

Harmful algal blooms and eutrophication: Examining linkages from selected coastal regions of the United States

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ABSTRACT

Coastal waters of the United States (U.S.) are subject to many of the major harmful algal bloom (HAB) poisoning syndromes and impacts. These include paralytic shellfish poisoning (PSP), neurotoxic shellfish poisoning (NSP), amnesic shellfish poisoning (ASP), ciguatera fish poisoning (CFP) and various other HAB phenomena such as fish kills, loss of submerged vegetation, shellfish mortalities, and widespread marine mammal mortalities. Here, the occurrences of selected HABs in a selected set of regions are described in terms of their relationship to eutrophication, illustrating a range of responses. Evidence suggestive of changes in the frequency, extent or magnitude of HABs in these areas is explored in the context of the nutrient sources underlying those blooms, both natural and anthropogenic. In some regions of the U.S., the linkages between HABs and eutrophication are clear and well documented, whereas in others, information is limited, thereby highlighting important areas for further research.

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1. Introduction

Virtually every coastal nation is affected by harmful algal blooms (HABs; Hallegraeff, 1993). It is now widely accepted that there are more toxic algal species, algal toxins, areas affected, fisheries resources impacted, and higher economic losses compared to several decades ago. Reasons for such expansion include natural dispersal of species by currents and storms; dispersal of species through human activities such as ballast water discharge and shellfish seeding; improved detection of HABs and their toxins due to better chemical instrumentation and improved communication among scientists; and stimulation of HABs as a result of cultural

eutrophication linked to the pressures of increasing human population including animal and plant agricultural runoff and non-point nutrient pollution (Anderson, 1989; Hallegraeff, 1993; Burkholder, 1998; Glibert et al., 2005a; Glibert and Burkholder, 2006).

In this latter context, there is now consensus on some aspects of the relationship between eutrophication and HABs (Heisler et al., 2008), recognizing that significant questions and challenges remain (Glibert, 2006). Various authors have investigated potential linkages between HABs and eutrophication at the global level (e.g., Smayda, 1989; Burkholder, 1998; Anderson et al., 2002; Glibert and Burkholder, 2006; Glibert et al., 2008). In some instances, the linkage is clear and unequivocal. For example, mandated reductions in pollution inputs to the Inland Sea of Japan in the mid-1970s led to a proportional decrease in the number of red tides and HAB events (Okachi, 1997). Likewise, increased nutrient loadings to the

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northwestern Black Sea in the 1970s and 1980s led to an increase and compositional shift in algal blooms (Bodeanu and Ruta, 1998). Subsequently, HABs declined in the 1990s coinciding with a decrease in nutrient loading due to reduced fertilizer usage following the breakup of the former Soviet Union and termination of its agricultural subsidies.

The pathways and mechanisms through which nutrients supplied by human activities can stimulate HABs are often complex and subtle. For example, it is now evident that in addition to the quantity of nutrients supplied through point and non-point sources of pollution, the relative abundance of the major nutrients (e.g., nutrient supply ratios) and the chemical form of those nutrients (e.g., inorganic versus organic) are all important (Smayda, 1989; Anderson et al., 2002; Glibert et al., 2001, 2005a). Furthermore, it is recognized that nutrient effects cannot be inferred from concentration data alone; in fact, there can be a negative relationship between ambient concentration and biomass due to incorporation of the nutrient into biomass. Nutrient loading or flux rates are the more appropriate measure, but much more difficult to quantify. In addition, the role of mixotrophy, or use of both phototrophic and heterotrophic nutrition, by some harmful algae increasingly has been recognized, and these organisms sometimes have been shown to be indirectly stimulated by nutrient enrichment through consumption of algal prey that are directly stimulated by eutrophication (Burkholder and Glasgow, 1997; Burkholder, 1998; Stoecker, 1999; Lewitus et al., 1999a; Glibert et al., 2005a; Burkholder et al., 2008).

Given that some HABs are stimulated by anthropogenic nutrient inputs, projections of increased nitrogen (N) and phosphorus (P) loadings to coastal waters are worrisome (Seitzinger et al., 2005; Harrison et al., 2005; Burkholder et al., 2006; Howarth, 2008; Bricker et al., 2008). Here we focus on some common HAB events in the U.S., particularly those that cause human illness, but this is not intended to be a comprehensive survey of all blooms, species or regions. For example, some blooms in the Northeast (e.g., Narragansett Bay; Li and Smayda, 2000), eastern Florida or Florida Bay (e.g., Phlips et al., 1999; Glibert et al., 2004b), the Texas Coast (e.g., Laguna Madre; Buskey et al., 2001), and San Francisco Bay (Lehman et al., 2005) are not reviewed herein.

2. Regional HAB phenomena

2.1. PSP in the Gulf of Maine

The most significant HAB problem in the northeastern U.S. is PSP caused by *Alexandrium fundyense*.¹ The affected resources are predominantly shellfish, but higher levels of the food web are also impacted, including lobsters, fish, and marine mammals. Blooms of *A. fundyense* fall into two categories: regional outbreaks occurring in open coastal waters, and “self-seeding” localized blooms in isolated embayments and sounds with little or no input or export of cells to the adjacent coastal waters (Anderson, 1997; Anderson et al., 2005c). A key feature of *A. fundyense* bloom dynamics is a dormant cyst stage that allows this species to overwinter. In the nearshore waters of the Gulf of Maine (GoM), blooms are initiated from two cyst seedbeds, one in the Bay of Fundy, and the other offshore of mid-coast Maine, with delivery of established populations to shore by episodic wind forcings as well as large-scale movements of water masses in the central Gulf (Anderson et al., 2005b). Along this extended transport pathway, cells within the

eastern and western segments of the Maine coastal current can enter embayments such as Casco and Massachusetts Bays with downwelling-favorable winds. It is important to recognize, however, that the source populations and associated water masses are delivered from upstream and offshore.

PSP toxicity in the western GoM was sporadic and poorly documented prior to a major bloom in 1972 (Hurst, 1975). PSP toxicity continued at high levels until the early 1990s, decreased for a decade thereafter, and recently has shown signs of increasing again (Anderson et al., 2005a).

2.1.1. Eutrophication linkages

An evaluation of potential linkages between northeastern U.S. PSP outbreaks and eutrophication needs to account for the two types of blooms in the region. Riley (1967) challenged the prevailing dogma that coastal nutrients in the GoM were derived primarily from riverine sources. Instead, he suggested that cross-shelf fluxes from the open ocean were important, an inference later validated by Fournier et al. (1977). Nutrients that enter the GoM at depth through the Northeast Channel overwhelm fluxes from the atmosphere or local rivers (Townsend, 1998; Townsend et al., 2006). There has been and continues to be significant inter-annual variability in the magnitude of that nutrient flux into the Gulf, reflecting the relative importance of the source waters and large-scale forcings such as the North Atlantic Oscillation (Townsend et al., 2006).

Coastal currents of the GoM carry populations of *A. fundyense* into embayments such as Casco and Massachusetts Bays where anthropogenic influences may be more significant. Local cyst germination might also provide an inoculum. Poulton et al. (2005), Martorano (1997) and Love et al. (2005) all provided evidence for increasing dissolved inorganic nitrogen (DIN) levels (ranging from 1 to 10 μM during *Alexandrium* bloom season) along a transect from offshore to inshore within Casco Bay. These data reflect land-based nutrient sources in the bay (i.e., the city of Portland) and riverine inputs.

Nutrient measurements in the region's rivers and coastal waters are relatively scarce, and suggest that nutrient loads in the Androscoggin and Kennebec (two of the four largest rivers emptying into the GoM) are highly variable (Fig. 1A). Nitrate + nitrite ($\text{NO}_3^- + \text{NO}_2^-$) levels average about 7.6 μM over an annual cycle, with highest levels (12.7 μM) in the high-runoff months (winter–spring) and the lowest (4.6 μM) during low-runoff months (June–October). These are comparable to or lower than values in other urban regions of the U.S., and once those freshwaters mix with coastal waters, the resulting nutrient concentrations are diluted (e.g., to $\sim 2.7 \mu\text{M}$ NO_3^-). Episodic high values of $\text{NO}_3^- + \text{NO}_2^-$ in excess of 10 μM can occur during bloom season (Fig. 1B), which could be important to *A. fundyense* populations in Casco Bay at that time. The average annual cycle shows no clear changes over the last 7 years, although a longer duration may be needed to detect NO_3^- -related changes (e.g., Rothenberger, 2007). Many HABs also use ammonium (NH_4^+) or dissolved organic nitrogen (DON) as their primary N substrate. In Casco Bay, NH_4^+ concentrations are very high, occasionally exceeding 20 μM , and tend to average $>2 \mu\text{M}$ (Bricker et al., 2007).

Analysis of samples collected from inshore and offshore waters throughout the northern GoM in high-, medium-, and low-runoff periods again suggest that terrestrial sources of $\text{NO}_3^- + \text{NO}_2^-$ are not significant, except for localized areas of inner Casco Bay as mentioned, based upon the available data. For example, mixing curves of NO_3^- concentrations versus salinity show that there was virtually no low-salinity (terrestrial, freshwater) NO_3^- contribution in July 2001 or June 2000 (Fig. 1C). There was evidence of a terrestrial, freshwater source in these coastal waters in April–May

¹ *Alexandrium tamarense* and *A. fundyense* frequently co-occur and are considered to be varieties of the same species (Anderson et al., 1994). The name *A. fundyense* will be used to refer to both forms.

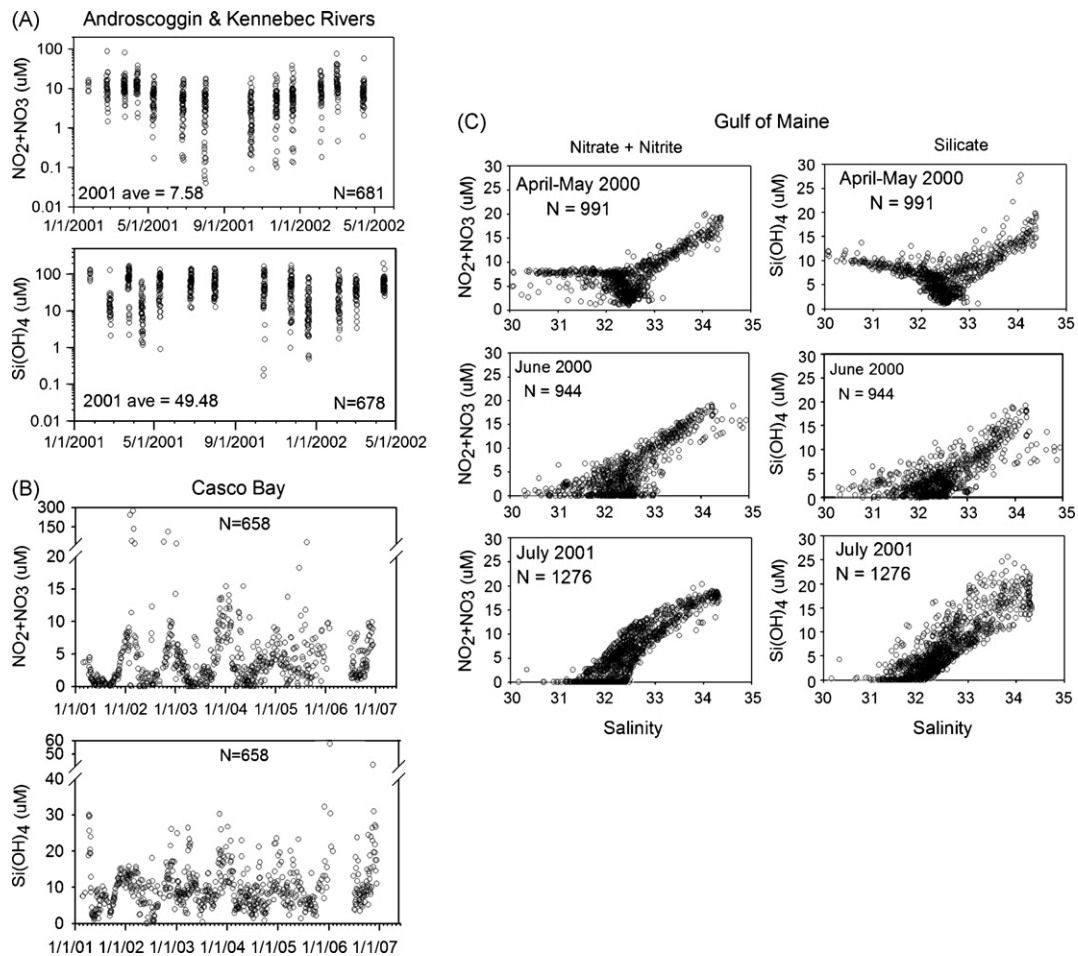


Fig. 1. Nutrients in Gulf of Maine nearshore waters. (Panel A) Concentrations of nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$) and silicate ($\text{Si}(\text{OH})_4$) in the Kennebec and Androscoggin Rivers in Maine over the period 1 January 2001 to 1 May 2002 (data from Vorosmarty et al., <http://www.gm-wics.sr.unh.edu/>). (Panel B) Concentrations of $\text{NO}_3^- + \text{NO}_2^-$ and $\text{Si}(\text{OH})_4$ collected in Casco Bay at the Southern Maine Community College dock, South Portland, Maine (from Townsend et al., <http://grampus.umeoce.maine.edu/>). (Panel C) Mixing curves for $\text{NO}_3^- + \text{NO}_2^-$ and $\text{Si}(\text{OH})_4$ vs. salinity for Gulf of Maine samples collected in a high- (April–May 2000), medium- (June 2000) and low-runoff period (July 2001) (Townsend et al., 2005). Assuming a northern Gulf of Maine coast-wide freshwater source concentration of nutrients similar to the Kennebec–Androscoggin (which was $32 \mu\text{M}$ $\text{Si}(\text{OH})_4$ and $12 \mu\text{M}$ $\text{NO}_3^- + \text{NO}_2^-$ in April 2000; $n = 49$; <http://www.gm-wics.sr.unh.edu/>), and coastal seawater concentrations of ca. $8 \mu\text{M}$ of $\text{Si}(\text{OH})_4$ and ca. $8 \mu\text{M}$ $\text{NO}_3^- + \text{NO}_2^-$ and salinity of 32.5, $\text{Si}(\text{OH})_4$ concentrations of $9.5 \mu\text{M}$ and $\text{NO}_3^- + \text{NO}_2^-$ concentrations of $8 \mu\text{M}$ at salinity of 30 in April–May are expected (in agreement with those values observed in the mixing curve in (C)).

2000, during and after the high-runoff period but, even then, the NO_3^- sources were primarily from offshore. Data are not available for other N forms offshore.

Considering localized blooms that occur along the New England coast, a separate analysis in each area would be needed to assess whether eutrophication is affecting *A. fundyense* blooms. There is a good likelihood that this is occurring, as these embayments, sounds, and estuaries are often surrounded by housing and other development, often with outdated septic systems. One example, the Nauset Marsh System on Cape Cod, lacks major river input, and NO_3^- -contaminated groundwater from septic systems is the largest source of N (Giblin and Gaines, 1990; Howes et al., 2003). Groundwater NO_3^- fluxes are ~5-fold greater than inputs from land runoff, and these two sources combined are comparable to inputs in river-dominated urban areas of the U.S. (Portnoy et al., 1998). In the more highly developed areas of the Nauset System, groundwater NO_3^- concentrations are more than 30-fold higher than in less developed areas. PSP outbreaks within the Nauset Marsh System have increased dramatically over the last several decades. Toxicity occurred in Salt Pond (Eastham) in 8 of 17 years (48%) from 1975 to 1991, and then in 15 of the last 16 years (94%). PSP is also occurring earlier and lasting longer (H. Lind, personal

communication). The growing nutrient load from NO_3^- contaminated groundwater is a likely reason for the increased frequency of PSP outbreaks within this system.

In summary, PSP outbreaks in the northeastern U.S. take two forms—large regional open-water blooms and localized nearshore outbreaks. For the open-water blooms, the supply of inorganic nutrients from oceanic sources dwarfs inputs from land, so that if there is an eutrophication effect, it is subtle and unquantified. These blooms do impact certain bays and sounds when offshore populations of *A. fundyense* are delivered by winds, and thus there is a potential for local sources of anthropogenic nutrients to enhance bloom magnitude and duration. The strongest linkage to eutrophication is with localized, nearshore PSP outbreaks that recur annually in small salt ponds, embayments, and sounds where flushing rates are low and development pressures can lead to high-nutrient inputs from sewage treatment plants, terrestrial runoff, and groundwater sources.

2.2. Brown tides in the northeast and mid-Atlantic

Aureococcus anophagefferens is the picoplanktonic pelagophyte that has caused destructive ‘brown tide’ blooms in northeast and

mid-Atlantic U.S. estuaries for two decades (Gobler et al., 2005). The first blooms occurred simultaneously in 1985 in Narragansett Bay, Rhode Island, and Great South Bay and the Peconic Estuary on Long Island, New York (Cosper et al., 1989). Blooms recurred annually in Long Island Bays from 1986 to 1988 and sporadically since then, but have not returned to Narragansett Bay. Even during years without blooms, *A. anophagefferens* populations of up to 10^4 mL^{-1} persist (Nuzzi and Waters, 2004). During the 1990s, brown tides expanded south along the U.S. East Coast into bays in New Jersey (Gastrich et al., 2004), Delaware (Popels et al., 2003), Maryland, and Virginia (Trice et al., 2004; Glibert et al., 2007). Low abundance of *A. anophagefferens* has been observed along the entire eastern seaboard of the U.S. from Maine to Florida (Anderson et al., 1993; Popels et al., 2003).

2.2.1. Eutrophication linkages

Brown tides are not directly caused by eutrophication from inorganic nutrients, but they may be linked to organic nutrients (see below). Other phytoplankton such as diatoms often out-compete *A. anophagefferens* when inorganic nutrient loads are high (Berg et al., 1997; MacIntyre et al., 2004). An examination of spatial and temporal patterns of concentrations of *A. anophagefferens* cells and inorganic nutrients indicates that blooms occurred when inorganic nutrient levels were low (Cosper et al., 1989; LaRoche et al., 1997; Gobler et al., 2002, 2004). Moreover, NO_3^- additions during mesocosm and bottle experiments consistently have yielded reduced *A. anophagefferens* cell densities relative to those of competing algae (e.g., Keller and Rice, 1989; Gobler and Sañudo-Wilhelmy, 2001a). The N-uptake characteristics of *A. anophagefferens* (low K_s and V_{max} for NH_4^+) suggest that this species is well adapted to low-nutrient environments (Lomas et al., 1996). The off-shore rerouting of sewage previously discharged directly into western Great South Bay during the early 1980s led to lower levels of DIN there, thus creating a nutrient regime which reduced total annual phytoplankton biomass, but favored dominance by *A. anophagefferens* as blooms began to first develop in the late 1980s (Fig. 2A).

Blooms of *Aureococcus* often occur after 'pre-blooms' of other algae which draw down inorganic nutrients to low levels. Nutrient remineralization processes during and following these pre-blooms can result in enhanced levels of dissolved organic matter (DOM)

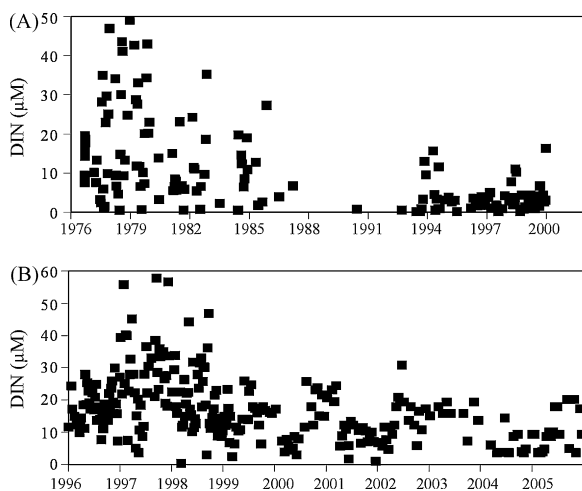


Fig. 2. (A) Concentrations of DIN in western Great South Bay, NY (Suffolk County Department of Health Services Station 250) from 1976 to 2000, before and after the onset of brown tides. (B) Concentrations of DIN in Great Peconic Bay, NY (Suffolk County Department of Health Services Station 130) from 1996 to 2005, since the last occurrence of brown tide in this system.

which can serve as a source of DON and dissolved organic carbon (DOC) (LaRoche et al., 1997; Gobler and Sañudo-Wilhelmy, 2001b). Cultures (both axenic and non-axenic) and field populations of *A. anophagefferens* have been shown to obtain N from a variety of organic compounds, including urea, amino acids, proteins, chitin, and acetamide (Berg et al., 1997, 2002, 2003; Mulholland et al., 2002; Kana et al., 2004). Experimental additions of DOM (glucose, amino acids, DOM from macroalgae) have enhanced the growth and relative abundance of *A. anophagefferens* during field experiments (Gobler and Sañudo-Wilhelmy, 2001a; Kana et al., 2004). Concentrations of DON and DOC often are elevated during bloom initiation, and their drawdown has been associated with bloom development (LaRoche et al., 1997; Gobler et al., 2004).

Brown tides commonly occur in shallow bays where diffusive fluxes from the benthos are important sources of organic nutrients. For example, in the shallow (~1.5 m) lagoonal estuaries of NY, brown tides are persistent events and DON levels are high, due in part to strong benthic–pelagic coupling (Lomas et al., 2004; Gobler et al., 2005). In Maryland's lagoonal bays, both the DON concentrations and the strength of brown tide blooms have increased steadily over the past decade (Trice et al., 2004; Glibert et al., 2007). Since the mid-1990s, mean concentrations of DON in these bays have more than doubled, and the fraction of total chlorophyll composed of brown tide in the summer has increased to an even greater extent (Glibert et al., 2007).

In deeper estuaries where benthic–pelagic coupling is weaker, DON concentrations typically are lower than in shallow lagoons and brown tides occur less frequently. This is the case, for example, in the Peconic Estuary (mean depth >5 m; Gobler et al., 2005). Both brown tide and DON levels there have decreased since 1996 (Fig. 2B), presumably due to decreased N loading, but DIN levels have remained unchanged. Hence, it is possible that lower DON levels, in conjunction with higher grazing rates on *A. anophagefferens* by the zooplankton community (Deonaraine et al., 2006), may be responsible for the absence of brown tides in the Peconic Estuary since the 1990s.

In summary, *A. anophagefferens* thrives in environments where nutrients are dominated by organic rather than inorganic forms. In regions where inorganic nutrient loading is elevated, other phytoplankton with faster growth rates tend to dominate. Thus, brown tides are not directly related to inorganic nutrient loading, but may be indirectly related to eutrophication processes as inorganic nutrients are assimilated and regenerated as organic forms. In some regions, such as the Maryland Coastal Bays, DON is increasing from agricultural sources, animal operations and organic fertilizers (e.g., Glibert et al., 2007) and direct sources of DON should be considered as contributing to eutrophication in these regions, and therefore to brown tides.

2.3. HABs in the mid-Atlantic region

In the mid-Atlantic, the frequency of occurrence and, in many cases, the intensity of HABs is increasing relative to previous decades. The region has a wide range of high-biomass and/or toxic HABs involving species such as *Prorocentrum minimum*, *A. anophagefferens*, *Microcystis aeruginosa*, *Pfiesteria piscicida*, *Pfiesteria shumwayae*, *Karlodinium veneficum* (formerly *Karlodinium micrum*, *Gyrodinium galatheanum*), *Heterosigma akashiwo*, *Chattonella subsalsa* and *Chattonella cf. vericulosa*, and *Fibrocapsa japonica* (Marshall et al., 2005a; Burkholder et al., 2005; Moeller et al., 2007; Lewitus et al., 2008).

Numerous other potentially toxic or harmful species are also present; for example, six species of *Pseudo-nitzschia* have been found, and of these, 46% contained low levels of domoic acid (Thessen and Stoecker, 2008). Marshall et al. (2005b) identified 34

harmful species for Chesapeake Bay, while [Tango et al. \(2004\)](#) identified 13 in Maryland Coastal Bays. The trend in brown tides in Maryland's Coastal Bays was discussed above, and only a few species and trends are highlighted here.

2.3.1. Eutrophication linkages

A recent comprehensive assessment of eutrophication in the nation's waters revealed that most of the estuaries affected by HABs are in the mid-Atlantic, and that this region is the most affected by eutrophication of all coastal regions of the U.S. ([Bricker et al., 2007, 2008](#)). With the exception of the Mississippi plume, N loads were found to be highest in the mid-Atlantic. The mid-Atlantic has the nation's two largest estuaries in areal extent (Chesapeake Bay and the Albemarle-Pamlico Estuarine System), which drain watershed areas that are rapidly growing in human and animal populations and changing in land use and N loads. Since 1960, for example, the watershed for Chesapeake Bay has sustained more than a doubling in human population and in use of N-based fertilizers ([Kemp et al., 2005; Fig. 3](#)).

Land use in the region also has changed with a large expansion of confined animal feed operations (CAFOs), primarily swine and poultry ([Mallin and Cahoon, 2003; Rothenberger et al., in press](#)). These have contributed to nutrient loads through surface runoff, leachate into groundwater, and enhanced atmospheric emissions ([Burkholder et al., 1997; Mallin, 2000](#)); approximately 80% of emissions of NH_3 from swine operations in the U.S. originate in North Carolina ([EPA, 1998; Aneja et al., 2003](#)). Thus, the total N load to the Albemarle-Pamlico water from atmospheric deposition is among the highest for U.S. watersheds ([EPA, 2000](#)). CAFOs also have altered the composition of nutrients reaching the estuarine and coastal waters, in particular increasing NH_4^+ and in some cases, urea ([Glibert et al., 2005b; Burkholder et al., 2006](#)). Retention ponds also have been shown to serve as incubation sites for many species ([Lewitus et al., 2003, 2008](#)). These major estuaries are also sustaining major loss of wetlands, depletion of shellfish stocks, and global warming, all of which can act synergistically to increase nutrient loads and alter trophic relationships.

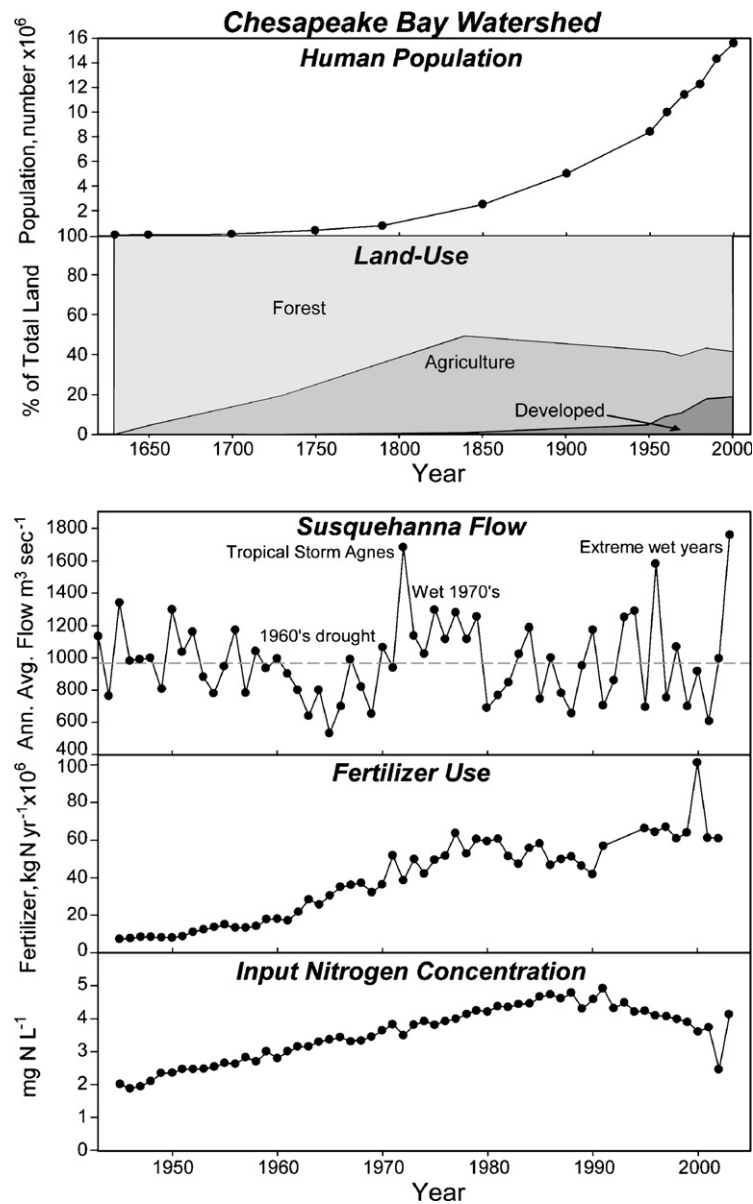


Fig. 3. Temporal changes in land use, river flow, fertilizer use, and river N concentration in the Chesapeake Bay watershed. From [Kemp et al., 2005](#) with permission of the publisher.

An example of frequent high-biomass bloom formers is *P. minimum*. Well established to be stimulated by eutrophication (Heil et al., 2005; Rothenberger, 2007; Glibert et al., 2008), this species frequently blooms following precipitation events that add significant quantities of nutrients. Blooms are most common in late winter–spring (Albemarle-Pamlico) through early summer (Chesapeake Bay) following major agricultural fertilizer applications (Glibert et al., 2001; Springer et al., 2005; Tango et al., 2005). These blooms now appear to be 10–100-fold higher in maximum density in Chesapeake Bay than blooms of the same organism recorded a few decades ago (Tyler and Seliger, 1978).

Blooms of *K. veneficum* are also increasing in frequency in Chesapeake Bay, and have been linked to some fish kills (Deeds et al., 2002; Goshorn et al., 2004). These blooms tend to occur when NO_3^- concentrations are low, and when NH_4^+ or urea concentrations and ambient PO_4^{3-} are elevated. Mixotrophy through consumption of algal prey that are directly stimulated by eutrophication also contributes to *K. veneficum* nutrition and supports faster growth rates (Adolf et al., 2006, 2008).

Other harmful algae that have been linked both directly and indirectly to eutrophication are the potentially toxic, heterotrophic *Pfiesteria* spp. (*Pfiesteria piscicida*, *Pfiesteria shumwayae*), which mostly have affected the Albemarle-Pamlico and Chesapeake Bay (Burkholder and Glasgow, 1997; Burkholder et al., 2005; Glibert et al., 2001, 2006a; Marshall et al., 2006; Moeller et al., 2007; Lewitus et al., 2008). Field studies with supporting laboratory experiments have shown that *Pfiesteria* spp. thrive in nutrient over-enriched estuaries where they consume cryptophytes and other microbial prey when preferred fish resources are not available (Burkholder and Glasgow, 1997; Lewitus et al., 1999b; Glasgow et al., 2001; Parrow et al., 2002). They can also act as mixotrophs by retaining kleptochloroplasts from cryptophytes for short periods, apparently used to augment their nutrition (Lewitus et al., 1999b). *Pfiesteria* spp. depend mostly on grazing for their nutrient supplies, but can also take up dissolved nutrients directly (Burkholder and Glasgow, 1997; Lewitus et al., 1999a,b; Burkholder et al., 2001; Glibert et al., 2006a). *Pfiesteria* outbreaks in Chesapeake Bay tributaries also have been associated with high DON and DOC levels (Glibert et al., 2004a). Laboratory studies have shown that *Pfiesteria* can be stimulated by P (Burkholder and Glasgow, 1997), and that the preference for N form follows a trend of amino acids > urea > NH_4^+ > NO_3^- (Glibert et al., 2006a). Urea is now the dominant agricultural N form in the region, and is also a dominant N form in poultry manure (Glibert et al., 2005b). The major effect of eutrophication on *Pfiesteria* spp., nonetheless, appears to be indirectly mediated through abundance of prey that is directly stimulated (Burkholder and Glasgow, 1997; Glibert et al., 2006a).

Large blooms of the toxic cyanobacterium *M. aeruginosa* are common in the summer months in the low-salinity reaches of the estuaries and tributaries of the region (e.g., Jaworski, 1990). In recent years, these blooms have increased as nutrient concentrations have been escalating (Marshall et al., 2005b).

Raphidophytes have caused fish kills and recurring impacts to some mid-Atlantic ecosystems, especially *H. akashiwo*. Based on an analysis of historical phytoplankton monitoring data, these raphidophytes, as well as *F. japonica* and *C. subsalsa*, have increased significantly in abundance over the past 20 years in the Coastal Bays of Maryland (Tango et al., 2004). While inorganic nutrient concentrations decreased from the 1980s to the mid-1990s in the bays where these species are most common (Wazniak et al., 2007),

significant increases have since been documented in both P and N, especially as NH_4^+ and DON (Wazniak et al., 2007; Glibert et al., 2007). In laboratory experiments, Zhang et al. (2006) found that cell yield for *C. subsalsa* and *H. akashiwo* was higher on NH_4^+ and NO_3^- , respectively, and that *C. subsalsa* did not use urea while *H. akashiwo* readily used this N form. The levels of N used in these experiments were comparable to natural conditions in the highly eutrophic Delaware Inland Bays.

In summary, the mid-Atlantic region has many HAB species, most of which have increased in frequency, abundance, regional extent and impact over the past few decades as population, agriculture and animal operations, and fertilizer usage have increased. In addition to increased nutrient loads, the estuaries, rivers and embayments of the region are also highly modified by declines in shellfish stocks and wetlands (e.g., Steel, 1991; Rothschild et al., 1994), leading to multiple stressors which collectively and synergistically lead to habitat change and alterations in trophic structure, including HAB proliferations.

2.4. *Karenia brevis* blooms in the Gulf of Mexico

The most significant HAB species in the Gulf of Mexico is the ichthyotoxic dinoflagellate *K. brevis* (formerly *Gymnodinium breve*, *Ptychodiscus brevis*), although other HAB species (e.g., *Pseudonitzschia* spp., *P. minimum*) are present (Parsons et al., 2002; Heil et al., 2005). Published accounts of widespread West Florida Shelf *K. brevis* blooms predate extensive development on that coast (Lund, 1936; Tester and Steidinger, 1997; Magaña et al., 2003). Although *K. brevis* is the primary species associated with toxic blooms in the Gulf of Mexico, there are now at least five described *Karenia* species known from Gulf waters (Haywood et al., 2004). Recent blooms are now known to exhibit a sequence of *Karenia* species (Heil et al., in press) but the toxicity of species other than *K. brevis* is presently under investigation.

2.4.1. Eutrophication linkages

There are two views on the role of nutrients and eutrophication in *K. brevis* blooms. Walsh et al. (2006) examined potential linkages between *K. brevis* outbreaks on the West Florida Shelf and the Texas Shelf with riverine flux and eutrophication. Increases in nutrient loads to the Caloosahatchee River during the 1970s and 1980s were followed by decreases in the 1990s (Fig. 4). Overall, Walsh et al. (2006) did not discern differences in the magnitude or frequency of West Florida Shelf red tides, or correlations with nutrient data, although the data records were sporadic and the change in total flux relative to earlier periods is unknown. Using a similar approach, Vargo et al. (2004, 2008) evaluated nutrient sources for support of blooms after initiation and transport into coastal waters and estimated that estuarine fluxes of N and P from Tampa Bay, Charlotte Harbor, and the Caloosahatchee River were sufficient to support a major portion of the nutrients needed to sustain moderate *K. brevis* blooms (3×10^5 cells L^{-1}) in localized nearshore areas, but would contribute a low proportion of the nutrients needed to support larger blooms over broader areas.

On the other hand, Brand and Compton (2007) suggested that there has been a significant increase in nutrient inputs to the nearshore waters of West Florida over the past 50 years. Based on their analysis of the State of Florida long-term HAB database, which emphasized bloom periods, they reported that higher nearshore abundance of *K. brevis* during blooms over the 1994–2002 timeframe, compared to the 1954–1963 timeframe, appears to be related to elevated nutrient flux into nearshore coastal waters from urban and agricultural development in the Caloosahatchee River watershed, and eutrophication of Lake Okeechobee, the headwaters for the Caloosahatchee. Turner et al. (2006) used

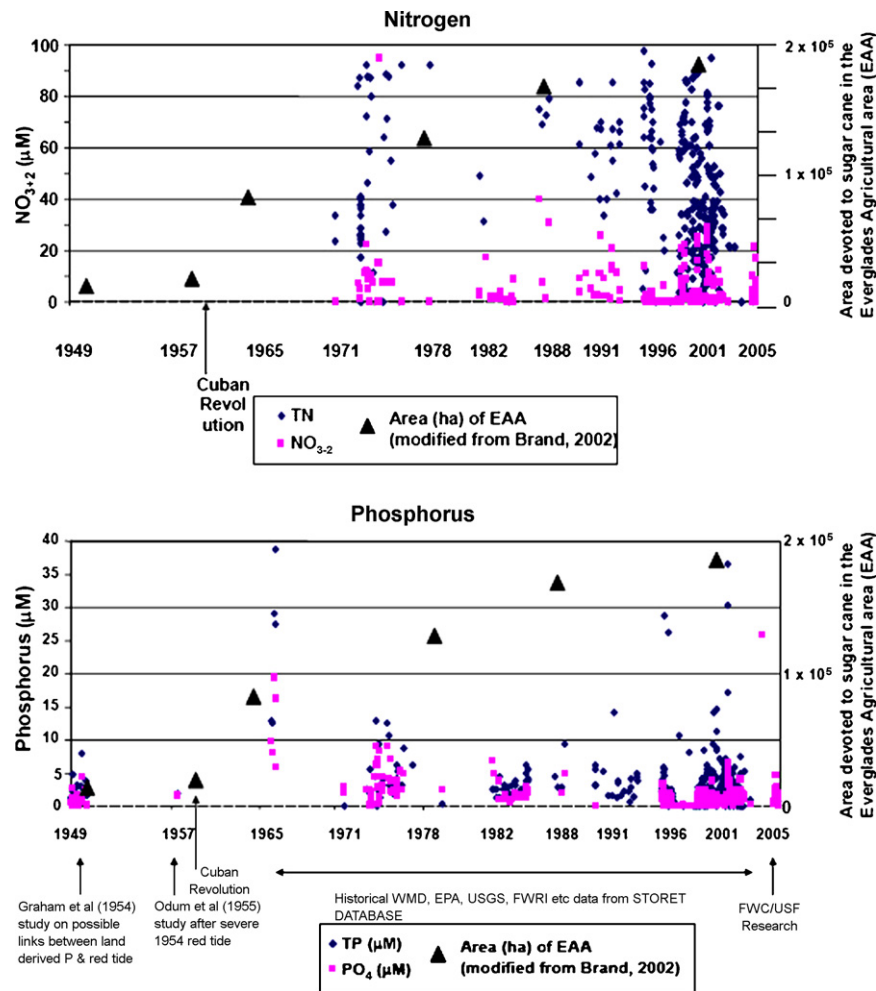


Fig. 4. Available data for total and inorganic N and P concentrations for a 2 km² area at the Caloosahatchee River mouth and the extent of everglades agricultural area (EAA) which is devoted to sugar cane fields for the time frame of 1949 through 2005. Nutrient data has been retrieved from the state of Florida STORET database; available data for the river from a variety of sources are listed in the figure. The change in the areal extent of the EAA has been modified from Brand (2002).

paleo-indicators to assess long-term water quality changes in Charlotte Harbor and found evidence of a 3-fold increase in N loadings between the 1800s and the present, with significant increases in water-column NO_3^- concentrations between 1960 and 1980 which have remained essentially constant since the 1980s (see their Fig. 3).

Walsh and Steidinger (2001) and Walsh et al. (2006) hypothesized that N_2 fixation by blooms of the pelagic cyanobacterium *Trichodesmium* spp. and subsequent release of DON, coupled with use of remineralized nutrients from dead fish, can lead to *K. brevis* bloom initiation, growth and maintenance on the West Florida and Texas shelves. They estimated that N_2 fixation could supply up to $0.16 \mu\text{M L}^{-1} \text{day}^{-1}$ based on *Trichodesmium* biomass and N excretion rates measured over a 3-year period (Mulholland et al., 2006). Subsequent decay of dead fish might then be sufficient to supply all of the required N and P for blooms on the order of $10^6 \text{ cells L}^{-1}$ or greater. Mulholland et al. (2006) also concluded that observed N_2 fixation and subsequent release of DON by *Trichodesmium* could provide substantial support for a moderate *K. brevis* bloom. A source of P would be required for the Saharan dust-*Trichodesmium*-dead fish hypothesis since P concentrations are extremely low in shelf waters (Vargo and Shanley, 1985; Vargo et al., 2008) and *Trichodesmium* spp. compete with *K. brevis* for available P. Further, based on stable N-isotope measurements of particulate organic matter (POM) collected

during 4 years of West Florida Shelf red tides, Havens et al. (2004) reported values of $\delta^{15}\text{N}_{\text{POM}}$ from -2 to 6% , which excludes sewage and upwelled N as a source, but does not exclude commercial fertilizers derived from atmospheric N, which have an isotopic composition close to 0 (e.g., del Amor et al., 2008). However, the low- $\delta^{15}\text{N}_{\text{POM}}$ values indicative of fixed N recorded by Havens et al. (2004) were found only in samples collected in close proximity to a *Trichodesmium* bloom whereas the majority of bloom values (71 in 5 separate blooms) were in the range of 3 – 5% . Thus, N from a variety of sources appears to fuel West Florida Shelf *K. brevis* blooms.

Mixotrophy may also provide nutrients for *K. brevis* blooms (e.g., Bronk et al., 2004; Jeong et al., 2005a,b; Glibert et al., in press; Procise and Mulholland, submitted for publication), as described above for *K. veneficum* and *Pfiesteria* spp. Dissolved organic N (DON) concentrations in West Florida estuaries and coastal waters are about 10-fold higher than inorganic N concentrations, and while inorganic N:P ratios are low, DON:DOP (dissolved organic P) ratios are consistently higher than the Redfield ratio (Heil et al., 2007). Notably, Hu et al. (2006) found much higher DON flux compared to DIN and DIP. Collectively these data suggest that species capable of using DON, such as *K. brevis*, would be favored over those relying on inorganic N sources (Heil et al., 2007). Concentrations of DON, presumably both terrestrial and marine derived, are sufficient to support blooms $>10^5 \text{ cells L}^{-1}$ but the

extent to which this complex N is used by *K. brevis* and other *Karenia* spp. is unknown (Hu et al., 2006; Vargo et al., 2008). Thus, N from various sources appears to fuel West Florida Shelf and nearshore *K. brevis* blooms and different nutrient sources may play a role in initiation versus maintenance stages of these blooms.

Hu et al. (2006) hypothesized that “submarine ground water discharge provides the ‘missing’ nutrients that can trigger and support *Karenia* red tides off west-central Florida”. They suggest that increased development and population growth have increased groundwater nutrient levels and this, in turn, contributes to longer and higher biomass West Florida Shelf blooms. While Vargo et al. (2008) report elevated near-bottom nutrient concentrations, they generally detected such concentrations only at the 50 m isobath during years when shelf-break upwelling due to Loop Current meanders occurred.

Elsewhere in the Gulf of Mexico, a link between eutrophication and the frequency and magnitude of *K. brevis* blooms along the Texas Coast has been suggested (Buskey et al., 1996; Denton and Contreras, 2004; Biegalski and Villareal, 2005; Walsh et al., 2006). This linkage has been based upon data for nutrient inputs from the Mississippi River (Turner and Rabalais, 1994; Villareal et al., 2001), combined with fish kill and bloom information (Trebatoski, 1988). Walsh et al. (2006), for example, postulated that doubling of the NO_3^- loads in the Mississippi River every decade since the 1950s has led to massive increases in phytoplankton biomass in the river plume. Considering measured water column and near bottom N:P ratios off both Texas and Southwest Florida coastal areas where red tides are prevalent, together with modeling results (Walsh et al., 2006), remineralization of this elevated biomass leads to low-N:P ratios that favor development of *K. brevis* blooms. Notably, the first documented bloom off Texas occurred in 1955 followed by another in 1976 and 1986, but blooms have occurred almost annually after 1996. Similarly, the increased NO_3^- loading from the Mississippi River coupled with reduced N:Si ratios have been presented as causative factors leading to increased abundance of potentially toxic *Pseudo-nitzschia* spp. in the northern Gulf of Mexico (Parsons et al., 2002).

In summary, *K. brevis* populations may derive nutrients as DON from the cyanobacterial blooms and other aquatic food web sources such as decomposition of fish killed by *K. brevis*, as well as land-based sources. Initiation and development of *K. brevis* blooms in open waters along the West Florida Shelf are apparently supported by sources within the aquatic food web, whereas in localized nearshore areas, land-based nutrients may also supply a proportion of the nutrients that sustain the blooms. While it is well known that eutrophication in coastal regions is increasing globally as a result of development and fertilizer use (e.g., Cloern, 2001; Glibert et al., 2005a, 2006b; Howarth, 2008; Bricker et al., 2007), clear evidence to support hypotheses about increased bloom frequency and biomass on the West Florida Shelf is still not yet available. Blooms of *K. brevis* along the Texas Coast, which are influenced by major nutrient loads from the Mississippi River, have been more clearly linked to stimulation from land-based sources, and additional experimental data will help to clarify the strength of that linkage.

2.5. ASP and PSP in California

California coastal HAB problems are dominated by two organisms: *Alexandrium catenella* which produces saxitoxin (STX), the causative agent of PSP, and several *Pseudo-nitzschia* species whose toxic strains produce domoic acid (DA), the causative agent for amnesic shellfish poisoning (ASP; alternately called domoic acid poisoning). While other HAB species are present, some of which are linked to nutrient loading (e.g., the dinoflagellate

Lingulodinium polyedrum and the raphidophyte *H. akashiwo*; Kudela and Cochlan, 2000; Herndon et al., 2003), here we emphasize ASP and PSP syndromes that are regularly monitored by state agencies in California.

Unlike many other ecosystems impacted by HABS, the physical, chemical, and ecological characteristics of the coastal waters of California are largely dominated by upwelling. The boundary along the coast between the upwelled water and the warmer adjacent surface water is usually a front with an associated equatorward jet (Smith, 1992). Consequently, upwelling circulation overrides both the nutrient limitation of stratified waters and the light limitation of well-mixed waters (Hood et al., 1992), and generally nourishes these waters with macronutrients in excess of anthropogenic sources.

2.5.1. Eutrophication linkages

ASP. Potentially toxic *Pseudo-nitzschia* spp. are ubiquitous in California coastal waters, and major toxin events often occur over large spatial and temporal scales (Trainer et al., 2000). Prior to 2000, toxic blooms were considered rare and unusual in southern California (Lange et al., 1994); however, in recent years ASP has become increasingly important in southern regions (e.g., Trainer et al., 2000; Busse et al., 2006; Schnetzer et al., 2007). The apparent synchrony of ASP events in California suggests that there must be large-scale forcings, such as upwelling relaxation, responsible for the otherwise coincidental timing of major DA outbreaks.

Multiple factors have been shown to trigger the production of DA by *Pseudo-nitzschia* (Bates, 1998), but the most thoroughly characterized are macronutrient limitation by either PO_4^{3-} or silicate ($\text{Si}(\text{OH})_4$) in cultures (Pan et al., 1996a, b). *Pseudo-nitzschia* previously has been associated with both eutrophication and a reduction in the ratio of N:Si (cf. review by Bates et al., 1998; Parsons et al., 2002), and in California there is circumstantial evidence that a massive DA event in Monterey Bay in 1998 was triggered by post-El Niño runoff (Scholin et al., 2000). Recently, Anderson et al. (2006) reported a correspondence between limiting Si concentrations, the ratios of $\text{NO}_3^-:\text{Si}(\text{OH})_4$ and $\text{PO}_4^{3-}:\text{Si}(\text{OH})_4$ and the concentrations of *Pseudo-nitzschia* and particulate DA, among other factors.

DA production by *Pseudo-nitzschia* spp. has also been linked to iron (Fe) and copper (Cu) stress. These elements may be indirectly linked to anthropogenic changes, as excess availability of Cu is associated with runoff (Ladizinsky, 2003), and decreasing Fe is associated with modifications to stream and river flow (Johnson et al., 2001). Limitation by Fe directly modulates Si:N ratios in diatoms, as DA may serve as an Fe-acquisition mechanism (Rue and Bruland, 2001; Wells et al., 2005). Recent laboratory and field data also demonstrate that *Pseudo-nitzschia* spp. may increase toxicity when using urea as an N source (Howard et al., 2006), which would come predominantly from anthropogenic inputs (Cochlan et al., 2008). Thus, cultural eutrophication may have the unanticipated consequence of both selecting for *Pseudo-nitzschia* spp. and promoting toxin production (Kudela et al., 2008).

Despite correlative evidence for a connection between ASP and coastal runoff and/or eutrophication, studies are, as yet, lacking to test whether there are direct linkages. In general, blooms of *Pseudo-nitzschia* in California occur during anomalously weak (but not absent) upwelling conditions, typically during a transition from excess to limiting macronutrients (Kudela et al., 2004). However, there is no consistent evidence that *Pseudo-nitzschia* blooms are correlated with runoff events, nor is there direct evidence for trace-metal limitation or stimulation of DA during most blooms (Kudela et al., 2004). An apparent south-to-north trend in bloom events in coastal California waters is consistent with large-scale physical forcing, suggesting that the spatial pattern is indicative of a change in environmental conditions.

PSP. PSP toxin events associated with *A. catenella* occur most years (Price et al., 1991), and large-scale outbreaks appear to exhibit a northward temporal trend (Langlois and Smith, 2001). As with ASP, there are correlative links between PSP occurrences in California and cultural eutrophication, but direct linkages have not yet been established. PSP outbreaks typically initiate on the open coast, and only then move into bays and estuaries (Langlois, 2001). A consistent pattern associated with PSP events is an increase of *A. catenella* in offshore waters, followed by onshore transport during relaxation-favorable winds, with subsequent intoxication of shellfish (Price et al., 1991; Langlois and Smith, 2001). Thus, as with ASP, PSP events appear to be correlated with large-scale oceanographic events, in particular the upwelling-relaxation cycle and the onshore transport of toxic cells.

In summary, both PSP and ASP dynamics in California appear to be dominated by large-scale oceanographic forcings in nutrient dynamics. This does not, however, preclude the possibility that the growth of these algae, their toxicity, and the frequency or duration of toxic events may be exacerbated by anthropogenic nutrient inputs once these populations reach nearshore waters. For example, there is both direct (Cochlan et al., 2008) and indirect (Collos et al., 2004) evidence that some toxic strains of *A. catenella* and *Pseudo-nitzschia* spp. can use DON for growth, such as urea (presumed to be from anthropogenic sources) that has been measured in appreciable concentrations in California nearshore waters (Cochlan et al., 2008). Although the extent to which such nutrient pulses occur during natural upwelling or runoff is not known for this region, their utilization by HAB species normally found in coastal California suggests that anthropogenic N sources could be potential factors in bloom initiation or maintenance. As with the Gulf of Maine, these localized blooms are significant since they generally occur in populated coastal zones, despite the fact that the total flux from these nutrient sources likely is a minor component in comparison to seasonal upwelling inputs along the open coast (Kudela et al., 2008).

2.6. PSP, ASP, and *H. akashiwo* in the Pacific northwest

The dinoflagellate *A. catenella* is responsible for shellfish harvesting closures in the Pacific Northwest due to PSP toxins. The occurrence of PSP toxins in Washington shellfish was once restricted to the open coast, the Strait of Juan de Fuca and northern Puget Sound. A large bloom originating in the Whidbey Island basin in 1978 spread through large areas of central Puget Sound that were previously unaffected (Nishitani and Chew, 1988; Rensel, 1993) and since then PSP incidents have progressed southward into the remaining inlets of southern Puget Sound (Trainer et al., 2002).

More than 10 *Pseudo-nitzschia* spp. are found in the oceanic and inland waterways of Washington. The primary species believed to cause DA-related shellfish harvesting closures are *Pseudo-nitzschia pseudodelicatissima*, *Pseudo-nitzschia cuspidata*, and *Pseudo-nitzschia australis* (Trainer et al., 2007). Since 1991, DA has been a recognized problem on the outer Washington Coast (e.g., Trainer and Bill, 2004), but over this same period low levels of DA have been measured in Puget Sound shellfish (Trainer et al., 1998). Puget Sound is presumed to be less susceptible to DA closures due to the absence of DA-retaining razor clams in this region.

Fish-killing blooms of the raphidophyte *H. akashiwo* have occurred in Puget Sound and adjacent inland waters of British Columbia, Canada for an unknown period. This alga was observed in the 1960s before marine fish farms were first installed in either region. All evidence from Puget Sound to date indicates that blooms originate in areas remote from the fish farms such as the U.S.–Canada border waters of North Puget Sound and the southern

Georgia Strait or in shallow backwaters of central and northern Puget Sound. The blooms are transported by estuarine circulation (seaward moving brackish river plume) tidal action and winds to net-pen locations in Puget Sound where finfish have been killed (Rensel, 2007).

In Washington inland waterways, there is evidence that both flagellate and non-flagellate HAB species are expanding their scope and magnitude, in some cases possibly due to anthropogenic influences. Most of this area is naturally replete with high levels of DIN (10–25 μM) due to oceanic upwelling and advection into inland marine waters, but there are seasonally nutrient-sensitive backwaters where HAB development may be related to human-caused perturbations as discussed below.

2.6.1. Eutrophication linkages

Along the open coast and adjacent fast-fluxing channels, episodic upwelling is the dominant source of nutrients to surface waters, and thus blooms of *Alexandrium catenella* and potentially toxic *Pseudo-nitzschia* spp. in those areas are not likely to be sensitive to anthropogenic influence. However, there are two general systems where the linkage between HABs and nutrient pollution in the Pacific Northwest should be examined more closely. Within Puget Sound and the adjacent Strait of Juan de Fuca, DIN concentrations are usually high year-round, and are considered saturating for phytoplankton growth except in poorly flushed terminal inlets which make up only ~7% of the area (Mackas and Harrison, 1997). Anthropogenic sources likely have contributed to the elevated NH_4^+ concentrations commonly found in surface waters of the region (W. Cochlan, unpublished data; Rensel, 2007). Ambient concentrations of reduced N substrates (such as NH_4^+ and urea) are generally about 10-fold lower than NO_3^- , which is primarily of oceanic origin within Puget Sound. In the absence of directed studies to test influences of anthropogenic nutrient enrichment, linking nutrient loading to blooms of *H. akashiwo* remains an elusive possibility in the Pacific Northwest.

With regard to PSP, some anthropogenic stimulation may be occurring since the magnitude, frequency and geographical distribution of shellfish bed closures from PSP toxins have increased over the past 50 years since monitoring began (Trainer et al., 2003). Comparison of maximum yearly PSP toxin values for Puget Sound (averaged for each of the last 5 decades using all shellfish monitoring data) with population estimates of the counties bordering Puget Sound shows a high correlation. The data suggest that increased nutrient loadings to Puget Sound may be contributing to the spatial and temporal increases in PSP in nutrient-sensitive regions that are vertically stratified in the summer months and poorly flushed.

For the occurrence of DA closures, there also may be a linkage to anthropogenic nutrients within Puget Sound. Several species of *Pseudo-nitzschia* are present in Puget Sound and have been for decades (Bill et al., 2006; Horner, 2003), but only since 2003 has their toxicity resulted in shellfish harvesting closures (Bill et al., 2006; Trainer et al., 2007). One possibility is that more potentially toxic strains have entered Puget Sound from offshore initiation sites such as the Juan de Fuca Eddy (Trainer et al., 2002) via occasional summertime reverse flow of surface waters along the south shore of the Strait of Juan de Fuca. It is also possible that environmental factors within the inland waters are stimulating *Pseudo-nitzschia* growth and/or DA production as discussed below.

Aquaculture activities (e.g., fish farms) have been suggested to be stimulatory to the raphidophycean flagellate *H. akashiwo* and eutrophication has been linked to *H. akashiwo* blooms in various locations worldwide (e.g., Wang et al., 2008). In Puget Sound, however, where fish farms are few in number, the evidence is to the contrary. Salmon excrete mostly NH_3 and low levels of urea

(Brett and Zala, 1975), but elevated concentrations of reduced N substrates have not been measured downstream of the fish farms in Puget Sound. NH_4^+ found within the pens is partly oxidized to NO_3^- and diluted within a few meters downstream so that the DIN increase represents only about 5% of the high-background flux levels at farm sites (Rensel, 1991).

All commercial fish farms in Puget Sound are, by state aquatic lease requirement, located in non-nutrient sensitive (N-replete) areas (SAIC, 1986) where sunlight, not macronutrients, limits phytoplankton productivity. Certain subareas of Puget Sound are seasonally nutrient-sensitive either by short-term, river-induced vertical stratification during the spring or by summer and fall solar-heating induced vertical stratification of backwaters that allows nutrient stripping of DIN by algae in the surface mixed layer. As *H. akashiwo* cells can migrate to sub-surface, nutrient-rich waters, they might potentially have a competitive advantage over non-motile species. Only some blooms (e.g., Rensel, 1995) occur in such conditions, however, whereas others occur, or at least are transported through, moderately N-depleted mixed layers (Rensel, 2007). The geographic scale of many blooms of *H. akashiwo* (affecting nearly all of Puget Sound in several cases), the brevity of the blooms (a few days to at most a week in duration), and the apparent dependency on warm weather periods and physical transport mechanisms all highlight the importance of naturally occurring physical forcing factors (Rensel, 2007).

Isolates of both *H. akashiwo* and *P. cuspidata* from the Pacific Northwest can grow equally well on NH_4^+ and NO_3^- when supplied as the sole N source (Auro et al., 2006; Herndon and Cochlan, 2007; Auro, 2007), so there is a potential for anthropogenic stimulation of these blooms. For example, several *H. akashiwo* blooms in central Puget Sound have co-occurred precisely with summertime municipal sewage spills into nutrient-sensitive backwater areas in Kitsap County, Washington (Rensel, 2007). Likewise, Trainer et al. (2007) suggested that a toxic bloom of *P. pseudodelicatissima* developed following a pulse of inorganic N (up to $13 \mu\text{M NO}_3^-$ and $13 \mu\text{M NH}_4^+$) after weeks of N-limited conditions in Sequim Bay in 2005. They speculated that a failing septic system was the source of the elevated NH_4^+ concentration in this poorly flushed bay.

In summary, anthropogenic sources of nutrients are considered insignificant for HABs along the outer coast of Washington, but within Puget Sound and the Strait of Juan de Fuca, the potential contribution of pollution-related loading to HAB development remains to be fully understood and quantified. The ability of *H. akashiwo* and *Pseudo-nitzschia* spp. to achieve good growth by using various N sources suggests that reduced N forms may contribute to their recent success. In these and other cases, the spread of a toxic HAB species into or within new areas such as Puget Sound may be linked to anthropogenic nutrient sources, but as yet directed studies to confirm or refute this link are largely lacking.

2.7. Ciguatera

Ciguatera fish poisoning (CFP) is a circumtropical seafood poisoning caused by the ingestion of marine fish (especially reef fish) that have accumulated toxins produced by species of the benthic dinoflagellate genus, *Gambierdiscus*, especially *Gambierdiscus toxicus* (Yasumoto et al., 1977) and possibly other co-occurring dinoflagellates (e.g., *Ostreopsis lenticularis*; Tosteson et al., 1986).

2.7.1. Eutrophication linkages

The role played by nutrient enrichment in CFP remains unclear because the topic is understudied. Fewer than 10 known field-based studies have measured nutrient concentrations concurrently

with the abundance of ciguatera dinoflagellates, and only four of these studies were conducted for at least 1 year and reported statistical results (Yasumoto et al., 1980; Carlson and Tindall, 1985; Parsons and Preskitt, 2007). Of these, Carlson and Tindall (1985) reported a significant, positive correlation between the abundance of ciguatera dinoflagellates and nutrient concentrations. Parsons and Preskitt (2007) did not report a positive correlation in their study of six Hawaiian sites, but *Gambierdiscus* concentrations were highest at the site (Puako) exhibiting the highest amounts of $\text{NO}_3^- + \text{NO}_2^-$.

Culture-based studies also have been limited. Lechat et al. (1985) reported that growth rates of *G. toxicus* were greater when using higher media enrichments (ES 4%) versus more diluted enrichments (ES 1% and 2%). Durand-Clement (1986) reported that growth of *G. toxicus* increased when the urea concentration was increased from 0 to 1 mM, although this concentration is higher than would be expected in natural habitats. Sperr and Doucette (1996) reported that growth rates did not vary over a range of N:P ratios from 5:1 to 50:1.

The role of nutrients in toxin production is unclear as well. Durand-Clement (1986) reported no differences in toxin production across different media recipes or nutrient concentrations. In contrast, Lechat et al. (1985) indicated that cellular ciguatoxin content increased 10-fold when the metallic salt content (PII-mix) was increased 10-fold. Bomber (1987) did not discern any difference in cellular toxicity for *G. toxicus* grown in regular ES media and low-N ES media. Cellular toxicity also was constant over the range of N:P ratios used by Sperr and Doucette (1996), although toxin levels spiked at an N:P of 30:1 for an unknown reason.

Ciguatera dinoflagellates have two potential sources of nutrients, the water column and benthic substrata. Since they are primarily epiphytic, they can obtain nutrients from macroalgal substrata or co-occurring epiphytes (i.e., the thallosphere; Yasumoto et al., 1980; Withers, 1981). The most likely role of eutrophication in CFP is through coral reef degradation (Bagnis, 1994). Researchers early on noted that CFP outbreaks often followed disturbances to coral reef environments (e.g., Randall, 1958; Cooper, 1964). The role of nutrient loading in coral reef degradation is complex and some reef sites appear to be more susceptible to nutrient degradation than others (Lapointe, 1999; Parsons et al., 2008). Eutrophication can cause an increase in macroalgae (Lapointe et al., 2004; Smith et al., 2001), providing more habitat for ciguatera dinoflagellates.

In summary, the limited evidence available indicates that any linkages between eutrophication and increased incidents of CFP remain inconclusive. There may be indirect linkages between eutrophication and increased growth of ciguatera dinoflagellates, but further assessment is required to determine the strength of these linkages, and the potential for direct links remains to be examined. Outbreaks of CFP often follow impacts to coral reef ecosystems, of which nutrient loading can be a factor, including the expansion of macroalgal-based habitat. As ciguatera dinoflagellates are benthic organisms, rigorous assessment of eutrophication linkages will require analysis of not only water-column nutrient loadings, but also of indirect effects mediated through benthic nutrient sources.

3. Conclusions

HAB events in the U.S. are diverse in many ways, spanning a wide range of algal species, poisoning syndromes, and other negative impacts. A common observation is that the initiation of large-scale HABs along *open coasts* appears to be unrelated to anthropogenic nutrients, since nutrients supplied by upwelling or advection from offshore water masses (e.g., New England and the

Pacific Northwest), or by N₂ fixed from co-occurring blooms (e.g., Gulf of Mexico) can be much larger than terrestrial or atmospheric sources, although data on the diversity of nutrient sources (including organic) are often lacking in these regions. *Localized, nearshore* pollution effects are possible in embayments, estuaries, and sounds, and thus HAB cells delivered to these locations from open waters can be stimulated and sustained by anthropogenic inputs. In regions where HABs originate within estuaries, embayments or nearshore coasts, the role of anthropogenic nutrients is much larger, and in some cases, a dominant factor in HAB species success. Overall, there is an obvious need for additional research on the relationship between HABs and eutrophication in U.S. estuaries and coastal waters, including many species and regions not covered here. In particular, there is a need for additional information on the fluxes of nutrients (not only concentrations), the role of varying nutrient composition in HAB proliferation, and the interactions between nutrient loads and the complexity of other factors contributing to HABs.

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