

# The Global, Complex Phenomena of Harmful Algal Blooms

Figure 1. Many HABs produce vividly colored blooms of cells that accumulate on surface water. These high biomass blooms can cause hypoxia, can contribute to toxicity of fish and shellfish, and can cause other environmental problems. Main photo: A bloom off Heron Island, Australia caused by cyanobacteria (*Trichodesmium theibautii*). Photo by P. Glibert. Insets: (Left) A bloom in Hong Kong, China caused by caused by dinoflagellates (*Gymnodinium* sp.). Photo by M. Dickman. (Middle) A bloom in the Choptank River, one of the tributaries of the Chesapeake Bay, USA caused by dinoflagellates (*Prorocentrum minimum*). Photo by P. Glibert. (Right) A bloom in the Baltic Sea caused by caused by cyanobacteria (*Anabaena* sp.). Photo by K. Kononen.



BY PATRICIA M. GLIBERT, DONALD M. ANDERSON,  
PATRICK GENTIEN, EDNA GRANÉLI, AND KEVIN G. SELLNER

### WHAT ARE HABs?

Marine and fresh waters team with life, much of it microscopic, and most of it harmless; in fact, it is this microscopic life on which all aquatic life ultimately depends for food. Microscopic algae also play an important role in regulating atmospheric CO<sub>2</sub> by sequestering it during production and transporting it to deeper waters. Yet some of the microscopic “algae” cause problems when they accumulate in sufficient numbers, due either to their production of endogenous toxins, or to their sheer biomass or even their physical shape. These are known as the harmful algae, or, when in sufficient numbers, harmful algal blooms (HABs). These blooms were formerly called “red tides” because many were composed of dinoflagellates containing red pigments that in high densities colored the water red, but blooms may also be green, yellow, or brown, depending on the type of algae present and their pigmentation (Figure 1). As with all blooms, their pro-

liferation results from a combination of physical, chemical, and biological mechanisms and their interactions with other components of the food web that are for the most part poorly understood. Most HABs are dinoflagellates or cyanobacteria, but other classes of algae, including diatoms, have members that may form HABs under some conditions. As stated by J. Ryther and co-workers many years ago, “...there is no necessity to postulate obscure factors which would account for a prodigious growth of dinoflagellates to explain red water. It is necessary only to have conditions favoring the growth and dominance of a moderately large population of a given species, and the proper hydrographic and meteorological conditions to permit the accumulation of organisms at the surface and to effect their future concentrations in localized areas” (Ryther, 1955).

HABs have one unique feature in common—they cause harm, either due to their production of toxins or to the

manner in which the cells’ physical structure or accumulated biomass affect co-occurring organisms and alter food-web dynamics. Dangerous conditions can also occur when the water is clear with very low cell concentrations if a highly toxic HAB species is present. The term “HAB” also applies to some non-toxic micro- or macroalgae (seaweeds) that can grow out of control and cause major ecological impacts such as the displacement of indigenous species, habitat alteration, or oxygen depletion in the bottom waters. Some HABs are not algae at all, but rather are small animal-like protists that obtain their nutrition by grazing not by photosynthesis. Thus, the term “HAB” is operational and not technical, but this distinction is irrelevant in terms of their human health and economic impacts.

### THE HARMFUL PROPERTIES OF HABs

HABs are harmful in two fundamental ways, although not all HABs have both harmful properties. The first is the production of toxins that may kill fish and shellfish or harm human consumers. The range of toxins produced by HABs is quite extensive, including brevetoxins,



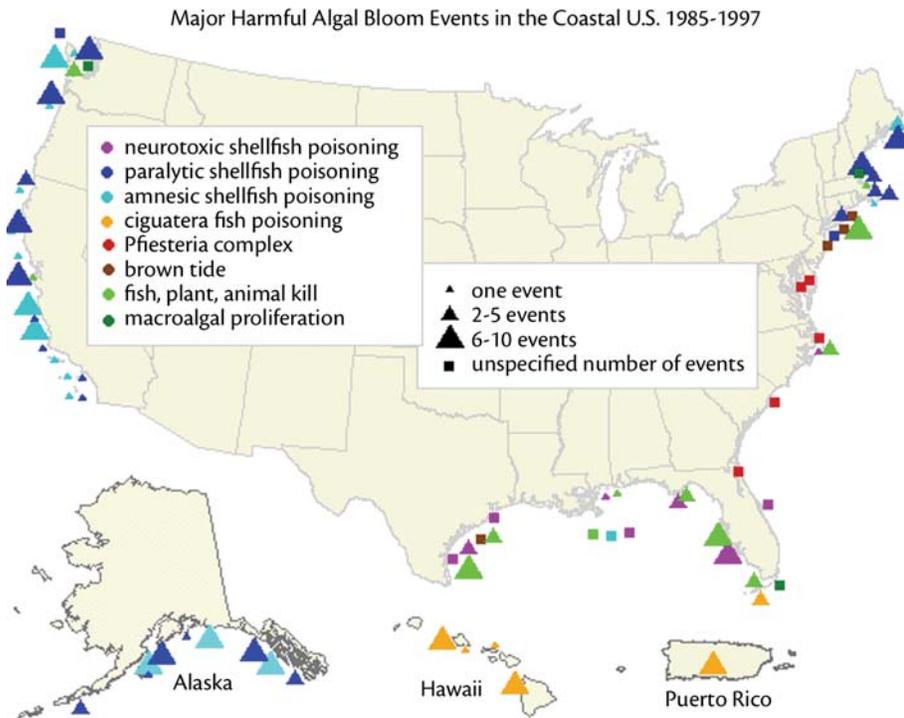


Figure 2. Virtually every coast in the United States has been affected by harmful algae. Highlighted in this map are the regions affected by each type of HAB poisoning and an indication of the general frequency of these outbreaks from 1985 to 1997. Graphic by D. Anderson, WHOI National Office for Marine Biotoxins and Harmful Algal Blooms.

the cause of neurotoxic shellfish poisoning (NSP); saxitoxins, the cause of paralytic shellfish poisoning (PSP); okadaic acid, the cause of diarrhetic shellfish poisoning (DSP); domoic acid, the cause of amnesic shellfish poisoning (ASP); and azaspiracid, the cause of azaspiracid shellfish poisoning (AZP); and numerous others (Landsberg, 2002). Toxins may kill shellfish or fish directly, or may have little effect on them, but may cause illness or death when shellfish that have accumulated the algal toxins are eaten by people or other consumers in the food web (Landsberg, 2002). There are no known antidotes for poisonings caused

by HAB toxins. Some HABs, while not directly toxic, have physical structures, such as spines, that can lodge in gills, and can cause irritation and eventual suffocation. The other fundamental way in which HABs are harmful is through high biomass accumulation, which may lead to environmental damage, including hypoxia, anoxia, and shading of submerged vegetation, each of which in turn can lead to a multitude of negative environmental consequences. These are the blooms that cause visible water discoloration (Figure 1).

Human illness and death are the primary impact of HABs, but effects on

other wildlife are also important. Some fish kills due to HABs can be spectacular in size, with millions of fish and millions of dollars lost to local economies. Deaths of birds and mammals, such as dolphin, manatees, and sea lions, have also been related to HABs and their toxins and are of immense public and economic concern when they do occur. In addition, HABs impact aquaculture industries, and losses can be staggering as the impacted organisms are typically in confined areas and rapidly succumb to toxins or to excessive accumulations of cells. In some areas, HABs have indirect but significant impacts on local economies through impairment of water quality, leading to losses in the tourism and recreational industries. The overall economic impact of HABs is difficult to determine, but the costs range from the direct expenses of public health and medical care for those affected to losses in commercial and recreational fishing and in tourism-related activities from water-quality deterioration. For example, as recently as 2003 it was estimated that

---

**Patricia M. Glibert** ([glibert@hpl.umces.edu](mailto:glibert@hpl.umces.edu)) is Professor, University of Maryland Center for Environmental Science, Horn Point Laboratory, Cambridge, MD, USA.

**Donald M. Anderson** is Senior Scientist, Woods Hole Oceanographic Institution, Woods Hole, MA, USA. **Patrick Gentien** is Director, CREMA, a Joint Research Unit between Ifremer and CNRS, L'Houmeau, France. **Edna Graneli** is Professor, Department of Marine Sciences, Institute of Natural Sciences, University of Kalmar, Kalmar, Sweden. **Kevin G. Sellner** is Director, Chesapeake Research Consortium, Edgewater, MD, USA.

more than \$6 million dollars in revenue from sport fishing and tourism due to fish kills were lost in Texas due to a bloom of a small flagellate in inland rivers and reservoirs (*Prymnesium parvum*). Another economic cost of HABs is that of sustained environmental monitoring.

The production of specific toxins is typically restricted to one, or at most a very few, species. Unique to HABs, in contrast to non-HAB algae, is that the same species can sometimes have widely different impacts in two regions (i.e., the same species can be toxic in one location, and non-toxic in another) (Anderson et al., this issue). Underlying these observations is the realization that morphological species identifications sometimes do not provide the resolution needed to explain differences among HAB events. In many cases, what was formerly considered a single species is in fact a mixture of genetically similar strains of that species. Considerable genetic diversity has now been documented within a single species, and evidence indicates that only some of these genotypes bloom under a given set of environmental conditions. Morphologically, all cells might look like exactly the same species, but genetic differences abound, and environmental selection is acting on those differences to select one genotype over others. The factors that regulate toxin production are still not well understood for most species.

## RECENT TRENDS—NATIONAL AND GLOBAL CHANGES

Over the past few decades, the world's coastal waters have experienced an increase in the number and type of HAB events. In the United States, only a few regions were previously affected by

HABs, but now virtually every coastal state has reported major blooms, frequently involving multiple species (Figure 2). Similar trends are reported for freshwater HABs in inland states. Freshwater cyanobacterial outbreaks due to *Microcystis* are expanding and costly, and impact large water bodies such as the Great Lakes as well as smaller lakes, ponds, and rivers. Cyanobacterial outbreaks in these waters are of great concern because many of these water bodies serve as reservoirs for drinking water and the microcystin toxin levels have, on occasion, exceeded advisory limits.

Several examples demonstrate the national and global expansion of HABs. In the Gulf of Maine, occurrences of the causative dinoflagellate *Alexandrium tamarense* and PSP toxicity were rare prior to about 1970, but have been frequent in the past three decades. In fact, PSP occurrences have increased globally in this same time frame (Figure 3). PSP tox-

**Human illness and death are the primary impact of HABs, but effects on other wildlife are also important. Some fish kills due to HABs can be spectacular in size, with millions of fish and millions of dollars lost to local economies.**

icity has increased in proportion to the growth of human population in Puget Sound, Washington State (Trainer et al., 2003). The bloom-forming dinoflagellate *Prorocentrum minimum* is also now documented to cover most coasts throughout the world (Heil et al., 2005). Based on

analyses of frustules preserved in cores, blooms of the diatom *Pseudo-nitzschia* spp. in the Gulf of Mexico were also rare prior to the 1950s, but have increased significantly in abundance and frequency since then, concomitant with increases in nutrient loading (Parsons et al., 2002). In Europe and Asia there are also more blooms with more toxic effects than in previous decades (Granéli et al., 1999).

Although some of the factors contributing to national—and global—expansion are natural, such as biological species dispersal, many others are considered to be a result of human activities. Increases in nutrient loading, changes in agriculture and aquaculture practices, overfishing, ballast water discharge, and global climate change may all be important in the global increase in HABs. Another factor that must be recognized is that improved tools and capability have led us to detect more species more often. In other words, years ago we were not

aware of the size or complexity of the HAB problem, but as we have become better at detecting toxins and recognizing HAB phenomena we have more clearly defined the extensive boundaries of the problem. Some species are expanding their geographic range; in other

instances new toxic species are being identified that were previously considered harmless. For example, the number of known toxic dinoflagellates has increased from about 20 a decade ago to more than 60 today (Burkholder, 1998). The fact that some of the increase is sim-

ply a result of better detection or more observers does not diminish the seriousness of the problem, nor does it explain all of the global expansion.

There is a wealth of evidence that the expansion of HABs may also be related, in whole or in part, to many other global-

change phenomena. Climate change, for example, may influence HAB expansion because some of these blooms may reflect the major changes in ecosystem structure that occur in response to inter-annual oscillations, such as those related to the El Niño Southern Oscillation (ENSO), or longer term cycles, such as North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO). In the northern Iberian Peninsula, for example, the abundance of the harmful dinoflagellate *Gymnodinium catenatum* was high during the mid-1980s when there was a transition from downwelling-favorable conditions to upwelling-favorable conditions following a shift in the NAO index (Alvarez-Salgado et al., 2003).

Climate ultimately controls the fundamental parameters regulating algal growth, including water temperature, nutrients, and light, and thus can be expected to result in changes in the species composition, trophic structure, and function of marine ecosystems. Examples can be found throughout U.S. and European coasts, where long-term data are available, that show correlations between shifts in HAB species and the timing of their outbreaks and increases in mean water temperature.

The past several decades have witnessed dramatic changes globally, many of which could have direct or indirect impacts on HAB species distribution. In addition to changes in climate, human activities have altered the nutrient regimes of coastal waters tremendously, primarily as a result of increased applications of synthetic fertilizers. The export of phosphorus to the coastal zone has increased at least three-fold compared to pre-industrial levels, while export of

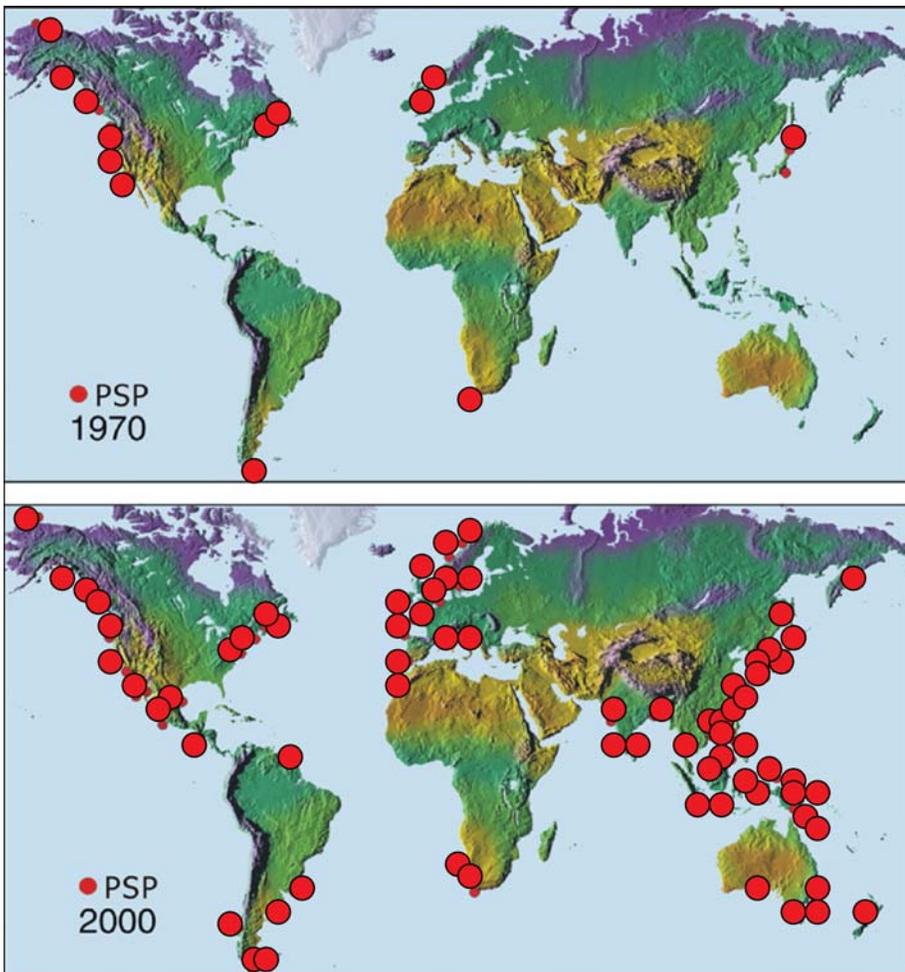


Figure 3. Paralytic shellfish poisoning is but one syndrome caused by HABs and occurring with increasing frequency throughout the world. Paralytic shellfish poisoning (PSP) can cause diarrhea, nausea, vomiting, and respiratory paralysis when shellfish, which have consumed the toxic algae, are eaten by humans. The upper panel shows the recorded occurrences of PSP by 1970, while the lower map shows the recorded occurrences in this syndrome up through the year 2000. The expansion has been particularly large throughout Southeast Asia, Europe, and South America. Modified from GEOHAB (2001).

nitrogen has increased to an even greater degree (Smil, 2001). Population growth and development, and the production of food (crop and animal production systems) result in dramatic alteration of the landscape as well as large sewage inputs, and increased runoff from land. Increased nutrient inputs to enclosed and nearshore ecosystems have resulted in widespread coastal eutrophication throughout Europe and the United States. Production and consumption of energy also results in increased atmospheric inputs from NO<sub>x</sub> emissions, which can then lead to increased nitrogen deposition. The eutrophication of coastal systems and its relationship to HAB development cannot be understood without knowledge of the sources and composition of the nutrients, as well as the physiological rates and mechanisms by which HABs acquire these nutrients (Glibert et al., this issue).

Another significant alteration in nutrient loading to the coastal zone comes from the increase in aquaculture activities. From cultured salmon in Norway, which has grown from less than 10,000 t/yr in 1970 to greater than 500,000 t/yr, to shellfish culture through Europe, Asia, and elsewhere, these industries have altered ecosystems through input of feed and feces, only a small percentage of which is incorporated in food biomass. Fish and shellfish harvesting has also altered ecosystems, leading to changes in food chains. The exploitation of natural fish stocks has, in some cases, led to a decrease in the control of HAB species by removal of the primary grazers through trophic cascade effects. This is exemplified for the brown tide in Long Island bays where the overfishing of the quahog

and other shellfish is now thought to be a factor in the emergence of *Aureococcus anophagefferens* brown tides. Since its first appearance in large numbers in 1985, this tiny alga blooms frequently along the mid-Atlantic U.S. coast. In Long Island, it is well documented that the dense brown tide blooms devastated the local scallop population and destroyed submerged aquatic vegetation by shading. Altered food webs and trophic interactions, through overfishing and the invasion of the predatory ctenophore *Mnemiopsis leidyi*, have also been suggested as possible factors leading to increased HABs in the Black Sea (Lancelot et al., 2002).

For decades, HABs have been studied in all areas of the globe, but the underlying reasons for these blooms, the ability to predict their occurrence, and the means to mitigate them when they do occur, are not well known. Most studies are conducted at local levels, or in a reactionary mode following HAB outbreaks, rather than with the overarching goal of understanding the underlying processes behind the development or outbreak of HABs. As the papers in this issue demonstrate, this approach is beginning to change, with the implementation of U.S. programs such as ECOHAB (Ecology and Oceanography of Harmful Algal Blooms), MERHAB (Monitoring and Event Response of Harmful Algal Blooms), and related international efforts, such as EUROHAB (European Harmful Algal Blooms) and GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms). Consequently, a better understanding of the oceanography and ecology of HABs is beginning to emerge. Many of the causative factors that are only touched on in this

overview are dealt with in more detail in the following papers. In addition, new methodological approaches and future needs are addressed.

## THE RANGE OF FACTORS INFLUENCING HABs

Varying forcing functions, including physical dynamics, climate change, nutrient loading, and other anthropogenic influences such as reductions or changes in the grazing community through fishing or aquaculture select for different groups of algae—including HABs—in several distinct oceanographic systems (Figure 4). This selection, and the resulting bloom and population dynamics of those groups, are a consequence of these factors and the physiological, behavioral, and trophodynamic interactions of HABs with their environment. For example, the initiation of a bloom requires successful recruitment of a population into a water mass. This may result from excystment of resting cells during a restricted set of suitable conditions, transport of cells from a source region where blooms are already established, or exploitation of unusual climatic or hydrographic conditions.

Once a bloom is initiated, physical processes controlling bloom transport are of paramount importance. Coastal currents driven by wind, buoyancy, or other factors can transport blooms hundreds or even thousands of kilometers along the coast, often from one management area to another. Understanding the physical dynamics underlying these transport pathways is essential to effective management and mitigation of HAB effects. A population's range and biomass are affected by physical controls such as

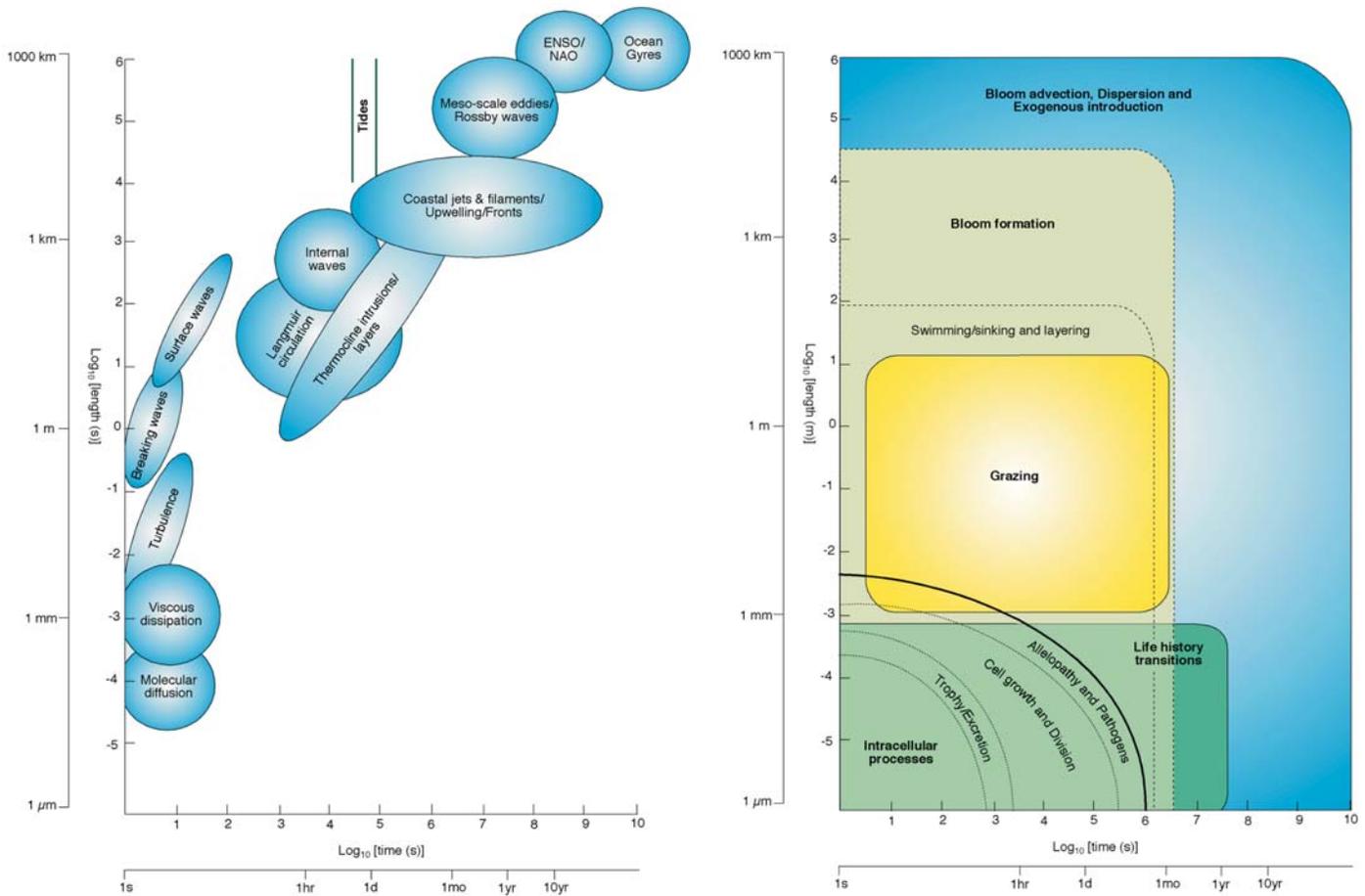


Figure 4. Many physical and biological interactions control HABs on many different temporal and spatial scales. For some HABs, the physical processes such as large-scale advection, transport, and even climate change are significant in HAB development. In other cases, biological factors such as ability to exploit particular nutrients, swimming, aggregation, allelopathy, and interactions with other members of the microbial community are the dominant processes affecting the distribution of HAB species. It is therefore important that ecological studies of HABs be conducted in a multidisciplinary context in which both oceanographic and physiological/trophodynamic controls are taken into consideration. SOURCE: GEOHAB (2001).

long-distance transport, accumulation of biomass in response to water flows and swimming behavior, and the maintenance of suitable environmental conditions (including temperature and salinity, stratification, irradiance, and nutrient supply). Thus, physical forcings, nutrient supply, and the behavior of organisms all interact to determine the timing, location, and ultimate biomass achieved by a bloom, as well as its impacts.

### PHYSICAL PROCESSES AND HABs

Physical processes that are likely to influence the population dynamics of HAB species are operative over a broad range of spatial and temporal scales. Large-scale, mean circulation affects the distribution of water masses and biogeographical boundaries. Many examples may be found of the influence of mesoscale circulation on HAB population dynam-

ics. Eddies from the deep ocean can, for example, impinge on slope and shelf regions, affecting the transfer of algae and nutrients across the shelf break. This type of transport may be involved in the delivery of the Florida red tide organism *Karenia brevis* to nearshore waters from an offshore zone of initiation. Although eddies are difficult to resolve through sampling at sea, they can usually be detected through remote sensing of temperature,

sea-surface height, or ocean color. The understanding of the main features of mean circulation is often sufficient to devise models that may be used to guide decision-makers on the movement and development of HABs, although such predictions are still mostly rudimentary.

Processes at intermediate scales result in the formation of convergence zones, fronts, and upwelling. The retentive nature of some semi-enclosed coastal systems, such as estuaries and fjords, can produce long residence times leading to prolonged suitable periods for cells to thrive (Cembella et al., this issue). The importance of fronts in HAB development is now recognized and included in some modeling efforts. A linkage has been demonstrated, for example, between tidally generated fronts and the sites of massive blooms of the toxic dinoflagellate *Gyrodinium aureolum* (= *Karenia mikimotoi*) in the North Sea (Holligan, 1979). The typical pattern is that of a high surface concentration of cells at the frontal convergence, contiguous with a subsurface chlorophyll maximum, which follows the sloping interface between the two water masses beneath the stratified side of the front. The signature of the chlorophyll maximum, sometimes visible as a “red tide,” may be 1 to 30 km wide. Chlorophyll concentrations are generally lower and much more uniform on the well-mixed side of the front. The significance of this differential biomass accumulation is best understood when movement of the front and its associated cells brings toxic dinoflagellate populations into contact with fish and other susceptible resources, resulting in massive mortalities. This is an example where physical-biological

coupling results in biomass accumulation, and larger-scale advective mechanisms interact synergistically in ways that result in harmful effects. The timing and duration of upwelling is another physical feature that plays an important role in many blooms, as in the case of the Benguela upwelling system, where HABs accumulate subsurface as stratification increases during the upwelling season and move onshore as upwelling relaxes (Kudela et al., this issue).

The importance of small-scale physical processes in HAB development is observed in the layering of the physical, chemical, and biological environment in stratified coastal systems. Off the French coast, for example, a thin layer of dinoflagellates, including the HAB species *Dinophysis* cf. *acuminata*, has been observed in the region of the thermocline (Gentien et al., this issue). The same pattern is found for *Dinophysis norvegica* in the Baltic Sea, where a 1 to 2 m thick layer with up to 80,000 cells/L is usually situated between 20 and 25 m depth, where light is less than 1 percent (Gisselsson et al., 2002). Several HAB species are well known for their ability to form these thin, subsurface layers of uncertain cause and unknown persistence, at scales as small as 10 cm in the vertical and 10 to 1000 km in the horizontal (Gisselsson et al., 2002). One explanation is that these layers result from the stretching of horizontal inhomogeneities by the vertical shear of horizontal currents. This produces an environment potentially favoring motile organisms that can maintain their position in this layer. Any comprehensive study of HABs must now incorporate an understanding of the physical conditions that can lead to cell aggrega-

tion and dispersion. The study described in this issue by Ryan et al. in Monterey Bay, California illustrates how diverse physical phenomena over a range of spatial and temporal scales can influence development of dinoflagellate blooms.

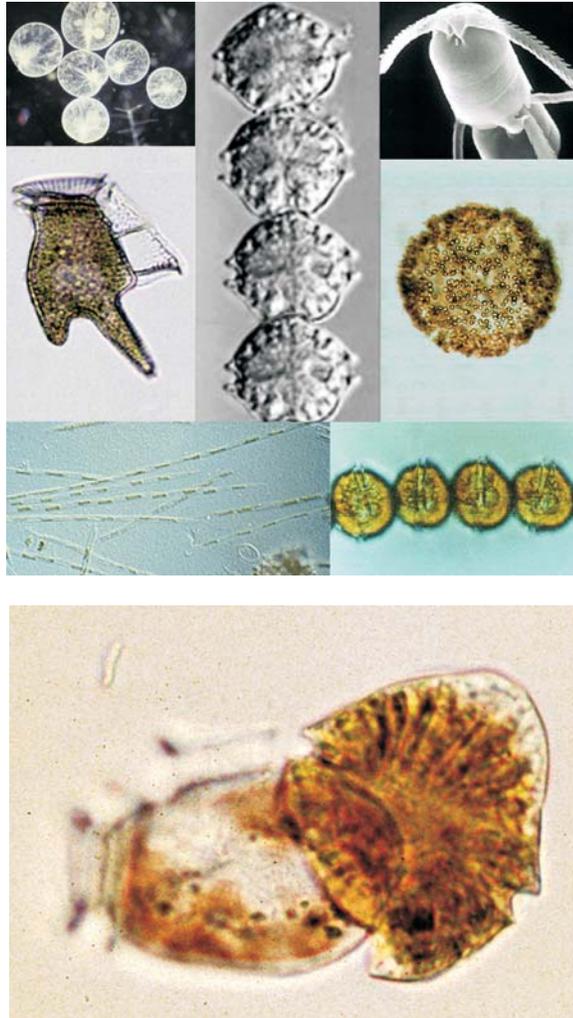
## POPULATION DYNAMICS OF HABs

The proliferation of HABs reflects the metabolism and specific growth of algal cells as well as the selection of a species within an ecosystem. Studies of species responses at the ecosystem level are therefore essential if we are to understand the population dynamics of HABs. The specific growth rate of a species is determined by many metabolic processes, including photosynthesis and nutrient uptake and assimilation, which are under genetic control. The net population growth of a species is controlled by external environmental factors, including nutrients, physical transport, grazing, and other community interactions.

HAB species do not typically appear to have higher intrinsic growth rates than many other phytoplankton. Rather, the expression of harmful algae is dependent on a suite of biological characteristics of the ecosystem and the HAB species, all of which are embedded in the physical and nutrient regimes described above. Some cells have morphological or physiological adaptive strategies that may aid their survival or competitiveness (Figure 5).

A survival and growth strategy that is important to many HAB species is a complex life cycle, or a life cycle involving resting or benthic stages, such as spores or cysts. These cysts or spores provide a recurrent seed source or inoculum for planktonic populations, and this

Figure 5. HAB species display a diversity of morphological and physiological adaptations. These adaptations may permit them to compete and thrive. These adaptations include such features as buoyancy/sinking regulation through adjustment of ion balance, gas vacuoles, colony formation, spines, and the formation of chains. In addition, some species have the ability to consume prey as shown in the second panel. SOURCE: GEOHAB (2001).



characteristic may be a critical factor in determining not only the geographic distribution of species but possibly their eventual abundance as well.

Interactions between HAB species and other algae may be an important survival strategy for some HABs. For example, it has long been argued that production of allelopathic exudates allows some harmful species to outcompete co-occurring phytoplankton (e.g., Smayda, 1998; Granéli and Johansson,

2003). Some species may even use cyst formation as a survival strategy against strong allelochemicals produced by another HAB species (Fistarol et al., 2004). It may well be that some of the HAB species that form thin, subsurface or surface layers of cells at extraordinary densities do so because this allows them to change the ambient water chemistry and light penetration in a manner that deters grazing, inhibits co-occurring algal species, or facilitates sexuality and

gamete encounter rate. These ecological strategies are appealing, but direct investigations of these mechanisms or their effects on the plankton community are few. Quantitative estimates of these effects in the context of HAB population dynamics studies are just emerging (Gentien et al., this issue).

There are numerous explanations for the growth and accumulation of the cells that cause HABs, and many of those explanations are rooted in the interactions of those cells with other members of the planktonic community. Many HAB species produce more toxin under stress, thereby allowing them to avoid predation and competition by killing their predators and the competing algal species (Granéli and Johansson, 2003). Fish and zooplankton avoid dense concentrations of certain HAB species (Fiedler, 1982) and laboratory studies indicate that toxic species are rejected by at least some predators or grazers (e.g., Ives, 1987). The extent to which toxins or other bioactive compounds impact grazers is far from understood. The ability of a HAB species to build up population size under specific conditions is therefore related to the availability of sufficient nutrients to sustain it and to reduction in grazing and mortality rates.

Reductions in grazer abundance can also play a key role in bloom development. This might result from physical factors or behavioral strategies that lead to spatial separation of harmful algal species and grazers. Local reductions in grazer abundances may also be in direct response to HABs (e.g., avoidance or mortality induced by the HABs) (Granéli and Johansson, 2003), or in response to the effects of past HAB events on

grazer populations. In those cases where grazers are abundant, grazing control may still not be exerted because toxins or prey size reduce the ability of the grazers to ingest the HAB species. The response of zooplankton and other grazers to toxic algae is often species-specific in terms of behavioral responses and toxin susceptibility.

Grazing control of HABs can also depend on the population density of the harmful algae, as demonstrated for the brown tides in Narragansett Bay, United States, where suppression of grazing occurs above a threshold concentration (Tracey, 1988). A threshold effect may also occur if the daily production of new harmful cells becomes large enough to saturate the ingestion response of the grazers and the ability of grazers to increase their populations. In that case, population growth can accelerate dramatically (Donaghay, 1988). There is, however, little quantitative information on how the nature of the grazer response influences the timing, magnitude, and duration of HABs. Model parameterization of these effects is thus in very early stages of development.

Viruses are also now known to have significant impacts on the dynamics of marine communities and some have been found to infect algae and have been implicated in the demise of red or brown tide blooms (Fuhrman and Suttle, 1993). Likewise, bacteria play an important role in controlling many HABs and regulating their impacts, including their toxicity. Bacteria may also interact with HABs in a positive manner by stimulating their growth (Fistarol et al., 2004). Cyanobacteria, in particular, establish mutually beneficial consortia by chemotactically

attracting and supporting microorganisms involved in nutrient cycling and the production of growth factors (Paerl and Millie, 1996). A different type of bacterial interaction with HAB species was described by Bates et al. (1995) who showed that the toxicity of the diatom *Pseudo-nitzschia* was dramatically enhanced by the presence of bacteria in laboratory cultures. The extent to which any of the above interactions occur in natural waters and affect HAB dynamics is not well known and represents an important line of inquiry.

Moving higher in the food web, zooplankton impaired by ingesting harmful algae may be more susceptible to predation, and thus may become an important vector for transferring toxins in the pelagic food web. Alternatively, zooplankton fecal pellets may be important sources of toxin to benthic communities. Herbivorous fish can accumulate and transfer toxins, and even cause mass mortalities of the marine birds that consume them. During food-web transfers, toxins may be bioaccumulated, excreted, degraded, or structurally modified. To understand the effects of HAB species on the marine food web, both the direct as well as the indirect, more subtle pathways by which toxins are transferred and transformed, and the differential susceptibility of marine organisms to these toxins must be characterized. In some cases, HABs may insult, but not kill, other members of the food web, leaving them stressed and therefore more susceptible to other sources of mortality, such as infection by pathogens (Burkholder and Glasgow, 1997; Glibert et al., 2002).

The physical environment is also

intrinsically intertwined with the biology and ecology of these organisms. Turbulence has, for example, significant consequences for the growth and decline of HABs through its influence on the transport of nutrients, the mixing of phytoplankton through gradients of light, and even through direct impairment of growth. Many HAB species are motile and their swimming behavior or buoyancy may result in the formation of high-density patches under certain environmental conditions. Some cyanobacterial species are able to regulate their vertical positioning by synthesis and collapse of gas vesicles and by accumulation of photosynthetic ballast. Vertical movement by cells in a stratified environment undoubtedly has functional significance, maximizing encounter frequencies for sexual reproduction, minimizing grazing losses, and allowing cells to obtain nutrients at depth and light at the surface. The challenge is to identify which conditions allow a particular species to bloom or to cause its strategy to fail.

The above represent some well-established examples of the effects of various processes on the distribution of harmful algae. There are, however, many examples where the physical and/or biological processes common to particular ecosystems are poorly characterized and understood and therefore their influence on HAB population dynamics and their harmful properties remain uncertain.

## MOVING FORWARD

In summary, the HAB problem is significant and growing worldwide and poses a major threat to public health, ecosystem health, as well as to fisheries

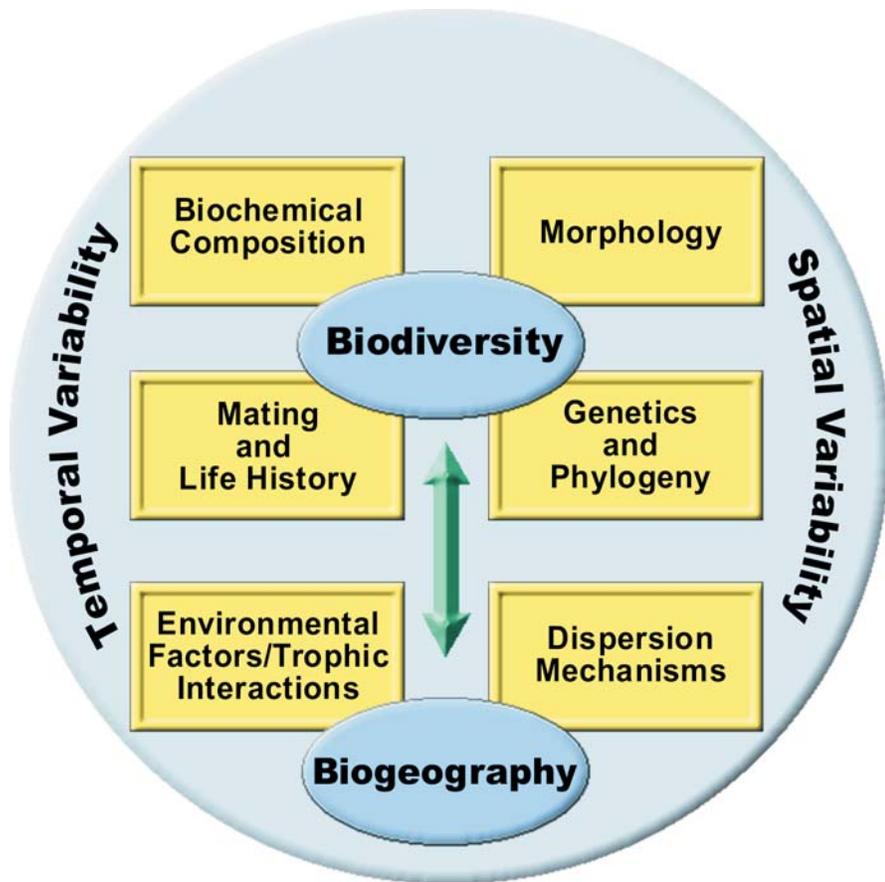


Figure 6. Understanding biodiversity and biogeography of HAB species requires that many biological, chemical, and physical factors be considered on a range of temporal and spatial scales. SOURCE: GEOHAB (2001).

and economic development. The HAB problem and its impacts are diverse as are the causes and underlying mechanisms controlling the blooms. HABs may be caused by the explosive growth of a single species that rapidly dominates the water column, but may also be the result of highly toxic cells that do not accumulate in high numbers. Winds, tides, currents, fronts, and other features can create discrete patches or streaks of cells at all scales. A full understanding of the many biological, chemical, and physical processes that underlie HABs will con-

tinue to be a challenge, given the many different species and hydrographic systems involved (Figure 6).

As highlighted in this issue, HAB research is proceeding along many different lines, and great progress is being made in some areas. The development of multi-lateral international programs such as EUROHAB (1999, 2002) and GEOHAB (2001, 2003) and bi-lateral initiatives like the EU-US Scientific Initiative on Harmful Algal Blooms (2003) program are bringing scientists together from different countries and different

disciplines in a concerted attack on this complex and multi-faceted issue. Better methodologies are becoming available for predicting the occurrence, distributions, toxicity, and other deleterious effects of HABs and these tools are being incorporated in observing systems yielding real-time data that can aid in management response or prediction (Babin et al., this issue; Trainer and Suddleson, this issue). A deeper understanding of the physical and environmental mechanisms underlying the diverse array of HABs will emerge as these tools are applied more routinely and as new tools are developed. On a broader level, these programs will contribute to the improved global observation systems that are required to resolve influences of environmental factors (anthropogenic and climate-related) on distributions and trends in HAB occurrence.

HABs are a serious and growing problem in the global coastal ocean—one that requires the interplay of all oceanographic disciplines, as well as others such as public health and resource management (Anderson and Ramsdell, this issue). Only through recognition of the diversity of these interactions will progress be made towards our goal of scientifically based management of HAB-threatened resources.

#### ACKNOWLEDGEMENTS

This short review is the outcome of many interactions with many people. In particular, the authors wish to thank the past and present members of the GEOHAB Scientific Steering Committee, and the participants at the EU-US Joint Workshop on Harmful Algal Blooms in Trieste, Italy, September 2002. Funding

for these activities has been provided by NSF, NOAA, and the European Commission DG Research-Environment Directorate. GEOHAB is an initiative of SCOR (Scientific Committee on Oceanic Research) and IOC (Intergovernmental Oceanographic Commission of UNESCO). P. Glibert and D. Anderson were funded by the National Oceanic and Atmospheric Administration (NOAA), ECOHAB, MERHAB and NSF. This is contribution number 127 from the ECOHAB Program, 3836 from the University of Maryland Center for Environmental Science, and 11334 from the Woods Hole Oceanographic Institution. 

## REFERENCES

- Alvarez-Salgado, X.A., F.G. Figueiras, F.F. Perez, S. Groom, E. Nogueira, A. Borges, L. Chou, C.G. Castro, G. Moncoiffe, A.F. Rios, A.E.J. Miller, M. Frankignoulle, G. Savidge, and R. Wollast. 2003. The Portugal coastal counter current of NW Spain: New insights on its biogeochemical variability. *Progress in Oceanography* 56:281-321.
- Bates, S.S., D.J. Douglas, G.J. Doucette, and C. Leger. 1995. Enhancement of domoic acid production by reintroducing bacteria to axenic cultures of the diatom *Pseudonitzschia multiseriata*. *Natural Toxins* 3:428-435.
- Burkholder, J.M. 1998. Implications of harmful microalgae and heterotrophic dinoflagellates in management of sustainable marine fisheries. *Ecological Applications* 8:S37-S62.
- Burkholder, J.M. and H.B. Glasgow, Jr. 1997. *Pfiesteria piscicida* and other *Pfiesteria*-like dinoflagellates: Behavior, impacts, and environmental controls. *Limnology and Oceanography* 42:1052-1075.
- Donaghay, P.L. 1988. The role of temporal scales of acclimation, food quality and trophic dominance in controlling the evolution of copepod feeding behavior. *Bulletin of Marine Science* 43:469-485.
- EU-US Scientific Initiative on Harmful Algal Blooms. 2003. *EU-US Scientific Initiative on Harmful Algal Blooms: A Report from a Workshop Jointly Funded by the European Commission-Environmental and Sustainable Development Program and the U.S. National Science Foundation*. The European Commission, Brussels, Belgium, 57 pp. [Online] Available at: [http://www.whoiedu/science/B/redtide/announcements/EU\\_US\\_Sci-Init.pdf](http://www.whoiedu/science/B/redtide/announcements/EU_US_Sci-Init.pdf) [April 5, 2005].
- EUROHAB. 1999. European Initiative on Harmful Algal Blooms (EUROHAB): Harmful Algal Blooms in European Marine and Brackish Waters, E. Graneli, G.A. Codd, B. Dale, E. Lipiatou, S.Y. Maestrini, and H. Rosenthal, eds. European Commission, Directorate General Science Research and Development, Brussels, Belgium, 93 pp.
- EUROHAB. 2002. EUROHAB Science Initiative Pat B: Research and Infrastructure Needs. E. Graneli and E. Lipiatou, eds. National European and International Programmes, Office for Official Publications of the European Communities, Luxembourg, 142 pp.
- Fiedler, P.C. 1982. Zooplankton avoidance and reduced grazing responses to *Gymnodinium splendens* (Dinophyceae). *Limnology and Oceanography* 27:961-965.
- Fistarol, G.O., C. Legrand, K. Rengefors, and E. Granéli. 2004. Temporary cyst formation in phytoplankton: a response to allelopathic competitors? *Environmental Microbiology* 6(8):791-798.
- Fuhrman, J.A. and C.A. Suttle. 1993. Viruses in marine planktonic systems. *Oceanography* 6:50-62.
- GEOHAB. 2001. *Global Ecology and Oceanography of Harmful Algal Blooms, Science Plan*, P. Glibert and G. Pitcher, eds. SCOR and IOC, Baltimore and Paris, 86 pp.
- GEOHAB. 2003. *Global Ecology and Oceanography of Harmful Algal Blooms, Implementation Plan*, P. Gentien, G. Pitcher, A. Cembella, and P. Glibert, eds.. SCOR and IOC, Baltimore and Paris, 36 pp.
- Gisselson, L.-Å., P. Carlsson, E. Granéli, and J. Pallon. 2002. *Dinophysis* blooms in the deep euphotic zone of the Baltic Sea: Do they grow in the dark? *Harmful Algae* 1:401-418.
- Glibert, P.M., J. Landsberg, J. Evans, M.A. Al-Sarawi, M. Faraj, M.A. Al-Jarallah, A. Haywood, S. Ibrahim, P. Klesius, C. Powell, and C. Shoemaker. 2002. A fish kill of massive proportion in Kuwait Bay, Arabian Gulf, 2001: The roles of infectious bacteria, harmful algae, and eutrophication. *Harmful Algae* 1:1-17.
- Granéli, E., P. Carlsson, P. Tester, J.T. Turner, C. Bechemin, R. Dawson, and F. Azam. 1999. Effects of N:P:Si- ratios and zooplankton grazing on phytoplankton communities in the northern Adriatic Sea. I. Nutrients, phytoplankton, biomass, and polysaccharide production. *Aquatic Microbial Ecology* 18:37-54.
- Granéli, E. and N. Johansson. 2003. Effects of the toxic haptophyte *Prymnesium parvum* on the survival and feeding of a ciliate: the influence of different nutrient conditions. *Marine Ecology Progress Series* 254:49-56.
- Heil, C.A., P.M. Glibert and C. Fan. 2005. *Prorocentrum minimum* (Pavillard) Schiller—A review of a harmful algal bloom species of growing worldwide importance. *Harmful Algae* 4:449-470.
- Holligan, P.M. 1979. Dinoflagellate blooms associated with tidal fronts around the British Isles. Pp. 249-256 in *Toxic Dinoflagellate Blooms*, D.L. Taylor and H.H. Seliger, eds. Elsevier North Holland, New York, USA.
- Ives, J.D. 1987. Possible mechanisms underlying copepod grazing responses to levels of toxicity in red tide dinoflagellates. *Journal of Experimental Marine Biology and Ecology* 112:131-145.
- Lancelot, C., J.M. Martin, N. Panin and Y. Zaitsev. 2002. The North-western Black Sea: A pilot site to understand the complex interaction between human activities and the coastal environment. *Estuarine, Coastal and Shelf Science* 54:279-283.
- Landsberg, J.H. 2002. The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science* 10:113-390.
- Paerl, H.W. and D.F. Millie. 1996. Physiological ecology of toxic aquatic cyanobacteria. *Phycologia* 35 (6 Suppl.):160-167.
- Parsons, M.L., Q. Dortch, and R.E. Turner. 2002. Sedimentological evidence of an increase in *Pseudo-nitzschia* (Bacillariophyceae) abundance in response to coastal eutrophication. *Limnology and Oceanography* 47:551-558.
- Ryther, J. 1955. Ecology of autotrophic marine dinoflagellates with reference to red water conditions. Pp. 347-413 in *The Luminescence of Biological Systems*, F.H. Johnson, ed. American Association for the Advancement of Science, Washington, D.C., USA.
- Smayda, T.J. 1998. Ecophysiology and bloom dynamics of *Heterosigma akashiwo* (Raphidophyceae). Pp. 113-131 in *Physiological Ecology of Harmful Algal Blooms*, M. Anderson, A.D. Cembella, and G.M. Hallegraeff, eds. NATO ASI Series Vol. G 41. Springer-Verlag, Berlin, Germany.
- Smil, V. 2001. *Enriching the Earth: Fritz Haber, Carl Bosch, and the Transformation of World Food*. The MIT Press, Cambridge, MA, USA.
- Tracey, G.A. 1988. Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 "brown tide" in Narragansett Bay, Rhode Island. *Marine Ecology Progress Series* 50:73-81.
- Trainer, V., B.-T.L. Eberhart, J.C. Wekell, N.G. Adams, L. Hanson, F. Cox, and J. Dowell. 2003. Paralytic shellfish toxins in Puget Sound, Washington State. *Journal of Shellfish Research* 22:213-223.