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Toxic red tides and harmful algal blooms: A practical challenge in coastal oceanography

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Introduction

The debate over the relative value of practical or applied versus fundamental research has heated up considerably in recent years, and oceanography has not been spared this re-evaluation of science funding policy. Some federal agencies with marine interests have always focused their resources on practical problems, but those with a traditional commitment to basic research such as the National Science Foundation have increasingly had to fight to maintain their freedom to fund quality science without regard to practical or commercial applications.

Within this context, it is instructive to highlight the extent to which certain scientific programs can satisfy both sides of this policy dilemma - i.e. address important societal issues through advances in fundamental or basic research. One clear oceanographic example of such a program involves the phenomena called "red tides" or "harmful algal blooms". This paper describes the nature and extent of the problems caused by these outbreaks, emphasizing the alarming expansion in their incidence and their impacts in recent years, both in the U.S. and worldwide. The objective is to highlight fundamental physical, biological, and chemical oceanographic question that must be addressed if we are to achieve the practical goal of scientifically based management of fisheries resources, public health, and ecosystem health in regions threatened by toxic and harmful algae.

Background

Among the thousands of species of microscopic algae at the base of the marine food chain are a few dozen which produce potent toxins. These species make their presence known in many ways, ranging from massive "red tides" or blooms of cells that discolor the water, to dilute, inconspicuous concentrations of cells noticed only because of the harm caused by their highly potent toxins. The impacts of these phenomena include mass mortalities of wild and farmed fish and shellfish, human intoxications or even death from contaminated shellfish or fish, alterations of marine trophic structure through adverse effects on larvae and other life history stages of commercial fisheries species, and death of marine mammals, seabirds, and other animals.

"Blooms" of these algae are commonly called red tides, since, in some cases, the tiny plants increase in abundance until they dominate the planktonic community and change the color of the water with their pigments. The term is misleading, however, since non-toxic species can bloom and harmlessly discolor the water; conversely, adverse effects can occur when algal cell concentrations are low and the water is clear. Given the confusion surrounding the meaning of "red tide", the scientific community now prefers the term "harmful algal bloom", with HAB as the obligatory acronym. This new descriptor applies not only to microscopic algae but also to benthic or planktonic macroalgae which can proliferate in response to anthropogenic nutrient enrichment, leading to major ecological impacts such as the displacement of indigenous species, habitat alteration, or oxygen depletion. The causes and effects of macroalgal blooms are thus similar in many ways to those associated with harmful microscopic phytoplankton species.

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HAB phenomena take a variety of forms. One major category of impact occurs when toxic phytoplankton are filtered from the water as food by shellfish such as clams, mussels, oysters, or scallops, which then accumulate the algal toxins to levels which can be lethal to humans or other consumers (reviewed in *Shumway*, [1990], *Ahmed* [1991]). Typically, the shellfish are only marginally affected, even though a single clam can sometimes contain sufficient toxin to kill a human. These poisoning syndromes have been given the names paralytic, diarrhetic, neurotoxic, and amnesic shellfish poisoning (PSP, DSP, NSP, and ASP). Except for ASP, all are caused by biotoxins synthesized by a class of marine algae called dinoflagellates. ASP is produced by diatoms that until recently were all thought to be free of toxins and generally harmless [*Bates et al.*, 1989]. A fifth human illness, ciguatera fish poisoning (CFP) is caused by biotoxins produced by epibenthic dinoflagellates attached to surfaces in many coral reef communities (reviewed in *Anderson and Lobel* [1987]). Ciguatera toxins are transferred through the food chain from herbivorous reef fishes to larger carnivorous, commercially valuable finfish. In a similar manner, the viscera of other commercially important fish such as herring or sardines can contain PSP toxins, endangering human health following consumption of whole fish. Whales, porpoises, seabirds, and other animals can be victims as well, receiving toxins through the food chain via contaminated zooplankton or fish [*Geraci et al.*, 1988; *Anderson and White*, 1992]. All of these poisoning syndromes except DSP are known problems within the U.S. and its territories.

Another type of HAB impact occurs when marine fauna are killed by algal species that release toxins and other compounds into the water, or that kill without toxins by physically damaging gills or by creating low oxygen conditions as bloom biomass decays. Farmed fish mortalities from HABs have increased considerably in recent years, and are now a major concern to fish farmers and their insurance companies. The list of finfish, shellfish and wildlife affected by algal toxins is long and diverse (Table 1) and accentuates the magnitude and complexity of the HAB phenomena. In some ways, however, this list does not adequately document the scale of HAB impacts. A general trophic routing and impact model proposed by *Smayda* [1992] is perhaps a better representation of the many ways in which HAB species affect other organisms within marine ecosystems, not just

Table 1. U.S. Finfish, Shellfish and Wildlife Affected by Toxic or Harmful Microalgal Species (Adapted from Anderson et al., 1993)

Harmful Algal Species	Geographic Area	Affected Organisms *
Alexandrium spp. (PSP)	Northern Atlantic and Pacific Coast of North America	Mussels, surfclams, softshell clams, sea scallops, butterclams, ocean quahogs, oysters, gastropods, lobsters, crabs Herring, salmon, menhaden, sandlance, mackerel and possibly other fish species. Whales, sea lions[+], sea otters[+], sea birds Squid, zooplankton, benthic invertebrates
Alexandrium monilata	Gulf of Mexico	Oysters, coquinas, mussels, gastropods, fish
Pseudonitzschia pungens f. *multiseries* (ASP)	Gulf of Maine; Eastern Canada, Puget Sound, WA	Mussels
P. pseudodelicatissima (ASP)	New Brunswick, Canada	Mussels
P. australis (ASP)	California	Anchovies, sea birds
Probably *P. australis* (ASP)	Washington, Oregon	Razorclams[+], Dungeness crabs[+]
Unidentified (ASP)	Massachusetts, Maine	Bay scallops[+]
Dinophysis spp. (DSP)	Nova Scotia, Gulf of St. Lawrence, Canada	Mussels[+]
Prorocentrum lima (DSP)	Nova Scotia, Canada	Mussels[+]
Prorocentrum spp.	Long Island Sound	Northern quahogs, bay scallops
Gyrodinium aureolum	Northern New England (Maine)	Mussels, softshell clams[+]
Aureococcus anophagefferens	New York, Rhode Island, New Jersey	Bay scallops, mussels *Anchoa* sp., cladocerans
Gymnodinium breve (NSP)	Gulf of Mexico, South Atlantic Bight	Bay scallops, surfclams, oysters, southern quahogs, coquinas. Tunicates Many commercial/recreational fish species Sea birds[+], sea turtles, manatees[+], dolphins[+]
Chaetoceros convolutus *C. concavicornis*	Pacific northwest	Salmon aquaculture, possibly other species
Heterosigma carterae	Pacific northwest Narragansett Bay	Salmon aquaculture Zooplankton
Unnamed gonyaulacoid	Mid-Atlantic region	Striped bass, flounder, croaker, mullet, menhaden, sea trout, pinfish, blue crabs, scallops
Gambierdiscus toxicus *Prorocentrum lima*[+] *P. concavum*[+] *P. hoffmannianum*[+] *Ostreopsis lenticularis*[+] *O. siamensis*[+]	South Florida, Florida Keys Puerto Rico, U.S. Virgin Islands Hawaii, Guam	Grouper, snapper, mackerel, jack, goat fish, barracuda, parrot fish, tang, and others Gastropods

* Found to contain algal toxins, or be adversely affected by marine algae

[+] Causative algae implicated, not confirmed.

those that are commercially important or easily visible to humans (Fig. 1). This model shows where adverse effects on viability, growth, fecundity, and recruitment can occur within different trophic levels, either through toxin transmitted directly from the algae to the affected organism or indirectly through food web transfer. In virtually all trophic compartments of the marine food web, there can be impacts from toxic or harmful blooms. Smayda points out that the model resembles energy flow dia-

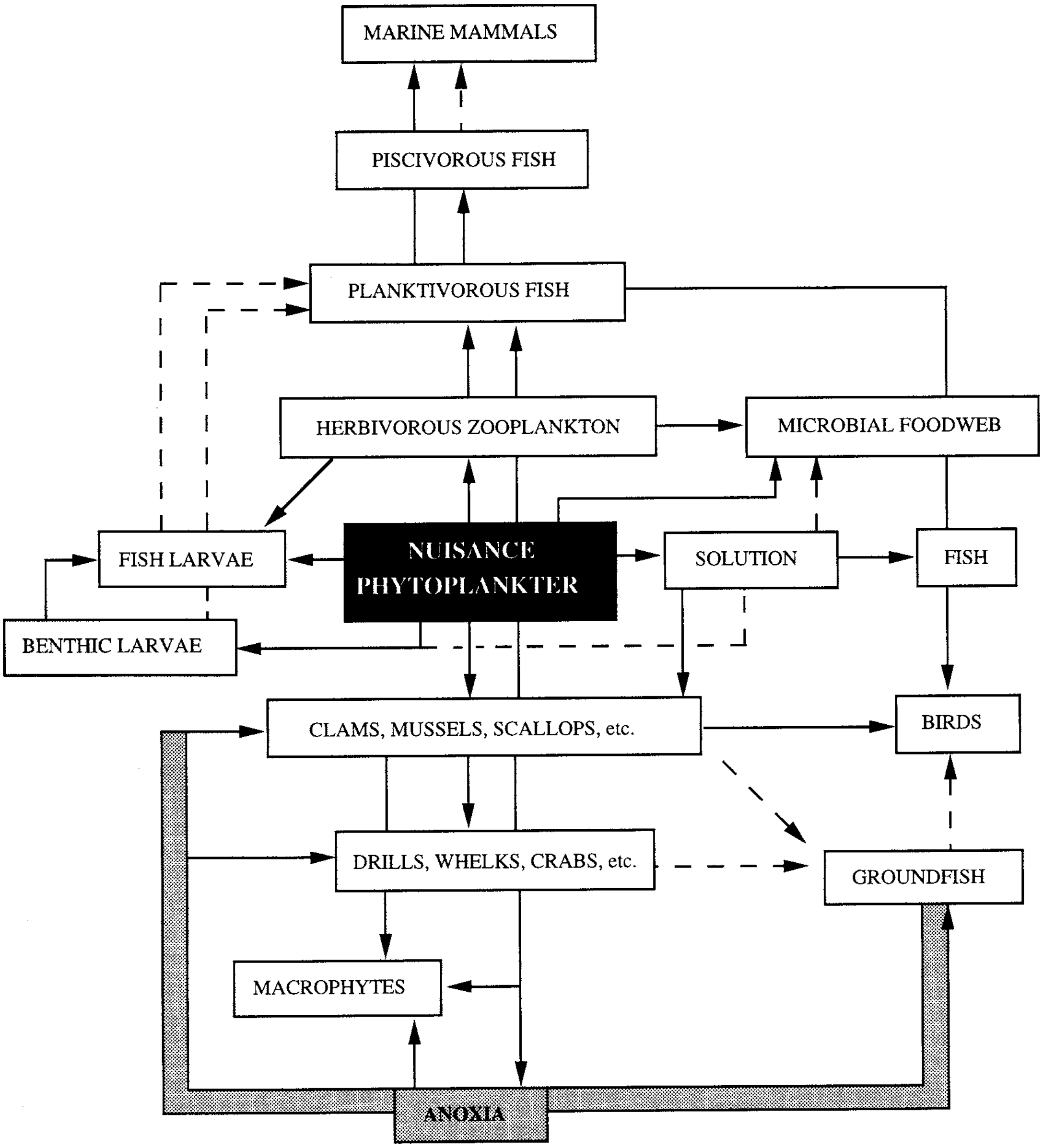

Figure 1. A trophic routing and impact model showing possible linkages between nuisance or harmful algal blooms and various marine food web compartments. The arrows illustrate direct and vectored routes through which toxins and anoxia can impact the depicted trophic compartments, causing recruitment failure and/or mortality. (From *Smayda*, [1992]).

grams because bloom events impact ecosystems via the movement of toxins in a manner that is analagous to the flow of carbon or energy. Examination of Figure 1 in light of our present knowledge of HAB impacts quickly reveals the many areas where information is lacking. Most HAB research activity has focused on shellfish, fish, and zooplankton, but many other organisms are being affected by toxins in ways that we can only guess at right now. This is a good example where expanded research on HAB phenomena can provide useful information to many other disciplines in marine biology and geochemistry.

Recent Trends

The nature of the HAB problem has changed considerably over the last two decades in the United States (Fig. 2). Where formerly a few regions were affected in scattered locations, now virtually every coastal state is threatened, in many cases over large geographic areas and by more than one harmful or toxic algal species. Few would argue that the number of toxic blooms, the economic losses from them, the types of resources affected, and the number of toxins and toxic species have all increased

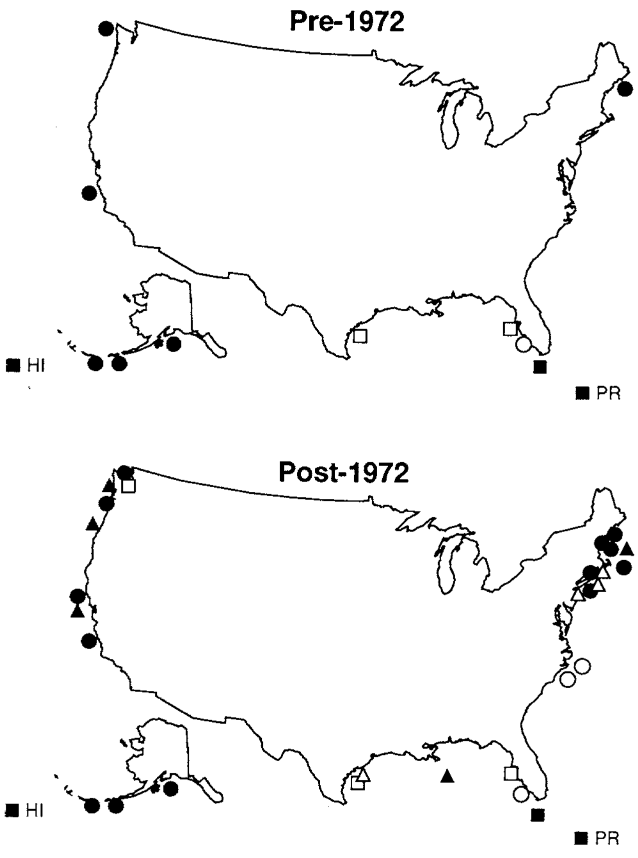

Figure 2. Expansion of the problems caused by harmful phytoplankton species in the U.S. over the last two decades. The maps show the HAB outbreaks known before (top) and after (bottom) 1972. This is not meant to be an exhaustive compilation of all events, but rather an indication of major or recurrent HAB episodes. In addition to the toxic impacts shown, harmful (but non-toxic) micro- and macroalgal species have caused whale and other marine mammal or animal mortalities, occasional anoxia, habitat destruction, and a general decline in coastal aesthetics in many coastal areas during the last 20 years. Legend: Open circles - neurotoxic shellfish poisoning (NSP); Darkened circles - paralytic shellfish poisoning (PSP); Open squares - recurrent fish kills; Darkened squares- ciguatera fish poisoning (CFP); Open triangles - brown tide; Darkened triangles - amnesic shellfish poisoning (ASP).

dramatically in recent years in the United States and around the world [*Anderson*, 1989; *Smayda*, 1990; *Hallegraeff*, 1993]. Disagreement only arises with respect to the reasons for this expansion. Possible explanations include: a) species dispersal through currents, storms, or other natural mechanisms (e.g. *Anderson et al.*, [1982]); b) nutrient enrichment of coastal waters by human activities, leading to a selection for, and proliferation of, harmful algae [*Smayda*, 1990]; c) increased aquaculture operations which can enrich surrounding waters and stimulate algal growth [*Gowen and Bradbury*, 1987]; d) introduction of fisheries resources (through aquaculture development) which then reveal the presence of indigenous harmful algae in waters formerly "free" from HAB problems [*Anderson*, 1989]; e) dispersal of HAB species via ship ballast water or shellfish seeding activities [*Hallegraeff and Bolch*, 1992]; f) long-term climatic trends in temperature, wind speed, or insolation [*Reid et al.*, 1990]; and g) increased scientific and regulatory scrutiny of coastal waters and fisheries products and improved chemical analytical capabilities that lead to the discovery of new toxins and toxic events [*Work et al.*, 1993].

If we accept that the expansion is real, and that it has many causes, both natural and human-assisted, what can be done about it in a practical sense? What information is needed to efficiently manage the affected fisheries resources, protect the public health, encourage and support aquaculture development, and contribute to policy discussions about coastal zone issues such as pollution or dredging? If human activities are making the HAB problem worse, how can that be demonstrated, and what steps should be taken to minimize further impacts? These are important practical issues, and the apparent trends in HAB incidence make them even more pressing. The need for focused research is clear, and fortunately, far from being mundane, the issues requiring investigation are of fundamental importance to many oceanographic disciplines. A few of these are highlighted below.

Physical/Biological Coupling

Despite the diverse array of HAB species and the many hydrographic regimes in which they occur, one common characteristic of such phenomena is that physical oceanographic forcings play a significant role in both bloom dynamics and the patterns of toxicity or adverse impacts. Furthermore, the interplay or coupling between the physics and biological "behavior", such as swimming, vertical migration, or physiological adaptation, holds the key for understanding many HAB phenomena. This physical/biological coupling can occur at both large and small scales.

Large-scale Forcings. Years ago, many attributed sudden red tide outbreaks to the rapid, in situ growth of the causative algae, yet numerous studies have since shown that much of the variability in the distribution of HABs can be explained by large-scale advective processes such as wind-driven, buoyancy-driven, and tidally-generated motions of water masses. Several prominent examples illustrate the importance of this type of transport, the different mechanisms involved, and the areas where our knowledge is deficient.

The Rias Bajas of northwest Spain are a group of oceanic bays noted for their prolific production of blue mussels. This productivity is due in large part to intermittent enrichment of the rias by nutrient-rich deep water during upwelling, driven by persistent winds from the north [*Otto*, 1975; *Tenore and Gonzalez*, 1975]. Beginning in 1976, these mussels have been affected by outbreaks of PSP which are often quite sudden; toxicity can rise from undetectable to extremely high levels in a few days. *Fraga et al.*, [1988] argue that the PSP toxicity is linked to the relaxation of upwelling following a change in wind direction and speed. Upwelling is driven by north or northeast winds, but winds from the south or west cause downwelling that transports offshore surface waters into the rias, carrying established dinoflagellate populations with it. The resulting changes in the composition of the phytoplankton community are not due to in situ growth of the red tide algae, but instead to the transport or delivery of blooms that originated elsewhere.

Documentation of this linkage between PSP outbreaks in Spain and upwelling relaxation relied heavily on quantification of the degree of upwelling using an index [*Bakun*, 1973] representing the onshore or offshore transport of surface water by winds. This "upwelling index" is a simple calculation from meteorological pressure fields, but it has tremendous practical importance since it can serve as the basis for a predictive capability for toxic blooms [*Fraga, et al.*, 1988]. Further research is needed to confirm the validity of this concept in the Spanish rias [*Figueiras and Pazos*, 1991] and to better define other necessary conditions. Nevertheless, the concept of linking toxic outbreaks to easily measured meteorological or oceanographic parameters is compelling and worth exploring, not only in Spain, but in other areas of the world where seasonal upwelling is a prominent feature.

In this context certain similarities between the hydrography, meteorology, and patterns of PSP in California and northwest Spain are noteworthy. In both areas: a) the dominant hydrographic feature is coastal upwelling, driven by persistent northerly winds; b) sudden outbreaks of PSP toxicity occur, with toxicity increasing far faster than is possible from localized, in situ growth of the causative dinoflagellates; and c) PSP typically occurs during months when a cessation or relaxation of upwelling is common [*Price et al.*, 1991]. Studies are now underway to see if certain California PSP events can be correlated with upwelling relaxation. If so, state health authorities can look forward to the time when they can manage affected shellfish resources using remote sensing or moored instrument arrays to detect such events in real time. The first step, however, is to develop a fundamental understanding of the linkage between large-scale physical forcings and the pattern of PSP outbreaks.

Another example of how long-distance bloom transport mechanisms can be identified and characterized is found in the southwestern Gulf of Maine. There, the temporal and spatial pattern of persistent PSP outbreaks have been linked to the behavior of a buoyant plume or coastal current originating in several rivers that empty into the Gulf [*Franks and Anderson*, 1992a,b]. Concentrations of the toxic dinoflagellate *Alexandrium tamarense* are much higher within the lower salinity waters of the plume than without, and toxicity in coastal shellfish rises and falls with the movement of the plume. This is in turn driven by the local wind stress, by rainfall and snowmelt patterns, and by the general circulation of the Gulf. As in Spain, downwelling conditions are conducive to toxicity development, since such conditions trap the plume and its associated cells tightly against the coast and accelerate them to the south. In contrast, upwelling favorable winds push the plume offshore, spreading it out laterally and dramatically decreasing the concentration of *A. tamarense* in nearshore waters due to the upwelling of deeper, saltier waters that contain no toxic cells.

Studies of this coastal current are ongoing, with the objective of better characterizing the nature of the association between the toxic cells and the low salinity water mass, as well as the physical forcings that determine plume behavior. Circulation models are under development that should prove very useful in a predictive capacity, and additional insights are coming from remote sensing detection of the plume using its warm surface temperature signature [*Keafer and Anderson*, 1993]. Here, as in Spain, basic oceanographic studies of large-scale physical transport mechanisms may someday lead to a predictive capability of great practical importance.

Small-scale Interactions

The movements and interactions of water and cells on scales of a few kilometers to a few micrometers is an active research area in the HAB field. At the larger end of this spectrum lies the explanation for enhanced phytoplankton biomass at hydrographic features such as fronts of various types. This enhanced biomass is the result of the interaction between physical processes such as upwelling, shear and turbulence, and physiological processes such as swimming, enhanced nutrient uptake, or biochemical adaptation. Examples of the importance of fronts in phytoplankton bloom dynamics are many, and several prominent studies involve HAB species. Pingree, Simpson and co-workers have demonstrated the linkage between tidally generated fronts and the sites of massive blooms of the toxic dinoflagellate *Gyrodinium aureolum* [*Pingree et al.*, 1975; *Simpson et al.*, 1979] in the North Sea. The pattern generally seen is 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 surface signature of the chlorophyll maximum (sometimes a visible red tide) may be 1-30 km wide. Chlorophyll concentrations are generally lower and 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 *G. aureolum* populations into contact with fish and other susceptible resources, resulting in massive mortalities [*Holligan*, 1979]. This is an example where small-scale physical/biological coupling results in biomass accumulation, and larger-scale advective mechanisms cause the biomass to become harmful.

The biological and physical mechanisms that account for enhanced phytoplankton biomass at fronts are diverse, as they must be to account for the different physical and chemical gradients associated with frontal regions. Many suggested mechanisms relate to differences in nutrient availability and light. High nutrient concentrations are often found at or below the pycnocline, but the rate of supply of nutrients across this interface to the accumulating cells is not well known, nor has the relative importance of recycled versus "new" nutrients been quantified with respect to biomass accumulation. Physical processes which can influence nutrient exchange across a front include interfacial friction and Ekman pumping [*Garvine*, 1974; *Garrett and Loder*, 1981], baroclinic eddies [*Simpson*, 1981], and tidal stabilization/destabilization [*Demers et al.*, 1986].

If cells behaved as passive, neutrally buoyant particles, they could not accumulate. Thus for HAB species, many explanations of enhanced biomass accumulation invoke the swimming behavior of the organisms as a mechanism to take advantage of the gradients in nutrient availability in the frontal region. This may manifest itself as vertical migration in which the cells traverse the top layer of the water column in a daily pattern of directed swimming (e.g. *Heaney and Eppley*, [1981]). *Eppley et al.*, [1968] suggested that downward migration of dinoflagellates at night into deeper, nutrient rich layers at or below the pycnocline allows them to increase their uptake of nitrate, which could then be transformed into cell biomass during photosynthesis when the cells reside in illuminated surface waters during the day. Subsequent work has confirmed that deep nutrients are indeed utilized by some nutrient-starved dinoflagellates (e.g. *Cullen et al.*, [1985]). Alternatively, swimming may simply allow a species to persist at some optimum depth in the presence of vertical currents. One striking observation about *G. aureolum* blooms is that highly concentrated subsurface layers of cells can sometimes be only tens of centimeters thick (*O. Lindahl, personal communication*). The behavioral and physiological strategies that lead to these accumulations are important unknowns.

Clearly, more is involved in the accumulation of cells at fronts and other interfaces than simple enhanced nutrient uptake. Other mechanisms which may be involved include photoadaptation, the inhibition of growth due to wind-driven turbulence, or the different chemical composition of water masses comprising the frontal system. Of special interest is the relative importance of water chemistry (e.g. micronutrients that stimulate growth) versus behavior and hydrography (that physically concentrate cells) as factors responsible for the observed elevated cell concentrations in buoyant plumes and estuarine fronts. Furthermore, *Thomas and Gibson*, [1990] provide evidence that cell division of one red tide dinoflagellate species is directly affected by levels of turbulence similar to those expected from moderate wind stress at the water surface. If the concept of microscale effects of turbulence on HAB species is a general phenomenon, and if the inhibitory levels of shear are shown to be realistic for conditions commonly encountered in the surface mixed layer, the patchy distribution of HAB species in frontal regions may reflect a microscale level of physical interaction. Before such inferences can be drawn, however, several fundamental oceanographic questions must be addressed. For example, direct physical measurements of turbulence at the scale of the individual algal cell are needed during blooms to determine if natural conditions can in fact cause growth inhibition. Likewise, multiple HAB species must be screened for their susceptibility to turbulence, and the actual physiological mechanism for the turbulence inhibition determined so that sensitive species can be identified. Here again, the practical implications of the basic research on these questions are large with respect to our ability to understand and predict the patterns of blooms.

In general, the physical and biological features of frontal regions have often been studied in isolation, whereas major advances in our understanding of HAB phenomena require cooperative studies in which the distribution, physiology, and behavior of the algae are studied at the same spatial and temporal scales as the physics. In the latter instance, high-resolution measurements of flow and density fields at the interfaces where enhanced algal biomass is observed would provide important insights, especially if they are incorporated into coupled physical/biological models which allow the relative importance of the processes described above to be evaluated.

Nutrient Dynamics

One of the explanations given for the increased incidence of HAB outbreaks worldwide is that these events are a reflection of increased pollution and nutrient loading in coastal waters. Some argue that we are witnessing a fundamental change in the phytoplankton species composition of coastal marine ecosystems throughout the world due to the changes in nutrient supply ratios from human activities [*Smayda*, 1990]. There is no doubt that this is true in certain areas of the world where pollution has increased dramatically. It is perhaps real, but less evident in areas where coastal pollution is more gradual and unobtrusive. A frequently cited dataset from an area where pollution is a significant factor is from Tolo Harbor in Hong Kong, where population growth within the watershed grew 6-fold between 1976 and 1986. During that time, the number of observed red tide events increased 8-fold [*Lam and Ho*, 1989]. The underlying mechanism is presumed to be increased nutrient loading from pollution that accompanied human population growth. A similar pattern emerged from a long-term study of the Inland Sea of Japan, where visible red tides increased steadily from 44 per year in 1965 to over 300 a decade later, matching the pattern of increased nutrient loading from pollution [*Murakawa*, 1987]. Japanese authorities instituted effluent controls in the mid-1970's, resulting in a 50% reduction in the number of red tides that has persisted to this day.

These two examples have been criticized, since both could be biased by changes in the numbers of observers through time, and both are tabulations of water discolorations from algal blooms, not just toxic or harmful episodes. Nevertheless, the data demonstrate that coastal waters receiving industrial, agricultural, and domestic effluents, which frequently are high in plant nutrients, do in fact experience a general increase in algal growth. These nutrients can stimulate or enhance the impact of toxic or harmful species in several ways. At the simplest level, toxic phytoplankton may increase in abundance due to nutrient enrichment but remain as the same relative fraction of the total phytoplankton biomass (i.e. all phytoplankton species are affected equally by the enrichment). Alternatively, some contend that there has been a *selective* stimulation of HAB species by pollution. This view is based on the nutrient ratio hypothesis [*Smayda*, 1990] which argues that environmental selection of phytoplankton species is associated with the relative availability of specific nutrients in coastal waters, and that human activities have altered these nutrient supply ratios in ways that favor harmful forms. For example, diatoms, the vast majority of which are harmless, require silicon in their cell walls, whereas most other phytoplankton do not. Since silicon is not abundant in sewage effluent but nitrogen and phosphorus are, the N:Si or P:Si ratios in coastal waters have increased through time over the last several decades. Diatom growth in these waters will cease when silicon supplies are depleted, but other phytoplankton classes (which have more toxic species) can continue to proliferate using the "excess" nitrogen and phosphorus.

This concept is controversial, but is not without supporting data. A 23-year time series off the German coast documents the general enrichment of coastal waters with nitrogen and phosphorus, as well as a four-fold increase in the N:Si and P:Si ratios [*Radach et al.*, 1990]. This was accompanied by a striking change in the composition of the phytoplankton community, as diatoms decreased and flagellates increased more than ten-fold.

As coastal communities and countries struggle with pollution and eutrophication issues, the implications of these studies are profound. Increasingly, the possible stimulation of HAB species by domestic or industrial effluent is being raised by those in opposition to public works projects. One example is a proposed new sewage outfall that will release up to 1 billion gallons of effluent each day into Massachusetts Bay at a point near the pathway of the coastal current described above for the PSP dinoflagellate *A. tamarense*. Opponents of the project cite the time series described above and argue that an adverse impact of the outfall will be an increase in harmful or toxic algal species within the Bay. The stakes in this controversy are huge and the scientific uncertainty significant. The public, the press, and regulatory officials are demanding predictions and answers, yet their expectations exceed our present capabilities. Competitive outcomes in phytoplankton species selection and succession cannot yet be predicted, nor can the relative effects of natural versus anthropogenic factors be resolved. To address the concern that the phytoplankton species composition will change with the different quantities and ratios of nutrients in the effluent from the new outfall, ecosystem-level models of the Bay are required that are a decade or more away. Even when the focus is narrowed to a few key HAB species, their responses within the Bay ecosystem cannot be estimated with any accuracy because their nutrient requirements have not been well-characterized in laboratory studies, nor do we even have ways to determine their nutrient status during present-day blooms.

The potential stimulatory influence of anthropogenic nutrient inputs on HAB incidence is certainly one of the more pressing unknowns we face, and it will require a focused commitment of resources and effort greatly in excess of what has been devoted to the topic until now. Time-series analysis of existing data bases for phytoplankton communities and variables such as major nutrients or pollutants is required, and where such data are lacking, long-term monitoring programs of at least 10-years duration must be initiated in key regions where anthropogenic changes are anticipated. Laboratory studies of the stimulatory effects of chemicals contained in effluents or terrestrial runoff are also needed, as are kinetic studies and other experiments that can quantify the nutritional requirements and uptake capabilities of HAB species.

Emerging Technologies

Molecular Probes. Many of the gaps in our knowledge of HAB oceanography and ecology stem from the autecological or species-specific nature of the phenomena. A common problem in research and monitoring programs occurs when the HAB species of interest is only a minor component of the mixed planktonic assemblage. Many potentially useful measurements are thus not feasible because of the co-occurrence of numerous organisms and detritus. Autecological studies must rely on tedious microscope counts to enumerate the target species, and unlike many other problems in phytoplankton ecology, bulk or community measurements of water samples such as chlorophyll or ^{14}C uptake are of little use. Another constraint arises from the difficulties in adequately identifying and distinguishing between species or strains which are morphologically similar. Considerable time and effort are required to identify a particular species when its distinguishing characteristics are difficult to discern under the light microscope. Such fine levels of discrimination are not generally feasible in monitoring programs or other studies which generate large numbers of samples for cell enumeration. This situation is encountered frequently in studies of harmful or toxic algae. For example, the diatom *Pseudonitzschia pungens* occurs in two varieties, one toxic and the other non-toxic, but these cannot be distinguished from each other using the light microscope [*Smith et al.*, 1990]. Likewise, toxic and non-toxic varieties of toxic dinoflagellates are known to co-occur within a given region [*Yentsch et. al.*, 1978].

Whether the problem is distinguishing between closely-related strains or enumerating a single species in large numbers of samples, the need for species- or strain-specific "probes" is clear - probes which can be used to label only the cells of interest so they can then be detected visually, electronically, or chemically. To date, the two most common probes of this type for harmful algae are antibodies (both polyclonal and monoclonal) that bind to cell surface proteins, and oligonucleotide probes which target nucleic acid sequences inside cells.

Antibody probes are produced by inoculating cells of a target species into animals to stimulate an immune response (e.g. [*Shapiro et al.*, 1989; *Campbell et al.*, 1989; *Anderson et al.*, 1989]). The animal then produces antibodies in response to the presence of the intact foreign organism or compounds derived from it. Cultured algal cells have been inoculated into laboratory animals and antibodies obtained that are specific for proteins on the outer cell wall of the target algae. Using a simple series of steps, a plankton sample can be treated with the antiserum in such a way that the cells of the target species are labeled with antibodies to which fluorescent compounds are attached [*Shapiro et al.*, 1989]. Visual detection of the labeling is possible using an epifluorescence microscope (Fig. 3a,b). Alternatively, the samples can be processed using a flow cytometer or other instruments that can detect and quantify fluorescence. Assays can also be conducted on filters using fluorescent, chemiluminescent, or colorimetric detection.

Both polyclonal and monoclonal antisera have been developed for HAB species with excellent specificity. For example, a polycolonal antiserum developed for the brown tide chrysophyte *Aureococcus anophagefferens* is species-specific, showing no cross reactions with 46 phytoplankton cultures representing 5 algal classes [*Anderson et al.*, 1989]. An even higher level of specificity was demonstrated for the diatom *Pseudonitzschia pungens*, where a polycolonal antiserum is able to distinguish toxic from non-toxic varieties of the same species [*Bates et al.*, 1993].

Much of the effort in immunological detection of harmful algal species has thus far been focused on development and characterization of antibodies for individual species. Applications of this probe technology to field populations of harmful algae are accordingly limited, but will surely increase as more highly specific antisera become available. Experience with an antibody for the brown tide organism *A. anophagefferens* suggests that antibody-based recognition of target species has a large role to play in HAB field programs. That antibody has been used for cell enumeration [*Anderson et al.*, 1993] and grazing studies [*Caron et al.*, 1989], and was recently used to map the geographic distribution of this species over a large region [*Anderson et al.*, 1993]. The latter study was able to detect *A. anophagefferens* at extremely low concentrations (10-20 cells ml^{-1}), and demonstrated that the species is present in many areas with no known history of harmful brown tides. This degree of resolution is noteworthy since *A. anophagefferens* is so small and non-descript that normal microscopic identification and enumeration are highly uncertain at low cell concentrations.

One obvious application of antibody probes would be in automated cell enumeration for field programs. As with other field applications, this has not yet been accomplished, however, but is under active investigation using solution and solid support-based formats. A useful instrument in this context is the flow cytometer, which uses a laser beam to excite individual cells in a flow stream, and characterizes their fluorescence and several other optical properties simultaneously. One current obstacle to flow cytometric analysis of immunolabeled cells is that the intensity of positive labeling is often not significantly higher than the background fluorescence of control or unlabeled cells. Signal enhancement is clearly necessary, and several promising approaches are being explored. Another problem is the loss of cells during the multiple steps involved in antibody labeling. Expectations are high that these problems can be overcome, but at this writing, automated applications of immunofluorescent techniques for harmful algae await further technique development.

Another promising probe technology targets particular genes or gene products inside cells using short, synthetic deoxyribose nucleic acid (DNA) segments (termed "oligonucleotides") which bind selectively to DNA or ribonucleic acid (RNA) sequences specific for a particular organism. For marine systems, this technique has thus far been used primarily on prokaryotes (e.g. [*DeLong et al.*, 1989; *Amann et al.*, 1990; *Distel et al.*, 1991]). Work is in its early stages on HAB species, with only two species or genera under investigation - the PSP dinoflagellates in the

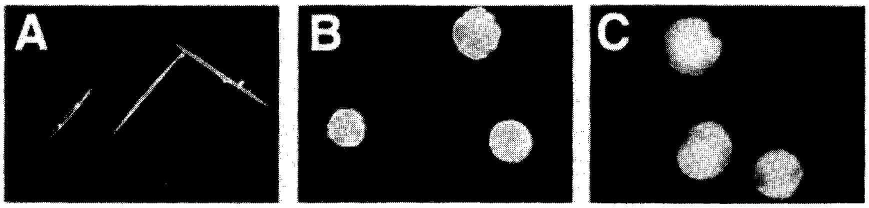

Figure 3. Antibody and oligonucleotide probe-labeled HAB cells, visualized using fluorescence. A). Immunofluorescent image of ASP-producing *Pseudonitzschia pungens* var. *multiseries* labeled with polyclonal antisera developed by *Bates et al.* [1993]. Note the bright fluorescent outline around the frustule of the diatom, and the autofluorescence of chloroplasts inside the cell; B). Immunofluorescent image of *Alexandrium fundyense* (causes PSP) labeled with monoclonal antiserum produced by *Sako et al.* [1993]; C). Fluorescence image of *A. fundyense* labeled with oligonucleotide probe targeting ribosomal RNA or rRNA (*Anderson, unpublished data*). Note that the rRNA label is throughout the cytoplasm.

genus *Alexandrium* [*Scholin and Anderson*, 1993; *Scholin*, 1992] and the ASP diatoms in *Pseudonitzschia* [*Scholin et al.*, 1994].

One of the problems that arises immediately when such work is initiated with HAB species is that little or no sequence information is available. The specificity of a probe will depend on the degree to which a particular sequence is unique, yet that determination requires that sequences of many closely-related or co-occurring algal species be known. Molecular studies of HAB species are still very much in their infancy. If the target gene or gene fragment has not been sequenced previously for the species, genus, or class of interest, it is necessary to establish the sequence database at the outset. This can be both time consuming and expensive.

Many current detection protocols immobilize extracted DNA on a solid surface such as a nitrocellulose or nylon membrane to which a probe is added and allowed to hybridize and establish a double-stranded molecule. Excess unbound probe is washed off, and the hybrid (target + probe) sequences is detected using radioactivity, fluorescence, chemiluminescence, or enzyme-coupled, colorimetric methods. In situ hybridization is also possible, using intact cells that are either immobilized on a microscope slide or suspended in solution. In this format, the probe enters the cell and binds to target sequences, excess probe is washed out, and the complex is detected with fluorescence or radioactivity. As with antibodies, the probe can be directly conjugated to a fluorescent reported molecule such as fluorescein isothiocyanate (FITC), or it can be biotinylated and detected using fluorescent avidin conjugates. Figure 3c shows an epifluorescent image of an *A. fundyense* cell labeled with a ribosomal RNA probe. Multiple variations of these detection strategies exist as well.

As with antibodies, much of the effort in oligonucleotide detection of harmful algal species has been focused on development and characterization of probes for individual species, so applications of this technology to field populations of harmful algae are limited to a few unpublished analyses of field samples. Considerable research is thus needed to fully realize the potential that probes have to change the nature of HAB research and monitoring. Nevertheless, it is evident that antibody and oligonucleotide probes have great potential to alter the manner in which research is conducted on harmful algae. They can be valuable in quick, qualitative assays to indicate the presence or absence of a target organism, and they can assist in the identification of harmful species when trained taxonomists are not available. Once the limitations of these methods are better understood, probes will be used for the direct (and automated) enumeration of HAB species, and someday, to assist in physically separating those cells from co-occurring organisms for physiological or toxicological analyses. One can already envision the time when monitoring of HAB species will involve arrays of instrumented buoys that apply these probe techniques in an automated fashion and telemeter the data to shore. It is likely that both antibody and oligonucleotide probes will have roles to play in these detection systems, but there is a great deal of work to be done to reach these goals and to expand the availability of probes to all HAB species. Furthermore, the species-specific methods developed of necessity for HAB studies can have significant benefits to many other areas in biological oceanography where probe technology has yet to be applied. In all of these cases, there is a high probability of commercialization of the probe technology, demonstrating once again that fundamental science can lead to practical applications. This area of HAB research will clearly be active and productive for many years.

Remote Sensing. Remote sensing was long considered an obvious tool for studying the distribution of HAB organisms over larger spatial and shorter time scales than is possible with ship-based sampling [*Tester et al.*, 1991; *Keafer and Anderson*, 1993]. It has only recently lived up to its potential, however. Although multi-spectral scanners (e.g. Coastal Zone Color Scanner; CZCS) can be used to detect the reflectance of chlorophyll *a* and other pigments, these efforts have been constrained by the inability of the sensors to discriminate phytoplankton populations at the species level. This is, of course, a fundamental requirement of HAB programs. Instead, progress has been made by first linking specific water masses to HAB organisms and then identifying and tracking that water mass with an appropriate remote sensing technique. In particular, remotely-sensed sea surface temperatures (SST) have been used to follow the movement of fronts, water masses, or other physical features where HAB species accumulate. The coastal current discussed above that dominates PSP dynamics in the southwestern Gulf of Maine is easily identified by its temperature signature (Fig. 4). Likewise, the long-distance advection of *Gymnodinium breve* from Florida into the nearshore waters of North Carolina via the Gulf Stream was documented with this approach [*Tester et al.*, 1991].

A few years ago, remote sensing images were expensive and difficult to obtain in a timely manner for all but those closely linked to a satellite receiving station or processing center. The advent of the National Oceanic and Atmospheric Administration (NOAA) Coastwatch Program has since brought this technology on a near real-time basis to the small user at little or no cost [*Keafer and Anderson*, 1993]), so the prospects are bright for an expansion in the application of remote sensing to HAB issues. In

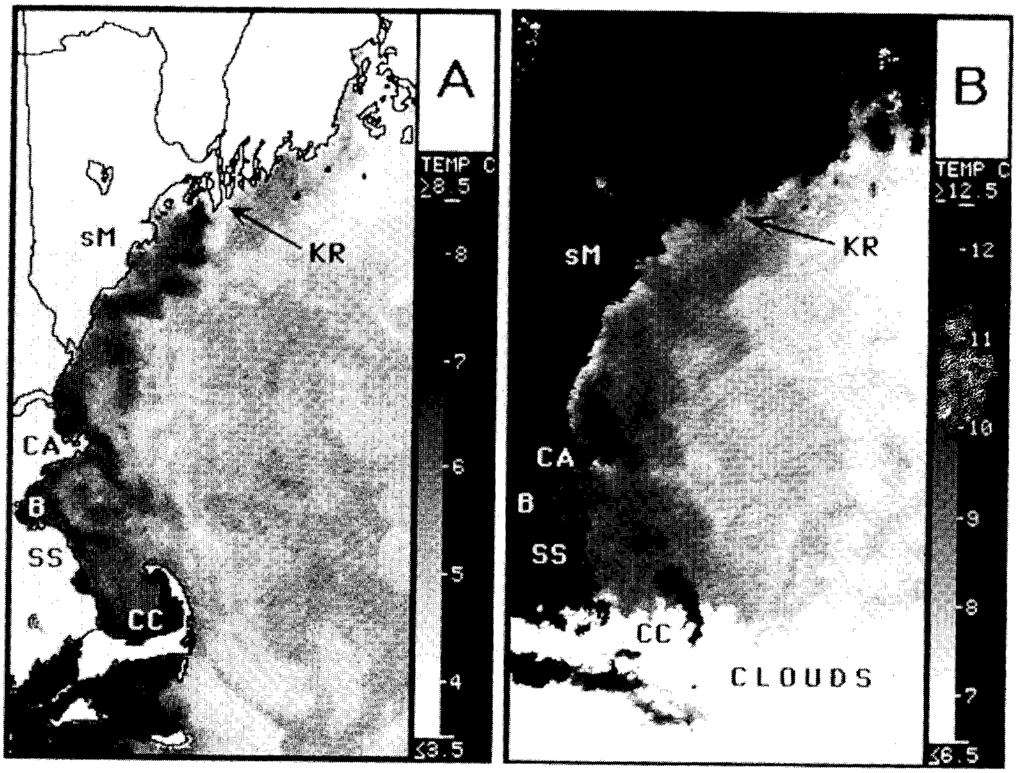

Figure 4. (A) NOAA Coastwatch sea surface temperature (SST) image from April 26, 1991 at 0305 hrs local time during an early spring runoff event. The warmer (darker) coastal current that plays a dominant role in PSP dynamics within the region is seen originating near the mouth of the Kennebec River (KR) and extending past Cape Ann (CA) and into Massachusetts Bay near Boston (B). PSP toxicity was detected only in southern Maine (sM) at this time. Low concentrations of *A. tamarense* were detected within the plume further to the south, but well offshore in Massachusetts Bay just north of Cape Cod (CC). (B) Image from May 12, 1991 at 1447 hrs local time, about two weeks after FIG. 4A. The narrow band of colder water (white) along the coast north of Cape Ann signifies nearshore upwelling which has moved the warmer plume (dark) and *A. tamarense* cells offshore, resulting in decreasing toxicity in southern Maine shellfish and no toxicity in Massachusetts during this time. (From *Keafer and Anderson*, [1993]).

an offshoot of remote sensing technology, the same automated buoys that will someday be searching for HAB cells using molecular probe technology can also be measuring the physical and optical characteristics of the water column to provide the complementary information needed to make "algal forecasts" of impending toxicity.

Models. Models of dinoflagellate blooms have been developed from several different perspectives. [*Kamykowski*, 1979, 1981] examined the response of a swimming dinoflagellate to internal waves and showed that accumulation of motile and non-motile cells may occur due to an internal wave field, with the accumulation of vertically migrating cells being most significant. These models consider only the physics of the wave field and the swimming behavior of the phytoplankton, without regard to the phytoplankton response to nutrients or light. Others have examined the response of phytoplankton to the flow field of Langmuir cells [*Evans and Taylor*, 1980; *Watanabe and Harashima*, 1986] or to 2-dimensional, cross-frontal circulation [*Franks*, 1992], to name just two of many physical systems that have been studied in this theoretical context.

The growth and accumulation of individual harmful algal species in a mixed planktonic assemblage are exceedingly complex processes involving an array of chemical, physical, and biological interactions. Our level of knowledge about each of the many HAB species varies significantly, and even the best-studied remain poorly characterized with respect to bloom or population dynamics. Resolution of various rate processes integral to the population dynamics (e.g., input and losses due to growth, grazing, encystment, excystment, and physical advection) has not been accomplished, but is fundamental to the long-term management of fisheries resources or marine habitats affected by harmful algae. Many of the processes are difficult to quantify in the field because harmful species are often only a small fraction of the biomass in natural samples. The end result is that despite the proven utility of models in so many oceanographic disciplines, there are no predictive models of population development, transport, and toxin accumulation for any of the major harmful algal species in the United States. There is thus a clear need to develop realistic physical models for regions subject to HAB events, and to incorporate biological behavior and population dynamics into those simulations.

The primary method for exploring the details of the interactions of HAB populations with coastal circulation should be through the incorporation of biological and physical field data into circulation models. The physical dynamics of the model can be constrained by the equations used to describe the flow and by physical data gathered in field programs. Numerical experiments can then examine the distribution and fate of cells under a variety of forcing mechanisms. HAB cells can initially be treated as passive tracers, but it will most likely be necessary to include factors such as grazing or physiological adaptation in the models to accurately simulate observed cell distributions. It should then be possible to show, for instance, under what conditions directed swimming behavior will cause cell accumulation and blooms, or to evaluate the relative importance of physical losses (advection, sinking) and biological losses (grazing, cyst formation) in bloom termination. The flexibility of such models allows certain aspects of the field data to be explored in a way that would be impossible through direct sampling. Another advantage is that the behavior and physiology of a single HAB species can be better understood and simulated than that of an entire community. This is an area long neglected in HAB research, and one that should be strengthened in the coming years. The insights to be gained from modeling studies will do much to advance our general understanding of the dynamics and consequences of HABs.

Management Issues. The ultimate of goal of much of the ongoing HAB research in the U.S. is to generate the scientific information needed for effective management of fisheries resources and the public health in regions where natural marine biotoxins of algal origin can occur. Many of the investigations mentioned above are making excellent progress towards this goal. Monitoring programs for HAB species and for their toxins will likely change dramatically in the coming years as remote sensing (in the broadest sense of the term) and automation provide real-time data. Likewise, coupled physical/biological models will be used to predict the effects of changes in wind forcings, rainfall, or other meteorological variables that are measured routinely for other purposes. Site selection for fish farms and other aquaculture facilities will become more quantitative, based on observed and simulated cell distributions or on toxicity patterns revealed by geographic information systems. Ocean engineers will have important roles to play as well, as aquaculture facilities will need to be re-designed to function in higher-energy coastal environments where the probability of HABs is lower than in sheltered, quiescent systems.

Program and Policy Issues. At the national level, a new era has begun with respect to HAB programs and policies. In the past, no single federal agency had assumed a leadership role in coordinating and supporting the studies needed to optimize management and mitigation strategies, and research funding has been sporadic and limited. Now, in response to heightened public and governmental awareness of the growing problems in seafood safety and the changing nature of the coastal marine environment, more funding is being targeted on marine biotoxins, harmful algae, and their impacts. Recognizing that the optimum allocation of these resources can benefit greatly from scientific guidance as new programs are formulated and implemented, the National Marine Fisheries Service, the National Science Foundation, and several NOAA programs have joined with the academic community in an effort to develop a national consensus on directions and priorities. The first step was the publication and widespread distribution of *Marine Biotoxins and Harmful Algae: A National Plan*, [*Anderson et al.*, 1993]. This report identified numerous impediments to progress and issued a series of recommendations to accomplish the goal of assuring the safe consumption of seafoods through the prediction, control, and mitigation of the effects of HABs on the marine biota of the United States. The list of impediments identified at the *National Plan* workshop is diverse and long.

The rate and extent of progress from here will depend in large part on how effectively the recommendations in the *National Plan* are implemented. State and federal agencies are already using the document to identify topics that relate to their particular responsibilities or purviews, and scientists and private industry are using those ideas to guide their activities as well.

No single agency can address all of the identified impediments, but most can be covered by the combined efforts of several organizations. For this reason, an *ad hoc* Interagency Task Force on Marine Biotoxins and Harmful Algae has been created, consisting of program managers and other high-level officials from federal agencies and programs with interests or responsibilities in HAB issues. This task force meets several times a year to discuss new developments in the field and to coordinate activities and initiatives. A framework for national action has thus been established and the network created to implement it. Concerted efforts will be necessary to keep the lines of communication and coordination open, but the momentum is there to sustain support for fundamental scientific investigations of an oceanographic phenomenon that is of great practical importance to society.

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