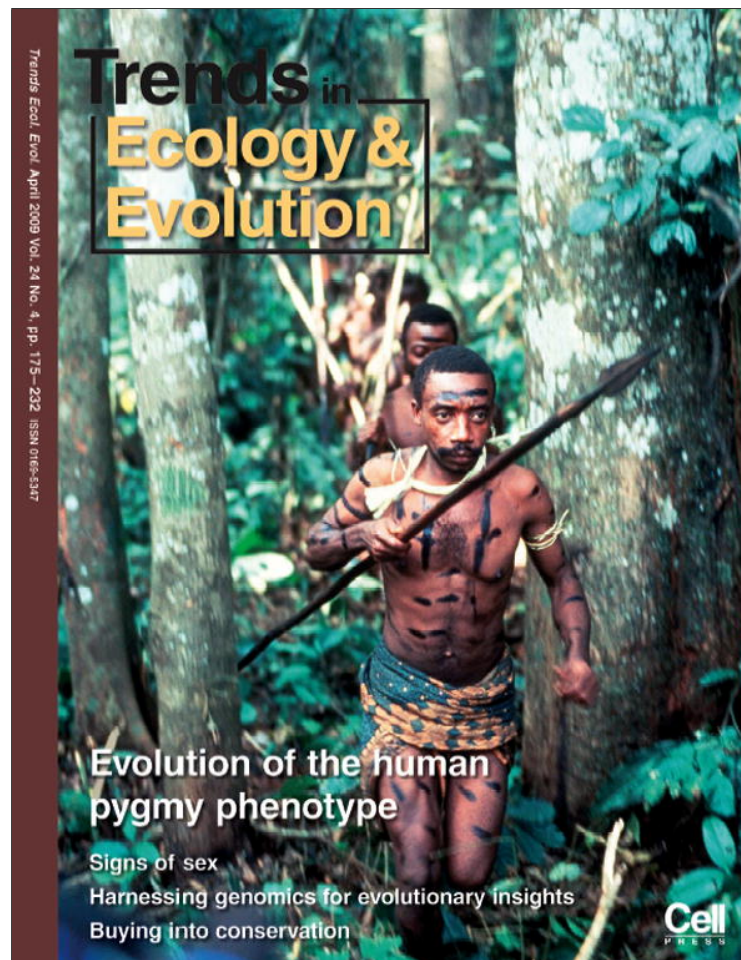


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Eutrophication science: where do we go from here?

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Cultural eutrophication has become the primary water quality issue for most of the freshwater and coastal marine ecosystems in the world. However, despite extensive research during the past four to five decades, many key questions in eutrophication science remain unanswered. Much is yet to be understood concerning the interactions that can occur between nutrients and ecosystem stability: whether they are stable or not, alternate states pose important complexities for the management of aquatic resources. Evidence is also mounting rapidly that nutrients strongly influence the fate and effects of other non-nutrient contaminants, including pathogens. In addition, it will be important to resolve ongoing debates about the optimal design of nutrient loading controls as a water quality management strategy for estuarine and coastal marine ecosystems.

Introduction

Cultural eutrophication (excessive plant growth resulting from nutrient enrichment by human activity) is the primary problem facing most surface waters today. It is one of the most visible examples of human changes to the biosphere ([1,2]; Figure 1), affecting aquatic ecosystems from the Arctic to the Antarctic [3]. Eutrophication has many undesirable side effects (Table 1), major economic costs and transnational implications [4,5]. Many studies have concluded that managing phosphorus and, in coastal waters, managing nitrogen inputs is critical to maintaining desirable water quality and ecosystem integrity [6,7]. Evidence has also accumulated to favor nutrient restriction as a means of restoring eutrophic waters [2,6]. However, nutrient enrichment interacts with many site-specific conditions, especially the ecological stability of the system, and the presence of other contaminants, including infectious disease agents. Moreover, a consensus has yet to be reached concerning optimal nutrient loading controls in coastal zone eutrophication management. Our review addresses these knowledge gaps.

Nutrient loading and ecosystem stability

Interactions between nutrients, producers and their consumers remain poorly understood for most aquatic ecosystems. Major food web disturbances (e.g. winter fish kills [8], or the addition or deletion of piscivorous predators [9,10]) can cause shifts in ecosystem structure and function that

persist over extended periods of time. Two strikingly different alternative states are frequently observed in shallow, nutrient-enriched aquatic systems: the first is a clear water state dominated by benthic macro-vegetation, and the second is a more turbid state dominated by algae. Many freshwater studies [11,12] show that these regime shifts can be abrupt and sometimes catastrophic [13]. Similar regime changes have been observed in shallow marine ecosystems [14]. Alternative system states have, for example, been observed in coastal soft sediment communities, which dominate the shallow (0–1 m depth) zone along the Swedish west coast [15]. Previously unvegetated shallow sediment areas now appear to be locked into a state of recurring green algal mat development that is resistant to restoration efforts. The cause of this shift could be related to an anoxia-driven ‘vicious cycle’ that enhances algal growth by efficiently recycling phosphorus from bottom sediments [16].

Regime shifts can also result from anthropogenic changes in the catchments and airsheds of aquatic ecosystems. For example, clearing forested catchments causes long-term increases in the loss of nutrients [17]. Applications of manure or commercial fertilizer further increase terrestrial nutrient exports: fertilized soils can become nutrient saturated, leaking nutrients into receiving waters for decades after external nutrient additions are reduced or discontinued [18]. Gaseous nitrogen emissions can occur hundreds of kilometers upwind of affected ecosystems, yet their subsequent atmospheric deposition can constitute the predominant anthropogenic nitrogen source in downwind regions [19,20].

There is recent evidence that not all regime shifts are stable, and that some alternative states are not mutually exclusive. Bayley *et al.* [21] found that alternative states in shallow lakes of the Boreal Plain in Canada were unstable. Over 70% of studied lakes shifted alternative states from two to nine times in a 6 year period. At very high nutrient concentrations, both submersed aquatic vegetation and high algal turbidity occurred. They hypothesized that due to harsh winter conditions (ice thickness, winterkill caused by anoxia) these ecosystems were strongly abiotically regulated, and lacked the biological mechanisms that maintain stable states in more temperate climates.

Whether stable or not, alternate states pose important complexities for the management of aquatic resources, and could be one of the most important issues facing aquatic ecologists today. Regime shifts need extensive further study in eutrophic lakes, estuaries and coastal

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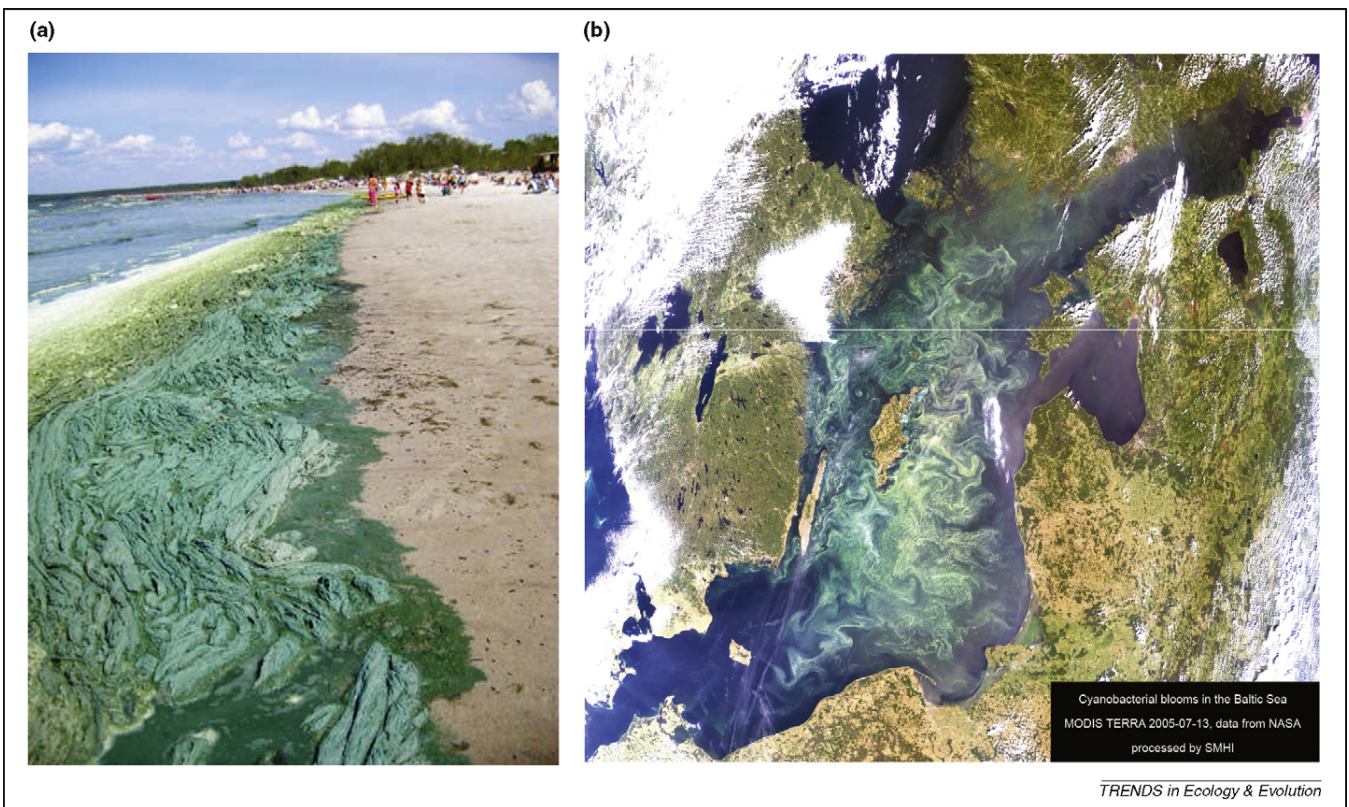


Figure 1. Excessive nutrient enrichment, or eutrophication, of surface waters frequently results in the appearance of harmful algal blooms in both freshwater lakes and coastal ecosystems. (a) Surface bloom of cyanobacteria at Grand Beach, Lake Winnipeg, Canada (photo by Lori Volkart). (b) Extensive surface blooms of cyanobacteria in the Baltic Sea (NASA, GES Distributed Active Center, as processed by SMHI, http://www.smhi.se/weather/baws_ext/info/2005/Baltic_algae_2005_en.htm). Reproduced, with permission, from University of Alberta Press [57].

zone ecosystems. In particular, it is imperative that we understand both when and where unstable regime shifts imposed by harsh climates, climate change or other physical conditions can override the stability that has been widely demonstrated.

Eutrophication and the fate of non-nutrient contaminants

In addition to receiving major inputs of anthropogenic nutrients, surface waters worldwide serve as reservoirs and conduits for heavy metals, pesticides, pharmaceuti-

cals, hormones and other non-nutrient pollutants. Accumulating evidence suggests that the fates of such contaminants can be strongly influenced by nutrient availability, and that these interactions deserve extensive further study.

The supply of nutrients can directly and indirectly limit the metabolic activity of heterotrophic microorganisms. For example, there is evidence for direct positive effects of N and P on bacterial growth [22] and, accordingly, total bacterial biomass is very strongly correlated with concentrations of total phosphorus in freshwater and marine ecosystems [23]. In addition, the diversity of organic substrates that aquatic bacteria are able to metabolize appears to increase under conditions of higher water-column productivity (Figure 2a). The fate of non-nutrient contaminants thus can be strongly influenced by the trophic state of the waterbodies that receive them: increasing supplies of N and P can enhance the biodegradation of petrochemicals, aromatic hydrocarbons and pesticides in many aquatic ecosystems [24]. For example, the rate of phenol biodegradation increases with the productivity of the lake from which the water was taken (Figure 2b).

Eutrophication also enhances the biogeochemical cycling of both organic and inorganic contaminants. For example, Lake 227 in the Experimental Lakes Area was kept highly eutrophic for three decades, while another nearby lake (Lake 110) remained oligotrophic. Both lakes had similar access to atmospherically derived PCBs, and dissolved PCB concentrations were similar in the two

Table 1. Potential effects of cultural eutrophication, caused by excessive inputs of phosphorus and nitrogen to lakes, reservoirs, rivers and coastal oceans^a

Effects of eutrophication
• Increased biomass of phytoplankton and macrophyte vegetation
• Increased biomass of consumer species
• Shifts to bloom-forming algal species that might be toxic or inedible
• Increases in blooms of gelatinous zooplankton (marine environments)
• Increased biomass of benthic and epiphytic algae
• Changes in species composition of macrophyte vegetation
• Declines in coral reef health and loss of coral reef communities
• Increased incidence of fish kills
• Reductions in species diversity
• Reductions in harvestable fish and shellfish biomass
• Decreases in water transparency
• Taste, odor and drinking water treatment problems
• Oxygen depletion
• Decreases in perceived aesthetic value of the water body

^aSee Ref. [2] and references therein.

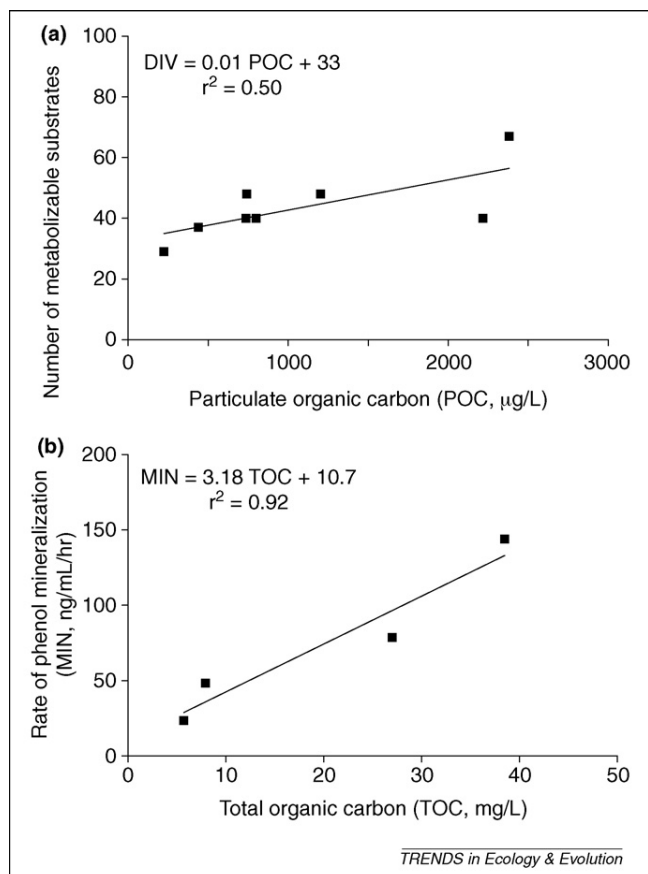


Figure 2. Eutrophication influences the microbial processing of non-nutrient contaminants. **(a)** The number of different kinds of organic substrates that can be metabolized by aquatic microbes increases with aquatic ecosystem productivity, as measured by particulate organic carbon (POC) concentrations (data from Table 1 in Ref. [58]). **(b)** The biodegradation rate of an experimental addition of 1.98 ng/ml phenol is dependent upon the nutrient enrichment status of the system from which the water was taken, as measured by its total organic carbon (TOC) concentration (data replotted from Ref. [59] with permission from the American Chemical Society).

lakes. However, greater biotic uptake of PCBs in Lake 227 decreased the dissolved PCB concentrations in water, causing enhanced air-to-water PCB exchange. As a result, PCB sedimentation with organic particles was significantly higher in eutrophic L227 than in oligotrophic L110, and eutrophication also resulted in lower volatilization of dissolved PCBs into the atmosphere during stratification [25]. This result shows that eutrophication can cause enhanced uptake of airborne toxic contaminants by lakes.

In Moab Lake, Canada, forest fire increased the inputs of both nutrients and mercury [26]. Higher nutrient loading resulted in enhanced recruitment of juvenile rainbow trout, which in turn were preyed upon by several fish taxa, including species that were previously benthivores. As a result, the apparent trophic position of these fish species shifted, and their growth increased. Normally, increased growth caused by eutrophication would be expected to cause growth dilution, resulting in lower concentrations of tissue mercury in fish [27–29]. However, in this case, higher mercury concentrations were observed in all fish species, probably indicating that increased mercury inputs outweighed the effects of nutrient-stimulated growth

dilution. This hypothesis is supported by parallel analyses of organic contaminants (OCs), which did not increase as the result of forest fire, presumably because they were degraded by high temperatures. Unlike mercury in Moab Lake, OC concentrations in fish decreased as the result of growth dilution [30]. Contaminant concentrations in fish therefore appear to be the result of complex interactions between nutrient supplies, characteristics of aquatic communities and the biogeochemical properties of particular contaminants in the catchments of eutrophied lakes.

In the case of riverine ecosystems, contaminant concentrations in some organisms appear to increase with eutrophication, apparently as a result of rapid cycling between water and benthic communities [31]. Thus, eutrophication can affect contaminant metabolism, cycling and biomagnification in diverse ways in different ecosystems. We urge further research to identify and quantify the complex mechanisms that regulate organic and inorganic contaminant processing and attenuation in nutrient-enriched systems.

Eutrophication and infectious disease risk

There might also be direct linkages between eutrophication and disease risk. Water-related diseases are a major cause of human morbidity and mortality worldwide [32], and recent evidence suggests that diseases can cause major impacts among aquatic organisms [33]. Clearly, biological waste disposal activities such as manure applications to cropland can simultaneously increase the loading of phosphorus, nitrogen and potentially hazardous coliform bacteria to surface waters [34]. However, enhanced nutrient loading alone might also influence the abundance, composition, virulence and survival of pathogens that are already resident in aquatic ecosystems. For example, increased nitrogen and phosphorus availability enhances the replication rate of aquatic viruses [35]. Similarly, lesions in marine coral communities caused by infections by *Aspergillus* fungi grow at faster rates under high nitrate availability [36]. Another potential nutrient–pathogen interaction involves changes in food quality: if eutrophication influences the nutrient content of food consumed by host organisms, then changes in host nutrition could alter host–pathogen dynamics and the ultimate outcome of infection [37].

Eutrophication can also influence the abundance of pathogens indirectly by modifying the abundance and distribution of their hosts and vectors [38]. For example, eutrophication-driven increases in host abundance increase the contact rate between infected and uninfected individuals [39]. Similarly, by increasing the abundance of the copepod vector of *Vibrio cholerae*, increases in nutrient loading can influence the probability of cholera epidemics in susceptible human populations [40].

Potential linkages between pathogens and nutrient availability could have important implications for managing human health in areas of lakes and oceans that have significant bathing-related activity. Recreational use of waters can spread fecal-oral viruses (enteroviruses, hepatitis A viruses, rotaviruses and others) that cause a broad range of gastrointestinal, respiratory, eye, nose, ear and skin infections [41]. We hypothesize that the risk of such infections could increase in eutrophic systems. If we are correct,

then such a trend could have important economic consequences as well as personal health concerns.

Such nutrient–pathogen interactions make it important to explore the effects of eutrophication on disease in much greater detail, especially in the face of major climate change [42]. Johnson and Carpenter [43] emphasized the need to integrate scientific experiments and ecological modeling to identify thresholds and feedbacks in the interactions between nutrient loading and host–pathogen dynamics. However, little is known about feedbacks in the other direction: can epidemic disease in aquatic systems exacerbate eutrophication? Such a scenario might result from diseases affecting the structure of food chains, possibly triggering a trophic cascade (Box 1). More research thus is needed on the mechanisms by which eutrophication interacts with other environmental stressors to influence disease [44]. Carefully designed studies are needed to clarify eutrophication–pathogen interactions, and to assist in the further development of disease risk models.

Harmful algae, nutrient management and the control of coastal eutrophication

The growth and abundance of aquatic organisms is typically enhanced by nutrient inputs. This enhanced productivity is sometimes channeled primarily into species

Box 1. Controlling nuisance blooms by manipulating food chains

The possibility of controlling the symptoms of eutrophication in North American lakes by ‘biomanipulating’ higher members of aquatic food chains instead of controlling nutrient inputs was pioneered by Joseph Shapiro and his students [60,61]. Early efforts focused on removal of bottom-feeding fishes such as carp, which increase the nutrient return from bottom sediments by physically stirring them and excreting nutrients obtained by benthic feeding. A later synthesis of northern freshwater lakes [9] showed that eutrophication can be exacerbated by the removal of piscivorous predators such as bass, pike and walleye by overfishing. This causes an increase in zooplanktivores, which in turn reduce grazing herbivores to low levels. The decreased grazing pressure allows phytoplankton to flourish. The trophic cascade caused by removal of piscivorous predators could thus cause a lake to move from a low algal phase to a high algal phase at the same nutrient loading. Similar results have been demonstrated in several whole-ecosystem experiments (see e.g. Refs [9,10]). High biomass algal phases generally occur when lakes contain one or three trophic levels, and low algal biomass phases are common when two to four trophic levels are present. These results have given rise to the idea that to reduce eutrophication, lakes should be managed to contain an even, rather than uneven, number of trophic levels.

There is also evidence that some grazers also increase the supply of nitrogen relative to phosphorus, by selective excretion of nitrogen [10,12]. *Daphnia*, an obligate freshwater herbivore, is known to do this because it selectively sequesters phosphorus [10]. The high N:P ratio in grazer-excreted nutrients in some systems thus can allow nitrogen-fixing cyanobacteria to be outcompeted by other species.

Deliberate manipulation of food chains in temperate lakes to contain an even number of trophic levels has thus shown some promise in controlling the symptoms of eutrophication. To be successful, it appears that interactions between trophic levels must be strong, with few consumer species feeding at more than one trophic level [62]. Given that cascading ecological interactions can occur in coastal waters as well, biomanipulation needs extensive further investigation in estuaries and coastal marine ecosystems to determine whether it is feasible or advisable.

that are directly harvestable for human consumption [45,46]. Unfortunately, however, excess nutrients often are instead utilized by taxa that are undesirable or harmful. For example, some nutrient-stimulated phytoplankton species are of a form or size that hinders their utilization by consumers, and accumulate as intense nuisance blooms [47]. A diverse set of algal species including diatoms, flagellates, chrysophytes and dinoflagellates can cause nuisance blooms, and many produce toxins that harm other organisms [48,49] and human health [50].

The frequency and intensity of harmful algal blooms (HABs) are thought to be increasing [51,52], and often accompany increased nutrient loading. Such blooms can cause surface or shoreline accumulations (Figure 1) and many other problems. The global economic impacts of HABs have not been fully calculated, but the cost of eutrophication on fisheries, drinking water treatment and the health of humans and livestock is likely to be billions of dollars per year. Red tides in US coastal waters alone created almost \$500 million in economic costs between 1987 and 1992 [53].

Extensive research worldwide indicates that increased nutrients are not the sole cause of all HABs [47,51], and a complete treatment of this topic is beyond the scope of this review. However, developing methods and tools to regulate undesirable algal growth is critical. Here we focus on nitrogen-fixing cyanobacteria, where freshwater studies have made extensive progress in terms of understanding how to manage blooms by controlling nutrient concentrations or ratios, or by manipulating higher members of food chains. We hypothesize that, like in lakes, the mean and peak summer biomass of nitrogen-fixing cyanobacteria in estuarine and coastal marine waters is closely dependent on the magnitude of phosphorus loading to the system (Figure 3; Box 2). Moreover, we conclude that reductions in nitrogen loading should in many cases be geared to reductions in phosphorus, so that N:P loading ratios are kept sufficiently high to discourage N₂-fixing cyanobacteria. However, we agree with other authors (e.g. [54]) that the freshwater-based phosphorus hypothesis of cyanobacterial growth will require extensive evaluation to test

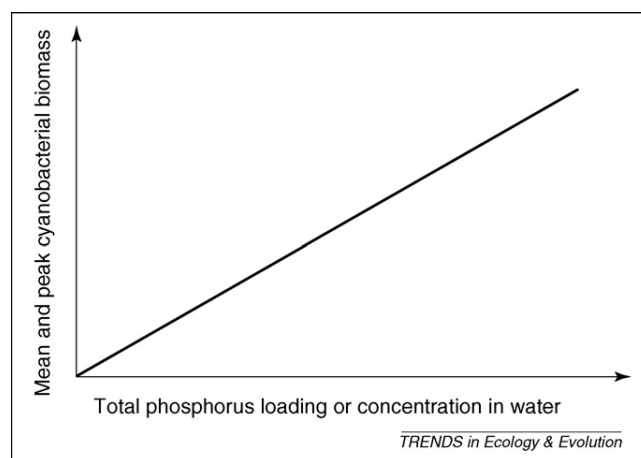


Figure 3. The mean and peak summer biomass of nitrogen-fixing cyanobacteria in estuarine and coastal marine ecosystems are predicted to be positively dependent upon phosphorus availability, as has been consistently observed in freshwater lakes (see text).

Box 2. Controlling nitrogen-fixing cyanobacteria blooms by managing nutrient inputs: phosphorus as a key element

In freshwaters, controlling or reversing eutrophication has relied largely on controlling inputs of one nutrient, phosphorus. However, it required ecosystem-scale experiments to reveal that phosphorus control was necessary. Despite evidence that nitrogen was often limiting during the summer months, whole-lake nutrient experiments at the Experimental Lakes Area (ELA) showed that phytoplankton always responded in proportion to added phosphorus, regardless of how much nitrogen was added as fertilizer. If the ratio of N:P in the fertilizer was below the average found in phytoplankton biomass, cyanobacterial species capable of fixing atmospheric nitrogen were favored. Over a period of years, fixation from the atmosphere and return from sediments allowed the total mass of nitrogen in the lake to increase relative to phosphorus. When nitrogen fertilization was decreased, symptoms of nitrogen limitation increased, and nitrogen-fixing cyanobacteria were increasingly favored [63]. Short-term nitrogen limitation in lake ecosystems was thus a response to excess phosphorus availability, and was not an indication that nitrogen loading to the system should be exclusively reduced instead of phosphorus.

Given the demonstrated success of small ecosystem-scale lake experiments in devising nutrient controls in inland sea-like Lake Erie [64] and in embayments such as Saginaw Bay, Lake Huron [65], we suggest that a similar approach might be useful in estuaries and coastal marine ecosystems, assuming proper implementation. The Stockholm Archipelago, for example, responded to reduced phosphorus loading, suggesting that phosphorus control measures will succeed in some low-salinity estuaries where nitrogen-fixing cyanobacteria are a problem [20,66]: in a 3 week seawater experiment, some mesocosms were fertilized with nutrients at high N:P ratios, while others were supplied with low N:P [16]. In all cases, low N:P ratios in the total nutrient supply were key to favoring bloom-forming N_2 -fixing cyanobacteria. Water column ratios of total N:P and inorganic N:P, by contrast, are imperfect predictors of cyanobacteria dominance, because they represent the overall result of external nutrient inputs, nitrogen fixation and within-system recycling.

Similarly, summer blooms of the cyanobacterium *Nodularia* in the Harvey Estuary (Western Australia) were directly related to total riverine phosphorus loadings during the previous winter [67]. Coastal marine simulation models [68] further suggest that phosphorus removal at St. Petersburg, Russia would reduce the biomass of nitrogen-fixing cyanobacteria in the entire Gulf of Finland. Similarly, reducing phosphorus loads in the most polluted rivers could be the most cost-effective way of improving water quality in the Baltic Sea [69].

The effects of nutrient loading on nuisance cyanobacteria could also depend on the structure of the local food web, however, because food web manipulations in coastal waters have provided results similar to those in many freshwaters [63]. In both kinds of systems, zooplankton might be able to suppress cyanobacterial populations by grazing, which keeps the size of the bacterial colonies too small to form nitrogen-fixing heterocysts. When zooplankton abundances are reduced, filament sizes increase, heterocysts form and N_2 fixation begins. This implies that food web structure might strongly interact with phosphorus availability to control heterocystous cyanobacterial abundance.

its applicability to estuarine and coastal marine water quality management, where water chemistry can differ strongly from that in freshwater, and HABs other than cyanobacteria are also a concern.

We stress, however, that the above conclusions might differ strongly for estuarine or coastal marine systems that exhibit objectionable growth of other taxa. Extensive evidence (reviewed e.g. in Refs [2,3]) suggests that controlling the diverse symptoms of eutrophication in many coastal systems will require careful management of nitrogen as

well as phosphorus loading. Whereas phosphorus control was successful in reducing algal blooms in the upper Neuse Estuary (North Carolina, USA), high nitrogen concentrations remained in the river water and transport of this excess N caused enhanced algal blooms in the more saline waters downstream [55]. Moreover, control of atmospheric nitrogen deposition could be needed for reasons unrelated to eutrophication, such as to avoid N deposition-related acidification of forest soils and lakes or high concentrations of nitrate in drinking water.

Whereas it is thus clear that phosphorus should be restricted [20], controlling the eutrophication of many estuaries and coastal marine waters will likely require careful basin-specific reductions in both N and P [7], with special attention to the type of eutrophication-related issues that must be controlled in the targeted system. It is noteworthy in this regard that the water framework of the European Union [56] has mandated removal of nitrogen as well as phosphorus. A consensus on optimal nutrient loading controls has not yet fully emerged for estuarine and coastal marine ecosystems, where many species of phytoplankton, macroalgae and macrophyte vegetation must be managed, and other key issues including hypoxia must be controlled. We suggest that only large-scale, long-term experiments and restoration attempts in diverse types of coastal waters, analogous to those performed in freshwater lakes, are likely to resolve current questions over the effectiveness of nutrient loading controls. However, it is clear that recovery of individual systems from eutrophication might require years or even decades (Box 3).

Conclusions

Remarkable advances have been made in our understanding of eutrophication during the past half-century (see e.g. Refs [3,6]). With relatively few exceptions (Box 3), reductions in phosphorus inputs have led to successful recovery from eutrophication in many lakes and a few low-salinity estuaries. The role of nitrogen in eutrophication of estuaries appears to be more complicated owing to the wide variety of potentially HAB-forming species and the effects of variable salinity on algal species composition. We note that to date, there is not a single well-documented case where reductions in nitrogen input alone have been shown to reduce eutrophication of a water body. Long-term ecosystem-scale experiments with phosphorus and nitrogen, similar to those that clarified the problem of eutrophication in freshwater, are needed for estuarine and coastal ecosystems. In short, our ability to predict the occurrence and composition of harmful algal blooms has lagged well behind our ability to control total algal biomass, and we urgently need advances in our ability to predict and to prevent the growth of undesirable algae and other nuisance-forming organisms. Moreover, we require a much better understanding of the significant but as yet poorly understood interactions that occur between nutrient enrichment and key physical, chemical and biological characteristics of receiving waters. In particular, we suggest that future research be focused on the cumulative effects of nutrient loading and other human-caused insults to lakes, especially inputs of toxic contaminants

Box 3. Recovery from eutrophication

Controlling nutrient inputs has allowed many lakes and several river, estuarine and coastal ecosystems to recover rapidly from eutrophication [2,3,55,57]. In some systems, however, recovery has been slow or negligible. Internal regeneration of nutrients could in many cases be responsible for the observed delays in recovery.

Whether or not lakes recover quickly once external phosphorus sources are reduced appears to depend on the concentration of iron. Most lakes with high concentrations of iron have little or no return of phosphorus from lake sediments. By contrast, lakes with low iron concentrations typically exhibit seasonal recycling of phosphorus from sediments. Although the mechanism is not fully understood, a possible reason for this phenomenon is that in high-iron lakes, phosphorus coprecipitates with ferric hydroxide when oxygen is abundant in the water column. If iron is scarce, phosphorus is free from control by iron coprecipitation, and is free to diffuse into overlying water, where it facilitates increased algal growth. Whereas all new phosphorus must originate from external sources, when concentrations of iron are low this externally supplied phosphorus can be recycled between sediments and water for many years. In extreme cases, internal recycling can contribute over 90% of phosphorus annually available to plankton. In some studies, iron or alum has been added to lakes to prevent the internal recycling of phosphorus. Such treatments have had variable success, reducing phosphorus concentrations for a few to several years [70]. Without such chemical treatments, however, it can take years or decades for a lake to reach a new steady state with reduced nutrient loading [62].

Decades of evidence indicate that the successful control of eutrophication in lakes involves reducing inputs of phosphorus to lake waters, whether the sources are external, such as sewage or land-use changes, or internal, by the recycling of phosphorus from sediments. Extensive new studies are needed to clarify and ultimately to manage the key physical, chemical and biological factors that determine the abilities of estuaries and coastal marine systems to recover from enrichment with both nitrogen and phosphorus.

and pathogens. We conclude that, as in lakes, carefully implemented restrictions of anthropogenic nutrient inputs will be an essential feature of eutrophication management efforts in estuarine and coastal marine ecosystems.

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