CELEBRATING 50 YEARS OF THE
INTERGOVERNMENTAL OCEANOGRAPHIC COMMISSION

BY DONALD M. ANDERSON,
BEATRIZ REGUERA, GRANT C. PITCHER,
AND HENRIK O. ENEVOLDSEN

The IOC International Harmful Algal Bloom Program

HISTORY AND SCIENCE IMPACTS

ABSTRACT. Harmful algal blooms (HABs) have become an important subdiscipline within oceanography. Heightened attention to this topic as well as significant research advances reflect the global nature of the problem and the development of strong national and international programs for HAB research and management. The planning, communication, coordination, and capacity-building activities of the Intergovernmental Oceanographic Commission (IOC) have been a key factor in this growth. Here, we highlight selected advances in science and management capacity for HABs and document the impressive growth of the field in the context of activities supported directly or indirectly by IOC. As we look to the future, the field has significant momentum and stability. Nevertheless, it will require scientific guidance and coordination going forward. With an appropriate commitment of resources from member states, the IOC HAB program can continue to be a major factor in the sustained growth of this important scientific discipline and its delivery of improved observation and management systems.

Figure 1. HABs and their impacts. (A) A visible red tide of *Noctiluca*, a nontoxic dinoflagellate that can cause damage when the high cell biomass in blooms of this type decay and deplete oxygen, leading to mortality in bottom waters or shallow areas. These cells produce ammonia, which is also thought to contribute to marine mortality events. (B) A closure sign prohibiting all shellfish harvesting due to an algal biotoxin. (C) A dead sea lion linked to consumption of domoic acid, the amnesic shellfish poisoning (ASP) toxin. (D) A "bloom" of a seaweed overgrowing a coral reef. Negative impacts include shading and alteration of habitat and food web, and thus this is considered a HAB. *Images courtesy of M. Godfrey (A), Judy Kleindinst (B),* Five Cities Gazette *(C), and Brian LaPointe (D)*

BACKGROUND

Virtually every coastal country in the world is affected by harmful algal blooms (HABs, commonly called "red tides"). Many of these phenomena are caused by blooms of microscopic algae or phytoplankton, although the term also applies to blooms of macroalgae (seaweeds), which cause impacts such as the displacement of indigenous species, habitat alteration, and oxygen depletion. Some phytoplankton species are toxic; their blooms cause illness and death in humans, fish, seabirds, marine mammals, and other oceanic life, often as a result of toxin transfer through the food web (Figure 1). Six human poisoning syndromes are caused by consumption of seafood contaminated by HAB toxins: amnesic shellfish poisoning (ASP), ciguatera fish poisoning (CFP), diarrhetic shellfish poisoning (DSP), neurotoxic shellfish poisoning (NSP), paralytic shellfish poisoning (PSP), and azaspiracid shellfish poisoning (AZP). Other threats to human health are posed by toxic aerosols and water-borne compounds that cause respiratory and skin irritation.

Sometimes the direct release of compounds that are, strictly speaking, not toxins (i.e., reactive oxygen species, polyunsaturated fatty acids, mucilage) can be lethal to marine animals. Nontoxic HABs cause damage to ecosystems, fisheries resources, and recreational facilities, often due to the biomass of the accumulated algae that can shade other plant species, or decay and deplete oxygen.

The nature of the HAB problem has changed considerably over the last several decades, in part because of an actual expansion in events and impacts, but also because we are better able to perceive the true scale of the problem. The number of toxic blooms, the resulting economic losses, the types of resources affected, and the number of toxins and toxic species reported have all increased dramatically (Figure 2; Anderson, 1989; Hallegraeff, 1993). Some of this expansion may be attributed to natural events, as well as to heightened and more effective scientific attention to the problem, but human activities are also implicated. Increased exploitation of the coastal environment has contributed through the transport of HAB species in ballast water and imports of live shellfish; by the release of industrial, agricultural, and sewage effluents to coastal waters; and by the restriction of water circulation with new harbors and dams. The steady expansion in fertilizer use for agriculture represents a large and worrisome source of nutrients that promote high biomass HABs (Anderson et al., 2002; GEOHAB, 2006).

The diversity in HAB species and their impacts present a significant challenge to those responsible for management of coastal resources. HABs are complex oceanographic phenomena that require multidisciplinary study, ranging from molecular and cell biology to large-scale field surveys, numerical modeling, and remote sensing. Our understanding of these phenomena is increasing dramatically, and IOC's International Harmful Algal Bloom Program has been central to this progress.

PROGRAM DEVELOPMENT

Thirty years ago, HAB science was primarily the province of a few individuals working with algal taxonomy, toxin chemistry, and phytoplankton ecology. An established research community did not exist, nor were there significant multidisciplinary research programs. Expertise was scattered nationally and globally, and not only were there major gaps in scientific coverage, but some topic areas such as taxonomy were in decline. Only a few countries had well-established monitoring and management programs for toxic shellfish or fish, and few governmental or nongovernmental organizations had the issue on their agendas.

The earliest effort to coordinate HAB activities on a regional level was through the International Council for the Exploration of the Seas (ICES), which in 1984 held a special meeting on the causes of exceptional algal blooms and further established a Working Group on Phytoplankton and Management of their Effects (WGPME; for convenience, this acronym, and others used in this document are listed in Box 1.) This group focused on the morphological and toxicological descriptions of the causative species, on the compilation of HAB events in the ICES realm, and on recommendations for procedures to monitor HABs and their toxins. In 1991, the name and focus of the group changed as IOC joined as a co-sponsor. The need for a population dynamics approach to the study of HABs became a top priority, and as a result, the ICES-IOC Study Group on Harmful Algal Bloom Dynamics was established in 1991 and consolidated in 1993 as a working group (WGHABD), whose activities continue to date. The compilation of HAB events was maintained by WGHABD and led to the establishment of the IOC-ICES Harmful Algae Events Database (HAEDAT). The difficult dialogue among biologists, physical oceanographers, and modelers

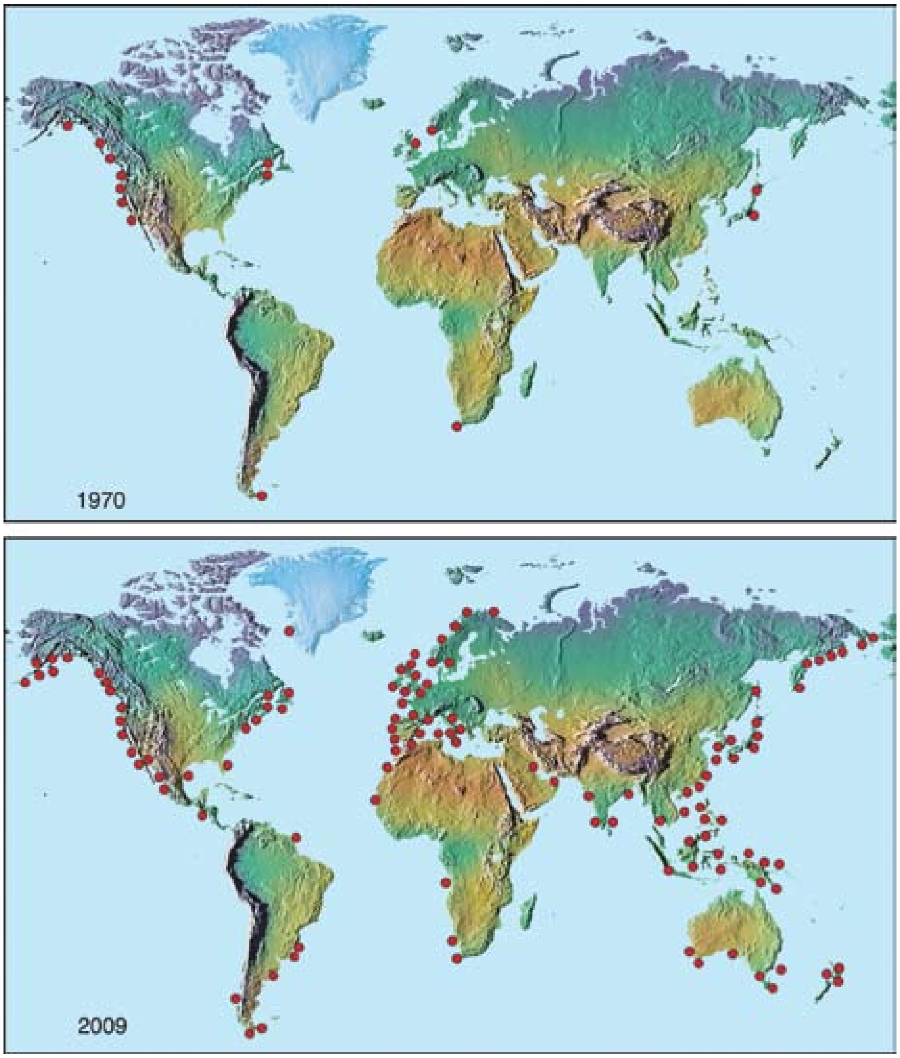

Figure 2. The global expansion in the distribution of PSP toxins–1970 compared to 2009. Red circles denote locations with documented measurements of PSP toxins in shellfish, fish, or plankton samples. *US National Office for Harmful Algal Blooms, Woods Hole Oceanographic Institution, Woods Hole, MA*

was encouraged through joint meetings of WGHABD and the working groups on Shelf Seas Oceanography (WGSSO) and Physical-Biological Interactions (WGPBI).

Another milestone was the 1987 International Symposium on Red Tides held in Takamatsu, Japan, as it was the first with co-sponsorship from multiple governmental and nongovernmental organizations, reflecting recognition of the issue at many levels of society. This meeting has been followed by a series of international conferences on HABs, with the fourteenth in the series scheduled for Crete later this year. The IOC HAB program has been a major participant in the planning of many of these meetings, as well as in the publication of the conference proceedings.

The Takamatsu meeting was followed by an IOC workshop on international cooperation in the study of "red tides and ocean blooms." This activity, which was critical in the eventual formulation of the IOC HAB program, was motivated by the IOC Assembly earlier that year, which noted that the Commission had the mandate and position "to take the lead in developing an overview of relevant research, to formulate research strategies for a global program on harmful algae and to identify major research topics."

Early in 1990, IOC co-sponsored the work of an ad hoc group of experts on HABs that met in Paris to formulate an international program based on the recommendations of the Takamatsu workshop. This was also the time that the term "harmful algal bloom" was formally adopted as a substitute for "red tides" in order to include any algal proliferation (regardless of cell concentration) that was perceived as a nuisance because of negative impacts on ecosystems or human resources.

The draft plan was endorsed during IOC's 14th assembly in 1987 and fully elaborated at an IOC-SCOR workshop in Rhode Island in 1991. That workshop provided the final focus for IOC efforts and formulated the overall goal of the International HAB Program:

Donald M. Anderson *(danderson@whoi.edu) is Senior Scientist, Woods Hole Oceanographic Institution, Woods Hole, MA, USA.* **Beatriz Reguera** *is Researcher, Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Vigo, Spain.* **Grant C. Pitcher** *is Marine Scientist, Marine and Coastal Management, Rogge Bay, Cape Town, South Africa.* **Henrik O. Enevoldsen** *is IOC Project Coordinator, IOC Science and Communication Centre on Harmful Algae, Department of Biology, Botanical Institute, University of Copenhagen, Copenhagen, Denmark.*

> *To foster and organize the management and scientific research of Harmful Algal Blooms in order to understand the causes, predict the occurrences, and mitigate the effects.*

To govern the new program and identify priorities and required resources, IOC and FAO established an Intergovernmental Panel on Harmful Algal Blooms (IPHAB), which met in 1992 with 14 nations participating. Today, 43 nations and organizations are members of IPHAB, which has met nine times thus far. The existence of an intergovernmental mechanism for HABs has clearly raised the visibility and awareness of the issue at the national and global levels, and has led to major advances in both outreach and science. One important development was establishment of the IOC Science and Communication Centers on Harmful Algae in Denmark and Spain. These centers have proven to be important nodes of expertise in the development and coordination of international collaboration and networking on HABs.

One major requirement identified by IOC member states was training and capacity building. Since the inception of the International HAB Program, IOC has run (often through co-sponsorship) many workshops on HAB species identification, toxin detection, and monitoring and management. Over the past 20 years, IOC has by itself or with partners organized more than 60 training courses in species identification, toxicity testing, and monitoring and management strategies. Emphasis has been in the regions most unprepared to meet HAB impacts, such as Southeast Asia and Latin America, but the need for upgraded skills has been global and systematic.

Another significant training activity has been through the IOC subcommission for the western Pacific (WESTPAC) and related bilateral projects, led by Yasuwo Fukuyo of the University of Tokyo. Since the 1980s, he and his coworkers have initiated training in HAB monitoring and species identification in Southeast Asia, exhibiting a strong commitment to the region, leading to the inclusion of HABs on the agenda of the UNEP Regional Seas Programme for the North West Pacific.

One noteworthy accomplishment under the category of outreach and training is the publishing of IOC manuals on HABs. The first was issued in 1995 (Hallegraeff et al., 1995), and a revised version in 2003 (Hallegraeff et al., 2003). The latter provides nearly 800 pages of material covering all aspects of the methods used for HAB research and monitoring.

Another scientific accomplishment derived from IPHAB is the establishment of national or regional research programs. One example is the ECOHAB (Ecology and Oceanography of Harmful Algal Blooms) program in the United States. The idea for this program was raised during an IPHAB session on international cooperation in HAB science. Recognizing that it made little sense to discuss participation in an international science program when there was no national program in the United States at the time, the US delegation returned to

BOX 1. ACRONYMS FOR HAB PROGRAMS AND ORGANIZATIONS

ASP	Amnesic Shellfish Poisoning
AZP	Azaspiracid Shellfish Poisoning
CEOHAB	Chinese Ecology and Oceanography of Harmful Algal Blooms
CFP	Ciguatera Fish Poisoning
CRP	Core Research Project
DSP	Diarrhetic Shellfish Poisoning
ECOHAB	Ecology and Oceanography of Harmful Algal Blooms Program (US)
EUROHAB	European Science Initiative on Harmful Algal Blooms (EU)
FAO	United Nations Food and Agricultural Organization
GEOHAB	Global Ecology and Oceanography of Harmful Algal Blooms
GOOS	Global Ocean Observing System
HABs	Harmful Algal Blooms
HAEDAT	IOC-ICES-PICES Harmful Algae Events Database
ICES	International Council for Exploration of the Seas
IOC	Intergovernmental Oceanographic Commission of UNESCO
IPHAB	IOC Intergovernmental Panel on Harmful Algal Blooms
NATO	North Atlantic Treaty Organization
NSP	Neurotoxic Shellfish Poisoning
PSP	Paralytic Shellfish Poisoning
SEED	EU-NSF project on HAB life history stages
SCOR	Scientific Committee on Oceanic Research (International Council for Science)
UNEP	United Nations Environment Program
WGHABD	ICES-IOC Working Group on Harmful Algal Bloom Dynamics
WGPBI	ICES Working Group on Physical-Biological Interactions
WGPME	Working Group on Phytoplankton and Management of their Effects
WGSSO	ICES Working Group on Shelf Seas Oceanography
WESTPAC	IOC subcommission on the Western Pacific

America and organized the workshop that developed the ECOHAB Science Agenda (Anderson, 1995) that has guided that program through more than a decade of highly productive research. Nearly $100M has been awarded to date. ECOHAB has been emulated by other regional or national programs with a similar focus—including EUROHAB for the EU (Granéli et al., 1999), and CEOHAB in China (Zhou et al., 2008).

With respect to facilitation of HAB science, IOC joined with the Scientific Committee on Oceanic Research (SCOR) in sponsoring a Working Group on the Physiological Ecology of Harmful Algal Blooms, leading to a NATO-funded Advanced Study Institute in 1996 (Anderson et al., 1998). In the late 1990s, IOC formed a new partnership with SCOR to develop a coordinated international scientific program on the ecology and oceanography of HABs. GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms) was thus formed to foster international cooperative research on HABs in ecosystem types that share common features (GEOHAB, 2001). The GEOHAB goal of improved prediction was to be achieved through a better understanding of the critical features and mechanisms underlying the dynamics of HAB species in a variety of oceanographic regimes, using a comparative approach.

Central to the implementation of GEOHAB was the establishment of Core Research Projects (CRPs), which were intended to facilitate comparative studies within specified ecosystems, through oceanographic field studies supported by observation and modeling activities (GEOHAB, 2003). CRPs related to four ecosystem types—upwelling systems, fjords and coastal embayments, eutrophic systems, and stratified systems—were initiated through Open Science Meetings (GEOHAB, 2005, 2006, 2008). A fifth CRP on Benthic HABs will be initiated at an Open Science Meeting in 2010.

In addition to CRPs, GEOHAB encourages targeted research projects to address specific objectives in the science plan. For example, a workshop on Real-Time Coastal Observing Systems for Ecosystems Dynamics and Harmful Algal Blooms was held in 2003 in response to a resolution by ICES-IOC WGHABD and endorsed by GEOHAB. The monograph on this workshop (Babin et al., 2008) details the theory, instrumentation, and modeling requirements for HAB detection and prediction. Fundamental to prediction is the continued development of models, and in response to this requirement, GEOHAB convened a GEOHAB Modeling Workshop in 2009. This workshop was intended to energize the interface between models and observations in HAB research, building on what has been learned in the broader fields of physical-biological interactions and plankton ecosystem modeling. Papers from this workshop will be published in a special issue of *Journal of Marine Systems.*

SCIENCE PROGRESS

In the context of this retrospective examination of IOC's role in the development of the International HAB Program, it is instructive to demonstrate how far HAB science has advanced over the last several decades. Clearly, not all of this progress can be attributed to the HAB program, yet without doubt, IOC/ICES/SCOR working groups, workshops, and open science meetings promoted discussion, exchange of ideas, and inspiration for national and regional research proposals that followed. Further, the international recognition that the field has achieved through IOC involvement has led to improved visibility and funding opportunities for scientists in many countries, thereby contributing to the advances described below.

System-Based Studies

Several studies of HABs within particular ecosystems have been particularly successful in advancing our knowledge on the ecology and oceanography of HABs. Well-documented cases include investigation into blooms of *Karenia brevis* within the Gulf of Mexico (Walsh and Kirkpatrick, 2008) and of *Alexandrium fundyense* blooms in the Gulf of Maine (Anderson et al., 2005b). More recent examples of system-based studies include those HABs in upwelling regions, in fjords and coastal embayments, in stratified systems, and in eutrophic systems, as facilitated by GEOHAB and detailed below.

HABs in Upwelling Systems

Several comparative research projects have been initiated within major eastern boundary upwelling systems in order to compare ecosystems of similar function. GEOHAB extended this approach to the study of HABs (GEOHAB, 2005). Unlike many other ecosystems impacted by HABs, upwelling systems are dominated by a common set of physical parameters and are likely to respond similarly, regardless of locale (Kudela et al., 2005).

Much of our current understanding of HABs in upwelling systems is synthesized in a special issue of *Progress in Oceanography* (Pitcher and Pillar, 2010). Upwelling systems are susceptible to HABs largely as a result of their high productivity and the consequent high-

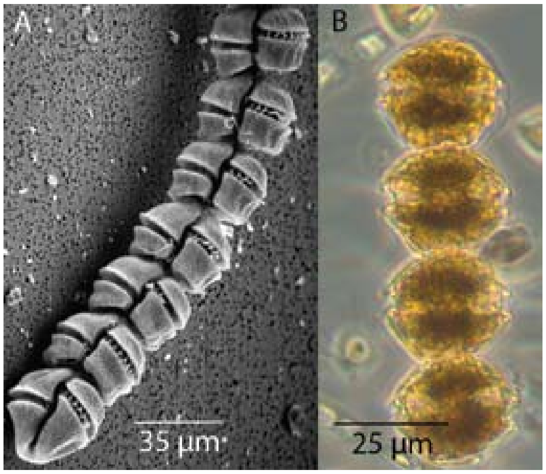

Figure 3. The two chain-forming species, (A) *Gymnodinium catenatum* and (B) *Alexandrium catenella*, are the primary causes of paralytic shellfish poisoning in upwelling systems. These chains increase swimming speed, a property previously considered to favor these species during periods of downwelling (Fraga et al., 1989). However, the general underrepresentation of chain-forming species in upwelling systems indicates that the complex habitat mosaic within these systems provides growth opportunities to a variety of life forms (Smayda, 2010b). *Photos courtesy of (A) C.J. Bolch and G.M. Hallegraeff and (B) A. Reñe*

biomass blooms that characterize the shelf environment. Although the vast majority of HAB species in upwelling systems are dinoflagellates, there is no HAB flora unique to these systems (Smayda, 2010a), and there are notable inconsistencies in the presence and impacts of HAB species among the major upwelling systems (Trainer et al., 2010). Common biophysical adaptations of HAB species to the conditions associated with upwelling systems are not evident; rather, the mosaic of habitats offers growth opportunities to a variety of dinoflagellate life forms. Even the added swimming power that dinoflagellates gain through chain formation (Figure 3) does not appear to provide an advantage in their selection or success in upwelling systems, as was once proposed (Fraga et al., 1989; Smayda, 2010b). Also, in contrast to previous thinking, upwelling HABs exhibit a moderate to high affinity for nitrate, with a capacity to utilize several forms of nitrogen. The clear linkage between nutrient availability and supply, and the physical dynamics of upwelling systems, indicates the critical need to understand the nutrient ecophysiology of HAB species in attempting to predict HAB events in these environments (Kudela et al., 2010).

The timing of HABs in upwelling systems is controlled by wind-stress fluctuations and buoyancy inputs at seasonal, event, and interannual scales (Pitcher et al., 2010). HABs are especially prominent in nearshore areas, where changes in coastline configuration and orientation, and bottom topography determine the distribution of HABs through their influence on water stratification and retention. Studies of wind forcing have revealed complex patterns of interaction with coastal topography in ways that are being coupled to increasingly realistic ocean models that can be used to simulate the complex three-dimensional structure of coastal flow and the corresponding changes in the physical properties of water. Equations describing the transport and fate of constituents in the water, such as HABs, can be coupled to the equations of these hydrodynamic models. Future linkage to the observation and modeling activities of the coastal module of the Global Ocean Observing System (GOOS) is therefore likely to result in improved management of HABs in upwelling systems through better detection and prediction.

HABs in Fjords and Coastal Embayments

Within the international research framework of GEOHAB (GEOHAB 2001, 2003), a spectrum of coastal embayments (including fjords), characterized by different water retention times and bathymetries, are being identified as sites for detailed comparative studies on the physical, chemical, and biological factors that affect HABs (GEOHAB, 2010). Embayments are typically zones of high primary productivity and biodiversity and often serve as spawning areas, nurseries, or refuges for key populations of fish and invertebrates (Valiela, 1991). Embayments are often focal points of land-sea margins and are therefore particularly vulnerable to anthropogenic influences driven in many cases by terrigenous runoff and sediment transport. Owing to the geomorphological and hydrodynamic constraints within embayments, dilution is restricted. Such systems are therefore specifically susceptible to eutrophication, which is often considered to promote HAB development. Other anthropogenic changes more likely to occur in embayments result from the introduction of exotic species either from shipping activities or the transfer of aquaculture stock.

Coastal embayments may be broadly defined as enclosed or semi-enclosed aquatic environments along a landmass margin, characterized by diverse hydrodynamic regimes, determined often by the varying degree of physical isolation from the open coastal environment. The physical constraints imposed by fixed land boundaries and embayment bathymetry dictate increasing importance of small-scale processes in defining water circulation within these systems. Subcategorization of coastal embayments with respect to the effects of basin morphology on water exchange and retention, and their influence on HAB dynamics, is considered a useful approach. Therefore, descriptions of horizontal circulation patterns, the magnitude and frequency of water exchange with the open coast, the mechanisms of vertical stratification, and the distribution of turbulent energy in response to external forcing generated by wind, tides, and freshwater input are central to the study of HAB dynamics in coastal embayments (GEOHAB, 2010).

The role of benthic-pelagic coupling in HAB dynamics is of specific importance in embayments. The reduced depth of embayments compared to open coastal environments provides increased likelihood of the benthos serving as a possible source of seed material for pelagic blooms, whereas the contribution of benthic grazers to the control of phytoplankton biomass is also considerably greater within a bay environment. A further contribution of embayments' shallow benthic environments is the provision of suitable substrates for colonization by toxic epiphytic dinoflagellates, thereby providing sites of toxicity associated with ciguatera fish poisoning in the tropics and diarrhetic shellfish poisoning in temperate embayments.

HABs in Stratified Systems

A feature of some HAB events is that populations accumulate in subsurface layers in stratified waters. These dense populations may then be advected to the coast where they cause harm. Stratified water columns are encountered in upwelling systems, fjords, and coastal embayments and eutrophic systems; thus, HABs in Stratified Systems was identified as a crosscutting GEOHAB project (GEOHAB, 2003). HABs in thin layers (TLs) is an extreme case of HAB layering, where congregations of plankton are only a few tens of centimeters to a few meters in vertical thickness, although they may extend horizontally for kilometers. Until recent years, these structures were detected either by chance—an oceanographic bottle cast at the right time and place—or by divers. TLs of phytoplankton can be defined by cell numbers, chlorophyll concentrations, and other biological parameters; they must have a minimum spatial coherence horizontally, be less than 3-m thick, and the magnitude of the property must be significantly higher (> 5 times) than background (Sullivan et al., 2010).

The temporal and spatial scales of TLs pose problems for sampling and modeling. The coupling of physical effects (turbulence, shear, advection) to biological behavior (migration, physiological adaptation) holds the key to understanding vertical distributions, bloom dynamics, and toxicity patterns. Advances in sophisticated observing instruments with high vertical resolution and in situ processing are leading to rapid progress in this field (Babin et al., 2008; GEOHAB, 2008). Key questions are: (1) are HABs in TLs passive accumulations of cells driven by physical factors, or rather do they result from active congregations of swimming flagellates? and (2) what are the mechanisms that control TL initiation, maintenance, and dissipation?

These extraordinary concentrations of cells have important implications for HAB growth dynamics, predator-prey interactions, life history transitions, and allelopathy. Advantages include: (1) selection of optimum depth (i.e., in the upper part of the nutricline) where conditions are most suitable for cell growth, and (2) the effects of toxins, allelopathic substances, or grazer deterrents are multiplied, and the probability of sexual encounters increased. Thin layers of domoic acid producers *Pseudo-nitzschia* spp., often located in the base of the pycnocline, have been well described in East Sound (Washington, United States; Rines et al., 2002) and in the Galician Rías (Northwest Spain) where they are formed during relaxation periods in the upwelling season, and coexist with TLs of toxigenic *Dinophysis* spp. aggregated around the diurnal thermocline (Figure 4; Velo-Suárez et al., 2008).

A particular case of HABs in TLs is that of mucilage-forming blooms. These blooms can disrupt artisanal fisheries, cause mortalities of benthic resources, and depress revenues from tourism. Diatom blooms, harmless in most systems, may at times and places (e.g., in the Adriatic Sea) exude large quantities of polysaccharides that, once established in the pycnocline, trap sinking organic matter, including materials that enhance mucilage persistence. Some dinoflagellate species, such as *Gonyaulax hyaline/fragilis* (e.g., MacKenzie et al., 2002), are known to secrete large amounts of mucilage in culture and have been identified as the major cause of massive production of mucilage at some events in New Zealand and the Mediterranean Sea. Mucilage formation can be a form of bioengineering or manipulation of the physical environment, for example, to regulate rates of turbulent diffusion, such as by the naked dinoflagellate *Karenia mikimotoi*. In any case, mucilage outbreaks formed by phytoplankton populations that have been linked to high N/P ratios, and whose frequency in the Mediterranean Sea has been attributed to increased stratification (Danovaro et al., 2009), constitute a microcosmic layer where complex microbial interactions take place.

HABS in Eutrophic Systems

Increased nutrient loading from human activities is considered to be one of the multiple reasons that HABs have been expanding in frequency, duration, and harmful properties (Anderson, 1989; Hallegraeff, 1993; GEOHAB, 2006). A Core Research Project on HABs in Eutrophic Systems was therefore established within GEOHAB to further investigate the extent to which increased eutrophication influences the occurrence of HABs and their harmful effects.

Worldwide, strong relationships have been observed between increases in nutrient loading and proliferations of specific types of HABs, and recent advances in our understanding of the physiology of these organisms has yielded important insights as to why these algae respond so favorably to these nutrients (GEOHAB, 2006). To further advance our knowledge on the role of eutrophication in HAB proliferation, the comparative approach of GEOHAB was considered highly beneficial in that it provides the ability to compare gradients of responses and differential HAB occurrences within systems subjected to varying degrees of eutrophication (GEOHAB, 2006).

Many of the recent advances in our understanding of HABs in eutrophic systems are synthesized in a special issue of *Harmful Algae* (Glibert et al., 2008). Within this publication, Heisler et al. (2008) provide a scientific consensus on the relationship between eutrophication and HABs. They conclude that: (1) degraded water quality from increased nutrient pollution promotes both the development and persistence of HABs, (2) both the composition and total quantity of the nutrient pool are important in HAB development, (3) exogenous nutrients are required to sustain high-biomass blooms, (4) both chronic and episodic nutrient delivery may promote HABs, (5) recently developed tools and techniques will allow advancement toward operational status for the prediction of HABs in eutrophic systems, (6) experimental studies are required to further understand the role of nutrients in the expression of HABs, and (7) the management of nutrient inputs to the watershed can lead to significant reduction in HABs.

Historically, the conceptual understanding of HABs in eutrophic systems has been based on the simplistic notion that more nutrients yield higher algal biomass. However, there is now a greater appreciation for the interactive influences of the composition and relative proportional availability of nutrient pools, the range of physiological responses by different phytoplankton, and the interactions of other dynamic factors such as physics and grazing in controlling responses to cultural eutrophication by HAB and other algal populations (Glibert et al., 2008).

Genetics and Taxonomy

For many years, workers in the HAB field established unialgal cultures that were studied as representatives of regional populations. Due to the species-specific nature of HAB research, it soon became apparent that there was considerable heterogeneity within individual bloom populations in terms of toxicity, physiology, genetics, and behavior (e.g., Scholin et al., 1994; John et al., 2003). This realization, in turn, led to conflicts with traditional taxonomic approaches to defining population structure. For example, phylogenetic studies used genetic markers such as rRNA to group isolates into clades, but many of these clades did not coincide with groups established on the basis of morphology. A prominent example is the *Alexandrium tamarense* species complex, in which isolates belonging to the same morphospecies cluster into multiple phylogenetic clades using rRNA sequences (Scholin et al., 1994; Lilly et al., 2007). This example has called into question the morphological criteria used for species definitions,

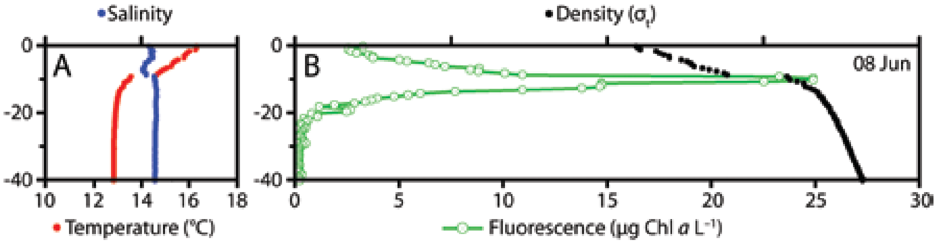

Figure 4. High-resolution (Ifremer Particle Profiler) vertical profiles of temperature and salinity (A) and a thin layer of domoic acid-producers *Pseudo-nitzschia* spp. (B) in a Galician ría (estuary) in northwest Spain during relaxation between consecutive upwelling pulses. Vertical displacement of these layers during downwelling leads to fast accumulation of domoic acid (above regulatory levels) in bottom shellfish (scallops, razor clams) before detection in suspended raft mussels. *Modified from Velo-Suárez et al. (2008)*

and led to reevaluation of the "species concept" in the context of HAB populations. In contrast, rRNA sequencing has not proven to be very useful for specific discrimination within the genus *Dinophysis*, so additional genetic markers need to be explored for that purpose (Jensen and Daugbjerg, 2009). One of the arguments proposed by HAB workers has been that morphology-based species designations can sometimes be of little use for ecological purposes (e.g., Beam and Himes, 1982; Brand, 1991; Anderson et al., 1994).

Consistent with the GEOHAB goal of comparative analysis of species distributed globally, this line of investigation turned to hypervariable microsatellite markers as a new tool to explore population genetics. This approach provides extraordinary resolution, allowing workers to identify individuals and subpopulations in much the same way that our eyes distinguish individuals and races of humans. The resolution of this technique was recently demonstrated by Massaret et al. (2009), who examined strains of *Alexandrium catenella* and revealed relationships that were not apparent from rRNA studies on the same group. In particular, Mediterranean populations previously thought to have been introduced by ballast water discharges from Asia (Lilly et al., 2002) were shown to be a distinct lineage, and therefore other origins must now be explored. This analysis highlights intraspecific diversity that was not detected with classical rRNA gene markers and demonstrates that microsatellites are well suited to investigations of the population genetics of globally distributed HAB species.

Nutrition and Physiology

There is increasing evidence of mixotrophy (the combination of autotrophic and heterotrophic nutrition) in many HAB species, which increases their flexibility under changing environmental conditions (e.g., Jeong et al., 2007). A good example is the *Dinophysis* spp. responsible for DSP outbreaks worldwide. After numerous failed attempts to establish these species in culture for over a decade, *D. acuminata* was recently grown successfully with the ciliate *Mesodinium rubrum* as food, the latter fed in turn with the cryptophyte *Teleaulax* (Park et al., 2006). Advances in molecular biology (the three species in the food web share a common plastid sequence) and their common pattern of orange autofluorescence were key factors in this achievement. Well-fed specimens in culture can survive months without prey. Therefore, field populations, intermittently feeding on their ciliate prey, can persist for months and cause prolonged closures of shellfish harvesting (González-Gil et al., 2010).

Dinophysis spp. is also a good example of regional intraspecific variation in toxin production. A few hundred cells per liter are sufficient to contaminate shellfish with DSP toxins above regulatory levels in Western European waters, whereas concentrations at least two orders of magnitude higher are required in southeastern US oysters (Swanson et al., 2010). Whether these differences are genetic or reflect modulation by environmental conditions needs to be ascertained.

Some HAB species perform diurnal vertical migration and can thus reach deeper, nutrient-rich waters at night. These species must somehow be able to take up nutrients and store them for use when light is available for photosynthesis. However, when stratification is more pronounced, species like *K. mikimotoi* stop migrating and remain within the pycnocline (Gentien, 1998) at a depth where a trade-off between nutrient availability (fluxes from below the pycnocline) and light exists. A single species may be able to switch behavior patterns from migrating to layer forming during different nutritional modes and/or stages of population growth (GEOHAB, 2008).

Many HAB species exhibit complex life cycles with multiple morphotypes and pathways that expand the tolerance range of the species and its geographical distribution. Some species, like *Alexandrium* spp. in the Gulf of Maine, rely on benthic resting cysts for the initiation of blooms, whereas other species (*Karenia* spp., *Dinophysis* spp.) adopt strategies that involve overwintering motile forms and aggregation during the growth season. The importance of life cycle transitions in the initiation and decline of HABs was the object of a GEOHAB-promoted workshop (LIFEHAB; Garcés et al., 2002) followed by a large EU-US project—known as SEED—the results of which have been reported in a special issue of *Deep-Sea Research Part II* (Garcés et al., 2010).

Cell Detection and Bloom Observations

HAB research and monitoring usually requires identifying and enumerating one or several species in plankton samples. Normally, this activity requires taxonomic expertise because identification is based on morphological characters that are often difficult to discern. Indeed, taxonomic training has been a major element of IOC HAB program outreach and education activities. However, sometimes toxic and nontoxic forms of the same species co-occur, and in many cases, HAB species of interest are present as only a minor component of the planktonic community. These challenges led to the development of a variety of new technologies that have revolutionized HAB research and management, meeting the GEOHAB goal of improved observational tools and strategies.

Two approaches are highlighted here. One uses optical characters unique to the target organism. A major success story in this regard is for *Karenia brevis*, the Florida red tide organism, which produces a pigment called gyroxanthin-diester. This carotenoid is sufficiently unique to be a useful biomarker for *K. brevis* and other potentially toxic *Karenia* species (Kirkpatrick et al., 2000; Richardson and Pickney, 2004). Instruments have been developed that quantify this pigment in water samples, and they have been mounted on research vessels (Kirkpatrick et al., 2003) and inside an autonomous underwater vehicle called *BreveBuster* (Figure 5; Robbins et al., 2006). This approach thus has great potential for the monitoring of HAB species that have this unique pigment, but for the vast majority of other species, alternative approaches to automated detection are needed.

A more broadly applicable approach involves the development of species- or strain-specific molecular "probes" that can label HAB cells of interest so they can be detected visually, electronically, or chemically. Progress has been rapid, and probes and assays of multiple types are already available for many of the HAB species. The most promising of these techniques uses short pieces of synthetic DNA (probes or primers) that bind to complementary portions of those molecules in the target HAB species. These targets, typically ribosomal RNA,

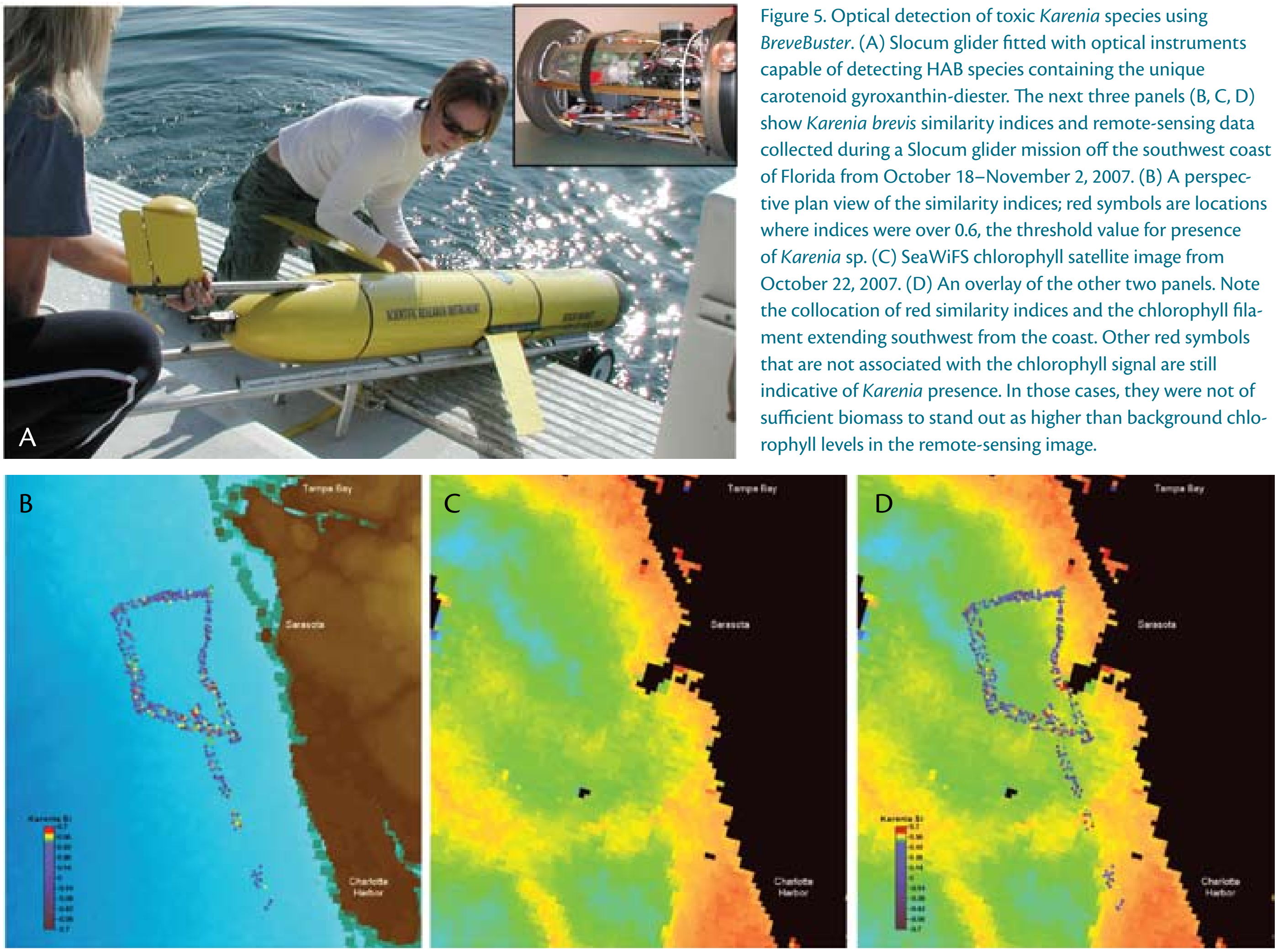

Figure 5. Optical detection of toxic *Karenia* species using *BreveBuster*. (A) Slocum glider fitted with optical instruments capable of detecting HAB species containing the unique carotenoid gyroxanthin-diester. The next three panels (B, C, D) show *Karenia brevis* similarity indices and remote-sensing data collected during a Slocum glider mission off the southwest coast of Florida from October 18–November 2, 2007. (B) A perspective plan view of the similarity indices; red symbols are locations where indices were over 0.6, the threshold value for presence of *Karenia* sp. (C) SeaWiFS chlorophyll satellite image from October 22, 2007. (D) An overlay of the other two panels. Note the collocation of red similarity indices and the chlorophyll filament extending southwest from the coast. Other red symbols that are not associated with the chlorophyll signal are still indicative of *Karenia* presence. In those cases, they were not of sufficient biomass to stand out as higher than background chlorophyll levels in the remote-sensing image.

can be visualized and/or quantified using a variety of techniques such as fluorescent in situ hybridization (FISH; Anderson et al., 2005a); sandwich hybridization assays (SHA; Scholin et al., 1996), and a variety of PCR-based assays (e.g., Penna and Magnani, 1999; Coyne et al., 2005; Bowers et al., 2006). These developments have reached the stage where the new molecular counting methods are routinely employed in major research programs, as well as in some monitoring programs (e.g., Rhodes et al., 2001; Anderson et al. 2005b; Haywood et al., 2009).

> “...THE IOC HAB PROGRAM CAN CONTINUE TO BE A MAJOR FACTOR IN THE SUSTAINED GROWTH OF THIS IMPORTANT SCIENTIFIC DISCIPLINE AND ITS DELIVERY OF IMPROVED OBSERVATION AND MANAGEMENT SYSTEMS.”

Given this rapid development, ICES-IOC WGHABD convened a workshop to intercalibrate these different molecular methods with traditional cell counting procedures (IOC, 2010). Seventeen different techniques (nine classical microscopic-based and eight molecular) were compared. The workshop highlighted the differences between methods and the difficulties in measuring the absolute, true target cell concentration in samples.

Modeling and Forecasting

Forecasting is a major goal of the IOC HAB program, and is central to GEOHAB. In the context of the foregoing discussion, the value of data from ocean observatories is greatly enhanced by numerical modeling techniques that can lead to forecasts of HAB transport and dynamics. A region in which HAB-specific instruments are deployed should therefore take steps to develop and validate numerical models of local HAB dynamics. The most advanced of these models are coupled physical-biological models that resolve a region's circulation and include biological components that simulate the bloom dynamics of a HAB species (McGillicuddy et al., 2003, 2005). These models are used predominantly in hindcast mode at present (i.e., in simulating past observations; He et al., 2008), but they are advancing rapidly toward operational use for short-term forecasts similar to those used for weather. The ultimate goal is to obtain data on HAB cells and toxins through instruments in an observatory system, assimilate these data and contextual meteorological and oceanographic observations into the models, and provide continually updated forecasts of bloom behavior. For many areas of the world, there are significant challenges to achieving this goal, as neither conceptual models nor numerical models exist for regional HAB problems.

Numerical models of blooms of HAB species span a large range of sophistication and validation. Some use remote sensing to detect blooms, with particle transport models then used to predict transport and landfall. This is the case in the Gulf of Mexico, where a forecasting system is now used operationally to detect *Karenia* blooms (Stumpf et al., 2003), and in the Great Lakes, where a similar approach is used for toxic cyanobacterial blooms (Wynne et al., in press). This capability is not easily transferred to other HABs, however, as the blooms must be dense and monospecific, which is not often the case.

One of the most complex physical-biological models is that used for *A. fundyense* bloom dynamics in the Gulf of Maine (McGillicuddy et al., 2005; He et al., 2008). Near-real-time nowcasts and forecasts have been run routinely each year since 2006 and made available to more than 150 managers and scientists involved with PSP outbreaks in the northeastern United States. Web interfaces provide the latest model simulations, with one-week forecasts driven by meteorological predictions. Forecasts have also been sent to researchers at sea to aid in sampling. In both 2008 and 2009, seasonal forecasts or advisories of regional bloom magnitude were issued based on model simulations initiated using large-scale maps of *A. fundyense* cyst abundance. In advance of each bloom season, the physical-biological model was used to make a seasonal forecast using a cyst abundance map obtained the winter before, as well as an ensemble of scenarios based on past weather and hydrographic conditions. Results were made available to resource managers and the public via press releases. This information was then used by resource managers to make staffing decisions in advance of the bloom and was seen by many as a major factor in the controlled and moderate response of the public and press to both outbreaks, which were indeed significant in size. Initial evaluation of the accuracy of the model simulations has been favorable (Figure 6).

A significant constraint to numerical model development is the need to identify initial conditions for the biological fields (i.e., HAB species distribution). In the Gulf of Maine, *A. fundyense* cyst abundance and distribution in bottom sediments are used as the initial condition for that model, with germination of those cysts producing the vegetative cells that ultimately grow and form the bloom (McGillicuddy et al., 2005). In other HAB systems, and in particular those without cyst populations, cell concentrations measured by instruments in an observing system may well provide the initial conditions for subsequent model runs and forecasts of bloom dynamics.

OUTLOOK FOR THE FUTURE

IOC showed admirable foresight and persistence in identifying HABs as an important and expanding societal problem and building an international program to address it. IOC's impact is evident in the enhanced management and science capabilities of many countries, as well as in effective international communication. The HAB scientific community is large and growing, with impressive scientific advances that benefit not only the HAB field, but oceanographic science in general.

As we look to the future, HABs will always be with us. Some large biomass blooms will be linked convincingly to pollution, possibly leading to policy decisions that reduce nutrient inputs and diminish blooms. Other HABs that are natural, with no human influence, will always occur, but their impacts will be managed and mitigated using both simple and sophisticated instruments and technology, from handheld monitors to networks of remotely deployed, robotic sensors. The latter will detect species and their toxins and send those data to shore, where they will be incorporated into numerical models and used for forecasts of bloom transport and longevity. We will also better understand the genetic heterogeneity that underlies all bloom populations, and begin to reveal the mechanisms that lead to the dominance of particular genotypes under a specific set of conditions, with clear implications for public and ecosystem health. This knowledge will be increasingly important, given the possible expansion of HABs or their movement to new areas as a result of global climate change.

This vision is only part of what we can expect, and it is indeed ambitious, but the field has significant momentum and stability, so it is not unrealistic. Nevertheless, it will require scientific guidance and coordination going forward. With an appropriate commitment of resources from member states, the IOC HAB program can continue to be a major factor in the sustained growth of this important scientific discipline and its delivery of improved observation and management systems.

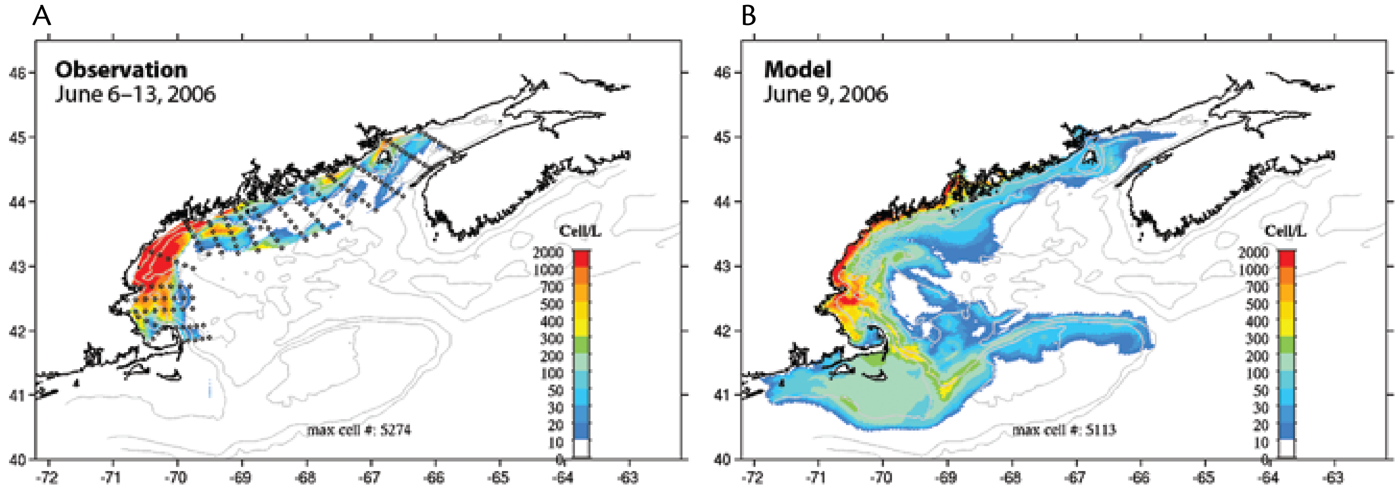

Figure 6. Comparison of observed and modeled surface *A. fundyense* cell concentration in June 2006. Cruise observations (A) are similar to the model-simulated bloom for that time period (B). See McGillicuddy et al. (2005) and Li et al. (2009).

ACKNOWLEDGMENTS

This effort was supported in part by the following grants to D.M. Anderson: NOAA Cooperative Agreement NA17RJ1223, NOAA Grant NA09NOS4260212, NIEHS Grant 1 P50 ES01274201, and NSF Grants OCE-0430724 and OCE-0911031.

REFERENCES

Anderson, D.M. 1989. Toxic algal blooms and red tides: A global perspective. Pp. 11–16 in *Red Tides: Biology, Environmental Science and Toxicology*. T. Okaichi, D.M. Anderson, and T. Nemoto, eds, Elsevier.

Anderson, D.M. 1995. *ECOHAB—The Ecology and Oceanography of Harmful Algal Blooms: A National Research Agenda*. Woods Hole Oceanographic Institution, Woods Hole, MA, 66 pp.

Anderson, D.M., A.D. Cembella, and G.M. Hallegraeff, eds. 1998. *The Physiological Ecology of Harmful Algal Blooms*. Springer-Verlag, Heidelberg, 662 pp.

Anderson, D.M., P.M. Glibert, and J.M. Burkholder. 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25(4b):704–726.

Anderson, D.M., D.M. Kulis, G.J. Doucette, J.C. Gallager, and E. Balech. 1994. Biogeography of toxic dinoflagellates in the genus *Alexandrium* from the northeast United States and Canada as determined by morphology, bioluminescence, toxin composition, and mating compatibility. *Marine Biology* 120:467–478.

Anderson, D.M., D.M. Kulis, B.A. Keafer, K.E. Gribble, R. Marin, and C.A. Scholin. 2005a. Identification and enumeration of *Alexandrium* spp. from the Gulf of Maine using molecular probes. *Deep-Sea Research Part II* 52(19–21):2,467–2,490.

Anderson, D., D. McGillicuddy, D. Townsend, and J. Turner. 2005b. The ecology and oceanography of toxic *Alexandrium fundyense* blooms in the Gulf of Maine. *Deep Sea Research Part II* 52:2,365–2,836.

Babin, M., C.S. Roesler, and J.J. Cullen, eds. 2008. *Real-time Coastal Observing Systems for Marine Ecosystem Dynamics and Harmful Algal Blooms*. UNESCO, Paris, 807 pp.

Beam, C.A., and M. Himes. 1982. Distribution of members of the *Crypthecondinium cohnii* (Dinophyceae) species complex. *Journal of Protozoology* 29:8–15.

Bowers, H.A., C. Tomas, T. Tengs, J.W. Kempton, A.J. Lewitus, and D.W. Oldach. 2006. Raphidophyceae [Chadefaud ex Silva] systematics and rapid identification: Sequence analyses and real-time PCR assays. *Journal of Phycology* 2:1,333–1,348.

Brand, L.E. 1991. Review of genetic variation in marine phytoplankton species and the ecological implications. *Biological Oceanography* 6:397–409.

Coyne, K.J., S.M. Handy, E. Demir, E.B. Whereat, D.A. Hutchins, K.J. Portune, M.A. Doblin, and S.C. Cary. 2005. Improved quantitative real-time PCR assays for enumeration of harmful algal species in field samples using an exogenous DNA reference standard. *Limnology and Oceanography Methods* 3:381–391.

Danovaro, R., S. Fonda-Umani, and A. Pusceddu. 2009. Climate change and the potential spreading of marine mucilage and microbial pathogens in the Mediterranean Sea. *PLoS ONE* 4(9):e7006, doi:10.1371/journal.pone.0007006.

Fraga, S., S.M. Gallager, and D.M. Anderson. 1989. Chain-forming dinoflagellates: An adaptation to red tides. Pp. 281–284 in *Red Tides: Biology, Environmental and Science and Toxicology*. T. Okaichi, D.M. Anderson, and T. Nemoto, eds, Elsevier, New York.

Garcés, E., M. Montresor, D.M. Anderson, J. Lewis, and K. Rengefors, eds. 2010. Phytoplankton life cycles. *Deep-Sea Research Part II* 57:(3–4):159–322.

Garcés E., A. Zingone, M. Montresor, B. Reguera, B. Dale, eds. 2002. *LIFEHAB: Life History of Microalgal Species Causing Harmful Blooms.* European Commission. Research in Enclosed Seas Series No.12, Brussels, 214 pp.

Gentien, P. 1998. Bloom dynamics and ecophysiology of the *Gymnodinium mikimotoi* species complex. Pp. 155–173 in *The Physiological Ecology of Harmful Algal Blooms*. D.M. Anderson, A.D. Cembella, and G.M. Hallegraeff, eds, NATO ASI Series G41, Springer Verlag, Berlin, Heidelberg.

GEOHAB. 2001. *Global Ecology and Oceanography of Harmful Algal Blooms, Science Plan*. SCOR and IOC, Baltimore and Paris, 86 pp.

GEOHAB. 2003. *Global Ecology and Oceanography of Harmful Algal Blooms, Implementation Plan*. SCOR and IOC, Baltimore and Paris, 36 pp.

GEOHAB. 2005. *Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Upwelling Systems*. SCOR and IOC, Paris and Baltimore, 82 pp.

GEOHAB. 2006. *Global Ecology and Oceanography of Harmful Algal Blooms: Eutrophication and HABs*. SCOR and IOC, Paris and Baltimore, 74 pp.

GEOHAB. 2008. *Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Stratified Systems.* SCOR and IOC, Paris, France, and Newark, Delaware, USA, 59 pp.

GEOHAB. 2010. *Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Fjords and Coastal Embayments*. A. Cembella, L. Guzmán, S. Roy, J. Diogène, eds, IOC and SCOR, Paris, France, and Newark, Delaware, 57 pp.

Glibert, P.M., J.M. Burkholder, E. Granéli, and D.M. Anderson. 2008. Advances and insights in the complex relationships between eutrophication and HABs: Preface to the special issue. *Harmful Algae* 8:1–2.

González-Gil, S., L. Velo-Suárez, P. Gentien, I. Ramilo, B. Reguera. 2010. Phytoplankton assemblages and characterization of a *Dinophysis acuminata* population during an upwelling-downwelling cycle. *Aquatic Microbial Ecology* 58:273–286.

Granéli, E., G.A. Codd, B. Dale, E. Lipiatou, S.Y. Maestrini, and H. Rosenthal, eds. 1999. *EUROHAB Science Initiative: Harmful Algal Blooms in European Marine and Brackish Waters.* Office for Official Publications of the European Communities, Luxembourg.

Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32:79–99.

Hallegraeff, G.M., D.M. Anderson, and A.D. Cembella. 1995. *Manual on Harmful Marine Microalgae*. IOC Manuals and Guides No. 33. UNESCO.

Hallegraeff, G.M., D.M. Anderson, and A.D. Cembella. 2003. *Manual on Harmful Marine Microalgae*. Monographs on Oceanographic Methodology, 11, UNESCO, 794 pp.

Haywood, A.J., CA. Scholin, R. Marin III, K. Petrik, R. Pigg, M. Garrrett, K.A. Steidinger, and C. Heil. 2009. Detection of *Karenia brevis* in Florida coastal waters using sandwich hybridization assays in two formats. Pp. 95–100 in *Proceedings of the 6th International Conference on Molluscan Shellfish Safety.* Royal Society of New Zealand Miscellaneous Series No. 71, Blenheim, Marlborough, New Zealand.

He, R., D.J. McGillicuddy Jr., B.A. Keafer, and D.M. Anderson. 2008. Historic 2005 toxic bloom of *Alexandrium fundyense* in the western Gulf of Maine: 2. Coupled biophysical numerical modeling. *Journal of Geophysical Research* 113, C07040, doi:10.1029/2007JC004602.

Heisler, J., P.M. Glibert, J.M. Burkholder, D.M. Anderson, W. Cochlan, W.C. Dennison, Q. Dortch, C.J. Gobler, C.A. Heil, E. Humphries, and others. 2008. Eutrophication and harmful algal blooms: A scientific consensus. *Harmful Algae* 8:3–13.

IOC (Intergovernmental Oceanographic Commission of UNESCO). 2010. *Microscopic and Molecular Methods for Quantitative Phytoplankton Analysis*. B. Karlson, C. Cusack, and E. Bresnan, eds. IOC Manuals and Guides, no. 55, IOC/2010/MG/55, Paris, 110 pp.

Jensen, M.H., and N. Daugbjerg. 2009. Molecular phylogeny of selected species of the order Dinophysiales (Dinophyceae): Testing the hypothesis of a Dinophysioid radiation. *Journal of Phycology* 45:1,136–1,152.

Jeong, H.J., J.E. Song, N.S. Kang, S. Kim, Y.D. Yoo, and J.Y. Park. 2007. Feeding by heterotrophic dinoflagellates on marine heterotrophic nanoflagellates. *Marine Ecology Progress Series* 333:151–160.

John, U., R.A. Fensome, and L.K. Medlin. 2003. The application of a molecular clock based on molecular sequences and the fossil record to explain biogeographic distributions within the *Alexandrium tamarense* "species complex" (Dinophyceae). *Molecular Biology and Evolution* 20(7):1,015–1,027, doi:10.1093/molbev/msg105.

Kirkpatrick, G.J., D.F. Millie, M.A. Moline, and O. Schofield. 2000. Optical discrimination of a phytoplankton species in natural mixed populations. *Limnology and Oceanography* 45(2):467–471.

Kirkpatrick, G.J., C. Orrico, M.A. Moline, M. Oliver, and O.M. Schofield. 2003. Continuous hyperspectral absorption measurements of colored dissolved organic material in aquatic systems. *Applied Optics* 42(33):6,564–6,568.

Kudela, R., G. Pitcher, T. Probyn, F. Figueiras, T. Moita, and V. Trainer. 2005. Harmful algal blooms in coastal upwelling systems. *Oceanography* 18(2):184–197.

Kudela, R.M., S. Seeyave, and W.P. Cochlan. 2010. The role of nutrients in regulation and promotion of harmful algal blooms in upwelling systems. *Progress in Oceanography* 85:122–135, doi:10.1016/j.pocean.2010.02.008.

Lilly, E.L., K.M. Halanych, and D.M. Anderson. 2007. Species boundaries and global biogeography of the *Alexandrium tamarense* complex (Dinophyceae). *Journal of Phycology* 43:1,329–1,338.

Lilly, E.L., D.M. Kulis, P. Gentien, and D.M. Anderson. 2002. Paralytic shellfish poisoning toxins in France linked to a human-introduced strain of *Alexandrium catenella* from the western Pacific: Evidence from DNA and toxin analysis. *Journal of Plankton Research* 24(5):443–452.

MacKenzie, L., I. Sims, V. Beuzenberg, and P. Gillespie. 2002. Mass accumulation of mucilage caused by dinoflagellate polysaccharide exudates in Tasmanian Bay, New Zealand. *Harmful Algae* 1:69–83.

Masseret, E., D. Grzebyk, S. Nagai, B. Genovesi, B. Lasserre, M Laabir, Y. Collos, A. Vaquer, and P. Berrebi. 2009. Unexpected genetic diversity among and within populations of the toxic dinoflagellate *Alexandrium catenella* as revealed by nuclear microsatellite markers. *Applied and Environmental Microbiology* 75:2,037–2,045.

McGillicuddy, D.J. Jr., D.M. Anderson, D.R. Lynch, and D.W. Townsend. 2005. Mechanisms regulating large-scale seasonal fluctuations in *Alexandrium fundyense* populations in the Gulf of Maine: Results from a physical-biological model. *Deep-Sea Research Part II* 52(19–21):2,698–2,714.

McGillicuddy, D.J. Jr., R.P. Signell, C.A. Stock, B.A. Keafer, M.D. Keller, R.D. Hetland, and D.M. Anderson. 2003. A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine. *Journal of Plankton Research* 25(9):1,131–1,138.

Park, M.G., K. Sunju, H.S. Kim, G. Myung, Y.G. Kang, and W. Yih. 2006. First successful culture of the marine dinoflagellate *Dinophysis acuminata*. *Aquatic Microbial Ecology* 45:101–106.

Penna, A., and M. Magnani. 1999. Identification of *Alexandrium* (Dinophyceae) species using PCR and rDNA-targeted probes. *Journal of Phycology* 35:615–621.

Pitcher, G.C., and S.C. Pillar. 2010. HABs in eastern boundary upwelling systems. *Progress in Oceanography* 85:1–4, doi:10.1016/j.pocean.2010.02.001.

Pitcher, G.C., F.G. Figueiras, B.M. Hickey, and M.T. Moita. 2010. The physical oceanography of upwelling systems and the development of harmful algal blooms. *Progress in Oceanography* 85:5–32, doi:10.1016/j.pocean.2010.02.002.

Rhodes, L., C.A. Scholin, J.V. Tyrrell, J. Adamson, and K. Todd. 2001. The integration of DNA probes into New Zealand's routine phytoplankton monitoring programs. Pp. 429–432 in *Harmful Algal Blooms 2001*. G.M. Hallegraeff, S.I. Blackburn, C.J. Bolch, and R.J. Lewis, eds, Intergovernmental Oceanographic Commission, UNESCO, Paris.

Richardson, T.L., and J.L. Pickney. 2004. Monitoring of the toxic dinoflagellate *Karenia brevis* using gyroxanthin-based detection methods. *Journal of Applied Phycology* 16:315–328.

Rines, J.E.B., P.L. Donaghay, M.M. Dekshenieks, J.M. Sullivan, and M.S. Twardowski. 2002. Thin layers and camouflage: Hidden *Pseudo-nitzschia* spp. (Bacillariophyceae) populations in a fjord in the San Juan Islands, Washington, USA. *Marine Ecology Progress Series* 225:123–137.

Robbins, I.C., G.J. Kirkpatrick, S.M. Blackwell, J. Hillier, C.A. Knight, and M.A. Moline. 2006. Improved monitoring of HABs using autonomous underwater vehicles (AUV). *Harmful Algae* 5(6):749–761.

Scholin, C.A., K.R. Buck, T. Britschgi, G. Cangelosi, and F.P. Chavez. 1996. Identification of *Pseudo-nitzschia australis* (Bacillariophyceae) using rRNA-targeted probes in whole cell and sandwich hybridization formats. *Phycologia* 35:190–197.

Scholin, C.A., M. Herzog, M. Sogin and D.M. Anderson. 1994. Identification of group- and strain-specific genetic markers for globally distributed *Alexandrium* (*Dinophyceae*) species. II. Sequence analysis of a fragment of the large-subunit ribosomal RNA gene. *Journal of Phycology* 30:999–1,011.

Smayda, T.J. 2010a. Adaptations and selection of harmful and other dinoflagellate species in upwelling regions. 1. Morphology and adaptive polymorphism. *Progress in Oceanography* 85:53–70, doi:10.1016/j.pocean.2010.02.004.

Smayda, T.J. 2010b. Adaptations and selection of harmful and other dinoflagellate species in upwelling regions. 2. Motility and migratory behaviour. *Progress in Oceanography* 85:71–91, doi:10.1016/j.pocean.2010.02.005.

Stumpf, R.P., M.E. Culver, P.A. Tester, M. Tomlinson, G.J. Kirkpatrick, B.A. Pederson, E. Truby, V. Ransibrahmanakul, and M. Soracco. 2003. Monitoring *Karenia brevis* blooms in the Gulf of Mexico using satellite ocean color imagery and other data. *Harmful Algae* 2:147–160.

Sullivan, J.M, M.A. McManus, and P.L. Donaghay, eds. 2010. The ecology and oceanography of thin plankton layers. *Continental Shelf Research* 30:1–118.

Swanson, K.M., L.J. Flewelling, M. Byrd, A. Nunez, and T.A. Villareal. 2010. The 2008 Texas *Dinophysis ovum* bloom: Distribution and toxicity. *Harmful Algae* 9:190–199.

Trainer, V.L., G.C. Pitcher, B. Reguera, and T.J. Smayda. 2010. The distribution and impacts of harmful algal bloom species in eastern boundary upwelling systems. *Progress in Oceanography* 85:33–52, doi:10.1016/j.pocean.2010.02.003.

Valiela, I. 1991. Ecology of coastal ecosystems. Pp. 57–76 in *Fundamentals of Aquatic Ecology*, 2nd ed., R.S.K. Barnes and K.H. Mann, eds, Blackwell Scientific, Oxford, UK.

Velo-Suárez, L., S. González-Gil, P. Gentien, M. Lunven, C. Bechemin, L. Fernand, R. Raine, and B. Reguera. 2008. Thin layers of *Pseudo-nitzschia* spp. and the fate of *Dinophysis acuminata* during an upwelling–downwelling cycle in a Galician ría. *Limnology and Oceanography* 53(5):1,816–1,834.

Walsh, J.J., and G. Kirkpatrick, eds. 2008. Ecology and oceanography of harmful algal blooms in Florida. *Continental Shelf Research* 28(1):1–214.

Wynne, T.T., R.P. Stumpf, M.C. Tomlinson, D.J. Schwab, G.Y. Watabayashi, L. Lanerolle, J.D. Christensen. In press. Ecological forecasting: Estimating cyanobacterial bloom transport by coupling remotely sensed imagery and a hydrodynamic model. *Limnology and Oceanography*.

Zhou, M.-J., Z.-L. Shen, and R.-C. Yu. 2008. Responses of a coastal phytoplankton community to increased nutrient input from the Changjiang (Yangtze) River. *Continental Shelf Research* 28:1,483–1,489.