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Eutrophication of freshwater and marine ecosystems

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Abstract

Initial understanding of the links between nutrients and aquatic productivity originated in Europe in the early 1900s, and our knowledge base has expanded greatly during the past 40 yr. This explosion of eutrophication-related research has made it unequivocally clear that a comprehensive strategy to prevent excessive amounts of nitrogen and phosphorus from entering our waterways is needed to protect our lakes, rivers, and coasts from water quality deterioration. However, despite these very significant advances, cultural eutrophication remains one of the foremost problems for protecting our valuable surface water resources. The papers in this special issue provide a valuable cross section and synthesis of our current understanding of both freshwater and marine eutrophication science. They also serve to identify gaps in our knowledge and will help to guide future research.

Knowledge of the links between nutrients and aquatic productivity began with the pioneering work of Weber (1907) on German peat bogs and with Johnstone's (1908) studies of the North Sea. A crystallization of freshwater eutrophication concepts took place soon thereafter in Northern Europe, where the first trophic classification systems for surface waters were developed. These early classification systems were based on the intensity of aquatic organic matter production, as well as nutrient supply conditions and ecosystem-level consequences of increased production (e.g., hypolimnetic oxygen depletion; Rodhe 1969). There was a lot of uncertainty in the subsequent 50 yr about the physical, chemical, and ecological details of the eutrophication process, and hot debates raged about the relative roles of different mineral nutrients as constraints on, or regulators of, primary productivity, especially the macronutrients nitrogen (N), phosphorus (P), and carbon (C).

Work on the eutrophication process accelerated in the 1960s and 1970s. Particularly important was the landmark 1971 American Society of Limnology and Oceanography (ASLO) eutrophication symposium that culminated in the publication of the first special issue of *Limnology and Oceanography* (L&O) on nutrients and eutrophication, edited by G. E. Likens (Likens 1972*a*). This special issue was similarly stimulated by a symposium that the three of us hosted almost exactly 32 yr later at the February 2003 ASLO meeting in Salt Lake City, Utah. The 36 papers in this special issue were derived from oral presentations made at this symposium, as well as from manuscripts submitted in response to an open call to freshwater and marine eutrophication scientists.

Research motivation

In both textbooks and popular press articles, eutrophication in freshwaters has commonly been portrayed as a logical consequence of the natural aging of lake basins, which are often considered to become steadily less deep and more biologically productive over geological time (Rodhe 1969). However, recent evidence suggests that this classical pattern of succession from oligotrophic (nutrient-poor) to eutrophic (nutrient-rich) conditions is not necessarily followed in lake basins that are unaffected by human activity. For example, a study of chemical and biological trends in 33 lakes formed after landscape deglaciation in Glacier Bay National Park (Alaska) revealed an opposite trend: these relatively recent lakes grew more dilute and less productive during the past 10,000 yr (Engstrom et al. 2000).

Isolated lakes such as those studied by Engstrom et al. (2000) are increasingly rare, however; few if any surface waters worldwide remain undisturbed, either directly or indirectly, by human activities. We now know that anthropogenic nutrient loading to aquatic ecosystems (i.e., *cultural eutrophication*; Hasler 1947) from both point and nonpoint sources typically results in rapid increases in the rate of biological production and significant reductions in water column transparency and can create a wide range of undesirable water quality changes in freshwater and marine ecosystems (Carpenter et al. 1998; Howarth et al. 2000; National Research Council 2000). The global nature of the cultural eu-

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trophication problem (Smith 2003), its economic costs (Hoagland et al. 2002; Pretty et al. 2003), and the transnational implications of nutrient fluxes and eutrophication management (Howarth et al. in press) are abundantly clear.

As Schindler (2006) has stressed in this volume, our understanding of nutrient limitation and cultural eutrophication, as well as our ability to manage the consequences of nutrient overenrichment of freshwaters, has advanced dramatically during the past two decades. Schindler's comprehensive review traces advances in freshwater eutrophication from 1967 to present. A recent issue of *Estuaries* dedicated to nutrient overenrichment in coastal waters (Rabalais and Nixon 2002) provided an excellent overview of the state of knowledge in marine eutrophication research. This explosion of eutrophication-related research has made it unequivocally clear that a comprehensive strategy to prevent excessive amounts of nitrogen and phosphorus from entering our waterways is needed to adequately protect our lakes, rivers, and coasts from water quality deterioration (Howarth et al. 2000). Implementing this strategy successfully will require the best possible aquatic science, as well as good communication between scientists, policy makers, and water resource managers.

The papers in this special issue provide a valuable cross section and synthesis of our current understanding of both freshwater and marine eutrophication science. They also serve to identify gaps in our knowledge, and we believe that they will help to guide future eutrophication research.

Recent accomplishments in eutrophication science

Nutrient limitation of marine productivity—With rare exceptions (Schindler 1981), for much of the 20th century the study of eutrophication in estuaries proceeded in relative isolation from that of lakes. For example, in the first special L&O issue on eutrophication, the vast majority of papers were about freshwater lakes. There was little discussion about whether estuaries and nearshore marine waters might respond to nutrient loading differently from lakes, or which nutrient (nitrogen or phosphorus) might be primarily responsible for the eutrophication of coastal marine ecosystems (*see* Howarth and Marino 2006). Eutrophication-related water quality policy in the United States and Europe became directed primarily toward P control for both lakes and estuaries (OECD 1982; National Research Council 2000; Howarth et al. in press).

During the past 5–10 yr, great advances have been made in understanding marine eutrophication (Howarth et al. 2000; Rabalais and Nixon 2002). In this special issue, Howarth and Marino (2006) highlight the strong consensus that has developed among the scientific community that excess N loading is the primary cause of eutrophication in many coastal ecosystems. Smith (2006) compared the N and P dependence of chlorophyll *a* (Chl *a*) in 92 coastal ecosystems and showed a strong positive response of marine phytoplankton growth to N and P enrichment that was highly consistent with the general patterns that were reported previously in the limnological literature for freshwater lakes and reservoirs.

Nutrient limitation of stream and wetland productivity—Of the 18 papers published in the first L&O eutrophication special issue, none dealt with the effects of nutrient loading on stream ecosystems. In retrospect, this is surprising, given that streams and rivers constitute the most visible delivery mechanism for watershed- and atmosphere-derived nutrients to most lakes, reservoirs, estuaries, and coastal marine zones. This omission might be attributable to the prevailing early view that primary producers in flowing waters were nutrient saturated and that river ecosystems thus were insensitive to changes in nutrient inputs (Correll 1998; Smith 2003). However, both this concept and the related conclusion that physical factors such as light limitation and short hydraulic residence times will always prevent any algal responses to nutrient enrichment in rivers are no longer tenable. Numerous studies (Moss et al. 1989; Smith et al. 1997; Köhler and Gelbrecht 1998) clearly demonstrated eutrophication in many rivers worldwide. Because some skeptics have questioned whether algal biomass in river ecosystems will respond to nutrient controls, it is especially noteworthy that Donabaum et al. (2004) reported that suspended algal biovolume in the Old Danube River (Austria) responded sensitively to changes in total phosphorus concentrations, even though this response was hysteretic.

In this issue, Chételat et al. (2006) concluded that both nanoplankton and total potamoplankton biomass were significantly correlated with water column total phosphorus concentrations and were not related either to water residence time or to light availability. Building on the trophic state classification systems for lakes (Carlson 1977; OECD 1982), Dodds (2006) developed a new trophic state classification system for rivers and streams. Dodds' study revisits some of the ideas discussed 30 yr ago by Gene Likens, who presented a conceptual diagram of relationships between allochthonous inputs, autochthonous inputs, and the trophic state of freshwater lakes (*see* fig. 2 in Likens 1972*b*). Mallin et al. (2006) also considered the relative importance of allochthonous and autochthonous inputs in their comparative study of factors that control hypoxia in rivers, lakes, and streams.

Effects of eutrophication on food web structure—Nutrient enrichment causes an intensification of all biological activity and typically leads to dramatic changes in the composition and structure of aquatic food webs. Two of the most consistent eutrophication effects are a shift in algal species composition and an increase in the frequency and intensity of nuisance algal blooms, which in eutrophic freshwater lakes are typically dominated by harmful cyanobacteria (Downing et al. 2001; Huisman et al. 2005). One of the most important recent advances in our understanding of freshwater eutrophication is the discovery that the biological responses of producer organisms to nutrient availability can be strongly modified by consumer communities (Hrbacek et al. 1961; Shapiro and Wright 1984; Carpenter et al. 1995).

Eutrophication and grazing can also profoundly alter the biotic community structure of marine ecosystems (Worm and Lotze 2006). Olsen et al. (2006) found that mesozooplankton dominated by doliolids (Tunicata), but not by copepods, appeared to buffer the responses of autotrophs to high rates of nutrient loading. Among the many factors that potentially modify the responses of marine primary producers to nutrients, they suggested that the timescale over which the enrichment is made and the precise mode of nutrient enrichment could be very important.

Although the effects of nutrient loading have been much less well studied in wetland ecosystems (Crosbie and Chow-Fraser 1999), they too can be strongly affected by eutrophication. Gaiser et al. (2006) examined periphyton along transects in five Florida Everglades marshes and related their community structure and function to phosphorus gradients caused by nutrient-enriched inflows. Diatom species composition was strongly related to P availability, but the total phosphorus optima of many species varied between marshes. Although potential recovery trajectories in wetlands are not yet well understood, periphyton indicators should serve as excellent metrics for the progression or amelioration of eutrophication-related effects in wetland ecosystems like the Everglades.

Effects of eutrophication on aquatic biogeochemistry—Nutrient enrichment of aquatic ecosystems typically results in significant alterations in biogeochemical cycling over both space and time. Elemental fluxes can be followed with a variety of tools, including mass balance methods. Although mass balances for an aquatic system were first calculated by Johnstone (1908) in his studies of the North Sea, more than five additional decades elapsed before mass balance models became an integral part of the eutrophication modeling process (Smith 1998). Moosman et al. (2006) used mass balances to follow the internal fate of P in five lakes on the Swiss Plateau that were restored through a combination of external nutrient loading reductions and in situ aeration/oxygenation. Current P retention estimates were not found to differ between lakes with aeration or oxygenation and lakes with anoxic hypolimnia.

Nitrogen biogeochemistry in coastal waters was explored by several papers in this issue, in sharp contrast to the first special issue in which only the biogeochemistry of P was discussed. Dong et al. (2006) used an isotope pairing technique to monitor rates of denitrification and nitrous oxide (N_2O) formation and the sources of N_2 and N_2O in three U.K. estuaries of different trophic states. Ménesguen et al. (2006) used a new numerical technique for tracking chemical species in a multisource coastal ecosystem to help predict the growth and spatial distribution of *Ulva* in the Bay of Brest (France). Gardner et al. (2006) conducted continuous-flow experiments on intact sediment cores to evaluate internal N sources, sinks, and retention mechanisms in four Texas estuaries having different salinities. These three papers highlight how differences in internal N processing can influence the effects of N enrichment in estuaries.

Historical and paleoecological studies—In the first L&O special issue, Edmondson (1972) documented striking changes in the chemistry and biology of Lake Washington (Seattle, Washington) in response to nutrient enrichment and control. In the following three decades, it has become clear that historical reconstructions of past environments, as well as retrospective case studies of individual systems, provide important insights into the dynamics and potential reversibility of eutrophication-related change in aquatic ecosystems. Turner and Rabalais (2003), for example, showed that two centuries of land use change in the Mississippi River watershed are strongly reflected in the water quality of its streams and in the continental shelf ecosystem receiving its discharge.

Not surprisingly, analysis of temporal dynamics is a major focus of more than half of the papers in this special issue. Building significantly on their earlier study, Schelske et al. (2006) examined temporal dynamics in silicon and phosphorus biogeochemistry of the Laurentian Great Lakes in the 19th and 20th centuries. They concluded that biogenic silica (BSi) accumulation in lake sediments is a sensitive proxy for P enrichment because BSi production by diatoms integrates silica use over an annual timescale, silica is recycled slowly relative to P, and sedimented BSi is focused into depositional zones. Parsons et al. (2006) used sediment cores from three salt marsh ponds in coastal Louisiana to explore the usefulness of paleoecological records of eutrophication. Both sedimentary Chl *a* and a diatom-based trophic index were significantly and positively correlated with riverine or local nutrient indices. Their results suggest that these variables can be used as potential indicators of trophic state in coastal wetlands. Turner et al. (2006) used dated sediments and a suite of biological and geochemical proxies to reconstruct two centuries of water quality change in the shallow, subtropical Charlotte Harbor estuary (Florida). They concluded that without management intervention, an anticipated doubling of the watershed's population will result in much higher phytoplankton biomass accumulation, exacerbating current hypoxic conditions.

Case studies of individual ecosystems also provide valuable insights into both the dynamics and the direction of environmental change. For example, Foy and Lennox (2006) reported evidence for a delayed response of riverine P exports to agricultural intensification in the Lough Neagh (Ireland) watershed. In North America, Alexander and Smith (2006) modeled trends in total phosphorus and total nitrogen concentrations and associated changes in trophic state in 250 large U.S. rivers between 1975 and 1994. They found that the trophic state had improved at 25% of the monitoring sites and had worsened at fewer than 5% of the sites; approximately 70% of the study sites were unchanged.

As noted above, the biological expressions of eutrophication in aquatic ecosystems can be strongly modified by the activity of consumers, and flowing waters are no exception. Caraco et al. (2006) used a 15-yr data record to examine the controls of suspended algal biomass in the tidal freshwater Hudson River (New York). Their results add to a growing literature suggesting that ecosystem changes linked with high phytoplankton biomass depend on a diverse range of ecosystem characteristics, as well as whether phytoplankton biomass is controlled by food web interactions or nutrient availability.

Long term, real-time data sets also provide potential opportunities to tease out the relative importance of human versus natural drivers of change in aquatic ecosystems. For example, Paerl et al. (2006) examined the effects of anthropogenic and climatic perturbations on nutrient–phytoplankton interactions and eutrophication in the Chesapeake Bay (Virginia/Maryland) and Neuse River Estuary/Pamlico Sound (North Carolina) ecosystems. They cautioned that seasonal hydrologic perturbations can overwhelm nutrient controls on the floral composition of these estuaries, underscoring potential difficulties in predicting the responses of phytoplankton production and species composition to nutrient input reductions aimed at controlling the eutrophication of large estuarine ecosystems.

The Choptank and Patuxent tributaries of Chesapeake Bay have become eutrophic during the last 50–100 yr. Fisher et al. (2006) concluded that low N : P of sewage inputs to the Patuxent have resulted in an N-limited, P-saturated system; in contrast, the Choptank is primarily limited by N, with P limitation of phytoplankton during spring river flows. Carstensen et al. (2006) reported the responses of Danish waters to very strong nutrient control measures undertaken during the past two decades, which were aimed at reducing riverine N and P discharges to the sea by 50% and 80%, respectively. Their case study is among the first to document, at a large regional scale, significant decreases in water column nutrient concentrations resulting from active management strategies designed to reduce both diffuse and point source nutrient loading. The study by Soetaert et al. (2006) of long-term trends in dissolved inorganic nutrients in the tidal portion of the Scheldt estuary (Belgium/The Netherlands) provided further evidence of the sensitivity of marine systems to changes in nutrient loading.

Conclusions

The papers presented in this volume present current knowledge about the causes, consequences, and management of eutrophication. Although advances made during the 30 yr since the first L&O eutrophication special issue have been most rapid in freshwater lakes and reservoirs, our knowledge base has also expanded greatly for estuaries, coastal marine ecosystems, rivers, and wetlands. In particular, we conclude that it has been clearly established that two primary nutrients (P and N) can regulate aquatic primary productivity in most lakes and coastal marine ecosystems, although the actual response of primary producers to N and P enrichment can be modified by factors such as light limitation, hydrology, and grazing. In addition, the intensity and frequency of eutrophication-related water quality problems are often (but not always) correlated with the supply rates of N and P to the receiving waters. The management of nutrient loading thus can be expected to remain a keystone to maintaining desirable quality in our surface waters. However, we have also begun to better understand the ways in which the local biological expression of nutrient enrichment can be modified by site-specific factors, including food web structure.

We thus echo here the conclusion of Schindler (2006) that despite these very significant advances, eutrophication remains one of the foremost problems in protecting freshwater and coastal marine ecosystems. Many critically important questions remain to be answered in eutrophication science (Boesch 2002; Howarth et al. 2003).

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