

# 1 Eutrophication and the Ecosystem

## 1.1 Background

Eutrophication of surface waters is generally recognised as a matter for environmental concern. Eutrophication is characterised by increased algal growth, with an increased incidence of toxic cyanobacteria blooms and a decrease in the abundance of species.

Some of the manifest problems brought about by prolific algal biomass include: turbid waters; anoxic conditions; bad smell and chironomid and *Culex* midge plagues (Vollenweider 1990; Moss et al. 1996a; Carpenter et al. 1998). Such eutrophication problems (“eutrophication” *sensu lato*) are generally considered to be the consequence of enhanced nutrient loadings (“eutrophication” *sensu stricto*) (Likens 1972; Vollenweider 1990; Reynolds 1992; Moss et al. 1996a; Carpenter et al. 1998). Therefore, the management of eutrophicated water bodies is usually primarily focused on the reduction of nutrient loading, supported by a policy of reduced environmental releases of phosphorus from laundry detergents, sewage and agriculture.

However, it became apparent over the past decade, that reduced grazing of algae by daphnids can be a crucial factor determining whether or not nutrient enrichment will lead to eutrophication problems (Moss et al. 1991; Moss et al. 1996b; Reynolds 1994). Biomanipulation of eutrophicated shallow water bodies, thereby improving ecological conditions for daphnids, became a regular tool applied in eutrophication management practice (Benndorf 1990; McQueen 1998; Harper et al. 1999).

Biomanipulation is mainly focussed on the improvement of biological conditions leading to a higher survival rate for daphnids as part of the aquatic foodweb. Examples of biomanipulation measures include: reduction of predation by planktivorous fish and improvement to the submerged vegetation as a shelter for daphnids against predation. More recently, the palatability of suspended particles as a factor determining the grazing efficiency of daphnids has become a topic of interest. High concentrations of resuspended inorganic particles hamper daphnid grazing, while at the same time stimulating algal growth due to increased nutrient releases (Kirk and Gilbert 1990; Ogilvie and Mitchell 1998). Top-down control by daphnids under eutrophicated conditions may also be reduced by the presence of unpalatable algal species (mainly cyanobacteria) that may gain competitive advantage over the heavily grazed palatable algal species.

This book covers another important aspect regarding the improvement of environmental conditions for daphnids, which is necessary for successful eutrophication management, i.e. optimisation of the abiotic water conditions. Bales et al.

(1993) suggested that the sensitivity of daphnids to saline conditions may be a significant reason for the higher susceptibility of brackish waters to eutrophication. From this perspective, ecotoxicologically reduced daphnid grazing due to micropollutant loadings could be a crucial factor leading to problems associated with eutrophication (Hurlbert et al. 1972; Hurlbert, 1975; Gliwicz and Sieniawska, 1986).

The toxic effects of pesticides and other chemicals on the viability of cladoceran populations reduce their capacity to graze the surplus algal growth caused by increased nutrient availability. In ecotoxicological semi-field studies, it has been observed that cladocerans are amongst the most sensitive species when it comes to toxicant exposure, consequently resulting in a reduction in the top-down control of the algal growth (Day 1989; Yasuno et al. 1993). Based upon the analysis of sediment cores, Stansfield et al. (1989) argued that a switch from submerged plant dominance to phytoplankton dominance (eutrophication) in a series of shallow lakes, i.e. the Norfolk Broads, U.K, during the 1950s and 1960s, was likely to have been due to the poisoning of cladocerans (viz. *Daphnia*) as a result of liberal organochlorine pesticide use.

The aim of this book is to provide a better understanding of the ecotoxicological aspects of eutrophication processes in shallow, temperate fresh waters, so that these processes may become a recognized factor in the restoration of eutrophicated water bodies.

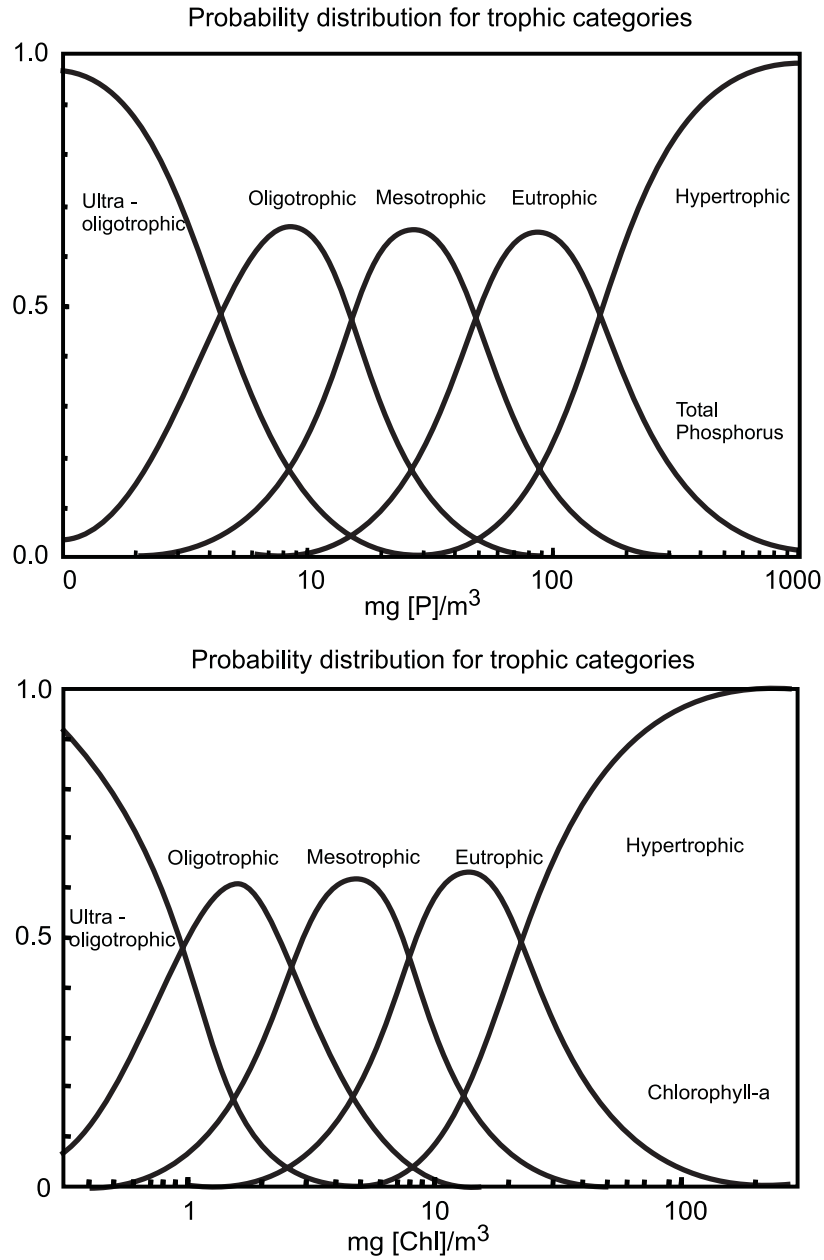
Some basic limnological ecology, which is fundamental to the further contents of this book, is presented in the first chapter. Chapter 2 provides more information on daphnids, encompassing their ecology, grazing efficiency and any subsequent consequences for the control of algal densities. Chapter 3 concerns daphnid ecotoxicology, and provides information on toxicity induced reduction of daphnid grazing effectiveness (so called “toxic anorexia”) in experimental settings. Variation in daphnid grazing effectiveness in the field situation is described for two Dutch lakes in Chap. 4. The applicability of an ecotoxicological assessment of eutrophicated water bodies is discussed, and practical tips given, in Chap. 5.

## 1.2 Eutrophic and Eutrophicated Waters

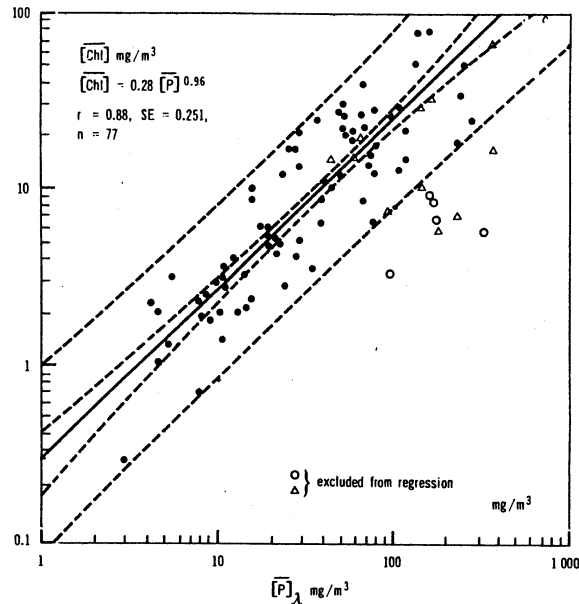
### *Nutrients or Algae*

In order to acquire a better understanding of the causes of eutrophication in fresh water ecosystems, it is helpful to make a distinction between “**eutrophic**” waters (classification of water according to its intrinsic nutrient status, eutrophication *sensu stricto*) and “**eutrophicated**” (or “eutrophied”) waters (perception of manifest water quality problems related to ecological malfunctioning such as turbid water, bad smell and high algal density, eutrophication *sensu lato*).

The total phosphorus concentration of fresh surface waters is generally used as an indicator for the trophic status of that water body. Phosphorus is one of the essential nutrients for algal growth. It is considered to be the prime limiting element determining the biological productivity (algal productivity, and subsequent higher order productivity) in many freshwater aquatic systems.



**Fig. 1.1.** Classification of waters according to the OECD (1982). Above: on the basis of P-loading, and below: on the basis of average algal density



**Fig. 1.2.** The “Vollenweider-model” (OECD 1982) illustrating large variation in the P:chl-a ratio

Other main nutrient elements present in potential limiting concentrations are nitrogen and silicate. Nitrogen is not a suitable indicator, because it is poorly retained by soils and leaches easily to aquatic systems. Additionally, transformations between various fractions of particulate (organic) nitrogen, dissolved (organic/inorganic) nitrogen and atmospheric (inorganic) nitrogen occur at high rates, ensuring a continuous supply of available nitrogen under most circumstances.

Silicate (ortho-silicic acid) is only essential for the growth of diatoms, which incorporate silicic acid into their frustuliers. Therefore, it is not a suitable indicator for total system productivity.

In the classification of the trophic state of waters according to the OECD (1982), no distinction was made between eutrophic and eutrophicated waters. Waters are referred to as mesotrophic, eutrophic or hypertrophic on the basis of their P-loading as well as on the basis of algal densities (Fig. 1.1), with the underlying assumption that nutrient status (P loading) is positively and causally correlated with algal density (Fig. 1.2).

### **The Vollenweider Regression**

The OECD classification was based upon a regression model (known as the “Vollenweider” model) in which the phosphorus concentration (as indicator for the trophic status) of surface waters and mean algal density (as indicator for manifest “eutrophication” problems) were related to each other. The regression model was based upon observed relationships between phosphorus and algal densities in vari-

ous deep upland lakes during the nineteen seventies (Vollenweider and Kerekes 1980). The model has been used often and validated in many situations (CUWVO 1976, 1980, 1988; OECD 1982; Klein 1989). This has led to the perception that the ecological water quality problems related to high algal densities were solely due to “eutrophication” (i.e., nutritional or, more specifically, phosphoric loading of waters).

It should, however, be noted that the “model” demonstrates a broad variation in the relationship between the two indicator parameters (a factor of 10 at 99% confidence), even after plotting on a log-log scale (Fig 1.2). This means that many eutrophic waters exist with relatively low algal densities; and oligotrophic/ mesotrophic waters with relatively high algal densities. Additionally, it should be noted that examples of eutrophic lakes with a relatively low algal density were excluded from the regression (open symbols in Fig 1.2).

### ***Beyond Nutrients***

Although phosphorus is a suitable rough indicator for the trophic status of a water body, this does not imply that it is a reliable (causal) predictor of manifest eutrophication problems (Reynolds 1992). The relationship between phosphorus content and eutrophication problems is not fixed, due to the fact that there are many other variables, in addition to phosphorus concentrations, that influence the manifestation of eutrophication problems. In certain circumstances, eutrophic waters are not eutrophicated, while mesotrophic waters sometimes appear to be eutrophicated.

The “Vollenweider-model” had its function in clarifying the role of excessive phosphorus loads in the manifestation of severe eutrophication problems, but for successful eutrophication management it is necessary to look beyond nutrient loads in order to arrive at reliable and sustainable water management options (Golterman 1991; Moss et al. 1994). Nutrient-algal relationships are only a fraction of the complete aquatic food web (Hosper et al. 1992; Scheffer et al. 1993; Leibold and Wilbur 1992; Vijverberg et al. 1993). An extensive statistical data analysis of 231 lakes in the Netherlands (Portielje and van de Molen 1997a; 1997b; 1998) has made it clear that top-down control of algal density development by submerged vegetation (competition) and daphnids (grazing) is a significant factor explaining variation in chlorophyll nutrient ratios. In eutrophication management it is important to understand what has caused the eutrophicated state of the waters, and to recognise the bottleneck situations inhibiting their restoration.

## **1.3 Trophic Cascades in Freshwaters**

### ***The Foodweb***

The availability of nutrients is a basic requirement for the development of organic biomass. Algae can respond quickly and opportunistically to increases in nutrient availability. However, the capacity of individual algae to store nutrients is limited. It is the population that retains the nutrients, but only during the growing season.

Decaying algae release nutrients and the following season all nutrients must be re-acquired.

Macrophytes on the other hand, cannot respond as quickly as algae to changing nutrient levels, but do retain nutrients individually within storage organs. Macrophytes are also able to acquire nutrients, both actively and passively, from the substrate on which they grow. This gives them a competitive advantage over algae. The shade created by macrophyte leaves may inhibit algal growth. Some macrophytes can even suppress algal growth by releasing allelochemicals (Mjelde and Faafeng 1997). By preventing algal growth, macrophytes may also gain access to nutrients in the water that might otherwise be utilised by the more rapidly responding algae. As a result, macrophytes are the predominant primary producers in shallow waters where sunlight can reach through to the sediment, whereas algae are the primary producers in deeper waters.

The primary production of algae and macrophytes is the basis of aquatic food webs (see Fig 1.3). The main groups of algal consuming secondary producers in fresh water ecosystems are cladocerans and other zooplankton groups (viz. copepods and rotifers) and filter feeding benthic species (viz. bivalves). Zooplankton (especially cladoceran water fleas) plays a key role in aquatic ecosystems by effectively responding to variations in algal production through its opportunistic population dynamics. Bivalves, though individually capable of filtering large volumes of water, do not play such a central role, since they cannot multiply at the same rate as their algal food source. Therefore, bivalve populations are limited by the minimum amount of food available.

The algal biomass density is the nett result of algal production and algal losses due to sedimentation and grazing by zooplankton or other secondary producers. The production of herbivore biomass in aquatic ecosystems is approximately 2–6% of the primary (i.e., algal) production, which is extremely high compared to terrestrial ecosystems (<< 1%) (Barnes and Mann 1993). Accounting for respiration and defaecation losses, this means that in a healthy aquatic ecosystem that 30–90% of the primary production is consumed and ends up in the aquatic food chain. In plankton dominated systems this is at the higher end of the scale (up to 90–95%). Only a small fraction of the primary production is allocated for the establishment of a standing vegetation (e.g., reed and rush marshes) and temporary algal blooms. Sedimentation and shore deposition of unconsumed algal and plant debris (detritus) brings about decay by benthic detritivores.

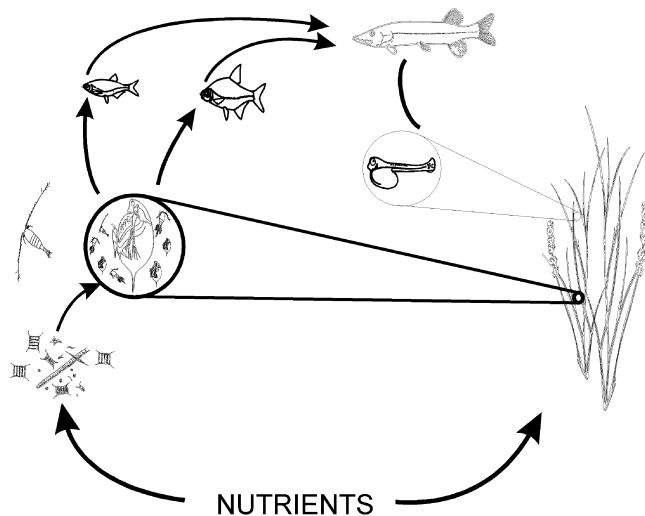
Zooplankton is consumed by small fish (e.g., roach and smelt, and the juveniles of larger species) and amphibians, which, in turn, are food for predatory fish (e.g., pike and perch). Zooplankton predation, especially of the larger cladoceran species, may be very high. Therefore, cladocerans usually seek refuge in the macrophyte vegetation and migrate out into open water only during the night when the risk of predation is low (Timms and Moss 1984; Lauridsen and Lodge 1996; Stephen et al. 1998). Zooplanktivorous fish, on the other hand, avoid macrophyte vegetation due to the fact that predators such as pike may be concealed there.

The aquatic food chain provides a food source for many birds (e.g., waterfowl) and various mammals (e.g., otters).

### ***The Role of Macrophytes***

Macrophytes as seen in figure can play substantial role in shallow lakes and ponds as they contribute to primary production of organic material that give organic matter to the bacterial loop and invertebrates. Of course, in high trophic and turbid lakes, this process do not occur as a significant contribution in nutrient cycles as lack of light is limitant factor for their growth.

We must distinguish the different types of macrophytes as shown in the (following) figure:



**Fig. 1.3.** The position of zooplankton (i.e. cladocerans) in the foodweb

As any plants, macrophytes participate to the productivity of the ecosystem. When rooted macrophytes are present, they can export nutrient from sediments and at their decay and senescence contribute to the enrichment of the water column. This phenomenon may be temporarily decreased by periphyton fixed on leaves and stems, nevertheless, N and P are rapidly available for small algae and heterotrophic microflora. Senescing macrophyte tissue and attached algae, as well as organic matter and nutrients retained in them stay in sediments where they collapse in the littoral zone of lakes. The accumulative retention of these inputs of nutrients and carbon can be very high. It should be recalled that most aquatic macrophytes are perennials and much of certain nutrients as phosphorus extracted by plant growth from the sediments is largely translocated back to the rooting tissues at the end of the growing season and taken off from the nutrient pelagic cycle of lakes. In case of shallow lakes and high development of littoral zone, the total nutrient releases to the pelagic zone is reduced. The tendency is for the littoral developments and metabolism to reduce total phytoplankton growth of the lake to levels below the growth potential that would occur if most of the nutrient loads entered the pelagic zone directly. Wetzel (1990) has shown that in these conditions, “in the ecosystem with profundal sedimentation patterns and the converse differ-

ences in system components and their metabolism, one finds a overall decrease in the phytoplanktonic efficiency of nutrient utilization". The relations between P and macrophytes have been discussed also for a long time and it is known that these plants are able to keep quite large quantities as "luxury consumption". In summer, this contribution of macrophytes in the P cycle can participate of decreasing concentrations of the growth capacity of algae in the littoral zones of the lakes, but in autumn, large amounts of P are released. In the same way, the allocation of macrophytes in toxicants explains the leaching of these compounds under specific conditions ( pH, redOx...).

### ***Balanced Foodchains***

In a healthy ecosystem, a finely tuned balance exists between production and consumption within each link in the food chain (Carpenter et al. 1985). In shallow freshwater bodies, macrophytes are important for the stabilisation of this balance. Their long-term accumulation of nutrients tempers phytoplankton dynamics and at the same time they offer shelter for zooplankton, protecting it from predation. To a certain extent, bivalves also have a stabilising function, as they graze a base level of algae and clear the water of any suspended particles that may interfere with zooplankton grazing.

However, zooplankton, especially cladocerans, controls the short-term variation in phytoplankton dynamics, through their opportunistic response to food availability. The opportunistic response of cladocerans to algal (food) conditions is thus a critical and central step in the trophic cascade of aquatic foodchains. A well-balanced and synchronised coupling of cladoceran development to algal development is, required therefore, especially under mesotrophic or eutrophic conditions.

### ***The Trophic Basis of the Cascade***

Nutrients for algal growth become available through the mineralisation of organic materials, organism excretions and leaching from sediments. The cycles of the macronutrients C, N and P are the best understood and are briefly described below. Trace elements may limit primary or secondary production both spatially and temporarily. This may, for instance, be the case for Si, which is an important element for diatoms (Hecky and Kilham 1988; Moss and Balls 1989). The cycles and importance of trace elements are less well understood and will, therefore, not be further considered here.

The *carbon cycle* is the basis of all biogenic processes. Atmospheric CO<sub>2</sub> is fixed by autotrophs and enters the food chain, where a major portion of it is rereleased by means of heterotrophic metabolism. Heterotrophic consumers rely, both directly and indirectly, on this autotrophic fixation of CO<sub>2</sub> for their carbon supply. Carbon is, therefore, often used to quantify energy fluxes in ecosystems. Generally, carbon is not considered to be a limiting nutrient for primary production, due to the large available pool of atmospheric CO<sub>2</sub>. In the aquatic environment, however, C may become temporarily limiting, especially during summer stratification, when the rate of autotrophic CO<sub>2</sub> fixation exceeds the combined fluxes of heterotrophic CO<sub>2</sub> production and the transport of atmospheric CO<sub>2</sub> into the water.



The *nitrogen cycle* is very dynamic and is characterised by many transformations, in which (micro)biological processes play an important role. Nitrogen primarily enters the biogenic cycles by microbial nitrogen fixation of atmospheric  $N_2$  (Vitousek et al. 1997; Galloway 1998; Pastor and Binkley 1998). Nitrogen compounds are not absorbed by soil, clay or ferric hydroxide, etc. A large fraction of the N, therefore, dissolves in either inorganic (ammonia, nitrate, nitrite) or organic (amino acids, proteins, nucleotides) forms and easily leaches to surface waters (Overbeck 1989). Part of the N is lost to the atmosphere due to denitrification. In contrast to terrestrial ecosystems, which are often characterised by N limitation, most freshwater systems have a sufficient supply of N from terrestrial run off. Within aquatic systems, the N cycle is primarily controlled by microbial processes (nitrification, denitrification, ammonification), which are strongly dependent on the redox status of the system (Overbeck 1989; Stumm and Morgan 1996).

The *phosphorus cycle* is mainly driven by physico-chemical processes. P readily adsorbs to soil and, thus, most P is particle bound and only a fraction is directly available to biota (Sharpley and Rekolainen 1997). The most important natural route from terrestrial to aquatic ecosystems is terrestrial run off and erosion of particulate P (Sharpley et al. 1995). The bulk of the P in water is in particulate form and much P is bound to the sediment. The bioavailable fraction, the soluble orthophosphate (SRP), is very small and has an extremely high turnover rate (minutes). The P cycle in lakes is heavily dependant on the redox conditions of the system. Under anoxic conditions, the soluble P fraction drastically increases and substantial amounts of P may be released from the sediment. Under oxygenated conditions, soluble inorganic P is readily bound by adsorption to ferric hydroxide and  $CaCO_3$  and by precipitation as ferric phosphate. The oxygenated surface layer of the sediment acts as an efficient P trap (Overbeck 1989; Grobbelaar and House 1995). Under certain conditions, P bound to sediment may be utilised by phytoplankton (Golterman 1977; Grobbelaar 1983; Grobbelaar and House 1995). However, this is negligible in clear shallow water due to the presence of a layer of benthic diatoms, which stimulate an oxygenated sediment surface layer and arrest nutrient fluxes from deeper sediment layers. The remaining P fraction is used by benthic diatoms for growth (Van Luijn et al. 1995). Additionally, the layer of benthic diatoms stabilises the sediment surface, thereby reducing the amount of resuspended sediment particles. Bioturbation by sediment-dwelling organisms may increase P-fluxes from the sediment, but this effect is counteracted by the increased oxygenation of the surface layer of the sediment (Andersson et al. 1988). Assimilation in the biomass (e.g., submersed and shoreline vegetation, aquatic food chain) is an important factor in the P-cycle.

### **Hydrological Aspects**

Resuspension of inorganic sediment particles is mainly caused by wave action and, occasionally, by foraging fish. These resuspended particles can act as an internal source of phosphate (Ogilvie and Mitchell 1998). The dynamics of nutrients is also determined by the depth and stratification of lakes. In deep lakes, thermal stratification occurs during winter and summer. Nutrients present in the epilimnion (upper water layer) will be transported to the hypolimnion (bottom wa-

ter layer). The epilimnion of a stratified lake can lose up to 50% of its total phosphorus during the summer (Scheffer 1998). The 'turn over' in autumn and spring makes the nutrients from mineralised material in the hypolimnion available to the epilimnion. There is no stratification in shallow lakes and there is a continuous exchange of material between sediment and water. The mineralisation rate of sediment and the subsequent release of nutrients will increase due to higher temperatures in summer (Jeppesen et al. 1997).

Other environmental factors such as flushing rate, water temperature, pH and water hardness also influence growth rates and the composition of algal communities (Reynolds 1989; Moss and Balls 1989; Moss et al. 1991; Beklioglu and Moss 1995). However, since nutrients form the basis of ecosystem production, nutrient availability is the key factor affecting the functional role of algae as basic producers in the food web.

### ***Nutrients and Algal Growth***

The relative availability of different nutrients changes over time, as the nutrient cycles are not synchronised. In order to assess the relative availability of nutrients, the concentrations of macronutrients may be compared with the molar Redfield ratio of 106C:16N:1P (Goldman 1979). As only one growth factor can be limiting at a time (Liebig's Law of the Minimum), the Redfield ratio is considered to be an optimum ratio for algal growth, at which transitions from one nutrient limitation to another occur (Grobbelaar and House 1995). The Redfield ratio is an average ratio of algal elemental composition in marine waters, which is relatively stable compared to the nutrient concentrations in fresh waters. Such a stable elemental composition is thought to have evolved because algal cells perform similar metabolic functions and have quantitatively similar structural requirements (Hecky and Kilham 1988).

It should, however, be realised that different algal species have different optimum nutrient requirements, resulting in changes in community structure with changes in nutrient ratios (Grobbelaar and House 1995). This is especially true for fresh water systems, where algal elemental composition seems to be more variable, with respect to the Redfield ratio, than in marine systems (Hecky et al. 1993).

Since the relative availability of nutrients is not constant, but varies over time and between water bodies, most aquatic systems are resource limited. N and P are often the primary limiting nutrients. For our mesocosm studies (see Chap. 3), it has been observed that up to a depth of 80 cm, the P-flux from the sediment is sufficient to sustain algal growth and that the remineralisation of N, which is proportional to the height of the water column, is the limiting factor for optimal algal growth conditions. However, at a water depth of 180 cm, the P-flux, which was primarily related to the sediment surface area, was not sufficient to sustain algal growth. In lakes, this deeper water is the exclusive domain of algae.

To ensure survival, a competitor must be able to maintain nett population growth at resource levels less than those required by other species (Tilman et al. 1982). Algae are particularly well adapted for scavenging their environments for resources. Concurrent with the observation that P is most often the nutrient struc-

turally limiting in their environment, these strategies are particularly suited to compensating for P shortage.

In response to nutrient limitation, algae may react with three different strategies, or a combination of these (Sommer 1989):

- affinity-strategists can utilise low nutrient concentrations very efficiently;
- growth-strategists utilise transient periods with high nutrient concentrations to achieve a rapid population growth, compensating for periods with low concentrations and slow growth;
- storage-strategists build up internal reserves of nutrients during periods of high nutrient concentrations (luxury uptake), which are utilised during transient periods with low nutrient concentrations.

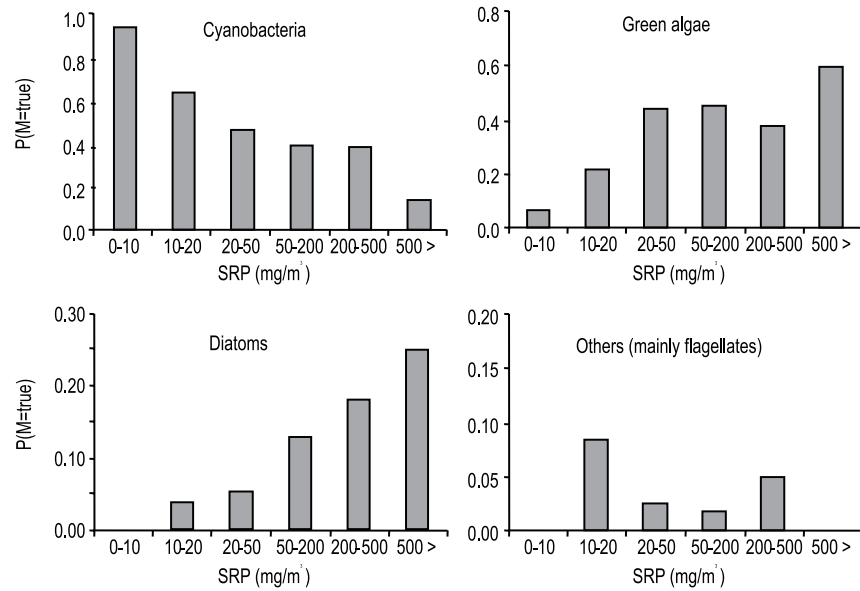
Affinity strategists are not only very efficient in the uptake of scarce nutrients, they also release substances that increase the availability of bound P (Grobbelaar 1983; Grobbelaar and House 1995). The cyanobacterium *Anabaena*, for instance, excretes extracellular phosphatases almost immediately upon the onset of P limitation (Healy 1973). Algae may also change the pH of their surroundings, which also increases the availability of adsorbed P (Grobbelaar 1983). Flagellates may be seen as behavioural affinity strategists, since due to their motility, they can utilise patches of any available nutrients caused by zooplankton excretion (Sommer 1989).

Storage strategists may have internal P reserves that may be sufficient for 5 to 10 cell divisions. The storage capacity for other elements, on the other hand, is substantially lower; ca. 5 times lower for N and negligible for Si, even in the case of diatoms (Fisher et al. 1995).

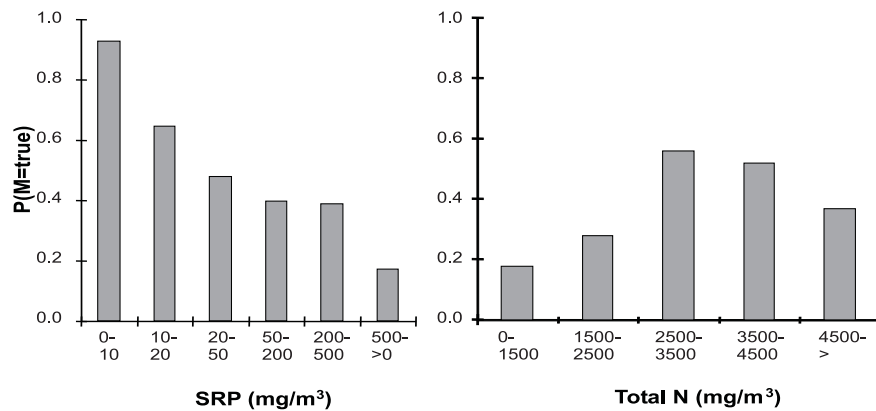
### **Nutrients and Algal Communities**

Varying nutrient concentrations, in an absolute as well as in a relative sense, will result in the development of different algal communities, depending on the outcome of intraspecific competition (Sommer 1989; Valiela 1993). The rate and quality of algal production is heavily dependent on the availability of both phosphate and nitrogen, and the subsequent N:P ratios. An analysis of phytoplankton data in European lakes (Schreurs 1992) shows that cyanobacteria dominate lakes with relatively low fractions of soluble reactive phosphorous (SRP), while green algae dominate systems with higher SRP (Fig. 1.4). Blue-green dominance increases with total N concentrations (Fig. 1.5). On the basis of total P, cyanobacteria dominate moderate classes (100–800 mg.m<sup>-3</sup>), while green algae dominate at higher levels (>800 mg.m<sup>-3</sup>). Lakes with low nutrient concentrations encompass a significant representation of flagellates in their phytoplankton communities.

The observations of blue-green dominance at high N:P ratio is contrary to what is generally assumed and observed in chemostate experiments (Andersen 1997), where cyanobacteria prefer a low N:P ratio. The dominance of cyanobacteria in fresh waters is, on the basis of these observations, often attributed to their ability to fix N by means of heterocysts. As N-limitation can be avoided by N-fixation, it has been hypothesised that the P-demand of blue-greens is high and that cyanobacteria may therefore have an advantage at low N:P ratios. On the contrary, however, it can be argued that high N:P ratios favour blue-green algae, since eco-



**Fig. 1.4.** Data from European lakes show that cyanobacteria have a lower frequency of dominance in P-rich waters, which favour green algae and diatoms (from Schreurs 1992)



**Fig. 1.5.** Probability of cyanobacteria dominance in freshwaters at various P or N conditions (from Schreurs 1992)

physiological studies with these algae have demonstrated their more efficient use of P in comparison to other algal taxa and/or their better storage abilities. This high affinity for phosphorous results in a high nitrogen demand, and this may be the reason for the evaluation of facilities for cyanobacteria to fix nitrogen gas. From this point of view, a high availability of N in relation to P may increase the incidence of nitrogen fixing cyanobacterial blooms.

Although nutrients are often limiting for algal growth, other factors might be just as important (Reynolds 1989). Light, used as the energy source for obligatory autotrophic algae, is often available at low intensities due to high water turbidity or deep mixing of the water column (Bleiker and Schanz 1997). In water containing high levels of suspended matter or algal cell concentrations, light is scattered by particles and absorbed by algal pigments and dissolved organic matter, and it may become the limiting factor.

### ***Nutrients and Zooplankton***

Planktonic algae are heavily grazed by zooplankton. Cladocerans are the most efficient grazers, due to their relatively large size and indiscriminate feeding habit. Because of differences in elemental stoichiometry, different types of zooplankton have a markedly different influence on the nutrient cycle. Relative to their food (algae), zooplankton species have low C:N and C:P ratios, which means that the caloric value of the food is generally sufficient, but that the macronutrients N or P may be limiting for growth. Copepods have relatively high N:P ratios (40–50:1) and, consequently, N is often the limiting nutrient in their diet (Hessen 1997). Copepods, therefore, preferentially select N-rich algal cells (Butler et al. 1989). Copepod excretion is fluid and does not sedimentate. Non-assimilated nutrients are, therefore, instantly replaced to the benefit of algal growth (Lyche et al. 1996a).

Cladocerans typically have a low N:P ratio of ca. 12–15 (Hessen 1997). Although they do not actively select P-rich food particles, cladocerans retain P from their food very efficiently (Lyche et al. 1996a). Cladocerans have solid faecal pellets that easily sedimentate and thus attribute to a nutrient loss from the epilimnion. Sedimentation of (dead) animals may reinforce P-limited conditions (Urabe et al. 1995; Rothaupt 1997). In this way daphnids create P-limited conditions in which they have a competitive advantage over other zooplankton, due to their efficient P-scavenging.

Cladocerans are the preferred prey of zooplanktivorous fish, resulting in increased P recycling within the system (Carpenter et al. 1992; 1995b; Vanni and Layne 1997). Predatory fish, on the other hand, reduce the number of zooplanktivorous fish, thereby releasing predatory pressure on cladocerans and retaining P in the biomass (Carpenter et al. 1995a).

## **1.4 Eutrophicated Waters: Disturbed Trophic Cascades**

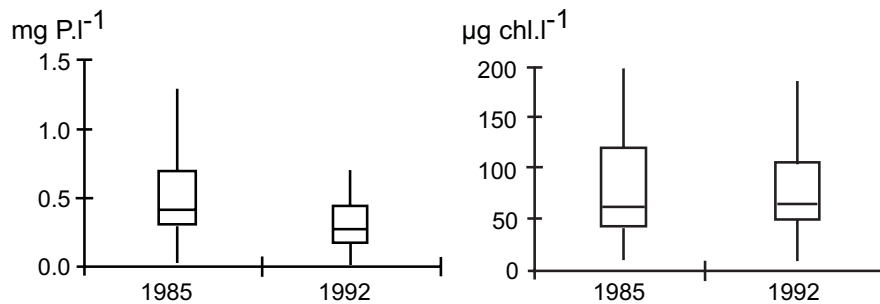
### ***Eutrophication***

Eutrophication problems are related to excessive algal densities. These problems arise due to prolific algal growth caused by nutrients becoming available to the algae in excess of the ecosystem's capacity to stabilise their concentrations in combination with the inability of its zooplankton to control algal development.

Manifest eutrophication problems are, thus, related to a complex of factors: an ecological imbalance between nutrient loading or mobilisation on the one hand, and herbivorous algal grazing and the development of water plants on the other. In “eutrophicated” water bodies, most of the algal biomass remains ungrazed (resulting in algal blooms) and ends up in the decomposition pathway (eventually resulting in oxygen depletion).

From the 1950s on, the nutrient load in lakes started to increase because of the rapid increase in the human population, and agricultural intensification accompanied by intense use of fertilizers. Other perturbations, such as chemical pollution (e.g., pesticides) toxic to zooplankton and the loss of lake-marginal wetlands, have also contributed to the effects of nutrient enrichment (Hosper 1997). These continuous and incidental sources led to higher algal production, eventually resulting in problems associated with eutrophication. Until recently, increased nutrient loads were considered to be the main source for the deterioration of the lake ecosystems. Eutrophication resulted in turbidity of the water and the increased production of algae reduced the light available to the macrophytes which, therefore, disappeared. The elevated production of algae and the decaying macrophytes produced large amounts of detritus, which accumulated on the bottom of the lakes to form loose sediment. Resuspension of this loose sediment by wind, waves and benthivorous fish further enhanced the turbidity of the water (Meijer 2000).

Although the increased nutrient loads in themselves are necessary prerequisites to prolific algal development, attempts to restore water bodies showed that nutrient reduction alone is not sufficient, unless extensive reductions are achieved. A survey of the trophic status of 231 Dutch lakes, covering the period 1980–1996, indicated a significant reduction in nutrient levels and chlorophyll concentration in nearly half of the lakes (Portielje and Van der Molen 1998). However, a more close evaluation of water quality data from the Netherlands shows that this is mainly due to reduced peak levels and that the reduction in chlorophyll concentrations is much less pronounced than the reduction in the P-loads (Fig. 1.6).



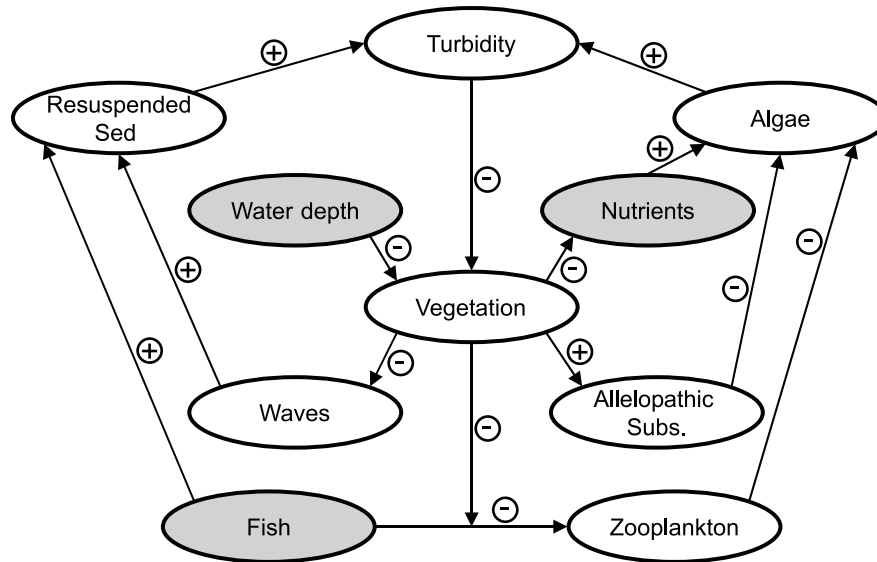
**Fig. 1.6.** Calculated trends in phosphate levels (left panel) and algal densities (right panel) measured in 1985 and 1992 (RIVM 1995)

### **Top-Down Control**

Daphnids are key organisms for maintaining the clear water state. As long as they are able to consume the algal production facilitated by the increased nutrient concentrations, the system will remain clear. However, anything that affects the performance of daphnids, either directly or indirectly, may induce a shift to the turbid state. The daphnid community is influenced by the rate of consumption of individuals by planktivorous fish, which in their turn are influenced through predation by piscivorous fish. The effect brought about by fish on phytoplankton dominance via zooplankton, is known as a trophic interaction or a trophic cascade, as the impact cascades down the trophic levels in the food chain (Scheffer 1998; Carpenter 1993). Top-down control is frequently confirmed in lakes by responses to biomanipulations and changes in plankton communities after fish immigrations or a fish dieoff (Vanni et al. 1990; Vanni and Layne 1997). On the other hand, investigations comparing lakes with different trophic conditions show a positive correlation of phosphorus not only with the phytoplankton biomass, but also with the biomass of the total zooplankton, the crustacean zooplankton, the fish populations, and with harvested fish. These studies support the bottom-up hypothesis (more available nutrients → more algae → more zooplankton → more planktivorous fish → more piscivorous fish) which is based on the idea that the biomass depends on the fertility of the habitat. Year-to-year comparisons within the same lake usually support the top-down hypothesis, whereas comparisons of different lakes tend to support the bottom-up hypothesis (Lampert and Sommer 1997).

However, it should be realised that top-down and bottom-up forces are two sides of the same coin and that they act complementary to each other. The extent to which each of these processes influences the aquatic food web may vary, depending on environmental conditions as well as human perturbations.

In several studies, food web models have been developed with the aim of acquiring more insight into the underlying mechanisms of eutrophication in lakes. The models have been utilised as a tool for the management of eutrophicated water bodies (Jørgensen 1986). The relations between nutrients and phytoplankton growth are quite complex in shallow eutrophicated water systems. Removing nutrient sources will not always lead to an improvement of the water quality in eutrophicated lakes and additional measures are usually needed. An improvement in the water quality of various shallow lakes was observed when combining nutrient reduction programmes with biomanipulation techniques (Moss et al. 1996a; Lathrop et al. 1996). Daphnid grazing has proven to be a crucial process in the top down control of phytoplankton biomass and the maintenance of the water clarity over a number of years, and has therefore been an important aspect in the biomanipulation of eutrophicated lakes over the last few decades (Meijer, 2000). Consequently, much is known about the biology of *Daphnia* and a large number of different models are available for the purpose of describing daphnid dynamics (Hallam et al. 1990; Scheffer et al. 1993).



**Fig. 1.7.** Main feed-back loops thought to be responsible for the existence of alternative equilibria in shallow lake ecosystems. The qualitative effect of each route in the diagram can be determined by multiplying the signs along the way. In this way it can be seen that both the vegetated and the turbid state are self-reinforcing. The shaded boxes are possible steering variables for lake management and the effects of measures can be determined in a similar way (Scheffer et al. 1993; Hosper 1997).

### Feedback Loops

The daphnid-algae relationship can be modelled with different types of models. For example, McCauley et al. (1988) and Scheffer (1998) used a simple predator-prey model; its dynamics are affected by factors such as the nutrient level and spatial and temporal heterogeneity. Simulation models for the dynamics of various size classes of daphnids feeding on various size classes of phytoplankton at limiting phosphorus concentrations and the responses of food webs to fish manipulations have also been developed (Carpenter and Kitchell 1993).

Daphnid populations are directly influenced by the availability of food (bottom-up) and by the presence of zooplanktivorous fish (top-down). However, these direct causal relationships are embedded within the freshwater ecosystem that comprises many components which encompass a large number of direct and indirect interrelations. These relations are influenced by biological variables as well as system characteristics, resulting in several positive and negative feedback loops. Scheffer et al. (1993) proposed a schematic representation for such feedbacks (Fig. 1.7). The presence of submerged vegetation is central in this scheme. Vegetation has a direct negative influence on algal growth, by competing for available nutrients and by the release of allelopathic substances. Indirect effects on algal development are offset by the positive effects of vegetation on daphnid populations, since vegetation offers daytime refuge to daphnids and ambush cover for piscivorous fish. By dampening wave action, the vegetation prohibits exces-

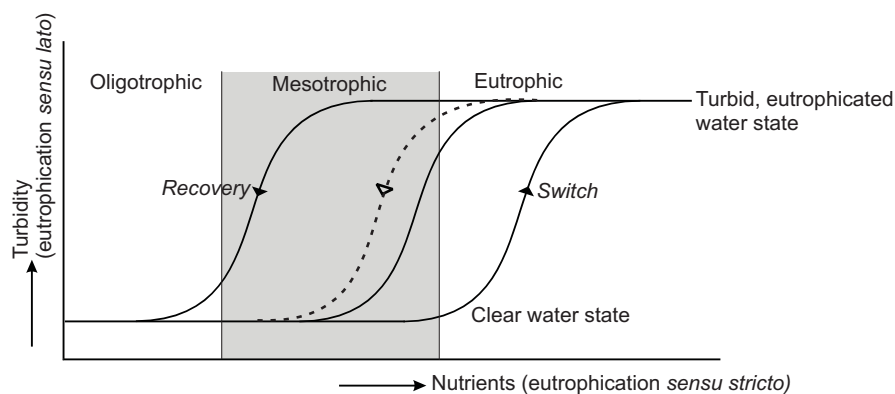


rous fish. By dampening wave action, the vegetation prohibits excessive resuspension of sediment which might inhibit its own growth.

### Hysteresis

Once a system is turbid, vegetation cannot persist and populations of daphnids and piscivorous fish (e.g. pike and perch) decline. The fish community in turbid waters is comprised mainly of benthivorous (benthos-eating) and planktivorous (zooplankton-eating) fish e.g. bream and roach. The abundant planktivorous fish control the zooplankton, resulting in low grazing of algae and increased recycling of phosphorus. Large numbers of benthivorous fish, if unhindered by vegetation, stir up the mud and thereby contribute to turbidity and phosphorus release (Hosper 1997; Scheffer 1998) and hamper the settlement of new submerged vegetation. These conditions are unfavourable to daphnids, resulting in dominance by less efficiently grazing copepods and rotifers in the zooplankton and prolific algal growth, often dominated by cyanobacteria which are considered to be an inferior food source for daphnids (Moss et al. 1991).

As a consequence, two alternative stable equilibria can occur over a range of nutrient concentrations in shallow lakes: a clear water state, characterised by the dominance of macrophytes, and a turbid water state, in which the phytoplankton is dominant (Scheffer et al. 1993). Below a concentration of ca. 25–50  $\mu\text{g}/\text{total P}$  and 250–500  $\mu\text{g}/\text{l total N}$ , a shallow lake is likely to be in a clear water state (Moss et al. 1996a). Above this concentration, the water will remain clear, unless the system is disturbed (Scheffer et al. 1993), which might initiate a rapid switch to the turbid state (Fig. 1.8). There is probably no upper limit above which a turbid state only can exist but, at higher nutrient concentrations, the clear water state becomes very unstable (Moss et al. 1996a).



**Fig. 1.8.** Hysteresis effect in the response of lake turbidity to changes in the nutrient status (adapted from Scheffer et al. 1993)

The presence of two alternative stable states, and the hysteresis that is observed when forcing the system from one stable state into the other, has important management implications, because the way in which the system responds to measures is very different from that of non-hysteretic systems (Hosper 1997; Scheffer 1998).

The turbid water state can be referred to as “eutrophicated water”. Figure 1.8 clearly shows that eutrophication problems can occur over a wide range of nutrient conditions suitable for non-eutrophicated clear waters. The model also indicates that restoration from a turbid, eutrophicated state back to a clear water state is not an easy reversion.

### Switches

Eutrophicated, turbid, shallow lakes can be resistant to nutrient reduction. The turbid and the clear water state are both hysteretic stable states, as changes in the nutrient concentration within a certain range will not affect the state these lakes are in. Only at certain threshold levels for nutrients do the systems show drastic changes (‘shifts’) in their algal biomass. Special events or actions (‘switches’) may trigger a shift from the one state to the other. Buffering mechanisms can prevent or promote switches between the two states for a broad range of nutrient concentrations (Table 1.1 and Table 1.2).

**Table 1.1.** Stable states, buffering mechanisms maintaining the stable states and switches to trigger a shift from a stable turbid state to a stable clear water state (forward switch) (adapted from Hosper 1997)

Factors contributing to stability of turbid water	Buffering mechanisms	Forward switches to ‘clear water’
Oscillatoria bloom	<ul style="list-style-type: none"> <li>– Resistant to low TP, low light and low temperature</li> <li>– Reduced edibility for <i>Daphnia</i> grazers</li> <li>– Bloom results in high pH, high sediment oxygen demand and thus high internal P loading, more blooms</li> </ul>	<ul style="list-style-type: none"> <li>– Prolonged snow-covered ice</li> <li>– Washout by winter flushing</li> <li>– Control P release by sediment removal, sediment treatment or ‘hard water’ flushing</li> </ul>
Phytoplankton bloom	<ul style="list-style-type: none"> <li>– Bloom results in turbid waters, low piscivores, high planktivores, low grazing, more blooms</li> </ul>	<ul style="list-style-type: none"> <li>– Lower water level in spring to promote submerged vegetation</li> <li>– Natural winter fish kills</li> <li>– Reduce planktivores and promote piscivores</li> </ul>
Non-algal turbidity	<ul style="list-style-type: none"> <li>– Wind-induced resuspension of sediments in plant-free lakes</li> <li>– Fish-induced resuspension of sediments by benthivores, unhindered by plants</li> </ul>	<ul style="list-style-type: none"> <li>– Reduce wind exposure of sediments or complete draw-down and drying of sediments</li> <li>– Reduce benthivores</li> </ul>

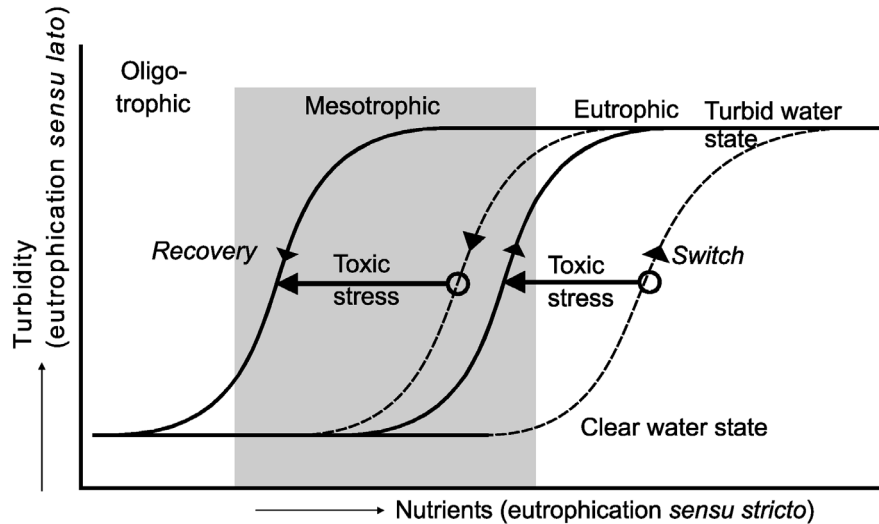
**Table 1.2.** Stable states, buffering mechanisms maintaining the stable states and switches to trigger a shift from a stable clear state to a stable turbid water state (reverse switch) (adapted from Hosper 1997)

Factors contributing to stability of clear water	Buffering mechanisms	Reverse switches to 'turbid water'
Benthic diatoms	<ul style="list-style-type: none"> <li>– Reduce susceptibility of lake sediments to wind-induced resuspension</li> <li>– Compete with phytoplankton for N,P</li> <li>– Promote N loss by denitrification</li> </ul>	<ul style="list-style-type: none"> <li>– Benthivore stocking</li> <li>– Storm events</li> </ul>
Submerged vegetation	<ul style="list-style-type: none"> <li>– Competes with phytoplankton for N,P</li> <li>– Promotes N loss by denitrification</li> <li>– Reduces susceptibility of lake sediments to wind-induced resuspension</li> <li>– Excretes substances allelopathic to phytoplankton</li> <li>– Promotes grazing of phytoplankton by providing refuge to Daphnia</li> <li>– Promotes phytoplankton grazing by providing refuge to pike and subsequent top-down control of planktivores</li> <li>– Reduces fish induced resuspension by hindering bottom feeding</li> </ul>	<ul style="list-style-type: none"> <li>– Mechanical destruction of vegetation</li> <li>– Chemicals toxic to vegetation</li> <li>– Macrophyte grazing by birds</li> <li>– Increase water level during spring</li> <li>– Benthivore stocking</li> <li>– Grass carp stocking</li> <li>– Chemicals toxic to Daphnia</li> <li>– Storm events</li> </ul>

### ***Disturbance of the Trophic Cascade Due to Toxic Stress***

In many shallow lakes in countries such as England, the Netherlands and Denmark, the shift from a clear water state towards a turbid state is thought to have taken place during the nineteen sixties and seventies. The challenge presented in the restoration of a lake is to reverse this shift, and recreate stable clear-water in that lake.

It is worthwhile considering the toxic state of eutrophicated waters, especially where biomanipulation has failed. Toxic stress can trigger a forward shift from a clean water state into a eutrophicated state, as suggested by Hurlbert (1975) and Stansfield et al. (1989), at lower nutrient (trophic) conditions, and may, on the contrary, hamper the recovery of eutrophicated waters back into clear water in response to nutrient reduction (see Fig. 1.9).



**Fig. 1.9.** Hysteresis effect in response of lake turbidity to changes in nutrient status (adopted from Scheffer et al. 1993), extended for the impact of toxic stress

Some evidence for reduced daphnid grazing effectiveness due to the presence of pesticides in the field situation is known from literature (see also Chap. 5). Poisoning of the cladoceran (viz. *Daphnia*) community might have caused a switch from dominance by submerged plants to phytoplankton dominance in the Norfolk Broads, a series of lakes, during the 1950s and 1960s. This allowed phytoplankton to take advantage of the increased nutrient loadings and to increase in number. The 1950s and 1960s were periods of liberal organochlorine pesticide use (Stansfield et al. 1989).

In sediment cores with residues of dieldrin and DDD, no remains of *Daphnia* were found. In addition, the phytoplankton related *Bosmina* rather than submerged macrophyte associated *Chydorus* were found in these cores.

The experimental studies reviewed in this book provide some more insight into and information on the hypothesis that toxic stress may contribute to the shifting of water bodies into eutrophied states, due to disturbances to the trophic cascade at the level of daphnid function.

Eutrophication Management and Ecotoxicology

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