

Continuity and change in environmental systems: the case of shallow lake ecosystems

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Abstract: Traditional ideas concerning environmental management tend to be based upon simple relationships between cause and effect. Such approaches make the design of environmental management strategies fairly straightforward: once the cause of a problem has been identified, it is necessary only to address the cause and/or help the system to recover through some sort of attempt at restoration. In the case of shallow lake eutrophication, research in the 1960s and 1970s identified phosphorus as the key control on the trophic state of a lake and, hence, recommended reductions in the supply of phosphorus to lakes as the necessary remedial measure. However, subsequent research has illustrated that such measures were not always successful. This article reviews the science of shallow lake eutrophication to demonstrate the role of ecosystem-specific biological and chemical interactions in conditioning the response of lakes to remedial measures and, hence, shows how new ideas of complexity help us to understand the behaviour of lake ecosystems so that we can develop alternative environmental management strategies.

Key words: biomanipulation, complexity theory, eutrophication, limnology, multiple stable states, phosphates, predator–prey dynamics, restoration.

I Introduction: approaches to environmental management

Wiman (1991) identifies three approaches to the concept of environmental change: nature benign, nature linear and nature nonlinear. Nature benign has its origins in classical ecological ideas, and is associated with strong negative feedbacks that serve to maintain a system in some sort of equilibrium – the environment is capable of absorbing the stresses applied to it. Nature nonlinear (which has different origins, notably in meteorology and the study of turbulence) argues that positive feedbacks

dominate environmental change – small events are amplified through positive feedback to create much larger events. The environment responds catastrophically and chaotically to environmental stress. In between these approaches is the nature linear view, which reconciles these ideas of continuity (nature benign) and change (nature nonlinear) by arguing that the environment does indeed respond to stress but that it does so in readily identifiable, explicable and often predictable ways. This view ties in with the classic Newtonian view of mechanics (Janstch, 1980), whereby human activity is thought to force a given environment in a particular direction; if that activity is stopped, the environment will relax back, perhaps with some help (i.e., the concept of restoration). The nature linear view has clearly dominated much thinking about environmental management. First, much thought about environmental change has assumed simple relationships between cause and effect. Classic examples of this include both climate change and ozone depletion. Climate change, for example, is often characterized by the term ‘global warming’, and both advocates (e.g., Hulme, 1999) and critics (e.g., Balling, 1992; Michaels, 1992; Bate and Morris, 1994) of the ‘global warming’ concept have placed much emphasis upon the statistical properties of temperature records and on proving or disproving that there has been a detectable secular temperature increase. Secondly, much ecological policy is now concerned with environmental restoration. While this is in itself a hotly contested concept, it is based upon the principle that we can rebuild those things we have learnt to value as a result of their loss. Once gone, appropriate human activity can return the environment to what it once was. Thirdly, and following on from the idea of restoration, there remains a tendency (despite the growth of concepts like the precautionary principle) to await the identification of environmental damage before action is undertaken. Although the possibility that climate change might be more spatially and temporally complex is increasingly being acknowledged (and the need to situate anthropogenic effects within the context of natural feedback processes is recognized), there remain some who argue it is better to wait to see how much global warming there is – following the implicitly modernist dictate (O’Riordan, 1981) that, should it become a serious issue, humans possess the requisite means to control and redress any changes.

The aim of this article is to illustrate the implications of complex ecosystem interactions for environmental management and, in doing so, to illustrate the need to move away from simple assumptions of cause–effect and of nature linear towards a more holistic form of environmental management based upon the recognition of complexity. The article does this through a consideration of shallow lake eutrophication – an environmental problem that has not only received considerable scientific attention but that has also seen a shift away from acceptance of simple cause–effect relationships based upon nutrient limitation towards a full acceptance of the implications of complex ecosystem dynamics. The article begins by considering the traditional management approach of external nutrient loading. It then reviews the role of biotic components in ecosystem dynamics and systematics, citing the case of nutrient loading as an example of characteristic lake behaviour. The article concludes by demonstrating the importance for environmental management of thinking through the implications of complex lake behaviour, showing how such behaviour causes us to question the simple assumption that, once we have degraded an environment, we can readily restore it to some sort of natural state. In such a way, this links into wider geographical thinking about the nature of interactions between humans and their environment (e.g., Harvey, 1996).

II The traditional view of shallow lake eutrophication: a nature 'linear' paradigm

The traditional definition of eutrophication is that it involves the enrichment of nutrients (notably N and P) above natural levels (Reuss, 1970; Keeney, 1973; Harper, 1992), resulting in an increase in the net primary productivity of ecosystems and an associated loss of ecosystem services, such as the decline of water quality. This enrichment has to be coupled to the intrinsic characteristics (e.g., morphometry, geographical location, fluvial links) of aquatic ecosystems to determine the speed, degree and types of eutrophication. For instance, eutrophication characteristics in lotic systems (e.g., rivers) tend to be very different from lentic systems (e.g., lakes), owing to differences in environmental and ecological conditions. Amongst water bodies in general, temperate freshwater lakes (especially those of significant conservation and amenity value) have been the focus of eutrophication investigation (Schindler, 1974). Compared to deep-water lakes, shallow lakes tend to be more prone to eutrophication as they have a smaller dilution capacity, and provide more opportunity for contact between the euphotic zone and the hypolimnion, where nutrients are stored (Holdren and Armstrong, 1980; Lennox, 1984). This may be because the euphotic zone extends to the bed, or because the water is well mixed, so allowing a generally higher nutrient input from the sediment.

Nitrogen and carbon are associated with natural biological mechanisms that can rectify any deficiency (Schindler, 1977). Thus, phosphorus is most commonly in shortest supply relative to biological demand, and is thus widely recognized as the major factor that limits primary productivity in freshwater (Schindler, 1978; Reynolds, 1984). Nitrogen deficiency still matters as, whilst it may not affect primary production rates, it can affect primary production types (e.g., competitive growth of nitrogen-fixing blue-green algae). Phosphorus levels in lentic systems tend to increase with age. Unlike nitrogen and carbon, which may leave the lake ecosystems via decay and decomposition (e.g., respiration and denitrification), phosphorus has no natural gaseous state. Thus, external phosphorus loading may be enhanced by human activity (Schindler, 1974; 1977), may substantially increase eutrophication above natural rates and may leave a legacy of high internal phosphorus loading that may serve to maintain high levels of eutrophication even if external loading is addressed (e.g., Bengtsson, 1978; Nürnberg and Peters, 1984).

Given the identification of phosphorus as a critical limiting nutrient, much emphasis was placed upon the reduction of phosphorus supply to lakes whose trophic levels had increased to unacceptable levels. Figure 1 shows the general model upon which the restoration of eutrophic lakes is based (Cullen and Forsberg, 1988). By reducing the level of phosphorus sufficiently, it is hypothesized that the growth of phytoplankton will be limited and there will hence be the desired change in trophic level. However, this simple linear view suffers in two senses. First, there are many examples where reducing external phosphorus loading does not result in lake recovery (e.g., Larsen *et al.*, 1981; Welch *et al.*, 1986) and the system remains unacceptably eutrophic. Cullen and Forsberg (1988) note that in only 44% of cases did a eutrophic ecosystem revert to a mesotrophic system in response to a reduction in nutrient loading. Secondly, even if the level of eutrophication is reduced, the effects of eutrophication upon trophic structure mean that significant time may be required before the ecosystem recovers to its previous state (e.g., Björk, 1972; Golterman, 1977). Thus, as eutrophication proceeds,

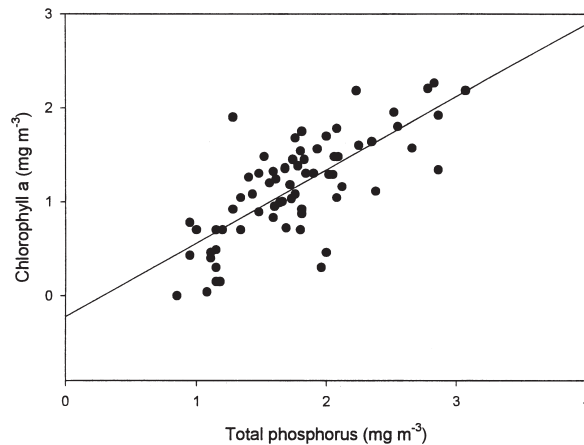


Figure 1 Simple linear log-log relationship between chlorophyll a and total phosphorus in the summer

characteristic symptoms of overfertilization occur: macrophytes tend to be replaced by microscopic phytoplankton, with a decrease in water clarity. 'Nuisance' algal blooms are amongst the most severe symptoms of eutrophication (Shapiro, 1973): these can eradicate macrophytes, can kill animals (e.g., fish, invertebrates) and can cause illness in humans. This is the basic limitation of the linear view: the reasons why we want to reduce trophic level and eutrophication rates (e.g., nuisance algae) are themselves indicative that the trophic structure of the lake has changed in a manner that may affect the restoration process. Thus, the 'bottom-up' view that nutrient limitation controls organisms at the lower (photosynthetic) levels of food webs and hence determines the nature and production of those in the intermediate and upper levels (Moss *et al.*, 1996a) has been combined with a recognition of the role of the biotic community in lake ecosystems (Shapiro, 1980), and attempts to manipulate food chains at higher levels via top-down control. This is often labelled biomanipulation and involves a manipulation of organisms at the upper (predator) levels of food webs to control the intermediate and lower (photosynthetic) levels.

However, even attempts at combined bottom-up and top-down control represent a linear conceptualization of the system, and the results of combined nutrient reduction and biomanipulation experiments have not necessarily produced reliable and consistent responses. The reason for this is that interacting ecological processes involve feedback mechanisms and time lags that may have profound effects upon resource storage, cycling and availability, so decreasing the potentially expected effect and power of restoration. Thus, the aim of the next section is to review the lake ecology of eutrophication through a consideration of trophic-level interactions in eutrophic shallow lakes and their functioning in regulating and maintaining eutrophication and oligotrophication (i.e., the process that is a reverse of eutrophication).

III Biotic components and their role in eutrophication

Figure 2 demonstrates the basic links between the biotic components (macrophytes, phytoplankton, zooplankton, planktivorous fish and piscivorous fish). Each of these links represents a generalization of both the form and function of typical interactions: it is common for the nature of interactions not only to be species specific but also dependent upon the state of the ecosystem (levels of inter- and intraspecies competition, abundance of food, etc.).

1 Phytoplankton-zooplankton links

The interaction between phytoplankton and zooplankton often plays an important role in determining whether a water body is eutrophic or not, and this has been a focal point in eutrophication management, in particular in phytoplankton modelling. In a biological sense, the two plankton are reciprocally related: phytoplankton biomass is limited by the grazing pressure exerted by its predator filter-feeding zooplankton (Shapiro, 1979). In the simplest terms, under an exploitation limit, an increase in zooplankton biomass can efficiently control and reduce phytoplankton biomass and, correspondingly, reduce trophic level and increase water transparency. However, as is common to many predator-prey cycles, the relationship between zooplankton and phytoplankton can be nonlinear (Bergquist and Carpenter, 1986). With respect to species composition, variations of the type and abundance of zooplankton are of major importance for governing the species composition of phytoplankton, and so determining eutrophication state (Shapiro, 1980). The total biomass of phytoplankton may not decrease correspondingly with an increase in zooplankton biomass, for example, but may change species abundance, size distribution and composition (McCauley and Kalff, 1981). This may be due to the fact that some species will be grazed whilst species that are not grazed are favoured or competitively released (Porter, 1977). Another plausible reason is associated with the availability of alternative prey or food in lake ecosystems. Zooplankton may not always be herbivorous and microbes (e.g., bacteria), and suspended detritus may be an alternative food source (Scheffer, 1990). Moreover, with respect to the functional response of consumers to prey, the efficiency with which the predator consumes the prey should decline as the prey density

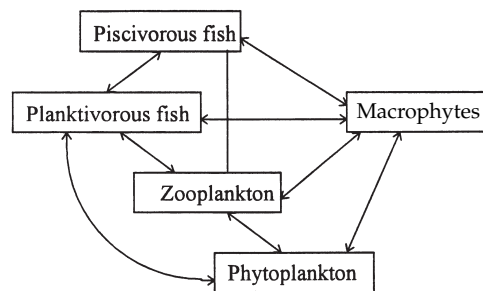


Figure 2 Basic links between some important components in a eutrophic lake (see text for details)

increases. Importantly, the choice of prey by a predator may be selective between different species, as well as between individuals of the same species.

Below the exploitation limit, there are possibilities that phytoplankton and zooplankton are mutually beneficial to each other, but not inversely related. Zooplankton (e.g., *Daphnia*), which can excrete substantial quantities of nutrient into the water column (Wright and Shapiro, 1984), might increase nutrient availability to phytoplankton and hence stimulate their growth and abundance (Wynne and Gophen, 1981). Thus, whilst there may in some circumstances be a sensitive balance between phytoplankton and zooplankton levels (dominated by negative feedback), changes in phytoplankton or zooplankton populations of sufficient magnitude may cause indirect feedbacks that eventually set into chain positive feedback and a major and high-magnitude change in ecosystem behaviour. Indeed, severe phytoplankton blooms in eutrophic lakes commonly involve algal species that cannot be efficiently grazed by zooplankton. This is related to the size selectivity of herbivory: filter-feeding zooplankton cannot graze upon all algal cells, only those within a limited size range (Dawidowicz, 1990). Grazing rates per zooplankton increase geometrically with zooplankton body size (Burns and Rigler, 1967). Moreover, the ineffectiveness of zooplankton grazing capability may be associated with their prey; such algae may have a form which is difficult to handle, have a large cell or colony size or be toxic to animals (Lampert, 1981a; 1981b). Concentrations of filamentous blue-green algae are a good example, as associated blooms may represent a deterioration in food quality and thus limit the growth of zooplankton (Arnold, 1971; Breukers *et al.*, 1997). This may in turn lead to increased mortality of zooplankton by fish predation. The occurrence of blooms may also be associated with ecological feedbacks that lead to macrophyte loss which serves to help to increase phytoplankton levels to a state where other factors (e.g., nutrient availability) become limiting. Indirect effects as a result of changes in water chemistry associated with abundant phytoplankton may also promote uncoupling of the zooplankton grazing on phytoplankton. High pH in algal-dominated eutrophic waters has been shown to influence the survival and reproduction of zooplankton and to suppress the zooplankton biomass (O'Brien and deNoyelles, 1972). When over-exploitation of phytoplankton occurs, this may lead to a collapse of the total zooplankton population as a result of resource competition associated with food depletion (Scheffer, 1998).

2 Phytoplankton–macrophyte links

In lake eutrophication, phytoplankton and macrophytes represent two contrasting plant groups which dominate in turbid and clear-water states, respectively, although under some circumstances they may coexist. Because of reduced resuspension, water in lakes tends to be less turbid if there is a high coverage or abundance of aquatic macrophytes (Jackson and Starrett, 1959; Canfield *et al.*, 1984; Dieter, 1990; Jeppesen *et al.*, 1990). The two plant groups interact principally in terms of competition for available resources, particularly light and nutrients in a complex manner. When phytoplankton concentration is too high, phytoplankton may increase water turbidity and prevent light penetration through the water column. At a critical threshold, lower-growing macrophytes may be shaded out in response to low levels of light reaching the bed

(Jupp and Spence, 1977; Phillips *et al.*, 1978). Importantly, the effects of light limitation may vary depending on the dominance of various algal groups. Certain algae, such as periphyton (i.e., algae attached to plants), may pose as great a competitive threat to macrophytes as phytoplankton algae (Phillips *et al.*, 1978; Sand-Jensen and Søndergaard, 1981), as they may cover the surfaces of macrophytes and compete for light and nutrients. However, this light limitation on macrophytes may not occur if phytoplankton assemblage is dominated by benthic algae, which form a soft crust on top of the sediment surface.

Chemical defences (e.g., allelopathy) may also affect shifts in plant dominance. Allelopathy involves the production of inhibiting compounds by macrophytes that may limit algal growth (Szczepanski, 1977; Wium-Anderson *et al.*, 1982; Hootsmans and Blindow, 1993). When phytoplankton composition changes to being blue-green algae dominated, toxin produced by the algae may act in a manner that limits macrophyte re-establishment and growth. Macrophyte stands (which reduce water movement and turbulence) may provide a calm-water condition that leads to sinking of immobile phytoplankton (James and Barko, 1990). Macrophyte and phytoplankton may also interact indirectly by influencing habitat availability for phytoplankton grazers. Predation refuges provided by macrophytes for zooplankton may enhance the grazing pressure upon phytoplankton. However, macrophytes may benefit phytoplankton growth as nutrients taken up by macrophytes from sediments may be released into the water column during senescence and decay and thus become available for phytoplankton growth (Carpenter, 1980; Barko and Smart, 1981). Thus, the macrophyte–phytoplankton link is critical to the way in which nutrients interact with phytoplankton, both because of the direct effects of macrophytes upon phytoplankton and because of the way in which macrophytes condition other predator–prey interactions.

3 Zooplankton–macrophyte links

The major link between macrophytes and zooplankton is that macrophyte stands (e.g., water lily) can act as a refuge for zooplankton against fish predation (Timms and Moss, 1984; Phillips *et al.*, 1996). Refuge effectiveness may depend not just on plant species but also on macrophyte growth rates, densities, coverage, fish species and density, and time of the day. Grazing on phytoplankton in open water adjacent to the plant stands is greatest at night, suggesting that the large zooplankton (e.g., cladocerans) use the macrophytes as a daytime refuge to escape predation by fish (Scheffer, 1998). This in turn suggests that the refuge effect depends critically on plant density: sparse stands are less protective (Schriver *et al.*, 1995). In practice, macrophyte–zooplankton–fish interactions are more complex than this. For instance, if fish density is too high, dense macrophytes may not prevent zooplankton populations from collapsing (Schriver *et al.*, 1995). Similarly, macrophytes may provide refugia for juvenile planktivorous fish against predation by larger fish (Scheffer, 1998), which can lead to poor protection for zooplankton as fish enter dense macrophyte stands and suppress zooplankton populations (Kairesalo *et al.*, in press). Moreover, similar to the allelopathic effects associated with phytoplankton, macrophytes may have a repellent effect upon certain zooplankton (e.g., *Daphnia*) due to the excretion of inhibiting substances (Pennak, 1973).

4 Fish–phytoplankton links

The composition of fish species is an important factor in determining the relationship between fish and phytoplankton. In terms of feeding preference, piscivores (i.e., fish-eating fish, for example, pike) and zooplanktivores (i.e., zooplankton-eating fish, for example, bream and roach) function differently in lake ecosystems. Piscivorous fish prey upon zooplanktivorous fish, and this may decrease the predation pressure of zooplanktivorous fish on zooplankton and hence decrease phytoplankton biomass as a result of the presence of more zooplankton. In contrast, zooplanktivorous fish may increase phytoplankton biomass. An increase in zooplanktivores may lead to a decrease in zooplankton, so reducing predation pressure upon phytoplankton. This results in an increase in phytoplankton population. Most importantly, both piscivorous and zooplanktivorous fish may have a strong impact on phytoplankton community structure, independent of their effects upon zooplankton grazing rates (Vanni and Findlay, 1990). This may be related to the wide range of size class of alternative prey and thus selective feeding. This can be demonstrated, for example, in the way the predation preference of fish alters invertebrate assemblages (Sih *et al.*, 1985; Thorp, 1986). As fish selectively feed on and reduce the densities of larger prey, densities of other smaller prey may be enhanced (Crowder and Cooper, 1982). The presence of macroinvertebrate predators such as *Chaoborus* (e.g., gnats) and *Neomysis* (e.g., shrimps), which are common in lakes, would alter the relationship between zooplanktivores and zooplankton by acting as alternative zooplankton predators to fish (Benndorf, 1990). Moreover, the feeding habits of fish communities may be dependent upon their species, age structure and size. Young bream are zooplanktivores, whilst adult bream are piscivores. Some fish species may have direct predatory effects upon phytoplankton. Roach, for example, have also been found to consume and utilize algae when animal food is scarce (Persson, 1983).

As regards feeding behaviour, bioturbation (e.g., due to the foraging activities of certain fish) – in particular by benthivores such as bream – affects phytoplankton by disturbing bottom sediments, so transforming and translocating phosphorus and altering nutrient cycling rates (Lamarra, 1975). Fish may render nutrients more available, not only by direct excretion and egestion but also as a result of nutrient mobilization from fish death and decomposition (e.g., Shapiro *et al.*, 1975). High phytoplankton biomass may act indirectly on fish by reducing visibility and thus the feeding efficiency of fish (Moss *et al.*, 1991). This may have profound consequences for fish communities, both indirectly through changes in the abundance and diversity of available invertebrate prey and also directly through a reduction in refuges and spawning sites (or in some cases food) (Willemsen, 1980; De Nie, 1987).

5 Fish–macrophyte links

An increase in macrophyte density is known to increase the abundance of fish. The beneficial effects are attributable to a number of mechanisms. Most likely, these are related to the fact that macrophytes create very distinct aquatic microclimates (e.g., by modifying habitat structure) and this can affect the distribution of other organisms (Lodge *et al.*, 1988). The clear-water condition created by macrophytes provides fish with a favourable ground for spawning and foraging (De Nie, 1987) as it minimizes suffocation. Macrophyte beds that provide favourable conditions for piscivorous fish

may subsequently limit the number and distribution of zooplanktivorous fish (Werner *et al.*, 1983; Grimm, 1989). Hence, in clear-water lakes where macrophytes are present, there is a high piscivore:zooplanktivore ratio (Grimm, 1983; Kipling, 1983).

The presence of macrophytes may also be important for the structuring of fish communities in eutrophic turbid waters (Lammens, 1989). In turbid waters, where macrophytes are sparse, cyprinids, such as bream (*Abramis brama*), roach (*Rutilus rutilus*) and carp (*Cyprinus carpio*), are dominant. In benthivorous fish-dominated lakes, fish-induced turbidity (i.e., bioturbation), and thus the low underwater light, may affect macrophyte growth and development. In some lakes, even where underwater light conditions are relatively good, macrophyte development may be prevented (Ten Winkel and Meulemans, 1984). This may be the result of the physical damage caused by fish during food-searching activities. However, it has to be recognized that macrophytes provide a habitat and food source for fish but also, at high densities, a hindrance to their feeding activity. It has been shown that dense macrophyte stands may affect the foraging and feeding efficiency of benthivorous fish (Diehl, 1988; Scheffer, 1998). Hence, the positive relationship between macrophytes and fish is dependent on macrophyte density and fish predation and production. Furthermore, some fish species may switch to alternative prey, in particular when the environment changes. Rudd (*Scardinius erythrophthalmus*) and roach (*Rutilus rutilus*) may utilize macrophytes as food (Andersson *et al.*, 1988). Sometimes, indirect effects can be important. With respect to the grazing ability of macroinvertebrates (such as snails) on feeding macrophytes (Bronmark, 1985; Lodge, 1986), fish predation on these grazers may indirectly control macrophyte abundance.

6 Implications of these links

The above sections provide an introduction to the inter-relationships amongst biotic components but do not provide a complete picture of the totality of lake ecosystems. The interconnectivity amongst all the components is obviously much more complex and interactive than this, and the full range of interactions between the variables (such as the age structure and body size of the biotic community; size-specific and food-specific selectivity during predation; omnivory; alternative predator; alternative prey; indirect competition; additive and nonadditive effects of different predators; behavioural variability; and spatial and temporal heterogeneity, to name but a few) will be highly lake specific. The generation of general rules may thus be difficult (e.g., Sih *et al.*, 1985; Knisely and Geller, 1986; Van Buskirk, 1988; Bern, 1990).

Inherent variability in a lake ecosystem affects not only the structure and abundance of one trophic level, but may also transfer or propagate directly and indirectly to other components and trophic levels in the system. The simple linear inverse predator-prey interaction may not be achieved hierarchically at every successive trophic level. Direct extrapolation of observations in the laboratory to the field should also be taken into account as certain processes, such as allelopathy, are only evident in laboratory studies and have not been observed in field observations (Forsberg *et al.*, 1990).

The last part of this review aims to demonstrate the difficulty of extrapolating the specific findings of a particular laboratory study or field case to a general model without careful consideration of exactly what it is possible to generalize about. Simple

recommendations (e.g., remove planktivorous fish and reintroduce piscivorous fish) are unlikely to be successful (e.g., Meijer *et al.*, 1994) unless careful investigation is given into the exact structure of the ecological system under investigation, as well as the possibility that intermittent external events (e.g., a drought or a storm) may induce positive feedbacks that switch the system back to a higher trophic level. The next section discusses the ways in which researchers have attempted to produce generalizations that could be applied to shallow lakes.

IV Integration of biotic interactions with nutrient perspectives in order to understand eutrophication

1 Food web properties

In biological terms, connectivity between components of the food web results in feedbacks (both positive and negative) which will be conditioned by, and themselves condition, the environmental characteristics of a given lake ecosystem. The dominance of either positive or negative feedbacks determines the ecosystem structure and functioning and affects eutrophication. An important consequence of hierarchical organization in a trophic structure is that as components are combined to produce larger functional wholes, new properties emerge that may not have been present or evident at the level below (Forrester, 1976). What is observed in a particular lake is a product of the linkages between components in that lake: i.e., it is emergent or 'the whole is more than the sum of its parts'. This represents a real challenge for eutrophication research, as an 'emergent property' of an ecosystem may not be predicted from a study of components that are isolated or decoupled from the whole system (Forrester, 1976). This may make every eutrophic lake ecosystem unique in its response to the same restoration tool. For example, some features of predator-prey interactions (such as the particular patterns of behaviour in response to a specific predator) may only be obvious when the two species are observed together (Salt, 1979). Many other biological systems on different scales, such as population biology and landscape ecology, also exhibit emergent behaviour. All these suggest that a systems view of lake eutrophication may help to understand lake dynamics, provided those systems are defined openly, both in terms of what we think we know about the behaviour of a particular lake and what we allow to be incorporated into our analysis. This section reviews the reasons and essentials of a systems view – an increasingly recognized part of eutrophication research.

Central to the systems approach to eutrophication is the recognition that nutrient control alone may not be practically feasible, partly due to the resistance (i.e., capacity to withstand a disturbance) of the food web to enforced changes (Gulati *et al.*, 1990; Van der Vlugt *et al.*, 1992) which can prevent a eutrophic lake from recovering (Janse, 1997). In terms of eutrophication, lake ecosystems may show a resistance to change even when nutrient loading is reduced, and improvements to water quality may only begin once a critical threshold or time period is passed. In many cases, homeostasis (i.e., the maintenance of an ecosystem by self-adjusting mechanisms to achieve a relatively constant state of internal balance, under ever-changing conditions) in the biological structure (Hosper, 1989; Hosper and Jagtman, 1990), which is the direct result of the net

interactions of populations, has caused lake restoration to be ineffective, even with bio-manipulation. Since many of the organisms (both vertebrate predators (e.g., fish) and invertebrate predators (e.g., *Chaoborus*) which are involved in indirect and feedback mechanisms) have generation times spreading over several years, a top-down manipulated food web will only reach a new steady state after a period of several years or even a decade (Benndorf, 1990).

The system is further complicated by interactions between biotic and abiotic components through feedback mechanisms (de Bernardi, 1985): changes in one component will induce corresponding changes in others. For example, the feeding strategies of a particular fish species may maintain a turbid state by suspending the bottom sediment which, in turn, results in a competitive advantage for that species, so resisting the restoration of water quality (Cazemier, 1982; Lammens, 1986; Hosper, 1989; Hosper and Jagtman, 1990). Virtually every top-down impact (i.e., every change in predation strength) automatically causes feedback responses at the bottom-up level (Kerfoot and Sih, 1987; Carpenter, 1988; Benndorf, 1990). Increased predation intensity of zooplanktivorous fish by piscivorous fish, for instance, can improve the food resources of other zooplanktivorous fish which, consequently, grow faster to reach a critical body size above which they switch to food resources other than zooplankton. This long-term adjustment process can result in surprising feedback effects: after an initial success, the ecosystem may begin to change due to longer-term biological adjustments, so eliminating the initial success.

2 Alternative stable states

Theoretically, more than one equilibrium in ecosystems has been shown to exist (Sutherland, 1974; May, 1977; 1981), and May (1977) suggested how the gradual change of a parameter can lead to a sudden shift in the stable state of a system. Further, discontinuous response in a simple mathematical model of a nutrient-limited algae–fish ecosystem has been demonstrated (Bondi, 1985). All these theories, with observations of the presence of both clear and turbid water states in eutrophic lakes, have to the introduction of the concept of ‘alternative stable states’ (Figure 3) (Balls *et al.*, 1989; Moss, 1989; Scheffer, 1989).

3 Negative feedbacks and the maintenance of clear or turbid water states

Negative feedbacks, by definition, are the mechanisms that act to counter the direction of initial change in a variable (Roberts, 1978). Negative feedbacks are important for the regulation of many processes in nature. In lakes, they are essential to maintaining a lake in a given state (e.g., clear or turbid), normally involving mechanisms that are specific to that state (Timms and Moss, 1984; Hosper, 1989; Scheffer, 1989). Thus, both the clear and turbid states in shallow lakes represent strongly contrasting community states (Figure 3).

Figure 4 shows one representation of the links shown in Figure 2. Negative feedbacks could maintain a noneutrophic lake in a clear-water state and thus prevent the system from becoming eutrophic and turbid. In comparison to algal abundance in turbid water, the clear-water state in shallow lakes is usually associated with aquatic macrophytes.

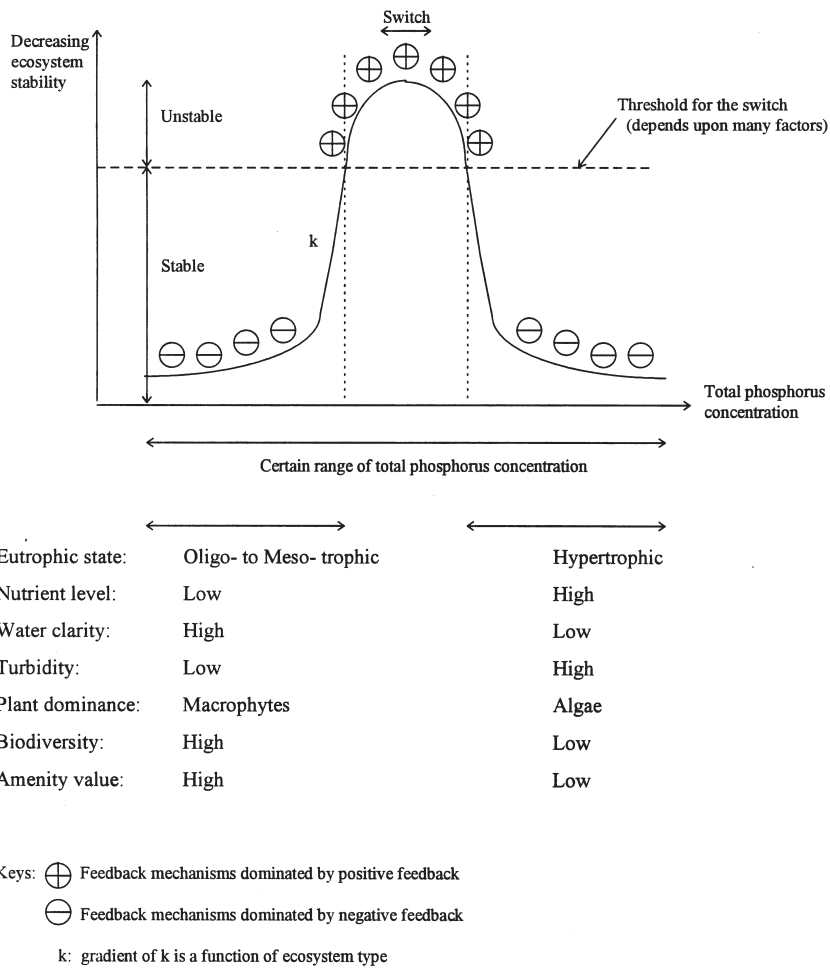


Figure 3 The hypothesized model of alternative stable states in shallow lakes

Source: Modified from Scheffer, 1989

Good underwater light is the key factor for the establishment and maintenance of aquatic macrophytes, and thus their dominance (Phillips *et al.*, 1978; Chambers and Kalff, 1985). The feedbacks that improve light accessibility for macrophytes are therefore important in self-sustaining the clear-water state. Primarily, macrophytes physically reduce water movement and velocity, and thus help to prevent sediment resuspension and water turbidity and the release of nutrients from sediment (Lohammar, 1966; Schiemer and Prosser, 1976), enhancing deposition and increasing water clarity. Thus, macrophytes may provide a firm, structured sediment suitable for the germination and support of plant propagules. Light accessibility may be improved by limiting phytoplankton biomass. Importantly, macrophytes themselves can reduce phytoplankton biomass by means of nutrient limitation (Stephen *et al.*, 1998), by creating daytime refuges for zooplankton from predation of zooplanktivorous fish

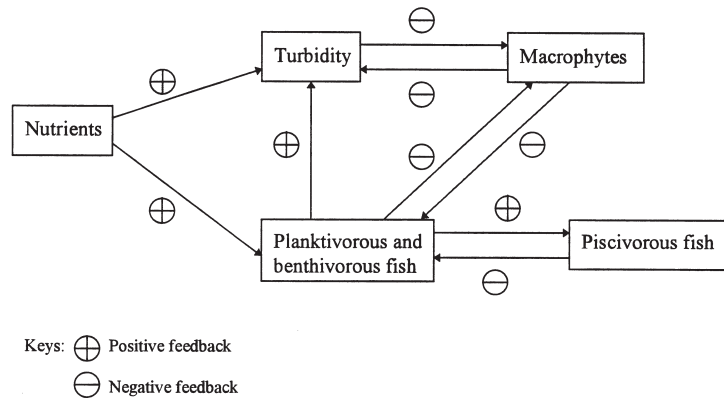


Figure 4 Positive and negative feedbacks in shallow lakes
Source: Scheffer, 1990

(Timms and Moss, 1984; Tuzen and Mason, 1996), by allelopathic reactions (Vermaat *et al.*, 1990), and by reducing wind-induced resuspension by stabilizing the sediment (Van Donk *et al.*, 1993). Also, macrophytes may oxidize the surficial sediment to reduce nutrient release across the sediment–water interface, as compared to greater release rates under anoxic conditions (Carpenter *et al.*, 1983; Meijer *et al.*, 1990; Van Donk *et al.*, 1990). All these mechanisms contribute to the self-stabilizing property of high water clarity in shallow lakes.

Negative feedback mechanisms have also been noted for the turbid state, in which phytoplankton are abundant and dominant. Most importantly, high phytoplankton density decreases the availability of both light and carbon dioxide, which gives them a competitive advantage over macrophytes (Moss, 1990). Some algal species, in particular blue-green algae, may release compounds that are toxic to macrophytes (Van Vierssen and Prins, 1985). The poor edibility of blue-green algae may reduce the grazing pressure of zooplankton (Gulati *et al.*, 1990). For some phytoplankton, their nutrient utilization efficiency may increase in response to turbid environments, so that they can produce the same biomass with fewer nutrients (Van Liere and Janse, 1992). A lack of shelter provided by macrophytes for zooplankton in turbid water exposes them to fish predation and results in a low grazing pressure upon phytoplankton; thus zooplankton are grazed by fish to densities that are insufficient to limit phytoplankton biomass, so sustaining water turbidity. The unprotected sediment may be frequently resuspended by wave action and by fish searching for food, and large amounts of suspended material in the water column not only reduce the filtering efficiency of zooplankton but also light availability (Hanson and Butler, 1990; Van Donk *et al.*, 1990). The turbid water creates a poor underwater light condition, and thus impedes the return of macrophytes (Van Dijk and Van Donk, 1991). The unprotected, unconsolidated sediment may also prevent re-establishment of macrophytes (Chesnut and Barman, 1974; Schiemer and Prosser, 1976). The turbid state may be maintained by nutrient addition of fish through mortality (Threlkeld, 1988), and nutrient regeneration by living fish (Vanni and Findlay, 1990) and zooplankton (den Dude and Gulati, 1988). Hence, all these mechanisms may maintain a eutrophic lake in its turbid state.

4 Positive feedbacks and the shifts between clear and turbid water states

Positive feedbacks involve amplification of a given factor, and result in a change from one state to another. Process rate increases as a state variable becomes larger, driving the system faster and faster and forcing the system away from an equilibrium position such that an exponential change is often produced. This may be labelled 'homeostasis breakdown'.

Positive feedbacks may operate to shift primary production from macrophyte-dominated clear water to phytoplankton-dominated turbid water in shallow eutrophic lakes (Figure 4) (e.g., Stone and Weisburd, 1992). The clear-to-turbid shift is triggered only if a disturbance is large enough to over-ride the self-stabilizing capacity (i.e., the net effect of negative feedbacks) of the aquatic system. A high nutrient loading is probably the ultimate cause of a collapse of the macrophyte-dominated state (Wetzel and Hough, 1973), mostly because of shading and carbon dioxide competition arising from an excessive proliferation of phytoplankton which outcompete macrophytes (Phillips *et al.*, 1978; Hosper and Jagtman, 1990). Such intrinsic biological characteristics as the short life-cycle and high surface:volume ratios of phytoplankton may also give them an advantage in resource competition as compared with macrophytes. This results in rapid change to high turbidity. At moderately high nutrient levels, such a shift of states may not occur as negative feedbacks are sufficient to prevent the system reaching a critical threshold.

Introducing and enhancing the positive feedback mechanisms that might shift the turbid water to a clear-water state are difficult and unpredictable. Drastic measures may be required. Attempts to restore eutrophic ecosystems have been made through nutrient control and biomanipulation. It is recognized that only a severe reduction (80%) of nutrient levels may result in a switch to clear water. Biomanipulation recognizes the linkages and complex interactions amongst various biotic components and involves manipulation of secondary or tertiary aquatic producers to cause changes to the aquatic community structure and to productivity at lower levels (Gophen, 1990). This may involve the artificial removal of zooplanktivorous fish (Shapiro and Wright, 1984; Benndorf, 1987; Van Donk *et al.*, 1989; Meijer *et al.*, 1994), the stocking of piscivorous fish (Shapiro and Wright, 1984; Benndorf *et al.*, 1988; Prejs *et al.*, 1994) or the provision of refuges for the zooplankters against predators (Irvine *et al.*, 1990; Moss, 1989; 1990). Removal of benthivorous fish (e.g., bream) usually leads to a dramatic increase in underwater light and thus improved growth conditions for macrophytes (Hosper and Jagtman, 1990). Significant drawdown of lakes to consolidate the loose sediments and thus to promote the growth of macrophytes is also suggested (Greening and Doyon, 1990). Another mechanism is based upon the trophic cascade effect that results from removal of planktivorous fish, and which allows populations of large-bodied zooplankters to peak and graze down the algal biomass, causing clear water (Carpenter, 1988). Other triggers may be responsible for such a shift, for example, varying water levels (Edberg, 1980), setting up artificial habitats (e.g., bundles of brushwood, polypropylene string plants or suspended netting) to increase the density of filter-feeding *Daphnia* (Moss, 1989; Scheffer *et al.*, 1993), or increasing the number and thus piscivorous activity of fish-eating birds, such as cormorants (Leah *et al.*, 1980).

However, the act of maintaining the system in a given state may not be neutral but may make the system more sensitive to future fluctuations. Similarly, other processes

may determine the sensitivity of the system to positive feedbacks. For instance, warm water in summer holds less dissolved oxygen and may discourage fish growth, resulting in a positive effect on macrophytes. During winter, sediment resuspension (because of wave action and erosion) will affect light conditions and therefore have a negative impact upon macrophytes (Karlsson *et al.*, 1976). Anthropogenic factors may also have an important role in inducing positive feedback. A reduction in the grazing of planktivores by zooplankton (e.g., *Cladocera*) in the presence of toxic substances may be responsible for the switch from a clear to turbid water (Stansfield *et al.*, 1989): insecticides and pesticides (e.g., organochlorines) can have a negative effect on the growth of zooplankton (Gaufin *et al.*, 1965; Hurlbert, 1975). Increased salinity, for example due to the effects of a change in tidal behaviour upon a freshwater lake, may be another trigger, as Daphnids are tolerable only up to 3–5 ppt salinity (Leah *et al.*, 1978).

What emerges from this is an important point: both small fluctuations and large fluctuations generated from outside the system may result in positive feedback – if the system is in the right state at the time they occur. For instance, chance events (such as bad weather) may trigger a shift to a phytoplankton-dominated state (Stansfield, 1995). In practice, the positive feedback mechanisms that are responsible for shifting the turbid water to a clear-water state may be difficult to identify with confidence, and this explains why attempts at biomanipulation have often produced surprising and conflicting results (e.g., Meijer *et al.*, 1994).

5 Links to nutrient loading

The existence of two alternative stable equilibria may be nutrient dependent. It has been shown that there exist two types of lakes (i.e., a phytoplankton-dominant turbid state and a clear state in which aquatic vegetation is abundant) at similar phosphorus concentrations (Jeppesen *et al.*, 1991). Specifically, it is suggested that two alternative stable equilibria may exist only over a certain range of nutrient concentrations, typically from $25 \mu\text{g P l}^{-1}$ to several mg P l^{-1} (Figure 3). Under oligotrophic conditions ($< 25 \text{mg P l}^{-1}$), alternative states have not been observed: the clear-water state represents the only stable equilibrium. At very high nutrient levels, the clear-water state is usually absent. Thus, the hypothesis of alternative stable states may be applicable only to a certain range of nutrient concentrations. This emphasizes the point that, unlike the continuous view of lake ecosystem change implied by the linear view of nutrient–phytoplankton interactions, sudden changes in lake productivity may occur according to how close the system is to its threshold for change. This is an intermittent process, conditioned by nutrient availability, but resulting in ecological feedbacks that may serve to maintain or reverse the effects of the intermittent event. This explains why there is a positive relationship between nutrient loading and eutrophication level, and also explains why simple attempts at lake restoration based upon the reduction of external nutrient loading may sometimes fail.

The significance of the hypothesis of alternative stable equilibria in eutrophic shallow lakes, the relationship of these equilibria to recovery and the implications for ecosystem management have been increasingly noted by various researchers (Scheffer, 1990; Blindow, 1992; Scheffer *et al.*, 1993; Moss *et al.*, 1996b; Hosper, 1997; Janse, 1997). System switches between alternative states are of importance to lake restoration as they are

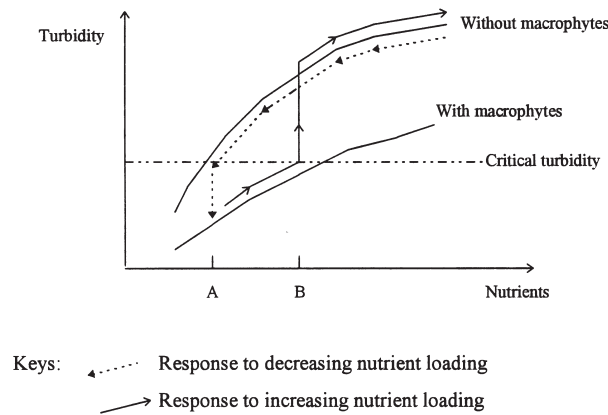


Figure 5 Nonlinearity of the nutrient–turbidity relationship in shallow lakes (Hosper, 1989). $A < B$ denotes that: 1) a very low reduction of nutrient loading has to be achieved for macrophyte redevelopment and recolonisation; and 2) macrophytes will only die off from phytoplankton shading when a relatively high nutrient loading is reached

associated with both hysteresis and sudden jumps in the system, instead of a smooth response to changes in external factors (Scheffer, 1990). For instance, nutrient addition may, surprisingly, cause the switch to be of a nonlinear manner (Figure 5), and the effects of the reverse change in oligotrophication may not necessarily be linear either (Balls *et al.*, 1989; Hosper, 1989). Restoration becomes more difficult and unpredictable than is implied by Figure 1.

V Implications for lake restoration in particular and for environmental management in general

Thus far, this article has reviewed recent research into the way in which biological interactions result in feedbacks that can both maintain a system in a particular stable state and, in some situations, produce rapid positive feedback between stable states. The aim of this section is to develop some of the implications of this review for lake restoration measures in particular and for environmental management more generally.

The reason for the stable states identified above was the continual operation of the system as a whole. This merits some attention as it contrasts with the more traditional ideas of cause and effect in aquatic ecosystems. Central to the above analysis is the idea that each state is self-referential: a system determines its own behaviour in the context of the environment in which it is operating. Stability is itself a misconception of system, as evolution is open, not only with respect to its products but also to the rules of the game it develops (Janstch, 1980). Form determines both form (i.e., the composition of the ecosystem) and structure (i.e., the interaction between ecosystem components), so determining the nature of future forms. Jantsch (1980: 6) describes this as follows

whereas a given spatial structure, such as a machine, determines to a large extent the processes which it can accommodate, the interplay of processes may lead to the open evolution of structures. Emphasis is then on the becoming – and even the being appears in dynamic systems as an aspect of becoming. A system now appears as a set of coherent, evolving, interactive processes which temporally manifest in global stable structures that have nothing to do with the equilibrium and the solidity of technological structures.

This has a number of implications for the way in which environment systems are viewed.

First, as illustrated above, it implies that lake behaviour will be sensitive to the state the lake is in. This is important as it challenges some of the basic principles upon which we manage environmental systems. We traditionally conceive of the environment as changing once some sort of threshold is reached: the environment can assimilate certain levels of human activity up to the point at which a threshold is reached, and change or damage begins. Thus, the development of environmental policy becomes grounded in a consideration of the magnitude and frequency of external events, as judged with respect to thresholds in the system under consideration. Dependence of change upon system state does not just mean that the threshold required for change will evolve, but also that this evolution will be determined by the system itself. In the case of eutrophication, even if phosphorus inputs to a lake may be small, there may be continued accumulation of phosphorus in bed sediments, particularly if flushing rates are low. This will result in slow and progressive changes in trophic structure, even with small levels of nutrient loading, such that system state is evolving to one in which further small fluctuations could have a much greater effect. Although an environment may appear to be resilient and stable, small amounts of pollution could be creating the subtle changes that mean that future pollution events in that system could have a much more dramatic affect. This issue is important as it is a reminder of the difficulty of setting assimilative capacities where the action of assimilation is not neutral but changes the way the system operates, albeit quite subtly: the susceptibility of an environment to pollution evolves through time as a result of the history of stress upon that environment.

Secondly, and following on from the above discussion, the possibility of general recommendations for the best means of lake restoration will be limited. As each history will be specific to particular systems, so locality or place become critical in terms of determining the way a system behaves. It is well established that deeper lakes are more responsive to reductions in external nutrient loading than shallow ones (Moss *et al.*, 1997). However, even categories like deep and shallow may need further disaggregation as the history of an ecosystem conditions the processes that are operating at any one point in time: the way a lake responds to restoration will depend upon the ecological interactions that have been created during the phase of increasing levels of eutrophication. These ecological interactions will then determine the way the lake responds to any one restoration method. The importance of system history as part of the evolutionary process, and the sensitive dependence of future behaviour upon initial state, suggests that tracing a system's footsteps may not be possible, which contrasts markedly with the nature linear view that characterizes some aspects of current environmental management (Figure 6).

What follows from this is the need to develop new ways of managing environmental systems. If there is a sensitive dependence of lake behaviour upon lake state, then recreating a different state will not necessarily produce a state that is sustainable. What

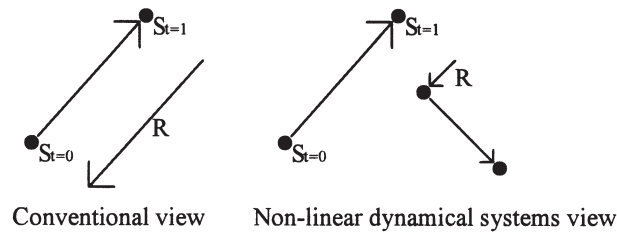


Figure 6 Linear and nonlinear views of current environmental management

the restorer can hope to do, at best, is to reintroduce the processes that may create a desired state, recognize that the way these processes will develop will interact with the existing state of a lake to create future lake states, and appreciate that there will almost certainly be an element of surprise in the restoration process as a result of the strong evolutionary link between lake state and lake process. This is the essence of biomanipulation, in which human activity tries to reintroduce certain processes through changing particular parts of a lake's state. It is also a reminder that biomanipulation measures will not always be successful when judged with respect to their original interaction, and that the probability of successful manipulation will increase with the number of processes that are manipulated. Jantsch (1980) calls this a switch away from *form-orientated* approaches, where we rebuild what we want, to *process or function-orientated* approaches, where we recreate the processes that will produce what we want. This is perhaps the true definition of a sustainable state: one that is capable of reproducing itself.

Thirdly, and following on from this, small things can have big effects if the time is right. This is in marked contrast to traditional views of environmental management and the way in which systems in general behave. For instance, Pattee (1973: 93) noted:

Many hierarchical structures will arise from the detailed dynamics of the elements . . . but the optimum degree of constraint for hierarchical *control* is not determined by the detailed dynamics of the elements. The dynamics of control is determined by how these elements are ignored. In other words, hierarchical controls arise from a degree of internal constraint that forces the elements into a collective, simplified behaviour that is independent of selected details of the dynamic behaviour of its elements.

This is developed by Bennett and Chorley (1978: 398) who conclude that ' . . . the secret of the successful interpretation and control of hierarchical systems is to ignore just the correct amount of detail at the relevant scale of space or time'. In the case of lake eutrophication, what is the correct amount of detail might actually be very small indeed.

The final point that emerges from this case study reinforces the view that the lake manager should recognize rather than exclude the idea that nature is itself a cultural construct. There is always uncertainty over what the environment would have looked like if we had done nothing, and this may be addressed through appropriate environmental reconstruction (e.g., Moss, 1978). However, we are still left with difficult questions. For instance, some environments are naturally eutrophic. We tend to advocate making the ecosystem oligotrophic by biomanipulation – i.e., by killing fish.

However, strictly speaking, eutrophication is a natural process which occurs where primary productivity rates are higher than the rates of removal of waste matter from the ecosystem. Thus, it follows that, according to this definition, lakes can be naturally eutrophic (Murphy *et al.*, 1983), with different trophic structures (e.g., clear water versus turbid water). Both systems can reproduce themselves and are hence sustainable. Thus, if we chose to restore the turbid system, we are clearly placing a value upon the clear-water system we wish to recreate. Hence, choice between these states is not just about the choice between which approach mimics nature in the most appropriate way but about what we believe as humans is natural (i.e., it is culturally constructed). This does not simply challenge the nature nonlinear perspective but reinforces its suitability as a metaphor through which one can consider ecosystem restoration. This perspective (Figure 5) emphasizes the difficulty of restoring a particular lake form: you cannot create what went before, as what goes on in the future is a product of what is going on now. Thus the *ecological* justification for a particular approach is poor, as *exact* ecosystem restoration is not possible. Thus, lake management, and other types of ecosystem management, is about different choices between particular culturally constructed views of what is natural and what we perceive to have a natural value. It is important not to exclude artificially an individual's or society's expectations under the umbrella of ecological objectivity as there is no 'form' to be objective about. The existence of very different levels of eutrophication for the same nutrient loading (e.g., Jeppesen *et al.*, 1991) as a result of ecosystem interactions emphasizes this point. Further, the very language of eutrophication, with its emphasis upon restoration, upon recreating natural lake systems, upon aesthetics, emphasizes the manner in which eutrophication is a concept embodied within society rather than being a pollution problem which exists independently of society.

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