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Eutrophication and Harmful Algal Blooms: A Scientific Consensus

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Abstract

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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 the world; 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 of the role of nutrients in HAB 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 is provided herein.

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, 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, J. Heisler, who originated and guided development of the meeting and chaired the discussion group, is now deceased and this paper is contributed 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 (auxotrophic, 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 were 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 supporting evidence and a few examples. These synopses are not intended to be thorough reviews. In keeping with the mission of the sponsoring agency for this roundtable, US EPA, 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 the data presented in the roundtable and provides new data where advancements in the field have been substantial.

The Consensus Statements

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 algal blooms, often of greater geographic extent and/or longer duration, with more toxic species observed, more fisheries affected, and higher associated costs with 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 storm or human activities such as dispersal of ballast water exchange or shellfish seeding operations by which algal cells or cysts may be transported. Both overfishing and increase 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.

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 and Burkholder 2002), increasing linkages between nutrient loading and estuarine/coastal marine HABs have more recently been recognized (Smayda, 1990, Smayda, 1997, Anderson et al., 2002, Glibert et al. 2005a, and Gilbert and Burkholder, 2006). For example, in the Gulf of Mexico, the sedimentary record of concentration of potentially toxic diatoms, *Pseudo-nitzschia 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 km² to tens of km², and from days to months, related to the increase in fertilizer use over the past two decades (Fig. 3; Anderson et al., 2002 and 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, Bodenaus, 1993 and 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 toxic 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 (Gilbert et al., 2001).

Although such 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 and 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 and Glibert et al., 2005a), and this complexity of HAB dynamics is a challenge for their management, as further described below.

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 ration or form (Smayda, 1990, Smayda, 1997, Anderson et al., 2002, Smayda and Reynolds, 2001, Smayda and Reynolds, 2003 and 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, Smayda, 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 4-fold 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 4-decade time series from Narragansett Bay 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 dinoflagellate 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 and 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 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 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 and 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, Granéli et al., 1999, Berg et al., 1997, Berg et al., 2002, Stoecker, 1999, Kudela and Cochlan, 2000, Berman, 2001, Glibert et al., 2001, Glibert et al., 2006a, Glibert et al., 2006b, Glibert et al., 2007, Lomas et al., 2001, Lomas et al., 2004, Mulholland et al., 2002, Mulholland et al., 2004, Gobler et al., 2005, Glibert and Legrand, 2006, Kudela et al. 2008 and 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 predominantly particulate rather than dissolved nutrients (e.g., Nygaard and Tobiesen, 1993, Stoecker et al., 1999, Parrow and Burkholder, 2003, 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 which may be stimulated by its preferred nutrient forms (Adolf et al., this issue).

Furthermore, some cyanobacteria also have the ability to convert or “fix” gaseous nitrogen into ammonia, 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 that 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, Lenex et al., 2001, Mullholland et al., 2004). Thus,

nutrient ratios based solely on dissolved inorganic nutrients often do not yield sufficient insights about influences of nutrient enrichment.

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-nitzschia* 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-nitzschia multiseriata* and *P. australis* produce increasing amounts of DA as a function of iron or copper limitation (Rue and Bruland, 2001, Maldonado et al., 2002 and 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 and 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., Lenex 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. 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 physiology of many HAB species and the interdependence of environmental factors in the outcome of any species succession (Glibert and Burkholder, 2006).

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 and 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 affect 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 and 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 and 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 and 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 and 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.

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 and 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 and 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 and 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).

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 and 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 and 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 and Glibert et al., 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., Scafer et al., 2004, Trainer and Suddleson, 2005, Whereat and Farestad, 2005 and 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 and Hood et al., 2006), although for most estuarine and coastal HABs, prediction has not yet been attained (see, e.g., Franks, 1997, Cembella, 1998 and 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 and Smayda and Reynolds, 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 and 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 and Flynn, 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 and 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.

6. Experimental studies are critical to further understanding about the role of nutrients on HAB 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 and 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 ploidy, expression of life history stages, and responses to environmental conditions such as salinity and nutrient regimes (reviewed in Wood and Leatham, 1992 and Burkholder and Glibert, 2006). *Pfiesteria* spp., for example, have been shown to lose 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 *Alexandrium lusitanicum* was also shown to lose 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 and Burkholder et al., 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 and Schindler, 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 and 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 (\pm bacteria, e.g., Bates et al., 1995 and 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.

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).

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 and 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, Berg et al., 2002, Mulholland et al., 2002 and Mulholland et al., 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 and 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 and 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 management 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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References

- Adolf JE, Bachvaroff T, Place AR. Cryptophyte abundance drives blooms of mixotrophic harmful algae: A hypothesis based on *Karlodinium veneticum* as a model system. *Harmful Algae*. 2008 this issue.
- Anderson, DM. Toxic algal bloom and red tides: a global perspective. In: Okaichi, T. Anderson, DM., Nemoto, T., editors. *Red Tides: Biology, Environmental Science and Technology*. Elsevier; 1989. p. 11-16.
- Anderson DM, Glibert PM, Burkholder JM. Harmful algal blooms and eutrophication: Nutrient sources, composition and consequences. *Estuaries*. 2002; 25:562–584.

- Anderson, DM., Kulis, DM., Keafer, BA., Gribble, KE., Marin, R., Scholin, CA. Deep-Sea Res II. 2005a. Identification and enumeration of *Alexandrium* spp from the Gulf of Maine using molecular probes; p. 2467-2490.
- Anderson DM, Stock CA, Keafer BA, Bronzino Nelson A, Thompson B, McGillicuddy DJ, Keller M, Matria PA, Martin J. *Alexandrium fundyense* cyst dynamics in the Gulf of Maine. Deep-Sea Res II. 2005b; 52(19–21):2522–2542.
- Anderson JT, Hood RR, Zhang X. Quantification of *Pfiesteria piscicida* growth and encystment parameters using a numerical model. Mar Ecol Prog Ser. 2003; 246:105–113.
- Armstrong-Howard MD, Cochlan WP, Ladzinsky NL, Kudela RM. Nitrogenous preference of toxogenic *Pseudo-nitzschia australis* (Bacillariophyceae) from field and laboratory experiments. Harmful Algae. 2007; 6:206–217.
- Ashworth, W. The Late, Great Lakes. Collins Publishers; Toronto, Ontario: 1986. p. 274
- Bates SS, Douglas DJ, Doucette GJ, Leger C. Enhancement of domoic acid production by reintroducing bacteria to axenic cultures of the diatom *Pseudo-nitzschia multiseries*. Natural Toxins. 1995; 3:428–435. [PubMed: 8612005]
- Bates, SS., Garrison, DL., Horner, RL. Bloom dynamics and physiology of domoic-acid-producing *Pseudo-nitzschia* species. In: Anderson, DM, Cembella, AD., Hallegraeff, GM., editors. Physiological Ecology of Harmful Algal Blooms. Vol. G41. Springer-Verlag; Berlin: 1998. p. 267-131. NATO ASI Series
- Beman JM, Arrigo KR, Matson PA. Agricultural runoff fuels large phytoplankton blooms in vulnerable areas of the ocean. Nature. 2005; 434:211–214. [PubMed: 15758999]
- Berg GM, Glibert PM, Lomas MW, Burford M. Organic nitrogen uptake and growth by the chrysophyte *Aureococcus anophagefferens* during a brown tide event. Mar Biol. 1997; 129:377–387.
- Berg GM, Repeta DJ, LaRoche J. Dissolved organic nitrogen hydrolysis rates in axenic cultures of *Aureococcus anophagefferens* (Pelagophyceae): Comparison with heterotrophic bacteria. Appl Environ Microbiol. 2002; :401–404. DOI: 10.1128/AEM.68.1.401-404.2002 [PubMed: 11772651]
- Berman T. The role of DON and the effect of N:P ratios on occurrence of cyanobacterial blooms: Implications from the outgrowth of *Aphanizomenon* in Lake Kinneret. Limnol Oceanogr. 2001; 46:443–447.
- Berman T, Bronk DA. Dissolved organic nitrogen: a dynamic participant in aquatic ecosystems. Aquat Microb Ecol. 2003; 31:79–305.
- Bodenau, N. Microbial blooms in the Romanian area of the Black Sea and contemporary eutrophication conditions. In: Smayda, TJ., Shimizu, Y., editors. Toxic Phytoplankton Blooms in the Sea. Elsevier; Amsterdam: 1993. p. 203-209.
- Bowers HA, Trice TM, Magnien RE, Goshorn DM, Michael B, Schaefer EF, Rublee PA, Oldach DA. Detection of *Pfiesteria* spp. in surface sediments collected from Chesapeake Bay tributaries (Maryland). Harmful Algae. 2006; 5:342–351.
- Burkholder, JM. Cyanobacteria. In: Bitton, G., editor. Encyclopedia of Environmental Microbiology. Wiley Publishers; New York: 2002. p. 952-982.
- Burkholder JM, Dickey DA, Kinder C, Reed RE, Mallin MA, Melia G, McIver MR, Cahoon LB, Brownie C, Deamer N, Springer J, Glasgow H Jr, Toms D, Smith J. Comprehensive trend analysis of nutrients and related variables in a large eutrophic estuary: A decadal study of anthropogenic and climatic influences. Limnol Oceanogr. 2006; 51:463–487.
- Burkholder JM, Gordon AS, Moeller PD, Law JM, Coyne KJ, Lewitus AJ, Ramsdell JS, Marshall HG, Deamer NJ, Cary SC, Kempton JW, Morton SL, Rublee PA. Demonstration of toxicity to fish and to mammalian cells by *Pfiesteria* species: Comparison of assay methods and multiple strains. Proc Natl Acad Sci (USA). 2005; 102:3471–3476. [PubMed: 15728353]
- Burkholder JM, Glibert PM. Intraspecific variability: An important consideration in forming generalizations about toxigenic algal species. African J Mar Sci. 2006; 28:177–180.
- Burkholder JM, Glasgow HB. *Pfiesteria piscicida* and other *Pfiesteria*-like dinoflagellates: behavior, impacts and environmental controls. Limnol Oceanogr. 1997; 42:1052–1075.

- Burkholder JM, Glasgow HB Jr, Deamer-Melia NJ, Springer J, Parrow MW, Zhang C, Cancellieri P. Species of the toxic *Pfiesteria* complex, and the importance of functional type in data interpretations. *Environ Health Perspect.* 2001; 109:667–679. [PubMed: 11677174]
- Burkholder JM, Mallin MA, Glasgow HB Jr, Larsen LM, McIver MR, Shank GC, Deamer-Melia N, Briley DS, Springer J, Touchette BW, Hannon EK. Impacts to a coastal river and estuary from rupture of a large swine waste holding lagoon. *J Env Qual.* 1997; 26:1451–1466.
- Buskey EJ, Liu H, Collumb C, Bersano JGF. The decline and recovery of a persistent Texas brown tide algal bloom in the laguna Madre (Texas, USA). *Estuaries.* 2001; 24:337–346.
- Bodenau, N. Microbial blooms in the Romanian area of the Black Sea and contemporary eutrophication conditions. In: Smayda, TJ., Shimizu, Y., editors. *Toxic Phytoplankton Blooms in the Sea.* Elsevier; New York: 1993. p. 203-209.
- Capone DG, Ferrier MD, Carpenter EJ. Amino acid cycling in colonies of the planktonic marine cyanobacterium *Trichodesmium theibautii*. *Appl Envir Microbiol.* 1994; 60:3989–3995.
- Cembella, AD. Ecophysiological processes and mechanisms: towards common paradigms for harmful algal blooms. In: Anderson, DM, Cembella, AD., Hallegraeff, GM., editors. *Physiological Ecology of Harmful Algal Blooms.* Springer; Berlin Heidelberg, New York: 1998. p. 381-403. NATO ASI Series 41
- Cloern JE. Our evolving conceptual model of the coastal eutrophication problem. *Mar Ecol Prog Ser.* 2001; 210:223–253.
- de Baar HJW, Boyd PW, Coale KH, Landry MR, Tsuda A, Assmy P, Bakker DCE, Bozee Y, Barber RT, Brzezinski MA, Buesseler KO, Boyé M, Croot PL, Gervais F, Gorbunov MY, Harrison PJ, Hiscock WT, Laan P, Lancelot C, Law CS, Levasseur M, Marchetti A, Millero FJ, Nishioka J, Nojiri Y, van Oijen T, Riebesell U, Rijkenberg MJA, Saito H, Takeda S, Timmermans KR, Veldhuis MJW, Waite AM, Wong C-S. Synthesis of iron fertilization experiments: from the Iron Age in the Age of Enlightenment. *J Geophys Res.* 2005; 110:C09S16. doi: 10.1029/2004JC002601
- Dzurica, S., Lee, C., Cosper, EM., Carpenter, EJ. Role of environmental variables, specifically organic compounds and micronutrients, in the growth of the chrysophyte *Aureococcus anophagefferens*, the “brown tide” microalga. In: Cosper, EM, Bricelj, VM., Carpenter, EJ., editors. *Novel Phytoplankton Blooms.* Springer-Verlag; New York: 1989. p. 511-541. Coastal and Estuarine Studies No 35
- Edmondson WT. Phosphorus, nitrogen and algae in Lake Washington after diversion of sewage. *Science.* 1970; 169:690–691. [PubMed: 5429903]
- Fan C, Glibert PM, Burkholder JM. Characterization of the nitrogen uptake kinetics of *Prorocentrum minimum* in natural blooms and laboratory cultures. *Harmful Algae.* 2003; 2:283–299.
- Flynn KJ. Modeling marine phytoplankton growth under eutrophic conditions. *J Sea Res.* 2002; 54:92–103.
- Flynn KJ. Castles built on sand: Dysfunctional plankton models and the failure of the biology-modeling interface. *J Plank Res.* 2005; 27:1205–1210.
- Franks PJS. Models of harmful algal blooms. *Limnol Oceanogr.* 1997; 42:1273–1282.
- Glibert, P., Pitcher, G., editors. GEOHAB, Global Ecology and Oceanography of Harmful Algal Blooms Programme. Science Plan. SCOR and IOC; Baltimore, MD, and Paris, France: 2001.
- Glibert, P., editor. GEOHAB, Global Ecology and Oceanography of Harmful Algal Blooms Programme. HABS in Eutrophic Systems. IOC and SCOR; Paris and Baltimore: 2006. p. 74
- Glasgow HB Jr, Burkholder JM, Reed RE, Lewitus AJ, Kleinman JE. Real-time remote monitoring of water quality: a review of current applications, and advancements in sensor, telemetry, and computing technologies. *J Exp Mar Biol Ecol.* 2004; 300:409–448.
- Glibert PM, Anderson DA, Gentien P, Granéli E, Sellner KG. The global, complex phenomena of harmful algal blooms. *Oceanography.* 2005a; 18(2):136–147.
- Glibert PM, Bronk DA. Release of dissolved organic nitrogen by the marine diazotrophic cyanobacterium *Trichodesmium* spp. *Appl Envir Microbiol.* 1994; 60:3996–4000.
- Glibert, PM., Burkholder, JM. The complex relationships between increasing fertilization of the Earth, coastal eutrophication, and HAB proliferation. In: Granéli, E., Turner, J., editors. *The Ecology of Harmful Algae.* Springer-Verlag; New York: 2006. p. 341-354.

- Glibert PM, Burkholder JM, Parrow MW, Lewitus AJ, Gustafson DE. Direct uptake of nitrogen by *Pfiesteria piscicida* and *Pfiesteria shumwayae*, and nitrogen nutritional preferences. *Harmful Algae*. 2006b; 5:380–394.
- Glibert PM, Conley DJ, Fisher TR, Harding LW Jr, Malone TC. Dynamics of the 1990 winter/spring bloom in Chesapeake Bay. *Mar Ecol Prog Ser*. 1995; 122:22–43.
- Glibert PM, Harrison J, Heil C, Seitzinger S. Escalating worldwide use of urea – a global change contributing to coastal eutrophication. *Biogeochemistry*. 2006a; 77:441–463.
- Glibert PM, Kelly V, Alexander J, Codispoti LA, Boicourt WC, Trice TM, Michael B, Wazniak C. *In situ* nutrient monitoring- A tool for capturing ephemeral nutrient pulses. *Harmful Algae*. 2008 this volume.
- Glibert, PM., Legrand, C. The diverse nutrient strategies of HABs: Focus on osmotrophy. In: Granéli, E., Turner, J., editors. *Ecology of Harmful Algae*. Springer; 2006. p. 163-176.
- Glibert PM, Magnien R, Lomas MW, Alexander J, Fan C, Haramoto E, Trice TM, Kana TM. Harmful algal blooms in the Chesapeake and Coastal Bays of Maryland, USA: Comparisons of 1997, 1998, and 1999 events. *Estuaries*. 2001; 24:875–883.
- Glibert, PM., O’Neil, J. Dissolved organic nitrogen release and amino acid oxidase activity by *Trichodesmium* spp. In: Charpy, L., Larkum, AWD., editors. *Marine Cyanobacteria*. Monaco Musée Océanographique, Bulletin de l’Institut Océanographique; Monaco: 1999. p. 265-272.
- Glibert PM, Seitzinger S, Heil CA, Burkholder JM, Parrow MW, Codispoti LA, Kelly V. The role of eutrophication in the global proliferation of harmful algal blooms: new perspectives and new approaches. *Oceanography*. 2005b; 18(2):198–209.
- Glibert PM, Wazniak CE, Hall M, Sturgis B. Seasonal and interannual trends in nitrogen and brown tide in Maryland’s Coastal Bays. *Ecol Appl*. 2007; 17(5):S79–S87.
- Gobler CJ, Lonsdale DJ, Boyer GL. A synthesis and review of causes and impact of harmful brown tide blooms caused by the alga, *Aureococcus anophagefferens*. *Estuaries*. 2005; 28:726–749.
- Granéli E, Anderson DM, Carlsson P, Maestrini SY. Light and dark carbon uptake by *Dinophysis* species in comparison to other photosynthetic and heterotrophic dinoflagellates. *Aquat Microb Ecol*. 1997; 13:177–186.
- Granéli E, Carlsson P, Legrand C. The role of C, N and P in dissolved and particulate matter as a nutritional source for phytoplankton growth, including toxic species. *Aquat Ecol*. 1999; 33:17–27.
- Granéli, E., Esplund, C. Minimizing economical losses with “real-time” HAB surveillance. 12th International Conference on Harmful Algae; Copenhagen, Denmark. September 2006; 2006. abstract only
- Hagy JD, Voynont WR, Keefe CW, Wood KV. Hypoxia in Chesapeake Bay, 1950–2001: long-term change in relation to nutrient loading and river flow. *Estuaries*. 2004; 27:634–658.
- Hallegraeff GM. A review of harmful algal blooms and their apparent global increase. *Phycologia*. 1993; 32:79–99.
- Harlin, MM. Changes in major plant groups following nutrient enrichment. In: McComb, J., editor. *Eutrophic Shallow Estuaries and Lagoons*. CRC Press, Inc; Boca Raton: 1993. p. 173-187.
- Harris, G. *Phytoplankton ecology: Structure, function, and fluctuation*. Chapman and Hall; 1986.
- Ramsdell, J. Anderson, D., Glibert, P., editors. *HARRNESS, Harmful Algal Research and Response: A National Environmental Science Strategy*. Ecological Society of America; Washington DC: 2005.
- Heil CA, Revilla M, Glibert PM, Murasko S. Nutrient quality drives phytoplankton community composition on the West Florida Shelf. *Limnol Oceanogr*. 2007; 52:1067–1078.
- Hodgkiss, IJ. The N:P ratio revisited. In: Ho, KC., Wang, ZD., editors. *Prevention and Management of Harmful Algal Blooms in the South China Sea*. School of Science and Technology, the Open University of Hong Kong; 2001.
- Hodgkiss IJ, Ho KC. Are changes in N:P ratios in coastal waters the key to increased red tide blooms? *Hydrobiologia*. 1997; 852:141–147.
- Hood RR, Zhang X, Glibert PM, Roman MR, Stoecker DK. Modeling the influence of nutrients, turbulence and grazing on *Pfiesteria* population dynamics. *Harmful Algae*. 2006; 5:459–479.
- Howarth RW, Marino R, Lane J, Cole JJ. Nitrogen fixation in freshwater, estuarine, and marine ecosystems. I. Rates and importance. *Limnol Oceanogr*. 1988; 33:669–687.

- Imai, I., Yamaguchi, M., Watanabe, M. Ecophysiology, life cycle, and bloom dynamics of *Chattonella* in the Seto Inland Sea, Japan. In: Anderson, DM, Cembella, AD., Hallegraeff, GM., editors. *Physiological Ecology of Harmful Phytoplankton Blooms*. Springer-Verlag; Berlin: 1998. p. 95-112.
- Irigoiien X, Flynn KJ, Harris R. Phytoplankton blooms: a “loophole” in microzooplankton grazing impact? *J Plank Res*. 2005; 27:313–321.
- Kana TM, Lomas MW, MacIntyre HL, Cornwell JC, Gobler CJ. Stimulation of the brown tide organism, *Aureococcus anophagefferens*, by selective nutrient additions to in situ mesocosms. *Harmful Algae*. 2004; 3:377–388.
- Kemp WM, Boynton WR, Adolf JE, Boesch DF, Boicourt WC, Brush G, Cornwell JC, Fisher TR, Glibert PM, Hagy JD, Harding LW, Houde ED, Kimmel DG, Miller WD, Newell RIE, Roman MR, Smith EM, Stevenson JC. Eutrophication in Chesapeake Bay: Historical trends and ecological interactions. *Mar Ecol Prog Ser*. 2005; 303:1–29.
- Kudela RM, Cochlan W. Nitrogen and Carbon Uptake Kinetics and the Influence of Irradiance for a Red Tide Bloom Off Southern California. *Aquat Microb Ecol*. 2000; 21:31–47.
- Kudela RM, Lane JQ, Cochlan W. The potential role of anthropogenically derived nitrogen in the growth of harmful algae in California, USA. *Harmful Algae*. 2008 this issue.
- Jeong HJ, Yoo YD, Park JY, Song JY, Kim ST, Lee SH, Kim KY, Yih WH. Feeding by phototrophic red-tide dinoflagellates: five species newly revealed and six species previously known to be mixotrophic. *Aquat Microb Ecol*. 2005; 40:133–150.
- Johansson N, Granéli E. Cell density, chemical composition and toxicity of *Chrysochromulina polylepis* (Haptophyta) in relation to different N:P supply ratios. *Mar Biol*. 1999; 135:209–217.
- Lam, CWY., Ho, KC. Red tides in Tolo Harbour, Hong Kong. In: Okaichi, T, Anderson, DM., Nemoto, T., editors. *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier; New York: 1989. p. 49-52.
- LaRoche J, Nuzzi R, Waters R, Wyman K, Falkowski PG, Wallace DWR. Brown tide blooms in Long Island’s coastal waters linked to variability in groundwater flow. *Global Change Biol*. 1997; 3:397–410.
- Larsson U, Elmgren R, Wulff F. Eutrophication and the Baltic Sea – causes and consequences. *Ambio*. 1985; 14:9–14.
- Lenes JM, Darrow BP, Cattrall C, Heil CA, Callahan M, Vargo GA, Byrne RH, Propsero JM, Bates DE, Fanning KA, Walsh JJ. Iron fertilization and the *Trichodesmium* response on the West Florida Shelf. *Limnol Oceanogr*. 2001; 46:1261–1270.
- Li A, Stoecker DK, Coats DW. Mixotrophy in *Gyrodinium galatheanum* (Dinophyceae): Grazing responses to light intensity and inorganic nutrients. *J Phycol*. 2001; 36:33–45.
- Lomas MW, Glibert PM, Berg GM. Characterization of nitrogen uptake by natural populations of *Aureococcus anophagefferens* (Chrysophyceae) as a function of incubation duration, substrate concentration, light, and temperature. *J Phycol*. 1996; 32:907–916.
- Lomas MW, Glibert PM, Clougherty DA, Huber DR, Jones J, Alexander J, Haramoto E. Elevated organic nutrient ratios associated with brown tide blooms of *Aureococcus anophagefferens* (Pelagophyceae). *J Plank Res*. 2001; 23:1339–1344.
- Lomas MW, Kana TM, MacIntyre HL, Cornwell JC, Nuzzi R, Waters R. Interannual variability of *Aureococcus anophagefferens* in Quantuck Bay, Long Island: natural test of the DON hypothesis. *Harmful Algae*. 2004; 3:389–402.
- MacIntyre HL, Lomas MW, Cornwell J, Suggett DJ, Gobler CJ, Koch EW, Kana TM. Mediation of benthic-pelagic coupling by microphytobenthos: an energy- and material-based model for initiation of blooms of *Aureococcus anophagefferens*. *Harmful Algae*. 2004; 3:403–437.
- Madden, C. Case study: Florida Bay. In: Glibert, P, Madden, C, Boynton, W, Flemer, D, Heil, C., Sharp, J., editors. *Estuarine Nutrient Criteria Development: State of the Science 2007*. EPA Office of Water; 2007. in press
- Mallin MA, Corbett CA. How hurricane attributes determine the extent of environmental effects: Multiple hurricanes and different coastal systems. *Estuaries and Coasts*. 2006; 29(6A):1046–1061.
- Malone TC, Conley DJ, Fisher TR, Glibert PM, Harding LW, Seller KG. Scales of nutrient-limited phytoplankton productivity in Chesapeake Bay. *Estuaries*. 1996; 19:371–385.

- Marshall HG, Egerton T, Burchardt L, Cerbin S, Kokocinski M. Long-term monitoring results of harmful algal populations in Chesapeake Bay and its major tributaries in Virginia, U.S.A. *Oceanol. Hydrobiol. Stud.* 2005; 34:35–41.
- McGillicuddy DJ Jr, Anderson DM, Lynch DR, Townsend DW. Mechanisms regulating large-scale seasonal fluctuations in *Alexandrium fundyense* populations in the Gulf of Maine: Results from a physical-biological model. *Deep-Sea Res II.* 2005; 52(19–21):2698–2714.
- Mitra A, Flynn KJ. Promotion of harmful algal blooms by zooplankton predatory activity. *Biology Letters.* 2006; 2:194–197. DOI: 10.1098/rsbl.2006.0447 [PubMed: 17148360]
- Miller, WD., Harding, LW., Adolf, JE. The influence of Hurricane Isabel on Chesapeake Bay phytoplankton dynamics. In: Sellner, KG., editor. Hurricane Isabel in Perspective. Chesapeake Research Consortium Publication 05–160; Edgewater, MD: 2005.
- Miller WD, Harding LW, Adolf JE. Hurricane Isabel generated an unusual fall bloom in Chesapeake Bay. *Geophys Res Lett.* 2006; 33:LO6612.doi: 10.1029/2005GL025658
- Moncheva S, Gotsis-Skretas O, Pagou K, Krastev A. Phytoplankton blooms in Black Sea and Mediterranean coastal ecosystems subjected to anthropogenic eutrophication: similarities and differences. *Estuar Coast Shelf Sci.* 2001; 53:281–295.
- Mulholland MR, Gobler CJ, Lee C. Peptide hydrolysis, amino acid oxidation, and nitrogen uptake in communities seasonally dominated by *Aureococcus anophagefferens*. *Limnol Oceanogr.* 2002; 47:1094–1108.
- Mulholland, MR., Heil, CA., Bronk, DA., O'Neil, JM., Bernhardt, P. Does nitrogen regeneration from the N₂ fixing cyanobacteria *Trichodesmium* spp. fuel *Karenia brevis* blooms in the Gulf of Mexico?. In: Steidinger, KA.Landsberg, JH.Tomas, CR., Vargo, GA., editors. Harmful Algae 2002. Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography and Intergovernmental Oceanographic Commission of UNESCO; 2004. p. 47-49.
- Neely, MB., Heil, CA., Murasko, S., Dziemiela, K., Faltin, E., Garrett, M., Truby, E., Carlson, D., English, D. HAB's and hurricanes in Florida. American Geophysical Union, Fall Meeting; 2006; abstract only #B41E-0226
- Nygaard K, Tobiesen A. Bacterivory in algae: a survival strategy during nutrient limitation. *Limnol Oceanogr.* 1993; 38:273–279.
- Nuzzi R, Waters RM. Long-term perspective on the dynamics of brown tide blooms in Long Island coastal waters. *Harmful Algae.* 2004; 3:279–294.
- Okaichi, T. Red tides in the Seto Inland Sea. In: Okaichi, T., Yanagi, Y., editors. Sustainable development in the Seto Inland Sea – from the viewpoint of fisheries. Tera Sci Publ Co; Tokyo, Japan: 1997. p. 251-304.
- Paerl HW. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnol Oceanogr.* 1988; 33:823–847.
- Paerl H, Valdes LM, Peierls BL, Adolf JE, Harding LW. Anthropogenic and climatic influences on the eutrophication of large estuarine systems. *Limnol Oceanogr.* 2006; 51:448–462.
- Parrow MW, Burkholder JM. Estuarine heterotrophic cryptoperidinioids (Dinophyceae): Life cycle and culture studies. *J Phycol.* 2003; 39:678–696.
- Parsons ML, Dortch Q, Turner RE. Sedimentological evidence of an increase in *Pseudo-nitzschia* (Bacillariophyceae) abundance in response to coastal eutrophication. *Limnol Oceanogr.* 2002; 47:551–558.
- Radach G, Berg J, Hagmeier E. Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at Helgoland and at V ELBE 1 in the German Bight. *Contin Shelf Res.* 1990; 10:305–328.
- Riegman R. Nutrient-related selection mechanism in marine phytoplankton communities and the impact of eutrophication on the planktonic food web. *Water Sci Technol.* 1995; 32:63–75.
- Riegman, R., Row, A., Noordeloos, AAM., Cadee, GC. Evidence for eutrophication induced *Phaeocystis* sp. blooms in the Narsdiep area (The Netherlands). In: Smayda, TJ., Shimizu, Y., editors. Toxic Phytoplankton Blooms in the Sea. Elsevier Science; New York: 1993. p. 799-805.
- Romdhane, MS., Eilertsen, HC., Yahia O, KD., Yahia, MND. Toxic dinoflagellate blooms in Turisian lagoons: causes and consequences for aquaculture. In: Reguera, B.Blanco, J.Fernández, ML.,

- Wyatt, T., editors. Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO; Vigo: 1998. p. 80-83.
- Schindler DW. Evolution of phosphorus limitation in lakes. *Science*. 1977; 196:260–262.
- Schindler DW. Determining ecosystem responses to anthropogenic stress. *Can J Fish Aquat Sci*. 1987; 44(Suppl 1):6–25.
- Schindler DW. Recent advances in the understanding and management of eutrophication. *Limnol Oceanogr*. 2006; 51:356–363.
- Scholin, CA., Anderson, DM. Detection and quantification of HAB species using antibody and DNA probes: progress to date and future research objectives. In: Requera, B., Blanco, J., Fernandez, M.L., Wyatt, T., editors. Harmful Algae. IOC, UNESCO; Paris: 1998. p. 253-257.
- Scholin, C., Vrieling, E., Peperzak, L., Rhodes, L., Rublee, PA. Detection of HAB species using lectin, antibody, and DNA probes. In: Hallegraef, GM., Anderson, DM., Cembella, AD., editors. Manual on Harmful Marine Microalgae. 2. UNESCO Monographs on Oceanographic Methodology; Paris, France: 2003. p. 131-164.
- Sellner KG, Doucette GJ, Kirkpatrick GJ. Harmful algal blooms: causes, impacts and detection. *J Ind Microbiol Biotechnol*. 2003; 3:383–406.
- Seitzinger SP, Sanders RW, Styles RV. Bioavailability of DON from natural and anthropogenic sources to estuarine plankton. *Limnol Oceanogr*. 2002; 47(2):353–366.
- Smayda, TJ. Primary production and the global epidemic of phytoplankton blooms in the sea: A linkage?. In: Coper, EM., Bricelj, VM., Carpenter, EJ., editors. Novel Phytoplankton Blooms. Springer-Verlag; New York: 1989. p. 449-484. Coastal and Estuarine Studies No. 35
- Smayda, TJ. Novel and nuisance phytoplankton blooms in the sea: Evidence for a global epidemic. In: Granéli, E., Sundstrom, B., Edler, L., Anderson, DM., editors. Toxic Marine Phytoplankton. Elsevier; New York: 1990. p. 29-40.
- Smayda TJ. Harmful phytoplankton blooms: their ecophysiology and general relevance. *Limnol Oceanogr*. 1997; 42:1137–1153.
- Smayda, TJ. Ecophysiology and bloom dynamics of *Heterosigma akashiwo* (Raphidophyceae). In: Anderson, DM., Cembella, AD., Hallegraef, GM., editors. Physiological Ecology of Harmful Algal Blooms. Vol. G41. Springer-Verlag; New York: 1998. p. 113-131. NATO ASI Series
- Smayda, TJ., Borkman, DG., Beaugrand, G., Belgrano, AG. Ecological effects of climate variation in the North Atlantic: Phytoplankton. In: Stenseth, NC., Ottersen, G., Hurrell, J., Belgrano, A., editors. Ecological effects of climate variations in the North Atlantic. Oxford Univ Press; 2004. p. 49-54.
- Smayda TJ, Reynolds CS. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *J Plank Res*. 2001; 23:47–461.
- Smayda TJ, Reynolds CS. Strategies of marine dinoflagellate survival and some rules of assembly. *J Sea Res*. 2003; 49:95–106.
- Springer JJ, Burkholder JM, Glibert PM, Reed RE. Use of a real-time remote monitoring network and shipborne sampling to characterize a dinoflagellate bloom in the Neuse Estuary, North Carolina, U.S.A. *Harmful Algae*. 2005; 4:533–551.
- Stoecker D. Mixotrophy among dinoflagellates. *J Eukaryot Microbiol*. 1999; 46:397–401.
- Strom, SL., Bright, K. Effects on planktonic food webs of organic nitrogen use by bloom-forming phytoplankton. Abstract. Proceedings of the Biennial Meeting of the Estuarine Research Federation; Seattle, Washington, USA. Port Republic, MD: Estuarine Research Federation; 2003.
- Sunda WG, Granéli E, Gobler CJ. Positive feedback and the development and persistence of ecosystem disruptive algal blooms. *J Phycol*. 2006; 42:963–974.
- Tango, P., Brown, CW., Gross, TF., Ramers, DL., Hood, RR., Michael, BD. Assessing the validation of a preliminary *Karlodinium micrum* nowcast model system in Chesapeake Bay and its tributaries: A framework for HAB nowcasts and forecasts. HABs and Eutrophication Open Science Meeting; Baltimore MD. March 2005; 2005. abstract only
- Tilman D. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology*. 1977; 58:338–348.
- Trainer VL, Adams NG, Bill BD, Stehr CM, Wekell JC, Moeller P, Busman M, Woodruff D. Domoic acid production near California coastal upwelling zones, June 1998. *Limnol Oceanogr*. 2000; 45:401–440.

- Trainer VL, Le Eberhart BT, Wekell JC, Adams NG, Hanson L, Cox F, Dowell J. Paralytic shellfish toxins in Puget Sound, Washington. *J Shellfish Res.* 2003; 22:213–223.
- Trice TM, Glibert PM, Lea C, Van Heukelem L. HPLC pigment records provide evidence of past blooms of *Aureococcus anophagefferens* in the Coastal Bays of Maryland and Virginia, USA. *Harmful Algae.* 2004; 3:295–304.
- Turner RE, Rabalais N. Changes in Mississippi river water quality this century and implications for coastal food webs. *BioScience.* 1991; 41:140–147.
- Vargo, GA., Heil, CA., Ault, DN., Neely, MB., Murasko, S., Havens, J., Lester, KM., Dixon, LK., Merkt, R., Walsh, J., Weisberg, R., Steidinger, KA. Four *Karenia brevis* blooms: a comparative analysis. In: Steidinger, KA, Landsberg, JA, Tomas, CR., Vargo, GA., editors. *Harmful Algae 2002 - Proceedings of the Xth International Conference on Harmful Algae.* Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography, and the Intergovernmental Oceanographic Commission of UNESCO; St. Petersburg (FL): 2004. p. 14-16.
- Walsh JJ, Jolliff J, Darrow BP, Lenos JM, Milroy SP, Dieterle D, Carder KL, Chen FL, Vargo GA, Weisberg RH, Fanning KA, Muller-Karger F, Steidinger KA, Heil CA, Prospero JS, Lee TN, Kirkpatrick G, Whitedge TE, Stockwell DA, Tomas C, Villareal TA, Jochems AE, Bontempe PS. Red tides in the Gulf of Mexico: Where, when and why? *J Geophys Res.* 2006; 111:C11003. doi: 10.1029/2004JC002813
- Whereat, E., Farestad, M. Volunteer HAB monitoring provides a “first watch” for resource managers and researchers in the Delaware Inland Bays. U.S.A. HABs and Eutrophication Open Science Meeting; Baltimore MD. March 2005; 2005. abstract only
- Wood AM, Leatham T. The species concept in phytoplankton ecology. *J Phycol.* 1992; 28:723–729.
- Yung YK, Wong CK, Broom MJ, Ogden JA, Chan SCM, Leung Y. Long-term changes in hydrography, nutrients, and phytoplankton in Tolo Harbour, Hong Kong. *Hydrobiologia.* 1997; 352:107–115.
- Zhou, M. Which is the trigger factor to the outbreak of large scale *Prorocentrum* blooms in the East China Sea?. HABs and Eutrophication Open Science Meeting; Baltimore MD. March 2005; 2005. abstract only

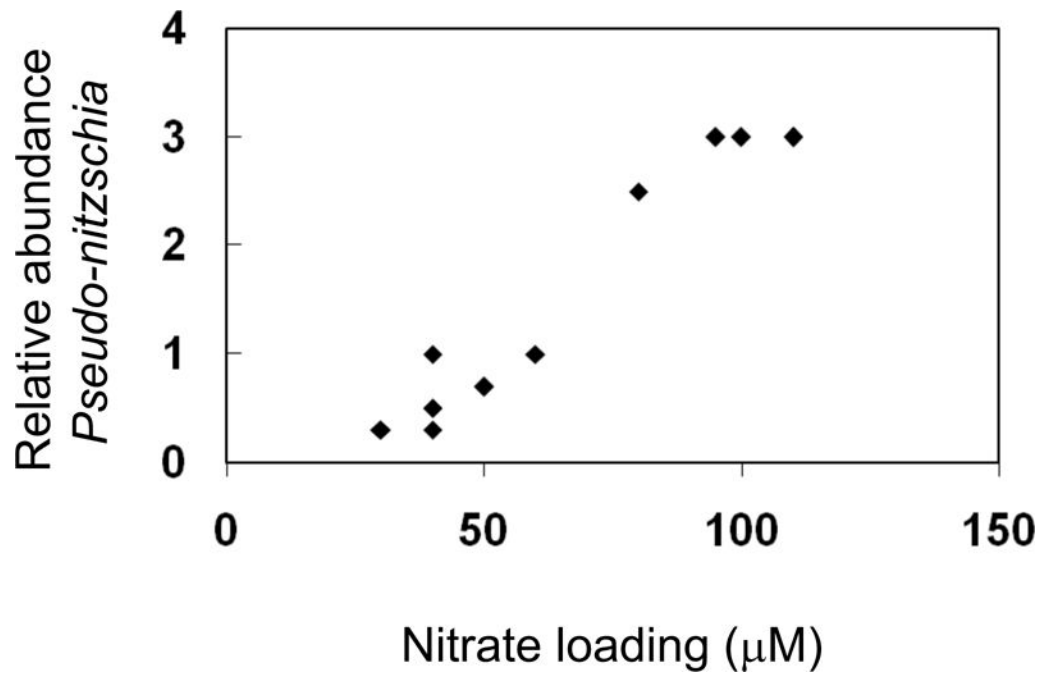


Figure 1. Average abundance (%) of the diatom *Pseudo-nitzschia* in the sedimentary record as a function of the nitrate loading in the northern Gulf of Mexico (redrawn from Turner and Rabalais 1991 and Parsons et al. 2002).

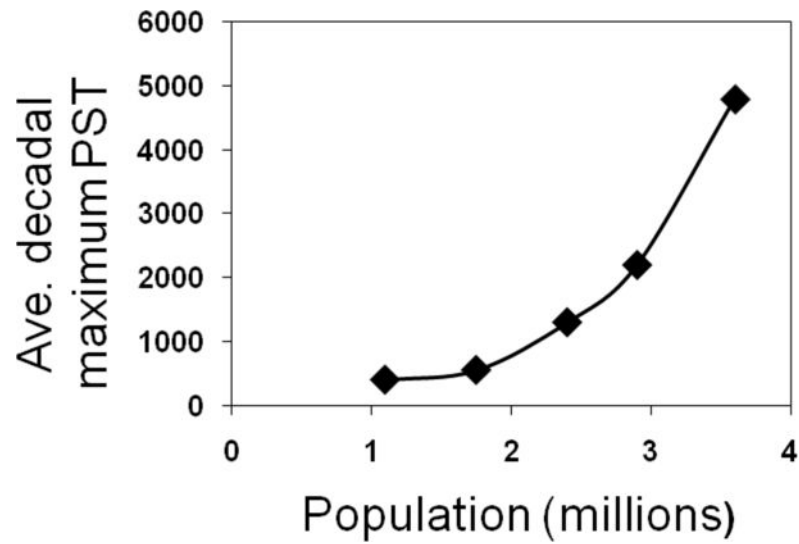


Figure 2. Relationship between the growth in human population (and presumably their nutrients) and HABs from Puget Sound, Washington State, where continuous monitoring of paralytic shellfish poisoning has been ongoing since the mid-1950's. Plotted here is the relationship between human population in the region for the past 40 years (data were derived from the U.S. census) and the average decadal maximum recorded amount of paralytic shellfish toxins, PST (redrawn from Trainer et al. 2003).

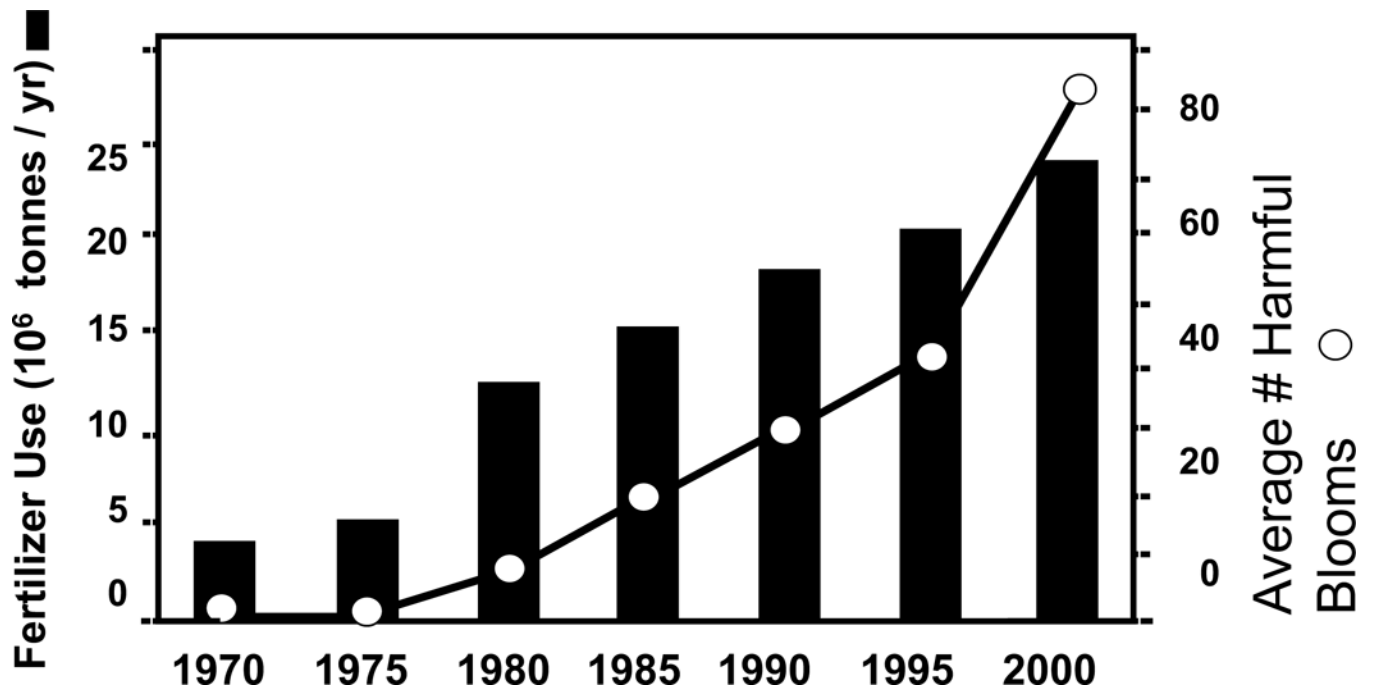


Figure 3. Long term trends in the use of nitrogen based fertilizers and the number of occurrences of red tide blooms in Chinese coastal waters (modified and redrawn from Anderson et al. 2002 and Zhou et al. 2005).

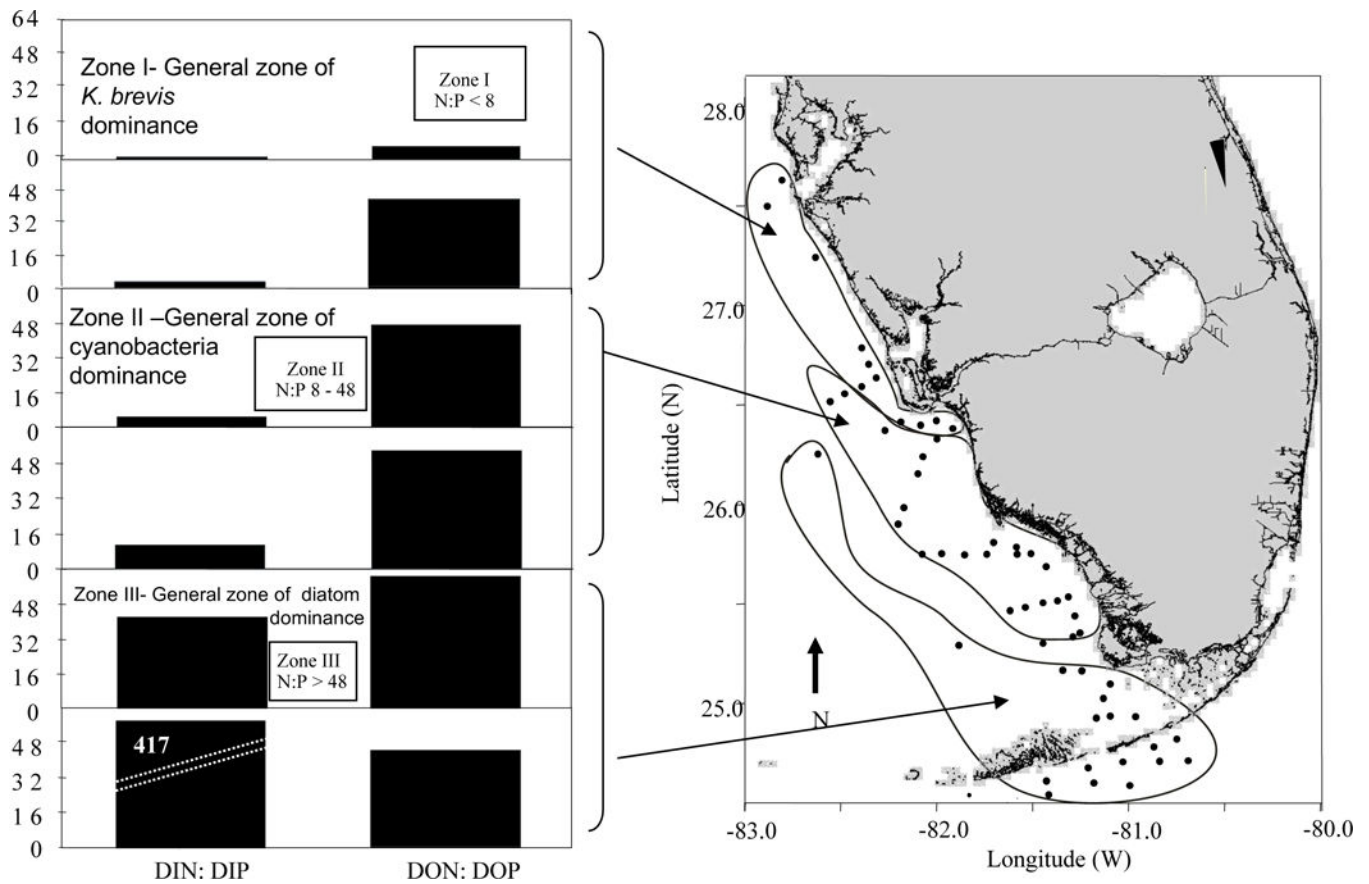


Figure 4. Mean dissolved inorganic and organic N:P ratios for each of the major riverine systems of western Florida shelf sampled during the dry season of May 2004. Each bar represents the means of the stations sampled along an individual riverine transect. The insert box indicated the mean particulate N:P ratio. The general zones are indicated on the companion map of southern Florida (modified from Heil et al. 2007).

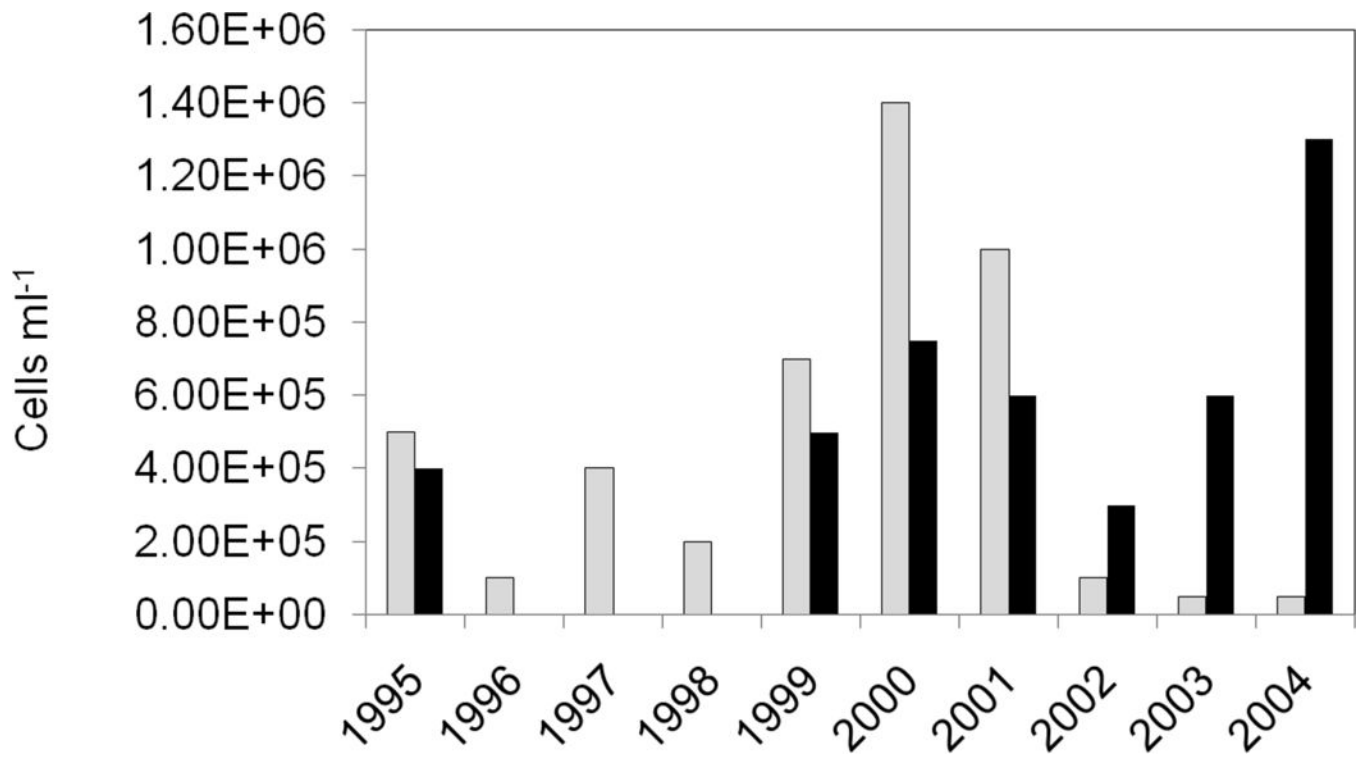


Figure 5. Long- term trends in brown tide in Peconic Estuary Long Island (open bars) and in Maryland Coastal Bays (closed bars; redrawn from Gobler et al. 2005 and Glibert et al. 2007).