

## Recent advances in the understanding and management of eutrophication

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### Abstract

Major advances in the scientific understanding and management of eutrophication have been made since the late 1960s. The control of point sources of phosphorus reduced algal blooms in many lakes. Diffuse nutrient sources from land use changes and urbanization in the catchments of lakes have proved possible to control but require many years of restoration efforts. The importance of water residence time to eutrophication has been recognized. Changes in aquatic communities contribute to eutrophication via the trophic cascade, nutrient stoichiometry, and transport of nutrients from benthic to pelagic regions. Overexploitation of piscivorous fishes appears to be a particularly common amplifier of eutrophication. Internal nutrient loading can be controlled by reducing external loading, although the full response of lakes may take decades. In the years ahead, climate warming will aggravate eutrophication in lakes receiving point sources of nutrients, as a result of increasing water residence times. Decreased silica supplies from dwindling inflows may increasingly favor the replacement of diatoms by nitrogen-fixing Cyanobacteria. Increases in transport of nitrogen by rivers to estuaries and coastal oceans have followed increased use of nitrogen in agriculture and increasing emissions to the atmosphere. Our understanding of eutrophication and its management has evolved from simple control of nutrient sources to recognition that it is often a cumulative effects problem that will require protection and restoration of many features of a lake's community and its catchment.

Despite 20th century advances in understanding eutrophication, it remains one of the foremost problems in protecting freshwater and coastal marine ecosystems. Here, I trace advances in the science of eutrophication since 1967, when the U.S. National Academy of Sciences held an international symposium on the topic in Madison, Wisconsin, providing a summary of earlier work. That symposium was my own introduction to the eutrophication problem.

*A brief introduction to eutrophication*—Eutrophication is a term that needs little introduction to limnologists. Hutchinson (1973) gave a clear history of the development and use of the term since Weber (1907) first coined the term to describe the appearance of wetlands. The early use of the term was largely descriptive, based on the appearance of lakes, hypolimnetic oxygen depletion, and key species of benthic macroinvertebrates. Needless to say, based on these criteria, many lakes proved to be difficult to categorize. Since the mid-1970s, the term appears to have taken on new meanings in a number of respects. As it became possible to measure the primary productivity of lakes directly, and the key role of human activities in a lake's catchment and the concept of water renewal became known, the term began to be used in a more dynamic sense, implying changes in both within-lake processes and land–water interactions. As Wetzel (2001) points out, using production or biomass as the key variable in classifying lakes eliminates most of the difficulties encountered when attempting to use earlier classification schemes.

By the mid-20th century, the eutrophication problem, if not the term, had been widely recognized by people who lived near lakes. Increased algal scums, macrophyte growth, and periodic fish kills were difficult symptoms to ignore. Early attempts to manage eutrophication largely involved treating symptoms, using copper sulfate or herbicides, rather than the source of the problem. It was not until the 1960s that scientists began to link the algal blooms with the increasing nutrient supply that resulted from human activities in the catchments of lakes.

*The Madison eutrophication symposium*—The Madison symposium volume (National Academy of Sciences 1969) illustrates the primitive state of our understanding of eutrophication four decades ago. Presentations and published papers described evidence that many chemical factors could cause eutrophication. No integrated view of how to attack and solve the problem was presented, and there was no focus on specific nutrients or other factors. Phosphorus and nitrogen, which are now the focus of eutrophication control in freshwaters and estuaries, were mentioned only in passing: “Substances other than inorganic phosphorus and nitrogen compounds contribute to eutrophication. Examples are vitamins, growth hormones, amino acids and trace elements” (National Academy of Sciences 1969, p. 4). The American Society of Limnology and Oceanography's symposium on eutrophication a few years later (Likens 1972) was only slightly more focused. Neither symposium proposed specific solutions to the eutrophication problem. Both ignored the role of changes to consumer communities as a cause of eutrophication.

*The International Biological Program*—Much of the funding for ecology and limnology in the 1960s was connected with the International Biological Program (IBP), to study the productivity of the world's ecosystems. Strangely, despite the rapidly increasing evidence for nutrient-driven

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eutrophication, in the earliest years of the IBP, nutrients were not considered to be an important determinant of productivity. The primary focus was on light, temperature, and latitude (Kajak and Hillbricht-Ilkowska 1972; Brylinsky and Mann 1973). By the later years of the IBP, the focus had changed to recognize the importance of nutrients in freshwater ecosystems (Schindler 1978). Despite the focus on production of upper trophic levels, top-down features of communities that affected eutrophication were overlooked.

*Vollenweider's models*—Ironically, one of the attendees at the Madison symposium who was not an invited speaker had the primary solution to the eutrophication problem with him in draft form. R. A. Vollenweider conducted an analysis of the eutrophication problem in the 1960s for the Organization for Economic Cooperation and Development (OECD). In a comprehensive review of the literature, he empirically deduced that controlling phosphorus inputs, and in some cases nitrogen inputs, to lakes was the primary key to reducing eutrophication. It was also the first study to link the changes in the watersheds of lakes to the eutrophication problem (Vollenweider 1968), dispelling the early focus on “The lake as a microcosm” (Forbes 1887). Vollenweider's first simple models linked eutrophication to nutrient input and the mean depth of lakes. His study was never published in the primary literature, but it became the basis for eutrophication management in the Great Lakes, in Europe, and in many other parts of the world. The focus of management was on phosphorus, the limiting element in most lakes. Changes to the formulations of laundry detergents, which contained up to 50% phosphorus at the time, and removing phosphorus from human sewage, were among the measures proposed.

*Challenges to the phosphorus limitation theory*—There were several who challenged Vollenweider's conclusions. For example, some used bioassay experiments to show that carbon, rather than phosphorus, controlled productivity (for example, Kuentzel 1969; Kerr et al. 1970; Lange 1970). These results were highly publicized by the soap and detergent manufacturers and their allies, who believed that the superb cleaning power of their phosphorus-based products should take precedence over environmental effects. However, many of these small-scale experiments were fundamentally flawed: they did not consider whether the state of the water bodies that they tested had already been influenced by phosphorus at the time bioassays were conducted. These articles resulted in an entire issue of Canadian Research and Development being devoted to questioning the rationale for managing phosphorus rather than carbon (Canadian Research and Development 1970).

*Evidence from Lake Washington*—For several decades, W. T. Edmondson documented the eutrophication of Lake Washington as the city of Seattle grew. Based on correlations between phosphorus and algal standing crops, he correctly deduced that phosphorus was the likely culprit in eutrophication. Persuaded by Edmondson's studies, the city decided to divert sewage from the lake. Lake Washington recovered rapidly, disproving early theories that once they had become

eutrophic, lakes would be unrecoverable (Edmondson 1970, 1991).

The soap and detergent interests (SDI) argued that Edmondson's conclusions were invalid because all nutrients had been diverted from the lake, rather than just phosphorus. Detergent propagandists claimed that decreases in phosphorus in Lake Washington following diversion of sewage from the lake did not cause the reductions in algae as Edmondson (1970) had argued. Instead, ignoring logical cause and effect arguments, they proposed that the reductions in phytoplankton had caused the reduction in phosphorus (Edmondson 1991)! The SDI used many other spurious arguments to delay legislation to control phosphorus, using arguments analogous to those used today by climate skeptics to disassociate global warming from increasing greenhouse gases in the atmosphere.

*The Freshwater Institute and the Experimental Lakes Area (ELA)*—W. E. Johnson was first director of the Freshwater Institute in Winnipeg, Manitoba. The Institute was a part of the Fisheries Research Board of Canada. Johnson hired J. R. Vallentyne to recruit and lead the Eutrophication Section, which was to study the eutrophication problem in Canadian lakes. Vallentyne hired R. A. Vollenweider to head a group that would study the Great Lakes directly, from a base at the Canada Center for Inland Waters in Burlington, Ontario. He hired me to find a suitable group of lakes for whole-lake manipulation experiments that would examine causes of eutrophication. Based on surveys in 1967, the Experimental Lakes Area (ELA) was located in northwestern Ontario, about 50 km southeast of Kenora. The lakes were deep enough to stratify thermally, in catchments that had not been modified by human activity, and had tight basins that were amenable to accurate hydrological measurements, essential for testing some of the eutrophication models under development by Vollenweider. Background on the ELA is given by Johnson and Vallentyne (1971) and other papers in Vol. 28, issue 2 of the Journal of the Fisheries Research Board of Canada. Based on work from the two groups, Vallentyne became a particularly effective advocate for phosphorus control in the Great Lakes, effectively using scientific results to counter the claims of the SDI.

As mentioned earlier, in 1969, there was great controversy over the role of carbon in controlling eutrophication. The ELA surveys revealed that lakes in the area were all oligotrophic. As a result of their setting in Precambrian granites and gneisses with little overburden, they contained unusually low concentrations of major ions and dissolved inorganic carbon (DIC), far lower than those in the microcosm experiments used as the basis for the SDI's claims. We decided to see whether the lakes could be made eutrophic by adding phosphorus and nitrogen, despite their low carbon content. Lake 227 was the lake with the lowest DIC in the entire ELA. Beginning in 1969, we added nitrogen and phosphorus at a ratio of 14:1 by weight, without any carbon, to focus the experiment on the phosphorus versus carbon hypotheses. The phosphorus loading was chosen to be roughly 10 times natural levels, based on our few measurements at the time.

Lake 227 quickly became eutrophic, despite low concentrations of DIC (Schindler et al. 1971, 1973). As photosyn-

thesizing algae depleted the dissolved inorganic carbon reserves in the lake, they were replenished by exchange with CO<sub>2</sub> from the atmosphere (Schindler et al. 1972). Clearly, carbon management was not an issue.

We also conducted bottle bioassays in Lake 227 similar to those that the SDI were claiming as evidence for carbon limitation. They indicated that carbon was indeed limiting to algal production following addition of nitrogen and phosphorus (Schindler 1971). The carbon limitation was a *response* to eutrophication, and not the cause, a classic example of the confusion that can be caused by basing ecosystem-scale management on seemingly precise but inappropriate small-scale experiments (Schindler 1998). As the result of the Lake 227 studies, the carbon limitation arguments collapsed.

The SDI further argued that studies by Hutchinson and Bowen (1947, 1950) and others showed that phosphorus was recycled extremely rapidly in lakes and could never be controlled well enough to reduce eutrophication. The ELA group was able to address that proposal in Lake 226, a double basin lake shaped roughly like a figure 8. The two basins of Lake 226 were separated at the narrows with a heavy vinyl-covered nylon curtain. Both halves of the lake were fertilized with nitrogen and carbon, but only the north basin received phosphorus as well. The half not receiving phosphorus remained in near-pristine conditions, while the part that received phosphorus as well as nitrogen and carbon developed algal blooms within weeks of beginning nutrient additions (Schindler 1974). An aerial picture of the lake was particularly convincing evidence for the control of phosphorus to policy makers who did not fully understand the scientific arguments.

As the result of further study of Lakes 226 and 227, it became clear that low N:P ratios further aggravated the eutrophication problem by favoring Cyanobacteria species that were capable of fixing atmospheric nitrogen (Schindler 1977). Smith (1983) reached similar conclusions based on observations of N:P ratios of lakes around the world. There seemed to be little point in controlling nitrogen if phosphorus was not controlled first.

As the result of accumulating evidence from limnologists, phosphorus control became the standard policy in most first-world countries. Many studies showed that controlling point sources of phosphorus effectively reduced eutrophication (for example, Edmondson 1970; Ahlgren 1978; Holtan 1981). In 1974, a resolution was read at the 19th International Congress of the International Limnological Society (SIL): "Because of the critical role of phosphorus in the rapid eutrophication of inland waters, be it resolved that in addition to secondary treatment of sewage it is necessary to control additions of this element to any inland water." Phosphates in cleaning products, sewage, septic tanks, and agricultural wastes were specified in subsequent wording. The resolution was carried by the roughly 1,000 delegates at the Congress.

The rapid control of eutrophication by reducing point sources of phosphorus is one of the clearest cases I know where science has contributed to quickly solving a major management problem. It is a success story that limnologists should be proud of. But controlling detergent phosphates and

point sources of sewage did not end the eutrophication problem. It was widely recognized by scientists that loading from diffuse sources like agriculture and recycling of phosphorus between sediments and water were problems that remained to be solved. But funding for studies of eutrophication problems was reduced in North America, and much of what we have learned about the topic on this continent since the 1970s has been the result of studies undertaken for other purposes. Fortunately, several strong European programs continued to study eutrophication in the intervening 30 years and continue to improve our ability to manage lakes on a scientific basis. Below, I briefly describe several of the most important recent advances in our understanding of the causes and control of eutrophication.

*Diffuse nutrient sources*—In the 1970s it was already clear that changing land uses as well as point sources were important in supplying nutrients to lakes. In the lower Laurentian Great Lakes, land use changes were identified as responsible for about 50% of the nutrient inputs (International Joint Commission 1980). Other studies showed that even partial conversion of forested land to pasture caused increases in nutrient losses (Dillon and Kirchner 1975). Conversion of natural landscapes to agricultural and urban uses has been ubiquitous in North America and Europe, and the implications for eutrophication are well known (for example, Soranno et al. 1996; Jeppesen et al. 1999). In addition, not all nutrient effluents from urban areas are controlled by treating sewage. Runoff from urban streets following storms is also an important diffuse source of phosphorus and nitrogen to lakes and streams (Cairns 1995). Unfortunately, reducing these sources is much more difficult than dealing with the point sources that were the target of legislation in the 1970s. Changes in agricultural practices, restoration of wetlands and riparian areas, and restoration of channelized streams have been some of the measures employed to make slow progress in curbing diffuse sources (for example, Jeppesen et al. 1999).

*Water renewal*—Eutrophication models developed during the 1970s (Dillon and Rigler 1974; Vollenweider 1976) clearly showed that the rate of water renewal was an important modifier of nutrient loading, where nutrient inputs were directly to lakes. Such models are still widely used as the basis for lake management today. In lakes where return of phosphorus from sediments is small, halving the outflow (therefore doubling the water renewal time of a lake) had roughly the same effect on the eutrophication of a lake as doubling the nutrient input (Schindler et al. 1978).

*Internal loading and eutrophication*—The classic experiments of Mortimer (1941, 1942) clearly showed the release of phosphorus, nitrogen, and other chemicals from anoxic lake sediments. In shallow polymictic lakes of the North American prairies, where natural soils contain high concentrations of phosphorus, repeated bouts of summer anoxia during calm periods cause high rates of phosphorus release from sediments. This is swept into the euphotic zone during following windy weather, renewing phosphorus supplies periodically during the ice-free season. Such lakes can be high-

ly eutrophic, even with few external anthropogenic nutrient sources (Schindler and Comita 1972; Barica 1975). In many cases, the calculated “internal loading” can exceed external sources of nutrients.

On the other hand, lakes of the Precambrian Shield, where precipitation is normally the only external source of phosphorus, have very low internal loading of phosphorus, even under anoxic conditions (Schindler et al. 1977; Levine et al. 1986).

These very different results lead one to question whether anoxia is the true control on phosphorus release, or whether the two are simply correlated. For example, Moosman et al. (2005) found that phosphorus exchange with sediments in lakes of the Swiss Plateau was a function of the capacity of sediments for sequestering phosphorus. There was little difference between lakes with oxic and anoxic hypolimnia.

Until the 1960s, it was believed that internal loading would render lakes permanently unrecoverable. Subsequent studies have shown that the importance of internal loading in delaying recovery of eutrophic lakes can be highly variable. In lakes that have received high nutrient loading for only a few years, internal loading delays recovery very little (Northcote 1972; Shearer et al. 1987). Results in lakes that had been eutrophic for years were slower. Ahlgren (1978) observed that once external loading was reduced, internal loading in Lake Norrviken declined slowly over several years. In some European studies, shallow lakes have taken 10 to 20 yr to reach new steady states after external loading was reduced (Jeppesen et al. 1999; Sondergaard et al. 2001). In deeper lakes, initially slow rates of recovery improved once surface sediments became less saturated with phosphorus (Moosman et al. 2005).

In many cases, liming, aeration, dredging, macrophyte harvesting, biomanipulation, and other methods have been used to attempt to accelerate the recovery process by reducing internal loading or accelerating the removal of phosphorus (Cooke et al. 1993; Keto et al. 2004). The success of these methods varies greatly from lake to lake, and costs are prohibitive in large lakes. It is generally agreed that such techniques are usually not worth considering unless external loads of phosphorus can also be reduced. In addition to point-source controls, reductions in agricultural runoff of nutrients, reestablishment of wetlands and littoral zones, and restoration of channelized streambeds have been shown to be necessary to restore many lakes (Jeppesen et al. 1999). Sondergaard et al. (2001) thoroughly review the role of internal phosphorus loading in eutrophication.

*Nitrogen and eutrophication*—Already in the 1960s, there was evidence that some lakes were naturally nitrogen limited, especially in mountains of western North America. In some cases, these were transformed to phosphorus-limited systems by rapidly increasing inputs of anthropogenic nitrogen (for example, Lake Tahoe, Goldman 1981). Later, many South American lakes were shown to be nitrogen limited (Soto 2002). Nitrogen-limited lakes were largely ignored in the efforts to manage eutrophication in the mid-20th century. However, the rapid increase in deposition of atmospheric nitrogen and the massive increases in use of nitrogen fertilizer that have occurred since that time were not recognized

until many years later (Vitousek and Howarth 1991; Tilman et al. 2001; Sickman et al. 2003). Eutrophication of estuaries and coastal zones has also emerged as one of the most pressing current aquatic problems of the 21st century (Cederwall and Elmgren 1990; Turner and Rabalais 2003).

*Community structure: trophic cascading, stoichiometry, benthic–pelagic coupling, and other effects*—In the 1960s and early 1970s, the widespread importance of food chain structure in eutrophication was not realized, even though several studies had documented the effects of high populations of grazing zooplankton on algal abundance (Hrbacek et al. 1961; Brooks and Dodson 1965; Schindler and Comita 1972). Shapiro and his colleagues were the first in North America to propose that it was possible to “biomanipulate” lakes to control eutrophication (Shapiro et al. 1975; Shapiro and Wright 1984). Carpenter et al. (1985) first clearly identified the common features of community structure as they related to eutrophication, terming the food-web effect the “trophic cascade.” In short, at constant nutrient loading, aquatic food webs with even numbers of pelagic trophic levels tend to have lower algal abundance than those with an odd number of trophic levels. In most larger northern lakes, pelagic food chains contain many species of phytoplankton, several species of zooplankton, several species of zooplanktivores, and a few species of piscivorous predators. Widespread overfishing and habitat destruction have increasingly depleted predatory fish species in both marine systems and freshwaters (Pauly et al. 2001; Post et al. 2002). As a result, zooplanktivores increase, depleting large grazing crustaceans, and the loss of “grazing power” allows phytoplankton to increase in abundance. Whole-lake experiments in northern lakes have clearly shown that removal of piscivorous predators can cause eutrophic lakes to change from a low to a high algal phase, whereas adding piscivores to a lake containing only planktivores has the opposite effect (Carpenter et al. 1995; Elser et al. 2000). In lakes with three trophic levels, removing zooplanktivorous fish also reduced algal blooms, supporting the cascading hypothesis (Meijer et al. 1994; Parker and Schindler in press).

*Alternative stable states*—There has been evidence for many years that shallow lakes could exhibit alternative stable states. A high algae, low macrophyte state characterized by low transparency could suddenly shift to a high macrophyte, clear water phase. Some lakes shift between the two states frequently, while others appear to exhibit considerable hysteresis after the shift has occurred (Bayley and Prather 2003). In extreme cases, shifts from a clear water, macrophyte to a turbid, phytoplankton-dominated state appear to be permanent and have caused the destruction of valuable fisheries (Schelske et al. 2000). Considerable study has been devoted to the reasons for the shifts in state. Various studies have proposed that the changes could be linked either to a trophic cascade, by changes in the abundance of large herbivorous grazers, or to the abundance of fishes that could promote nutrient exchange between water and sediment. Wind has also been found to be associated with switches to a turbid state, by resuspension of nutrient-rich sediment in large lakes like Lake Apopka, Florida (Bachmann et al.

2001). In smaller lakes resuspension by wind appears to be of little consequence (Jeppesen et al. 2003).

In many cases, removal of benthivorous fishes has allowed a shift to a clear water phase, provided external loading is also reduced enough that total phosphorus concentrations are  $<100 \mu\text{g/L}$  (Sondergaard et al. 2000). While understanding of the mechanisms causing the phase shifts appears to be improving, there are still many documented cases where shifts cannot be attributed with confidence to any simple combination of mechanisms (Norlin et al. 2005). Scheffer (2001) reviews the subject in detail.

Very sophisticated trophic cascading experiments were done in Wisconsin, where several small lakes were used to perform combined manipulations of predatory bass and nutrients. As expected, the presence of piscivorous predators (i.e., an even number of trophic levels) caused phytoplankton abundance to be lower than when predators were absent, at both high and low levels of nutrient enrichment. The effect appeared to be more pronounced at high nutrient loading (Carpenter et al. 1996). Even the direction of carbon dioxide exchange between the atmosphere and lakes could be reversed by manipulating trophic structure, particularly in eutrophic lakes (D. E. Schindler et al. 1996a). The whole-lake experiments in Wisconsin and at the ELA (Schindler 1977) show clearly that organisms can change the biogeochemical interfaces between lakes, their catchments, and the atmosphere in ways that are important to the understanding and management of eutrophication.

Recent studies suggest that the strength of the trophic cascading effect on algal abundance is affected by stoichiometric considerations. Briefly, large *Daphnia* appear to be required for maximum trophic cascading effect to protect lakes. *Daphnia* contain a lower N:P ratio than their algal food (Andersen and Hessen 1991), so they excrete excess nitrogen. This helps to keep algae phosphorus limited. The grazing pressure can also keep the length of Cyanobacteria filaments short, suppressing heterocyst formation (Chan et al. 2004). *Daphnia* are obligate herbivores and ideal food for zooplanktivorous predators (Sterner et al. 1992; Elser et al. 2000). *Daphnia* are usually rare in lakes where there are not piscivorous predators because high populations of zooplanktivorous fish keep their populations low. In lakes where *Daphnia* are scarce, strong trophic cascades are rarely observed. This is the case at ELA, where most natural lakes have zooplankton dominated by Copepoda (Patalas 1971; Findlay et al. 1994).

Lake 227, still eutrophied, appeared to be an ideal site for an ecosystem-scale test of the theoretical link between stoichiometry and trophic cascading. Lake 227 had been fertilized with nitrogen and phosphorus since 1969. The N:P ratio in fertilizer had been kept low since 1975, at 5:1 instead of natural supplies of closer to 15:1 by weight (Schindler et al. 1987). The lake contained no piscivores, and the predominant fishes were fathead minnows *Pimephales promelas* and several species of dace (*Margariscus margarita*, *Phoxinus eos*, *Phoxinus neogaeus*). *Daphnia* were scarce, represented by the small species *D. galeata mendotae*. Smaller Cladocera and Copepoda predominated in the zooplankton.

We hypothesized that the low N:P ratio used to fertilize

the lake (5:1 or less after 1975) would allow *Daphnia* to dominate in the zooplankton in the absence of planktivorous minnows. To reduce minnows, in 1993 and 1994, 200 northern pike (*Esox lucius*) were added to the lake. The final density of pike was  $26 \text{ kg ha}^{-1}$ , six times higher than natural oligotrophic lakes in the area. By the end of 1995, minnows were rare in the lake, as shown by catch per unit effort. In 1996, none were caught. In the absence of zooplanktivorous predators, *Daphnia* increased greatly in abundance. *Daphnia pulicaria*, a large species, supplanted *D. galeata*. For the first time since 1975, Cyanobacteria were rare because of heavy grazing by *Daphnia*. The lake was more transparent. Dissolved N:P ratios were higher than in previous years, confirming the selective retention of phosphorus by *Daphnia* (Elser et al. 2000).

The results from Lake 227 and the Wisconsin lakes leave some remaining questions about the importance of trophic cascading to eutrophication. In all cases, the experiments lasted just a few years, giving predators insufficient time to reach stable age distributions and adjust their abundances to be in proportion to their food supplies. Young of the year of most predator species are planktivorous, and large year classes could “muddy” a clear-cut response to predator manipulation. It is important that future cascading experiments be long enough for species to reach natural abundances and age structures. At ELA, in both eutrophication and acidification experiments, fishes required 8 yr or more to adjust to new energy sources or food-web structures (Schindler et al. 1993).

Other studies have shown the role of mobile animals in moving nutrients from benthic to pelagic regions. D. E. Schindler et al. (1996b) showed that nocturnal forays by minnows from the littoral zone to pelagic regions of Wisconsin lakes contributed significantly to the nutrients of the latter region. Wilhelm et al. (1999) showed that *Gammarus lacustris*, a large crustacean, played a similar role in an alpine lake. Benthic flora can also be important in overall lake productivity. Vadeboncoeur et al. (2003) showed that as phosphorus loading increased along a gradient in lake productivity, there was an increasing tendency for benthic algal productivity to be replaced by planktonic productivity. This also caused a shift in the diets of zoobenthos from periphyton to phytoplankton, suggesting that eutrophication caused a decoupling of benthic primary production pathways. Sondergaard et al. (2002) suggested that the differences in seasonal phosphorus patterns in recovering shallow versus deep lakes was the result of stronger benthic–pelagic coupling in the former. Further investigation of the role of benthic organisms in eutrophication is clearly in order.

In 11 years of study on 18 recovering lakes, Jeppesen et al. (2002) found that removal of plankti-benthivorous cypripinids speeded the recovery of lakes following reduction in external phosphorus loading. Overall, there are enough differences in the responses of biomanipulated lakes to suggest that the result will depend greatly on the complexities of individual lake communities.

*The cumulative effects of direct human perturbation and climate warming*—We could not have foreseen a quarter century ago how climate warming and increasing human de-

mand have sapped the flow of water from many regions (for example, D. W. Schindler et al. 1996; Schindler 2001). During the past 30 years, many areas of central and western North America have recorded increasing temperatures, with associated increases in evaporation and evapotranspiration outstripping precipitation. In the western Great Plains, at least two periods of extreme drought occurred in the 20th century as well, the last extending for several years, from 1998 to 2003. The result has been lower lake levels, dry wetlands, greatly reduced river and stream flows, and increased water residence times and nutrient retention by lakes. For lakes receiving point-source nutrient additions, increasing evaporation and decreasing inflows and outflows can contribute to eutrophication of lakes by increasing nutrient retention, as discussed earlier with respect to water renewal.

The situation is different where diffuse nutrient sources in catchments, rather than point sources, are the major sources of nutrient inputs to lakes. In pristine catchments at the ELA, less water inflow has been associated with reduced inputs of phosphorus. The decrease in phosphorus input more than compensated for the effect of reduced water renewal, resulting in a slight oligotrophication of the already unproductive lakes (D. W. Schindler et al. 1996). In lakes where both point and diffuse sources of nutrients are important, the result of lower water renewal is less clear and may require specific studies on individual lakes.

Schelske and Stoermer (1971) showed that the eutrophication of Lake Michigan by increased phosphorus and nitrogen had caused larger spring diatom blooms, which depleted silica earlier each year as phosphorus and nitrogen concentrations increased over time. The ratio of nitrogen to phosphorus in anthropogenic nutrient inputs was low, favoring Cyanobacteria as the successors to diatoms after silica concentrations were depleted. Later studies showed silica to play a similar role in other great lakes. Nitrate, too, was more rapidly depleted as phosphorus increased, aggravating the problem with nitrogen-fixing Cyanobacteria blooms (Schelske 1975). Similar conclusions were reached from a study of 18 lakes in Europe (Sas 1989).

In most areas, silica is supplied to lakes largely by inflow because it is a product of weathering of bedrock and soils. Concentrations in precipitation are very low. Both the size and geology of the catchment are important in silica supply. Water, which is essential for geochemical weathering and the transport of dissolved weathering products to lakes, is a key factor. At the ELA, silica supplies to lakes declined as drought and climate warming reduced weathering and streamflow, resulting in lower concentrations in lakes (D. W. Schindler et al. 1996). In lakes receiving anthropogenic inputs of nitrogen and phosphorus with their generally low ratio of N:P, lower silica inputs might enhance the tendency of Cyanobacteria blooms to develop earlier in the season. Earlier ice-out and warmer waters would also be expected to aggravate nuisance bloom formation. It is, however, noteworthy that silica can be internally recycled within lakes, by release from lake sediments under anoxic conditions (Schindler et al. 1973). In large lakes, the recycling of silica from sediment appears to be less efficient (Schelske and Stoermer 1971).

*Eutrophication in the 21st century: a cumulative effects problem*—In summary, during the past 40 years, the understanding of eutrophication and its management have evolved from rather unfocused studies of algal nutrition to a very narrow focus on controlling one, sometimes two elements. However, the focus has broadened in other ways, this time including the effects of increasing human activities on climate, land use, global nitrogen cycles, and fisheries (Schindler 2001). Reducing eutrophication in the century ahead will require complex policy decisions that include controlling some combinations of the stresses described above in most waters. The control of eutrophication remains one of the greatest challenges to limnologists, estuarine scientists, and managers. Perhaps greater than the scientific challenges will be the education of policy makers, so that they understand the complexity of the problems that they face.

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