur, for instance, two out of three years (Fig. 4.41a), or two out of four years (Fig. 4.41b).

However, this parameter band also contains very long cycles that judging from the time-series can be considered erratic for all practical purposes (Fig. 4.41c). Obviously, such multi-year cycles are unlikely to be found in nature since they only occur over a very small region in the parameter space. Taking environmental variability into account, however, lakes which are 'close' to the border of having-or-not-having clear-water phases should be expected to behave in a rather unpredictable way. They may or may not display a clear-water phase in any given year. The simulation results (Fig. 4.41) suggest that in such lakes, the timing of clear-water phases can be rather erratic. Isolated clear-water episodes can occur in summer or even in the autumn.

This minimal model is of course a crude simplification of reality. The aim, however, is not to be complete, but rather to check which part of the bestuary of behaviour that is observed in the field can in theory be explained by the few ingredients included in the model. The analysis shows that in this case the ingredients are indeed sufficient to generate an array of seasonal patterns of plankton dynamics that corresponds surprisingly well to the patterns observed in the field. As in real lakes, a clear-water phase can be absent or occur up to four times a year, scenarios with more than two

Mendota where the relationship between fish and plankton dynamics has been analysed for many years, it has indeed been noted that the spring clear-water phase can come earlier when the density of planktivorous fish is low (Temte *et al.*, 1988; Vanni *et al.*, 1990; Rudstam *et al.*, 1993). Even the peculiar prediction that incidental isolated clear-phases can occur in the summer or autumn in lakes that normally show no clear-water phase (Fig. 4.41) is supported by data (Fig. 4.32).

Importantly, the results are quite independent of the precise model formulation. The use of more realistic time lags between the light and temperature forcing functions and variation in their amplitudes hardly changes the patterns produced. Also, the dynamic patterns produced by a comparable but much more elaborate model (Doveri *et al.*, 1993) are very similar to the repertoire of the minimal model shown here. In that model, nutrient recycling and the dynamics of young-of-the-year fish are modelled dynamically, the role of adult fish that prey on zooplankton facultatively is modelled explicitly, and realistic temperature and light scenarios at different latitudes are analysed.

But many more mechanisms operate in the field

This robustness of the results suggests that they are not an artifact of particular model formulations and that, indeed, much of the observed seasonal dynamics of *Daphnia* and algal biomass can be interpreted simply as the result of their predator – prey interaction and the fact that everything, including planktivory, speeds up in the summer and slows down in the winter. However, although the correspondence between generated patterns and field observations is encouraging, it does not imply that the modelled mechanisms need to be entirely responsible for all of these patterns in the field. Other mechanisms may cause the same patterns, or what is probably very common, help to cause the pattern (Scheffer *et al.*, 1994b).

Indeed, there are many more mechanisms involved in driving plankton dynamics in reality. Depletion of nutrients, for instance, may contribute to the collapse of the spring bloom of algae (Reynolds, 1984; Sommer *et al.*, 1986; Vyhnálek, 1989). Also, many organisms can produce dormant structures and the timing of production and emergence of such resting stages usually depends on temperature, light and other clues. Cladocerans, for instance, tend to produce inert resting stages ('ephippia') at the end of the spring clear-water phase. This has been interpreted as a strategy to survive a period of food shortage (Slobodkin, 1954; Hutchinson, 1967) or to avoid the early summer period of predation by juvenile fish (Hairston, 1987). In the spring these ephippia can emerge massively to form the off-set of the spring population peak that grazes down the spring bloom of algae (De Stasio, Jr, 1990). Although such mechanisms obviously have a large effect on the seasonal patterns, it could be argued that the fact that largely the same population dynamics can be generated without such biological timing mechanisms suggests that they are 'post-hoc' adaptations to optimize the reproductive moment with respect to food availability and predation risk, rather than the prime forces driving the seasonal pattern.

Importantly, in lakes with abundant submerged vegetation, summer plankton dynamics are usually very different from those in unvegetated systems. As explained in the previous section, phytoplankton productivity is often low in vegetation stands due to factors like nitrogen limitation, shading, increased sinking losses and allelopathy. As a result the food situation for zooplankters can be unfavourable. Indeed, densely vegetated lakes often have low densities of both phytoplankton and *Daphnia* during the summer (Meijer *et al.*, 1990; Van Donk *et al.*, 1990; Van den Berg *et al.*, 1997). On the other hand vegetation can act as a refuge against fish predation, and detritus may act as an alternative food source supporting a high *Daphnia* population throughout the summer in some situations (Carvalho, 1994). The effect of vegetation on plankton dynamics is discussed in detail in the next chapter.

Inedible algae

A potentially important aspect that is not considered in the model is the presence of inedible cyanobacteria. The analysis suggests that the absence of clear-water phases can be explained as the effect of a high density of planktivorous fish. The time-series analysis of Dutch and Danish data indicates that the absence of clear-water phases is especially frequent in hypertrophic lakes with high algal biomass (Fig. 4.34, Fig. 4.35b). Indeed, fish biomass is typically very high in such lakes, and this may well explain the absence of clear-water phases. However, hypertrophic shallow lakes are also frequently dominated by cyanobacteria as explained in the previous chapter. Several studies show that these algae are usually not well edible (Arnold, 1971; Schindler, 1971) and that *Daphnia* growth can be severely reduced in their presence (Gliwicz, 1990; Gliwicz and Lampert, 1990). Also, toxic substances released by cyanobacteria have been shown to reduce filtering rates of daphnids by 50% or more (Haney *et al.*, 1994). Obviously, such adverse effects of cyanobacteria may well contribute to the absence of clear-water phases.

At first sight the size structure of the zooplankton community of hypertrophic lakes seems to indicate that fish is the dominant factor involved. The community is typically dominated by small zooplankters. As explained earlier, this is thought to be characteristic of situations with a high predation pressure from planktivorous fish. Selective predation of fish removes the larger individuals (Brooks and Dodson, 1965; Shapiro and Wright, 1984; Hambright, 1994; Seďa and Duncan, 1994) and *Daphnia* also tends to change its life history strategy, becoming smaller in response to chemical cues released by fish (Weider and Pijanowska, 1993; Engelmayer, 1995). However, it has also been shown that large *Daphnia* species are less able than small ones to forage and grow in the presence of filamentous blue-green algae (Hawkins and Lampert, 1989; Gliwicz, 1990; Gliwicz and Lampert, 1990), thus the absence of large *Daphnia* from hypertrophic lakes may at least in part be caused by the poor food situation.

Causality is difficult to unravel in this matter, but an extensive analysis of data from many Danish lakes indicates that top-down control by fish is probably the dominant mechanism preventing large zooplankters from peaking and grazing down algal biomass in most cases (Jeppesen *et al.*, 1996). Many of the hypertrophic Danish lakes that entirely lack episodes of high zooplankton grazing pressure are dominated by easily edible green algae. Also the mid-summer decline of *Daphnia* in lakes of lower nutrient contents occurs every year in many Danish lakes, irrespective of whether or not cyanobacteria are present.

An interesting study showing the complexity of the interaction of inedible cyanobacteria and *Daphnia* in a eutrophic lake has been published by Sarnelle (1993). The natural seasonal pattern in the lake was that the species composition of algae switched from diatoms and green algae during the spring bloom to small flagellate algae during the clear-water phase and filamentous cyanobacteria after the clear-water phase. At first sight this seems to support the view that grazing favours dominance of the algal community by the 'grazing resistant' cyanobacteria as it eliminates edible competitors. However, after a fish kill, *Daphnia* grazing was able to retard succession to 'inedible' cyanobacteria in the summer. Instead the phytoplankton community remained dominated by edible small flagellates. The idea that in the absence of fish predation *Daphnia* could suppress filamentous blue-green algae was confirmed by enclosure studies in the lake. Thus cyanobacteria may affect *Daphnia* development negatively but *Daphnia* may also suppress cyanobacteria.

The observations of Sarnelle (1993) suggest that the effect of *Daphnia* grazing on algal composition may depend on grazing intensity. Strong *Daphnia* grazing seems to lead to a dominance by small flagellate algae, while mild grazing may favour 'inedible' cyanobacteria. This view is supported by observations of Danish workers (Jeppesen, pers. comm.). The mechanisms through which these two very different groups can survive grazing pressure are entirely different. Selection of grazers against the large colonies is an intuitively straightforward mechanism that may favour blue-green algae. On the other hand larger algae have lower growth rates in general (Reynolds, 1988). Therefore, if the population suffers losses due to grazing (or sinking or flushing) these are not easily compensated for by growth. The small flagellate algae that are typical for heavily grazed situations, on the other hand, have very high growth rates. Thus even severe losses can be compensated for by the fast reproduction. As explained in the previous chapter this is also the reason why fast growing

benthivorous fish is often by far the most abundant group in terms of biomass. In small eutrophic lakes it is not unusual for bream (*Abramis brama*), carp (*Cyprinus carpio*) and roach (*Rutilis rutilis*) to reach densities of over 500–1000 kg ha^{-1} (Grimm and Backx, 1990; Jeppesen *et al.*, 1990a; Meijer *et al.*, 1990). Although adults of these species feed mainly on benthic invertebrates relatively large bream have been shown to switch back to zooplanktonic food when large zooplankton is sufficiently abundant (Lammens, 1985; Lammens *et al.*, 1985). As a result, the potential predation pressure on *Daphnia* can be high in such lakes even when planktivorous young-of-the-year are rare. As argued in the previous section, the resulting high predation pressure all year round can prevent the occurrence of a spring clear-water phase (scenario I in Fig. 4.46). Thus, the systematic absence of clear-water phases in eutrophic shallow lakes (Fig. 4.34) could in fact be interpreted as an indirect effect of the high benthic production in such lakes. The high biomass of zoobenthos 'pumps up' fish density, leading to an increased predation pressure on the alternative but less important food source, zooplankton (Jeppesen *et al.*, 1996).

This mechanism has been described in a more general context by Holt (1977). When a generalist predator is food-limited, increase of one prey type can lead to decrease of another one due to an increase in predator abundance. Since at first glance the effect in the field can look much like that of direct competition between the two prey types the phenomenon is called 'apparent competition'.

The support of *Daphnia* populations by detritus as an alternative food source in (vegetated) shallow lakes mentioned earlier can also be seen as an apparent 'competitive' effect, in this case an indirect negative effect of detritus on phytoplankton. This is one of the mechanisms promoting *Daphnia* abundance in vegetated situations, whereas the apparent competition with benthos promotes top-down control of *Daphnia* in shallow lakes with little vegetation.

Competition for benthic food

The dense populations of benthivorous fish in many shallow lakes exploit the benthic food intensively. Individual growth is often very low ('stunted') in populations of benthivores, indicating a poor food situation. In Lac Hertel (Quebec) for instance, four of the five benthivorous fish species showed stunted growth, while the two non-benthivorous species grew well. The view of stunted fish populations that cause a continuously high predation pressure on benthos is confirmed by the typical response to reduction of the fish stock: an increase of invertebrate biomass and strongly enhanced growth of individual fish (Giles, 1992).

Note that such 'stunted' fish populations do not overexploit the food to a

fish stock in Great Linford, for instance, resulted in a doubling of benthic chironomid biomass (Giles, 1992).

Thus the impact of benthivorous fish on benthos is small compared with the impact of planktivorous fish on zooplankton. Nonetheless, from a wildlife conservation point of view the reduction of benthic invertebrates is often considered one of the main adverse consequences of a dense fish population. Chironomids and other insects emerging from their benthic larval form are a crucial source of protein for young ducks, and the reproductive success of ducks is thought to be closely related to the availability of this resource (Street, 1977). This has led the English 'Game Conservancy' to investigate the effect of benthivorous fish on duck reproduction. Indeed, patterns of duckling survival in an area with flooded gravel-pits support this causal link (Hill *et al.*, 1987). Many ducklings died during their first two weeks of life, but those feeding on the river where fish were scarce survived better than those feeding on the lakes where fish density was high. In parallel pond experiments, higher fish densities caused a decline in emerging chironomids. Ducklings feeding in these ponds travelled further and gained less weight than ducklings feeding in a low-fish pond.

Also experimental reduction of the benthivorous fish stock in a gravel-pit confirmed the idea that competition for food was crucial for ducks as well as fish (Giles, 1992). During a short intensive fishery campaign most of the fish stock was removed. Chironomid biomass and survival of ducklings increased markedly. Also the mean individual weight of the remaining bream increased from 1.5 to 2.2 kg in the subsequent season, indicating that growth had been severely stunted due to food limitation previously.

The role of competition between ducks and fish for invertebrate food is further illustrated by the changes in lakes that lose all fish due to acidification. As an example, consider the comparative study of two pairs of physically identical ponds in Maine, USA (Hunter *et al.*, 1986). In each pair of ponds, one of the two lacked fish due to acidification. Those ponds lacking fish had much higher invertebrate densities than the ones with fish. Consequently, black duck (*Anas rubripes*) ducklings grew faster, spent less time searching and moving, and more time feeding and resting in the acidic ponds than in the ponds with fish.

Top-down control of snails and periphyton

Some fish species are specialized at feeding on molluscs. Well-known examples from the American continent are the redear sunfish (*Lepomis microlophus*) and the pumpkinseed (*Lepomis gibbosus*). In Europe, tench (*Tinca tinca*) is probably the most important molluscivore (Fig. 4.46). It switches to other food when molluscs are rare, but it has a strong preference for molluscs and will feed on them almost exclusively when availability is high (Brönmark, 1994).

Molluscivorous fish can have a strong impact on snail density (Brönmark, 1988; Martin *et al.*, 1992). Since snails are known to reduce periphyton density when they are abundant (Brönmark, 1989; Swamikannu and Hoagland, 1989; Mulholland *et al.*, 1991; Daldorph and Thomas, 1995) molluscivorous fish may be expected to have an indirect positive effect on periphyton growth. Indeed clear cascading effects from fish to periphyton have been shown.

In experiments with cages in the littoral zone of two Wisconsin lakes (Brönmark and Weisner, 1992), for instance, snail biomass was significantly reduced in the presence of a natural density of pumpkinseed sunfish as compared with the control situation without sunfish. The biomass of periphyton increased in the fish enclosures due to a reduced grazing pres-

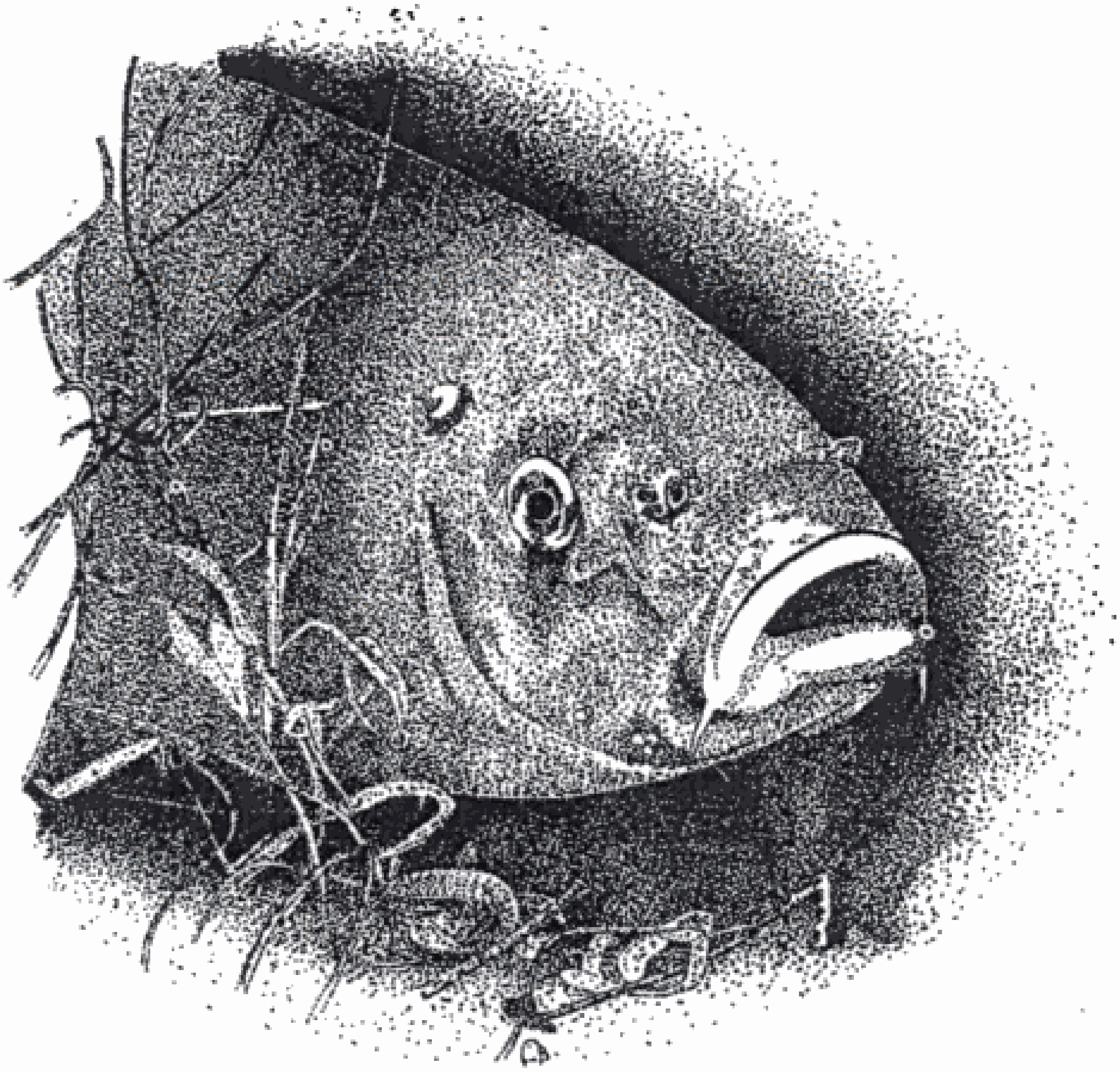


Fig. 4.46 Tench (*Tinca tinca*) can be a common fish in vegetated lakes. It eats all kind of macro-invertebrate prey but has a preference for snails.

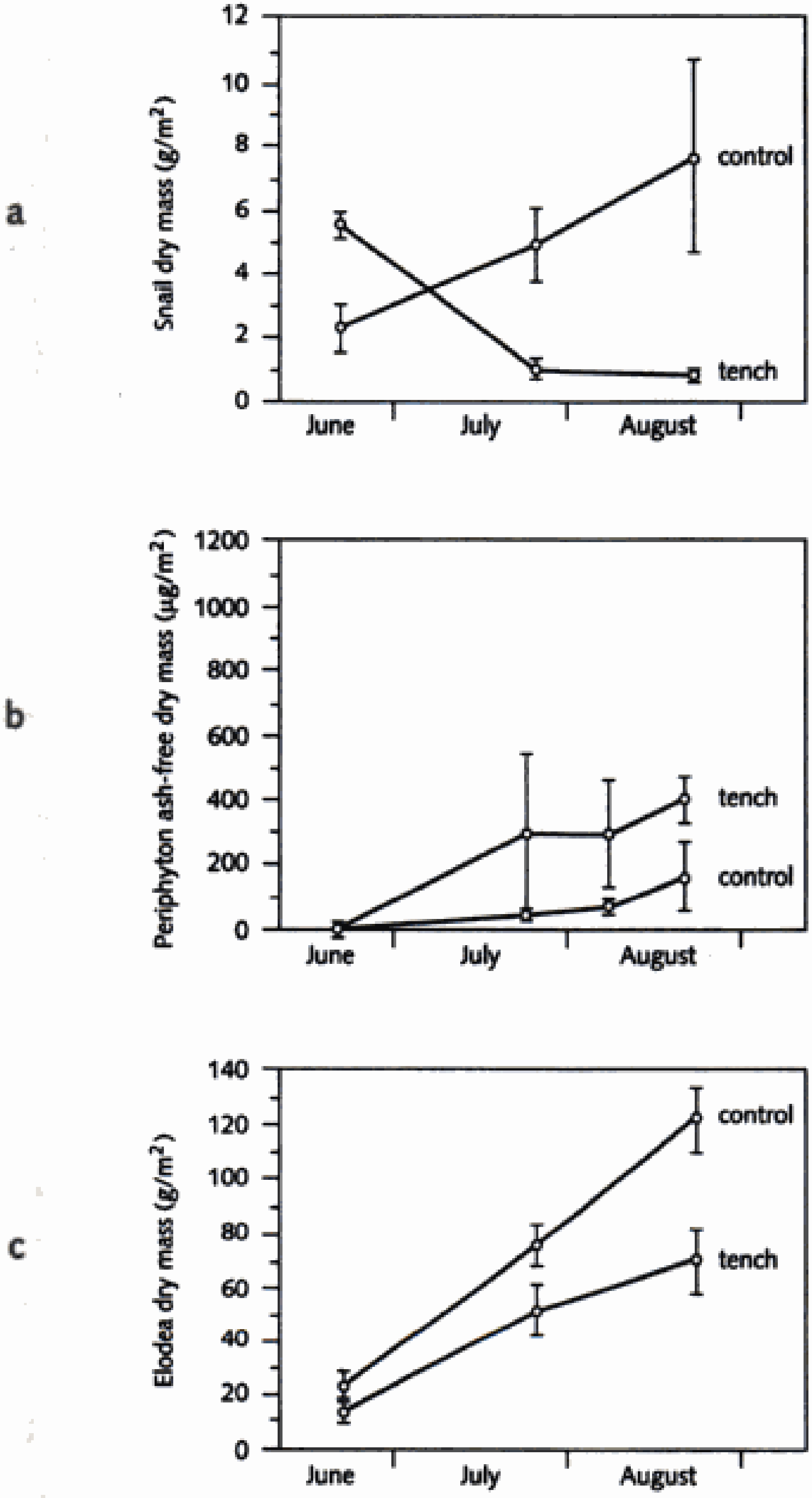


Fig. 4.47 Enclosure experiments in a shallow Swedish pond that in the presence of the molluscivorous fish tench, (a) snail biomass decreases (b) periphyton biomass increases and (c) the growth of the submerged plant *Elodea canadensis* is reduced. Error bars denote ±1 Standard Error. From Brönmark (1994).

sure by snails. Also the composition of the periphyton changed markedly with grazing. In the presence of fish, when snails were rare, large 'overstorey' species, such as stalked diatoms and filamentous algae dominated the community. When snail grazing was severe, small tightly adherent species became more abundant. This shift in species composition is commonly observed in studies of the effect of snail grazing (Brönmark, 1989), and is quite comparable to the effect of large herbivores on the structure of terrestrial vegetations.

Shading by a layer of periphyton can limit the growth of submerged plants (Sand-Jensen and Borum, 1984). It may therefore be expected that snails that graze down periphyton biomass should thereby indirectly enhance plant growth (Carpenter and Lodge, 1986; Thomas, 1987). Such a positive effect of snails has been shown in experiments with fresh-water macrophytes (Brönmark, 1985; Underwood, 1991; Daldorph and Thomas, 1995), and also the growth of seagrass (*Zostera marina*) has been shown to benefit from the activity of periphyton grazers (Hootsmans and Vermaat, 1985; Howard and Short, 1986). In view of this link between snails and plant growth, molluscivorous fish should potentially have an indirect negative effect on submerged macrophytes. Indeed, this effect has also been demonstrated. In a set of enclosure experiments in a shallow Swedish pond, tench was used as a molluscivore (Brönmark, 1994). Snail biomass decreased in the presence of this fish (Fig. 4.47a), leading to a increase of periphyton biomass (Fig. 4.47b) and a significant decrease in the biomass of *Elodea canadensis*, the dominant macrophyte (Fig. 4.48c). Comparable results were obtained by Martin *et al.* (1992) who found that the biomass of submerged plants increased when molluscivorous redear sunfish were excluded.

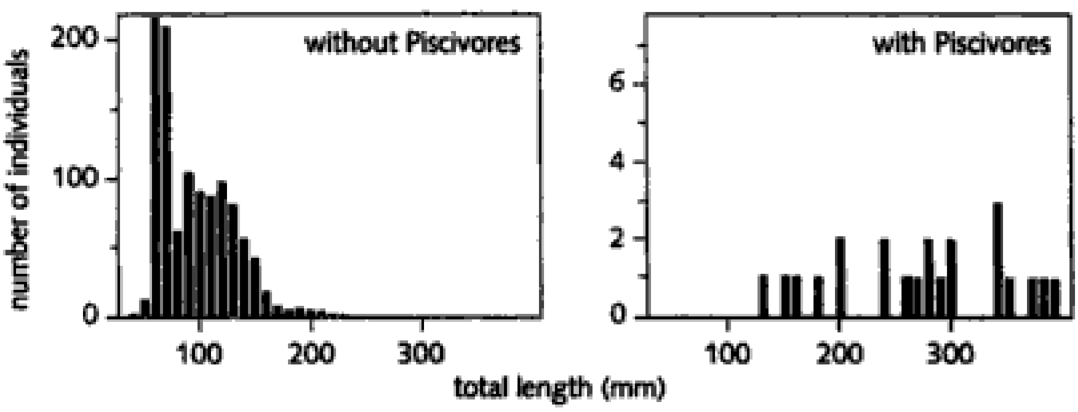


Fig. 4.48 Size distribution of crucian carp (*Carassius carassius*) in southern Swedish ponds with and without piscivores (data pooled from a survey of 46 ponds). From Brönmark *et al.* (1995)

4.5 PISCIVORES

The effects of piscivory on shallow lake food webs have been studied less intensively than the effects of planktivory and benthivory. Nonetheless it has become clear that predation is an important structuring force in fish communities. In the presence of piscivorous fish, potential prey fish often change their behaviour in order to reduce predation risk, and this can lead to crowding and increased food competition in safe vegetated areas (Werner *et al.*, 1983; Persson *et al.*, 1993). Although such predation avoidance strategies help reduce predation losses, marked impacts of piscivores on the abundance and size structure of fish populations have been found.

Impact on fish abundance and size

Effects of piscivores have been studied extensively in populations of crucian carp (*Carassius carassius*) in Finnish and Swedish lakes. It had long been known that in small lakes crucian carp populations usually consist of many small individuals, while in larger lakes there are few but large animals. It has now become clear that this difference is explained not by lake size per se, but by the absence of piscivores in many of the small lakes (Tonn *et al.*, 1989; Tonn *et al.*, 1994; Brönmark *et al.*, 1995). Long ice-cover in winter frequently leads to hypoxic conditions in such small shallow waters, killing virtually all fish except crucian carp, as this species is capable of anaerobic metabolism under low temperatures. Consequently, crucian carp is often the only species present in these lakes. In the absence of predators, mortality is low leading to dense populations in which the average individual size is small due to competition for food. These stunted populations contrast strongly with those of lakes in which predators are not wiped out by winter kills (Fig. 4.48). Here predation leads to almost complete elimination of small size classes, but the few individuals that survive grow to large sizes. Similar differences in size structure have been found for tench populations in the presence and absence of piscivores in Swedish ponds. The abundance of tench, however, is less affected by the presence of piscivores indicating that this species is not as vulnerable to predation as crucian carp (Brönmark *et al.*, 1995). It has been noted that extreme vulnerability to predation is also found in other species that can form dense populations in small ponds where piscivores are absent (Tonn *et al.*, 1990).

A shift from smaller to larger size classes of prey fish is probably the most commonly observed effect of piscivores. A comparative study of South-Swedish lakes, for instance, shows that the average size of roach systematically increases with the importance of piscivores in a lake (Persson *et al.*, 1991). A shift to larger size classes has also been found in response to experimental manipulation of piscivore density. Hambright (1994), for

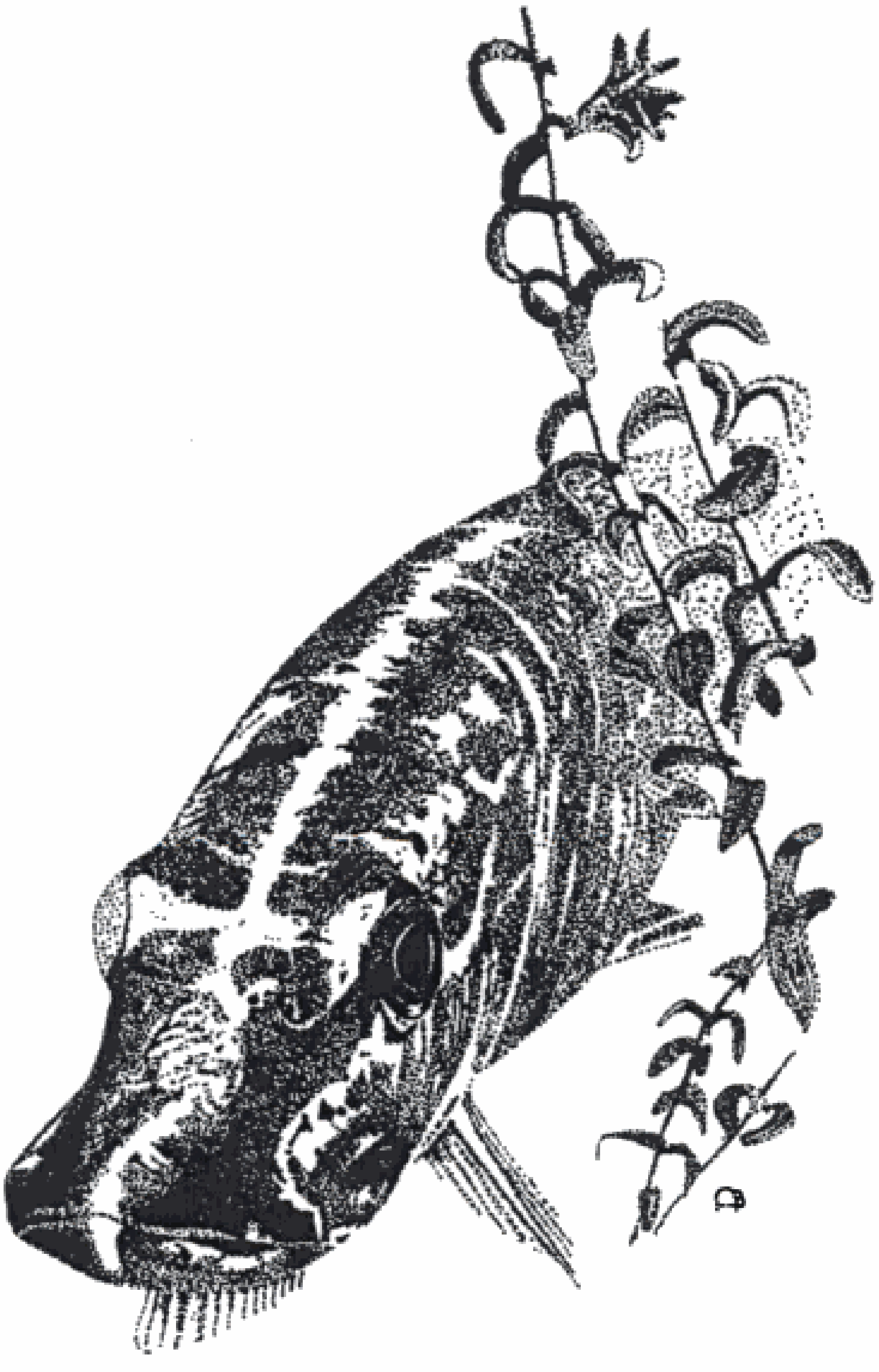


Fig. 4.49 Northern pike (*Esox lucius*) is a voracious predator that hunts from an ambush. It can swallow fish of up to half it own length. Cannibalism is a major source of mortality for juvenile pike and their survival depends largely on the presence of vegetation as a refuge.

The large impact of juvenile pike on their prey density can be understood from a back-calculation of how much food is needed to allow an individual pike to grow up to 18 cm in the first year as they usually do. Depending on the contribution of fish to the total diet such animals are estimated to consume up to about 600 juvenile cyprinids per capita during their first season (Grimm, 1989).

How far down does the cascade go?

Since small fishes usually exert the highest predation pressure on zooplankton, the repression of small size classes by piscivores may be expected to lead to a release of predation pressure on *Daphnia* and consequently to an enhanced top-down control of phytoplankton. Indeed such a cascading effect is observed in many studies.

The first experimental whole lake study showing a cascade from piscivores to phytoplankton is probably that of Carpenter and co-workers in Paul, Peter and Tuesday Lakes (Carpenter *et al.*, 1987). Since piscivores and planktivores were manipulated simultaneously in this experiment, the effects can not be ascribed purely to changes in piscivory. However, several later studies confirm that changes in piscivore populations can 'cascade' down to the plankton level. In Hambrights (1994) pond studies, for instance, reduced densities of small planktivores due to piscivory led to an increase in zooplankton biomass and cladoceran mean body sizes, and to a reduction of the chlorophyll concentration. Also the reduction in small planktivorous fish by juvenile pike in the Danish stocking experiment (Berg *et al.*, 1997) has caused an increase in *Daphnia* and a reduction of the chlorophyll concentration (Søndergaard *et al.*, 1997), while the enhancement of the pikeperch stock in Bautzen reservoir was followed by an increase in *Daphnia* size and abundance and the occurrence of spring clear-water phases that had been absent in previous years (Benndorf *et al.*, 1988). Especially spectacular are the reported effects of re-introduction of bass as a predator in a Michigan lake (Mittelbach *et al.*, 1995). The resulting dramatic decrease in planktivore density led to a recovery of large *Daphnia* that had disappeared upon extinction of bass eight years earlier. Total zooplankton biomass increased 10-fold and there was a marked increase in transparency.

Although, the causal links are not always well documented (Demelo *et al.*, 1992), the available evidence certainly illustrates that the reduction of small fish abundance by piscivores can have marked effects on zooplankton and on algal biomass. As a rule, however, top-down effects seem to become less pronounced when more trophic links have to be passed (McQueen *et al.*, 1989): piscivore effects on planktivorous fish may be strong, but indirect effects on zooplankton are often less pronounced and cascading effect on algae can be even weaker.

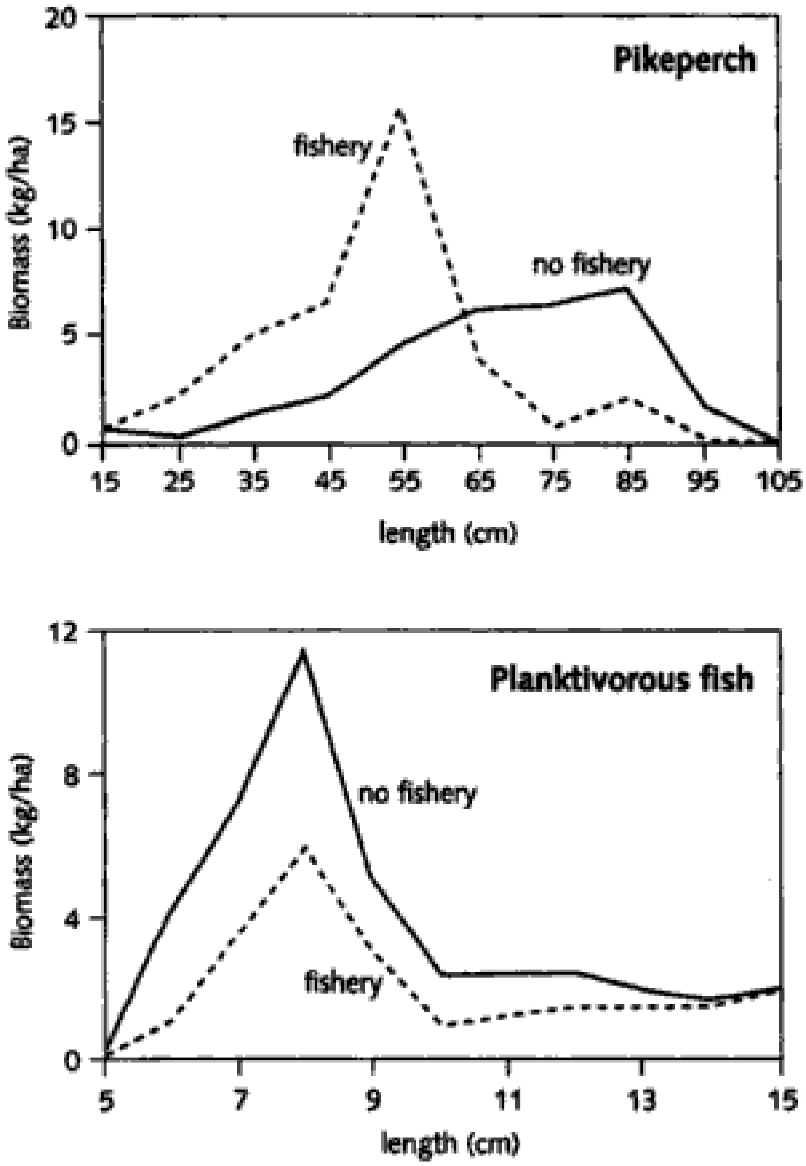


Fig. 4.51 An intensive gill-net fishery removing pike-perch >60 cm from a set of shallow lakes in The Netherlands has produced a shift to dominance by smaller size-classes (upper panel), while the density of small cyprinid prey-fish in the lakes decreased (lower panel) presumably due to an increase in predation pressure from the changed pike-perch population. After data from Lammens *et al.* (1997).

correlated with the abundance of 2–4-year-old pikeperch over a time-series of 14 years (Mooij *et al.*, 1996), suggesting that the observed decrease on small fish is indeed an indirect effect of the enhanced abundance of small pikeperch after the gill-net fishery.

Interestingly, the abundance of some piscivorous fish can also be controlled by competition with their future prey during early life stages. This 'juvenile competitive bottleneck' has been studied extensively for perch by Persson and co-workers (Persson, 1986; Persson, 1987a; Persson, 1987b; Persson and Greenberg, 1990b; Persson and Greenberg, 1990a). Perch has a relatively small gape size, and it can take some years before individuals

Scenedesmus has thicker cell walls and forms larger colonies in response to the presence of *Daphnia* presumably reducing its edibility (Hessen and Van Donk, 1993). In all of these cases the response occurs only when predators are present, and most work indicates that the presence of the predator is sensed largely through chemical cues.

Predation avoidance: costs and consequences

The above-mentioned body shape and size responses are just a small subset of the wide array of predation avoidance strategies that are found in aquatic ecosystems. Some strategies such as spines of some fishes and repellent tastes of many aquatic beetles and bugs (Scrimshaw and Kerfoot, 1987) are fixed in the course of the evolution. Very often, however, animals adjust their 'lifestyle' depending on the predation risk (Sih, 1987b). This makes sense as most predator avoidance strategies imply a cost, often reduction of foraging possibilities. Thus when predation risk is low, for instance, because predators are absent or because the individual is small or big enough to be invulnerable, it is obviously better not to display a costly predation avoidance strategy.

Moving to safer sites is one of the most conspicuous and well-studied strategies in aquatic systems. As explained earlier, zooplankton often concentrates in dense swarms where predation risk is lower (Kuenne, 1925; Colebrook, 1960; Klemetsen, 1970; Johnson and Chua, 1973; Malone and McQueen, 1983; Jakobsen and Johnsen, 1987), while in deep lakes they exhibit diel vertical migration, concentrating in dark·deep layers during daytime to avoid predation by visually hunting planktivores (Gliwicz, 1986; Leibold, 1990; Ringelberg, 1991; Lampert, 1992; Brancelj and Blejec, 1994; Loose and Dawidowicz, 1994; Ringelberg, 1995). These are costly strategies in terms of foraging possibilities. In zooplankton swarms, algal densities can be considerably reduced (Tessier, 1983; Jakobsen and Johnsen, 1987), and vertical migration has been shown to lead to reduced growth and reproductive rates (Lampert, 1987a).

In shallow lakes, as described in some detail in the next chapter, large zooplankton often aggregate in vegetation stands, swimming out only at night to the adjacent open water (Timms and Moss, 1984; Lauridsen and Buenk, 1996; Lauridsen *et al.*, 1996). Since phytoplankton biomass is usually very low in dense plant stands this strategy is likely to have a considerable price in terms of food intake. Indeed, vegetation basically has a repellent effect on *Daphnia* that is overridden only in the presence of fish (Lauridsen and Lodge, 1996). Interestingly, vegetation is also used as a refuge for small fish against predation by piscivores. Again there is a probably a price on the foraging side, as foraging efficiency is strongly reduced by the vegetation structure (Winfield, 1987; Diehl, 1988) and the animals prefer to forage in the open water when predators are absent (Persson *et al.*, 1993).

The cost of predator avoidance has marked implications for what predation effects look like in the field. Importantly, it can leave the hallmarks of food-limitation on prey-populations, as prey often pay a price in terms of foraging possibilities to minimize predation risk. Thus juvenile fish and large zooplankters may appear starved despite a high food availability in the risky parts of lakes where they are an easy prey for predators. Note that this implies a tricky caveat when interpreting the driving forces behind population dynamics from the condition of individuals. Starvation can really be an indirect effect of predators. Another way to look at the implications of predator avoidance is that predators do create a refuge for the food of their prey. For instance, the open water is a refuge against zooplankton grazing for phytoplankton when these herbivores are chased into vegetation refuges by planktivorous fish.

Note that despite the relative complexity of the mechanisms involved in these cascades of hide and seek, the net result of predation is still quite similar to that predicted by the simple food-chain theories proposed by Camerano (1880) and the HSS group (Hairston *et al.*, 1960). Predators have an indirect positive effect two trophic levels down. The main difference is that the negative effect of predators may partly appear as food-limitation in prey populations. Another important aspect is that avoidance of predators by crowding in refuges can stabilize predator – prey dynamics (Sih, 1987a), as discussed already in some detail for the *Daphnia* – algae interaction. Although locally food may be depleted to low levels, over-exploitation of food populations on a whole lake scale is less likely in the presence of refuges: in a lake with patches of vegetation, *Daphnia* is not easily driven to extinction by planktivorous fish, but likewise, juvenile fish have an increased survival probability and open-water phytoplankton is less likely to be grazed down to spring clear-water phase levels in the summer when planktivores prevent open-water use of *Daphnia* in the daytime.

Shifts in food-web structure with enrichment

Several studies show that the fish stock increases with the total phosphorus concentration of lakes (Hanson and Leggett, 1982; Jeppesen *et al.*, 1996). This is intuitively sound, as the primary productivity and thus the food availability on subsequent trophic levels will increase with nutrients until other factors such as light become limiting for primary production. Indeed, fish biomass levels off at high total-P concentrations where phosphorus limitation is unlikely to occur (Fig. 4.53).

The idea that primary productivity largely determines the carrying capacity for fish is also supported by the observation that lakes with a high concentration of suspended sediment have lower fish stocks than other lakes with the same nutrient level (Lind *et al.*, 1994). A good example of the latter is the difference between the lakes IJsselmeer and Markermeer, in fact artificially separated parts of the same basin. In Markermeer where the silty sediments are frequently resuspended by waves, algal biomass is approxi-

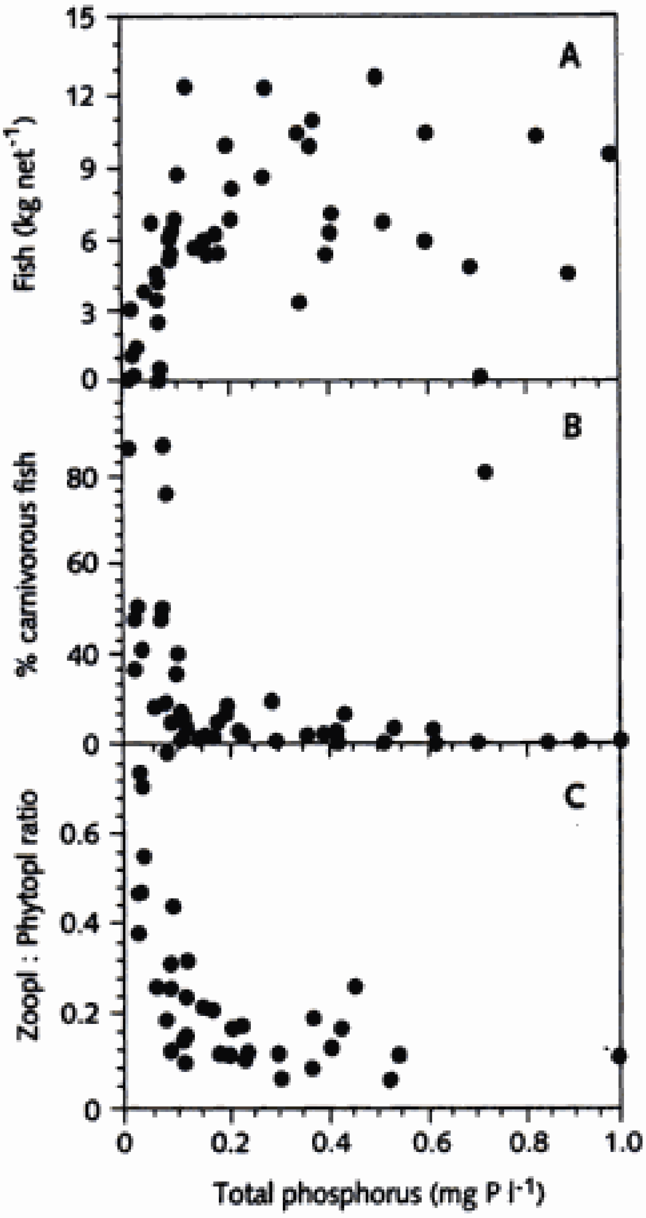


Fig. 4.53 Relationship between the total phosphorus concentration and fish biomass, the share of piscivores and the ratio of zooplankton to phytoplankton biomass in Danish lakes. From Jeppesen *et al.* (1996)

mately half the value found in the otherwise comparable IJsselmeer, supposedly due to light limitation. A very similar difference exists between the biomass of fish of the two lakes (Lammens *et al.*, 1996).

Fish biomass is often closely correlated to the biomass of benthic invertebrates (Hanson and Leggett, 1982), suggesting that benthos is an important food source that largely determines the total biomass of many fish communities. This is especially so in shallow lakes where benthos is relatively more important than in deep lakes. As argued earlier, the increase of (omnivorous) fish with eutrophication is thought to result in a disproportionally high predation pressure on zooplankton in such lakes (Jeppesen *et al.*, 1996).

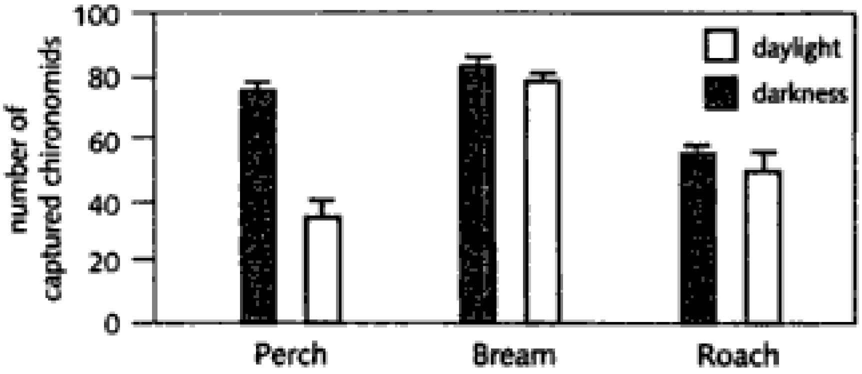


Fig. 4.54 Efficiency of perch, bream and roach in capturing chironomid larvae during experiments at daylight and darkness. From Diehl (1988).

More surprising than the increase of fish biomass with nutrients are the changes in trophic structure. Above a total-P level of 0.1 mg l^{-1} the share of piscivores in the fish community drops sharply and so does the ratio of zooplankton to phytoplankton biomass (Fig. 4.53b,c). This suggests a systematic shift in the role of top-down control with nutrients. At low nutrient levels piscivory is relatively important and planktivory is low allowing zooplankton to graze down algae. At high nutrient levels the strong top-down links have shifted one trophic level, and strong top-down control of phytoplankton by zooplankton is rare.

To understand the shift in the fish community it is necessary to consider the difference in species composition between lakes of different productivity in more detail. The general pattern is that in oligotrophic lakes Salmoniformes are the most important fish group, while in moderately productive lakes percids dominate and in eutrophic and hypertrophic lakes dominance shifts to cyprinids (Kitchell *et al.*, 1977; Leach *et al.*, 1977; Persson *et al.*, 1991). On the American continent there is another group, the centrarchids, that increases with eutrophication more or less like the cyprinids do (Oglesby *et al.*, 1987).

The shift from percids to cyprinids corresponds to the strong decrease in the percentage of piscivores with increasing nutrient status reported, for instance, in the Danish study (Fig. 4.53b). In European lakes the large proportion of piscivores in mesotrophic lakes is almost entirely due to dominance by perch, while roach and bream are usually the most important cyprinids (Persson *et al.*, 1991). The reason for the shift has been explained from the differences in competitive ability of these species depending on turbidity of the water and the presence of aquatic vegetation. As discussed further in the next chapter perch is a superior competitor for food in dense vegetation, which is predominantly found in the less eutrophic lakes. In turbid water, characteristic of hypertrophic lakes, roach and bream are the better competitors (Diehl, 1988; Persson *et al.*, 1991). Juvenile animals of these cyprinids have been found to feed at maximum rates even at very low

5 Vegetation

The presence of vegetation radically alters the functioning of shallow lakes. Macrophytes provide a refuge for small animals against predation by bigger ones, change the nutrient dynamics of the system, and prevent resuspension of the sediments. Vegetated lakes usually harbour a richer community of invertebrates and fish, and attract larger numbers of birds than lakes without vegetation. Even to a layman, the difference between a vegetated and an unvegetated shallow lake is striking. There is no real comparison with terrestrial systems, but with respect to the difference in habitat structure the parallel to a lush forest versus a landscape of barren sand-dunes comes close. In the first section of this chapter the effect of vegetation on the fauna of shallow lakes is reviewed. The next section treats the effect of vegetation on water clarity and reviews the mechanisms involved. In the third section the factors that regulate vegetation abundance and structure are discussed. The fact that vegetation needs clear water but also enhances clarity can lead to the existence of alternative stable states as discussed in the last section.

Aquatic macrophyte structural types

Aquatic plants differ quite strongly in shape (e.g. Fig. 5.1) and these differences are important with respect to their functional role in lake ecosystems.

In many lakes we find a sequence of growth forms along the depth gradient from the shore to the unvegetated deep parts of lakes. The area around the shoreline is occupied by emergent macrophytes (or 'helophytes'), such as reed, that have at least part of their shoot rising up in the air. These plants can reach very high productivities, obtaining water from the aquatic system and carbon from the air. Denitrification can be high in such marshy zones. Because of this process and the accumulation of nutrients in biomass helophyte beds can be used as biological filters for reducing the nutrient content of water (Chen and Barko, 1988; Weisner *et al.*, 1994).

In somewhat deeper water plants with floating leaves, such as water lilies, can be found if wave action is not too strong. Also submerged plants occur here, and these can be found at great depths if the water is not too turbid. Both submerged and floating plants can be rooted or non-rooted. In the tropics, free floating plant beds often become a nuisance in lakes with a high nutrient loading. In the temperate zone, such plants are usually restricted to small sheltered waters, such as ponds and ditches. Also filamentous macroalgae are often present in these situations. Such filamentous algae can

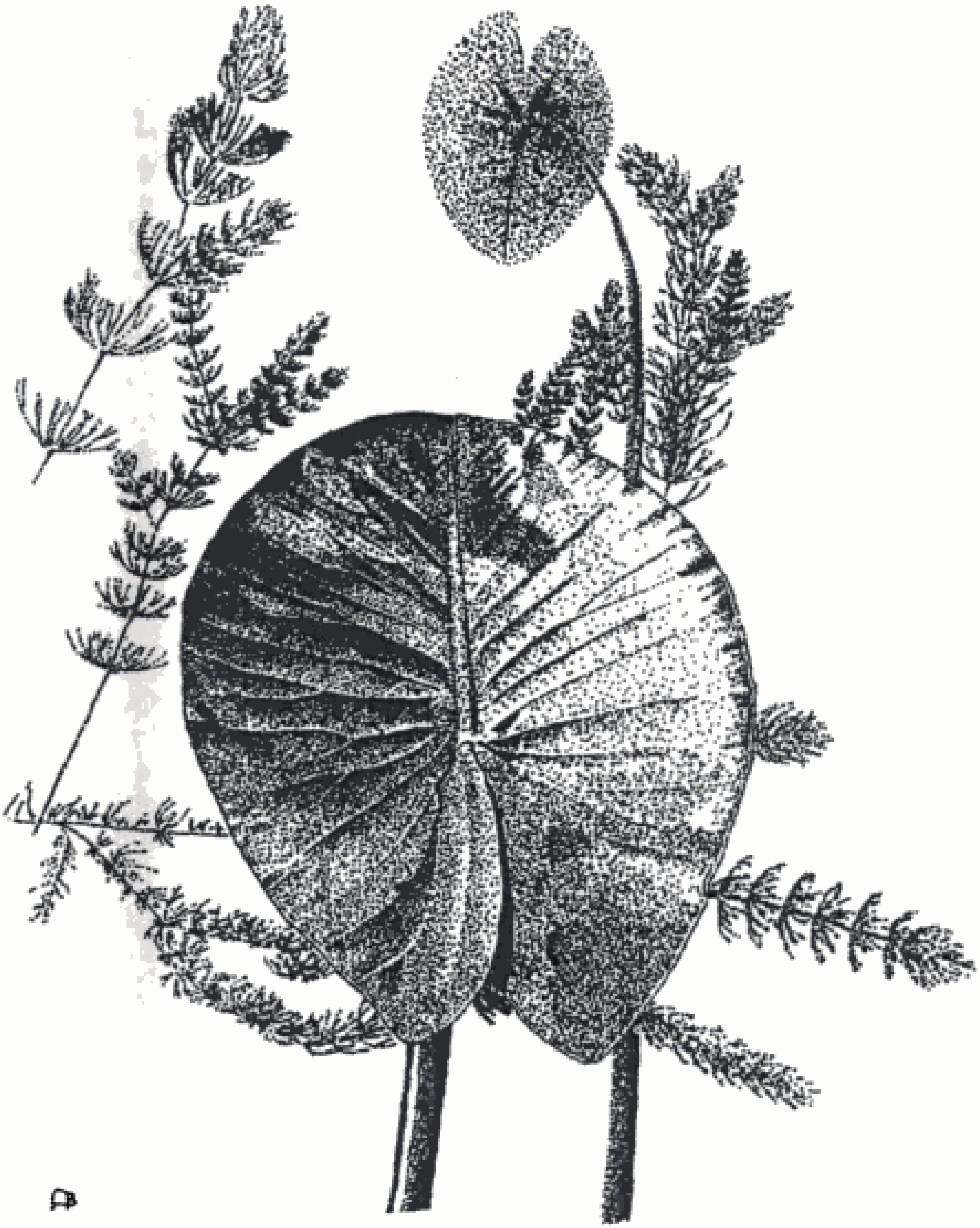


***Fig.** 5.1* The rounded leaves of the yellow waterlily (*Nuphar lutea*) and the finely dissected leaves of *Ceratophyllum* are extremes in the wide spectrum of plant forms that are found in lakes. The growth form of plants largely determines their effect on wave resuspension and their effectiveness as a refuge for small animals against predation by bigger ones.

develop rapidly at the sediment surface in the spring entangling and shading other submersed plants. Later such algal masses tend to become buoyant and form dense floating algae beds ('flab') that deteriorate gradually in summer. All of these structural groups have their specific impacts on the functioning of a lake, and in systems where vegetations with different growth forms co-occur, each one typically has its own associated invertebrate fauna (Dvořák and Best, 1982; Scheffer *et al.*, 1984; Dvořák, 1987).

With respect to the functioning of most temperate shallow lakes, rooted submerged plants are probably the most important group. They can develop massively over the entire lake bed, and have a tremendous impact on the system. Different types of submerged plants develop under different conditions and these types can have quite different impacts on the system. At least two extremes in growth form need to be distinguished: plants that can grow long and concentrate most biomass in a canopy just under the water surface in shallow situations, and plants that stay short and produce low but sometimes very dense vegetations. Vegetation in turbid shallow lakes is typically dominated by angiosperms that develop growth forms of the first type, such as sago pondweed (*Potamogeton pectinatus*) and *Hydrilla*. An example of the seasonal development of this vegetation structure has been described for an *Elodea* dominated weedbed in a Czechoslovakian fish pond (Pokorný *et al.*, 1984). Early in the growing-season plant biomass is distributed relatively evenly over the water column, but soon overall biomass increases and most plant matter becomes concentrated just below the water surface (Fig. 5.2).

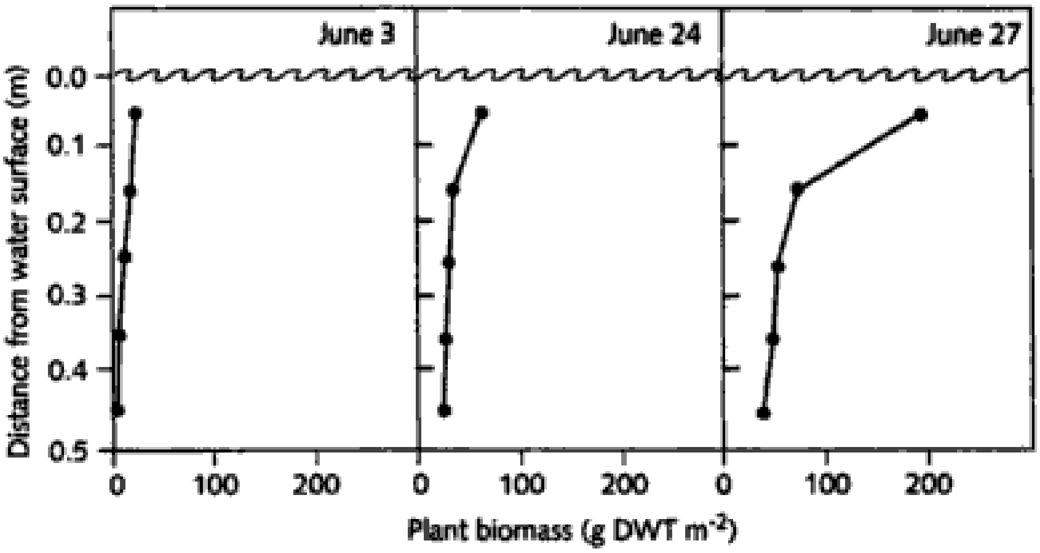


Fig. 5.2 Change in the depth distribution of plant biomass in an *Elodea* vegetation from spring to summer. By the end of July most of the biomass is concentrated close to the water surface. From Pokorný *et al.* (1984).

Isoetides are an extreme example of the low growing structural type. These rosette forming plants are typical of very clear water. Another very important group with a low growth form are the charophytes (Charophyceae). Despite the similarity in growth form to higher plants, charophytes are in fact algae. Consequently they differ strongly in physiology from other aquatic plants. Charophyceae can be characterized as typical r-select pioneers that have a high growth rate, and produce many small but highly persistent diaspores. They are often among the first species to colonize new water bodies, and although they usually represent a transitional vegetation stage, they can also form permanent vegetations in some situations (Wood, 1950).

Characterizing vegetation abundance

In terrestrial vegetation ecology it is common to describe and analyse the situation in certain plots in great detail. Submerged vegetations are usually less diverse than their terrestrial counterparts in terms of species richness and structure. Also the main interest of lake ecologists is often in the role of plants as a structuring element in the lake as a whole. It is therefore common to characterize the vegetation of a lake simply by estimating the percentage of the lake area that is occupied by submerged, floating or emergent plants. Note that this percentage of coverage is something different from the coverage used to characterize canopy density in terrestrial vegetation plots. The percentage of lake area covered by vegetation fields may give a flattered picture of vegetation abundance when vegetation within the fields is very sparse. Since the effect of vegetation on the ecosystem depends strongly upon its density it is useful to have some estimate of the latter. Biomass is a straightforward option. A third measure that is sometimes used to characterize total vegetation abundance in a lake is the percentage of the lake volume 'infested' with macrophytes (PVI) (Canfield *et al.*, 1984). The idea is that the impact of plants on the lake is larger if the total water column is occupied than when plants do not reach the surface.

5.1 IMPLICATIONS OF VEGETATION FOR THE ANIMAL COMMUNITY

As explained in the previous chapter there are systematic shifts in food-web structure of shallow lakes over a gradient from oligotrophic to hypertrophic conditions. Shifts in the species composition of the fish community with eutrophication can be attributed in part to increased turbidity, decreasing the efficiency of visual hunters such as perch (*Perca fluviatilis*) and pike (*Esox lucius*). However, the disappearance of aquatic vegetation as a refuge against predation is probably one of the main factors involved. Zooplankton and invertebrates are not easily caught in dense vegetation except by specialized species such as perch and tench (*Tinca tinca*). Also, small fish can escape predation by the larger piscivorous ones between the plants. Indeed, there are striking differences between the food web of vegetated and unvegetated sites in lakes.

Invertebrates

Vegetation stands usually have a much richer invertebrate community than unvegetated sites, both in terms of species numbers and total biomass (Gilinsky, 1984; Diehl, 1988; Engel, 1988; Hargeby *et al.*, 1994). The differences with open water fauna are especially pronounced if vegetation stands are dense. As an example consider the local differences in macroinvertebrate fauna found in Lake Krankesjön (Hargeby *et al.*, 1994). This lake has unvegetated sites, stands of sago pondweed and *Chara* fields. The heavy *Chara* mats have a 12 times higher vegetation biomass than pondweed stands. Macroinvertebrate biomass in the plant stands is higher than in the unvegetated parts, but the invertebrate biomass is much more elevated in the dense *Chara* fields than in the relatively sparse pondweed stands (Fig. 5.3).

Also diversity is higher in the vegetated areas. In the unvegetated areas Chironomidae and Oligochaeta consitute as much as 74–100% of the total biomass, whereas in the vegetation stands a wide range of invertebrate taxa is found. Again pondweed stands are intermediate in invertebrate fauna diversity between unvegetated parts and *Chara* beds.

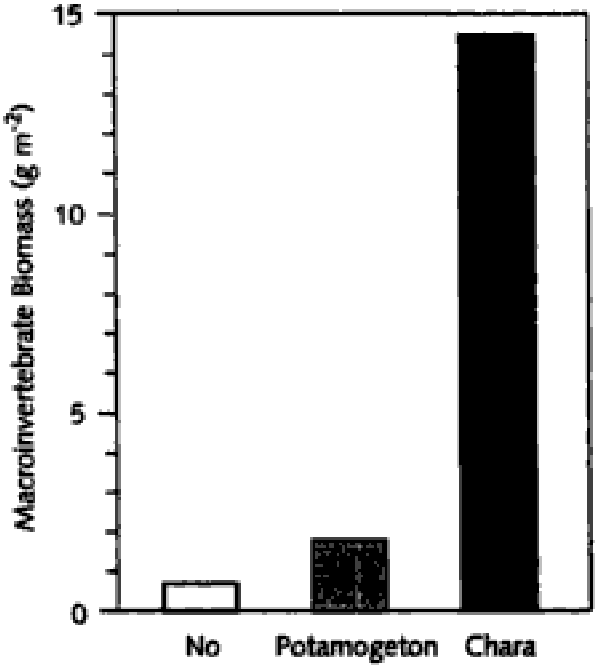


Fig. 5.3 Marcroinvertebrate biomass (g dry mass m^{-2}) in a *Chara tomentosa* vegetation, a *Potamogeton pectinatus* vegetation and in an unvegetated area in Lake Krankesjön. From Hargeby *et al.* (1994).

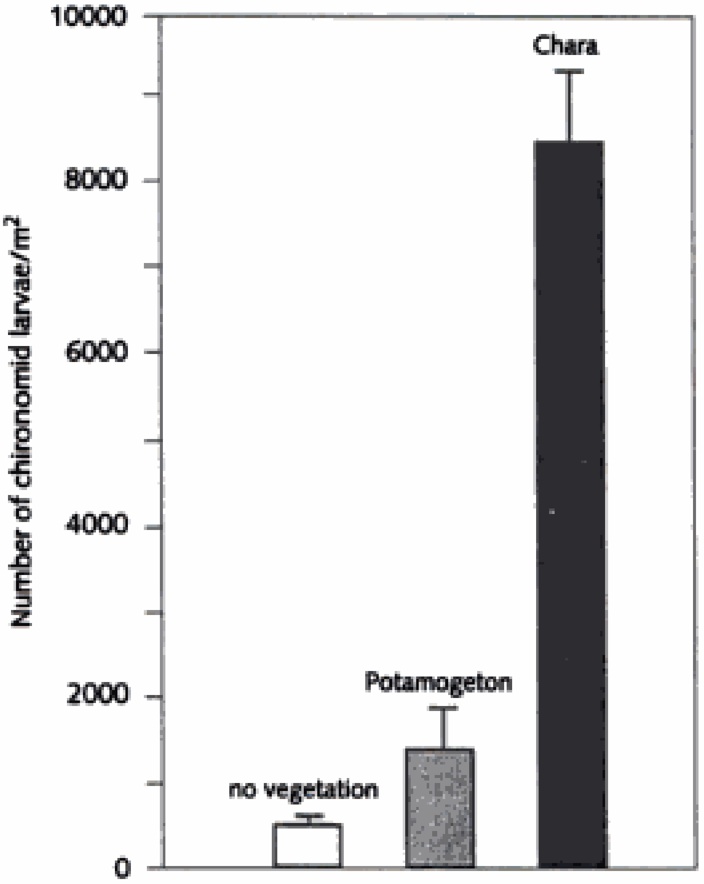


Fig. 5.4 Density of chironomid larvae in an unvegetated area, a *Potamogeton pectinatus* vegetation and in a *Chara tomentosa* vegetation in Lake Krankesjön. From Diehl (1988).

vertebrate groups than unvegetated areas, due mainly to the high availability of suitable food, and the relatively low predation pressure from fish.

Zooplankton

As mentioned earlier, vegetation stands can also be an important refuge for *Daphnia* and other pelagic copepods against fish predation. The first study indicating the importance of vegetation as a refuge for herbivorous zooplankton against fish addressed a striking difference in transparency between two small connected lakes in the Norfolk Broads area in eastern England (Timms and Moss, 1984). The smallest one, Hudsons Bay, had a large stand of water lilies, and the adjacent open water was clear. In contrast, the larger unvegetated Hoveton Great Broad had chlorophyll concentrations that were mostly an order of magnitude higher. Both lakes received their water from the same nutrient rich river, and bio-assays showed that the water in the clear Hudsons Bay could actually support a high algal growth. Indeed, phytoplankton densities in Hudsons Bay were high in the spring and autumn, but dropped strongly in the summer when the lilies were present. Zooplanktivorous fish was present in both basins, and in Hoveton Great

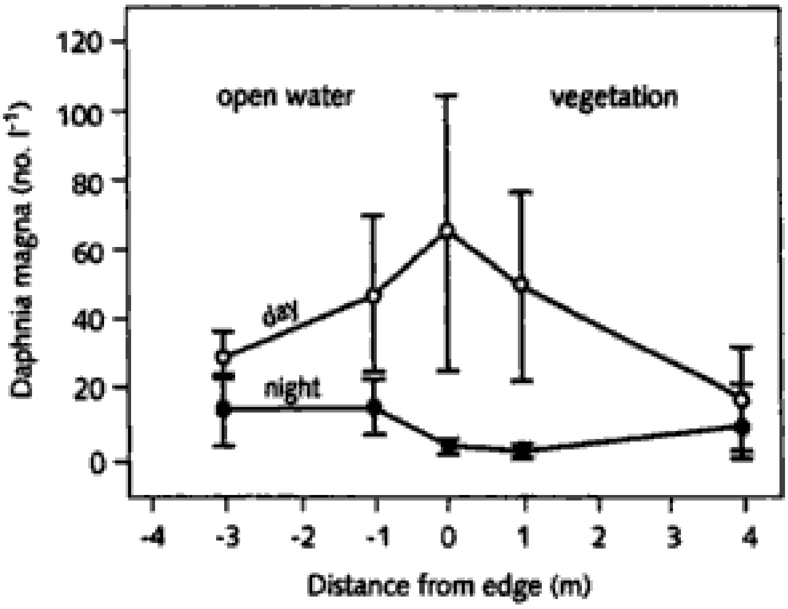


Fig. 5.6 Distribution of *Daphnia magna* in along a spatial gradient across the edge of a *Potamogeton pectinatus* field in the daytime (open symbols) and at night (closed symbols). From Lauridsen and Buenk (1996).

This suggests that large homogeneous fields of aquatic vegetation are not very effective as a daytime refuge for pelagic zooplankton as they have little edge relative to the surface area. This is confirmed by a study in Lake Stigsholm (DK) where diurnal fluctuations of zooplankton numbers in established vegetation stands with diameters of 2, 10 and 25 m were compared with open water dynamics (Lauridsen *et al.*, 1996). In the 2 m stands striking diurnal patterns occurred for *Ceriodaphnia* spp., *Bosmina* spp. and *Diaphanosoma brachyurum*, the decrease in density at night being mirrored by an increase in the open water (Fig. 5.7).

In the larger vegetation stands, *Ceriodaphnia* and *Bosmina* densities were much lower and diurnal fluctuations were found hardly at all. In contrast, *Sida crystallina*, *Eurycercus lamellatus* and *Simocephalus velutus* were abundant in the large vegetation stands but rare in the 2 m ones and absent in the open water. These cladocerans are known to be macrophyte associated (Quade, 1969; Paterson, 1994), and are suspected to have a considerable filtration capacity explaining at least in part the water transparency in some plant stands (Irvine *et al.*, 1990; Jeppesen *et al.*, 1996). Several species live largely attached to the plants. Therefore their abundance is easily underestimated with standard plankton sampling techniques.

Obviously, the high concentration of filter feeding zooplankton in plant stands leads to a high grazing pressure on phytoplankton, which already has a low productivity between the macrophytes due to shading, low nutrient availability allelopathic exudates and high sinking losses. As a result algal density is very low and in practice mainly small fast growing algae and bacterioplankton survive (Hasler and Jones, 1949; Schriver *et al.*, 1995;

hypolimnion of deep lakes (Dodson, 1988; Leibold, 1990; Loose and Dawidowicz, 1994), where chemical cues from fish induce a phototaxic response in *Daphnia* that drives them to the dark deep-water refuge at day (Ringelberg *et al.*, 1991).

It is not yet very clear how well submerged plants protect zooplankton against fish predation, but several experiments indicate that the refuge effectiveness depends among other things on the fish species and on the density of vegetation. Laboratory experiments with artificial reed and waterlily stands show that zooplankton consumption by juvenile roach (*Rutilis rutilis*) decreases with vegetation density, whereas capture rates of rudd (*Scardinius erythrophtalmus*) and perch can be enhanced by vegetation when it is not too dense (Winfield, 1987). The positive effect of sparse vegetation on prey capture of juvenile rudd and perch results in part from a higher activity of the animals, which, as Winfield suggests, may be due to a lower percepted risk of predation by larger piscivores in the vegetation.

The idea that the refuge effect depends critically on plant density is supported by experiments in Lake Stigsholm showing that daytime aggregation of pelagic zooplankton occurs in dense but not in sparse plant stands (Fig. 5.8).

A series of enclosure experiments (Schriver *et al.*, 1995) with different densities of *Potamogeton* plants and planktivorous fish confirms that sparse

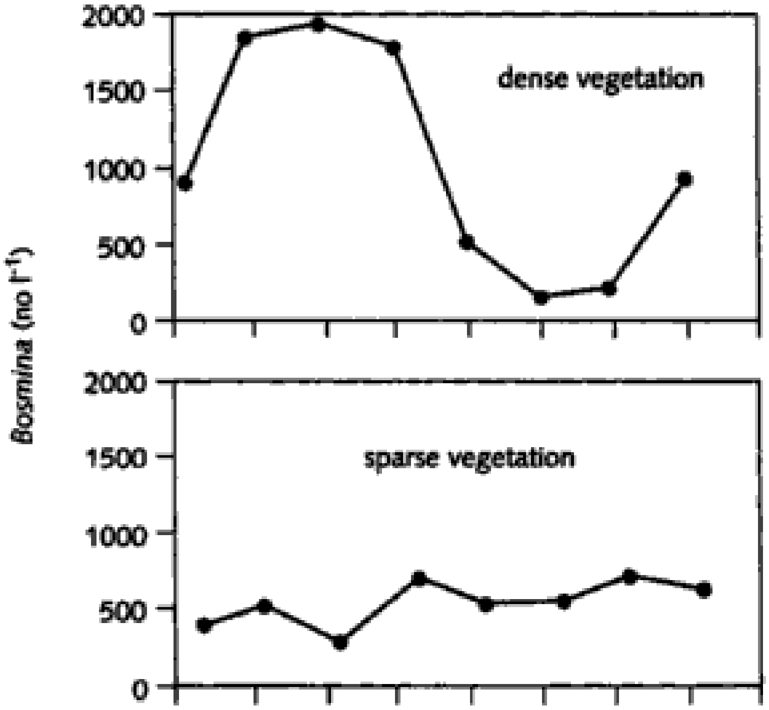


Fig. 5.8 Diurnal change in the density of *Bosmina* in a dense (PVI = 70%) and a sparse (PVI = 23%) vegetation stand in the Danish Lake Stigsholm. Only the dense stand is apparently used as a daytime refuge. From Jeppesen *et al.* (1996).

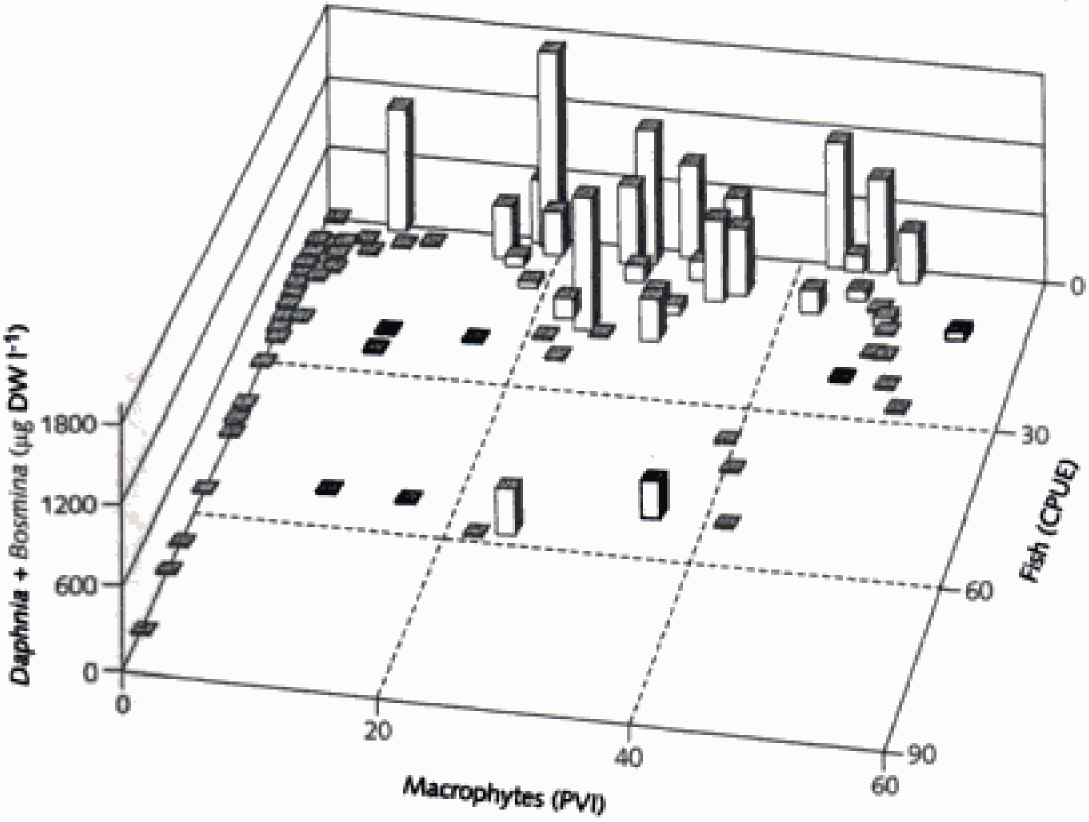


Fig. 5.9 Biomass of *Daphnia* and *Bosmina* in relationship to vegetation density (% PVI) and planktivorous fish density (10 CPUE ≈ 1 fish m^{-2}) in a series of enclosure experiments. Even dense vegetation cannot prevent *Daphnia* and *Bosmina* populations from collapsing when more than approximately 2 fish m^{-2} are present. From Schriver *et al.* (1995).

stands are hardly protective, and that even dense vegetation cannot prevent *Daphnia* and *Bosmina* populations from collapsing when the fish density is too high (Fig. 5.9).

Exclosure experiments in a macrophyte bed in a Finnish lake confirm that fish can enter even dense macrophyte stands and suppress *Daphnia* and *Bosmina* populations there (Kairesalo *et al.*, 1997).

In view of these results it seems surprising that even the sparse underwater structure of lily stands could act as an effective refuge as suggested by Timms and Moss (1984). In another study, juvenile fish have actually been found to be more abundant in *Nuphar lutea* vegetation than in the open water (Venugopal and Winfield, 1993). In practice the use of plant stands by fish and the resulting predation pressure on zooplankton apparently varies strongly from case to case. Importantly, vegetation is also a refuge against predation for juvenile fish, and crowding of small fish in the vegetation refuge may lead to high predation on zooplankton there. In fact fish predation avoidance patterns are quite similar to those observed in zooplankton. The most vulnerable individuals (in this case the smallest ones) use the vegetation more than the less vulnerable ones (Engel, 1988), and the use of

Birds

Shallow lakes that shift from a vegetated to an unvegetated state or vice versa show large shifts in the bird communities (Wallsten and Forsgren, 1989; Hanson and Butler, 1994b; Hargeby *et al.*, 1994). Some spectacular examples mentioned in the opening chapter are the lakes Veluwemeer, Ellesmere, Tåkern, Krankesjön, Linford, Tämnaren and Christina. The species that are involved are different from case to case but the general trend is usually the same. In vegetation-rich lakes large numbers of migrating swans, coots and ducks come to forage on vegetation and its associated invertebrates, while piscivores such as grebes forage on the fish. If the vegetation disappears only piscivorous birds remain abundant (Fig. 5.10).

The large numbers of migrating birds visiting vegetated lakes in the autumn and winter can be especially spectacular (Wallsten and Forsgren, 1989; Hanson and Butler, 1994b) and switches between macrophyte dominance and phytoplankton dominance in shallow lakes are often noted by the conspicuous change in bird abundance first by visitors. The developments in Lake Christina are a good example of the effect of macrophytes on lake use by migrating waterfowl (Fig. 1.9). Vegetation in the lake has been depressed from the late 1970s till the late 1980s and this is reflected by a tremendous drop in the autumn counts of ducks and coots that can be as high as 160 birds ha^{-1} in years when vegetation is abundant.

Summer breeding populations never reach such high densities. Typically only a few coots or ducks per hectare are present during the summer

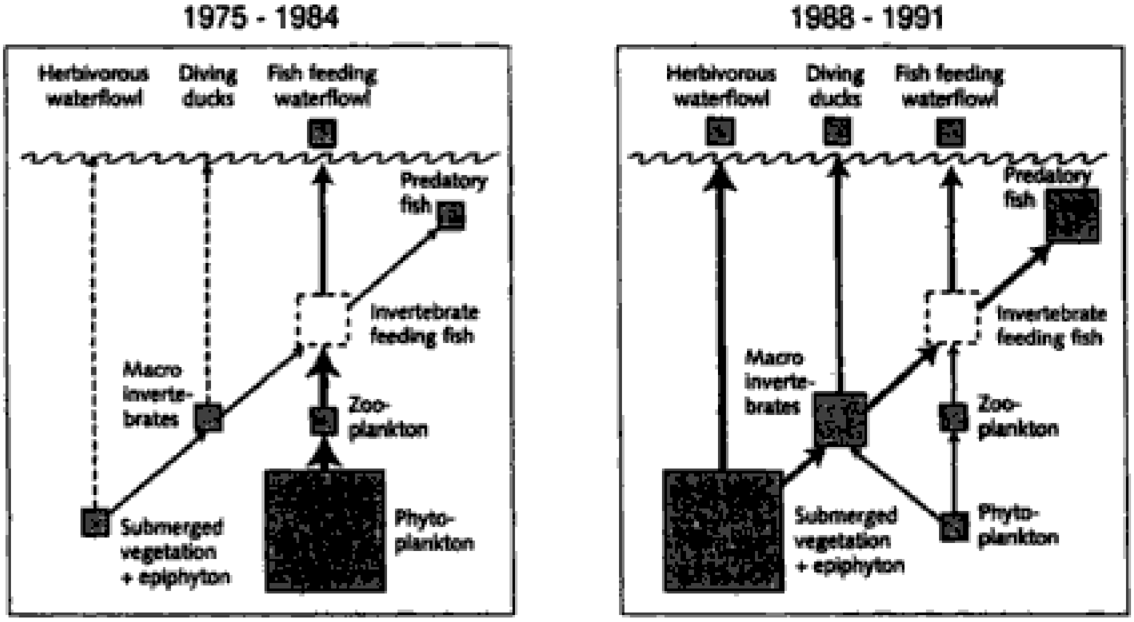


Fig. 5.10 Schematic description of the trophic web before (1975–1984) and after (1988–1991) the shift from a turbid to a clear state in the Swedish Lake Krankesjön. Boxes represent biomass, arrows represent energy flow. The estimation of invertebrate-feeding fish is uncertain. From Hargeby *et al.* (1994).

(Hargeby *et al.*, 1994; Perrow *et al.*, 1996; Søndergaard *et al.*, 1997). Shifts are usually observed in these breeding bird populations when vegetation becomes dominant (Fig. 5.11).

Not only plants but also invertebrates are used as a food source by many species. Invertebrate food is especially important to ensure a proper protein level in the diet of young ducks (Street, 1977), and duckling survival has been shown to increase with invertebrate abundance (Hunter *et al.*, 1986; Hill *et al.*, 1987). Thus the high invertebrate densities in vegetated lakes may be a major factor determining their suitability as a reproduction habitat for waterfowl.

Abundance and diversity of the resident bird community does not necessarily increase with vegetation coverage. Censuses in 46 Florida lakes revealed a shift in species composition with macrophyte abundance from mainly piscivorous to vegetation associated birds, but total bird numbers or species diversity did not change systematically with vegetation abundance (Hoyer and Canfield, 1994). However, many examples show that the autumn use by migrating waterfowl can differ by as much as two orders of magnitude between vegetated and non-vegetated situations.

5.2 EFFECT OF VEGETATION ON TURBIDITY

Correlations and causality

It has long been noted that the water tends to be less turbid if there is aquatic vegetation. The first publications result from work in fish culture ponds. Schreiter (1928), for instance, describes that the phytoplankton density of a pond was lowest in years with high aquatic macrophyte abundance. Many later studies report an enhanced water clarity in the presence of vegetation. Especially spectacular are the observations of whole lakes that switch between a clear and vegetated state and a turbid state with few

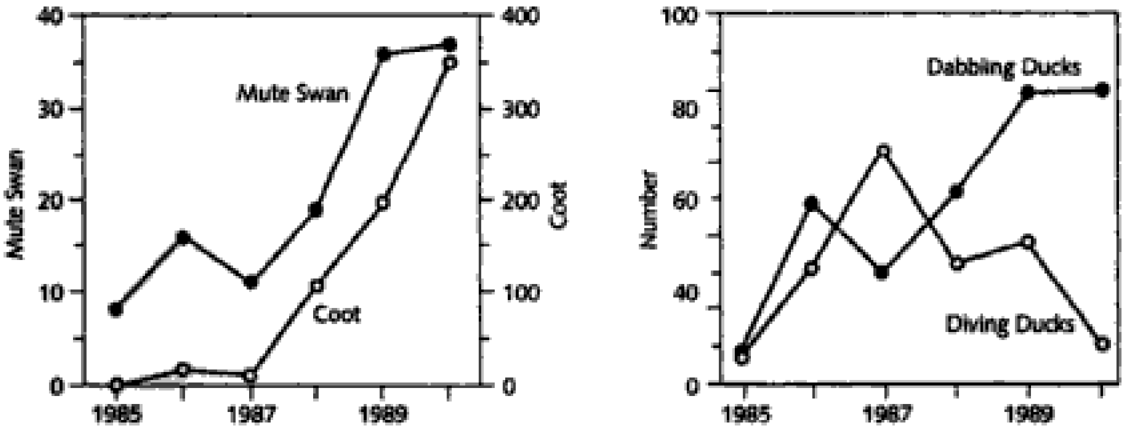


Fig. 5.11 Change in the summer populations of mute swan (*Cygnus olor*), coot (*Fulica atra*) and diving and dabbling ducks in the Swedish Lake Krankesjön during the switch from the turbid to the clear state. From Hargeby *et al.* (1994).

pattern in the vegetation dominated state fits well with those reported in the studies described in the previous section. The sequence of mechanisms that causes the pattern in this case is thought to be as follows: unlimited phytoplankton growth occurs at the end of winter when light is no longer limiting, and this spring bloom is followed by a period of severe zooplankton grazing. So far, this is the classical spring clear-water phase scenario. However, when vegetation appears, nitrogen availability drops sharply, and bio-assays reveal that this is the main limiting factor for phytoplankton in the summer. In the autumn when macrophytes become senescent, release of nutrients leads to a short period of unlimited phytoplankton growth again, followed by a second grazing limited episode. The spring clear-water phase (Meijer *et al.*, 1994a) and the autumn release of nutrients causing a phytoplankton peak at the end of the growing season (Landers, 1982) are probably quite common in vegetated lakes. The mix of mechanisms responsible for suppressing phytoplankton in the summer may differ from case to case, as demonstrated by other case studies.

The causes of the striking contrast in Veluwemeer between clear *Chara* fields and turbid open water have also been analysed (Van den Berg *et al.*, 1997). Regulation of algal growth has not been tested with bio-assays in this case, but the seston composition and sedimentation rates have been recorded in some detail, allowing inferences about the regulating processes. In this large exposed lake, turbidity is caused not only by phytoplankton, but also to a large extent by resuspended inorganic sediment particles and detritus (Fig. 5.18). The concentration of all of these seston fractions is lower inside the *Chara* fields than in the open water, but differences are especially pronounced for large particles. Since larger particles sink faster in general, this suggests that sedimentation in the absence of wave resuspension is an important reason why the water is clear in the *Chara* fields. This is confirmed by the sedimentation records. In the open water sedimentation is as much as 100 g DWT m^{-2} d^{-1}, whereas in the centre of the *Chara* field practically no deposition is measured in sediment traps despite the fact that some seston remains present here. Apparently this remaining seston is hardly prone to sedimentation. The same picture arises from the shift in phytoplankton composition over a gradient from the open water into the vegetation (Fig. 5.20). In the centre of the *Chara* bed motile flagellates that can swim up to prevent settlement dominate.

Cladoceran density is lower in the *Chara* fields than in the open water in the summer but to have an idea of the potential importance of zooplankton for phytoplankton regulation, it is necessary to relate the consumption by the animals to the available amount of algae. A simple way to estimate the potential grazing pressure is to assume that cladocerans can consume a daily amount of phytoplankton equal to their own body weight (Schriver *et al.*, 1995; Jeppesen *et al.*, 1996). It then appears that despite relatively low numbers of *Daphnia* and *Bosmina*, their potential daily grazing capacity is estimated to about 10 times the total phytoplankton biomass in the veg-

with changing tides is considerable, and that apparently algal loss processes in the vegetation are fast enough to clear up the water considerably in a matter of hours. There was no difference between photosynthetic rates of phytoplankton in the water from inside or outside the weed beds, indicating that severe nutrient limitation or allelopathic effects were not the cause of the observed differences in chlorophyll concentrations. This leaves zooplankton grazing, sedimentation and shading by the plants as possible explanations.

A Danish enclosure study designed to study the refuge effect of vegetation for zooplankton (Fig. 5.9) also provides some insight into the possible role of zooplankton grazing in reducing phytoplankton biomass in weed beds (Schriver *et al.*, 1995). In this case the main plant species are *Potamogeton pectinatus*, *P. pusillus* and *Callitriche hermaphroditica*. Phytoplankton biovolume in the enclosures decreases with vegetation abundance (measured as plant volume infested), but this effect is less pronounced when fish predation has eliminated *Daphnia* and *Bosmina* populations (Fig. 5.21).

Estimates of the potential grazing pressure of these cladocerans indicate

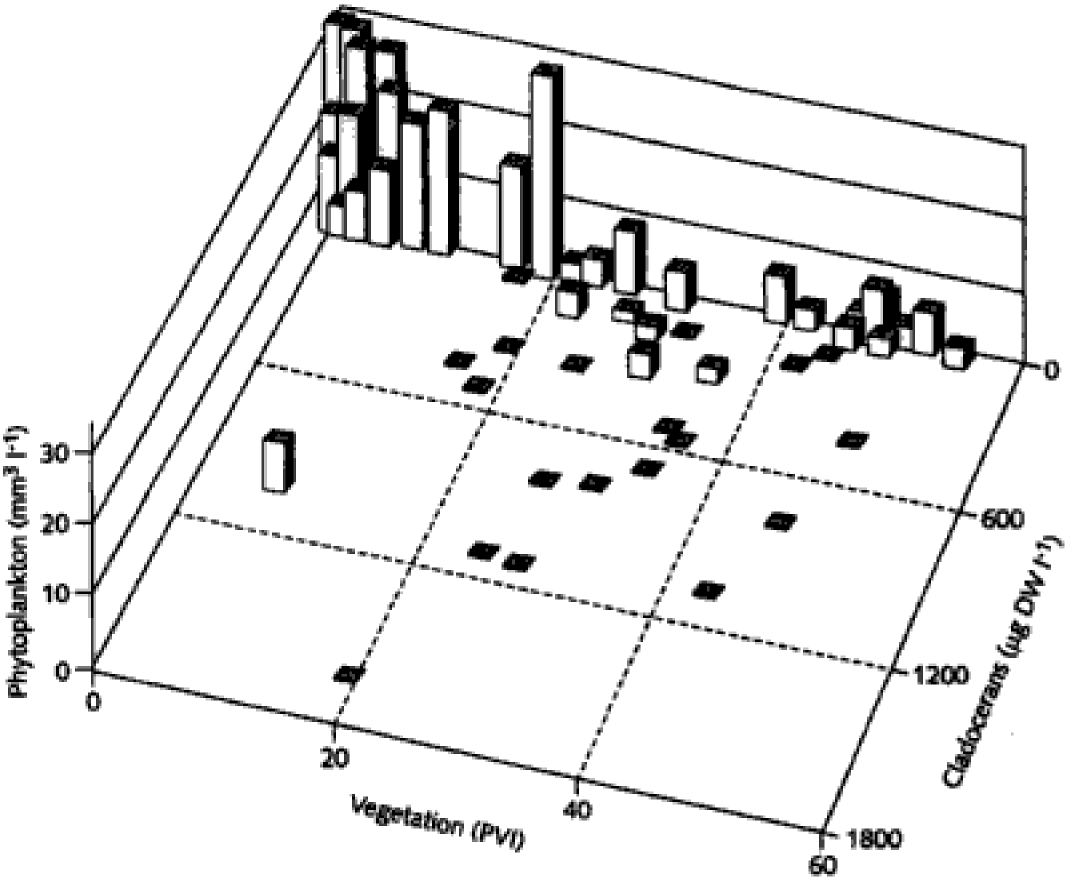


Fig. 5.21 Phytoplankton biovolume in relation to the vegetation density (PVI) and the biomass of planktonic cladocerans (*Daphnia* and *Bosmina*). From Schriver *et al.* (1995).

that their maximum daily consumption can be as much as 36 times the available amount of phytoplankton in the vegetated enclosures. Although other food sources such as detritus and periphyton apparently sustain cladoceran density at such high levels, grazing pressure on the preferred food, phytoplankton, is obviously severe under these conditions. Nonetheless, the fact that phytoplankton biovolume also decreases with vegetation abundance when these cladocerans are absent indicates that grazing by *Daphnia* and *Bosmina* is certainly not the only process involved (Fig. 5.21).

The importance of zooplankton grazing is also supported by the study by Timms and Moss (1984) who found clear water in the waterlily dominated Hudsons Bay, but not in the unvegetated Hoveton Great Broad receiving water from the same nutrient rich source. Bio-assays ruled out the possibility of nutrient limitation, and grazing by high numbers of large plant associated and pelagic cladocerans was probably the reason why chlorophyll concentrations in Hudsons Bay were less than 10% of those measured in the adjacent Hoveton Great Broad.

Are there general patterns?

The picture emerging from these case studies is that the importance of various mechanisms involved in the effect of aquatic macrophytes on water clarity varies considerably from case to case. This section summarizes the evidence for effects of shading, reduction of nutrient availability, excretion of allelopathic substances, reduction of resuspension and enhanced grazing, and shows how the interaction of these mechanisms may be understood using the theory of plankton interactions presented in earlier sections.

Shading

Although the role of shading by macrophytes in reducing phytoplankton productivity in plant beds is rarely mentioned, it may explain reduced algal abundance in vegetated areas at least in part as remarked already by Wetzel in his textbook on limnology (Wetzel, 1975). Light attenuation in the vegetation is among other things a function of plant biomass. Ikusima (1970) measured the specific attenuation coefficient of various plant types, and reports values of about $0.001\,\mathrm{m^2 g^{-1}}$. For submerged vegetation with a biomass of say $500\,\mathrm{g\,m^{-2}}$ this implies that even in crystal clear water less than 1% of the light that enters the water will reach the sediment ($I_D/I_0 = e^{-0.001 \cdot 500} = 0.0067$). How much shading will be experienced by phytoplankton depends on the vertical distribution of plant biomass, but clearly it is not an *a priori* negligible factor. Measurements of the vertical light gradient in a dense *Elodea* bed, for instance, show that irradiance can be reduced by more than 95% within the upper 20 cm of the water column (Pokorný *et al.*, 1984).

Nutrient limitation

Phosphorus availability in the water column may be reduced due to uptake by macrophytes (Kufel and Ozimek, 1994) but the majority of the studies show unaltered or even increased ortho-phosphorus levels (Moss *et al.*, 1990; Van Donk *et al.*, 1993; Perrow *et al.*, 1994; Van den Berg *et al.*, 1997). In contrast, very low inorganic nitrogen concentrations in the water column of vegetation stands are frequently found (Goulder, 1969; Van Donk *et al.*, 1993) and the importance of nitrogen as a limiting factor for algal growth has been confirmed in bio-assay experiments (Van Donk *et al.*, 1993). Low nutrient levels in vegetation stands may be due to uptake by plants but also to uptake by periphyton and in case of nitrogen by denitrification. Nonetheless, nutrient limitation has also been excluded as a possible explanation in various studies were reduced algal densities are observed among macrophytes (Pokorný *et al.*, 1984; Timms and Moss, 1984; Jones, 1990; Schriver *et al.*, 1995).

Allelopathy

Few studies indicate more than marginal allelopathic suppression of phytoplankton by macrophytes in natural situations, but the results so far indicate that cyanobacteria have a relatively high sensitivity to allelopathic exudates (see Chapter 3). Indeed the relative share of cyanobacteria in the phytoplankton community of weedbeds is often low (Hasler and Jones, 1949; Timms and Moss, 1984; Schriver *et al.*, 1995; Van den Berg *et al.*, 1997), but at least one study indicates that this is due to zooplankton grazing rather than plant exudates (Schriver *et al.*, 1995).

Resuspension prevention

Although several studies address the alteration of the sedimentation resuspension cycle of seston by macrophyte beds, only the Veluwemeer study (Van den Berg *et al.*, 1997) indicates the importance of this mechanism for the clearing effect of vegetation stands explicitly. Indeed in dense *Chara* stands in shallow water only motile or buoyant algae are likely to survive, as estimated sinking losses of more than 100% d^{-1} are unlikely to be compensated by growth. Although potential sinking losses in these *Chara* beds may be extreme, many studies demonstrate reduced resuspension in the presence of vegetation structure (Jackson and Starrett, 1959; Dieter, 1990; James and Barko, 1990; Petticrew and Kalff, 1992). In view of the rapid settling losses in shallow water, the presence of non-living suspended particles and most phytoplankton groups depends critically on resuspension, as explained earlier. Whether or not motile algae that are not affected by settling losses in dense vegetations can build up high biomasses depends on other factors. Note that one such factor is the residence time of water in the vegetation field. In some situations, residence time may be long enough to allow settling of particles, but too short to allow an alternative phytoplankton community to build up. The clearing of water in vegetation stands in the tidal Potomac river could potentially represent such a situation.

Zooplankton grazing

Several studies indicate that the amount of zooplankton in weed beds should be able to control the sparse phytoplankton populations present (Timms and Moss, 1984; Schriver *et al.*, 1995; Van den Berg *et al.*, 1997). Even in relatively dense vegetation, however, planktonic cladocerans can be driven to extinction by fish predation (Schriver *et al.*, 1995; Kairesalo *et al.*, 1997), and phytoplankton density can be reduced in the vegetation despite the absence of noticeable *Daphnia* and *Bosmina* populations (Schriver *et al.*, 1995). Plant associated cladocerans that hook up to the macrophytes may play a role in reducing algal biomass. These animals seem to be less vulnerable to fish predation (Kairesalo *et al.*, 1997) and their density is probably underestimated in standard sampling procedures. Nonetheless it is clear that grazing is just part of the story, and other factors may be more important in controlling phytoplankton at least in some cases (Van Donk *et al.*, 1993; Moore *et al.*, 1994).

How do things combine?

This overview leaves us with the rather general conclusion that various factors are responsible for the observed vegetation related increase in transparency and that the actual mix of effects differs from case to case. However, in using the basic theory of algal growth and grazing control presented in previous chapters something more can be said about the interaction of mechanisms leading to clear water in vegetation.

Importantly, grazing differs from the other factors in the fact that it can potentially cause a switch to an alternative stable state in which the algal food is over-exploited and can be kept at very low density even by a relatively small amount of grazers. Such over-exploitation of phytoplankton also happens during the spring clear-water phase, and usually leads to a collapse of *Daphnia* populations as a result of food shortage. In vegetation stands, high cladoceran densities can persist in the presence of very sparse phytoplankton densities, indicating that other food sources set the carrying capacity for daphnids and plant associated cladocerans here, and hence dynamics of filter-feeders are relatively independent of phytoplankton. As explained in the previous chapter, the effect of fixed grazer densities on food can be explored by plotting consumption and production as a function of food density in the same graph (Fig. 4.17). When production equals consumption the system is in equilibrium. Three such equilibria may arise: a stable one with a relatively high ('under-exploited') food density, another stable one at low ('over-exploited') food density and an unstable one that represents the breakpoint of the system. An increase in consumer density can cause the under-exploited equilibrium with high food concentrations to disappear, leading inevitably to a collapse of the food population (Figs. 4.18 and 4.19). Note, however, that the critical consumer density needed for the collapse of the food population depends on the productivity of the food. In terms of the graphical model (Fig. 4.17), a larger carrying capacity (*K*) of the food population is associated with a higher top of the humped production curve, sustaining higher consumer densities without collapsing.

In vegetation, nutrient limitation, shading and allelopathic substances will often reduce algal productivity, and the general conclusion of the graphical model therefore applies to the interaction of grazing and other mechanisms that reduce phytoplankton biomass in aquatic vegetation: when potential phytoplankton growth in the vegetation is reduced, even a relatively low density of filter-feeders may suffice to drive phytoplankton into an over-exploited state.

The combined effects of grazing and various productivity reducing factors on phytoplankton equilibrium biomass in vegetation can be visualized more completely using the minimal model of zooplankton controlled algal growth developed in the previous chapter:

$$\frac{dA}{dt} = rA\left(1-\frac{A}{K}\right) - g_z Z\frac{A}{A+h_a} + i\left(K-A\right) \qquad (1)$$

If we assume that (because of the availability of alternative food) zooplankton density is not directly dependent on phytoplankton biomass in the vegetation, the resulting phytoplankton biomass can be found as a function of zooplankton and algal carrying capacity (*K*) by solving the equation for $dA/dt = 0$. A plot of this equilibrium biomass of phytoplankton against *K* and zooplankton density summarizes the hypothesized combined effects of grazing and productivity reduction in the vegetation (Fig. 5.22).

Vegetation reduces phytoplankton biomass even in the absence of zooplankton, but extremely low algal biomass is found only when grazing leads to over-exploitation of phytoplankton. When vegetation is denser, factors such as shading and nutrient limitation reduce potential algal growth more strongly, and the threshold zooplankton density needed for the collapse of phytoplankton into the overgrazed state is lower. The catastrophe-fold that is characteristic for grazer over-exploitation (e.g. Fig. 4.19) becomes less pronounced and eventually disappears at very low algal productivities.

Although the minimal model is of course a crude simplification of the complex of intertwined mechanisms involved in regulating phytoplankton density in vegetation stands, it helps in seeing the forest through the trees in the somewhat confusing quest for 'the dominant' factor controlling algal

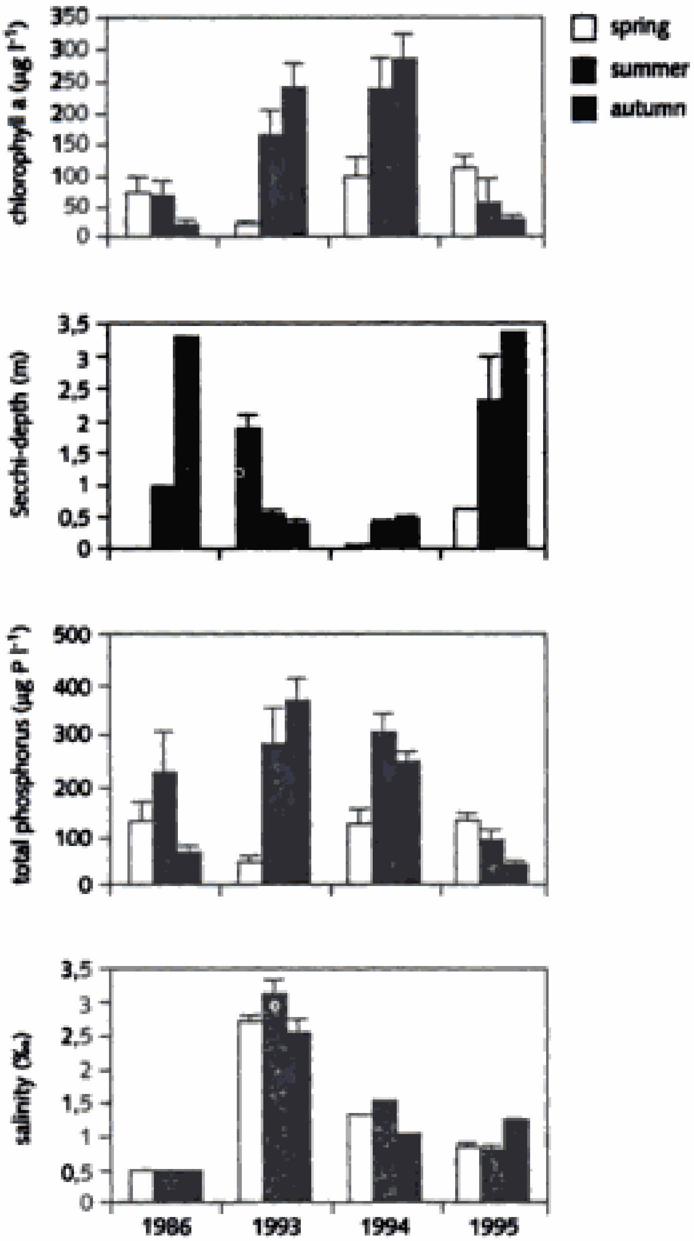


Fig. 5.24 In years with a higher salinity (lower panel) the concentrations of chlorophyll-a and total phosphorus are elevated and Secchi-depth is low in a shallow coastal Danish lake. From Jeppesen *et al.* (1997).

levels are much higher and Secchi-depths lower than in fresher years (Fig. 5.24).

Zooplankton composition in earlier years is not well documented, but the shift from turbid to clear in 1995 appears to be related to a strong increase in *Daphnia* numbers, as was observed in the Dutch Volkerak-Zoommeer. Interestingly, total-P levels are also elevated in the turbid years (Fig. 5.24) despite a relatively constant external loading. This is in line with the view presented in Chapter 3 that total-P concentration can in part be caused by high phytoplankton biomass, although causality behind their correlation is usually interpreted the other way round. Sulphide formation in the sediments of brackish water (which contains more sulphur than fresh water) may be another explanation of elevated phosphorus concentrations as it can cause part of the iron to become unavailable for phosphorus immobilization because Fe(II) is removed from the pore water due to precipitation with sulphide as insoluble FeS (see Chapter 2).

Comparison of the zooplankton communities of many brackish and fresh lakes confirms that substantial *Daphnia* populations are usually found hardly at all at salinities higher than 2–4 pp thousand (Jeppesen *et al.*, 1994; Moss, 1994). Instead, zooplankton in these situations is dominated by less efficient filter-feeders such as the copepods *Eurytemora* spp. and *Acartia* spp. and rotifers (Jeppesen *et al.*, 1994). Daphnids are known to be rather intolerant to salinity, and this may well be the main reason for their absence in brackish situations. An additional explanation may be that predation rates on zooplankton can be high in brackish lakes (Jeppesen *et al.*, 1997). The fish community is usually dominated by sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*). These animals may spawn several times during the summer leading to continuously high numbers of planktivorous juveniles. Since sticklebacks enter the vegetation, the refuge function of submerged plants for zooplankton in freshwater lakes may not work well against stickleback predation.

Mysid shrimps are another important component of the food web in most brackish lakes. This may be due to an adaptation to salinity per se, but the outbreak of *Neomysis* after strong reduction of the fish stock in Lake Wolderwijd (Meijer *et al.*, 1994a) shows that they can do well in fresh water. Possibly, the relative scarcity of larger planktivorous fish that prey on such relatively large invertebrates is an important factor explaining the abundance of mysid shrimps in brackish lakes. Mysids are omnivores that feed on detritus and periphytic and benthic algae but they are also known to consume zooplankton up to relatively large sizes (Chigbu and Sibley, 1994), which may be another stress factor to *Daphnia* populations in brackish lakes. Also, total-P levels may be elevated in the presence of *Neomysis integer* because excretion by these largely benthic feeders represents a net nutrient flow to the water column (Jeppesen *et al.*, 1997) a mechanism studied more extensively for benthivorous fish (Section 2.3).

Thus, predation pressure on *Daphnia* and nutrient regeneration by *Neomysis* may in part explain the turbidity of brackish lakes. However, the fact that daphnids respond more rapidly to decreasing salinity than the rest of the food web suggests that salinity per se is the main explanation for their absence in brackish water and the corresponding lack of top-down control of phytoplankton.

Note that the observations in brackish lakes also seem to suggest that cladocerans are crucial for causing water to clear up in aquatic vegetation. A caveat in this reasoning is that vegetation in brackish lakes is usually dominated by sago pondweed (*Potamogeton pectinatus*), a species that co-exists with turbid conditions in freshwater lakes too. In the lakes Krankesjön and Veluwemeer, for instance, the water becomes clear only after sago

$$Z_{max} = \frac{\ln\left(\frac{I_0}{I_{crit}}\right)}{E} \quad (3)$$

where the quotient (I_0/I_{crit}) is a constant depending on the daily radiation and the critical amount of light needed by the vegetation. Thus the maximum inhabited depth should be inversely related to the attenuation coefficient. Indeed, such a simple inverse relationship with the vertical attenuation coefficient has been found to describe the situation in the field quite well (Fig. 5.25) (Spence, 1982; Vant *et al.*, 1986).

For many lakes, light attenuation coefficients are not measured. Secchi disk transparency is easier to measure and data on the Secchi-depth are relatively abundant. As explained in Section 2.1, Secchi disk transparency (S_d) is approximately related inversely to light attenuation:

$$S_d = \frac{c_p}{E} \quad (4)$$

where c_p is the so-called Poole Atkins coefficient. Although this relationship is far from accurate (see Chapter 2) it suggests a linear relationship between z_{max} and transparency:

$$z_{max} = c_z S_d \quad (5)$$

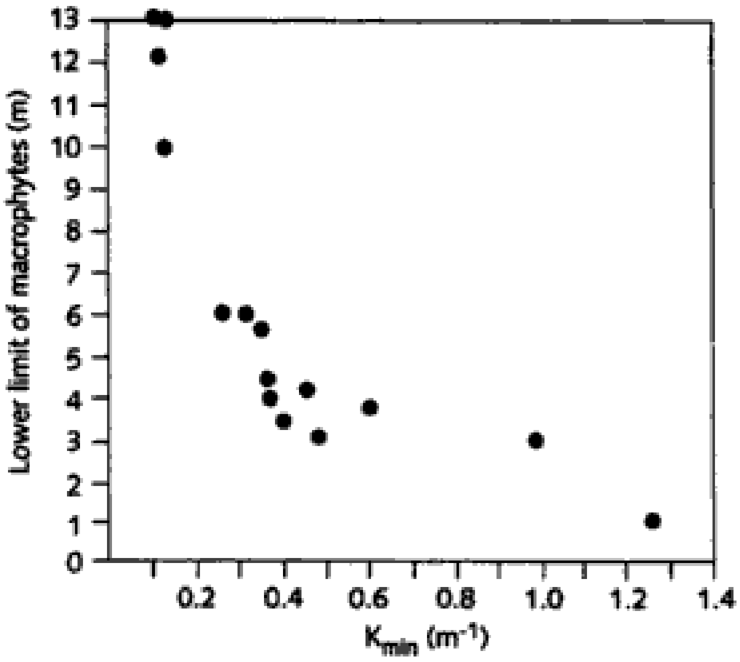


Fig. 5.25 Relationship between the maximum depth at which macrophytes occur (z_{max}) and the vertical attenuation coefficient of the most penetrating colours that can be used for photosynthesis (E_{min}) in a set of 15 UK lakes. Redrawn from Spence (1982).

where c_z is a constant depending on the Poole Atkins coefficient, the incoming radiation (I_0) and the critical light level needed by the vegetation (I_{crit}). Although this linearity is indeed confirmed remarkably well by some data sets, regression lines tend to intersect the y-axis (Fig. 5.26), suggesting that even under extremely turbid conditions, submerged plants can grow at shallow sites.

This can be represented by the formula:

$$z_{max} = z_c + c_z S_d \qquad (6)$$

where z_c is the maximum depth that can be colonized by submerged plants even under the most turbid conditions.

A simple explanation for this phenomenon is that it is not the light reaching the bottom that counts but the light reaching the canopy of the vegetation. This would imply that the effect of turbidity on plant growth in shallow lakes should critically depend on the growth form. Plants that stay low, such as many charophytes, depend more on a clear water column than plants that grow tall and concentrate much of their leaves just under the water surface. Indeed, canopy forming species such as *Potamogeton pectinatus* and *Hydrilla verticillata* usually dominate the vegetation in turbid shallow water, and there is a systematic increase of canopy forming species with the nutrient level (Chambers, 1987; Moss, 1988). Also, some plants respond to low light levels by extensive shoot elongation (Barko and Smart, 1981; Tanner *et al.*, 1993). It might be argued that the light that reaches the bottom remains crucial, as plants usually start their growth from the sediment surface in the spring. Many species in turbid lakes, however, overwinter in the form of vegetative underground structures. Such tubers

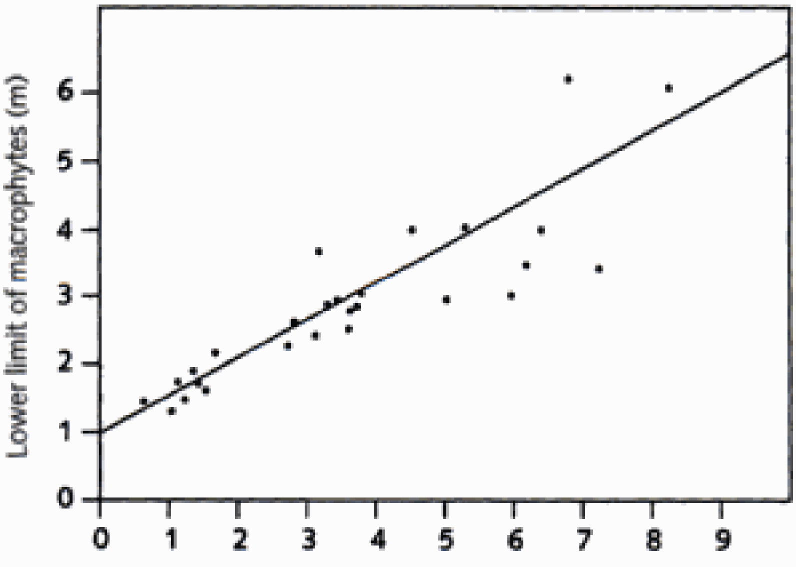


Fig. 5.26 Linear increase of the maximum depth inhabited by macrophytes with Secchi-depth in a set of 27 Finnish lakes. Redrawn from Hutchinson (1975).

(*Potamogeton pectinatus*). Mapping, however, has been continued ever since and also covers the gradual recovery of vegetation with improving water quality that started in the late 1980s. Since maps of lake depth, sediment characteristics and data on water quality and the abundance of fish and birds over that period are also available, a statistical analysis of the possible impact of these factors on the vegetation could be made (Scheffer *et al.*, 1992). To do this, 5% of the map surfaces were sampled at random in 50 × 50 m blocks. The presence of plants in these blocks was scored and related to the environmental factors.

As expected, the analysis suggests that turbidity and depth are the most important factors explaining vegetation abundance. However, although most of the plant beds are found in water shallower than 1 m, the probability of finding vegetation decreases with depth almost asymptotically, and no real limit is observed (Fig. 5.28).

Healthy plant stands are found at depths down to 3 m, even though Secchi-depth is less than 0.5 m. Model simulations (Scheffer *et al.*, 1993a) suggest that this can be explained by dispersal of diaspores from productive plant stands at shallower sites (Fig. 5.29).

The potentially large effects of propagule dispersal on plant distribution have also been reported in terrestrial plant ecology. A detailed study of the population regulation of the dune annual *Cakile edentula*, for instance, revealed that landward migration of seeds sustains substantial populations in areas where the species would otherwise not be able to persist (Watkinson, 1985; Watkinson and Davy, 1985). Obviously, variation in

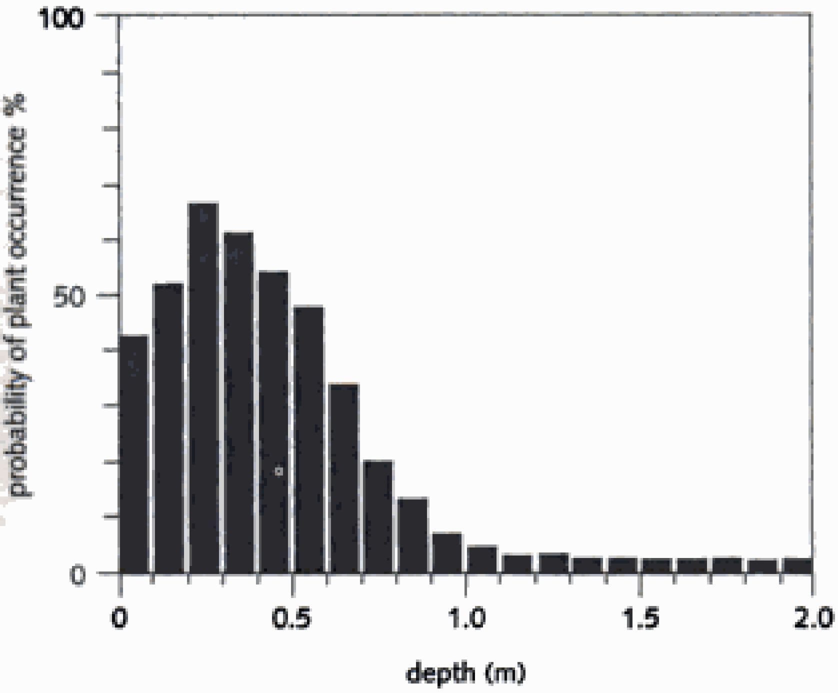


Fig. 5.28 Frequency of occurrence of *Potamogeton pectinatus* on 0.25 ha plots at different depth in the Randmeren. From Scheffer *et al.* (1992).

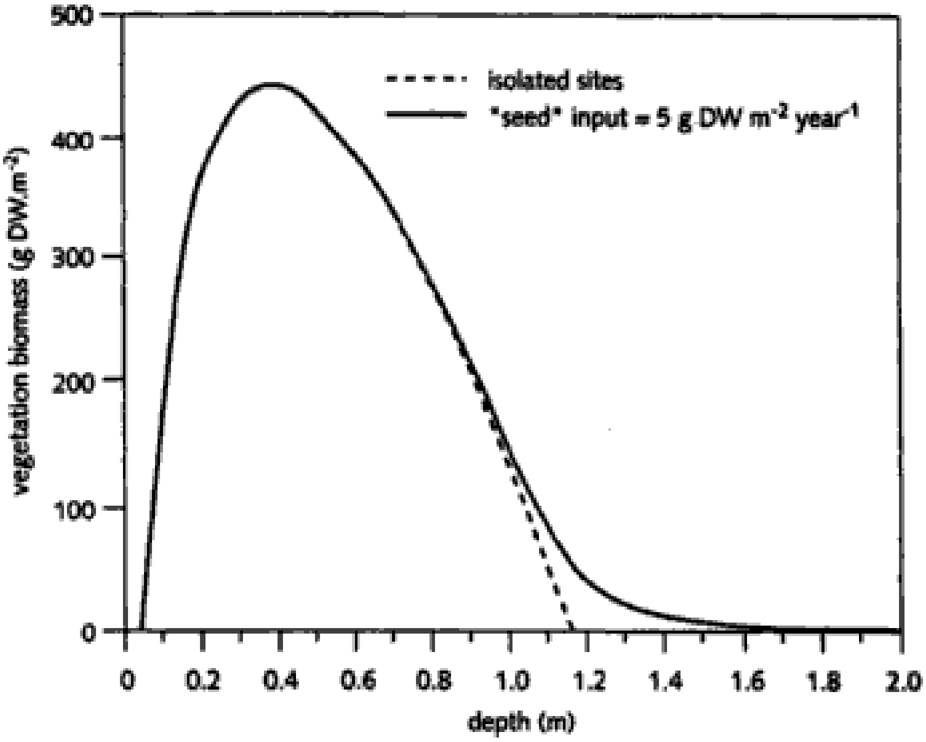


Fig. 5.29 Simulated effect of an input of seeds or other propagules on the equilibrium biomass of submerged vegetation over a range of water depths. From Scheffer *et al.* (1993a).

propagule rain from productive plant stands implies a caveat in relating vegetation distribution to local environmental conditions.

These observations also illustrate that even when a plant appears to be able to grow on a site, this does not necessarily imply that conditions are sufficient for a viable plant stand to survive there for a prolonged period. A positive net photosynthesis is a necessary but not sufficient condition for population persistence. In the absence of propagule import, plant stands will only persist if growth is sufficient to balance various losses in the course of the growing season, such as biomass loss in winter, herbivory losses and damage by waves (Scheffer *et al.*, 1993a). Indeed, light levels reported at the depth limit of macrophytes in deeper lakes are usually about 10–20% of the surface light (Chambers and Kalff, 1985b; Vant *et al.*, 1986) which is high compared with the light compensation point of individual plants. Also, a study by Golubi quoted by Hutchinson (1975) shows that the light compensation points of *Chara* and *Myriophyllum* in the Yugoslavian Lake Vrana are reached at depth 1.6 resp., 4.7 times greater than the actual maximum inhabited depth in the lake.

Periphyton

The practically floating canopies of *Potamogeton pectinatus* seem an almost perfect escape from the shading effect of turbid water. Indeed, the

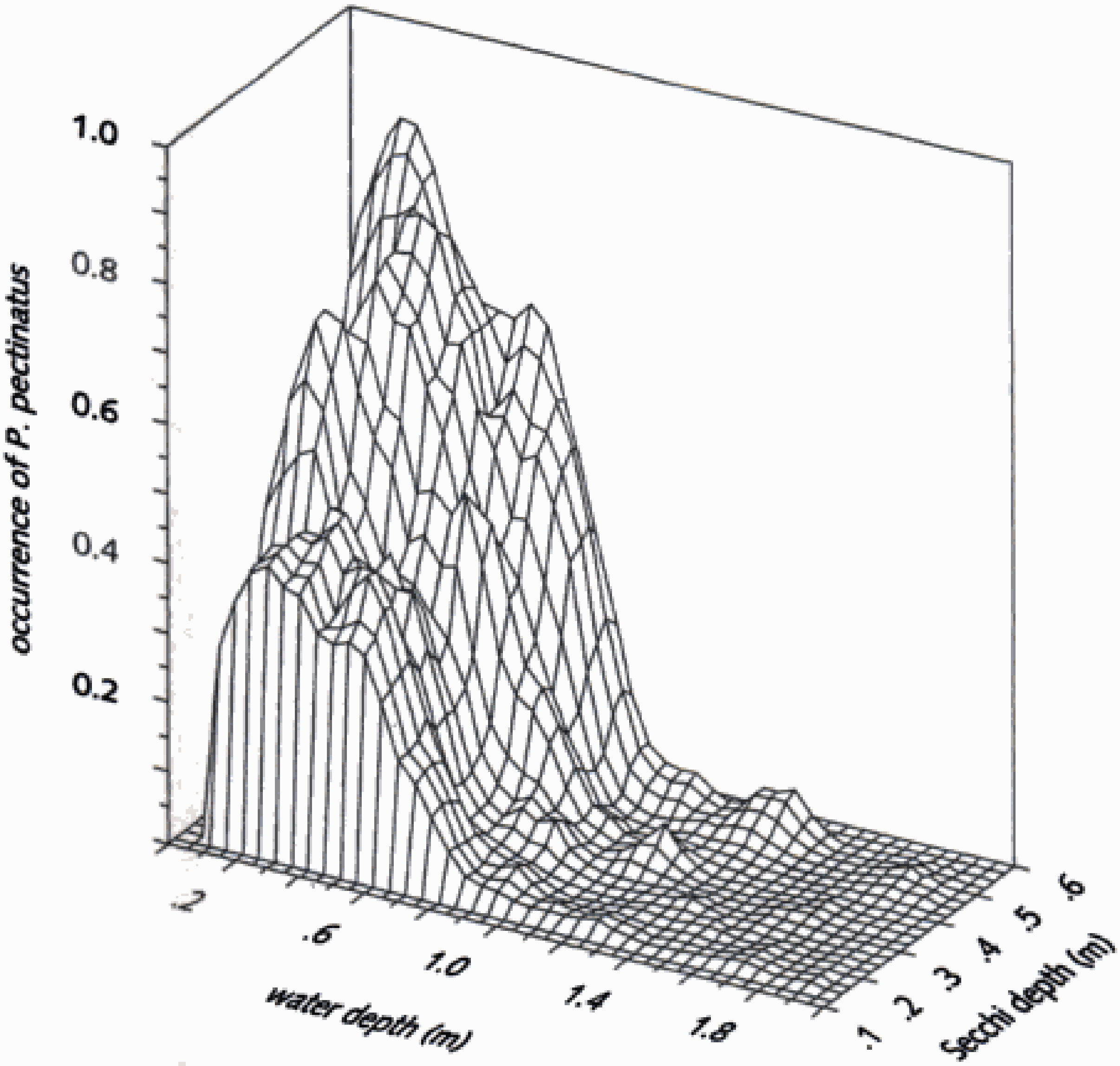


Fig. 5.30 Probability of occurrence of *Potamogeton pectinatus* as a function of water depth and Secchi disk transparency in the Randmeren. The response surface is interpolated through a set of presence–absence data for 0.25 ha plots, gathered over a period of 20 years. Vegetation is less abundant in turbid situations, but the depth range is largely independent of turbidity. From Scheffer *et al.* (1992).

Randmeren study shows that even under very turbid conditions plants stay present down to about 1 m depth. However, despite the growth form, abundance of this species does decrease with turbidity even in the shallow areas (Fig. 5.30).

Obviously, this decrease does not necessarily imply a direct causal link. The correlation may well have more indirect reasons (cf. Fig. 5.16). Turbidity increases with the nutrient loading, but so do other things that may affect the performance of submerged plants such as fish density and the growth of the periphyton covering the plants. To check if light was limiting the growth in the pondweed vegetation of the Randmeren, shade cloth of different

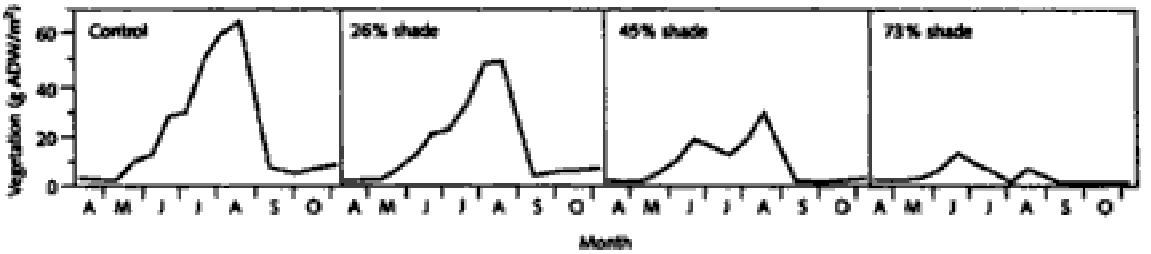


Fig. 5.31 Seasonal biomass development of artificially shaded vegetations of *Potamogeton pectinatus* in Lake Veluwemeer. From van Dijk and van Vierssen (1991).

densities was installed to reduce the incoming radiation in experimental plots in a large pondweed stand (Van Dijk and Van Vierssen, 1991; Van Dijk *et al.*, 1992). Even moderate shading reduced the growth (Fig. 5.31) indicating that the plants were indeed light-limited in the field.

However, it could also been shown that the periphyton layer covering the plants is responsible for much of the light attenuation in the field (Van Dijk, 1993). Since both periphyton growth and turbidity increase with the nutrient level, the decrease of sago pondweed with turbidity is likely to be at least partly due to the effect of periphyton.

Indeed, periphyton coverage is likely to be a major problem for submerged plants in many eutrophic lakes as it can reduce the light that reaches the plant by as much as 80% and limit the diffusion of carbon and other nutrients between water and plant (Sand-Jensen and Borum, 1984). The overall negative effect of periphyton on macrophyte growth is also indicated by the many experiments showing that removal of periphyton by grazers can result in greatly enhanced plant growth (Brönmark, 1985; Hootsmans and Vermaat, 1985; Howard and Short, 1986; Underwood, 1991; Daldorph and Thomas, 1995). It has been suggested that periphyton removal (by mysid shrimps) is also the clue to understanding the abundant growth of submerged plants despite the high turbidity in many brackish lakes (Bales *et al.*, 1993).

Periphyton is not simply a layer of algae. It can be a complex community on its own consisting of algae, bacteria and protozoa. In addition, considerable amounts of settling material can be trapped in it. In Veluwemeer, settled silt and clay particles and detritus represent the bulk of the periphyton layer (Van Dijk, 1993). The actual shading caused by periphyton on plants is difficult to estimate in practice, as plant tops usually have much less periphyton than older parts of the shoots. This is simply because the periphyton layer needs some time to grow. Thus, plants can minimize the impact of periphyton by sustaining a high growth rate. This implies a positive feedback. Fast growing plants keep ahead of the periphyton and maintain fast growth, whereas slow plant growth allows periphyton to overgrow the plant and reduce its performance further.

substrate than terrestrial plants. Nonetheless, within lake distributions are often correlated with substrate variation. In relatively nutrient poor Canadian lakes vegetation biomass is higher on clay than on sandy spots (Anderson and Kalff, 1987; Anderson and Kalff, 1988). Interpretation of this correlation is tricky, as sedimentation of clay particles is also higher in weed beds (Petticrew and Kalff, 1992). However, in situ pot experiments confirm that plant growth is better on nutrient rich clay than on sandy soils (Chambers and Kalff, 1985a). In eutrophic lakes nutrient supply through the shoots will help prevent nutrient shortage, and soil fertility is probably less important, although some relation to soil fertility has been demonstrated even in the hypertrophic Danish Lake Væng (Lauridsen *et al.*, 1993). In practice light is often the dominant limiting factor, obscuring effects of soil composition on within lake plant distributions (Scheffer *et al.*, 1992).

Nutrient content, however, is not the only important aspect of the substrate for plants. In highly organic soils toxic substances such as sulphide have been suspected to hamper vegetation development (Moss *et al.*, 1990; Smolders and Roelofs, 1993; Smolders and Roelofs, 1995). Also, very loose sediment may facilitate uprooting of plants by wave action. Since this normally coincides with a very high turbidity it may be difficult to infer the main reason for the absence of plants. In Lake Breukeleveen, for instance, the thick layer of very loose peaty sediment is resuspended almost every day, and it is hard to imagine any plant settling there. Transparency, however, is also very low (ca. 0.4 m), in part because of the same resuspension. In enclosures submerged plants grow well, indicating that sediment chemistry is not the reason for their absence in the lake (Van Donk *et al.*, 1994b). Wave action is blocked out here, suggesting that the combination of unstable sediment and waves was a problem for the plants. However, turbidity is also less in the absence of resuspension, and this obviously contributed to the improved conditions for plant growth.

Loose sediments may also facilitate uprooting by birds and fish causing the impact of these animals to be larger than that inferred from their consumption rates. Experiments with potted plants in Lake Væng, for instance, showed that macrophytes planted in clay were pulled out completely by coot while those planted in sandy soil were merely clipped off by the birds (Lauridsen *et al.*, 1993).

Wave action

Wave action can be an important factor for plants in shallow wind-exposed lakes even if the sediment is solid enough to prevent uprooting. The seasonal cycle of submerged plants, for instance, may differ with the degree of exposure. In the large, wind-exposed Randmeren the entire aboveground part of the vegetation is swept away with the first autumn storms. Van Wijk (1988) who compared the life cycle of sago pondweed vegetation in the Randmeren and several contrasting lakes, found that the growing season is shorter in the exposed Randmeren than in any other studied case. In small protected water bodies the species can even be perennial. Interestingly, the moment at which the vegetation is wiped out in the autumn has been shown to be related to the degree of eutrophication in the Randmeren. The growing season was longer in early years when the conditions were better. When eutrophication proceeded, lakes that were less affected kept vegetation longer at the end of the summer (Leentvaar, 1966). Also in the in situ shade experiments, heavily shaded plots lost aboveground biomass earlier at the end of the growing season (Van Dijk and Van Vierssen, 1991). Wave action thus seems to shorten the seasonal period over which submerged vegetation is present on exposed sites, and more so if growth conditions are bad due to light limitation.

Although vegetation abundance and species richness is often found to be better on sheltered sites (Spence, 1982), this is not necessarily the case in shallow lakes. In the Randmeren, even though the length of the vegetation period is limited by wave action, presence of submerged plants in summer is correlated positively with exposure (Fig. 5.32).

Apparently, positive effects of factors related with exposure overrule the effect of wave damage. One possible positive effect is that wave action partly removes the periphyton layer from the plants, whereas at sheltered sites, deposition of suspended solids on the vegetation only adds to the periphyton complex. Indeed, in Lake Krankesjön where vegetation abundance is also found to be reduced at sheltered sites, periphyton biomass is inversely related to wave exposure (Weisner *et al.*, 1997). Also, water movement caused by waves may enhance photosynthesis through an improved carbon exchange between water and plant. An even more indirect effect of

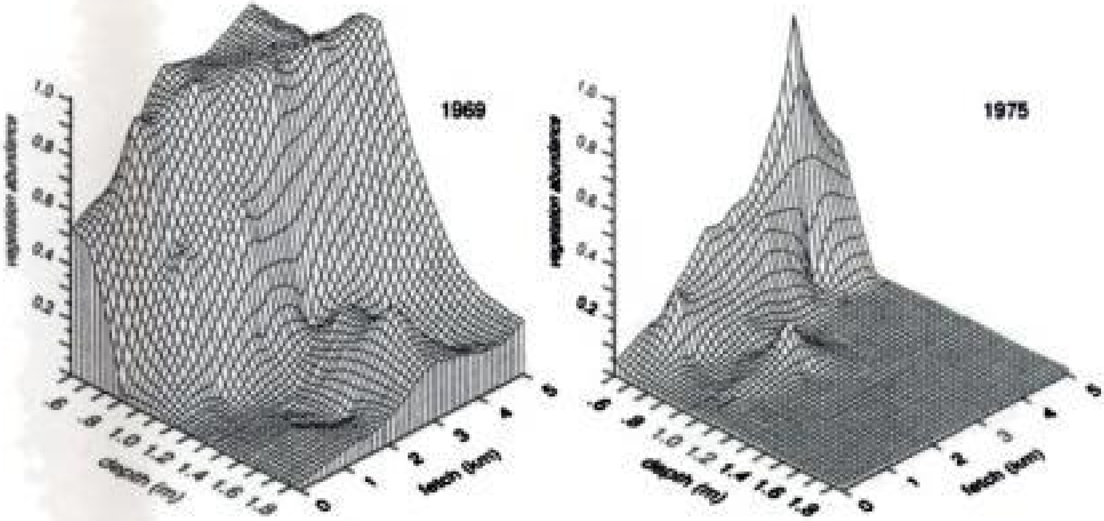


Fig. 5.32 Abundance of submerged vegetation in relation to water depth and wind exposure (fetch relative to the prevailing direction of the wind) in Lake Veluwe for a good year (1969) and a bad year (1975). The surfaces are obtained by interpolation through presence–absence data from 0.25 ha plots. From Scheffer *et al.* (1994a).

In the case of carp, the detrimental effect has been unequivocally demonstrated in many experimental studies (Threinen and Helm, 1954; Tryon, 1954; King and Hunt, 1967; Crivelli, 1983). Indeed the introduction of carp for sport fishery purposes is likely to be responsible for the disappearance of vegetation from many lakes in western Europe. In the United States, where carp was introduced more than a century ago, the devastating effect of this species on vegetation and its associated waterfowl and game-fish has been noted long since (Cahn, 1929). Several biomanipulation experiments 'avant la lettre' removing carp and other 'coarse fish' were conducted, resulting in vegetation recovery and enhanced transparency of the water (Rose and Moen, 1952; Cahoon, 1953; Threinen and Helm, 1954). In view of their destructive effects carp are even referred to as the swine of lakes (Threinen and Helm, 1954). King and Hunt (1967) found that while *Chara* plants were consumed by carp, pondweeds were damaged more by uprooting. Sediment resuspension may be another important way in which carp and other benthivorous fish affect vegetation performance. Not only does this cause a high turbidity, settling of the suspended sediment may also cover plants. The magnitude of this effect is illustrated by an observation of Threinen and Helm (1954). They found that wire exclosures helped little in stimulating vegetation growth, probably due to a deposition in the exclosures of as much as 20 cm of sediment within two months. As wave action was minor in the sheltered area where the experiments were conducted, carp was held responsible for these sediment dynamics.

5.4 VEGETATION AND PHYTOPLANKTON DOMINANCE AS ALTERNATIVE EQUILIBRIA

The cases presented in Chapter 1 show that many shallow lakes can switch abruptly between a vegetated state with clear water and a turbid situation with high concentrations of phytoplankton and other suspended solids. This section explains how such conspicuous and spectacular behaviour may be explained from the fact that these states represent alternative equilibria, a hypothesis that has been discussed extensively over the past decade (Timms and Moss, 1984; Hosper, 1989; Scheffer, 1989; Jeppesen *et al.*, 1990; Scheffer, 1990; Blindow *et al.*, 1993; Scheffer *et al.*, 1993; Moss, 1995; Blindow *et al.*, 1996; Moss *et al.*, 1996)

Stabilizing mechanisms

In the previous sections it has been shown that vegetation tends to enhance water clarity, but also that light limitation is one of the main problems for submerged plants in eutrophic lakes. This implies a positive feedback in the development of submerged vegetation: once they grow, the water clears up and they grow even better. Figure 5.33 summarizes the main mechanisms involved. A simple way of evaluating the overall effect of the depicted

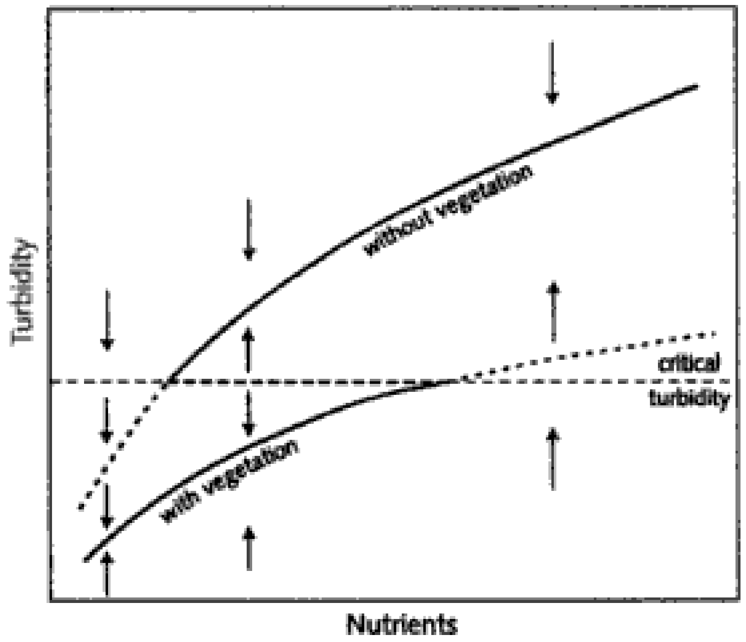


Fig. 5.34 Alternative equilibrium turbidities caused by disappearance of submerged vegetation when a critical turbidity is exceeded (see text for explanation). The arrows indicate the direction of change when the system is not in one of the two alternative stable states. From Scheffer *et al.* (1993b).

In some cases this may be very difficult; for instance when wave resuspension causes a high background turbidity that is not due to phytoplankton, or when sediments contain a large amount of buffered phosphorus. In such situations a disturbance, such as biomanipulation, that temporarily reduces the turbidity to a value below the critical level needed for macrophyte colonization may cause a permanent shift to the alternative stable state of clear water and vegetation dominance. This is discussed further in section 6.1.

Note that, at the extremes of the range of nutrient levels over which alternative stable states exist, either of the equilibrium lines approaches the critical turbidity that represents the breakpoint of the system. This corresponds to a decrease of stability. Near the edges, a small perturbation is enough to bring the system over the critical line and to cause a switch to the other equilibrium.

Water level in the lake is another important control variable with respect to aquatic macrophyte dominance. Since vegetation can resist a higher turbidity if the lake is shallower, the horizontal breakpoint line in the diagram will be at a higher critical turbidity in shallower lakes. It can be seen from the graphical model that a small shift in critical turbidity resulting from a change in water level can bring about a switch from one state to the other in lakes that are close to the breakpoint already. This is in line with observations in several lakes (Wallsten and Forsgren, 1989; Blindow *et al.*, 1993; Sanger, 1994).

It is not possible to find universally applicable values for E_c and E_v as both depend on various other factors than light availability. Nonetheless, something can be said about their relative positions. Both are related inversely to the depth of the lake (*D*). In the case of filamentous cyanobacteria the critical shade (*ED*) level in Dutch lakes seems to be in the range between 4 and 10 (Figs. 3.14 and 3.17). For submerged plants the maximum inhabited depth seems to indicate a shade level (*ED*) between 1 and 3 (Fig. 5.25). In shallow water, however, the latter value may be much higher as plants escape shading by growing to the surface. This suggests that in very shallow lakes the middle branch of the hysteresis may be very small, implying that cyanobacterial dominance and vegetation dominance are more likely to be the only two alternative stable states, whereas in somewhat deeper lakes dominance by other algae is a third alternative.

The vegetation–turbidity interaction elaborated

The assumption that vegetation is either abundant or absent is a major oversimplification. To allow a more careful approach, we need to be more specific about the effect of vegetation on turbidity and vice versa.

The effect of turbidity on vegetation

In practice the effect of turbidity on vegetation abundance will depend to a large extent on the shape of the lake. The simplest way to see this is to use the rule that the maximum inhabited depth (z_{max}) increases linearly with transparency (Fig. 5.27) and is inversely proportional to the light attenuation coefficient (Fig. 5.25). As argued, these relationships are not sufficient to describe the distribution of canopy forming species like sago pondweed in shallow water. Such plants can occur down to about 1 m water depth even at very high turbidities. However, their abundance in shallow water nonetheless tends to decrease with increasing nutrient level, and with respect to the impact on turbidity, sparse pondweed stands are not really relevant. Most studies indicate that significant effects on turbidity require dense weed beds, in the case of Veluwemeer and Krankesjön dense charophyte mats. As argued, the latter respond to changes in turbidity of the water column more strongly (Fig. 5.27). As a first approximation we therefore neglect the subtleties of vegetation shifts in turbid water and make the simplifying assumption that all parts of the lake that are deeper than z_{max} lack vegetation, whereas all the shallower areas are completely covered by macrophytes.

The effect of increasing turbidity on vegetation in a perfectly flat bottomed lake can now be derived easily (Fig. 5.36).

Vegetation coverage is 100%, as long as turbidity is low enough to let z_{max} exceed the lake depth. As soon as z_{max} becomes less than the lake depth, vegetation disappears completely. The other extreme case that allows a simple analysis is that of a lake in the form of a v-shaped channel. Here

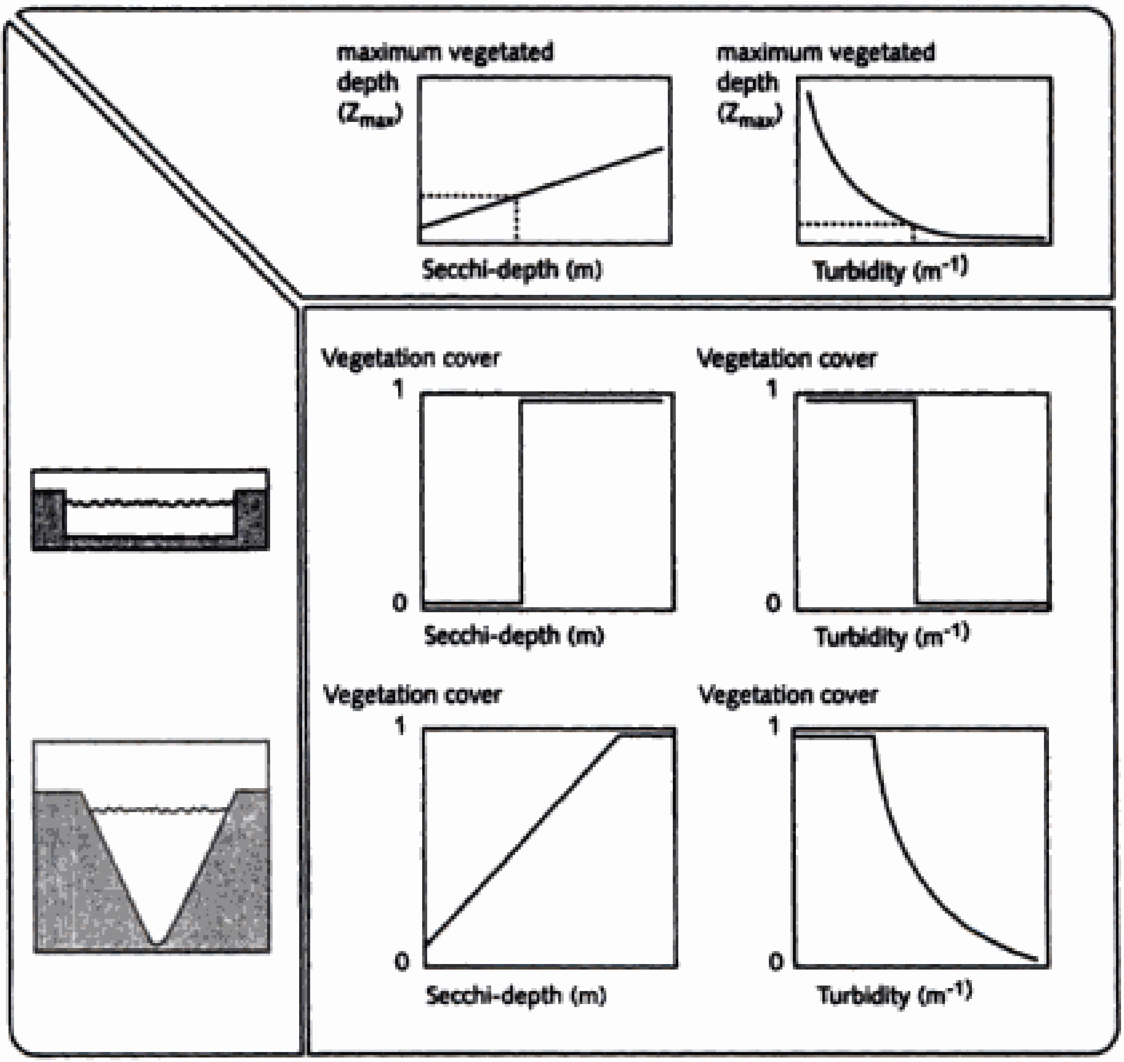


Fig. 5.36 Schematic representation of the response of the percentage of the lake area covered by aquatic vegetation to changes in Secchi disk transparency or turbidity (vertical light attenuation) in hypothetical flat bottomed lakes versus lakes with a v-shaped depth profile (the two left-hand drawings) as predicted from the empirically derived effects of transparency and turbidity on the maximum depth inhabited by plants (z_{max}) represented in the top two diagrams (see text).

vegetation will be unaffected as long as z_{max} exceeds the maximum lake depth. As soon as z_{max} becomes less than the maximum lake depth the percentage of the lake area that is vegetated will drop linearly with decreasing transparency and exponentially with increasing turbidity.

Although many shallow lakes resemble the flat bottomed caricature, real depth profiles usually combine large areas of equal depth with gradually declining slopes. Thus the drop in vegetation abundance with increasing turbidity becomes a combination of the caricatures. Also, we have to account for the fact that with increasing turbidity, vegetation abundance will already decrease before an area becomes too deep for vegetation according to the z_{max} threshold. Likewise, vegetation stands can often be found below this theoretical threshold. Relaxing the extreme threshold assumption and

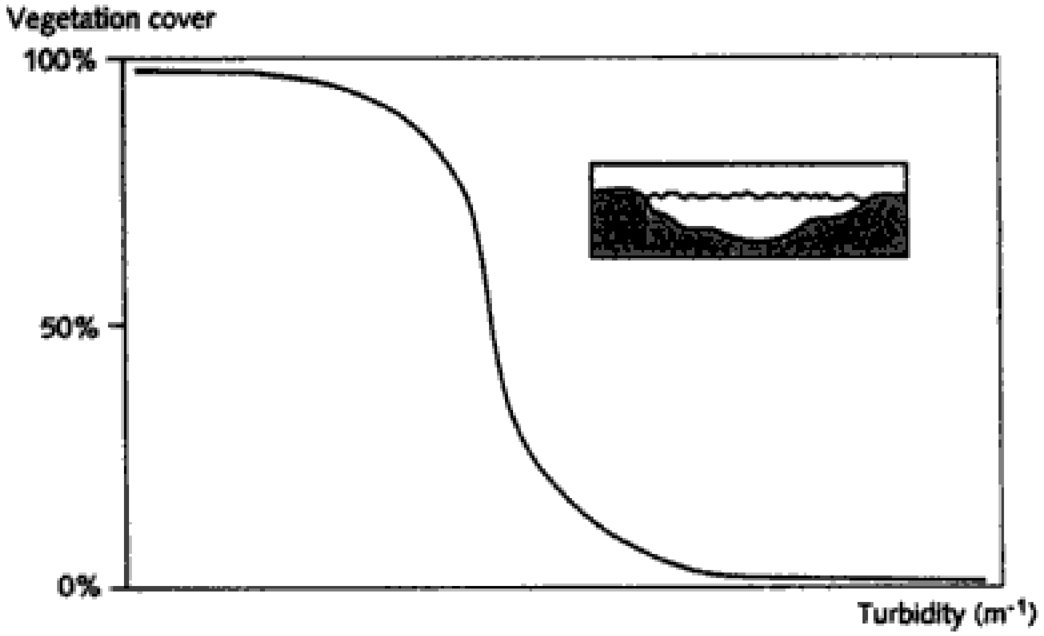


Fig. 5.37 Generalized response of equilibrium vegetation abundance in a shallow lake to turbidity (see text).

accounting for more realistic lake shapes, the overall response of vegetation abundance to turbidity should typically look sigmoidal for a shallow lake (Fig. 5.37).

Over a range of very high turbidities submerged plants will be virtually absent. Over a range of very low turbidities, the whole lake will be occupied by plants. Between these extremes there is a range of turbidities over which vegetation responds relatively strongly to turbidity. The response over this range is steeper if the bottom of the lake is flatter. Obviously, the critical turbidity where vegetation reacts relatively steeply to changes is higher if the lake is shallower.

The effect of vegetation on turbidity

As explained earlier, the picture of the suite of mechanisms through which vegetation reduces turbidity is not yet completely clear. Various studies show that sedimentation, nutrient, limitation, allelopathy and grazing can play a role but the relative importance of these mechanisms seems to differ from case to case. For the current purpose we can avoid going into too much detail and simply characterize the overall effect of vegetation on transparency.

Most of the case studies of the effect of vegetation on water clarity report reductions in seston concentrations or turbidity of about 90% (Table 5.1).

However, these studies all address local situations in weed beds or the effects of a switch to complete vegetation dominance of lakes. The impact of partial coverage by submerged macrophytes on whole lake turbidity can not simply be inferred from such maximum effects. In some cases plant beds will

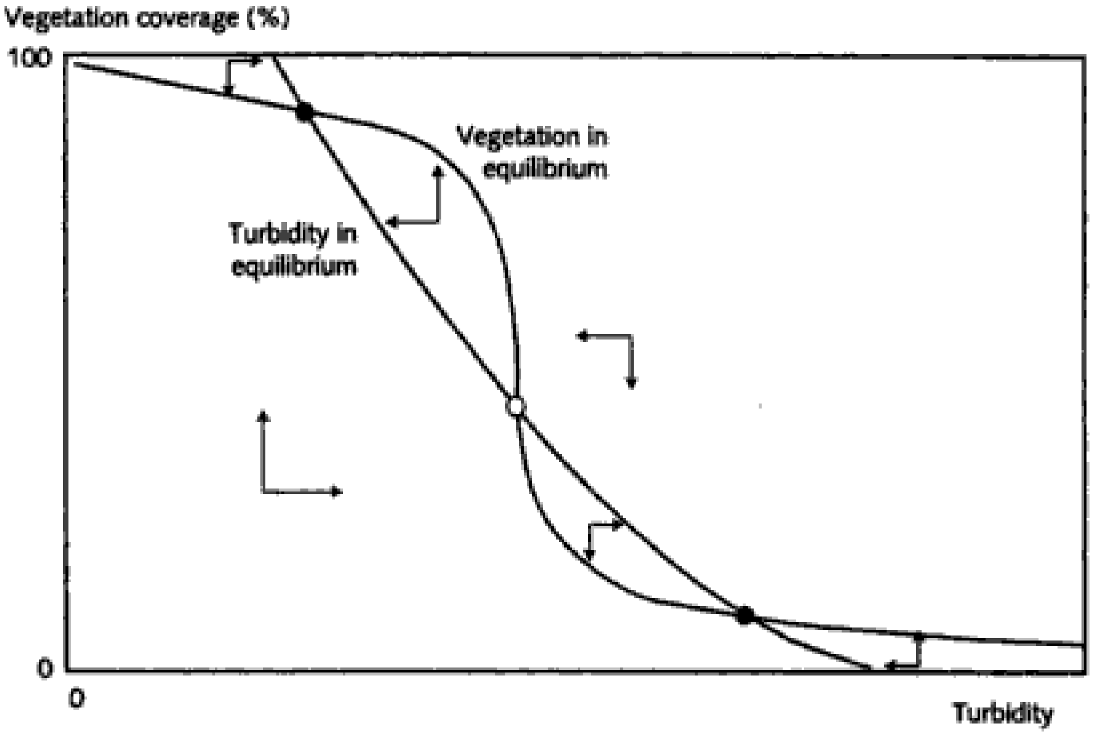


Fig. 5.39 Isoclines of turbidity (*dE/dt* = 0) and vegetation (*dV/dt* = 0) obtained by combining the equilibrium lines presented in Figs. 5.37 and 5.38. The intersection points are equilibria but the middle point (open dot) is unstable (see text).

dicular directions. Thus this point is an unstable equilibrium. It is a saddle point comparable to that in the competition model for cyanobacteria and algae. Again, it lays on a line called 'separatrix' that separates the basins of attraction of the clear and the turbid state. The origin, by definition, is another point of the separatrix, but since the growth equations are not specified, the complete separatrix can not be constructed.

The upper intersection point represents a clear vegetation dominated state, whereas the lower stable intersection point is a turbid state with little vegetation. The conditions for these alternative stable states to exist depend on the shapes and positions of the two isoclines. If the turbidity isocline (*dE/dt* = 0) shifts to the right, as may be expected when nutrient loading of the lake increases, the saddle point and the vegetation dominated equilibrium point will move together and eventually disappear. On the other hand, a shift of the turbidity isocline to lower values can lead to the disappearance of the turbid equilibrium point through collision with the unstable saddle. Plotting the vegetation density or turbidity in the intersections against nutrient loading (shifting the turbidity isocline horizontally), the familiar sigmoidal hysteresis curves arise, with the middle part representing the breakpoint of the system (Fig. 5.40a).

This qualitative result was also obtained with the more naive graphical approach (Fig. 5.34), but it can now be seen that the hysteresis does not necessarily always arise. Alternative equilibria only exist if the isoclines

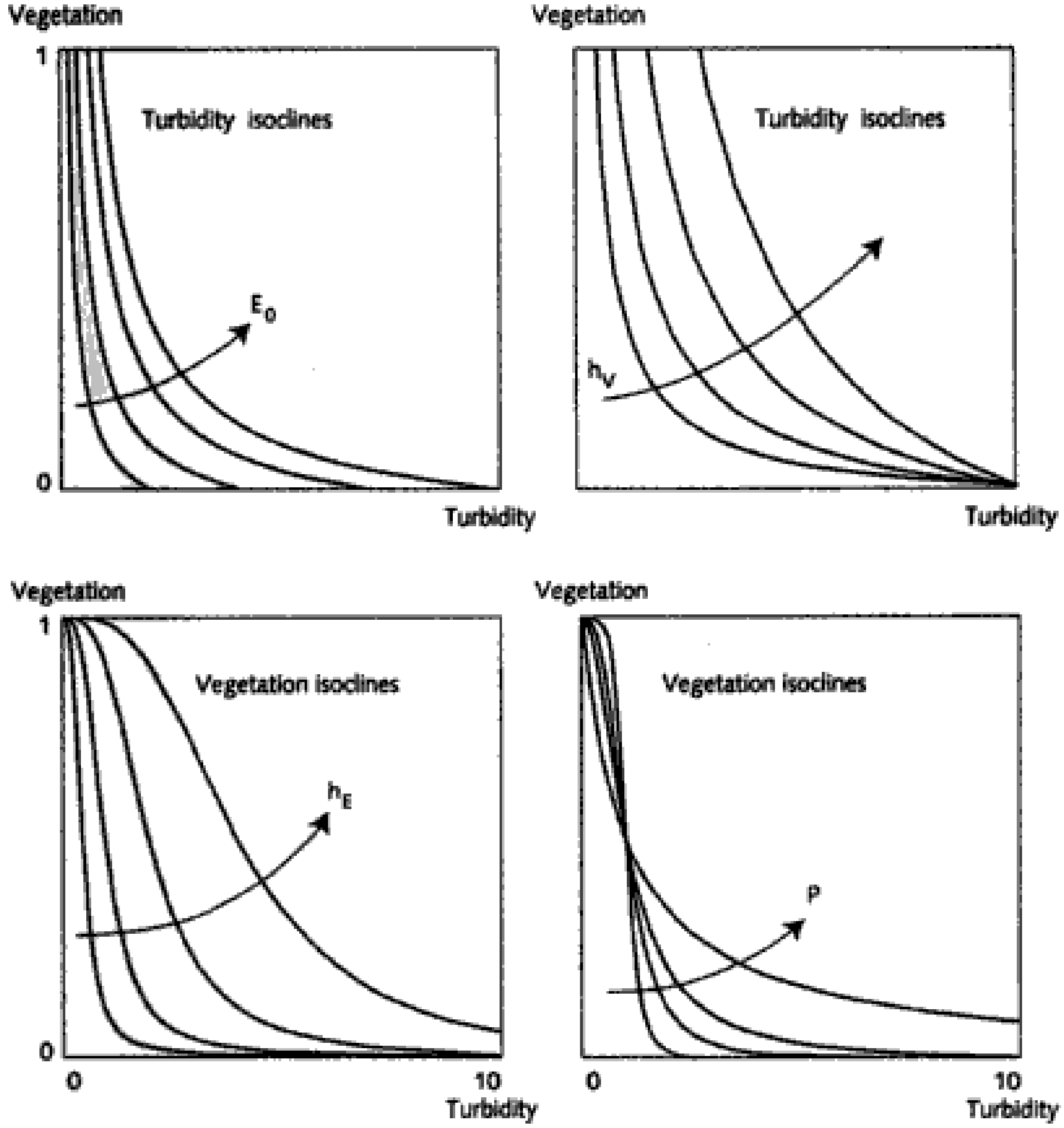


Fig. 5.41 Different shapes of the isoclines of turbidity ($dE/dt = 0$ upper panels) and vegetation ($dV/dt = 0$ lower panels) resulting from changes in the parameters E_0, h_v, h_E and p in the minimal mathematical model of the vegetation–turbidity interaction (Eqs. 69 and 70) (see text for interpretation of the parameters).

$$E^* = \frac{E_0 h_v}{h_v + \dfrac{h_E^p}{E^{*p} + h_E^p}} \tag{9}$$

$$V^* = \frac{h_E^p}{\left(\dfrac{E_0 h_v}{h_v + V^*}\right)^p + h_E^p} \tag{10}$$

The formulae look awkward, but we can now plot them with any appropriate software to see how the equilibria depend on the parameters.

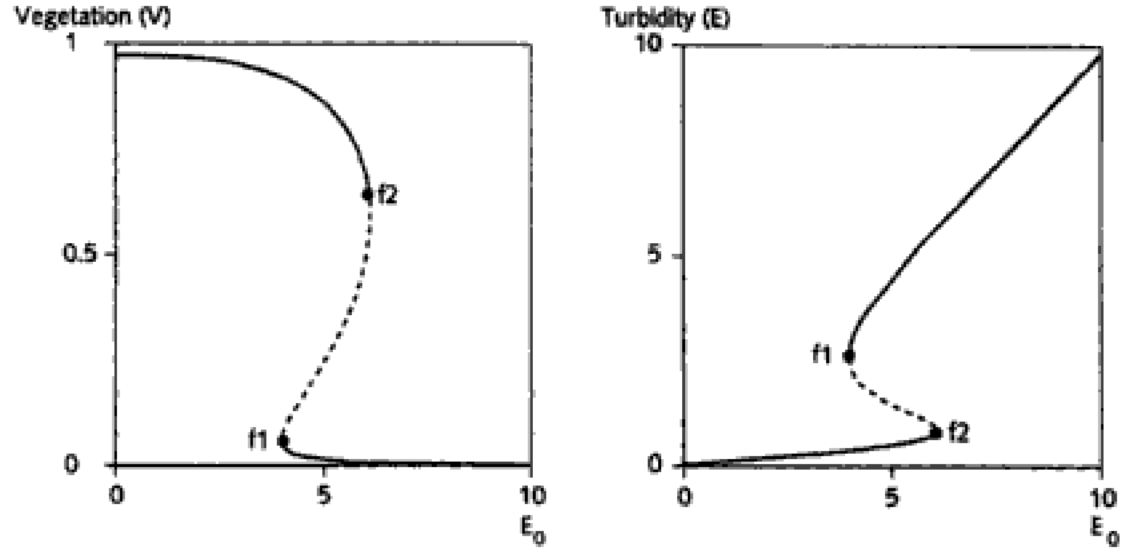


Fig. 5.42 Catastrophe-fold revealing hysteresis in vegetation abundance (V) and turbidity (E) computed from the minimal mathematical model of the vegetation–turbidity interaction (Eqs. 69 and 70) in response to turbidity of non-vegetated water (E_0) which depends (among other things) on nutrient loading (see text).

If we fix all parameters to their default values and plot turbidity and vegetation coverage as a function of E_0 to explore the response of the system to the nutrient level a folded line arises, indicating the hysteresis (Fig. 5.42).

The interpretation is similar to that of the hysteresis derived earlier. The upper and lower branch represent stable equilibria. The middle part is the unstable saddle equilibrium that marks the border of the basins of attraction of the stable states. The two inflection points (f_1 and f_2) are fold bifurcations where the saddle collides with either of the stable equilibria. For intermediate nutrient values the system has two alternative equilibria, a clear one with abundant vegetation and a turbid one with little vegetation.

As explained already for the simpler graphical model (Fig. 5.34) the resulting hysteresis with respect to changes in the nutrient level can be seen by slowly moving from the oligotrophic left end to the hypertrophic right end of the diagram. On the left where the basic turbidity (E_0) is low there is only one equilibrium, the clear vegetation dominated state. With increasing nutrient loading the lake tends to stay clear until f_2 is reached. Further eutrophication will cause a catastrophic transition to the turbid state. Subsequent reduction of turbidity does not have much effect, as the system stays in the turbid state. Only when nutrients have been reduced enough to reach the left-hand fold bifurcation (f_1), another catastrophic transition will return the lake to the clear water state.

A simple way to explore how this hysteresis depends on the other parameters of the model is to add these parameters as an extra dimension to the hysteresis plots (Fig. 5.43). The resulting three-dimensional plots show that the range over which the turbid and the clear state exist as alternative equilibria increases with h_E and p. Recalling the interpretation of these parameters, the model thus confirms the earlier conclusion that hysteresis should be most pronounced in shallow lakes with a flat depth profile. The hysteresis is also enhanced by a high vegetation impact (low h_v). This relative impact of macrophytes is likely to be higher in shallow water where wind resuspension can cause strongly increase turbidity in the absence of vegetation. All of these theoretical results lead to the same general conclusion: hysteresis due to the vegetation–turbidity feedback is more likely to occur in shallow water.

In fact, deep lakes are not even considered in the model. The maximum vegetation coverage in the model is 100%, occurring at zero turbidity. Even in very clear water, however, aquatic macrophytes do not completely colonize deep lakes. Obviously, the vegetation–turbidity feedback is unlikely to cause hysteresis in deep lakes where only a minor part of the total surface and an even smaller part of the overall volume can be colonized by macrophytes.

Predictions from a mechanistic vegetation model

The above models are based on simplifying assumptions about the overall effect of turbidity on vegetation abundance. The first graphical model (Fig. 5.34) assumes total disappearance of submerged plants beyond a critical turbidity. The subsequent graphical model and its mathematical counterpart are more realistic. They assume vegetation abundance to respond to turbidity in a smooth sigmoidal way rather than abruptly. The two reasons to use such a sigmoid are that vegetation biomass on a given site is not a sharp step-function of turbidity and that lakes are not uniform in depth allowing shallower parts to be colonized already at high turbidities. Although the reasoning behind these minimal models is plausible, the approach remains qualitative.

Another way to check the potential for alternative equilibria is to use a mechanistic simulation model for the dynamics of submerged macrophytes. Several simulation models for the growth of submerged macrophytes have been produced over the last decades (Titus *et al.*, 1975; Best, 1982; Wortelboer, 1990; Hootsmans, 1991), but the reduction of turbidity by the plants leading to the positive feedback that can cause alternative stable states is usually not considered. Here, the effect of including this feedback is shown using the model CHARISMA, a polished version of the model MEGAPLANT (Scheffer *et al.*, 1993a) tuned to represent the growth of *Chara aspera* as observed in Dutch lakes.

Although the model is relatively simple, it accounts for many more aspects than the presented minimal models. The frame of the model is the seasonal cycle (Fig. 5.44).

In winter the modelled vegetation can survive as shoots or in the form of overwintering structures. These structures can be seeds, tubers, turions etc., and are characterized by their individual weight. Growth is initiated in the

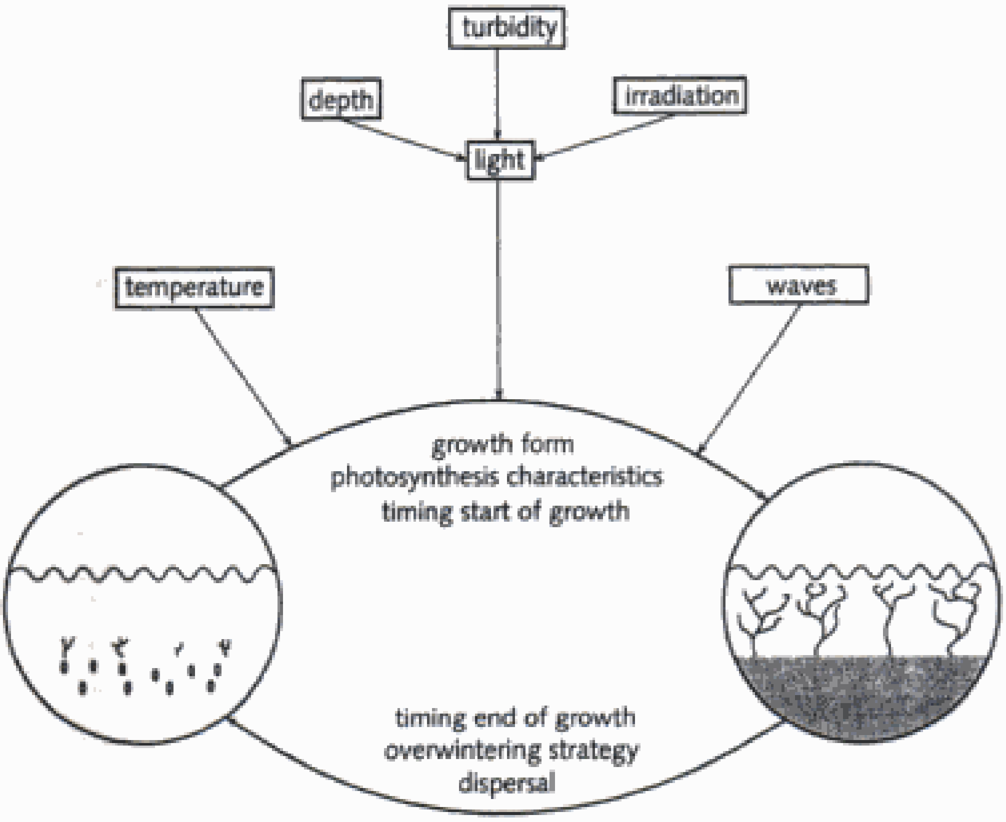


Fig. 5.44 Seasonal cycle represented in the simulation model MEGAPLANT with the main environmental factors (outside circle) and plant characteristics (inside circle) that are taken into account. After Scheffer *et al.* (1993a).

model at a fixed day in the spring. From that moment onwards, each overwintering structure starts transforming a daily percentage of its remaining biomass into sprout growth. At the end of the growing season, a proportion of the vegetation biomass is transformed into overwintering structures, and the remaining shoots disappear, although optionally part of the vegetation can be allowed to remain wintergreen. Growth depends on photosynthesis and respiration, both of which are temperature dependent. Photosynthesis on a given site on the plant also depends on in situ light and the distance from the tissue to the top of the plant. The latter is due to the decrease in activity with tissue ageing. Daily irradiance and temperature in the model follow a sine wave over the year. Light also follows a daily cycle and is attenuated in the water column according to the Lambert–Beer law (Section 2.1). In addition, in situ light is affected by self-shading. Plants grow until they reach a maximum length. After this a proportional increase in vegetation biomass over the whole length axis occurs. When plants hit the water surface, shoots spread just under the water surface, forming a canopy. Throughout the growing year mortality of plants occurs due to factors such as wave action or crowding effects.

As a first step in the analysis of the vegetation–turbidity feedback the impact of vegetation on turbidity is left out, and the effect of turbidity on the summer standing crop at a water depth of 1 m is computed (Fig. 5.45 upper panel).

The numerical procedure to produce this picture is to increase the turbidity (E) of the water in small steps from 0 till 8. Vegetation development is simulated at each of these intervals for several years until the summer biomass has stabilized. Then the equilibrium biomass is plotted and used as a starting point for simulations at the next turbidity step. This analysis gives the same result when it is run the other way around, decreasing turbidity stepwise from 8 till 0. The result is in line with the idea that vegetation declines relatively sharply at a critical turbidity. Note that these simulations give biomass at a lake depth of 1 m. As argued, the depth profile of a lake will affect the response of the total vegetated area to turbidity (used in the minimal models). The latter may be smoother than a local biomass response depicted here.

To check if the vegetation turbidity feedback may cause alternative equilibria, the model is expanded to include the effect of vegetation on turbidity. Turbidity in the vegetation (E) is assumed to be proportional to the turbidity of unvegetated water (E_0) and decline with vegetation biomass (B g AFDW m^{-2}) in a way that is analogous to the effect of vegetation coverage assumed in the previous model:

$$E = E_0 \frac{h_B}{h_B + B} \tag{11}$$

The half saturation constant h_B is set to 150 g DW m^{-2} which fits well to the data from Charophyte vegetation in Veluwemeer (Van den Berg *et al.*, 1997). It implies a turbidity reduction of 77% in a dense vegetation of 500 g m^{-2}. As explained earlier, as much as 90% reduction of turbidity is measured in various dense vegetations, and hence the used setting may be considered a conservative estimate of the vegetation effect.

When the equilibrium analysis is repeated for this version of the model, it appears that the vegetation collapse with increasing turbidity occurs at a much higher threshold (I in Fig. 5.45 lower panel). Obviously, this is the result of the implemented effect of vegetation on turbidity. By keeping the water within the vegetation clear it can survive even when turbidity in the absence of vegetation (E_0 displayed on the horizontal axis) would be high. Reversing the scenario, however, the vegetation biomass follows a different path (II). With decreasing turbidity vegetation does not recover until the critical turbidity where it also recovered in the simulation in which plants were not allowed to influence turbidity (Fig. 5.45 upper panel). The explanation is simple: in the colonizing phase plant biomass is insufficient to cause a significant reduction in turbidity. Therefore, the ability of macrophytes to keep the water clear helps vegetation to persist, but not to colonize a lake. As a result there is a range of conditions over which the vegetated and the unvegetated state are both stable. As in the previous hysteresis models, the dashed line (III) represents the threshold biomass for

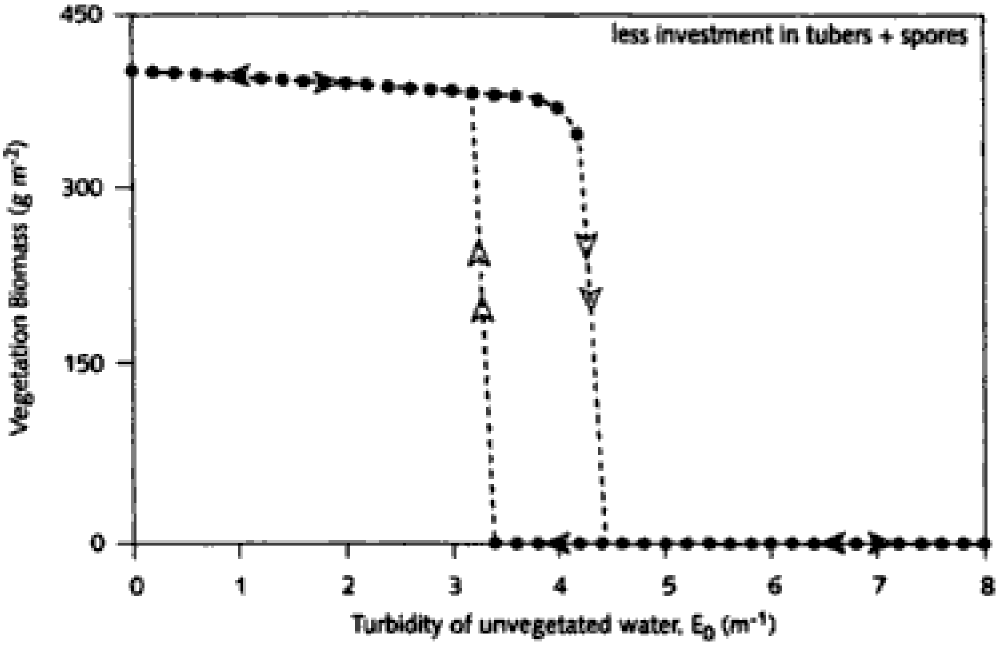


Fig. 5.47 Response of charophyte biomass to turbidity computed from the model MEGAPLANT as in the lower panel of Fig. 5.45 but reducing investment in overwintering structures such as tubers and spores to only 25% of the normal value. This reduces the extent of the stable upper branch of the hysteresis curve suggesting that large investments in survival structures are crucial for persistence of the vegetated state in lakes where aboveground biomass disappears seasonally.

that explains collapses as observed frequently, for instance, in monospecific *Elodea* vegetations. When wave action or consumption by overwintering flocks of coots and other birds diminish the standing crop too much, the potential for vegetation development in the spring is strongly reduced. This may bring the lake to an alternative stable turbid state, or allow colonization by other macrophyte species.

The observation that overwintering biomass can be critical for vegetation to maintain dominance in situations where an alternative turbid state is possible stresses the fact that winters in temperate regions should not be considered as simply 'resetting' the ecosystem. Overwintering densities of algae, plants and zooplankters may seem futile but are likely to be of critical importance to the spring development of a lake. The point is, that although biomasses of many populations become small in winter, they are likely to remain more or less proportional to the summer biomasses rather than being reset to a uniform low standard level. Winters 'shrink' rather than reset populations. As a result the community has a memory of the situation before the winter. Note that this holds not only for vegetation biomass, as assumed in CHARISMA, but for the entire community associated with vegetated conditions. This implies better chances for a spring clear-water phase in a vegetation dominated lake in view of the relatively high overwintering population of *Daphnia* individuals and ephippia, and low

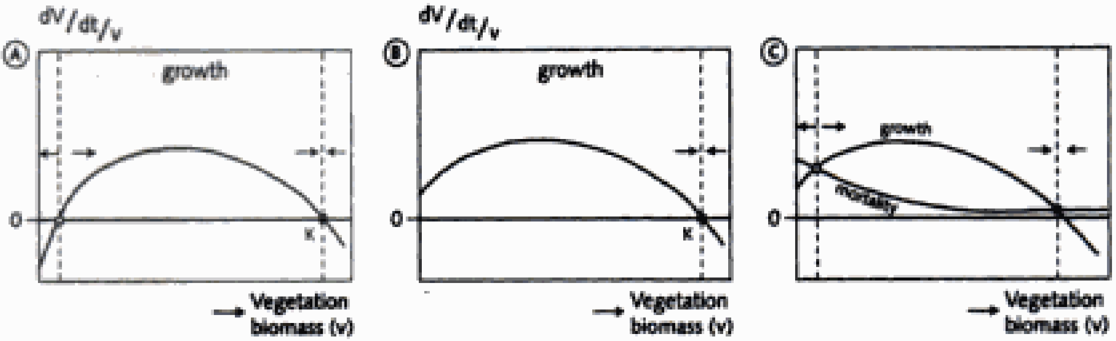


Fig. 5.49 (a) Relative growth of vegetation (*dV/dt/V*) as a function of biomass (*V*) in a situation with alternative stable states due to the fact that vegetation reduces turbidity. Below a critical threshold (open symbol) vegetation biomass is too low to make the water clear enough for growth and the vegetation become extinct. Above this threshold vegetation will stabilize at carrying capacity (*K*). (b) If turbidity in the unvegetated state is low enough to allow growth, the clearing effect will not lead to alternative stable states. However, unlike in the case of simple logistic growth (Fig. 5.48) relative growth will still tend to be a humped function of biomass. (c) In this situation (*b*) even a relatively low erosion mortality (cf. Fig. 5.48) may lead to alternative stable states.

the combination of these mechanisms will increase the chance that alternative stable states occur. To see this consider the way in which inclusion of the vegetation–turbidity feedback should be expected to modify the logistic growth. Instead of a linear decrease of growth rate with vegetation biomass, the relationship of growth to biomass will become humped (Fig. 5.49a).

At very low vegetation densities turbidity can be so high that growth is negative. Only if the biomass exceeds a critical threshold value can turbidity then be reduced sufficiently to allow a positive growth bringing the vegetation to carrying capacity. This represents a situation with alternative stable states. Even if turbidity in the absence of plants does not prevent growth and cause an alternative unvegetated equilibrium, however, the relative growth curve will remain convex as long as vegetation promotes water clarity (Fig. 5.49b). The combination of erosion mortality with the vegetation–turbidity feedback may now still cause alternative equilibria (Fig. 5.49c) even if each of these mechanisms separately would not be sufficient to have that effect: a moderate erosion mortality may be enough to prevent colonization if seedlings grow slowly due to high turbidity.

In conclusion, the vegetation–turbidity feedback tends to cause alternative stable states in shallow lakes but other mechanisms may well contribute to the hysteresis. Vegetationless lakes tend to stay unvegetated not only because they are turbid, but also because sediment disturbance by waves and benthivorous fish prevents plant settlement, and herbivory may help to prevent vegetation recovery, while vegetated systems, on the other hand, tend to stay vegetated because they are clear but also because the sediment is more stable, the fish community is more shifted towards piscivores, and the overall vegetation productivity is high enough to sustain a large population of herbivores.

Hallmarks of hysteresis

Although there is abundant evidence for the existence of mechanisms that tend to cause a positive feedback in the development of aquatic vegetation, our quantitative insight into the functioning of the system is still relatively poor. Obviously, we are still far from able to produce a mechanistic model that incorporates the discussed mechanisms in a way that allows us to predict whether a given lake will possess alternative clear and turbid equilibria and for which set of conditions.

Therefore, the best way to find out if hysteresis is important in real lakes is to check if specific predicted patterns can be found in the field. Obvious hallmarks of a system with alternative equilibria are the hysteresis in its response to a control variable and the catastrophic transitions at the fold bifurcations. In theory, experiments in which a control variable is gradually increased and subsequently decreased are obviously the best way to check this. Besides playing with the control variable, one may perturb the system state. Following small perturbations the system will return to its original state. A sufficiently large perturbation, however, should bring the system into an alternative stable state if the values of the control variables are in the range for which multiple equilibria exist.

The possibility for such controlled experiments with real lakes is limited, but we may also take advantage of natural experiments. The response of a hysteretic system to a variable environment leads to the expectation that states sampled over a long time-series should fall in two contrasting clusters as the contrasting stable states should occur more often than the unstable transients. Likewise, sets of comparable lakes should have bimodal state distributions at any given instant of time.

Summarizing there are four types of indicative observations (Fig. 5.50):

a. The response to a slow increase of a control factor (C) such as nutrient loading or water level should be discontinuous. The system switches to a contrasting state when a critical value of C is exceeded.
b. A subsequent decrease of the control variable should lead to a switch back, occurring at a lower threshold value of C than the forward switch.
c. It should be possible to bring the system from one stable state to another one by means of a perturbation, if the control variables are in the range that allows alternative equilibria.
d. Distributions of system states should be bimodal.

It is important to realize that most of these observations are not sufficient for a positive diagnosis of true hysteresis. Therefore we scrutinize them somewhat further:

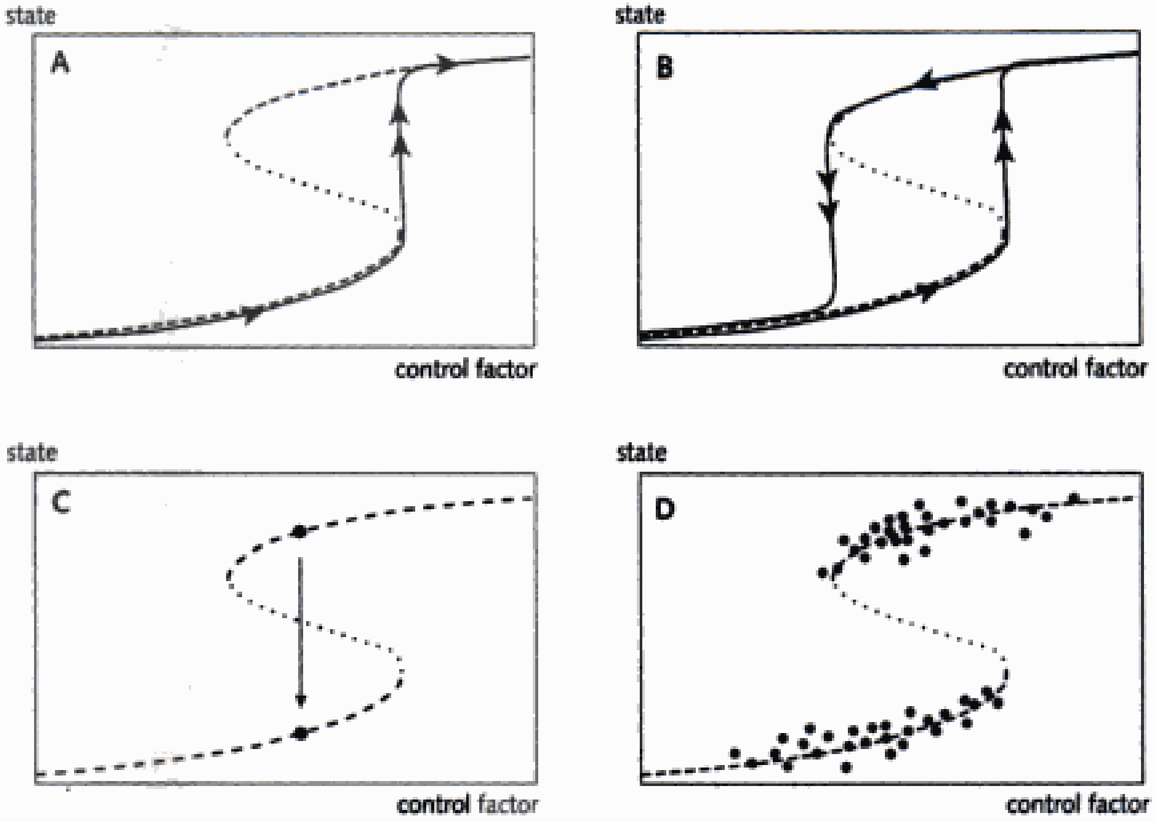


Fig. 5.50 Four types of observations indicating that a system may have alternative stable states: (a) The response to a slow increase of a control factor (*C*) such as nutrient loading or water level is discontinuous. The system switches to a contrasting state when a critical value of *C* is exceeded. (b) A subsequent decrease of the control variable leads to a switch back, occurring at a lower threshold value of *C* than the forward switch. (c) It is possible to bring the system from one stable state to another one by means of a perturbation, provided that the control variables are in the range that allows alternative equilibria. (d) Distributions of system states are bimodal.

a. Also in the absence of a real hysteresis, the response of the system to changes in the nutrient level can look discontinuous. In our minimal model the equilibrium curve remains sigmoid after the real fold has disappeared (Figs. 5.40 and 5.43). Thus, the sensitivity to a change in nutrients will normally be large in the 'critical range' where the response of vegetation and turbidity is steepest even if there is no hysteresis. As a consequence discontinuous responses do not necessarily imply hysteresis
b. The second observation (Fig. 5.50b) does not necessarily imply the existence of alternative stable states either. It may simply result from a slow response of the system to restoration measures. Phosphorus release from the sediment buffer, for instance, can cause decades of delay in the response of the lake water concentration to reduction in external loading. Although this behaviour can be called hysteresis, it is not a hysteresis in the sense of dynamic systems theory, indicating multiple equilibria.

c. The response to perturbation (Fig. 5.50c) is potentially more informative. Nonetheless there are some caveats in the interpretation of such observations. First, if after the perturbation the system returns to its original state, we can not reject the hypothesis that it is hysteretic. The perturbation may have been too small, or the conditions may be such that the system is not in the range where alternative equilibria exist. Secondly, if the system seems to stay in a new state, we need to wait sufficiently long to be able to judge if the new state is really stable. Unfortunately, it is hard to say how long is sufficiently long. Connell and Sousa (1983) suggest a wait of at least as long as the lifespan of the longest lived species. In view of the average lifespan of freshwater fishes this would be somewhere in the range of five to ten years. In practice it may be difficult, however, to distinguish a situation with real alternative stable states from one in which the system is not hysteretic but simply shows a steep response over a small critical range of nutrient levels or another control variable (Fig. 5.40). Disturbance of such a system close to this critical range will tend to cause the return to the original state to be very slow, as rates of change approach zero in the vicinity of the steep part of the equilibrium curve.

d. The bimodality pattern (Fig. 5.50d) can be checked in the time-series of one lake, along spatial gradients within one lake or in information from a set of similar lakes. Again, lakes that are not hysteretic but still respond steeply over a narrow range of control variables (Fig. 5.40) will also tend to show such a bimodality of the distribution of system states. Another caveat is that the bimodality may result from bimodality of an unknown control factor. There is of course no real way to rule out this possibility. As a first indication, however, this look at information may be useful as relatively low quality data on the system state suffice.

A review of evidence from the field

Discontinuous responses (Fig. 5.50a)

Many shallow lakes changed from clear and vegetated to turbid and vegetationless over the last century due to gradually increased nutrient concentrations. Unfortunately, good time-series of data that document the change are rare. However, there is much anecdotal information, suggesting that the change from the vegetated to the unvegetated state in the course of the eutrophication process has been abrupt in many lakes. Initially a slow increase in macrophyte biomass and a change to canopy forming growth forms is the main noticeable effect of nutrient loading, but when macrophytes start to decrease the complete transition to the turbid state can be quite fast. Similarly the studies of the Lakes Krankesjön, Tåkern, Rice Lake and Tämnaren (Chapter 1) suggest that relatively small changes in the water level can lead to dramatic and swift responses of the system state

(Wallsten and Forsgren, 1989; Blindow *et al.*, 1993; Sanger, 1994). Thus it seems to be true that shallow lake ecosystems can respond particularly strongly when conditions pass certain critical thresholds.

Hysteresis in response (Fig. 5.50b)

As discussed earlier, a large response to a small change in an environmental factor does not necessarily imply the existence of multiple equilibria. Additional information is required to reveal hysteresis. In the case of Rice Lake (Section 1.3) the water level has come back to the original state, and this did not lead to a recovery of the vegetation and the lake stayed turbid indicating that in this case the two states are truly alternative equilibria.

Nutrient loading has been reduced in many shallow lakes that lost their vegetation because of eutrophication. Indeed the response of shallow lakes to reduced nutrient loading is notoriously slow. It is, however, difficult to separate the mechanisms that cause this delay. Obviously, release of buffered phosphorus from the sediment is an important cause of the delayed response. On the other hand, the feedbacks discussed in this chapter will probably play a role in many cases. Vegetation settlement is prevented by high turbidity due to wave resuspension and algal growth, but also due to sediment disturbance by wind and benthivorous birds and to over-exploitation by herbivores. Nonetheless, the fact that internal phosphorus loading alone is not enough to explain the delayed response is illustrated by the fact that biomanipulation can sometimes restore a long lasting, probably stable clear state in such lakes.

Perturbations (Fig. 5.50c)

Biomanipulation experiments offer an outstanding opportunity to study the response of the shallow lake community to perturbations. The initial increase of transparency after biomanipulation is typically followed in shallow lakes by a strong development of submerged vegetation in the following years (Meijer *et al.*, 1990; Søndergaard *et al.*, 1990; Van Donk *et al.*, 1990). In a few years, the fish stock stabilizes to a new state but the recovery of the fish community does not usually lead to a switch back to the turbid state (Meijer *et al.*, 1994a). Several biomanipulated shallow lakes have been monitored for quite a long period after their shift from turbid to clear, and although some have returned to the turbid state, others have remained clear for as long as 10 years now. Nonetheless, the possibility that some of these lakes should be considered to be in slow transient phases rather than a stable vegetation dominated state cannot be ruled out as systematic changes were still observed (Van Donk, pers. comm.; Meijer, pers. comm.).

The result of disturbance induced switches from clear to turbid have been long lasting in several lakes. Lake Ellesmere, which lost its vegetation in a 1968 storm, and Lake Apopka, where a hurricane wiped out the vegetation in 1947, have not recovered since then (Section 1.2). Obviously, many storms will have occurred before, and the fact that such earlier disturbances have not caused a shift indicates that eutrophication or other changes in the conditions have reduced the stability of the clear state in these lakes.

Contrasting states (Fig. 5.50d)

Almost all of the examples in Chapter 1 illustrate that many shallow lakes tend to display strongly contrasting states. A good example of a set of shallow lakes showing bimodality of state is the Great Linford sand and gravel-pit complex in England (Section 1.4). The lakes have the same hydrology and shape, indicating that it is merely their history (dry- or wet-digging) that caused them to be in either of the two contrasting states. The fact that biomanipulation switched one of the turbid lakes to a long lasting clear and vegetated state further supports the idea that these lakes possess alternative stable states.

Another example of comparable lakes with contrasting states is the case of Hudsons Bay and Hoveton Broad. Although this is only one pair of lakes, the case is informative because the water quality of the lakes is identical. They are both fed with nutrient rich water from the same river and have short retention times. The lakes Tåkern, Krankesjön and Tomahawk Lagoon that switch repeatedly between greatly contrasting states as a result of small or unknown environmental changes are also good examples. The case of the *Chara* fields with clear water in Veluwemeer is interesting, as it combines the spatial and temporal aspects. For years, the whole lake has been turbid. Recently, however, *Chara contraria* has colonized large parts. The water has simultaneously cleared up, but only in the *Chara* fields, indicating that it is the vegetation itself rather than another changed factor that causes the high water clarity.

In summary, many field studies reveal the hallmarks of hysteresis in shallow lake dynamics. Even though the mechanisms involved are often not well demonstrated and several cases may be explained without the involvement of true alternative stable states, a large number of observations suggests that hysteresis is a common property of shallow lake ecosystems.

6 Managing the ecosystem

Much of the work presented in this book has been invoked by the need to find ways of restoring shallow lakes, but the emphasis in the text has been on unravelling the mechanisms rather than on the direct application to lake management. This chapter reviews the main points from an applied point of view. It is not meant as a practical guide for lake restoration. Several such guides including information on material, costs and legislation are available now. A good general treatise on reservoir and lake management is the work by Cooke and co-authors (Cooke *et al.*, 1993). Restoration guides that are more directed towards shallow lake problems are published in The Netherlands (Hosper *et al.*, 1992) and England (Moss *et al.*, 1996).

The following sections briefly summarize the implications of alternative stable states for management and the practical measures that can be taken to change the state of a lake.

6.1 IMPLICATIONS OF ALTERNATIVE STABLE STATES

As explained in the previous chapter a vegetation-dominated clear state and a turbid non-vegetated state are likely to be alternative equilibria over a range of nutrient levels in most shallow lakes. In the turbid state cyanobacteria often dominate the phytoplankton, the fish community consists mainly of benthivores and planktivores, and there is a relatively small bird community of piscivores and omnivores. In the clear vegetated state the fish community is more diverse, and large numbers of herbivorous and omnivorous waterfowl visit the lake. The tendency of these situations to be alternative stable states has important management implications, because the way the system responds to measures is very different from that of non-hysteretic systems. To clarify this, the following sections review the basic properties of the hysteresis briefly from a management perspective.

Stability properties

Although the mechanisms involved in causing alternative equilibria and the details of the resulting patterns can be quite intricate the overall stability properties can be summarized in a simple and intuitively straightforward way by means of a 'stability landscape' or 'marble-in-a-cup diagram' (Fig. 6.1).

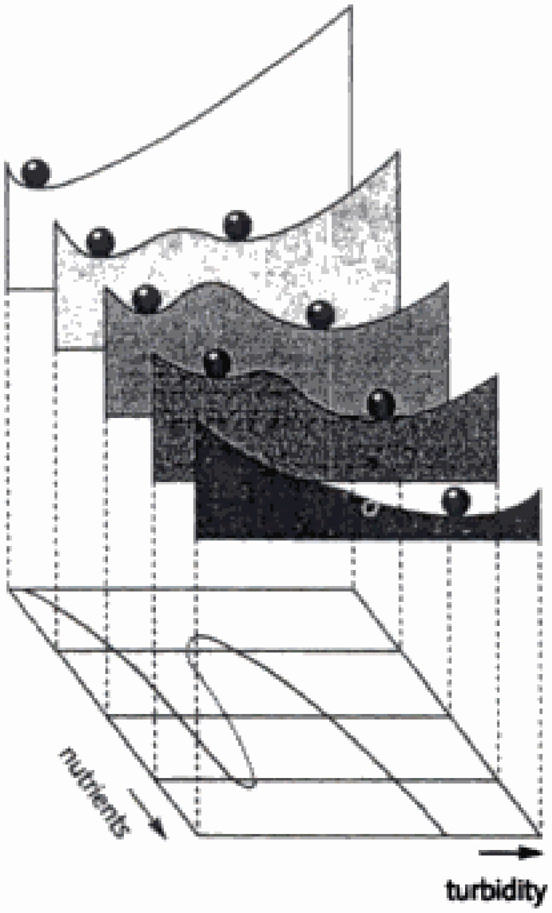


Fig. 6.1 'Marble-in-a-cup' representation of stability at five different levels of nutrient loading. The minima correspond to stable equilibria, tops to unstable breakpoints (see text). Modified from Scheffer (1990).

The system, like a ball, tends to move downhill and settle in the deepest point which is an equilibrium. The slope of the surface determines the direction and speed of movement. Such a stability landscape can be computed from a mathematical model of the system, for instance, by using the derivative of a state variable (such as turbidity) as the slope of the hills in the stability landscapes. As indicated in the figure they correspond to transverse sections through the familiar sigmoidal hysteresis curves presented in Chapter 5. On the hill-tops and in the deepest point of the valleys the slope is zero, corresponding to a derivative of zero and thus to an equilibrium. However, only the valleys of the stability landscapes represent stable equilibria. The hill-tops are unstable equilibria and represent the breakpoints that mark the limits of the basins of attraction of the stable equilibria.

With respect to the response of the lake to management it is important to distinguish between disturbances and measures that affect the stability properties. In terms of stability landscapes (Fig. 6.1), disturbances are displacements of the ball but do not alter the pattern of hills and valleys. Fish-kills, herbicide treatments and heavy storms are examples. If there is only one stable state (valley), the effect of a disturbance will be temporal as the system will always settle to this same state again. However, if two alternative stable states (valleys) are present, the system may settle to the alternative stable state if the disturbance has been strong enough to move it past the breakpoint (hill-top). The permanent loss of vegetation caused by a single heavy storm event as observed in Lakes Apopka and Ellesmere (Section 1.2), and the reverse switch to a vegetation dominated state in response to a single drastic reduction in fish stock as observed in Lakes Zwemlust and Linford (Section 1.4,5) illustrate this possibility. On the contrary, changes in external conditioning factors such as the nutrient loading (e.g. Veluwemeer, Chap. 1.1) or the average water level of the lake (e.g. Lake Tämnaren, Section 1.3) will change the stability properties (the landscape, 6.1) which may also cause a shift but has distinctly different implications with respect to management than disturbances.

Eutrophication and restoration

Changes in the nutrient loading are probably a major reason why the stability properties of shallow lakes have changed (Fig. 6.1). At low nutrient levels, the system has one globally stable equilibrium, a clear-water state. Increase of the nutrient level gradually changes the shape of the stability landscape, and gives rise to an alternative turbid equilibrium. However, if no major disturbances occur, the system will stay in its current state, responding only weakly to the enrichment. If the nutrient level is raised further, the stability of the clear state decreases, and slight perturbations are enough to cause a switch to the turbid equilibrium. At still higher nutrient levels the clear equilibrium disappears. This inevitably leads to an irreversible jump to the turbid state. Efforts to restore the system by reducing the nutrient level will change the stability landscape again, but even if nutrient levels at which the system was formerly clear are realized, the response may be minor. Despite the reappearance of an alternative clear equilibrium, the locally stable turbid state tends to be sustained. Only a drastic reduction of nutrient level will be sufficient to make the turbid state unstable, resulting in a switch to the clear state.

The two alternative equilibria are not equally likely to be found when they both exist. The probability of ending up in either of the equilibria in an environment with frequent stochastic events depends on the stability properties of the system, e.g. the size of the basins of attraction of the two alternative equilibria. The breakpoint (hill-top) moves towards either of the stable equilibria if the nutrient level changes, implying that the size of the basin of attraction of the vegetated equilibrium decreases with the nutrient level, while that of the turbid state increases with enrichment. As a result the vegetated state should be expected to be more robust to disturbances at lower nutrient values, whereas the system is more likely to settle to the turbid state when nutrient loading is higher. Consequently, disturbance-type measures are more likely to lead to a vegetated clear-water state if the nutrient loading is lower.

Clearly the stability properties of the system are of great importance to the expected results of management measures. Changes in conditioning factors such as nutrient loading and lake depth may have little effect over the range of conditions where two alternative stable states exist. On the other hand, one intentional disturbance can be enough to restore a turbid lake with long lasting results in this situation. Unfortunately, it is difficult to determine *a priori* whether an alternative stable state is possible in practice. However, if a clear system became turbid as a result of eutrophication, the nutrient level must already have been too high to allow a sufficiently stable clear equilibrium. Consequently, a stable clear state can never be established in such systems without a reduction of the nutrient level. The situation is different if a switch to the turbid state has resulted from large perturbations such as stocking with carp (*Cyprinus carpio*) or the complete removal of vegetation. This leaves the possibility that two alternative stable states exist under the current nutrient loading, and that the switch was forced. Obviously, without such indications disturbance measures such as biomanipulation should be preceded by a reduction of the nutrient loading or adjustment of the water level to allow the possibility of obtaining a stable clear-water state which does not require continuous care.

Hysteresis will be less pronounced or non-existent if a lake is deeper and has a less uniform depth profile (Chapter 5). Obviously, many situations exist between the extremes of a full-blown hysteresis and a smoothly responding deep lake (Fig. 6.2). Importantly, lakes that do not have a real hysteresis will still tend to respond strongly over a narrow range of conditions while being rather inert outside this critical range (Fig. 5.40b).

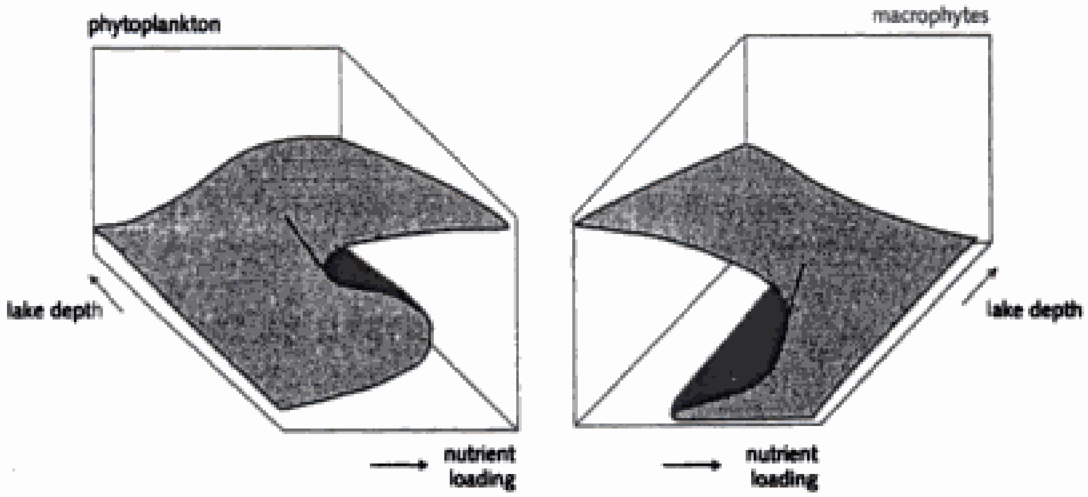


Fig. 6.2 Deep lakes are less likely to show hysteresis than shallow ones, but there is a continuum of possibilities between the extremes of a full-blown hysteresis and a smoothly responding deep lake.

Thus, even in lakes that are, for instance, too deep to have alternative stable states, reduction of the nutrient loading may have little effect until a critical concentration range is reached where the response becomes much stronger.

Note that in the discussion of hysteresis with respect to nutrients it is important to distinguish between nutrient loading and nutrient concentrations in the lake water. The change of the stability properties is a function of external nutrient loading which is a conditioning factor, whereas inlake nutrient concentration is a systems property that is strongly affected by the biological structure of the system. Plant dominance, for instance, often causes nitrogen concentrations to drop strongly even when external nitrogen loading remains the same.

Connected and heterogeneous lakes

In practice, lakes are usually not the isolated homogeneous systems we like to think of. Many lakes are connected through streams or channels, and large lakes can have shallow and deep regions that may behave very differently. Some of the presented case studies demonstrate that the clear and the turbid state can co-exist in open connection. In view of the management possibilities it would be relevant to know how connected potentially hysteretic systems may affect each other. Such spatial topics can be explored theoretically by studying models for two or more systems connected by diffusion, or more complicated rules of migration. However, a thought experiment suffices to understand the possible range of behaviour. Consider two hypothetical adjacent lakes both of which are hysteretic with respect to vegetation. The lakes are identical in all aspects except the average depth. The shallower one is clear and vegetated while the deeper one is turbid and unvegetated. By continuity, connecting the lakes by an extremely small exchange flow of water will not change the existing situation, although it will cause a slight increase the turbidity of the clear lake and decrease turbidity in the turbid lake. An extremely strong exchange on the other hand will change the two lakes into one completely mixed system. Because of the difference in depth, vegetation abundance may still differ in the sub-basins. However, in this hypothetical extreme mixing scenario, turbidity will be equal in both lakes. The result of intermediate exchange rates is more intricate, as there are many possibilities. Depending on the situation either of the lakes may go through a catastrophic or continuous transition towards the state of the other one. Obviously, exchange of water will let the final state of the whole system tend more towards that of the bigger and more stable subsystem.

Although water flows move the bulk of seston particles passively from one place to the other, most animals choose their habitat actively. The difference between vegetated and unvegetated parts may be amplified by such habitat choices. Benthivorous fish such as large bream (*Abramis*

ity at high nutrient loading is important. Phytoplankton biomass in vegetated systems is kept low by a combination of factors. Both shading by the plants and reduction of nutrients in the water column due to uptake by the macrophytes and enhanced denitrification tend to decrease algal productivity. The lower productivity makes it more likely that cladocerans drive the phytoplankton community into an over-exploited state (Chapter 5). Obviously, heavy nutrient loading reduces the probability of nutrient limitation, and therefore the potential of macrophytes to reduce algal productivity. As a result, more grazers are needed to control algal growth. However, predation pressure on zooplankton by fish tends to increase with enrichment in shallow lakes due to a relatively steep increase in benthos pumping up total fish biomass faster than plankton productivity (Section 4.5). Thus even in vegetated systems enrichment will tend to result in increased phytoplankton biomass as it reduces the chances of nutrient limitation and at the same time leads to increased predation on zooplankton.

An increase in periphyton growth with nutrient loading is probably another major factor involved in reducing macrophyte performance (Phillips *et al.*, 1978). Snails can control periphyton growth, but this works only if fish predation on snails is not too high (Section 4.5). Basically the same factors as described for phytoplankton are likely to be involved in reducing periphyton control when nutrient loading becomes too high. The biomass of fish such as tench (*Tinca tinca*) and roach (*Rutilis rutilis*) that feed on snails but also on other benthos such as chironomids, may increase strongly due to increased availability of such alternative food sources with eutrophication, while at the same time nutrient conditions for the perifytic algae improve, making top-down control less likely to be sufficient.

Surprisingly, very high nutrient concentrations do not necessarily lead to a turbid state. Heavy loading by sewage effluent may produce conditions in which most fish die, allowing dense populations of large *Daphnids* to control phytoplankton, as observed in the clear and vegetated English Little Mere (Carvalho, 1994). A comparable situation may sometimes occur when guano from dense concentrations of birds on roosting sites or breeding colonies causes a high local loading. Piscivory by birds may help to drive fish extinct on such sites. An extreme example can be observed in the Amsterdam zoo, 'Artis', where the pond in a small bird park is often literally turbid because of the high density of *Daphnia magna*. Also, very small and shallow ponds or ditches usually are clear and vegetated even if they have very high nutrient levels.

Note that since nitrogen is often the limiting nutrient for phytoplankton in vegetation dominated systems (Chapter 2), it may well be that nitrogen loading is more important than phosphorus loading in destabilizing the vegetated clear state of shallow lakes, although so far there are no studies that demonstrate this.

not long lasting. In the next sections I briefly review the way in which successful biomanipulation works, and the main reasons why it may fail. The literature on this topic grows exponentially, but as a starting point readers interested in shallow lake work may refer to the proceedings of a 1989 conference on the topic (Gulati *et al.*, 1990) for early case studies, and to a study of long-term responses of some lakes (Meijer *et al.*, 1994a) and a preliminary 'test' to assess the chances of success (Hosper and Meijer, 1993).

Biomanipulation as a shock therapy

The basic scenario through which a shallow lake can be switched to a clear state by means of biomanipulation is simple: a drastic reduction of the fish stock leads to clear water allowing submerged macrophytes to colonize the lake and these subsequently keep the water clear. There are many approaches possible but the most common strategy is to net out 75% or more of the fish stock between the autumn and early spring, or to kill most of the fish by applying rotenone. Often piscivores are stocked subsequently to slow down recruitment. In large lakes this shock therapy approach may be unfeasible. In such situations a continuous fishery pressure may still result in a reduction of algal biomass (Lammens *et al.*, 1997), but there is little experience in this approach. Also, massive stocking with juvenile pike (*Esox lucius*) alone has resulted in a reduction of chlorophyll levels (Prejs *et al.*, 1994; Søndergaard *et al.*, 1997). Here, I focus on the drastic stock reduction strategy.

There are two distinct mechanisms responsible for the initial clearing up of the water after fish removal. First, sediment resuspension by benthivores such as bream and carp is reduced. When benthivores dominate the fish stock most of the turbidity is often due to suspended sediment (Section 2.2). In that case, the water can clear up almost immediately after the fish removal due to settling of the suspended sediment particles. The other major effect of fish removal is through the trophic cascade. Predation pressure on zooplankton is reduced, leading to top-down control of phytoplankton. In eutrophic shallow lakes the spring clear-water phase is often absent due to year-round predation pressure on large zooplankton by omnivorous fish (Section 4.5). Drastic reduction of the fish biomass in winter allows *Daphnia* to peak in the spring and graze down phytoplankton to a very low level. In addition to reduction of resuspension and planktivory, the fish removal may imply a reduction of nutrient flux from the sediment to the water column (Section 2.3).

The resulting good underwater light conditions in the spring and the absence of sediment disturbance by benthivorous fish favour the development of submerged macrophytes. Often charophytes or other submerged plants develop a dense vegetation in the first summer after biomanipulation (e.g. Lake Bleiswijkse Zoom) although in other cases vegetation only covers large parts of the lake bottom after a couple of years (e.g. Lake Zwemlust), or remains largely absent (e.g. the Norfolk Broads).

The fish community tends to recover soon after biomanipulation (Meijer *et al.*, 1995). The remaining individuals spawn in the spring and when the spawning stock is not too small young-of-the-year fish will be abundant again in early summer. If vegetation develops rapidly enough the system is likely to remain clear, but otherwise planktivory by the new fish cohort can be a serious threat to the maintenance of clear water in the summer. Stocking with high densities of juvenile pike (Section 4.6) can help to control this recruitment, giving vegetation more time to recover and stabilize the clear state.

Requirements for success

For the above biomanipulation scenario to be successful, four basic steps have to work:

1. The fish stock must be reduced drastically.
2. The fish reduction must lead to clear water.
3. Submerged plants must develop.
4. The vegetation must stabilize the clear water state.

The experiences so far have pointed out some major risk factors for the success of each of these four steps.

1. First of all it must be possible to remove a substantial proportion of the fish. A review of Dutch case studies shows that none of the lakes where less than 75% of the fish was removed cleared up (Hosper and Meijer, 1993). Rotenone poisoning is an easy way to eliminate fish, but in many countries this approach is not allowed. Effective fishing with nets can be difficult if there are many tree trunks or other obstacles in the lake, preventing the use of efficient seine and trawl nets. Another prerequisite for drastic fish reduction is that the lake can be isolated from adjacent waters that are not manipulated. If isolation is not possible, remigration of fish can rapidly compensate for the fisheries effects.

2. Although all shallow lakes where the fish stock is reduced drastically have cleared up so far, there are some factors that might potentially prevent such an effect. First, wind resuspension of soft organic sediments or clay particles may be the dominant cause of turbidity in some exposed lakes (Chapter 2). It seems logical to expect that biomanipulation will not result in clear water in such situations, unless extra measures are taken to reduce the resuspension problem. There are, however, cases in which a lake with obvious wave resuspension nonetheless switched to a clear vegetation dominated state after biomanipulation (Little Wall Lake; Linford Main Lake).

Secondly, the trophic cascade route may not work out. This can be because *Daphnia* is controlled by factors other than fish, such as high salin-

With respect to manipulation of the water level, it should also be noted that extremely shallow water can be unfavourable for plant growth. Indeed, the dynamics of Lakes Krankesjön and Tåkern suggest that too low water levels may destroy the vegetation dominated state (Blindow *et al.*, 1993). Thus there will be an optimum water level for vegetation development. As explained earlier, the optimum depth will depend on various factors such as turbidity, wave exposure and plant type. However, in view of the cases reviewed in the first chapter the optimum depth seems to be less than 1 m in general. Lake Tämnaren, for instance, lost its vegetation when average lake depth increased from 1 to 1.5 m (Wallsten and Forsgren, 1989), and submerged plants in Veluwemeer are most abundant in the depth range between 0.3 and 1 m (Scheffer *et al.*, 1992; Van den Berg *et al.*, 1997). Small ephemeral ponds can have a lush charophyte vegetation even in a water layer of only 10 cm deep.

In practice the water level is rarely constant over a year. Many helophytes depend on the availability of bare moist soil for germination and therefore some water level fluctuation will enhance the diversity of the zone of emergent plants that fringes most shallow lakes (Coops, 1996). On the other hand, too strong fluctuations in the water level are disadvantageous to many submerged pants as shallow sites may dry out. Indeed, in the USA temporary reduction of the water level is frequently used to control nuisance submerged vegetation in reservoirs (Cooke *et al.*, 1993). Obviously, fluctuations of the water level are especially problematic for vegetation in turbid water where the shallow sites are the only places suitable for vegetation growth. In deep clear lakes, submerged plants have a larger depth range and are therefore less likely to be driven to extinction by moderate variations in the water level. Thus, although some fluctuation in water level stimulates development of a diverse helophyte zone, submerged vegetation in turbid shallow lakes is most likely to be promoted when the water level is kept relatively constant.

In the tropical Kariba Reservoir in Zimbabwe, stabilization of the water level is thought to have caused a switch from a dominance by nuisance floating plant beds to submerged vegetation (Marshall, 1983; Ramberg, 1987). Reduction of nutrients in the water column related to the expansion of submerged plants is probably the explanation for the disappearance of the free floating macrophytes that have no access to soil nutrients.

Draw-down

Complete draw-down is an extreme form of water level management. It is applied frequently to fish-ponds and reservoirs but there is less experience with applying this approach to natural lakes. In vegetated lakes, prolonged draw-down is used as a way to control aquatic plants as it usually results in the loss of most submerged species (Cooke *et al.*, 1993).

On the other hand, in unvegetated turbid lakes where sediment resuspension is a major problem, it seems reasonable to expect that draw-down could promote a shift to a clear vegetation dominated state. No case studies are available so far, but the potential scenario seems straightforward. When the sediment is left to dry out, consolidate and be colonized by terrestrial vegetation, resuspension is unlikely when the lake is allowed to fill up with water again. Helophytes that have developed will survive in the shallowest parts and subsequent colonization of the rest of the lake bottom by submerged vegetation will help stabilize the clear state in the lake.

Draw-down also facilitates other modifications that may help improving lake conditions. Sediment, for instance, can often be removed relatively easily with bulldozers and scrapers from a dry lake. Importantly, partial draw-down makes it much easier to remove the fish. As explained earlier, the chances of shifting a lake from a turbid to a stable clear state by means of biomanipulation increase strongly with the percentage of the fish stock that is removed. In Lake Zwemlust (Chapter 1) partial draw-down was used to be able to remove fish more effectively, and the fish reduction that was realized in this way has resulted in a spectacular shift to a plant-dominated state.

Ephemeral ponds that periodically experience a natural draw-down when they dry out are usually fishless. When they fill up they may have a rapidly growing vegetation of charophytes or other plants that have ways to survive the dry period. Such systems may have dense populations of Daphnids that filter the water.

Flushing

As mentioned in the section on nutrient management, flushing a lake with relatively clean water can reduce its nutrient level, but may also help to get rid of colonial cyanobacteria in a more direct way. This is because the growth rate of these algae is relatively small, causing the relative effect of an extra population loss due to wash-out larger. Put simply, an algal group can be eliminated from a lake if the loss rate due to flushing exceeds the growth rate (Section 3.1). Extreme flushing rates that replace more than about one third of the lake volume per day are likely to eliminate all phytoplankton, but slow growing species may be washed out at much lower flushing rates. Since growth rates are very low in winter, flushing in this season may be particularly effective. Indeed, winter flushing has probably been an important reason for the decrease of cyanobacterial density in Veluwemeer (Chapter 1). In practice even small increases in hydraulic flushing rates may lead to disappearance of blue-green algal in situations where the competitive balance with other algae is already close to shifting, due, for instance, to a reduction of the nutrient level in the lake (Section 3.2).

6.5 OTHER MEASURES

Barley-straw

The addition of barley-straw to ponds can lead to a remarkable reduction in phytoplankton biomass. The phenomenon is well known, and packages of straw are even sold in gardening shops for this purpose. There has been relatively little research on this straw effect, but the available work confirms the strong overall effect and gives some indications as to the mechanisms (Gibson *et al.*, 1990; Welch *et al.*, 1990; Everall and Lees, 1996). A recent case-study (Everall and Lees, 1996), for instance, shows that the addition of barley-straw ($50\,\mathrm{g\,m^{-3}}$) to a small English reservoir resulted in a reduction of summer chlorophyll concentrations from about $100\,\mathrm{mg\,l^{-1}}$ to about $20\,\mathrm{mg\,l^{-1}}$. The cyanobacterial blooms that occurred in the previous years were absent in the summer after the straw addition. These changes did not occur in an adjacent control.

It has been suggested that uptake of nutrients from the water by bacteria developing on the decomposing straw causes phytoplankton biomass to decrease as a result of nutrient limitation (Wingfield *et al.*, 1985). Another explanation is that the algal control results from release of phytotoxic compounds by the decomposing straw (Gibson *et al.*, 1990; Pillinger *et al.*, 1994). The mentioned reservoir study (Everall and Lees, 1996) shows no significant drops in available nutrients while showing that the total 'cocktail' of algicidal, phytotoxic, unidentified or toxicologically unknown organic compounds reaches concentrations of 0.48–$4.31\,\mathrm{mg\,l^{-1}}$ near the straw. Although toxic substances are thus likely to be the dominant cause of algal decline, rotifer density was also enhanced after straw addition, and grazing by these animals together with a moderate spring peak of *Daphnia* may have helped to reduce algal biomass.

Although the huge amounts of straw that would be needed make this approach unlikely to be useful for manipulating large lakes, it might help in clearing up ponds. Straw can also stimulate macro-invertebrate populations (Everall and Lees, 1996). Since invertebrates are an essential part of the diet of small ducklings (Section 4.5), straw addition has been promoted as a way to make unvegetated gravel-pits more suitable for duck reproduction (Street, 1978).

Dredging

Resuspension of a thick layer of unconsolidated sediment and phosphorus release from sediment are conspicuous causes of turbidity in many shallow lakes, and several ways to solve the sediment problem have been proposed. Removal of the accumulated sediment is the most straightforward approach, and it has been applied to many lakes over the years (1993). Dredging is the most common procedure for sediment removal, although bulldozer excavation can also work after lake draw-down.

Many different dredge types and dredging approaches have been developed. A problem of some dredging techniques is that they cause a considerable resuspension, with the associated problems of turbidity and release of nutrients and sometimes toxic substances. Another difficulty is the loose structure of the sediment layer in many shallow lakes. Often the substance behaves almost as a fluid. As a result local removal results in spreading out of the remaining material. The intense horizontal redistribution of loose sediment in shallow lakes can also be used to our advantage. Sediment tends to accumulate on deeper sites where wave action does not cause resuspension (Section 2.2). When a deep site is excavated in an otherwise shallow lake, sediment is trapped there and may be dredged out relatively efficiently.

The best studied case of sediment removal from a shallow lake is probably that of the Swedish Lake Trummen (Andersson, 1988). Dredging increased the mean depth of the lake from 1.1 to 1.75 m and resulted in a strong reduction of sediment phosphorus release into the water column. Since then numerous sediment removal cases have been published (Cooke *et al.*, 1993).

Enclosures and artificial refuges

Many experiments have shown that it possible to let vegetation develop inside exclosures that exclude birds and fish, and dampen wave action. A potential strategy to let an entire lake switch to a clear state is to build many of such exclosures in a lake to let plants establish (Jeppesen and Moss, pers. comm.). Since the resulting local vegetation patches may serve as a refuge for zooplankton against fish predation, reduce resuspension and enhance denitrification, this will help to reduce turbidity in the entire lake and might eventually induce a switch to the clear vegetation dominated state. Although the idea seems straightforward, no lake has so far been restored by means of this technique.

Another option that has been suggested is to introduce artificial plant-like structures to serve as a refuge for zooplankton against fish predation (Irvine *et al.*, 1990). Although plastic plants or plant-like structures do work as refuges against predators and have been successfully used as such in various experiments (Winfield, 1987; Irvine *et al.*, 1990; Persson, 1993), it seems unlikely that this approach could be scaled up sufficiently to induce a shift to a clear water state in real lakes.

Handling vegetation nuisance

Lakes may have clear water and sparse vegetation when their nutrient level is low, however this situation is uncommon in eutrophic shallow lakes. Such lakes tend to be either turbid with very little vegetation or clear with abundant submerged vegetation (Chapter 5). Although blue-green algal blooms and high turbidity are usually not appreciated, dense weedbeds can be a nuisance too for boating and angling visitors. Aquatic weed control is the topic of much research. Entire journals, conferences and books are devoted to it. It will be clear after reading this book that complete elimination of submerged plants from eutrophic shallow lakes will usually lead to turbid water and cyanobacterial dominance. If this is to be avoided, plant control should therefore preferably be limited to certain areas.

Probably the simplest way to control vegetation is by harvesting the plants in parts of the lake where they are a nuisance. When plants are removed after cutting, an advantage of this approach is that harvesting represents an export of nutrients. In Europe plant harvesting is common in ditches and canals, but large-scale harvesting in lakes is rare. Several effective harvesting machines are available on the American market that can cut and collect plants at water depths ranging from a few decimetres to about 2 m (Cooke *et al.*, 1993). Cooke's review of the American work shows that depending on the species involved and the conditions, regrowth of the plants can be quite fast and it may be necessary to repeat the treatment later in the growing season.

Another way of preventing plants from growing in certain areas is to cover the sediment with sheets that are impermeable for plant shoots and reduce light reaching the sediment. Again several materials are available commercially in the United States and have been tested in the field (Cooke *et al.*, 1993). A problem that can arise is 'ballooning' of some types of screens when they trap gas bubbles that are released from the sediment. Also sediment may accumulate on the screen and this new top layer can be colonized by plants again. The latter is likely to be a major problem when the screens are to be used in large shallow lakes where resuspension and redistribution of sediment is important during the unvegetated part of the year. Since screens are also relatively expensive, their use is limited to small-scale applications.

Although many shallow lakes are covered entirely by submerged plants, others have deeper areas that remain uncolonized. In Veluwemeer, for instance, macrophytes are largely limited to the area shallower than 1 m, while the large area with a depth ranging from 2 to 4 m has remained almost free of plants over the past 20 years. In some cases it may be possible to manipulate the water level of a lake in such a way that the deeper parts remain free of plants, while vegetation is preserved in shallower areas. Also dredging may increase water depth sufficiently in limited areas such as navigation channels to prevent nuisance vegetation from growing there.

Some species of submerged plants tend to cause much more nuisance than others. In shallow water canopy forming species such as *Potamogeton pectinatus* and *Hydrilla* can make it almost impossible to boat, swim or fish, while carpets of charophytes covering the sediment do not impair recreational activities too much. In the United States, the relatively recent invader Eurasian watermilfoil (*Myriophyllum spicatum*) can reach an extremely high biomass and forms a strong nuisance in lakes where the previous vegetation of native species had not caused such problems. Obviously, it would be useful to find management strategies that stimulate dominance by species that do not reach the water surface. In large shallow lakes such as Veluwemeer, Krankesjön and Tåkern, charophytes seem to form a stable vegetation outcompeting *Potamogeton pectinatus* when the water level and the nutrient loading are not too high. In general, however, the current knowledge of factors that determine the species composition of submerged vegetation is still too poor to suggest effective management methods.

Biological control of submerged plants by means of grass carp (*Ctenopharyngodon idella*) has been applied to many lakes. In practice these animals are not observed to exert the desired moderate control of vegetation. Various experiments show that at low densities their effect is negligible whereas at a slightly higher density they eliminate vegetation entirely (Small, Jr. *et al.*, 1985). This all-or-none effect is confirmed by experiences in many Florida lakes (Mark V. Hoyer, pers. comm.). Only if the stock is managed very carefully by sequential harvesting and restocking may grass carp balance the amount of vegetation to a desired level, but this requires a close monitoring of vegetation and carp. In that approach a simulation model may be used to aid in guiding the fish management decisions (Shireman *et al.*, 1985).

6.6 SELECTING RESTORATION MEASURES

Given some basic information on a lake it will usually be possible to make a reasonable selection of restoration measures that are most likely to be effective in restoring a lake. A combination of different measures is usually chosen. Obviously, this does not facilitate scientific interpretation of the effects of the separate measures, but chances of improving a lake are often better if several measures are combined. For instance, as explained in the previous sections the combination of nutrient reduction and biomanipulation can be a good way to restore a hypertrophic turbid lake in situations where each of these measures separately would be unsuccessful.

A diagnosis of the dominant forces that keep the lake turbid and prevent vegetation recovery facilitates choosing the best management options. As explained in Section 2.1 the contribution of phytoplankton and suspended sediment to turbidity can already be inferred roughly from the combination of Secchi-depth transparencies and the chlorophyll concentrations. Lakes with a low concentration of phytoplankton but a high turbidity due to suspended sediments are unlikely to clear up in response to nutrient reduction alone. In small lakes where wind impact is minor, high concentrations of suspended sediment are probably due to benthivorous fish, and biomanipulation is likely to have a large effect. Also, when carp has been introduced, removal of these animals may be a prerequisite to improve water clarity and conditions for vegetation development. When

7 The limits of knowledge

PROBLEMS OF PREDICTIVE MECHANISTIC MODELS

Going through the chapters of this book one may get the impression that much is known about the functioning of shallow lake ecosystems. It is tempting to try to combine all this knowledge into one big simulation model that accurately reflects the functioning of real lakes and that can be used to predict the response of the system to different management scenarios. Indeed, for many physical and chemical problems, simulation models have proven a useful tool to predict the system's behaviour, and in the early 1970s there was great optimism about the possibilities of constructing such detailed simulation models for predicting the dynamics of entire ecosystems. Cooperation of groups of experts on all relevant biological and technical sub-topics led to models integrating the available knowledge as much as possible. The model CLEAN (Bloomfield *et al.*, 1974), constructed as part of the International Biological Program is a good example of this approach. The model contains a diverse spectrum of components such as several fish species, algae, zooplankton, aquatic macrophytes, invertebrates and nutrients, formulated in 28 differential equations. The idea of such modelling approaches was that in the course of the modelling process missing information could be identified, and filled in after additional experimental research. The latter, however, turned out to be a 'mission impossible'. The number of parameters in such complex models is very large, and the values of many parameters can not be determined within a reasonable amount of time, if they are measurable at all.

The common solution is to estimate the remaining parameter values by fitting the model predictions to field data, so-called 'tuning'. A wide array of sophisticated numerical techniques is available for this purpose, and often an impressively good fit can be obtained with little effort. However, this success is illusory. The problem is that a certain system behaviour can often be produced from many different parameter settings. This phenomenon is nicely illustrated by Simons and Lam (1980) who show that even for relatively simple phytoplankton–nutrient models the same patterns can be produced with completely different parameter settings and also from totally different models. Thus, tuning of complex ecological models easily leads to good results for the wrong reasons. A good fit does not guarantee any realism of parameter values or model structure. Indeed, terms like model validation and verification promise more than can be realized in models for natural systems (Oreskes *et al.*, 1994). Basically, simulation models have the same problems as statistical input–output models. The assumed causal relations underlying the model need not be true, and therefore extrapolation to new situations easily leads to non-sense predictions.

Probably the most useful aspect of simulation models is that they can help analysing the contribution of different mechanisms to the system's behaviour, and generate hypothesis that can guide experimental research. This requires that the models are transparent enough to be understood by non-modellers working at the problem. In practice this inspiring role of models in research groups is the exception rather than the rule. The major problem is probably that it remains remarkably difficult for an outsider to understand the mechanisms that govern the behaviour of ecological simulation models if the models are not kept really simple.

Minimal models, as used throughout this book, are simple and may indeed help to get some insight into the often intricate effects of ecological feedback mechanisms. However, such models differ from the larger simulation models in that they do not attempt to include all quantitatively important aspects. Therefore, they can be used to study the properties of isolated mechanisms, but not to obtain a quantitative insight in the relative importance of different mechanisms operating in the field. As argued in the Introduction and illustrated by many examples in the different chapters, field patterns are often explained by an array of simultaneously operating mechanisms, rather than by a single dominant force. To help unravelling this interplay of mechanisms quantitatively, models need to be more complex, and necessarily lose part of their transparency.

A relatively new development that helps linking quantitative modelling and biological transparency is the use of individual based models. Individual animals or plants are the basic units in such models. Individual-based models have several advantages compared with traditional simulation models (Huston *et al.*, 1988; Hogeweg and Hesper, 1990; DeAngelis and Gross, 1992). Instead of implicitly assuming information processing on the population level, individuals are taken as the natural units, which is more realistic and intuitively straightforward. Also, model behaviour is often rather robust to variations in formulation of the processes. Perhaps most important is the fact that parameters needed in the models (such as speed of movement, amount eaten per day etc.) as well as the predicted variables (such as individual numbers, diets and conditions) are typically of the type measured by experimental biologists. This facilitates the communication between modellers and experimentalists, and thus the use of these models as a tool for inspiring and guiding research.

An obvious disadvantage of modelling populations individual by individual is that it takes too much computation time to simulate realistic numbers for most populations, although there are several ways out of this problem (DeAngelis and Rose, 1992; Scheffer *et al.*, 1995b). A more serious complication is that the range of complex patterns generated by such models are almost as bewildering as that observed in nature. As a consequence they are relatively difficult to study thoroughly and are usually not as appealing as some traditional minimal models for highlighting the consequences of an ecological mechanism in a transparent way. However, although simple differential equation models can handle some aspects of the effects of individual size variation on population dynamics (Scheffer *et al.*, 1995a) more elaborate individual based models are often the only option when size of individuals crucially determines their role in competition or predator–prey relationships as is the case in fish communities.

The fact that the output of individual based models has much biological details, such as stomach contents and size distributions, that can be checked against data makes it less likely to end up with 'good results for the wrong reasons' as in traditional large simulation models. Indeed, individual based models are considered a promising tool for predicting the response of fish communities to various factors (Vanwinkle *et al.*, 1993). However, even though this approach may have advantages over more traditional simulation models, most workers will probably agree that we are still far from being able to model ecosystems in a sufficiently complete and faithful way to allow accurate prediction of their responses to different management scenarios.

In conclusion, different types of models can contribute in different ways to the unravelling of ecosystem functioning, but our quantitative knowledge of the forces governing lake ecosystems simply remains insufficient to construct models that can predict their response in a detailed mechanistic way.

THE NECESSITY OF MECHANISTIC INSIGHT

From a scientific point of view all progress in unravelling mechanisms by means of model analyses and clever experiments is worthwhile. Whether or not we really need all these detailed insights in order to be able to restore a lake is less obvious. Despite the poor quantitative mechanistic insight into the functioning of lakes, experts are often quite capable of predicting what the response to a management measure will be. The explanation why some people do better than most models in predicting effects is probably that they take a very different approach to the problem. If an expert is asked to predict, for instance, what will happen if all the fish are removed from moderately eutrophic turbid pond, the prediction will probably be that the water will clear up and water fleas and aquatic plants will become abundant. This prediction is not based on a detailed mechanistic knowledge of the physiological characteristics of the organisms involved and their ecological interactions, but rather on the experience that this response has been observed in many comparable lakes. Indeed, such an empirical approach using information on similar cases is probably the most reliable basis for predicting the effects of measures. At first sight this may suggest that all the knowledge about the functioning of lakes is of little practical use after all. However, a more careful examination reveals that insight in the regulatory mechanisms is also an essential ingredient of the expert approach to prediction.

The need for more than examples alone is well illustrated by an unsuccessful attempt to predict the effect of biomanipulation by means of a neural network. Computer neural networks are simple models of real neural networks and can be 'trained' to give the right 'answer' to a 'question' by just presenting enough examples of correct answers to problems. We gave it information about 12 biomanipulation cases with varying outcomes. After training, the network could perfectly predict the 12 example cases in the hindsight. However, giving it new (hypothetical) problems and analysing the answers, it appeared that the 'internal rules' of the neural network made little sense. For instance, it systematically predicted stronger effects if less fish was removed.

In fact neural networks are comparable to very flexible statistical models that can be fitted well through most data sets. The danger of misinterpreting causality remains a crucial problem in applying empirical relationships to management. Of course, this is common wisdom, but since it is one of the main caveats in everyday applied science, it deserves repetition. As a caricatural example consider the relationship between wind and the swinging of trees. One could well imagine that swinging trees actually cause the wind: If they stop swinging the wind stops also. Such a lack of insight into the functioning of the system becomes a problem if one decides to manage the system by cutting down trees in order to reduce the wind. In practice, the caveats of applying empirical models for management purposes are more tricky than the simple cause–effect switch in this tree example. Algal biomass, for instance, is strongly correlated with the total-P concentration of lake water, but causality in the relationship is far from straightforward. The maximum algal biomass depends on phosphorus availability but algal blooms also stimulate phosphorus release from the sediment into the water column (Section 2.3). This is illustrated by the marked drops in total-P that can occur when *Daphnia* graze down phytoplankton (Meijer *et al.*, 1994b). The misinterpretation of causality behind the strong correlation between chlorophyll and total-P easily leads to an overestimation of the potential for restoring lakes by reducing phosphorus loading as a determinant of algal biomass, and consequently to an underestimation of the potential of other measures for controlling algal biomass.

Thus, even though our knowledge may be insufficient to predict effects of measurements in a mechanistic way, insight into the functioning of lake ecosystems is important to guide the pragmatic empirical approach to prediction. As argued, information on similar cases is a good basis to predict the effects of restoration measures, but the number of good case studies is still far too small to cover the wide range of different lake types. Insight into the functioning of these systems is indispensable for judging the importance of differences between lakes for the expected response, and for tailoring the restoration strategy to a specific situation.

Prospect

Although the recent intensive work on shallow lakes has led to an impressive expansion of our knowledge of these systems, the array of poorly understood problems remains equally impressive. To name just a few: Under which conditions do alternative stable states exist? How can switches of states be induced? How does vegetation as a refuge affect various predator–prey interactions? What are the implications of chemical signalling in trophic interactions for community dynamics? Could we use such signals to manipulate the food web? What is the role of inedibility and toxicity of cyanobacteria in their success? Why are brackish lakes turbid even when they have vegetation? How do predator–prey relations evolve over the seasons?

The best way to resolve these and other questions will differ from case to case, but as a rule a combination of approaches is often the most powerful strategy. Controlled experiments, whole lake manipulations, minimal models and elaborate simulation models all have their specific strong and weak points. Addressing the same question simultaneously with different approaches is the best way to identify artifacts of each of them. Clearly, well documented whole lake experiments are very valuable at this point. Not only do they reveal what works and what does not in restoring certain lakes, they can also help to identify the main regulatory mechanisms. The recent interest in biomanipulation, for instance, has catalysed the insight in the major forces that govern the dynamics of shallow lakes. On the other hand the conditions in whole lake experiments are difficult to control and there are usually no replicates. As a result it is often difficult to understand what happened for what reason in hindsight. Therefore, small-scale, well controlled and replicated experiments remain indispensable further to enhance our understanding, even though such experiments are necessarily conducted under rather unnatural conditions, and do not reveal how the specific mechanism addressed interacts with other mechanisms in the field. Elaborate individual based models and other simulation models can help in putting different processes into perspective but are difficult to study due to their mere complexity. Very simple 'minimal' models are easier to understand but do not help to reveal the relative importance of the addressed mechanism in the field.

Although the merits of combining modelling, laboratory experiments and fieldwork are broadly recognized the approaches remain quite segregated in practice. Whole lake manipulations are often disguised as rather crude and uninterpretable by experimentalists, and the lack of integration between modellers and 'real' biologists is notorious. Even within the modelling world there is a distinct separation between theoreticians working with abstract minimal models and groups working on more applied quantitative simulation models. Combining approaches requires an investment of time and energy to explain results and assumptions to relative outsiders, and

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Marten Scheffer

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Marten Scheffer wrote this book while at the Institute of Inland Water Management and Waste Treatment, RIZA, Lelystad, The Netherlands. He is currently at the Department of Water Quality Management and Aquatic Ecology of the Wageningen Agricultural University.

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