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Harmful Algal Blooms and Eutrophication: Nutrient Sources, Composition, and Consequences

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ABSTRACT: Although algal blooms, including those considered toxic or harmful, can be natural phenomena, the nature of the global problem of harmful algal blooms (HABs) has expanded both in extent and its public perception over the last several decades. Of concern, especially for resource managers, is the potential relationship between HABs and the accelerated eutrophication of coastal waters from human activities. We address current insights into the relationships between HABs and eutrophication, focusing on sources of nutrients, known effects of nutrient loading and reduction, new understanding of pathways of nutrient acquisition among HAB species, and relationships between nutrients and toxic algae. Through specific, regional, and global examples of these various relationships, we offer both an assessment of the state of understanding, and the uncertainties that require future research efforts. The sources of nutrients potentially stimulating algal blooms include sewage, atmospheric deposition, groundwater flow, as well as agricultural and aquaculture runoff and discharge. On a global basis, strong correlations have been demonstrated between total phosphorus inputs and phytoplankton production in freshwaters, and between total nitrogen input and phytoplankton production in estuarine and marine waters. There are also numerous examples in geographic regions ranging from the largest and second largest U.S. mainland estuaries (Chesapeake Bay and the Albemarle-Pamlico Estuarine System), to the Inland Sea of Japan, the Black Sea, and Chinese coastal waters, where increases in nutrient loading have been linked with the development of large biomass blooms, leading to anoxia and even toxic or harmful impacts on fisheries resources, ecosystems, and human health or recreation. Many of these regions have witnessed reductions in phytoplankton biomass (as chlorophyll *a*) or HAB incidence when nutrient controls were put in place. Shifts in species composition have often been attributed to changes in nutrient supply ratios, primarily N:P or N:Si. Recently this concept has been extended to include organic forms of nutrients, and an elevation in the ratio of dissolved organic carbon to dissolved organic nitrogen (DOC:DON) has been observed during several recent blooms. The physiological strategies by which different groups of species acquire their nutrients have become better understood, and alternate modes of nutrition such as heterotrophy and mixotrophy are now recognized as common among HAB species. Despite our increased understanding of the pathways by which nutrients are delivered to ecosystems and the pathways by which they are assimilated differentially by different groups of species, the relationships between nutrient delivery and the development of blooms and their potential toxicity or harmfulness remain poorly understood. Many factors such as algal species presence/abundance, degree of flushing or water exchange, weather conditions, and presence and abundance of grazers contribute to the success of a given species at a given point in time. Similar nutrient loads do not have the same impact in different environments or in the same environment at different points in time. Eutrophication is one of several mechanisms by which harmful algae appear to be increasing in extent and duration in many locations. Although important, it is not the only explanation for blooms or toxic outbreaks. Nutrient enrichment has been strongly linked to stimulation of some harmful species, but for others it has not been an apparent contributing factor. The overall effect of nutrient over-enrichment on harmful algal species is clearly species specific.

Introduction

Algal blooms, including toxic events, can be natural phenomena. Historically, indigenous tribes avoided shellfish at certain places or times of year (e.g., Lescarbot 1609 cited in Prakash et al. 1971), and the logs of early mariners such as Captains James Cook and George Vancouver (Vancouver and Robinson 1798 cited in Prakash et al. 1971) describe discolored water and poisonous shellfish. Over the last several decades coastal regions throughout the world have experienced what appears to be an escalation in the incidence of blooms that are toxic or otherwise harmful. Commonly called red tides, these events are now grouped under the descriptor harmful algal blooms or HABs. Although most of the species involved are plant-like, photosynthetic algae, a few are actually animal-like protozoans without the

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ability to photosynthesize on their own. HABs have one unique feature in common—they cause harm, either due to their production of toxins or to the manner in which the cells' physical structure or accumulated biomass affect co-occurring organisms and alter food web dynamics. Impacts of these phenomena include mass mortalities of wild and farmed fish and shellfish; human illness and death from toxic seafood or from toxin exposure through inhalation or water contact; illness and death of marine mammals, seabirds, and other animals; and alteration of marine habitats and trophic structure.

A distinction must be made between two different types of HABs—those that involve toxins or harmful metabolites, such as toxins linked to wildlife death or human seafood poisonings, and those which are nontoxic but cause harm in other ways. Some algal toxins are extremely potent, and low-density blooms can be dangerous, sometimes causing poisonings at concentrations as low as a few hundred cells l^{-1}. Many HAB species that do not produce toxins are able to cause harm through the development of high biomass, leading to foams or scums, the depletion of oxygen as blooms decay, or the destruction of habitat for fish or shellfish by shading of submerged vegetation.

Eutrophication is the natural aging process of aquatic ecosystems. The term was formerly used mostly in reference to the natural aging of lakes wherein a large, deep, nutrient-poor lake eventually becomes more nutrient-rich, more productive with plant and animal life, and slowly fills in to become a pond, then a marsh (Wetzel 1983). More recently, the term has been used to refer to cultural or accelerated eutrophication of lakes, rivers, estuaries, and marine waters, wherein the natural eutrophication process is advanced by hundreds or thousands of years by human activities that add nutrients (Burkholder 2000). Nixon (1995, p. 95) defined eutrophication as "the process of increased organic enrichment of an ecosystem, generally through increased nutrient inputs."

Two nutrients in human-derived sources, phosphorus (P) and nitrogen (N), are of most concern in eutrophication. In freshwaters, P is the least abundant among the nutrients needed in large quantity (macronutrients) by photosynthetic organisms, so it is the primary nutrient that limits their growth (Schindler 1977). P can also limit or co-limit algal growth in estuarine and marine environments that are sustaining high N inputs (Rudek et al. 1991; Fisher et al. 1992). In many temperate and polar coastal marine waters, N is the most important nutrient that limits primary production of photosynthetic organisms (Dugdale and Goering 1967; Glibert 1988). N is often the nutrient that first limits primary production at the estuarine interface between marine and freshwater habitats. In lower estuaries both N and P can co-limit phytoplankton production (Rudek et al. 1991; Fisher et al. 1992). If improved sewage treatment reduces P loading within freshwater segments of a given river system, corresponding reductions in freshwater phytoplankton blooms will allow more inorganic N to be transported down to estuarine segments where it can support larger blooms (Fisher et al. 1992; Mallin et al. 1993). Both N and P are considered here, and these nutrients should be co-managed in the development of strategies to minimize HABs. Other nutrients such as silicon (Si) and iron (Fe) also can significantly influence the outcome of species dominance and the structure and abundance of phytoplankton communities under cultural eutrophication (Heckey and Kilham 1988; Wilhelm 1995).

For more than 50 years scientists have recognized that noxious blooms of toxic or otherwise harmful cyanobacteria (blue-green algae), the most common harmful algae in freshwater lakes, reservoirs, and slow flowing rivers, are stimulated by P enrichment (reviewed in Schindler 1977; Smith 1983). These organisms can form rotting hyperscum mats up to ca. 1 m thick, with billions of cells ml^{-1} and chlorophyll *a* (chl *a*; index of algal biomass) as high as 3,000 $\mu g\ l^{-1}$ (Zohary and Roberts 1989). Many species produce bioactive compounds, including potent hepatotoxins and neurotoxins that have caused livestock and wildlife death in most countries throughout the world (Skulberg et al. 1993; Codd et al. 1997) and, more rarely, death of humans as well (Chorus and Bartram 1999). The relationship between cyanobacteria and P is sufficiently strong that in many lakes of moderate depth ($\geq$ 10 m) with low abiotic turbidity, the spring-season concentration of total P in lakes (specifically, during lake overturn or total water column mixing) has been used with reasonable success to predict the late summer maximum in cyanobacterial biomass (as water-column chl *a*; Wetzel 1983). This relationship has also held in estuarine and brackish coastal waters of Scandinavia and Australia, where blooms of the toxic cyanobacterium, *Nodularia spumigena,* have been related to excessive P enrichment (Chorus and Bartram 1999).

In freshwater reservoirs and rivers, mixing and flushing dynamics are more complex, and abiotic turbidity from episodic sediment loading is appreciable. Light can be the primary resource limiting algal growth, rather than nutrients. The increased flow and mixing maintains relatively high nutrient supplies, and P has not been used successfully to predict the occurrence and extent of late summer cyanobacterial blooms (Canfield and Bachmann 1981; Thornton et al. 1990). Modest success in understanding nutrient stimulation of harmful algae, and in being able to reliably predict HABs from nutrient inputs, has been achieved to date only for cyanobacteria in clear-water lakes of moderate depth and dependable mixing regimes. Reliable prediction of the growth of HAB species in rivers (including run-of-river impoundments), estuaries, and coastal waters, characterized by highly complex and stochastic mixing and flushing patterns, has remained a challenge (Thornton et al. 1990; Burkholder 2000).

The nature of the global HAB problem in estuarine and coastal waters has changed considerably over the last several decades, both in extent and its public perception (Anderson 1989; Smayda 1990; Hallegraeff 1993). Virtually every coastal country is now threatened by multiple harmful or toxic algal species, often in many locations and over broad areas. This trend has been referred to as the apparent global expansion of HABs because for many locations, poor historic data are available. It is not clear as to how much of the increase reflects heightened scientific awareness and scrutiny of coastal waters and seafood quality versus an actual increase in the number, severity, or frequency of outbreaks (Anderson 1989). Many new bloom species are believed to reflect the discovery of hidden flora populations (Smayda 1989) which had existed in those waters for many years, but which had not been detected or recognized as harmful until the advent of more sensitive toxin detection methods or an increase in the number and training of observers (e.g., Anderson et al. 1994). The number of known toxic dinoflagellates has increased from roughly 20 only a decade ago to at least 55 today (Burkholder 1998), yet none of these more recently known species appear to be mutants or species that have suddenly become toxic. Geological records or past monitoring data, where available, indicate that in many locations these species were present in the plankton all along, but were not discovered until recently. As underscored by Hallegraeff and Bolch (1992), the accidental introduction of HAB species into an area via ballast water discharge can also be a contributing factor to the global expansion.

Of considerable concern, particularly for coastal resource managers, is the potential relationship between the apparent increase in HABs and the accelerated eutrophication of coastal waters due to human activities. Linkages between HABs and eutrophication have been noted within the past two decades (e.g., Officer and Ryther 1980; Lam and Ho 1989; Smayda 1989, 1990; Riegman 1995; Richardson and Jorgensen 1996; Richardson 1997). Coastal waters are receiving massive and increasing quantities of industrial, agricultural, and sewage effluents through a variety of pathways (Vitousek et al. 1997). In many urbanized coastal regions, these anthropogenic inputs have altered the size and composition of the nutrient pool which may, in turn, create a more favorable nutrient environment for certain HAB species.

From innovative syntheses of available databases worldwide, Smayda (1989, 1990) made a compelling case for the increase in blooms of some HAB species being a result of coastal eutrophication. He presented a unifying framework that stressed analogies in phytoplankton community response across geographic regions and encouraged scientists and resource managers to consider the previously neglected role of accelerated eutrophication in HABs. Now, more than a decade later, the heavy public and scientific attention given to HABs and apparent increasing trends, new outbreaks, or, in a few cases, outbreaks that have diminished in size or frequency, suggest that it is time to assess scientific progress in some of the issues that relate to possible human-induced changes in HAB distribution and dynamics. In particular, emphasis is needed on the physiological, ecological, and environmental mechanisms involved. There is no question that nutrients are required by HABs, as they are by all algal species. Here we address current insights into the relationships between HABs and eutrophication, focusing on sources of nutrients, the known effects of nutrient loading and reduction, new understanding of pathways of nutrient acquisition among HAB species, and the specific relationships between nutrients and toxic algae. Through local, regional, and global examples of these various relationships, we offer both an assessment of the state of understanding, and the uncertainties that require future research efforts.

Sources of Nutrients and their Relationship with HABs

Many sources of nutrients can stimulate harmful algal blooms, including sewage and animal wastes, atmospheric deposition, and groundwater inflow, as well as agricultural and other fertilizer runoff. Yet another source is the growing aquaculture industry in many coastal areas.

Human activities have had a tremendous impact on the global cycling of nutrients in coastal systems. The export of P to the oceans has increased 3-fold compared to pre-industrial, pre-agricultural levels, and N has increased even more dramatically, especially over the last 4 decades (Caraco 1995; Smil 2001). During that time, the flux of N increased 4-fold into the Mississippi River and more than 10-fold into the rivers entering the North Sea

(National Research Council 2000; Smil 2001). Human activity is estimated to have increased N inputs to the coastal waters of the northeastern United States generally and to Chesapeake Bay specifically by 6–8-fold (Boynton et al. 1995; Howarth 1998).

Point sources generally are less important nutrient contributors than nonpoint sources, when considered on an annual basis (National Research Council 2000). Point sources can be a major source of nutrients for small watersheds within, or adjacent to, major population centers. Wastewater contributes an estimated 67% of the N inputs to Long Island Sound annually, largely due to sewage from New York City. Sewage treatment plants deliver from 40–80% of the N to Kaneohe Bay, Hawaii, and to Narragansett Bay, Rhode Island (Nixon and Pilson 1983; National Research Council 1993). More rarely, point sources can be major components of nutrient loads to moderately sized watersheds. One point source, the world's largest phosphate mine, added 50% of the total P loading to the mostly agricultural Tar-Pamlico watershed of the Albemarle-Pamlico estuarine system in North Carolina for nearly 30 years (ca. 2,800 metric tons of free phosphate dust added per day to the Pamlico Estuary; reduced by $> 90\%$ in the early 1990s; North Carolina Department of Environment, Health and Natural Resources [NC DEHNR] 1994).

Nonpoint sources of nutrients (from agricultural activities, fossil-fuel combustion, and animal feeding operations) are often of greater concern than point sources because they are larger and more difficult to control. Howarth et al. (1996) estimated that sewage contributes only 12% of the flux of N from the North American continent to the North Atlantic Ocean. Only ca. 25% of the N and P inputs to Chesapeake Bay come from wastewater treatment plants and other point sources (Boynton et al. 1995). Even in relatively large watersheds the importance of point source contributions increases during summer low-flow conditions, when treated and untreated wastewater can represent 50% or more of the river flow (e.g., the Neuse estuary of the Albemarle-Pamlico estuarine system; NC DEHNR 1994). This point becomes especially important, given the fact that many harmful algal species are most active in summer low-flow periods.

Fertilizer application on land remains a major contributor to nonpoint nutrient pollution, and this source is still increasing at an alarming rate in many geographic regions (Vitousek et al. 1997). Both industrial and developing nations are using significantly higher loadings of fertilizer in agriculture, with global N and P fertilizer usage increasing 8-fold and 3-fold, respectively, since the early 1960s (Constant and Sheldrick 1992; Caraco 1995; Matson et al. 1997; Smil 2001). There is a direct relationship between population development, fertilizer applications, and riverine N and P fluxes (Fig. 1a,b; Caraco 1995; Smil 2001). When these nutrient supplies reach lower rivers, estuaries, and coastal waters, they are available for phytoplankton uptake and growth. The nitrate component of fertilizers can travel long distances. For example, Mallin et al. (1993) demonstrated a significant relationship between nitrate, carried ca. 400 km downstream to the lower Neuse estuary (over a 2-wk period), and increased phytoplankton productivity.

Nutrient inputs from runoff vary not only in quantity (influenced by rainfall and other environmental factors), but also in composition (based on the form of fertilizer in use), and this has important implications for HAB development. A dramatic trend in world fertilizer production is the increased proportion of urea in world N production, especially in third-world countries (Fig. 1c; Constant and Sheldrick 1992). Urea now comprises roughly 40% of all N fertilizers produced (Constant and Sheldrick 1992). This is significant because data indicate that in some areas, this shift in fertilizer composition has resulted in a shift in the nutrient composition of runoff, potentially favoring some HAB species.

Ground water has also been identified as an important source of nutrients to receiving surface waters. Human population growth and agricultural practices have increased nutrient loadings to ground water, and this has the potential to affect algal growth in adjacent rivers, lakes, estuaries, and coastal zones. In lakes the linkages between groundwater nutrient inputs and HABs (mostly as cyanobacteria) has been clearly demonstrated; Jones and Bachmann (1975) and Dillon and Rigler (1975) were able to reliably predict late summer phytoplankton biomass in natural lakes by taking into account the P supplied from septic effluent leachate. In coastal areas such linkages can be more complex and more difficult to prove conclusively.

Some success has been achieved relating groundwater flow to the growth of the harmful brown tide species *Aureococcus anophagefferens* in Long Island, New York. This species has been associated with loss of eelgrass meadows and reduction in reproduction and growth of shellfish (Tracey 1988; Dennison et al. 1989; Gallagher et al. 1989). LaRoche et al. (1997) hypothesize that in specific coastal bays, years with high inputs of ground water lead to high dissolved inorganic nitrogen (DIN) concentrations. *A. anophagefferens* is not a strong competitor when DIN is high, as

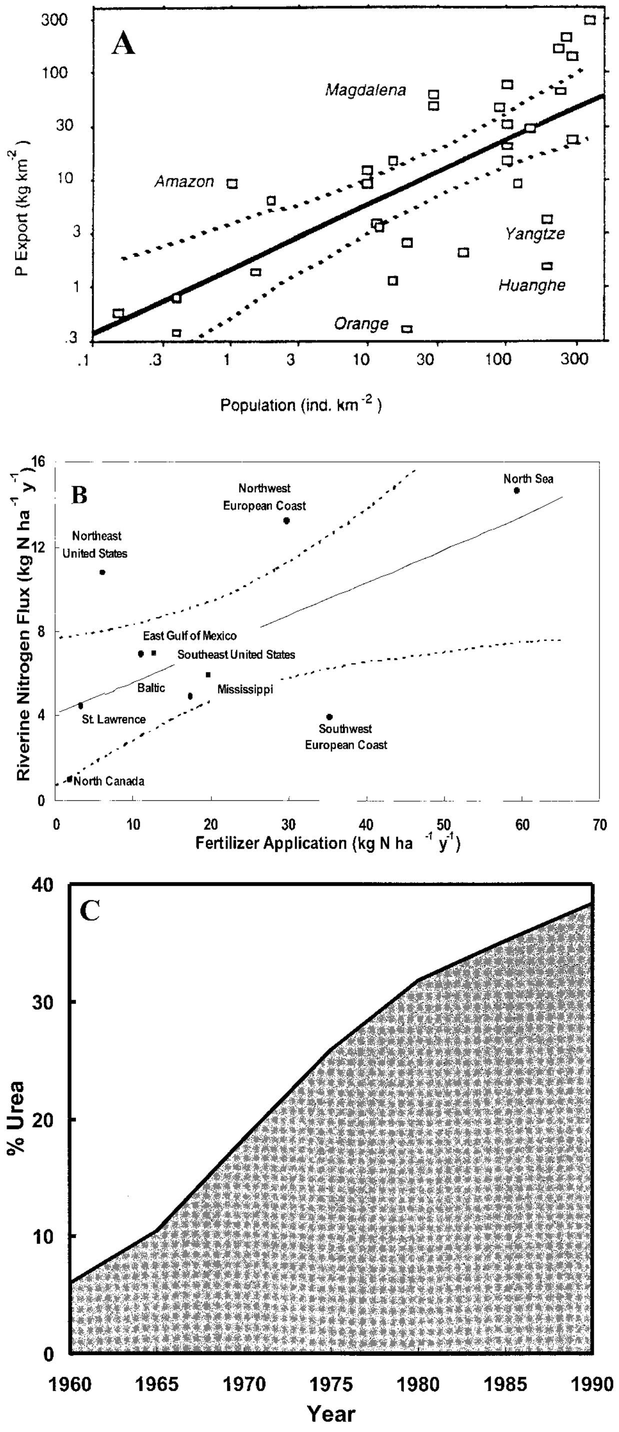

Fig. 1. Nutrient inputs to the world's oceans. A) The relationship between population density in watersheds and export of soluble reactive phosphorus (SRP) in river water, considering 32 major rivers (from Caraco 1995). B) The relationship between the rate of fertilizer applications and the flux of riverine nitrogen in many of the world's coastal ecosystems (from Smil 2001). C) Trends in the proportion of the contribution of urea to world N fertilizer production from 1960 to 1990 (from Constant and Sheldrick 1992).

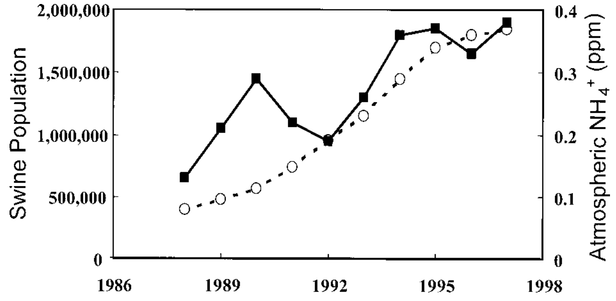

Fig. 2. Example of localized, significant increase in atmospheric ammonium (squares) from concentrated animal operations (circles; Sampson County, North Carolina, where there are 48 swine per person [ca. 2 million swine in total]). Approximately 72% of the variability in airborne ammonia during the past decade can be explained by the expansion of the county's swine population, alone. Much of the nitrogen volatilized as ammonia during spray-application of swine effluent onto fields is deposited into receiving rivers and streams within a distance of ca. 100 km radius (modified from Mallin 2000).

shown in nutrient enrichment studies in mesocosms, where the cell density of *A. anophagefferens* was inversely correlated with DIN concentrations (Keller and Rice 1989). When groundwater input is low, decay of the algal biomass created in previous years from high DIN leads to elevated levels of dissolved organic nitrogen (DON) which *A. anophagefferens* can use efficiently (Berg et al. 1997). A groundwater index relationship has been formulated that correctly hindcasts brown tide blooms in 9 of 11 years on Long Island, but the relationship has not held for all embayments in which this species blooms (Gobler 1999; Lomas et al. 2001; Borkman and Smayda unpublished data). If the groundwater hypothesis is valid, the LaRoche et al. (1997) study also suggests that there can be a significant time lag between human activities that enrich the ground water (such as heavy fertilizer usage) and the eventual HAB impact. In Long Island Sound, it is possible that the massive brown tides which began suddenly in 1985 may reflect heavy fertilizer usage on land 10 or 20 years earlier.

On local to global scales, one of the most rapidly increasing sources of nutrients to both freshwaters and the coastal zone is the atmosphere (Figs. 2 and 3). Phosphate adsorbed onto fine particulates, and nitrate derived from particulate or oxidized nitric/nitrous oxides in wet and dry deposition, have long been recognized as important sources of nutrients to streams and lakes, and can be major sources especially for softwater, nutrient-poor freshwater systems (Likens et al. 1979; Kilham 1982; Swedish Ministry of Agriculture 1982). In estuarine and coastal waters, it has been estimated that 20–40% of N inputs can be of atmospheric origin, from industrial, agricultural, and urban sources (Duce 1986; Fisher and Oppenheimer 1991; Paerl 1995,

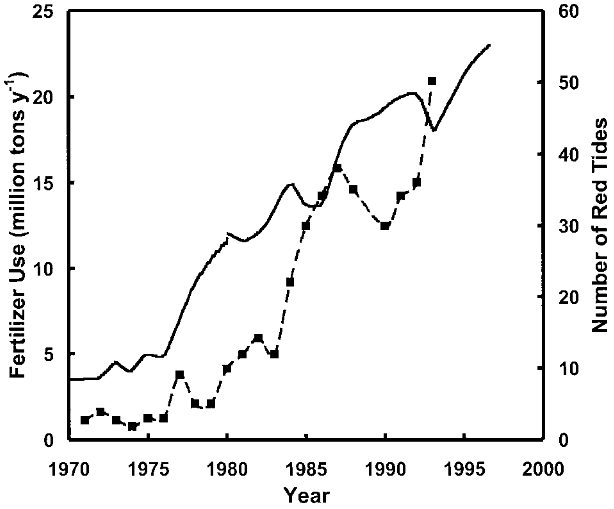

Fig. 3. Trends in fertilizer use and the number of red tides reported for Chinese coastal waters (data redrawn from Smil 2001 and Zhang 1994). While the general pattern is increasing for both parameters, it is thought that atmospheric deposition may also play an important role in the development of these blooms.

1997; Driscoll et al. 2001). In other areas more removed from such sources, this proportion can be lower, such as in the Gulf of Mexico where atmospheric inputs (1–2% of the total) are overwhelmed by contributions from the Mississippi and Atchafalaya Rivers (Paerl et al. 2000).

Atmospheric inputs are important not only because of their magnitude, but because the mix of atmospheric nutrients, like other nutrient sources, can stimulate some phytoplankton species disproportionately over others. Experimental manipulations have shown that rainwater can enhance productivity more than the addition of a single N source (Paerl 1997). The high proportion of DON in rainwater, representing up to 40% of its total N, is thought to be significant in this enhancement (Timperley et al. 1985; Paerl 1997). Blooms in the Yellow Sea of China, which have escalated in frequency over the past several decades (Fig. 3), have been related to atmospheric deposition in addition to direct nutrient runoff (Zhang 1994). It is estimated that a typical rain event over the Yellow Sea may supply sufficient N, P, and Si to account for 50–100% of the primary production of a HAB event (Zhang 1994).

The atmosphere, through both wet and dry deposition, may also be a source of key trace metals such as Fe (Church et al. 1991; Duce and Tindale 1991). Phytoplankton in many estuaries and coastal waters (where most HAB species occur) can be Fe-limited (e.g., Wells 1999), and additions of atmospheric Fe could therefore contribute to some bloom events (Martin and Fitzwater 1988; Cullen 1991; Coale et al. 1996). Interactions between Fe and N can influence plankton community structure (e.g., DiTullio et al. 1993), and may be a factor in the regulation of growth and encystment of dinoflagellates (Doucette and Harrison 1991) and possibly in the toxicity of diatoms such as *Pseudo-nitzschia* spp. (Rue and Wells unpublished data).

Aquaculture ponds and cage culture systems represent another source of nutrients, provided as feed or fertilizer and by the biological transformations occurring in these high biomass systems. It has been suggested that these enriched systems may promote the growth of harmful species not previously detected in the source water (Anderson 1989; Hallegraeff 1993). The cultured animals retain only a fraction of their food, the rest decomposes in the water column or settles to the bottom and decomposes, and either way, the nutrients released from this decomposition can stimulate phytoplankton growth (Cho et al. 1996; Burford 1997; Burford and Glibert 1999). The effect can be worsened if the aquaculture site is constructed in wetlands (e.g., salt marshes or mangrove swamps) that otherwise would serve as a sink rather than a source of nutrients to the system.

Sakamoto (1986) calculated that nutrients released from fish culture sites affect an area 3–9 times the size of the aquaculture zone. In a quiescent system, this sustained input could affect productivity in the area, but the extent of the nutrient impact may diminish with higher rates of flushing by tides and currents. Recognizing the need for dilution, fish farming operations in the northwestern U.S. have shifted from easily accessible but poorly flushed bays and coves to areas with much stronger currents resulting in a significant reduction in particulate and dissolved nutrient buildup and reduced planktonic and benthic impacts (Rensel personal communication). Many fish farms in developing countries are located in shallow, easily accessible bays where nutrients can accumulate and stimulate algal blooms (e.g., Wu et al. 1994). Benthic nutrient regeneration of the accumulated feces and decomposing feed may be a significant and sustained source of nutrients in such systems. The situation in these environments was described in harsh terms by Romdhane et al. (1998, p. 82), in referring to fish farms in Tunisian lagoons, “. . . eutrophication following increased human activity in and around these lagoons influences the magnitude and frequency of toxic blooms. Lagoons may function as traps for toxins or other exudates from algae. We therefore stress that aquaculture inside lagoons is a hazardous business.”

There is no simple generalization about the impacts of aquaculture operations on plankton communities, or specifically, on HABs, although it is clear that in waters with a high density of aquaculture operations and poor flushing, the cumulative input of nutrients has impacts on plankton productivity. As is the case with the other sources of nutrients to coastal waters, the increased nutrient loading will lead to increased phytoplankton production, but whether this leads to toxic impacts depends on whether toxic species are present and on the relative abundance of the nutrient elements, the mixing and hydrographic characteristics of the area, and other factors such as grazing intensity or light availability.

Nutrient Loadings, Nutrient Reductions, and High-Biomass HABs

On local, watershed, and global scales, strong correlations have been shown between total P input into freshwaters, and between total N input into estuaries and coastal waters and total phytoplankton production (Schindler 1977; Wetzel 1983; Nixon 1992; Mallin et al. 1993). HAB species, like all plant-like organisms require certain major and minor nutrients for their nutrition, and these can be supplied either naturally from freshwater and marine biogeochemical processes or through human activities such as pollution. These nutrient sources include dissolved inorganic and organic compounds of various types, as well as particulate nutrients in the form of other organisms or detritus.

In attempting to understand the impacts of nutrient availability and nutrient loading on an aquatic ecosystem, it is important to make the distinction between effects on physiological processes or productivity versus biomass accumulation. As initially developed conceptually by Caperon et al. (1971) and applied more recently to the Chesapeake Bay (Malone et al. 1996), nutrient loading responses can be viewed in a manner analogous to a saturating response curve (Fig. 4). The effects of nutrients may fall in the minimal response region, which is dominated by rapid physiological adjustment and low biomass accumulation, or alternatively, in the maximum response region, in which physiological processes have become saturated, but biomass accumulations continue. The minimum response region of the curve also represents the period of bloom initiation, whereas the maximum response region represents bloom maintenance. As the period of bloom initiation is characterized by minimal increases in biomass, the role of nutrients in bloom initiation is far less understood than for the period during which a bloom may have been maintained. Ultimately, the entire response may be saturated at exceptionally high loading rates due to limitation by some other factor. Within this framework, it is important to recognize that in the minimum response region, impacts are few, difficult to detect, and easy to reverse, while in the maximum response region, impacts are large and often easy to detect, but substantially more difficult to reduce and control.

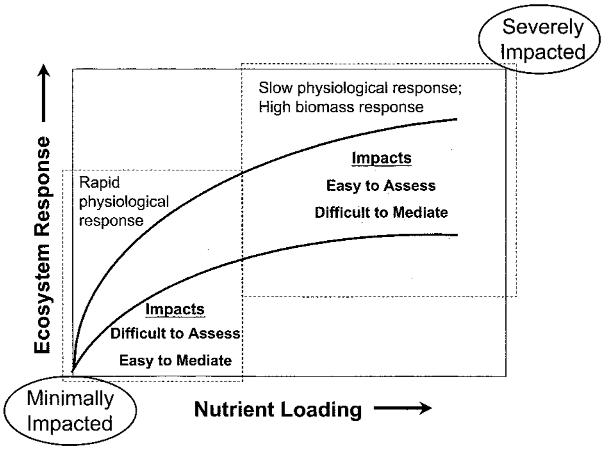

Fig. 4. Generalized ecosystem response to nutrient loading. At low levels of nutrient loading, the organismal response may be rapid, but biomass changes would be few. At high rates of nutrient loading, the physiological responses of the organism would be expected to be at or near saturating rates, and would show little increase, yet on a longer time scale, biomass would increase.

Nutrients can stimulate or enhance the impact of toxic or harmful species in several ways. At the simplest level, harmful phytoplankton may increase in abundance due to nutrient enrichment, but remain in the same relative fraction of the total phytoplankton biomass. Even though non-HAB species are stimulated proportionately, a modest increase in the abundance of a HAB species can cause it to become noticeable because of its toxic or harmful effects.

A more frequent response to nutrient enrichment occurs when a species or group of species begins to dominate under the altered nutrient regime. In deeper freshwater, estuarine, and coastal marine systems, phytoplankton dominate the algal flora. Macroalgae and benthic microalgae often dominate many lakes and shallow, poorly flushed estuaries, lagoons, and upper embayments, as well as coral reefs and rocky intertidal/subtidal habitats (Harlin 1993). In surface waters across the entire salinity gradient, there are many examples of overgrowth and high biomass blooms by phytoplankton, benthic microalgae (especially epiphytes), and macroalgae. In many cases, the responding dominant species are not toxic and, in fact, are beneficial to coastal productivity until they exceed the assimilative capacity of the system, after which anoxia and other adverse effects occur. When that threshold is reached, seemingly harmless species can have negative impacts.

In this context, much has been written about the links between freshwater flow, nutrient loading (as total P and phosphate), and increased nontoxic (as well as toxic) cyanobacterial blooms in lakes, and the associated bottom-water anoxia, benthic animal mortalities, and fish kills that can follow these outbreaks (Vallentyne 1974). Freshwater flow and nutrient loading (mostly as nitrate) have been linked to increased numbers of estuarine algal blooms (as diatoms and other typically benign microalgae or as macroalgae), followed by oxygen deficits and finfish and/or shellfish kills (Harlin 1993; Mallin et al. 1993).

Increases in high biomass phytoplankton blooms have been reported from the south China Sea (Qi et al. 1993), the Black Sea (Bodeanu and Ruta 1998), Hong Kong (Lam and Ho 1989), and many other locations, typically in parallel with the nutrient enrichment of coastal waters. In Chesapeake Bay, high phytoplankton biomass is typically observed in the spring, associated with high riverine nutrient inputs (Glibert et al. 1995; Malone et al. 1996). These large spring blooms eventually settle to the bottom, where heterotrophic bacteria process a major fraction of the organic material. This can result in depletion of oxygen as temperatures warm (Malone et al. 1986; Shiah and Ducklow 1994), leading to anoxia and benthic mortalities (e.g., Boynton et al. 1982; Malone et al. 1983; Fisher et al. 1988, 1992; Glibert et al. 1995). As another example, spring eutrophication from the N loading of the Mississippi and Atchafalya Rivers to the Gulf of Mexico has resulted in enhanced phytoplankton production and the development of anoxia in the Gulf of Mexico, a so-called dead zone that has altered benthic food web dynamics substantially (Turner and Rabalais 1994; Rabalais et al. 1996).

One of the clearest examples of the direct development of a toxic species in response to increased nutrient loading is the development of *Pseudo-nitzschia* spp. on the Louisiana shelf in the extended plume of the Mississippi River. Blooms of *Pseudo-nitzschia* spp. develop in high abundances during the spring when nutrient loading is highest (Dortch et al. 1997; Parsons et al. 1998, 1999; Pan 2001). Both historical data and frustules preserved in cores (Dortch et al. 1997, 2000; Parsons et al. 2002) indicate a large increase in *Pseudo-nitzschia* spp. abundance since the 1950s, concomitant with increases in nutrient loading. Studies in mesocosms have also demonstrated a disproportional increase in *Pseudo-nitzschia* spp. following nutrient pulsing (Dortch et al. 2000).

Flushing rate or turnover time (the rate at which all of the nutrient-laden water is exchanged or moved out of the lake, river, or estuary) and water depth play a major role in the duration of the period in which nutrients are available to algal assemblages. Lakes and reservoirs with high flushing rates and high P loading have significantly less algal production than similar systems with poor flushing (e.g., Dillon 1975; Canfield and Bachmann 1981). The same is true of flushing in estuaries and coastal waters, where shallow systems typically support more algal growth than deeper systems (Wetzel 1983; Day et al. 1989). Chesapeake Bay has an estimated mean turnover time of ca. 35 d and a mean depth of ca. 9 m (Magnien et al. 1992). N and P loads are estimated at ca. 80×10^6 kg N yr^{-1} and 4×10^6 kg P yr^{-1}, of which 55–70% is delivered during the winter-spring freshet (Magnien et al. 1992; Boynton et al. 1995). Phytoplankton biomass during early spring blooms that are supported by these nutrient supplies can exceed 50 μg chl *a* l^{-1} (Glibert et al. 1995; Malone et al. 1996). The Neuse estuary has a mean water turnover time of ca. 80 d and a mean depth of ca. 3.5–4 m (Glasgow and Burkholder 2000; Glasgow et al. 2001a). In this smaller, poorly flushed, shallow system, loadings of ca. 5×10^6 kg N yr^{-1} and $6–8 \times 10^5$ kg P yr^{-1} have supported late winter-spring blooms of benign (nontoxic) dinoflagellates with biomass as high as 300 μg chl *a* l^{-1} (Glasgow and Burkholder 2000; Glasgow et al. 2001a).

Repeated incidence of increased, high-biomass blooms provide evidence of a broadly based, stimulatory effect on phytoplankton from anthropogenic nutrients. The evidence for this relationship is further strengthened by repeated observations that HABs tend to decrease when nutrient loading is reduced. Among the most cited early reports of partial reversal of cultural eutrophication in freshwater involved removing sewage discharges from Lake Washington within metropolitan Seattle, Washington (Edmondson 1970). This lake had sustained noxious cyanobacteria blooms prior to the 1920s because of raw sewage inputs. Zero discharge of sewage to Lake Washington was imposed in 1968, and the cyanobacterial blooms declined. In a much larger system, Great Lake Erie, the green macroalga *Cladophora* had choked much of the west basin with massive growth until improved wastewater treatment and detergent phosphate bans in the early 1980s led to significant reduction in the nuisance blooms (Ashworth 1986).

Reduced nutrient loading similarly has promoted declines in estuarine and marine coastal HABs. Sewage discharges to the Mumford Cove, a shallow estuary in Connecticut were rerouted to another waterway in the late 1980s, and within two years massive nuisance blooms of the macroalga, *Ulva*

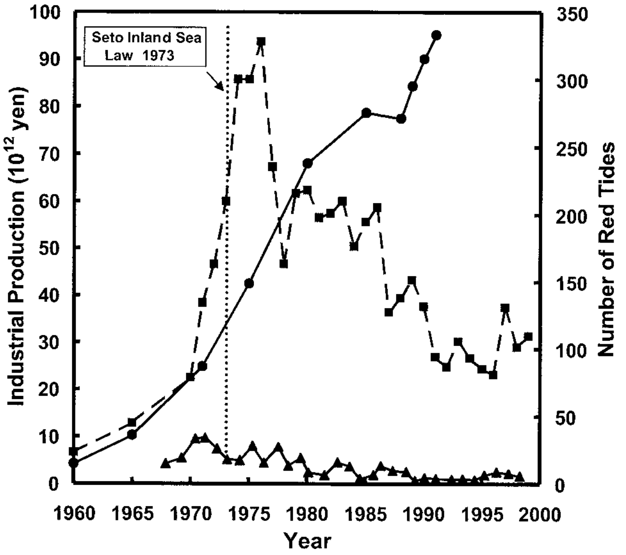

Fig. 5. Trends in industrial production (circles) and the number of visible red tides (squares) in the Seto Inland Sea of Japan. The vertical line represents the passage of the Seto Inland Sea Law in 1973, after which nutrient loadings were reduced to one-third of 1974 levels. The triangles denote the number of red tides with fisheries impacts (redrawn from Okaichi 1997 with additional data from Fukuyo).

lactuca, were eliminated (Harlin 1993). In the Seto Inland Sea in Japan between 1965 and 1976, the number of red tide outbreaks (high biomass blooms) increased 7-fold (Okaichi 1997), in parallel with the increase in industrial production and chemical oxygen demand (COD) from domestic and industrial wastes (Fig. 5). In 1973, Japanese authorities instituted the Seto Inland Sea Law to reduce COD loadings to half of the 1974 levels over a 3-yr period. The number of red tides began to decrease in 1977, eventually falling to less than 30% of the peak frequency, which had been in excess of 300 blooms yr^{-1} (Fig. 5). This lower level of bloom incidence has been maintained to the present. These data demonstrate a general increase in phytoplankton abundance due to overenrichment, and a proportional decrease in blooms when that loading was reduced. It is interesting that toxic blooms (in this instance, those that cause fish mortalities or other fisheries damage) also decreased after the loadings were reduced (Fig. 5).

Another important observation from the Seto Inland Sea is that as the waters became less eutrophic and large biomass blooms decreased, there was a shift in species composition, leading to a greater prevalence of some that are responsible for shellfish poisonings in humans, such as *Alexandrium tamarense* and *A. catenella.* Paralytic shellfish poisoning (PSP) caused by these species was not reported in the Inland Sea several decades ago, but is common now (Fukuyo personal communication). This emphasizes a common dilemma faced by coastal managers, namely that effluent controls may reduce the number of phytoplankton blooms, but those actions may not result in fewer HAB impacts. This can happen because some species (and their high biomass blooms) may decrease in frequency or disappear as the waters become cleaner, but there are other harmful or toxic species that can fill that niche and have negative impacts. This reflects the great variation among HAB species in the levels of nutrients that are optimal for growth. In some cases, oligotrophic HAB species that are not good competitors when nutrient loads are high can thrive as loadings from land diminish. PSP-producing *Alexandrium* spp. have long occurred in Alaska, northeastern Canada, and northern Japan; all areas with relatively unpolluted and historically pristine waters (e.g., Horner et al. 1997). On Long Island, shellfishermen who have been devastated by recurrent *A. anophagefferens* brown tides since 1985 point out that immediately prior to the outbreaks, the affected waters are cleaner with more transparency compared to the past when brown tides did not occur (McElroy 1996). Reductions in nutrients generally will reduce blooms, but may not necessarily reduce all the potentially harmful impacts of HABS or all of the HAB species.

Another example of the effect of nutrient reduction comes from the freshwater-to-brackish Potomac River, a tributary of the Chesapeake Bay, where phosphate removal from sewage began in the late 1970s. This region had previously experienced repeated blooms of *Microcystis* spp. with chlorophyll concentrations in surface waters exceeding 70 $\mu g\ l^{-1}$, but after the nutrient reductions, there were sustained decreases both in total chlorophyll and in the frequency and intensity of the *Microcystis* blooms (Jaworski 1990). Chlorophyll levels were generally $< 20\ \mu g\ l^{-1}$.

A final example is from the northwestern Black Sea, which experienced heavy pollution loading in the 1970s and 1980s due to industrialization, fertilizer use, and urbanization in eight countries within that watershed, followed by reductions in these loads in the 1990s. Significant increases in inorganic and organic nutrients were noted over that initial 20-yr interval: nitrate was 2.5–8 times higher, and phosphate was up to 20-fold higher (Bodeanu 1993). A consequence of this enrichment was an increase in the frequency and magnitude of algal blooms, as well as changes in the species composition. In the 1960s, high biomass blooms were rare, but during the two decades of intense eutrophication pressure, blooms became recurrent, with cell densities greatly exceeding past abundance levels (Bodeanu 1993). During the 1980s, when nutrient loadings peaked, 49 major blooms were reported, of which 15 had > 10 million cells l^{-1} (Bodeanu and Ruta 1998). Anoxia, fish mortalities, and other impacts were frequent. A characteristic of this interval was the decreased abundance of diatoms and larger algae, and their replacement by flagellates and nanoplankton. In a striking reversal, algal blooms began to decrease in 1991, both in number and size, and this trend has continued to the present. Diatoms became more dominant, and nanoplankton and flagellates decreased. From 1991–1996, there were only three blooms with cell concentrations in excess of 10 million cells l^{-1}. This reduction in blooms coincided with significantly decreased fertilizer usage as a result of the loss of economic subsidies that accompanied the breakup of the former Soviet Union (Bodeanu and Ruta 1998). It will be interesting to see if the positive trend in bloom incidence of recent years is reversed when economic development, and thus fertilizer usage, increase in the coming years.

There are a number of examples where increases and decreases in nutrient loadings due to human activities have resulted in parallel increases or decreases in bloom incidence. Many of these examples are of high biomass blooms, that cause harm through excessive population development and its decay. Other factors need to be considered in understanding phytoplankton compositional changes that lead to development of HAB outbreaks, but not necessarily to high biomass production.

Nutrient Composition and HAB Development

Many factors affect phytoplankton species composition and bloom development, and among these is the composition of the nutrient pool—the forms of the nutrients supplied, as well as the relative abundance of the major nutrient elements. Some generalities are beginning to emerge with respect to the preference of many bloom-forming species for specific forms of nutrients, as well as the tendency for some blooms to occur when the ratios of nutrient availability or supply are altered. The latter concept is based largely on the nutrient ratio hypothesis (Tilman 1977; Smayda 1990, 1997) which argues that environmental selection of phytoplankton species is associated with the relative availability of specific nutrients in coastal waters, and that human activities have altered these nutrient supply ratios in ways that change the natural phytoplankton community composition and possibly favor harmful or potentially toxic forms.

Perhaps the clearest demonstration of the effect of altered nutrient supply ratios involves the stimulation of non-diatom species following changes in the availability of N or P relative to silicate. Diatoms, the vast majority of which are harmless, require silica in their cell walls, whereas most other phytoplankton do not. Since silica is not abundant in sewage effluent but N and P are, the N:Si or P:Si ratios in some lakes, rivers, estuaries, and coastal waters have increased over the last several decades (Shelske et al. 1986; Smayda 1989, 1990; Rabalais et al. 1996). In theory, diatom growth will cease when silica supplies are depleted, but other phytoplankton classes can continue to proliferate using the excess N and P.

Research is ongoing in various geographic regions to further examine this concept, which is supported by several data sets. From a long-term database in Great Lake Michigan, Schelske et al. (1986) found evidence of silica depletion that was correlated with increased anthropogenic P loading through the early 1970s. By the 1980s, cyanobacteria and colonial green algae had increased to codominance with diatoms, but at that point P inputs began to decline. The phytoplankton community then shifted from ca. 50% cyanobacteria and colonial greens to replacement by flagellates in summer with diatoms dominant in the spring. Similarly, in marine waters of Tolo Harbor in Hong Kong, there was an 8-fold increase in the number of red tides (mainly dinoflagellates) per year between 1976 and 1989, in parallel with a 6-fold increase in human population density and a 2.5-fold increase in nutrient loading in that watershed that altered the nutrient ratios (Lam and Ho 1989). In the mid to late 1980s, as pollution loadings decreased due to the diversion of sewage effluent to Victoria Harbor, there was a resurgence of diatoms and a decrease in dinoflagellates and red tides (Yung et al. 1997).

These blooms in Tolo Harbor show a distinct relationship with nutrient ratios, but not just N:Si or P:Si. Hodgkiss and Ho (1997) demonstrated that the numbers of dinoflagellate red tides increased as the annually averaged N:P ratio fell from 20:1 to 11:1 between 1982 and 1989 (Fig. 6). In more detailed analysis of the patterns during a single year, Hodgkiss (2001) showed that whenever the N:P ratio fell below ~10:1 in Tolo Harbor, dinoflagellate cell numbers increased. These two inverse correlations are consistent with experimental data, whereby the three major dinoflagellate species in Tolo Harbor in the 1980s (*Prorocentrum micans, P. sigmoides,* and *P. triestinum*) were shown to have optimal N:P ratios for growth of 5–10, 4–15, and 8–15:1, respectively, all significantly below Redfield proportions. As the N:P ratio in Tolo Harbor decreased between 1982 and 1989, these species increased in abundance.

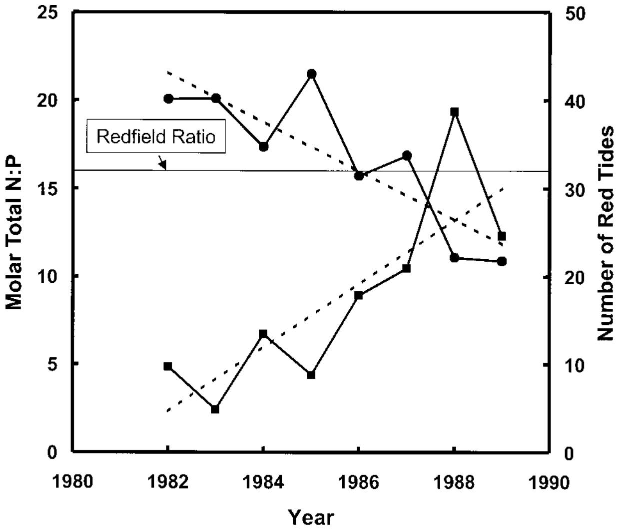

Fig. 6. Trends in the N:P molar ratio (circles) and the number of reported red tides (squares) in Tolo Harbor, Hong Kong from 1980 to 1990 (redrawn from Hodgkiss and Ho 1997).

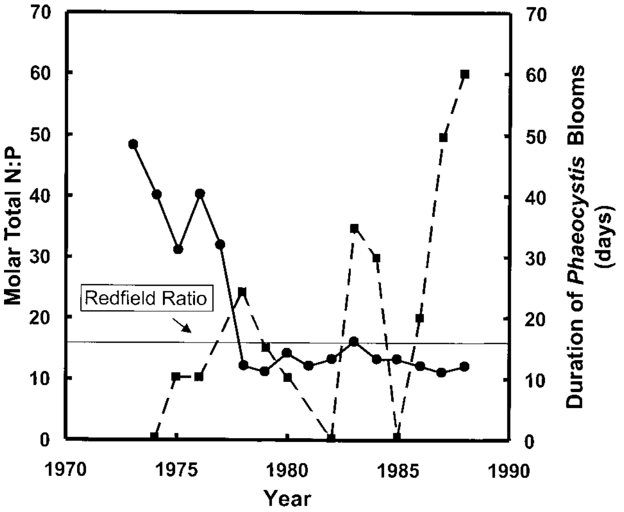

Fig. 7. Change in N:P molar ratio (circles) in Dutch coastal waters coincident with increase in *Phaeocystis* blooms (squares; redrawn from Riegman 1995).

In Tunisian lagoons where *Gymnodinium aureolumi* (formerly *Gyrodinium aureolum*) was found to be the cause of repeated fish kills in aquaculture systems, blooms occurred when the N:P ratio (which was normally very high) began to decline in the autumn (Romdhane et al. 1998). There is evidence to suggest that the ichthyotoxic dinoflagellate *Pfiesteria piscicida* may do disproportionately well when the ratio of N:P decreases following an increase in the availability of phosphate (Burkholder and Glasgow 1997; Burkholder et al. 2001b; Glasgow et al. 2001b).

Another prominent example of the importance of nutrient supply ratios in determining phytoplankton species composition is seen with the foam-producing prymnesiophyte *Phaeocystis poucheti.* A 23-year time series off the German coast documents the general enrichment of these coastal waters with N and phosphate and a 4-fold increase in the N:Si and P:Si ratios (Radach et al. 1990). This was accompanied by a decrease in the diatom community and an increase in the occurrence of *Phaeocystis* blooms. Mass occurrences of this species began in 1977 in the North Sea (Cadée and Hegeman 1986) and increased in cell abundance and bloom duration through 1985. The general N and P enrichment of that coastal area resulted in winter concentrations an order of magnitude higher than those in adjacent Atlantic waters (Lancelot 1995). The abundance of these nutrients is less of an issue than their relative proportions. These blooms were first related to the increase in N:Si ratios, particularly following the spring diatom blooms which depleted the silica but not the nitrate (Cadée and Hegeman 1986; Smayda 1990). Riegman (1995) further showed that in mixed phytoplankton assemblages in the laboratory, *P. poucheti* became dominant only when N:P ratios were 7.5 or lower, and at N:P ratios of 1.5, there was almost complete *P. poucheti* dominance. These relationships are consistent with the trends for summer blooms of *P. poucheti* in Dutch coastal waters, which accompanied a shift from P-limitation to N-limitation in the area; lower N:P ratios coincided with higher, and more variable, *P. poucheti* abundance (Fig. 7).

Nutrient ratios may also be affected by other types of human development in addition to direct nutrient pollution. The building of dams has numerous associated environmental problems, including the potential for altered water quality. Dam construction, coincident with increased P loading, has led to diatom blooms, and thus to the sequestration of silica (Turner and Rabalais 1991). In the development of the massive Three Gorges Dam in the upstream region of the Changjiang (Yangtze River), the potential for eutrophication and other massive environmental and cultural damage has been greatly debated (Zhang et al. 1999). In this system, it is thought that by the year 2010, silica will be significantly reduced due to diatom uptake and sediment trapping by the dam, and this combined with the trend of increasing N loading will lead to very high N:Si and N:P ratios downstream. As the Changjiang watershed supplies nearly 10% of the total world population's water resources and 40% of the Chinese national food production, the societal benefits from the dam are significant, as is the potential for negative impacts on the health of coastal ecosystems (Zhang et al. 1999).

The nutrient ratio concept has recently been expanded to include the relative abundance of different chemical forms of nutrients, such as organic versus inorganic N and carbon (C) compounds. Recent studies in enriched coastal areas have shown that while productivity may increase quantitatively with overall N availability, the DON component may contribute disproportionately to the changes in phytoplankton succession, apparently favoring the development of some HABs (Paerl 1988; Berg et al. 1997; LaRoche et al. 1997; Lomas et al. 2001). The DON pool is composed of a wide range of compounds from small amino acids and urea to complex molecules such as proteins and humic acids. Some are available for assimilation by the phytoplankton, whereas many other compounds are highly refractory and not readily used. One component of the DON pool, urea, has been shown to be highly correlated with the outbreak of harmful dinoflagellates in estuarine fish ponds (Glibert and Terlizzi 1999), where elevated levels of urea were associated with significant dinoflagellate outbreaks 73% of the time, but urea concentrations of < 1.5 μM were not associated with any dinoflagellate blooms. In several Chesapeake Bay tributaries, high urea concentrations have also been found to precede large blooms of the dinoflagellate *Prorocentrum minimum* (Glibert et al. 2001). The trend toward increasing applications of urea fertilizer (Constant and Sheldrick 1992) may increase the likelihood of blooms of organisms that grow well on this nutrient.

Several HABs have been shown to be related to an elevation in the ratio of dissolved organic carbon (DOC):DON. Three separate blooms in Chesapeake Bay occurring over a 3-yr period, including *P. piscicida, P. minimum,* and *A. anophagefferens,* were all correlated with elevated DOC:DON ratios relative to the long-term mean (Glibert et al. 2001; Fig. 8). The elevation in this ratio for these particular blooms was a reflection of both elevated levels of DOC as well as a depletion of DON. Lomas et al. (2001) have shown this relationship to be robust for numerous brown tide blooms in Long Island, New York (Fig. 8). During a bloom of *Gymnodinium* spp. in Kuwait Bay, the ratios of DOC:DON for stations collected within the bloom were approximately twice those determined for non-bloom stations with a mixed phytoplankton assemblage (Heil et al. 2001; Fig. 8). This relationship is deserving of additional study in other bloom conditions. Of particular interest in this context is the potential change in DOC:DON preceding blooms.

Pathways of Nutrient Acquisition

An understanding of physiological responses is further complicated by the fact that the rate of nutrient supply will not necessarily correlate with the rate of nutrient assimilation by the algae, as the latter is controlled by nutritional preferences, uptake capabilities, and physiological or nutritional status. The response by either the total phytoplankton community or individual species within the community also depends on many factors, including interactions with grazers and physical forcings such as turbulence. Grazers may inhibit the development of phytoplankton biomass through their feeding, while at the same time, enhance the regeneration of nutrients through their release and excretion. This in turn will alter the balance of reduced versus oxidized forms of N (Glibert 1998).

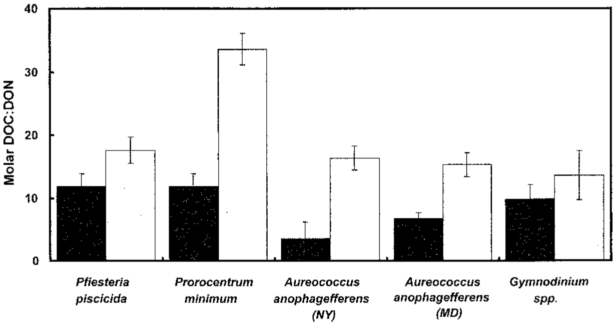

Fig. 8. Relationship between DOC:DON for numerous bloom periods and locations. In each case, the dark bars represent either long-term average non-bloom periods for the same sites or comparable sites outside of the bloom region. The gray bars represent the periods during the peak of bloom occurrence. The non-bloom data from the *P. piscicida* and *P. minimum* blooms represent long-term monitoring results for tributaries of Chesapeake Bay. The *P. piscicida* bloom occurred in these same tributaries in Maryland in 1997, and the *P. minimum* bloom occurred in the same region in 1998. The *A. anophagefferens* blooms were sampled either in New York or Maryland coastal bays in 1999. The *Gymnodinium* spp. bloom was sampled during a red tide event in Kuwait Bay, 1999 (data were derived and redrawn from Glibert et al. 2001; Lomas et al. 2001; and Glibert unpublished data).

The assimilation of nutrients by phytoplankton depends on environmental factors such as light, temperature, and water column stability with different environmental effects having differential impacts on different nutrient substrates. The uptake of ammonium and urea are usually thought to be less light dependent than the uptake of nitrate (MacIsaac and Dugdale 1972; Fisher et al. 1982), and the temperature dependence of ammonium uptake may also differ from that of nitrate (Lomas and Glibert 1999a). Water column stability is another critical factor influencing species composition. Blooms of *Karenia* cf. *mikimotoi* have been associated with warm, stable conditions, and can persist for extended periods with low light and low nutrients (Dahl and Tangen 1993). In Norwegian waters, these blooms initiate at the pycnocline in the summer or early autumn in offshore waters, then collect at hydrographic fronts in nearshore waters (Dahl and Tangen 1993). In Tunisian lagoons, where blooms of *G. aureolum* have caused repeated fish kills, a correlation has been found between the development of blooms and decreasing day length, consistent with the frequency of these blooms being greater in late summer or autumn (Romdhane et al. 1998). Any potential effects of nutrient stimulation on HAB biomass or productivity must be considered within the physical and environmental tolerances of the particular species of concern.

In recent years, the physiological strategies by which different groups of species acquire their nutrients have become better understood. Rapidly growing marine diatoms have been highly correlated with large and/or frequent additions of nitrate, in part because they have physiological adaptations which allow them to exploit nitrate-rich conditions (Takahashi et al. 1982; Goldman 1993; Lomas and Glibert 1999a,b, 2000). Microflagellates, including dinoflagellates, are most frequently associated with low nitrate concentrations, higher ammonium, urea, or DON supply, and consistent physiological preference for reduced N forms (e.g., Berg et al. 1997; Carlsson et al. 1998; Lomas and Glibert 1999b). Most estuarine and coastal marine HAB species are microflagellates. Harmful estuarine dinoflagellates tend to occur in waters that have seasonally high phosphate and nitrate, as well as high DOC and other organic nutrient forms (Burkholder and Glasgow 1997; Burkholder et al. 1997, 2001a,b; Magnien et al. 2000; Glasgow et al. 2001a; Glibert et al. 2001). Indeed, the brown tide species that blooms in Texas, *Aureoumbra lagunensis* is incapable of nitrate uptake, and thus must use reduced N forms (DeYoe and Suttle 1994).

An important physiological adaptation of many flagellate species, including some HAB species, is the ability to acquire both N and C via particle ingestion or by the uptake of dissolved organic compounds (reviewed in Granéli and Carlsson 1998). Such mixotrophic or heterotrophic tendencies have been linked with the ability of these cells to thrive in environments where inorganic nutrients or light may otherwise be insufficient to meet their nutritional or C demands. Toxic *Chrysochromulina polylepis* cultures have been shown to consume more algal food when limited by P compared to nutrient-replete and N-limited conditions (LeGrand et al. 1996). Mixotrophy is now considered essential for the survival and growth of many *Dinophysis* species, including those responsible for diarrhetic shellfish poisoning (DSP). This is supported by uptake of ^{14}C in the dark, either from direct ingestion of labelled algal prey or dissolved organic substances released by those algae (Granéli et al. 1997). Using different methods, Jacobson and Anderson (1996) found food vacuoles containing prey fragments (probably ciliates) in *Dinophysis norvegica* and *D. acuminata,* confirming these species' ability to ingest particulate food. Other common HAB species have also been shown to be mixotrophic, including *Heterosigma carterae* (= *H. akashiwo*), *A. tamarense* (Nygaard and Tobiesen 1993), and *Gyrodinium galatheanum* (= *Karlodinium micrum*; Li et al. 2000, 2001). Given the importance of mixotrophy in many species, as well as the development of new methods to measure ingestion and C uptake (Schnepf and Elbrächter 1992; Stoecker 1999; Stickney et al. 2000), the number of HAB species known to be mixotrophic will likely increase as more are examined for this characteristic (Burkholder and Glasgow 1995, 1997; Burkholder et al. 2001b).

A unique example of mixotrophic nutrition is the toxic *Pfiesteria* complex (two species—*P. piscicida* and *Pfiesteria shumwayae*; Burkholder et al. 2001a,b). These dinoflagellates are heterotrophs, yet they can be stimulated directly and indirectly by inorganic as well as organic nutrient enrichment (Burkholder and Glasgow 1997, 2001; Burkholder et al. 1998a, 2001a,b; Glasgow et al. 2001b; Parrow et al. 2001). Like other heterotrophic dinoflagellates (Schnepf and Elbrächter 1992), they can take up inorganic and organic nutrients directly (e.g., dissolved amino acids: Burkholder and Glasgow 1997; Glasgow et al. 1998; nitrate, ammonium, and urea: Lewitus et al. 1999a). *Pfiesteria* spp. are not capable of photosynthesis on their own, but zoospores can retain chloroplasts from algal prey (Burkholder and Glasgow 1997; Lewitus et al. 1999a,b; Glasgow et al. 2001c). This phenomenon, kleptochloroplastidy, is increasingly recognized in dinoflagellates and some protozoan ciliates (Stoecker 1998; Skovgaard 1998).

Kleptochloroplastidy allows *Pfiesteria* spp. to function as mixotrophs for hours to days (Lewitus et al. 1999a). In this mode, cells can take up N directly (Lewitus et al. 1999a). *Pfiesteria* spp. have also been shown to be stimulated indirectly by nutrient enrichment, mediated through the abundance of algal prey that they consume when fish are not present (Burkholder and Glasgow 1995, 1997; Glasgow et al. 1998; Parrow et al. 2001). The ability to consume an array of prey ranging from bacteria to mammalian tissues, as well as dissolved substrates, allows *Pfiesteria* spp. to thrive where food is abundant (Burkholder and Glasgow 1995, 2001; Burkholder et al. 2001b). Toxic *Pfiesteria* outbreaks have occurred in shallow, poorly flushed estuaries that have been highly impacted by nutrient overenrichment, including the Neuse, Pamlico, and New River estuaries of North Carolina and the tributaries of Maryland's eastern shore (Burkholder et al. 1995, 1997; Lewitus et al. 1995; Burkholder and Glasgow 1997; Glasgow et al. 2001a). In both laboratory and field studies, *Pfiesteria* zoospore production has been shown to be stimulated by human and animal wastes (Burkholder and Glasgow 1997, 2001; Burkholder et al. 1997). Nutrients provide a food-rich habitat for *Pfiesteria* spp., but other environmental conditions are required for toxic *Pfiesteria* activity, especially poor flushing, fish in abundance, and brackish salinities (Burkholder and Glasgow 1997; Glasgow et al. 2001a). The ability of these heterotrophic dinoflagellates to function photosynthetically, and to switch between modes of nutrition and among an array of prey types as conditions change, represents a significant survival mechanism.

Many phytoplankton have the ability to acquire some of their nutrients via extracellular oxidation or hydrolysis. Extracellular amino acid oxidation has been shown to occur in a wide range of flagellates and in a range of ecosystems, although this process appears to be expressed to a greater degree when ambient inorganic nutrient levels are at or near depletion (Palenik and Morel 1990a,b; Pantoja and Lee 1994; Mulholland et al. 1998). Proteins and peptides may also be hydrolyzed at the cell surface, producing smaller compounds that can be taken up by the cells (Hollibaugh and Azam 1983; Keil and Kirchman 1992; Pantoja et al. 1997; Pantoja and Lee 1999). While much is still to be learned about the role of this process in the development of HABs, there is some evidence that certain HAB species possess this ability (Mulholland et al. 2000).

The uptake of organic compounds may contribute to the C requirements of HAB cells, in addition to their N or P requirements. The suggestion that C acquisition may stimulate algal growth rates through organic uptake is by no means new (Schell 1974; Wheeler et al. 1974; Lewitus and Kana 1994). Specific examples of the linkage between DOC uptake and HAB development, however, are only now beginning to emerge. In 1998, a new species of dinoflagellate, *Kryptoperidinium carolinium* (sp. ined.; formal description ongoing by Lewitus unpublished data), was observed in the waters of coastal South Carolina. Following intensive monitoring of all forms of inorganic and organic nutrients, it was concluded that bloom initiation followed the pulsed delivery of organic nutrients (Lewitus et al. 2001). Bloom development was coincident with a greater than 3-fold decrease in both DOC and DON. These findings underscore the need to incorporate organic nutrients and heterotrophic potential in both monitoring and models of HAB population dynamics.

Indirect Nutrient Linkages with HABs

All too frequently, public perception of whether nutrient over-enrichment has reached undesirable levels has been based on acute, obvious or easily measured symptoms, such as high biomass algal blooms, massive fish kills, and oxygen deficits. Because of this focus, a broad array of indirect, chronic, often-subtle but serious impacts of nutrient pollution on aquatic ecosystems remain underemphasized and, in some cases, poorly understood. The available data indicate that these chronic, indirect impacts can be important in controlling the growth of HAB species over the long term in lakes, rivers, estuaries, and marine coastal waters.

As eutrophication progresses, for example, shifts in phytoplankton communities toward declines in certain diatom species in favor of less desirable nanoplankton and flagellates can lead to subtle but important changes at higher trophic levels. Some freshwater diatom species that grow best in low nutrient regimes produce lipids that are essential for zooplankton sexual reproduction. Under nutrient over-enrichment, these species are replaced by species that produce low or negligible quantities of these lipids (Kilham et al. 1997). In estuarine waters, spawning of green sea urchins and blue mussels appears to be triggered by a heat-stable metabolite that is released in high abundance by certain species of phytoplankton that decline with cultural eutrophication (Starr et al. 1990). Replacement species that thrive under nutrient enrichment produce low or negligible quantities of the substance. At the same time, excessive nutrient loading has led to the decline and, eventually, the disappearance of rooted vegetation that is critically important to the survival of animals such as certain zooplankton, finfish, and/or shellfish which graze on algae. Overfishing has led to significant declines in some shellfish species, such as oyster populations in Chesapeake Bay (Newell 1988; Rothschild et al. 1994). Such factors would interact in depressing grazing activity which, in turn, would indirectly encourage growth of phytoplankton, including HAB species, under nutrient enrichment (Burkholder 2000).

Nutrient loading seldom occurs alone. Atmospheric deposition contains nutrients as well as acid-imparting contaminants and toxic substances such as pesticides; cropland runoff carries not only nutrients, but pesticides and suspended sediments (Miller 2000). Nutrients in poorly treated human sewage and animal wastes are added to surface waters along with heavy metals and other toxic substances, suspended solids, estrogens and estrogen-mimic substances, and a wide array of microbial pathogens (Burkholder et al. 1997; Mallin 2000;

Miller 2000). Excessive nutrients act in concert with these other, co-associated pollutants to cause physiological stress and disease in sensitive grazing fauna which, again, could indirectly help to promote the growth of harmful algae through lowered grazing pressure and facilitated access to weakened fish by some harmful algae that consume them as prey.

Other factors such as suspended sediments or grazing pressure may reduce or negate a potentially stimulatory nutrient effect. In turbid lakes and reservoirs with high episodic sediment loading, and systems with relatively rapid flushing rates, high P loading may not stimulate phytoplankton blooms because of light limitation and short water turnover times (Dillon 1975; Cuker et al. 1990; Burkholder et al. 1998b). Cyanobacteria can bloom under low light availability by taking advantage of periods between episodic sediment loading events when the water clears, or by using mechanisms for buoyancy regulation to position themselves near the water surface (Burkholder et al. 1998b; Dortch unpublished data). In lakes with low to moderate nutrient loading, grazing pressure from large-bodied zooplankton can significantly reduce the populations of most phytoplankton species, balancing the nutrient stimulation effect (Harper 1992).

Similar observations have been reported in estuaries and coastal waters. The Pearl River estuary supplies a huge pollution load to the waters of the south China Sea, including the western waters of Hong Kong, yet the number of red tides and general chlorophyll levels are low compared to the conditions in Victoria Harbor and areas to the east. Tang et al. (2001) hypothesized that this inverse relationship between nutrient loading and algal biomass is due to the high sediment loads that accompany the Pearl River discharge. Light limitation would prevent the full utilization of the nutrients supplied to the phytoplankton.

In San Francisco Bay, increased nutrient loads have resulted in increased secondary production in the benthos, which in turn modulates the algal biomass (Cloern 1982). In an analogous manner, primary production in the Bay of Brest, France, is nutrient limited, even with large nutrient loadings from its tributaries. Nutrient inputs have increased 3-fold since 1975, yet chlorophyll levels have not changed significantly (Le Pape et al. 1996; Le Pape and Ménesguen 1997). Primary productivity has increased slightly, but grazing pressure has as well, particularly in the benthos. In this case, the main control of eutrophication pressures appears to relate to a strong tidal influence and hydrodynamic exchange. The resulting stirring hinders the formation of a persistent surface mixed layer where phytoplankton have access to nutrient inputs and to light. Horizontal tidal currents cause significant water exchange with the Iroise Sea, and reduce the accumulation of nutrients and plankton in the Bay. As has been observed in certain other systems, nutrient loading has been beneficial in that it supports increased productivity. Such beneficial effects should continue as long as those loadings fall within the assimilative capacity of the system.

In some cases, indirect relationships between nutrient loading or availability and the development of a HAB species may be difficult to establish, due to the complexities of the nutrient cycling pathways involved. These may be on short temporal and spatial scales, or on longer-term scales. One example of such pathways potentially leading to HAB development involves the release of DON following N fixation. Blooms of the N-fixing cyanobacterium *Trichodesmium* have been found to release a significant fraction of their newly fixed N in the form of ammonium and DON (Capone et al. 1994; Glibert and Bronk 1994). In dense blooms of this organism, the concentration of reduced N forms can be enriched several-fold over control sites (Karl et al. 1992; Glibert and O'Neil 1999; O'Neil et al. submitted). It has been suggested that this production of reduced N fuels red tide blooms of *Karenia brevis* (= *Gymnodinium breve*) off the coast of Florida (Walsh and Steidinger 2001; Lenes et al. 2001). Likewise, DON release by *Trichodesmium* has been shown to be correlated with an increase in the development of dinoflagellates such as *Dinophysis* off the coast of Australia (O'Neil et al. submitted).

Another example of indirect stimulation of HAB species by nutrients is the ichthyotoxic dinoflagellate, *P. piscicida*. In toxic strains of this organism, temporarily nontoxic zoospores are the precursors of actively toxic zoospores. These nontoxic zoospores have been found to increase in response to elevations in chlorophyll (Burkholder and Glasgow 1997; Glasgow et al. 2001a), and their growth rates have been shown to vary widely depending on the form of algal prey (Burkholder and Glasgow 1995; Glasgow et al. 1998; Burkholder et al. 2001a; Parrow et al. 2001). Nutrients may select for certain phytoplankton species which may promote *Pfiesteria* growth in temporarily nontoxic mode.

Links between Nutrients and Toxicity

The discussion thus far has centered on nutrient pools as they affect the growth and accumulation of HAB cells. There is evidence that nutrients can play a major role in the regulation of toxicity in some HAB species, and this can have significant implications to toxin monitoring programs and public health decisions. In some cases, toxicity can increase or decrease dramatically depending on the limiting nutrient. Saxitoxin production by *A. tamarense* can be 5–10-fold higher in P-limited versus N-limited cells (Boyer et al. 1987; Anderson et al. 1990). Likewise, domoic acid production by *Pseudo-nitzschia multiseries* is inversely correlated with the ambient Si concentration in batch culture (Pan et al. 1996a). In that study, cells began accumulating this toxin only when the division rate declined as a result of partial or total depletion of silica. When cultures were N-limited, no toxin was produced. Toxin production was greatly enhanced under P-deficient conditions in continuous cultures (Pan et al. 1996b). Recent results also suggest that Fe limitation can enhance toxicity in *Pseudo-nitzschia* spp. (Rue and Wells unpublished data).

For other HAB species a similar picture emerges: toxin production varies significantly with different degrees and types of nutrient limitation. The dinoflagellate *D. acuminata* produced elevated levels of the DSP toxin, okadaic acid, under both N and P limitation, but the enhancement was 6-fold larger with N-limitation (Johansson et al. 1996). In an analogous although opposite manner, *Chrysochromulina polylepis* was 6-fold more toxic under P enrichment than N-limited conditions (Johansson and Granéli 1999a). Another prymnesiophyte, *Prymnesium parvum,* increased toxicity under N-limited or P-limited conditions (Johansson and Granéli 1999b).

The chemical form of the nutrient supplied to the HAB species can also affect toxicity, although this is an area that has received relatively little study. *K. brevis* has been shown to increase its production of brevetoxin up to 6-fold when exposed to elevated urea levels of 0.5 to 1.0 mM in batch culture compared to controls without urea enrichment (Shimizu et al. 1993). The urea levels used in that experiment far exceed those found under natural conditions, but the implication is that certain compounds are more readily assimilated and incorporated into algal toxins than others. With the addition of urea or glycine, the cells switched from autotrophic to heterotrophic nutrition, using the C skeleton only after the N was used. In this study, toxicity was not influenced by the addition of leucine or aspartic acid (Shimizu et al. 1993).

The ecological implications of nutrient effects on toxicity are significant. What is not yet clear is how often the conditions that induce these changes actually occur in natural waters, and how human activities, and specifically eutrophication, affect overall toxin potential. One can envision several scenarios for eutrophic waters, depending on the extent of nutrient enrichment, the resulting nutrient availability ratios, and the HAB species and toxin involved. Due to the nutrient enrichment, HAB cells might be more abundant, but because of the altered nutrient ratios, their cellular toxicity could be higher or lower than with non-eutrophic conditions. Depending on the species, the net effect could thus be an increase, decrease, or no change in overall toxicity from a public health, fisheries, or ecosystem impact perspective. This is an area of obvious importance, but further research is needed before useful insights about nutrient form and HABs can be provided to coastal resource managers.

HABs with Little Apparent Link to Nutrient Enrichment

A common assumption by the public and the press is that new or unusual HAB events are somehow linked to pollution, and that all nutrient increases will result in algal blooms. The situation is far from that simple, but in many cases a link between blooms and eutrophication can be identified. It should be emphasized though that there are HABs that do not appear to have this linkage. These are blooms for which there may be no nutrient relationship, or one that has not yet been identified. There may be other factors that exert more control in regulating plankton community dynamics. This is true for some new outbreaks and for expansions of recognized or recurrent blooms. PSP toxicity from toxic *Alexandrium* species is a present-day problem in the relatively pristine waters of the Gulf of Maine, as well as along most of the U.S. west coast including Alaska. The blooms that occur undoubtedly use some nutrients that derive from human activities, given their proximity to the coast, but other factors seem to better explain the recent spreading of these organisms. The PSP problem has expanded into southern New England and into Puget Sound on the U.S. west coast over the last several decades, but these increases are thought to reflect the transport of cyst-forming *Alexandrium* species into those regions by natural storms and currents and with the deposition of cysts that have allowed the species to colonize the areas (e.g., Rensel 1993; Anderson et al. 1994). For *Alexandrium* spp. in the Gulf of Maine, increased nutrient loading and composition appear to be secondary factors influencing growth.

Conclusions and Cautions

Eutrophication is a global problem, and coastal areas throughout the world have been affected. There is little question that nutrient loading fuels high biomass algal blooms, and increases in chlorophyll have been shown to parallel increases in nutrient concentrations. There is clear evidence for direct stimulation of some HABs by nutrient over-enrichment. The linkages between other HABs and eutrophication, however, are more complex and include indirect as well as direct pathways; and linkages between some oligotrophic HAB species and eutrophication are not known. There have been many significant advances in our understanding of the physiological requirements for, and the mechanisms of nutrient acquisition by, HAB species. We have gained much knowledge of how certain nutrients, and their proportions, can regulate some species or groups of species.

It is important to recognize that the impacts of nutrient loading depend on many factors, from the species composition and nutritional state of the organisms at the time of the loading, to the physical features of the environment at that point in time, as well as the existence of grazers. Similar nutrient loads will not necessarily have the same effect on a different environment, or on the same environment at a different point in time. It is important to avoid ascribing the apparent global increase in HABs solely to pollution or eutrophication, although the public and the press often assume this linkage. There are many causes for the expansion and eutrophication is but one of these mechanisms.

Although there have been many successes in relating nutrient quantity and composition to outbreaks of HABs, in general the relationships between nutrient delivery and the development of blooms of many HAB species, and between nutrient enrichment and the potential toxicity of blooms or outbreaks of those species, remain poorly understood. Local, regional, and worldwide coordinated efforts, particularly those targeting comparative ecosystems that include both highly eutrophic waters and those that have experienced altered nutrient inputs will be required to better understand the underlying direct and indirect mechanisms that interact to control the complexities of these relationships.

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