

The Comparative “Systems” Approach to HAB Research

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Experimental and comparative methods have been referred to as “the two great methods of science” (Mayr, 1982). To reach valid scientific conclusions, the processes of interest should be studied through repeated investigations, preferably over a range of differing conditions. The most direct way to accomplish this is the experimental method, wherein controls are imposed that allow the scientist to systematically vary conditions of interest while holding other factors constant. Marine ecosystems, however, are not amenable to experimental control. One way to address this shortcoming is through the comparative method (Mayr, 1982), which allows the processes of interest to be examined on repeated occasions using naturally occurring temporal and spatial variations in existing conditions and phenomena. In this case, the range of natural variability in conditions and mechanisms substitute for controlled experimental treatments.

Harmful algal bloom (HAB) research has had a long history in many countries, and further advances in understanding of HABs are likely to benefit from international, collaborative efforts that will allow the assembly and comparison of data collected in different systems. A comparative approach will allow us to generalize previously obtained results and to establish the existence of recurrent patterns. By analyzing the response of particular HAB species from similarly functioning ecosystems distributed around the world, it should be possible to tease out significant trends from the noise within any single system. Likewise, similar HAB species can occur in geographically separated and environmentally distinct regions and as a result, may differ in their growth dynamics and expression of harmful attributes. Comparisons can reveal fundamental processes governing population development and toxin production. Furthermore, major anthropogenic and/or natural forcings, such as nutrient loading and climate variability, appear to have differing impacts on HABs in different regions, so understanding this gradient of responses may lead to better insight and better management of HAB events.



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Figure 1. Long chain of *Gymnodinium catenatum*, one of several chain-forming dinoflagellates associated with upwelling systems. Much as bicycle racers benefit from racing in single file, long chains of dinoflagellate cells swim faster than short chains, and thus are well suited for hydrographic systems in which water motion is strong. Photo courtesy of Yasuwo Fukuyo, Asian Natural Environmental Science Center, University of Tokyo, Japan.



There are, of course, disadvantages to the comparative approach that must be considered when setting up programs of this type. For example, costs can be high, as separate teams of investigators are often required, each with their own equipment and support needs. Nevertheless, the rationale for comparative studies of harmful algal taxa, functional groups, and the ecosystems in which

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they occur is compelling and has been incorporated into several international HAB programs. The GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms) Program created a Comparative Ecosystem Studies program element with the goal to “identify mechanisms underlying HAB population and community dynamics across ecosystem types through comparative studies” (GEOHAB, 2001). Central to the implementation of GEOHAB is the establishment of Core Research Projects (GEOHAB, 2003), which comprise oceanographic field studies in comparable ecosystems through identification of relevant organisms, and measurements of the physical, chemical, and biological processes that control their population

dynamics. A major objective of Core Research is the integration achieved by the application of models to HAB dynamics in geographically distinct ecosystems.

In a similar manner, the EU-U.S. Scientific Initiative on Harmful Algal Blooms (European Commission, 2003) builds on the recognition that comparable systems and species driven by similar factors are found within the EU and U.S. regions, as are systems in which the dominant forcing factors differ. Here we describe the types of “systems” that can be compared in this approach to HAB research, and offer examples of ongoing or planned studies where the approach can be particularly beneficial. The EU-U.S. program is highlighted because it provides many examples where comparative studies are of clear value.

COMPARABLE SYSTEMS

The comparative approach may be applied in several ways. HABs occur in both pelagic and benthic ecosystems that can be classified operationally according to their physical and chemical characteristics and their particular biology, and therefore offer the opportunity for an ecosystem approach to comparison. As an alternative, it is also possible to compare taxa or groups of HAB species that share common features or strategies, thereby dropping the ecosystem focus for a more organismal comparison.

Examples of ecosystem types that could be defined on the basis of hydrographic regimes include:

- **Upwelling systems, associated with eastern boundary current systems, such as the California Current, the Humboldt Current, the Canary Current and Iberian Coastal System, and the**

Benguela Current. Within the context of the seasonal succession of phytoplankton, several potentially harmful microalgae are common within these systems, including *Pseudo-nitzschia* spp., *Alexandrium* spp., *Gymnodinium catenatum*, and *Dinophysis* spp. (GEOHAB, 2005). Of particular interest is the association of blooms of chain-forming dinoflagellates, such as *Alexandrium catenella* and *Gymnodinium catenatum* (e.g., Fraga et al., 1988a; Pitcher and Calder, 2000), with these systems (Figure 1). This association is thought to relate to the strong swimming capabilities of chains of cells compared to solitary forms (Fraga et al., 1988b).

- **Fjords, as in Alaska, Canada, Scandinavia, and Chile.** These systems create retention and/or initiation zones that favor the proliferation of a particular suite of HAB species (e.g., *Alexandrium* spp., *Pseudo-nitzschia* spp., and various raphidophytes). Fjords are often only marginally affected by human activities because of low population densities, and thus are usually not subject to eutrophication, which can select for a different set of HAB species.
- **Coastal embayment systems, found in most coastal countries.** As with fjords, hydrodynamic processes may be complex, with an accentuated role of tidal flux, storm surges, wind-driven mixing, and salinity and thermal stratification. These systems are associated with a wide variety of HAB species, many of which are motile and have resting stages. Changes of position in the water column, in relationship with the tidal cycle, for example, may be important to avoid transport of the population

outside of the favorable habitat (e.g., Anderson and Stolzenbach, 1985). Resting stages may take advantage of the short distance between bottom sediments and surface waters.

- **Thin-layer-producing systems along most coasts, including the Atlantic coast of France, Sweden, California, and Washington state.** Several HAB species such as *Dinophysis acuminata* (Gentien et al., 1995), *Karenia mikimotoi*, and even *Alexandrium fundyense* (Townsend et al., 2001) are known to form thin, subsurface layers at scales as small as 10 cm in the vertical and as large as 10 km in the horizontal (Gentien et al., 2005). One kinematic explanation is that these layers result from the stretching of horizontal inhomogeneities by the vertical shear of horizontal currents. This produces an environment potentially favoring motile organisms that can maintain their position in this layer (Franks, 1995).

These are but a few of the many ecosystems classified on the basis of their hydrography and associated with various groups of HABs. Ecosystems can also be defined on the basis of their nutrient status or salinity characteristics. Examples of these types of ecosystems include:

- **Systems strongly influenced by eutrophication, such as the Black Sea, Baltic Sea, Adriatic Sea, Seto Inland Sea, and the waters near Hong Kong, and the mid-Atlantic regions of the United States.** HAB species that seem more prevalent in these systems include those within the genera *Phaeocystis*, *Chattonella*, *Heterosigma*, *Prorocentrum*, and *Pfiesteria*, to name just a few. Many factors can influence this

association, not just the quantity of ambient nutrients. The form of those nutrients (i.e., organic versus inorganic) can be a major determinant as well (Glibert et al., this issue).

- **Brackish systems, such as the Baltic Sea or portions of the Chesapeake Bay or the St. Lawrence.** These systems often are associated with cyanobacterial species of *Microcystis*, *Nodularia*, and *Anabaena*, but flagellates such as *Pfiesteria*, *Karlodinium*, and *Prymnesium* are also common.

Comparative studies need not be limited to ecosystems. It is also possible to conduct studies on taxonomic groups, or species with common life history or survival strategies. These species might include:

- **Cyst-forming dinoflagellates, haptophytes, prymnesiophytes, and cyanobacteria that are heavily reliant on the germination of dormant stages for bloom initiation** (Figure 2). HAB species or genera that can be compared within this context include *Alexandrium* spp., *Pyrodinium bahamense*, *Chattonella* spp., and *Gymnodinium catenatum*. These organisms can in turn be studied in different habitats where the relative importance of cyst germination may vary due to depth, advection, and other factors.
- **Mixotrophic species (i.e., those that obtain part of their nutrition through consumption of other organisms and compounds).** HAB genera such as *Chrysochromulina*, *Prymnesium*, *Alexandrium*, and *Prorocentrum* are among those capable of this strategy (Hansen, 1998). The challenge here is to quantify the role that mixotrophy plays in a particular organism's nutri-

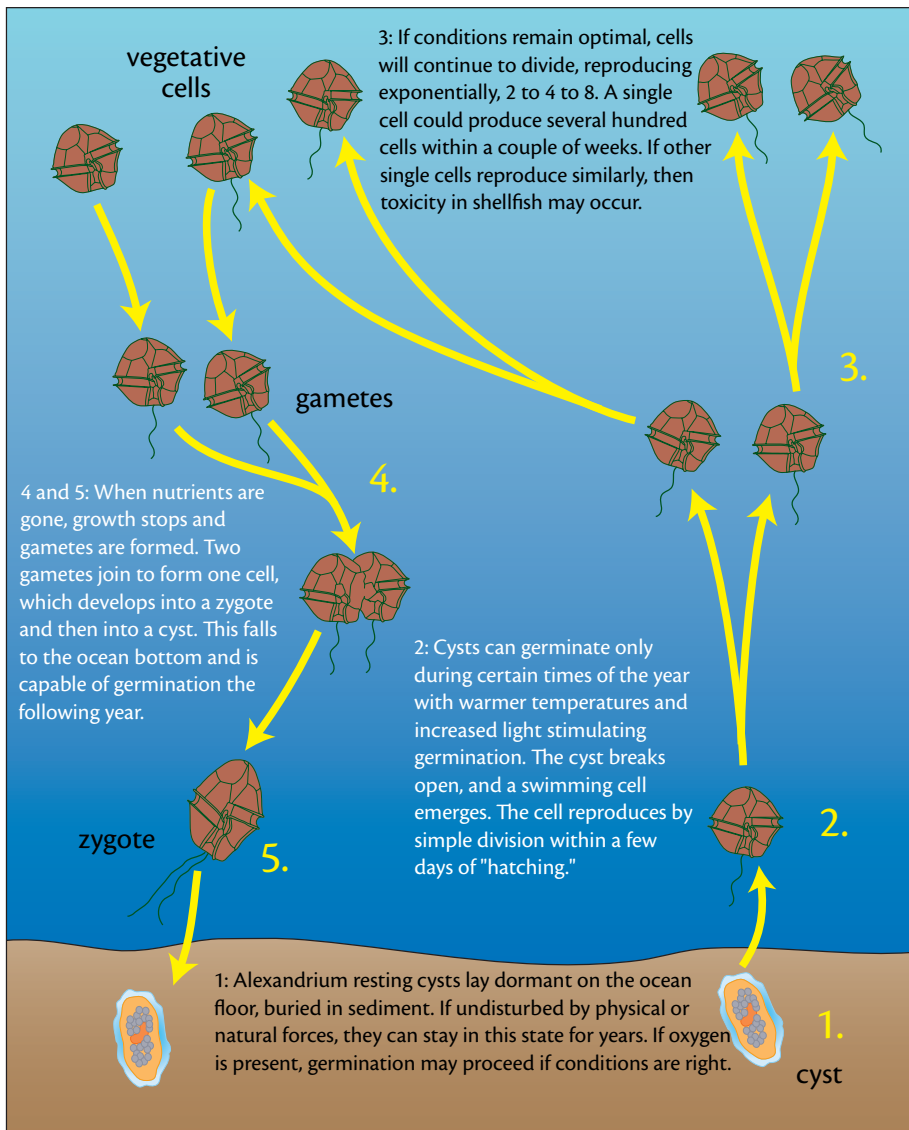


Figure 2. Meroplanktonic life cycle of the dinoflagellate *Alexandrium* sp. demonstrating the importance of a resting cyst in species survival through adverse conditions. Resting cysts and spores can have a profound impact on HAB dynamics, but the extent of this impact will vary with location and with environmental forcings. Comparisons among HAB species that share this life history strategy can be highly informative. SOURCE: McGillicuddy et al. (in press).

tion and to determine when this strategy is used. Many of these species are fully capable of surviving using only autotrophy; presumably they use mixotrophy as a strategy to supplement

their nutrition. The above examples are not intended to be comprehensive or exclusive; they demonstrate the latitude that can be followed in comparative studies.

COMPARATIVE STUDIES BETWEEN THE EUROPEAN UNION AND UNITED STATES

The EU-U.S. Scientific Initiative on Harmful Algal Blooms (European Commission, 2003) offers an outstanding opportunity to rapidly advance HAB science through comparative studies. In the following sections, examples are described that have a high probability of yielding new insights in HAB dynamics through the comparative approach in this bilateral program.

Comparisons among different species that inhabit the same ecosystem type can be highly informative. In this context, certain similarities between the hydrography, meteorology, and patterns of paralytic shellfish poisoning (PSP) in California and northwest Spain are noteworthy, even though the causative organisms (*Alexandrium catenella* and *Gymnodinium catenatum*, respectively) are different species. In both areas, the dominant hydrographic feature is coastal upwelling driven by persistent equatorward winds. Sudden outbreaks of PSP toxicity occur in both areas during months when a cessation or relaxation of upwelling is common (Price et al., 1991; Fraga et al., 1988a), suggesting the shoreward delivery of offshore water and its associated cells. Comparative studies developed to investigate the linkage between large-scale physical forcing and the patterns of PSP would clearly be informative. In this instance, identification of the specific characteristics of the two species that allow these species to persist in these upwelling systems is the goal. We already know that their ability to form long chains makes them exceptionally strong swimmers, able to withstand ver-

tical velocities that might otherwise carry them into deeper, unproductive waters (Fraga et al., 1988b) (Figure 1). Other factors must also come into play; however, these have yet to be identified. Both species form resting cysts, but this may not provide benefits that are specific to upwelling systems, particularly given the water depths in these systems. Likewise, both species are toxic, but again, this may not explain their dominance in these systems. Only through careful studies using similar methods and approaches can comparable data sets be obtained that can lead to the insights on factors that allow these species to inhabit this type of hydrographic system so successfully.

Physical processes controlling bloom transport are of paramount importance in all HABs. Coastal currents driven by wind, buoyancy, or remote forcings can transport blooms hundreds or even thousands of kilometers along the coast, often from one management area to another (e.g., Franks and Anderson, 1992). Understanding the physical dynamics underlying these transport pathways is essential to effective management and mitigation of HAB effects. In the context of comparative systems, *Karenia brevis* in the Gulf of Mexico develops offshore but is transported to and along the coast by complex interactions between coastal currents and shelf features (Steidinger et al., 1998). Similarly, *K. mikimotoi* is transported in coastal currents along the northwest European continental shelf, with delivery of subsurface populations to shore with specific wind conditions (e.g., Raine and MacMahon, 1998). There may or may not be common mechanisms underlying these blooms, but much can be learned by conducting

similar studies of each species, with an emphasis on the manner in which physical forcings regulate cell accumulation and delivery to shore.

Processes at much smaller scales are equally important to potential HAB expression. Accumulation at frontal interfaces (Franks, 1992) and fine-scale aggregation in subsurface thin layers are both strategies that can enhance the survival of a species. Examples of both are found in the EU and in the United States. For example, *Dinophysis norvegica* can grow and persist in thin layers within the Baltic Sea thermocline at 20 m during the summer months, reaching more than 100 cells m/l, similar to thin layers of the same organism in East Sound, Washington (P. Donaghay, Graduate School of Oceanography University of Rhode Island, Narragansett, Rhode Island, unpublished data, 2005). This is an example where comparative studies will require sophisticated equipment that can sample and document layers of cells that are sometimes a meter or less in thickness, without distorting them or altering their signature. Technologies to make these measurements are currently being developed both in the United States and Europe. The thin-layer fine spatial scale sampling technologies developed in the U.S. Thin Layers Program (e.g., Cowles et al., 2000) complement ongoing efforts in Europe (e.g., Marcaillou et al., 2000) and provide platforms for potential expanded capabilities through probe and toxin detection additions. Gentien et al. (this issue) describe some aspects of this type of collaborative effort.

One of the key questions facing scientists is the role of eutrophication in HABs and how the inputs, quality, and

fluxes of nutrients relate to HAB development and proliferation (Glibert et al., this issue). Here again, comparisons of systems in different regions can be informative. For example, some coastal systems in the EU are phosphorus-limited (e.g., Mediterranean Sea) compared to many regions of the U.S. coast, which are generally nitrogen limited. Shifts from nitrogen to phosphorus limitation have resulted from management intervention, such as implementation of advanced sewage treatment, and examination of present trends in the context of historical data sets may yield insights useful to managers. In the Northern Aegean Sea, phytoplankton populations were mostly diatom dominated until about 1996 when decreased N:P ratios developed following changes in sewage treatment policies and increases in phosphorus loading (Moncheva et al., 2001). These depressed ratios were subsequently correlated with increased dinoflagellate blooms, including *Dinophysis* species responsible for diarrhetic shellfish poisoning (DSP).

In the context of the EU-U.S. comparative HAB program, it is of note that European land discharge to coastal systems delivers, on average, five to ten times more nitrogen (per hectare) to coastal waters than is estimated for the United States (Seitzinger and Kroeze, 1998). This is likely a result of higher population density and more intensive and longer land use in Europe than in the United States. In the later context, there have been over 1000 years of land manipulation in the European countries compared to a modest 200 years in the United States. The higher loads of nutrients per hectare in the EU are intriguing consid-

ering the apparently increasing frequencies and duration of HAB events off Northern Europe and several Mediterranean countries (EUROHAB, 1999) *versus* the relatively small number of anthropogenically supported HABs in U.S. waters. These differences might suggest that as the United States ages, nutrient loads per unit land surface might follow the same pattern as in Europe, leading to the increasing HAB frequencies found in Europe today. Comparisons between similarly impacted and differentially impacted enclosed and semi-enclosed systems on both sides of the Atlantic would begin to provide the data needed to evaluate this worrisome possibility.

Several comparable HAB problems are of note in this regard. Beaches covered with foam and viscous waters that foul fishermen's nets are recurrent events in North Sea waters due to blooms of the colonial prymnesiophyte *Phaeocystis* (Lancelot et al., 1998). The mucilage-rich colonies are thought to bloom as a result of changing nutrient loads and ratios in the major rivers of the region. Diatoms flourish in early spring, sustained by the winter stock of dissolved silicate and phosphate, but the nitrate-enriched river waters in late April to May stimulate the growth of *Phaeocystis* colonies in the eastern Channel and southern North Sea, impacting areas of France, Belgium, the Netherlands, and Germany. In contrast, *Phaeocystis* has a limited range in the United States, occurring for short periods in the Gulf of Maine and Cape Cod Bay. Blooms are less frequent and less expansive, and only dominate surface biomass on rare occasions. Does this difference reflect lower nutrient loads or ratios, different species or strains of *Phaeocystis*, or

some other ecological factor? At present, we can only pose such questions. Answers await comparative studies.

Another example is found within the toxic dinoflagellate genus *Dinophysis* (Figure 3), in that some species in Europe are toxic and often contaminate mussels, leading to serious DSP outbreaks, whereas U.S. populations of the same species have undetectable or extremely low toxicity. Reasons for these differences remain unresolved and could reflect genotypic heterogeneity or differential toxin synthesis in response to nutrient availability or other factors that differ between the European and U.S. systems.

Yet another important example where comparative studies would lead to insights involves the toxic diatoms *Pseudo-nitzschia* spp. These species are found throughout Europe and the U.S., yet toxic outbreaks occur only in certain regions. For example, *P. australis* is the only species off the Atlantic coast of Spain that is toxic, although multiple other species of *Pseudo-nitzschia* are present (Bates et al., 1998). In contrast, *P. australis* is usually non-toxic off the U.S. Pacific Northwest but is commonly toxic in waters further south, off the coast of California, again in the presence of multiple (non-toxic) co-occurring *Pseudo-nitzschia* species. This intermingling of toxic and non-toxic species and strains within a given region or across regions suggests a series of natural experiments to determine the extent to which toxin variability reflects environmental forcings as opposed to genetic and physiological differences. Resolving these difficult issues requires comparative studies in multiple environments.

The change in genetic diversity that

can occur through time in comparable systems is also an important question in HAB dynamics. During a recent *Pseudo-nitzschia delicatissima* bloom in the Gulf of Naples, for example, a striking amount of genetic diversity was documented in the population of this species at the beginning of a bloom, but only a few genotypes were still present after the bloom was well established (Orsini et al., 2002). Clearly, genetic diversity changed through time, such that only a fraction of the resident population in the Gulf was ultimately responsible for the bloom. Such variability is important to resolve for other bloom taxa as well, and it must be taken into account if comparisons are being made of the "same" species in two different environments.

One outcome of comparative studies of different ecosystem types should be an ability to characterize HAB species into "functional groups" and to identify commonalities in plankton community structure in relation to environmental forcings. Functional groups provide a basis for simplification in order to improve our predictive ability relative to the dynamics of the system. The terms functional types, functional groups, or life forms, which some consider to be synonymous, can be defined in a number of ways. In the context of GEOHAB, a functional group follows the definition of Gitay and Noble (1997): a "non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors." The organisms within a functional group share "an adaptation syndrome... to recurrent patterns of selective factors" (Margalef, 1978). The term "syndrome" used in the above definitions highlights



Figure 3. *Dinophysis* species. A longstanding mystery has been why *Dinophysis* species such as these from Swedish waters (arrows) are toxic, producing DSP toxins, while the same species from U.S. waters are non-toxic. Resolution of this important unknown requires comparative studies. Photo by Donald Anderson.

the recurrence of specific sets of biological or environmental features.

Efforts to interpret the ecological implications of morphological or other phenotypical phytoplankton characteristics have been reviewed by Sournia (1982), Elbrächter (1984), Fogg (1991), and Kjørboe (1993), among others. Properties like size or shape may interact with water turbulence and with nutrient uptake ability, and swimming may allow control of the vertical position in the water column (Kamykowski et al., 1998).

However, very little is known of the functional significance of many features of phytoplankton (Sournia, 1982). It should be noted here that the toxicity or harmfulness of HAB species is generally defined from an anthropomorphic point of view and that the ecological relevance of these properties is generally unknown, and may be nil.

There have been many attempts to develop functional classifications of phytoplankton. Some have been useful in providing a conceptual framework, based

on empirically obvious morphological or physiological traits, such as that proposed by Margalef (1978), Margalef et al., (1979), Reynolds and Smayda (1998), and Cullen and MacIntyre (1998). The latter authors reconsidered Margalef's (1978) model and emphasized physiological and biochemical adaptations that could be quantified experimentally. They identified three main adaptation syndromes: "mixers," which are adapted to highly variable irradiance; "migrators," which have a well-developed capacity

for unbalanced growth and control of vertical movement, and “layer-formers,” which have developed efficient systems to harness light or nutrients in environments with highly predictable irradiance or nutrient supplies.

By analyzing the response of particular HAB species from similarly functioning ecosystems distributed around the world, it should be possible to tease out significant trends from the noise within any single system.

We are at the early stages of functional group classification for HAB species. In this context, a data-defined approach could use multivariate techniques to detect clusters of species based on the similarities in their distribution or on a set of characters. Many phytoplankton species tend to be cosmopolitan or to occupy a large biogeographical range. However, it is possible to detect recurrent patterns in the composition of phytoplankton communities at particular times or places. Taxa within a recurrent assemblage, or assemblages occupying similar ecological situations in comparable ecosystems, can be examined for common morphological, physiological, or life-history traits that could be considered as characterizing a functional group. The data needed for these analyses require comparative studies of many types.

In summary, a comparative approach to HAB research has been incorporated into several major international programs, and this should lead to a number of important contributions to our un-

derstanding of HAB dynamics. A few of the benefits from this approach include:

- Improved understanding of commonalities and differences in the physiologies and behaviors of individual HAB species or functional groups that determine their occurrence in particular ecosystem-types.
- Identification of the physical oceanographic forcings that play a significant role in bloom dynamics and are specific to particular ecosystem types.
- Models of HAB transport and dynamics in key hydrographic systems that can be used at multiple locales, leading to bloom forecasts and predictions.
- Models of HAB species or functional groups that can be modified for use with other species or groups, and that can be incorporated into physical circulation models for bloom forecasts and predictions.
- An understanding of the dynamics of particular organisms or groups of organisms that can be used in the design and implementation of mitigation strategies.

This comparative ecosystem approach compels the HAB community to synthesize knowledge and data in order to group HABs into categories based on

behavior, physiology, life history characteristics, or simply an ability to flourish under a particular set of conditions. Since it is not feasible to study all HAB phenomena at all locations, a series of studies targeting comparable ecosystem types, taxa, or functional groups is clearly an efficient use of limited scientific and financial resources.

ACKNOWLEDGEMENTS

This review reflects the views and efforts of many people. In particular, the authors wish to thank the past and present members of the GEOHAB Scientific Steering Committee, and the participants at the EU-U.S. Joint Workshop on Harmful Algal Blooms in Trieste, Italy, September 2002. Funding for these activities was provided by the National Science Foundation (NSF), the National Oceanic and Atmospheric Administration (NOAA), and the European Commission DG Research-Environment Directorate. GEOHAB is an initiative of SCOR (Scientific Committee on Oceanic Research) and IOC (Intergovernmental Oceanographic Commission of UNESCO). D. Anderson was funded by NOAA's ECOHAB (Ecology and Oceanography of Harmful Algal Blooms) program, the MERHAB (Monitoring and Event Response for Harmful Algal Blooms) program, and NSF. This is contribution number 129 from the ECOHAB Program and 11333 from the Woods Hole Oceanographic Institution. 

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