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Eutrophication and harmful algal blooms: A scientific consensus

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Eutrophication and harmful algal blooms: A scientific consensus

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ABSTRACT

In January 2003, the US Environmental Protection Agency sponsored a "roundtable discussion" to develop a consensus on the relationship between eutrophication and harmful algal blooms (HABs), specifically targeting those relationships for which management actions may be appropriate. Academic, federal, and state agency representatives were in attendance. The following seven statements were unanimously adopted by attendees based on review and analysis of current as well as pertinent previous data:

(1) Degraded water quality from increased nutrient pollution promotes the development and persistence of many HABs and is one of the reasons for their expansion in the U.S. and other nations;
(2) The composition–not just the total quantity–of the nutrient pool impacts HABs;
(3) High-biomass blooms must have exogenous nutrients to be sustained;
(4) Both chronic and episodic nutrient delivery promote HAB development;
(5) Recently developed tools and techniques are already improving the detection of some HABs, and emerging technologies are rapidly advancing toward operational status for the prediction of HABs and their toxins;
(6) Experimental studies are critical to further the understanding about the role of nutrients in HABs expression, and will strengthen prediction and mitigation of HABs; and
(7) Management of nutrient inputs to the watershed can lead to significant reduction in HABs.

Supporting evidence and pertinent examples for each consensus statement are provided herein.
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1. Introduction

This report represents the synopsis of a "roundtable discussion" on the links between water quality and eutrophication and the occurrence of harmful algal blooms (HABs). This meeting,

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sponsored by the US Environmental Protection Agency (US EPA), was held in Cambridge, Maryland, in January 2003, and included academic experts as well as federal, state and local agency representatives. The authors of this report represent all those in attendance; our colleague, John Heisler, who originated and guided development of the meeting and chaired the discussion group, is now deceased and this paper was written in his honor.

The goal of the meeting was to develop a set of consensus statements on presently understood relationships between eutrophication and HABs, with particular emphasis on implications for nutrient management programs. A broad definition (GEOHAB, 2001) of HABs was adopted for this purpose, including potentially toxic (both autotrophic and heterotrophic) species and high-biomass producers that can cause hypoxia and anoxia and indiscriminant mortalities of marine life after reaching dense concentrations, whether or not toxins are produced.

In advance of the meeting, succinct statements for discussion were provided to participants and a presentation was given on each statement by one member of the group. The presenter was asked to make a case "for" or "against" the given statement. In discussion, and through analysis of data and evidence presented, the goal was to accept, reject, or modify each statement so that a set of unanimously accepted statements was developed by the end of the meeting. Statements were specifically crafted so as to have management implications. The relevance and applicability for management of these consensus statements remain as valid at present as when they were developed.

One recommendation from the roundtable was to develop a GEOHAB Open Science Meeting on HABs and Eutrophication to broaden the discussion on this topic to a wider community of international participants. Such a meeting was held in 2005 and the scientific results from that meeting have been synthesized into a report (GEOHAB, 2006) and some of those results are further detailed in the other papers of this issue of *Harmful Algae*.

Herein, each consensus statement is summarized along with a synopsis of its rationale and examples of supporting evidence. These synopses are not intended to be thorough reviews. In keeping with the mission of the US EPA, the sponsoring agency for this roundtable, preference is given to US examples where available. It is recognized that, in some cases, significant new data have become available since the 2003 roundtable. This report generally uses examples presented in the roundtable and only provides new results where advancements in the field have been substantial.

2. The consensus statements

2.1. Degraded water quality from increased nutrient pollution promotes the development and persistence of many HABs, and is one of the reasons for their expansion in the U.S. and other nations

It is generally recognized that there have been more coastal algal blooms, often of greater geographic extent and/or longer duration, with more toxic species observed, more fisheries affected, and higher associated costs from HABs in the past decade than in previous decades (Anderson, 1989; Smayda, 1990; Hallegraeff, 1993; Anderson et al., 2002; Glibert et al., 2005a). Many possible reasons for the reported global expansion exist in addition to nutrient pollution. Species dispersal or introduction, through transport of cells or cysts, can occur via natural currents and storms or human activities such as dispersal by ballast water exchange or shellfish seeding operations by which algal cells or cysts may be transported. Both overfishing and increased aquaculture alter food webs which may, in turn, alter the community of grazers that feed on HABs. Finally, improved observation and tools for detection have increased public and scientific awareness (GEOHAB, 2001, HARRNESS, 2005). More than one cause is frequently involved, and the causes for global expansion of a given species can differ among species.

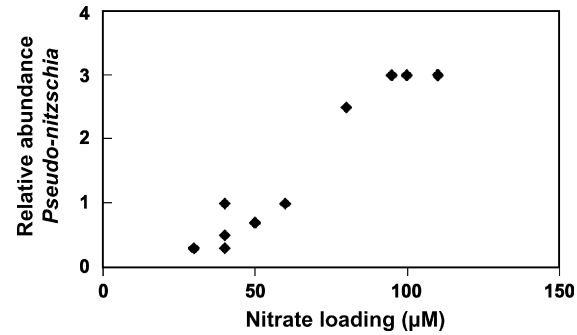

Fig. 1. Relative abundance (%) of the diatom *Pseudo-nitzschia* in the sedimentary record as a function of the nitrate loading in the northern Gulf of Mexico (redrawn from Turner and Rabalais, 1991 and Parsons et al., 2002).

There are numerous examples worldwide of increases in HABs linked to increased nutrient loading, a few of which are highlighted here. While strong relationships have been shown for many years in freshwater ecosystems between phosphorus loadings and harmful cyanobacteria blooms (Schindler, 1977; Burkholder, 2002), increasing linkages between nutrient loading and estuarine/coastal marine HABs have more recently been recognized (Smayda, 1990, 1997; Anderson et al., 2002; Glibert et al., 2005a,b; Glibert and Burkholder, 2006). For example, in the Gulf of Mexico, the sedimentary record of concentration of potentially toxic diatoms, *Pseudo-nitzcschia* spp., increased in parallel to increased nitrate loading over the past several decades (Fig. 1; Turner and Rabalais, 1991, Parsons et al., 2002). In Puget Sound, Washington, USA, a strong correlation has been reported between the increase in documented levels of paralytic shellfish toxins (PST) from toxic dinoflagellates over four decades and the increase in human population in the counties bordering Puget Sound (based on US census statistics; Fig. 2; Trainer et al., 2003). Although, as above, a statistical correlation does not establish a causal link, this relationship suggests that coastal eutrophication may be a causative agent of change (Trainer et al., 2003). Blooms off the coast of China, involving *Prorocentrum* sp., *Karenia mikimotoi* and other species, have expanded during recent years in geographic extent and duration, from km^2 to tens of km^2, and from days to months, related to the increase in fertilizer use over the past two

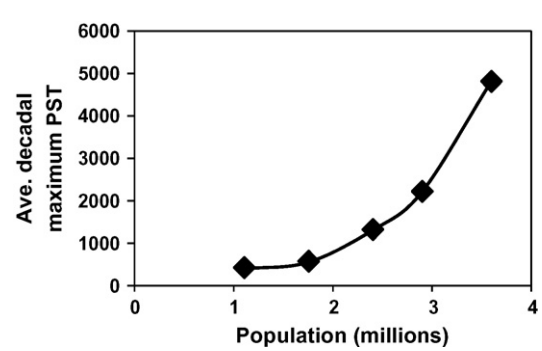

Fig. 2. Relationship between the growth in human population and the average decadal maximum paralytic shellfish toxins (PST) from dinoflagellate HABs from Puget Sound, Washington State, where continuous monitoring of paralytic shellfish poisoning has been ongoing since the mid-1950s. Human population data for the counties bordering Puget Sound for the past 40 years were derived from the U.S. census (redrawn from Trainer et al., 2003).

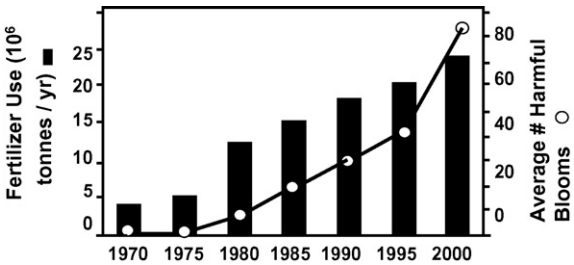

Fig. 3. Long-term trends in the use of nitrogen-based fertilizers and the number of occurrences of red tide blooms in Chinese coastal waters (modified and redrawn from Anderson et al., 2002; Zhou, 2005).

decades (Fig. 3; Anderson et al., 2002; Zhou, 2005). The Baltic Sea, Aegean Sea, Northern Adriatic, and Black Seas have all sustained increases in HABs coincident with increases in nutrient loading (e.g., Larsson et al., 1985; Bodenau, 1993; Moncheva et al., 2001). On a shorter time scale, Beman et al. (2005) reported, during a 5-year study, a strong positive relationship between nitrogen-rich agricultural runoff to the Gulf of California and the development, within days, of extensive phytoplankton blooms. In Sequim Bay, Washington, an intense bloom of the toxigenic diatom *Pseudo-nitzschia pseudodelicatissima* was found a week after elevated ammonium levels were reported in these waters (Trainer et al., 2007), and similarly, in Chesapeake Bay, blooms of *Prorocentrum minimum* have been found to follow within days of elevated levels of urea following agricultural applications (Glibert et al., 2001).

Although such field examples, supported by experimental and physiological data (e.g., Riegman, 1995; Bates et al., 1998; Imai et al., 1998; Smayda, 1998; Johansson and Granéli, 1999; Li et al., 2001; Fan et al., 2003; Glibert et al., 2006b), are increasing, recognition that degraded water quality from nutrient pollution contributes to the development and persistence of many HABs does not diminish the possibility that other factors may promote some HABs. Physical, biological, and other chemical factors may modulate harmful algal species' responses to nutrient loadings (e.g., Vadstein et al., 2004; Gobler et al., 2002; Sellner et al., 2003; Glibert et al., 2005a), and this complexity of HAB dynamics is a challenge for their management, as further described below.

2.2. The composition – not just the total quantity – of the nutrient pool impacts HABs

Specific algal species or species groups have numerous physiological adaptations that permit them to exploit nutrients differentially. Different species groups display preferences for specific nutrient regimes, including nutrient ratio or form (Smayda, 1990, 1997; Anderson et al., 2002; Smayda and Reynolds, 2001, 2003; Glibert and Burkholder, 2006). For example, diatoms require silicon for their growth, whereas certain dinoflagellates apparently have a higher phosphorus requirement than some other species groups. Thus, according to the nutrient ratio hypothesis (Tilman, 1977; Smayda, 1990, 1997), if nutrient loading leads to a proportional enrichment of phosphorus relative to silicon, then a proportional shift away from a diatom-dominated community toward flagellates might be expected over time.

The relationship between alteration in nutrient composition and the development of HABs is supported by examples in freshwaters, estuaries and marine coastal waters worldwide (reviewed by Anderson et al., 2002). Off the coast of Germany, time series analysis of nutrient concentrations over several decades showed that a fourfold increase in the N:Si ratio coincided with decreased abundance of diatoms and an increase in *Phaeocystis* blooms (Radach et al., 1990). Similarly, a nearly four-decade time series from Narragansett Bay, Rhode Island, shows a relationship between increases in the N:Si ratio and a proportional increase in flagellates (Smayda et al., 2004). Decreases in N:P ratios due to phosphorus loading have sometimes been related to increased abundance of certain harmful dino-flagellate species. For example, in Tolo Harbor, Hong Kong, where phosphorus loading increased due to human population growth in the late 1980s, a shift from diatoms to dinoflagellates was observed, coincident with a decrease in the ambient N:P ratio from ca. 20:1 to <10:1 (Hodgkiss and Ho, 1997; Hodgkiss, 2001). On shorter time scales, in Tunisian aquaculture lagoons, blooms of toxic dinoflagellates have been shown to develop when the N:P ratio drops in autumn (Romdhane et al., 1998), and along the eastern seaboard of the US, outbreaks of the toxic dinoflagellates, *Pfiesteria piscicida* and *P. shumwayae,* have been associated with low dissolved N:P ratios from high phosphate loading by effluent spills from concentrated animal operations (Burkholder et al., 1997). Blooms of *Karenia brevis* on the western Florida shelf are also found in waters with lower dissolved inorganic N:P ratios than in water directly to the south with higher N:P ratios, where diatoms tend to be more prevalent (Fig. 4; Heil et al., 2007).

The impacts of varying nutrient composition on HAB proliferation, however, are in many cases more complicated than the above examples. Some studies have shown, for example, that neither the quantity nor the ratio of inorganic nutrients alone can adequately explain sustained high biomass blooms of extended duration (e.g., Vargo et al., 2004). We now recognize that inorganic nutrients are not the only nutrients used by many HABs, and that many organic nutrients are bioavailable and dynamic in their composition (e.g., Seitzinger et al., 2002; Berman and Bronk, 2003). Many HAB genera, including dinoflagellates, cyanobacteria, and pelagophytes (e.g., brown tides), can use organic (dissolved or particulate) forms of nutrients for some or all of their nitrogen, phosphorus and/or carbon demands (e.g., Paerl, 1988; Burkholder and Glasgow, 1997; Granéli et al., 1997, 1999; Berg et al., 1997, 2002; Lewitus et al., 1999; Stoecker, 1999; Kudela and Cochlan, 2000; Berman, 2001; Glibert et al., 2001, 2006a,b, 2007; Lomas et al., 2001, 2004; Mulholland et al., 2002, 2004; Gobler et al., 2005; Glibert and Legrand, 2006; Lewitus, 2006; Herndon and Cochlan, 2007; Kudela et al., 2008; Cochlan et al., 2008).

Nutrient "packaging" can also be important. For example, many flagellate species, including various harmful dinoflagellates, are mixotrophic or heterotrophic phagotrophs, and consume pre-dominantly particulate rather than dissolved nutrients (e.g., Nygaard and Tobiesen, 1993; Stoecker, 1999; Jeong et al., 2005). Thus, the toxic, heterotrophic dinoflagellate *Pfiesteria* spp. can be indirectly stimulated by inorganic nutrient enrichment, mediated through an increase in the abundance of algal prey that may be directly stimulated by specific nutrient forms (Burkholder et al., 2001; Glibert et al., 2006a). Similarly, *Karlodinium veneficum* may be stimulated by the growth of cryptophytes, the abundance of which may be influenced by its preferred nutrient forms (Adolf et al., this issue).

Furthermore, some cyanobacteria also have the ability to convert or "fix" gaseous nitrogen into reduced nitrogen, enabling them to succeed in nitrogen-depleted conditions if other environmental conditions permit their growth (Howarth et al., 1988). The dynamics of nitrogen fixation by the cyanobacterium *Trichodesmium* have been related to increases in dissolved organic nitrogen which is released from the cyanobacteria and which may be available for subsequent uptake by dinoflagellates (e.g. Capone et al., 1994; Glibert and Bronk, 1994; Glibert and O'Neil, 1999; Lenes et al., 2001; Mulholland et al., 2004). Thus, nutrient ratios based solely on dissolved inorganic nutrients often do not yield sufficient insights regarding the influences of nutrient enrichment.

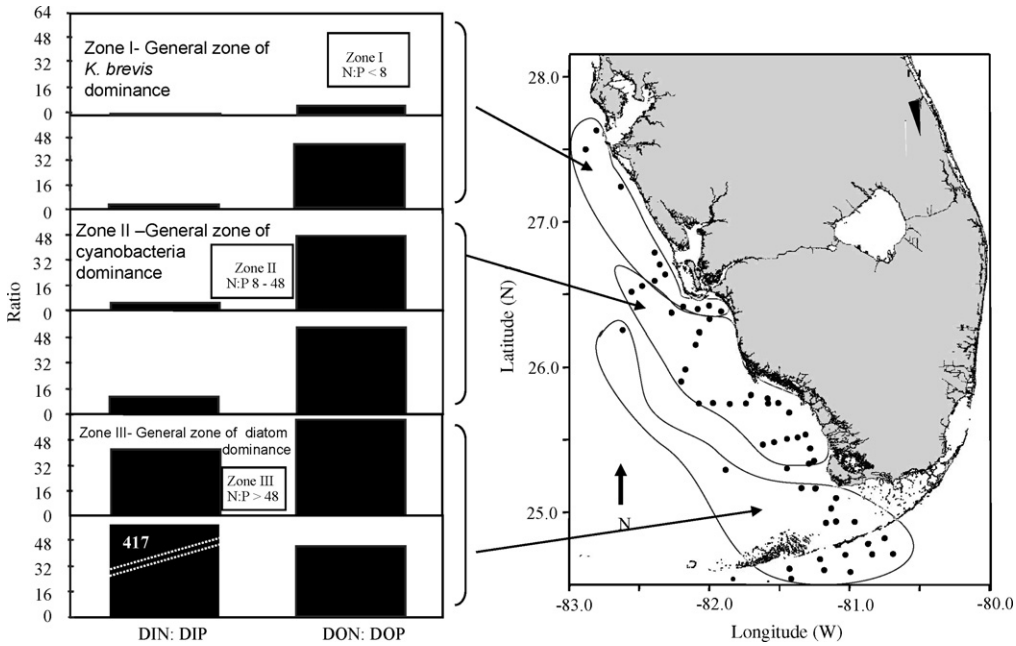

Fig. 4. Mean dissolved inorganic and organic N:P ratios at the mouths of each of the major riverine systems of western Florida shelf sampled during the dry season of May 2003. Each bar represents the means of the stations sampled along an individual riverine transect. The insert box indicates the mean particulate N:P ratio. The general zones are indicated on the companion map of southern Florida (modified from Heil et al., 2007).

Toxin production may also vary with nutrient form. For example, laboratory studies have revealed that the neurotoxin domoic acid (DA) production by the diatom *Pseudo-nitszchia* spp. can vary as a function of the nitrogen substrate being utilized for growth. For exponentially growing cultures of *P. australis*, nitrate and ammonium-grown cells produce equivalent amounts of dissolved and particulate DA, whereas DA production is enhanced in cultures growing solely on urea (Cochlan et al., 2005, Armstrong-Howard et al., 2007). However, for the smaller-celled species, *P. cuspidata*, the nitrate-grown cells are the most toxic (Auro, 2007).

In addition to macronutrients, micronutrients such as trace metals are essential for the growth of all phytoplankton and play critical roles in both photosynthesis and assimilation of essential macronutrients, and the toxicity of some HAB species (Sunda, 2006). For example, laboratory studies have shown that the toxigenic diatoms *Pseudo-nitszchia multiseries* and *P. australis* produce increasing amounts of DA as a function of iron or copper limitation (Rue and Bruland, 2001; Maldonado et al., 2002; Wells et al., 2005). Additionally, it has been seen that DA production in these diatoms increases under high copper concentrations, presumably to detoxify copper (Maldonado et al., 2002; Ladizinsky, 2003; Ladizinsky et al., 2005). Iron, besides being essential for phytoplankton growth and nitrogen assimilation, is also required for nitrogen fixation, and therefore the deposition of iron-rich dust in the Gulf of Mexico has been related to the strength of *Trichodesmium* blooms and, indirectly, to subsequent *K. brevis* blooms (e.g., Lenes et al., 2001).

In summary, nutrient preferences by different algal species groups are strongly supported by physiological evidence and by recognition of an array of adaptive mechanisms used by different species. The extent to which these adaptations are expressed depends on other environmental conditions at the time of nutrient supply, the types of nutrient supplied and other factors, including the micronutrient environment. The inability to apply a single criterion, such as the nutrient ratio, to an assessment of phytoplankton species dominance does not negate the utility of this approach; rather, it underscores the complexity of the physiology of many HAB species and the interdependence of environmental factors in the outcome of species succession (Glibert and Burkholder, 2006).

2.3. High-biomass blooms must have exogenous nutrients to be sustained

Algal proliferations, by definition, are due to increased *net* growth, and this must be accomplished either through increases in gross growth rate and/or through reductions in loss processes such as grazing (Harris, 1986). "New" nutrients from allochthonous sources can fuel biomass increases. While increased total algal biomass is often an obvious response to nutrient loading (see reviews in Cloern, 2001; Anderson et al., 2002), the overall species-specific response will depend upon the physiology of the organisms present, environmental conditions, and the form of nutrient supplied, as described above. Clear dose-response relationships between nutrient loading and biomass response (typically termed a "phase I" eutrophication model *sensu* Cloern, 2001) are more common in lakes, however, than in estuarine and marine systems.

The relationships between nutrient loading and algal proliferations are complicated by shifts in food webs, habitat changes, climate changes and other system alterations that affect the extent to which a given species may accumulate (typically termed a "phase II" model of eutrophication; Cloern, 2001). Increased nutrient enrichment can lead to a shift in plankton community composition, which in turn can afect predator–prey relationships, further altering the transfer of nutrients (e.g., Smayda, 1989; MacIntyre et al., 2004; Irigoien et al., 2005; Mitra and Flynn, 2006; Sunda et al., 2006). Incoming nutrients may be regenerated, recycled, or removed in space and time from the set of conditions that would otherwise support blooms. These links are frequently difficult to establish.

Inside blooms, ambient concentrations of inorganic nutrient forms may be reduced or depleted due to algal incorporation of the nutrients into biomass (e.g., Vargo et al., 2004; Springer et al.,

2005), leading to relationships between nutrient concentration and chlorophyll (or other biomass indicator) that may, in fact, appear to follow a saturation response, a negative relationship, or no relationship at all. Thus, the critical term is the flux of nutrient, not the absolute concentration that may be supporting the blooms.

The most complex nutrient sources to understand and regulate are non-point source inputs such as runoff, groundwater and atmospheric deposition. The relationship between increased exogenous inputs and increased algal biomass is often clearer over long time periods. Nitrogen loading, for example, in the Chesapeake Bay, which increased more than 2.5-fold from the mid-1940s to the mid-1990s, has been correlated with long-term increases in total chlorophyll, in the frequency and abundance of blooms of HAB species such as *P. minimum*, and in resulting hypoxic volume (Hagy et al., 2004; Kemp et al., 2005).

While exogenous nutrients are often necessary for high biomass blooms to be sustained, in some cases, blooms may be sustained on nutrients that are regenerated and recycled after an initial injection of new nutrients. Long-term sustained blooms, such as the bloom of *Aureoumbra lagunensis* evident in Laguna Madre for approximately 8 years in the 1990s, and the >20 month bloom of *K. brevis* that was sustained off western Florida in 2005, appear to have been fueled by an initial injection of nutrients, and then sustained on regenerated nutrients. In the former case, intense rains after years of drought led to a sequence of blooms and ecosystem conditions suitable for *Aureoumbra* (e.g., Buskey et al., 2001), while in the latter case, a series of hurricanes in preceding months may also have altered both nutrient availability and other habitat considerations (Mallin and Corbett, 2006; Neely et al., 2006). A third such example is that of the >18 months bloom of *Synechococcus* in eastern Florida Bay that followed an injection of phosphorus from two apparent sources: high freshwater discharge from Hurricanes Katrina, Rita and Wilma that impacted south Florida in 2005, and a very high organic loading from a unique situation of road construction that required mulching of significant amounts of mangroves (Madden, in press). Consequently, chlorophyll concentrations rose and were sustained at levels roughly eightfold higher than pre-bloom levels, while an increase in phosphorus concentration was only observed during the initiation stages of the bloom and then declined. A final example comes from brown tides (*Aureococcus anophagefferens*) in US mid-Atlantic estuaries (Gobler et al., 2005). These blooms are often preceded by a 'pre-bloom' of other algal species that are stimulated by nitrogen from groundwater flow (Gobler and Sañudo-Wilhelmy, 2001). When groundwater flow diminishes during summer and the initial bloom is remineralized, organic nitrogen levels increase, and *A. anophagefferens* becomes the dominant alga. Thus, nutrients may continue to serve as fuel for blooms long after the initial nutrient loading occurs.

2.4. Both chronic and episodic nutrient delivery promote HAB development

As described in some of the previous examples, the response of harmful algal species to changes in nutrient enrichment is often a chronic effect, becoming increasingly apparent only after long time intervals are examined (e.g., Lam and Ho, 1989; Smayda, 1989; Riegman et al., 1993; Yung et al., 1997; Marshall et al., 2005). Long-term, consistent monitoring records additionally can reveal relationships between harmful algal species composition and abundance versus other aspects of environmental change, such as climate variability or alterations in trophic control due to changes in dominant herbivorous species. Such long-term records are valuable in clarifying trends in nutrient loadings, and in identifying synergistic effects of changing climatic factors and nutrient enrichment (e.g., Smayda et al., 2004, Burkholder et al., 2006).

Episodic or "pulsed" nutrient inputs have also been related to outbreaks of harmful algal species on both small and large scales. Some of these, such as agricultural applications (timing and quantity), treated sewage discharge, and combined sewer outfalls, are amenable to management. As examples (reviewed in Harlin, 1993), in Boston Harbor, sea lettuce (*Ulva*) formed dense populations for many years near outfalls of poorly treated sewage. Along the intertidal area of the Baltic Sea, sewage inputs have been related to overgrowth of formerly dominant brown seaweeds (*Fucus* spp.) by opportunistic macroalgae. Episodic inputs resulting from storm events are, naturally, more difficult to manage.

Episodic storm events and climate variability affect the timing of freshwater flow, residence times, the magnitude and timing of nutrient pulses and resulting biotic responses (e.g., Miller et al., 2006; Burkholder et al., 2006; Mallin and Corbett, 2006; Paerl et al., 2006). In coastal lagoons, where riverine input is not the dominant source of nutrient delivery, climate variability can alter the input of groundwater nutrients (e.g., LaRoche et al., 1997). Hurricane Isabel in 2003 caused a large phytoplankton bloom to develop in Chesapeake Bay within days (Miller et al., 2005). Further, extensive hypoxia occurred in the lagoonal Neuse River Estuary after Hurricanes Dennis and Floyd, whereas a storm that caused less flooding, Hurricane Fran, led to more concentrated pollutants, extensive anoxia and massive fish kills (Burkholder et al., 2006). In the Choptank River subestuary of Chesapeake Bay, annual spring blooms of *P. minimum* generally follow within days of spring agricultural application of nitrogen fertilizer and its runoff from episodic spring rains (Glibert et al., 2001).

In some cases anthropogenic nutrients may not directly stimulate HABs, but may become linked to their growth and abundance following biogeochemical processing or following the stimulation of other components of the food web on which they may depend.

On a seasonal scale in Chesapeake Bay, USA, nutrient input in the spring is delivered largely in the form of nitrate and rapidly assimilated by diatoms which bloom, then sink and decompose as nutrients become depleted. Subsequently during warmer summer months, nitrogen, largely as ammonium, is released via decomposition in sedimentary processes which, in turn, supports an assemblage dominated by flagellates including potentially harmful dinoflagellates (Glibert et al., 1995; Malone et al., 1996; Kemp et al., 2005).

It is thus important in our interpretation of the relationships between nutrients and HAB occurrences that we move away from simplistic inorganic nutrient-dose-yield models and begin to incorporate nutrient loading parameters which encompass the increasing array of nutrient forms that are now recognized to be important. Furthermore, interpretations of nutrient effects on HABs as well as models that parameterize these relationships, need to incorporate indirect, time-lagged nutrient pathways, as well as the feedbacks and interactions of the effects of nutrient loads in ecosystems (Cloern, 2001).

2.5. Recently developed tools and techniques are already improving the detection of some HABs, and emerging technologies are rapidly advancing toward operational status for the prediction of HABs and their toxins

Due to the unpredictability of most episodic events, sampling programs historically have not "captured" the initiation phases of blooms. However, new *in situ* monitoring tools are beginning to permit resolution of the antecedent conditions and the time course response to some episodic events. Improved molecular probes, some

that can be incorporated into *in situ* microarrays, are allowing timely detection of cells. Molecular probes for individual HAB species and their toxins are now routinely applied for many species, making early detection possible (e.g., Scholin and Anderson, 1998; Scholin et al., 2003; Anderson et al., 2005a; Bowers et al., 2006). Optical sensors for *Karenia* species have been deployed on moorings and autonomous underwater vehicles (Schofield et al., 1999). *In situ* probes with telemetry for various key variables such as temperature, salinity, chlorophyll, turbidity, dissolved oxygen and pHs are also providing near-real time data for management applications (Glasgow et al., 2004; Springer et al., 2005). A suite of over 50 such probes in the State of Maryland are allowing managers and the public alike to monitor trends in Chesapeake Bay and rapidly respond when conditions warrant (www.eyesonthebay.net). *In situ* nutrient sensors are also advancing, with capability developing for some organic forms of nutrients as well as inorganic forms, so that relationships between pulses in nutrient delivery and alterations in salinity due to rainfall, for example, are now possible to establish (Glibert et al., 2005b, 2008).

In conjunction with the growing sophistication of tools, better citizen awareness and citizen monitoring can also be effective in capturing blooms or blooms conditions. Throughout the US and in many parts of the world, fishermen collect samples for cell and nutrient analyses, and local citizen groups and indigenous people participate in routine monitoring (e.g., Scaefer et al., 2004; Trainer and Suddleson, 2005; Whereat and Farestad, 2005; Granéli and Esplund, 2006).

Modeling is a rapidly developing tool advancing toward prediction of many HAB species and occurrences (e.g., Flynn, 2002; McGillicuddy et al., 2005; Hood et al., 2006), although for most estuarine and coastal HABs, prediction has not yet been attained (see, e.g., Franks, 1997; Cembella, 1998; Flynn, 2005). There are two general types of HAB models that are useful for management applications. The first is the development of models that predict "general likelihood of occurrence" of HAB species, whereas the second is the development of models that include "explicit" predictions of HAB occurrence in time or space. The former is useful for management in application of long-term actions to reduce the likelihood of future occurrences, i.e. prevention. The latter requires more refinement to understand the physics, biology and chemistry of the environment, but it can be of more value at the local community level. Models of a range of types are useful in predicting general likelihood of occurrence, from simple regression models that may yield correlation (without necessarily a biological foundation for cause and effect) and conceptual models that are useful in communicating general patterns (e.g., Smayda and Reynolds, 2001, 2003). In advancing toward more explicit predictions, mechanistic models that describe the physical, chemical and biological interactions are required. Spatially explicit models linked to hydrodynamic models are yielding some success in retrospectively tracking some species, such as for *Alexandrium* spp. in the Gulf of Maine and *K. brevis* in the Gulf of Mexico (McGillicuddy et al., 2005, Walsh et al., 2006). Multi-parameter physiological models that incorporate various organismal life stages and trophic interactions are also beginning to be developed (J. Anderson et al., 2003; D. Anderson et al., 2005b; Hood et al., 2006).

The development of explicit, reliable model predictions still needed for most HABs will require significant data on the species of interest as well as the environmental conditions (Flynn, 2002, 2005). Thus, for some species, "general likelihood" predictions are viable now and can be useful in guiding long-term management decisions with respect to nutrients. Furthermore, several types of real-time and near-real-time monitoring systems, coupled with conceptual, statistical, or mechanistic models, are also available now to assist in detecting and predicting some HABs in time and space. Now-cast models are being developed in the Chesapeake, Bay, for example, of the likelihood for *K. veneficum* blooms based on a statistical habitat relationship of the HAB with salinity and temperature, and a hydrodynamic model (Ramers et al., 2003; Tango et al., 2005). However, the prediction "window" for those species for which such mechanistic models are available is presently short, and considerable work will be needed to strengthen insights about the relationships between nutrient responses, physical dynamics, and climate change. Application of real-time monitoring of both environmental parameters and HABs species will continue to advance forecasting capabilities for these dynamic relationships.

2.6. Experimental studies are critical for further understanding about the role of nutrients on HABs expression, and will strengthen prediction and mitigation of HABs

Many physiological adaptations to nutrients are best examined under controlled laboratory conditions. For example, assessments of specific relationships that are required in models (such as parameters of nutrient uptake and growth kinetics) are better resolved under laboratory conditions where a culture of known physiological state can be established and where environmental conditions can be rigorously set (e.g., Lomas et al., 1996; Fan et al., 2003; Glibert et al., 2006b; Herndon and Cochlan, 2007; Cochlan et al., 2008). Laboratory culture studies of HAB species have been instrumental in resolving such species characteristics as life histories, toxigenesis, ecophysiological responses to specific nutrient forms, light and temperature regimes, and species-specific differences in rates of nutrient uptake and growth. As new insights are developed about various processes – for example, the extent of osmotrophy or mixotrophy within a species – generalizations based upon older laboratory data may have to be revisited, cross-confirmed, or assessed anew.

A critical but often overlooked consideration regarding experimental work is that major characteristics of species maintained in culture for extended periods (months to years) significantly change over time under (highly artificial) enclosed conditions. Over time in culture, highly toxic strains have lost their ability to make toxin; strains also have changed in polyploidy, expression of life history stages, and responses to environmental conditions such as salinity and nutrient regimes (reviewed in Wood and Leatham, 1992; Burkholder and Glibert, 2006). *Pfiesteria* spp., for example, have been shown to loose their toxicity when switched from a media that includes live to one with algal prey (Burkholder et al., 2001). Toxin production in a strain of *Alexandium lusitanicum* was also shown to loose toxicity after many years in culture, and although the exact reasons could not be ascertained, genetic mutations or prolonged use of antibiotics may have been the cause (Martins et al., 2004).

Many species have shown strain differences unrelated to extended period in culture. For example, Strom and Bright (2003) observed that strains of the haptophyte *Emiliania huxleyii* varied in their response to different forms of nitrogen. Whereas all four strains tested grew on nitrate and ammonium, three of the four could grow on organic nitrogen sources, while the fourth could not. The strains also showed distinct responses to various forms of organic nitrogen. Thus, in conducting laboratory studies, the history of the culture should be carefully considered (e.g., location of isolation and duration in culture). It is also important to compare multiple strains of the same species to assess whether the characteristic of concern is strain-specific, and generalizations at the species level (or higher) based upon one to a few strains should be avoided (Burkholder and Glibert, 2006; Burkholder et al., 2001, 2005).

Experiments should continue to build upon the knowledge gained from unialgal culture studies to assessment of more complex systems with multiple species, from microcosms to mesocosms, and from laboratory studies to field trials. Mesocosm studies and field experiments, if carefully designed and controlled, can enable *in situ* assessment of processes of trophodynamics and community interactions with individual species (e.g., Stoecker and Gustafson, 2002), and the importance of environmental fluctuations in light, temperature, and community-level responses to nutrient enrichment. Such approaches have significantly advanced understanding of nutrient limitation. As examples, the classic whole-lake studies undertaken decades ago in Canada yielded tremendous insights about phosphorus limitation in freshwater systems (Schindler, 1987, 2006). Analogously, much was learned about the regulation of marine phytoplankton production by iron in the multiple *in situ* iron enrichment experiments conducted in the high-nutrient-low-chlorophyll (HNLC) regions of the world (reviewed by de Baar et al., 2005). Smaller-scale mesocosms also have helped to resolve nutrient preferences by the harmful brown tide species, *A. anophagefferens* (Kana et al., 2004) and the effects of trophic structure on top-down regulation of phytoplankton biomass (Glibert, 1998; Granéli and Turner, 2002; Buskey et al., 2003; Vadstein et al., 2004).

As model sophistication and insights continue to develop about the dynamic regulation of adaptive characteristics of individual species, there will be a ongoing need to experimentally document specific processes under controlled conditions with clonal algal isolates, both as individual species (±bacteria, e.g., Bates et al., 1995; Burkholder et al., 2005) and as mixes of species in an increasingly complex but controlled environment (e.g., Flynn, 2002). Based upon the major insights gained from previous experiments, the data from such controlled conditions will surely strengthen scientists' abilities to predict and mitigate HABs.

2.7. Management of nutrient inputs to the watershed can lead to significant reductions in HABs

There are now multiple examples demonstrating both total algal biomass and HAB occurrence decreases after reduction in nutrient input. One of the classic examples involving decreases in cyanobacterial blooms is that of the removal of sewage discharges from Lake Washington within metropolitan Seattle, Washington (Edmondson, 1970). This lake had sustained noxious cyanobacteria blooms from the 1920s through the 1960s because of raw sewage inputs. An elimination of sewage discharges to Lake Washington was imposed in 1968, and the cyanobacterial blooms declined. In a much larger system, 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 Mumford Cove, a shallow estuary in Connecticut, were re-routed to another waterway in the late 1980s, and within 2 years massive nuisance blooms of the macroalga, *Ulva lactuca*, were eliminated (Harlin, 1993). In the Potomac River, a tributary of Chesapeake Bay, phosphate removal from sewage in the late 1970s was related to significant reductions in the frequency and intensity of *Microcystis* blooms that had been problematic in the previous decade (Jaworski, 1990). In the Seto Inland Sea in Japan between 1965 and 1976, the number of red tide outbreaks (high biomass blooms) increased sevenfold (Okaichi, 1997), in parallel with the increase in industrial production, but in 1973, Japanese authorities instituted the Seto Inland Sea Law to reduce loadings to half of the 1974 levels over a 3-year 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 year^{-1} (reviewed by Imai et al., 2006).

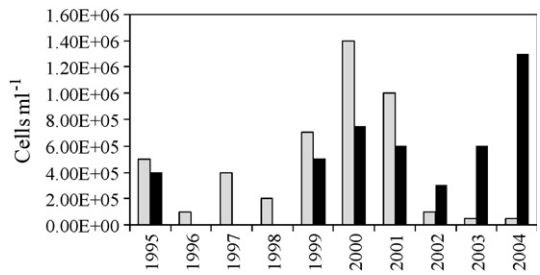

Fig. 5. Long-term trends in brown tide events in Peconic Estuary Long Island (gray bars) and in Maryland Coastal Bays (black bars; redrawn from Gobler et al., 2005; Glibert et al., 2007).

A more recent example appears to be that of the Long Island brown tides which, while so common in the early 1990s, were virtually absent from the Long Island embayments through the middle of the following decade (Fig. 5; Gobler et al., 2005). Although multiple factors have been suggested to be related to the decline in bloom intensity, the recent reductions in nitrogen levels in Peconic Estuary have been correlated with these declines (Nuzzi and Waters, 2004; Gobler et al., 2005). Blooms of *A. anophagefferens* are generally reliant on organic sources of nitrogen for growth (Dzurica et al., 1989; Lomas et al., 1996; Berg et al., 1997, 2002; Mulholland et al., 2002, 2004). In the Long Island embayments, the organic sources fueling these blooms are not thought to be a direct external nutrient source, but rather derive from the internal processing of other "new" nitrogen sources, including groundwater flow, which is elevated in nitrate. This nitrate delivery supports blooms of diatoms, as well as blooms of benthic microalgae which, as they begin to dissipate, can supply the necessary organic nitrogen for the brown tide (Gobler and Sañudo-Wilhelmy, 2001; MacIntyre et al., 2004; Gobler et al., 2005). From 1995 to 2006, levels of DON declined substantially and brown tides were absent from the Peconic Bays during those years (Gobler et al., 2005). In sharp contrast, however, in Maryland embayments, where brown tide also blooms, organic nutrient concentrations have been increasing annually over the past decade, leading to more significant blooms each year over the decade from the mid-1990s to the mid-2000s (Trice et al., 2004; Glibert et al., 2007).

Although these specific examples suggest that some successes may be possible in reducing incidences of HABs by reducing nutrient inputs, for many species these relationships may be complex. Long time scales may be involved, due to long-term storage of nutrient in sediments and alteration in the biogeochemistry of systems after years of nutrient loading (e.g., Kemp et al., 2005). Furthermore, for some systems, ecosystem dynamics may be permanently altered, and nutrient reduction strategies alone will not yield original ecosystem conditions. Eutrophication stressors such as loss of benthic habitat, development of hypoxia/anoxia, and alterations in food webs (Cloern, 2001) require long time scales for restoration and may require changes at the landscape scale.

With increasing pressures on the coastal landscape, it must be underscored that prevention of large blooms through nutrient control is far preferable than attempts to eradicate HABs once they are established. It is, however, a significant challenge and extremely costly to enact such policy decisions on large-scale nutrient reductions, so there will continue to be pressure to develop bloom control strategies. Furthermore, different nutrient actions may be required for different types of HABs, and organic as well as inorganic nutrients must be considered. Effective manage-

ment is an iterative process, involving adaptive management as new knowledge is gained, and must be sustained to be effective. Lastly, timely communication of results, to stakeholders and the public, is critical. Given projected increases in human population worldwide, eutrophication pressures and increased HAB occurrences will undoubtedly continue to increase in years to come.

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