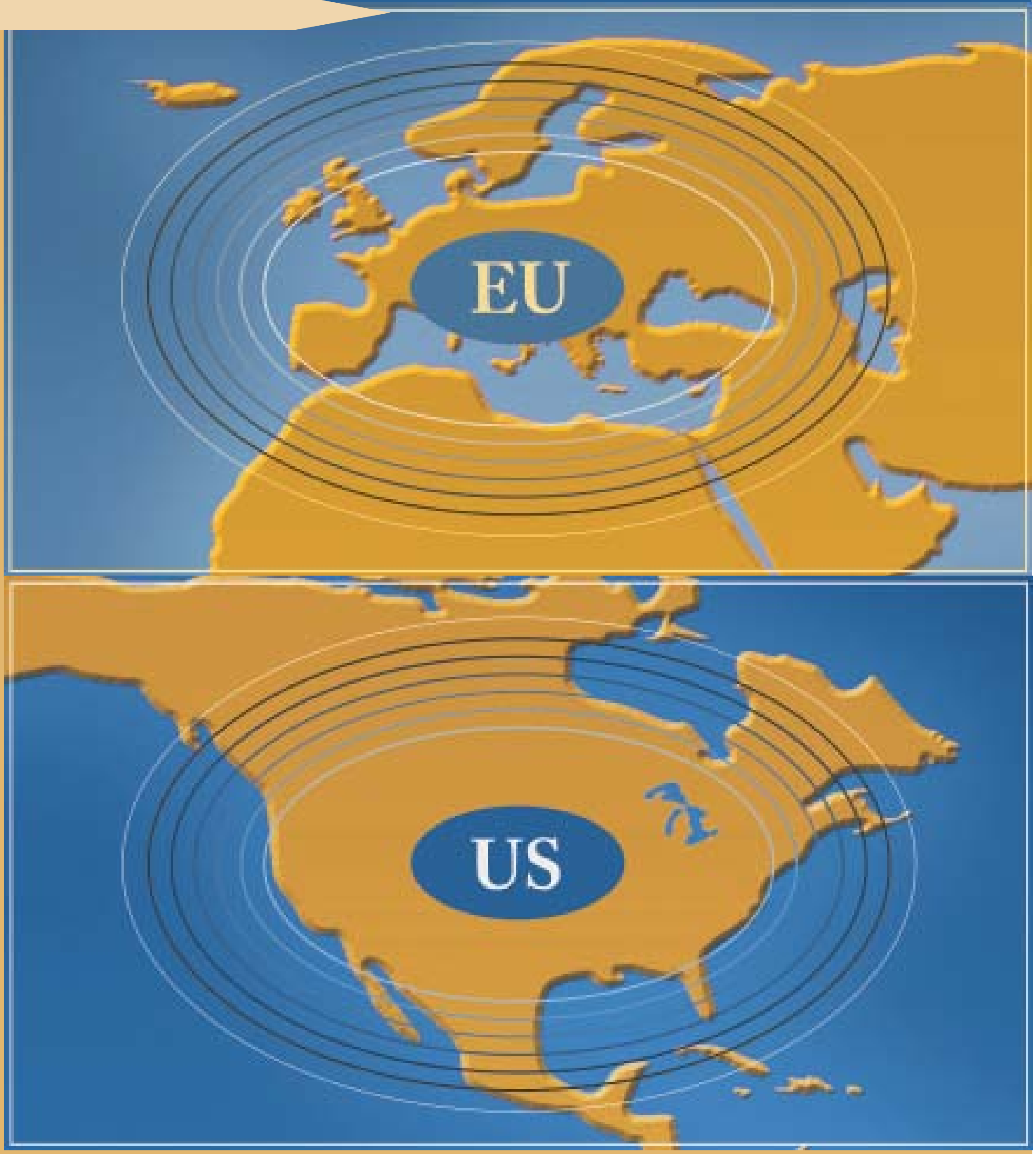
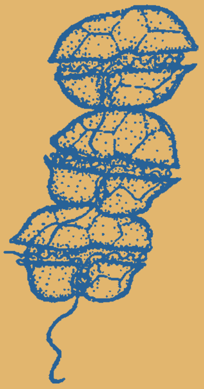
The EU-US Scientific Initiative on Harmful Algal Blooms

A Report from a Workshop Jointly Funded by the
European Commission - Environment and Sustainable Development Programme
and the U.S. National Science Foundation
5-8 September 2002 - Trieste, Italy





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I. Executive Summary

Over the last several decades, countries throughout the world have experienced an escalating and worrisome trend in problems associated with blooms of harmful and toxic algae, commonly called "red tides", but now termed "harmful algal blooms" (HABs). Impacts include mass mortalities of wild and farmed fish and shellfish, human illness and death from contaminated shellfish or fish, death of marine mammals, seabirds, and other animals, and alteration of marine habitats or trophic structure through shading, overgrowth, or adverse effects on life history stages of fish and other marine organisms. Several decades ago, relatively few countries were affected by HABs, but now most coastal countries are threatened, in many cases over large geographic areas and by more than one harmful or toxic species. It is still a matter of debate as to the causes behind this expansion, with possible explanations ranging from natural mechanisms of species dispersal to a host of human-related phenomena such as increasing nutrient-rich pollution, climatic shifts, or transport of algal species via ship ballast water. Whatever the reasons, coastal regions throughout the world are now subject to an unprecedented variety and frequency of HAB events. Many countries are faced with a bewildering array of toxic or harmful species and impacts, as well as disturbing trends of increasing bloom incidence, more impacted resources, larger areas affected, and higher economic losses.

For decades, HABs have been studied in relative isolation on both sides of the Atlantic. National and regional programs, such as EUROHAB in Europe and ECOHAB in the US, have been launched to focus co-ordinated research, technologies, and shared resources on HABs, but these efforts have not included significant international collaboration.

In recognition of the importance of scientific exchange among nations, the European Commission (EC) and the US National Science Foundation (NSF) signed an agreement in October 2001 to foster collaboration, with HABs identified as one of several topics of common interest. In September 2002, the EC Environment and Sustainable Development Programme and the US NSF jointly funded a workshop in Trieste, Italy to bring together scientists from both sides of the Atlantic to collectively assess the state of HAB science, to identify gaps in our knowledge, and to develop an international plan for co-operative, comparative studies. The efforts of that workshop form the basis of the plan presented herein. Subsequently, under the European Sixth Framework Programme, Bio-diversity and Marine Ecosystems theme, the need for and plans to implement a joint EU-US programme were articulated.

The Programmatic Approach

One of the challenges of designing and implementing a collaborative programme is the identification of areas where collaboration will lead to significant progress that would not be possible if similar studies were undertaken independently. HAB research has had a long history on both sides of the Atlantic and the scope of possible research areas is broad. However, there are areas where research would particularly benefit from collaborative efforts. First, there are common environments in the EU and the US where comparisons of processes controlling bloom dynamics of the same or similar organisms should lead to improved understanding. Second, similar HAB species occur in the EU and the US, but they differ in growth dynamics and expression of harmful attributes. Again, comparisons should reveal fundamental processes governing population development and toxin production. Third, major anthropogenic and/or natural forcings, such as nutrient loading and climate variability, appear to have differing impacts on HABs in the EU and the US, and understanding this gradient of responses may lead to better insight and better management of HAB events. The rationale for comparison of similar harmful algal events and taxa across environments and species is thus compelling.

Two broad hydrographic regimes have been identified as example systems: open coastal or basin-scale systems, and enclosed or semi-enclosed systems. While many exceptions exist, the former are more commonly subject to toxic outbreaks, whereas the latter are more commonly subject to high biomass blooms. In the context of the comparative ecosystems approach, open coastal and basin scale systems are more likely to be controlled by meso- to large-scale physical processes than are enclosed or semi-enclosed systems. Thus, understanding the dynamics of HABs in these systems may require a special focus on biophysical coupling processes, such as mechanisms that allow a species to survive and proliferate within these systems (e.g., resting cell formation or vertical migration), physical dynamics that lead to local accumulation or concentration of populations (e.g., eddies and/or stratified, thin layers), as well as advective processes that may transport blooms and cause harmful effects distant from where the blooms initially develop.

Enclosed and semi-enclosed coastal systems tend to retain materials introduced from land or the adjacent ocean. Ranging in scale from the Gulf of Mexico/Mediterranean/Baltic Seas, to large estuaries such as the Chesapeake Bay, to lagoons and small harbours, they share a susceptibility to bloom phenomena due to their relatively shallow depths and restrictive circulation and the pulsed delivery of fresh water and nutrients from land runoff and the atmosphere. In enclosed and semi-enclosed systems, the driving forces behind the initiation and success of a specific HAB species are also a combination of physical, meteorological, chemical, and biological factors. The most important physical process enabling HAB species to survive is, however, the stability of the water column. The introduction of buoyant fresh water stratifies the system, isolating the depths from vertical exchange and the replenishment of oxygen, and creates convergent circulation features such as fronts that may actively contribute to bloom formation. In addition, freshwater delivery sets up seaward gradients (salinity, nutrients) and thereby, a progression of habitats within which varying species subsist, falter, or thrive.

A number of example comparative studies are highlighted in this report. These are intended as examples only, as the scientific community will ultimately determine the focus of this proposed programme through submission of proposals within this framework and through their peer evaluation based on merit criteria. Suggested studies that emphasize the benefits of a proposed EU-US collaboration include:

- The toxic dinoflagellate *Dinophysis* spp. is common in the Baltic Sea and other European waters. In contrast, these taxa occur in the US but are essentially non-toxic. Reasons for these differences remain unresolved and could reflect genotypic heterogeneity or alternatively, differential toxin synthesis in response to low and high nutrients, respectively, of the European and US systems. Similarly, the toxic cyanobacterium *Nodularia spumigena*, the most conspicuous HAB species in the Baltic Sea, is not found in the US.
- Some species of *Pseudo-nitzschia* are commonly reported as toxic in one region but non-toxic in another. For example, *P. australis* is the only species off Spain that is toxic whereas the same species can be non-toxic off the US Pacific Northwest and is 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 provides a series of natural experiments to determine the

extent to which toxin variability reflects environmental forcings as opposed to genetic and physiological differences.

- Dinoflagellates within the *Alexandrium* genus bloom in the US and Europe in regions with wide and narrow shelves, with episodic and seasonal upwelling, and with deep and shallow cyst beds. These species are responsible for outbreaks of paralytic shellfish poisoning and spirolide poisoning and much can be gained from comparing the mechanisms for bloom formation in different regions.
- *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. Similarly *Karenia mikimotoi* is transported in coastal currents along the northwest European continental shelf.

European lands discharge on average 5-10 times more nitrogen to coastal systems than is estimated for the US, likely a result of more intensive and longer land use in Europe than in the US. These trends are intriguing considering the apparently increasing frequencies and duration of HAB events off Northern Europe and several Mediterranean countries *versus* relatively fewer anthropogenically-supported blooms in US waters. Conceivably, as the US ages, loads per unit land surface might follow the same pattern as in Europe, leading to the increasing HAB frequencies observed in Europe today. Contrasts between similarly impacted and differentially impacted enclosed and semi-enclosed systems are warranted.

Benefits of EU-US Comparative Studies

The proposed EU-US HAB Programme offers an outstanding opportunity to rapidly advance our science by providing multi-disciplinary intellectual input for specific HABs over a wide geographic area. Through formal workshops and training activities as well as basic research in laboratories, mesocosms, and ships, our understanding of HAB dynamics will be broadened considerably. Expansion of community knowledge will stimulate new research and exploration of approaches perhaps only considered on one side of the Atlantic. The collection of data on taxa in multiple environments provides an excellent means to assess our ability to forecast bloom development, maintenance, and dissipation. For example, numerical models developed to predict population development and distribution in one region can be evaluated in others. This exchange and application will allow assessment of model assumptions and parameterisations as model output deviates from observations.

Other benefits include distributing existing and new technologies and skills to wider areas (e.g., models, molecular probes, micropaleontological techniques, automated recognition systems, and remote sensing algorithms) allowing explorations not undertaken previously in one *versus* the other area. Additionally, some taxa are best studied initially at specific institutions on one side of the Atlantic or the other due to the maintenance of specific cultures or the existence of unique culture facilities for a given organism (e.g., *Pfiesteria*, which requires special biohazard facilities when it is in fish-killing form). Further, interrogation of time series data in Europe and the US will broaden the HAB communities' ability to ascertain the importance of mesoscale or global processes in plankton populations. Aperiodic and unusual deviations in HAB species in one area may be similarly identified at other locations, suggesting oceanic or global forcing rather than more local control. This synergy would be impossible without access to multiple data sets across the large geographic areas of the two regions.

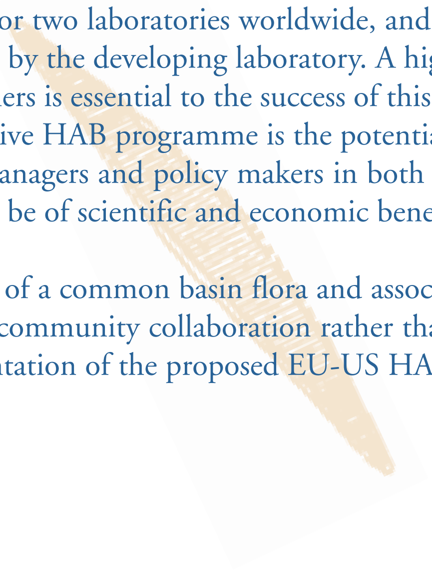
Timeliness

The EU and US HAB communities are primed to undertake a collaborative program. Research in HABs, as in many fields of geo- and biological sciences, has advanced tremendously in recent years, and new technologies now allow us to address questions – and pose solutions – that were previously not possible. From the rapid and accurate identification and enumeration of species on spatial and temporal scales that rival those for chemical and physical measurements, to our ability to monitor and model physical dynamics on scales relevant to organismal dynamics, advancements have been large, in part due to national and multi-national programmes such as EUROHAB and ECOHAB. The next step is to move these investigations to a higher level through international collaborative studies.

Educational Opportunities

The proposed EU-US HAB Programme will provide unique educational and training opportunities for both communities. For example, the critical problem of declining phytoplankton taxonomic expertise in the US research community could be partially alleviated by collaborations with taxonomic experts from the EU, as well as through joint training courses, incorporating classical and molecular techniques. Development of technologies such as *in situ* measurements, real-time biosensors, and remote sensing can more rapidly advance when such technologies are tested and calibrated in comparable ecosystems, or on similar species in different regions. In some cases, methodologies are being developed in only one or two laboratories worldwide, and opportunities to learn such techniques may require training visits by the developing laboratory. A high level of scientific exchange between EU and US researchers is essential to the success of this programme. Finally, one of the unique aspects of a collaborative HAB programme is the potential opportunity for agency staff development. Environmental managers and policy makers in both regions have technologies and experiences to share that could be of scientific and economic benefit to other regions developing management strategies.

The rapid advancement in our knowledge of a common basin flora and associated environmental forcing that will be provided by community collaboration rather than individual studies is a compelling motivation for implementation of the proposed EU-US HAB programme.



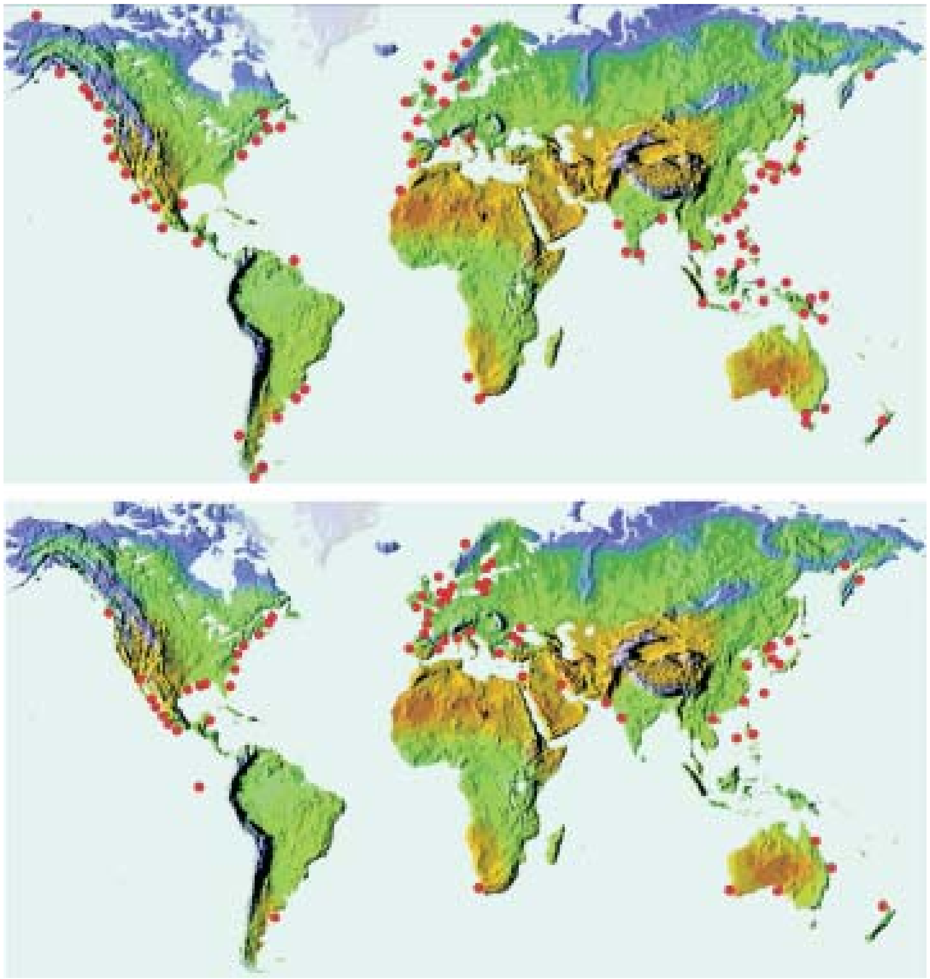
II. Overview

Introduction to the Problem of HABs

Harmful Algal Blooms (HABs) are due to proliferations of algae that can have devastating ecological and economic impacts in the world's oceans (Smayda 1990; Anderson et al. 2002). From a few isolated coasts several hundred years ago, their distribution now occupies virtually all areas of coastline throughout the world (GEOHAB 2001; Figure 1). Impacts of these events can include contamination of seafood with toxins; fish, shellfish, mammal, or bird kills (Figure 2); and altered marine ecosystems through changes in water quality and light penetration. Most dramatically, these events

Figure 1.

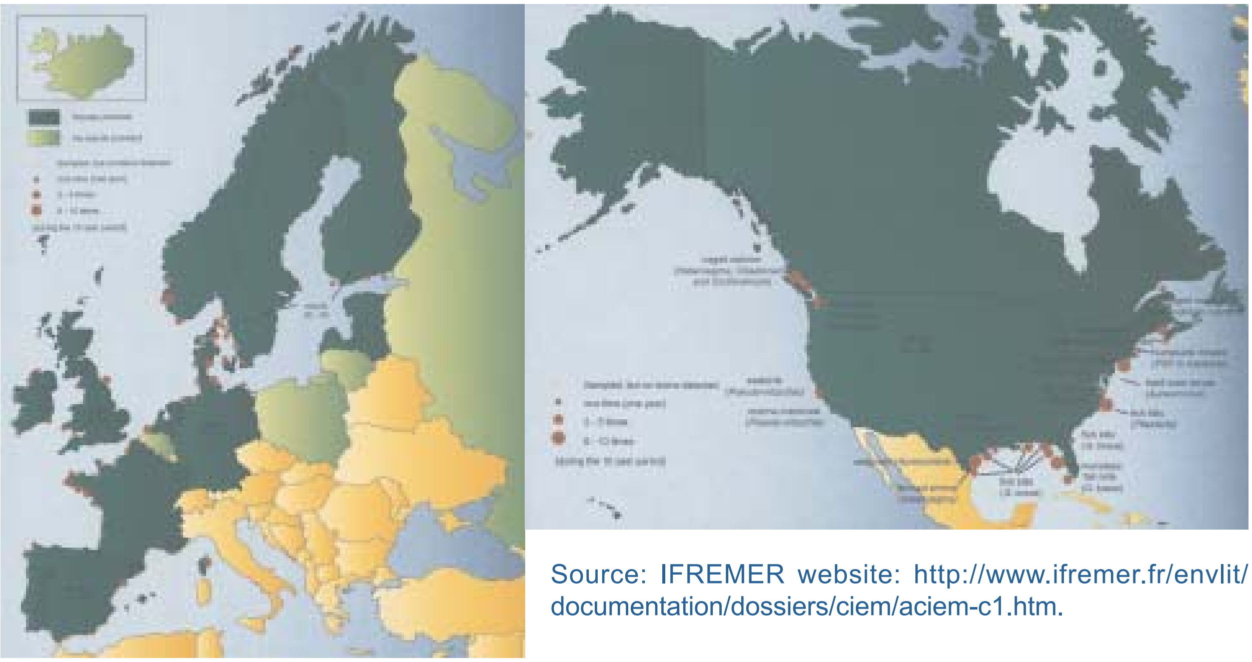
Global maps of the distribution of organisms known to be associated with the production of the toxic syndrome Paralytic Shellfish Poisoning (PSP): *Pyrodinium bahamense* var. *compressum, Alexandrium tamarense*, and *Gymnodinium catenatum* - upper panel; and with environmental problems associated with the production of one high biomass bloom-former: *Prorocentrum minimum* - lower panel.



Source: Modified from GEOHAB 2001 (upper panel) and Fan 2002 (lower panel).

Figure 2.

HAB-induced animal and plant mortalities in Europe and North America during the period from 1991-2000.



Source: IFREMER website: http://www.ifremer.fr/envlit/documentation/dossiers/ciem/aciem-c1.htm.

can induce human illness, leading to public demand for effective management of these bloom taxa. The study of their ecology and the factors that impact their development and toxin expression in Europe and the US are the subject of this proposed EU-US Scientific Initiative on Harmful Algal Blooms.

The problems identified above are associated with two general types of causative organisms: the toxin producers and the high-biomass producers. Some HAB species have characteristics of both groupings. The toxin producers may lead to harmful impacts even when present at low cell densities and are responsible to a greater extent for human health impacts while the high biomass producers may lead to harmful ecological impacts without toxin production *per se*. The distribution of these two HAB types include both sides of the Atlantic (Table 1). However, the expression of harmful properties appears to differ for many species between the EU and the US, leading to important fundamental questions regarding the regulation of HAB dynamics.

The research communities in both continents have been addressing HABs as a function of physics and environmental controls acting on the HAB species. Research communities also recognize that the expression of HABs is also a function of grazer interactions such that bloom formation and maintenance indicates decoupling from pelagic and benthic grazers; grazer strategies and top-down regulation are just as important as bottom up controls, whether through water quality, life cycle characters, or physics. Hence, HABs must be interpreted as a systemic-ecological phenomenon. The proposed mutual collaboration between the EU and US communities will foster critical observations of blooms constrained by the physical-chemical environment and the abilities of all organisms suspended in it.

Table 1. *Many HAB species have been documented to occur in both the US and EU. In some areas, these species, while present, have not led to detrimental effects. The asterisk in the table below indicates where such effects are known. Understanding when and why these species proliferate and lead to harmful effects is the objective of this comparative effort. Source: A. Zingone.*

Species	Location	Problem
Alexandrium acatenella	N California*	PSP
A. andersonii	Gulf of Mexico, Tyrrhenian Sea	PSP
A. balechii	Gulf of Mexico*, Tyrrhenian Sea	Fish mortality
A. catenella	NW Mediterranean*, W USA*	PSP, discolorations
A. fundyense	Gulf of Maine, Gulf of Mexico *, N Europe*	PSP
A. minutum	Mediterranean Sea*, Southern European Atlantic	PSP, fish kills, discolorations
A. monilatum	Gulf of Mexico*	Fish kills
A. ostenfeldii	N Europe, NE USA*	Spirolides
A. tamarense	Gulf of Mexico *, N EU*, Mediterranean Sea*	PSP, discolorations
A. taylori	W Mediterranean *	Discolorations
Amphidinium spp.	USA, Europe	Lipophylic toxins
Dinophysis acuminata	most coasts of USA and Europe*	DSP
D. acuta	Atlantic Europe*, Baltic Sea	DSP
D. caudata	S Europe*, S California	DSP
D. fortii	S. Europe*, California	DSP
D. norvegica	N Europe*, NE USA	DSP
D. sacculus	S Europe*	DSP
Gymnodinium catenatum	Atlantic Iberia*, Alboran Sea*	PSP
G. corsicum	W Mediterranean *	fish kills hemolisins
G. pulchellum	Gulf of Mexico*, Mediterranean lagoons	fish kills
Karenia brevis	Gulf of Mexico*, E Florida*	NSP, fish kills, respiratory problems
K. mikimotoi	Atlantic Europe*, Gulf of Mexico	fish kills
Karenia sp.	Greece*	fish kills
Karlodinium micrum	English Channel*	fish kills
Karlodinium veneficum	English Channel*	fish kills
Lingulodinium polyedrum	Gulf of Mexico, California, all over Europe*	Yessotoxins
Pfiesteria spp.	E USA*, N Europe	Fish kills, human illness
Prorocentrum minimum	German coast*, Black Sea*, Mediterranean Sea, N Europe, Chesapeake Bay*, Northern Gulf of Mexico*	Undetermined toxins
Protoceratium reticulatum	Europe* and USA	Yessotoxins
Protoperidinium crassipes, P. depressum	Europe*, USA	AZP
Pseudo-nitzschia australis	W USA*, Atlantic Iberia *	ASP, vertebrate mortality
P. delicatisima	USA and Europe	ASP
P. multistriata	Gulf of Naples	ASP
P. multiseries	USA* and Europe	ASP
P. pseudodelicatissima	USA and Europe	ASP
Heterosigma akashiwo	NW USA*, USA West Coast, Scotland*? Europe	Fish kills
Chattonella spp.	Skagerrak and Kattegat*, Norwegian coasts*	ichtyotoxicity
Fibrocapsa japonica	Southern Bight*, Germany* Mediterranean Sea*	ichtyotoxicity
Heterosigma akashiwo	Europe (Scotland?), NW USA (Washington DC)*	Fish kills
Chrysochromulina polylepis, C. leadbeateri	Skagerrak and Kattegat*, Norwegian coasts*, Mediterranean Sea, USA?	ichtyotoxicity?
Phaeocystis globosa	EU: Bay of Brest, Eastern Channel*, Southern Bight of the North Sea*, German Bight*, USA: Narragansett Bay	foam, anoxia, hindering shellfish
P. pouchetii	Norwegian fjords*, Barents Sea, Greenland Sea	toxic to fish larvae
Prymnesium spp.	Skagerrak and Kattegat*, Norwegian coasts*, Mediterranean Sea	fish kills
Aureococcus anophagefferens	Southern New England*	Fish, shellfish, eelgrass and macroalgal dieoffs, repressed copepod fecundity and growth
Aureoumbra lagunensis	Texas lagoons*	loss of submerged aquatic vegetation

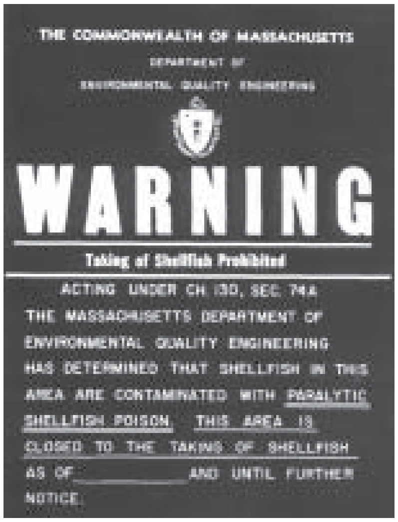
ASP = amnesiac shellfish poisoning; AZP = azaspiracid poisoning; DSP = diarrhetic shellfish poisoning; PSP = paralytic shellfish poisoning

Societal Impacts

The societal impacts of HABs are many and have led to large economic commitments in both the EU and the US toward reducing threats to local economies, living resources, and public health. The human health threat posed by HAB toxin production is by far the most important, with large monitoring programmes for toxins in shellfish, fish, and drinking waters designed to reduce public exposure. Both acute illnesses and mortality are now well established, while long-term debilitating symptoms associated with chronic exposures to low toxin levels, although of great concern, are less known and subjected to increasing investigation. In addition to direct human health concerns, public perception of coastal health in general, and thereby safety for consumers and coastal inhabitants more specifically, is intimately linked to water colour, clarity, and odour, fish and shellfish abundance, and governmental advisories for unseen microbes and toxins.

Figure 3.

Throughout the EU and the US, large expanses of coastline are posted with signs such as this, prohibiting the harvesting of shellfish due to the potent algal toxins they have accumulated.



A common consequence of recurrent HABs in coastal waters of both regions is depressed local or regional economies. Investments in monitoring programmes, public health advisories, and medical treatment are costly, but other associated costs from HAB events rapidly increase economic losses for given areas. Hardships induced from coastal HABs include public avoidance of tourist areas and tourism-related businesses, reduced seafood consumption and business in seafood-dependent commercial firms (e.g., restaurants), location, density, and relocation costs for coastal aquaculture or mariculture facilities, and lower productivity due to illness. Commitment to best management practices needed to address problems requires additional use of private and public funds. Further, the strong linkage between land use, nutrient loads, HABs, and decreasing fishery yield provides convincing evidence for human-induced threats to the sea's harvest. In the same manner, expanding frequencies and contributions of toxin-producing species could mean longer-term chronic exposure of valued living resources to sub-lethal toxin concentrations, as yet an unmeasured, but potential threat to some commercially-important fish and shellfisheries.

Impacts from HABs on coastal living resources often generate public outcry and concern in both the EU and the US. Otter, seal, sea lion, whale, and bird mortalities along coastlines of the two regions are widely covered in local and world press, with speculation often giving rise to public and political demands for controlling these natural disasters. The loss of submerged vegetation and benthic animal communities through shading or anoxia, respectively, are dramatic alterations in ecosystem structure, processing, and habitat, affecting fisheries production, watermen livelihoods, and nutrient and sediment dynamics on local-regional scales. Declining shellfish beds, crab populations, and increased turbidity and nutrient levels (poor water quality) are unacceptable environmental characteristics for coastal areas of the two regions leading to vocal concern and interest by EU and US citizens for "cleaning up" or "restoring" the systems.

The recognition of common problems associated with HABs in Europe and the US and the potential benefits gained from improved understanding and management of these problems are the

Introduction to a Proposed EU-US Collaborative HAB Initiative

For decades, HABs have been studied on both sides of the Atlantic, but the underlying reasons for these blooms, the ability to predict their occurrence, and the means to mitigate them when they do occur are not established. For the first time, joint research in Europe and the US is being proposed to address these problems of mutual concern, through financial support from the European Commission (EC) and the U.S. National Science Foundation (NSF).

Several efforts have been launched in the past decade to bring co-ordinated research, technologies, and shared resources to the issue of harmful algal blooms. These form an excellent foundation for the proposed EU-US HAB effort. It is now well recognised and accepted that our understanding of the population dynamics of HAB organisms, their impacts, and the potential management implications, is dependent on working within a global arena. Although HAB impacts may be local, solutions may be found in distant locales.

In recognition of the importance of scientific collaboration among nations, the European Commission and the US National Science Foundation signed an agreement in October 2001 to foster such collaboration.

National Science Foundation planning documents, such as "*Complex Environmental Systems: Synthesis for Earth. Life, and Society in the 21st Century"* (NSF Advisory Committee 2003), and on-going interest in increasing our understanding of the direct and indirect causes and consequences of HABs in our coastal regions, formed the basis for the inclusion of HABs as one of the scientific areas of collaboration under this agreement.

To further the development of such comparative studies, the EC - Environment and Sustainable Development Programme and the US NSF jointly funded a workshop in Trieste, Italy September 2002 to bring together scientists from both sides of the Atlantic (Appendix 1.) to collectively assess the state of the science, to identify gaps in our knowledge, and to develop an international plan for co-operative, comparative studies. The efforts of that workshop form the basis of the plan presented herein.

On-Going HAB Research Efforts in the US and the EU

For many years, US researchers and coastal managers struggled through piecemeal and fragmented efforts to address the problems of harmful algae. In 1994, this strategy was recognised to be inadequate, and NSF, together with the National Oceanic and Atmospheric Administration, co-sponsored a workshop on the Ecology and Oceanography of Harmful Algae. The participants, a group of 40 academic and government scientists and programme officers from numerous federal agencies, attended and developed a co-ordinated research strategy, *ECOHAB: The Ecology and Oceanography of Harmful Algal Blooms: A National Research Agenda* (1995). ECOHAB provided the framework needed to increase our understanding of the fundamental processes underlying the impacts and population dynamics of HABs. This involved a recognition of the many factors at the organismal level that determine how HAB species respond to and potentially alter their environment, the manner in which HAB species affect or are affected by food-web interactions, and how the distribution, abundance, and impact of HAB species are regulated by the environment.

Figure 4.

Many US agencies have contributed to the planning of ECOHAB as well as to the assessments of HABs and their economic impacts.

The ECOHAB programme identified three major research themes that encompass the priorities of national importance on the HAB phenomenon (ECOHAB 1995). These included: 1) Organisms – with a goal towards determining the physiological, biochemical, and behavioural features that influence bloom dynamics; 2) Environmental regulation – with a goal toward determining and parameterising the factors that govern the initiation, growth, and maintenance of these blooms; and 3) Food-web and community interactions – with a goal toward determining the extent to which food-webs and trophic structure affect and are affected by the dynamics of HABs. Information in these areas, in turn, supported a critical goal of the ECOHAB programme: the development of reliable models to forecast bloom development, persistence, and toxicity. Projects funded through ECOHAB include regional and targetted studies on the biogeochemical, ecological, and physical processes that contribute to bloom formation and maintenance, as well as specific biological and physical processes that regulate the occurrence of specific HABs. Research results have been applied through another programme, Monitoring and Event Response for Harmful Algal Blooms (MERHAB), to foster innovative monitoring programmes and rapid response by public agencies and health departments to safeguard public health, local economies, and fisheries.

Figure 5.

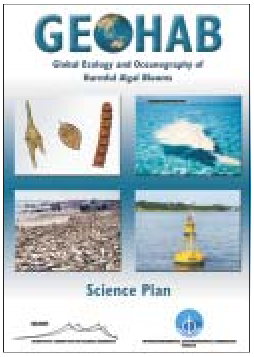
A science planning document and a regional assessment contributed to the implementation of EUROHAB.

Within the European community, it has also been recognised that the problems of HABs are increasing, and that these problems know no national borders. From fish-killing flagellate, toxic dinoflagellate, and high biomass *Phaeocystis* and cyanobacteria blooms in Scandinavia, to shellfish-intoxicating dinoflagellates in Ireland, France, Spain, and Portugal, to high biomass, mucilaginous, and toxic blooms of the northern Mediterrenean, Europe faces recurring frequent impacts to its societies and regional economies. HABs in one country may have been initiated through nutrient delivery or other source from another country and thus must be studied collectively. Furthermore, the transport of species and water via currents and shipping poses additional mechanisms by which these problems spread from one country to another. The European Commission (EC) has, over the past decade or more, funded numerous, individual projects related to harmful algae and there are many efforts devoted to monitoring and research on a local scale in many European countries. Yet, until very recently, there have been no co-operative efforts aimed at understanding harmful algae in European waters in a co-ordinated, comprehensive fashion. In 1998, an international workshop organised by the EC and the University of Kalmar, Sweden was held to develop a directed scientific initiative, resulting in the EUROHAB programme (EUROHAB 1999). The following were identified as important research areas: 1) Algae-producing toxins accumulating in the food web; 2) Fish-killing species; 3) High biomass HABs; 4) Cyanobacterial blooms and toxins; 5) Field studies of physical-biological interactions; 6) Tools and technology development; and 7) Mitigation.

Under the subsequent EUROHAB Initiative, projects were undertaken on eutrophication and biological control of HABs; importance of organic matter from terrestrial sources in HAB formation; transfer and fate of HAB toxins; development of predictive systems; and most recently, a project on the socio-economic impact of HABs (EUROHAB 2002).

Figure 6.

The GEOHAB Science Plan was published in 2001 outlining a broad plan for international collaborative work.



Another international effort aimed at co-ordinating and building on related national and international efforts is the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) programme, sponsored by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC). Although not a research-funding programme *per se*, GEOHAB helps to facilitate those activities that require co-operation among nations (GEOHAB 2001). The Scientific Steering Committee of GEOHAB has agreed that a focus on comparative ecosystems is a powerful way to ford boundaries and political realms while gaining important insights into population dynamics of HABs, and have therefore endorsed this EU-US collaborative programme. The proposed EU-US Scientific Initiative on HABs is one example of a regional project in GEOHAB.

ECOHAB, EUROHAB, and GEOHAB have produced extensive Science Plans over the past several years, outlining the vast array of issues that still need to be addressed to understand HAB population dynamics. This proposed EU-US initiative will build on these plans and focus on those issues where collaborative studies will be most fruitful through merit-evaluated proposals developed in response to this programme.

The Programmatic Approach

One of the challenges of designing and implementing a collaborative programme on HABs is the identification of areas where such collaboration will lead to significant progress that would not be possible if similar studies were undertaken independently. HAB research has had a long history on both sides of the Atlantic and the scope of possible research areas is very broad. However, there are several areas where research would clearly benefit from collaborative efforts. First, there are comparative environments in the EU and the US where comparisons of similar processes controlling bloom dynamics should lead to new understanding. Second, apparently similar species occur in the EU and in the US, but they differ in growth dynamics and expression of harmful attributes. Third, major anthropogenic and/or natural forcings, such as nutrient loading and climate variability, appear to have some differing impacts on HAB bloom dynamics in the EU and the US, and understanding this gradient of responses may lead to better insight and better management of

HAB events. Thus, the rationale for comparison of similar harmful algal events and taxa across environmental and species is compelling. Advances will be mutual and both research communities will benefit. Whereas this document emphasises the comparative ecosystems approach, it is well recognised that any study will have elements of both comparative ecosystems and comparative species, and any effort to distinguish the two approaches is organizational and does not preclude an effort that would take an alternate comparative approach.

Strengths of EU-US Comparative Studies

The proposed EU-US HAB Programme offers an outstanding opportunity to rapidly advance our science by providing a larger multidisciplinary intellectual input for specific HABs over a wide geographic area. Collaboration will lead to:

- Better hypothesis formulation
- Identification of species and sites facilitating hypothesis testing
- Establishment of sentinel sites to evaluate long-term changes resulting from anthropogenic/climatological drivers
- Development of approaches to evaluation of the impacts of increasing maricultural activities on HAB events and the effect of the latter on mariculture.

There is exceptional strength among European and US scientists, when combined, in addressing these issues. Further, through formal workshops and training activities to basic research in laboratories, mesocosms, and ships, information on HAB dynamics will be broadened considerably. Expansion of community knowledge will stimulate new research and exploration of possibilities perhaps only considered on one side of the Atlantic.

The collection of additional data on taxa in new environments provides an excellent means to assess our ability to forecast bloom development, maintenance, and dissipation. As EU and US researchers more clearly define growth, ecological, chemical, and physical limits for a taxon, predicting population success and distribution through model development in one area can be evaluated in another. This exchange and application will allow further assessment of model assumptions and parameterisations as model output deviates from observations.

Other benefits in the proposed EU-US HAB effort include distributing existing and new technologies and skills to wider areas (e.g., models, molecular probes, micropaleontological techniques, automated recognition systems, and remote sensing systems). Additionally, some taxa can be best initially studied in specific institutions or facilities on one side of the Atlantic or the other due to the maintenance of specific cultures or specifically designed and unique institutional capabilities. For example, the discovery of *Pfiesteria* in European waters will lead to investigations of comparative toxicity and life cycles between EU and US clones and strains, and experience gained in the US on safe laboratory maintenance of toxic forms of this organism will greatly benefit European researchers. Historical data records are also distinct to each side of the Atlantic. Interrogation of long time series data across the spectrum of records in the two areas will broaden community ability to ascertain the importance of mesoscale to global processes in plankton populations. For example, aperiodic and unusual deviations in HAB species in one area, such as the oscillation in *Gymnodinium catentatum* that occurs along the northern Iberian Peninsula as a function of the North Atlantic Oscillation, may be similarly identified in other locations, suggesting oceanic or global forcing rather than more local control. This synergy would be impossible without access to multiple data sets across the large geographic areas of the two regions.

The rapid advancement in knowledge provided by community collaboration, rather than individual studies, on a common basin flora is the largest driver for implementation of the proposed EU-US HAB Program. Cross-basin differences in training, approaches, and experiences assure new ideas and insights for each region's investigators, piquing interests and possible explanations for HAB expression.

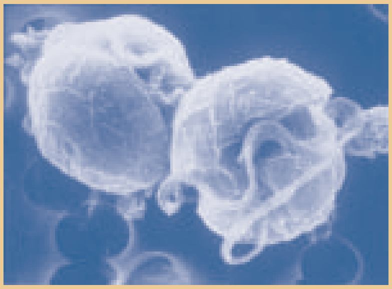
Worldwide distribution of *Pfiesteria*

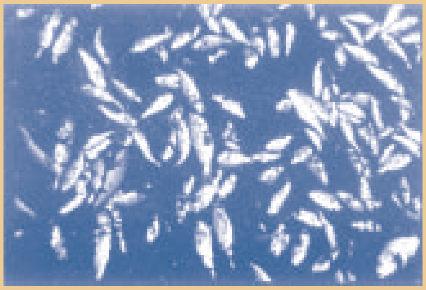
The toxic dinoflagellate *Pfiesteria* has been the subject of much scientific and public press in the U.S., first recognised as a correlate of fish kills in aquaria and in the Abermarle-Pamlico estuaries system of North Carolina beginning in the early 1990s. Large-scale public and legislative attention for this organism did not begin until 1997 when *Pfiesteria*-associated fish kills were documented in the Chesapeake Bay of Maryland.

Since the late 1990s, numerous microscopic, molecular, and physiological studies on this organism have been conducted. Such efforts have established among their many findings that *Pfiesteria* is but one member of a species complex with similar behaviours (Burkholder et al. 1992, 1995). Also, like many species of toxic algae, it has a range of toxicity, and culture strains are now classified according to whether they are toxic, inducible, or benign (Burkholder et al. 2001). Lastly, and of significance to this project, *Pfiesteria* is no longer known as only a U.S. East Coast phenomenon. Not only have isolates of *Pfiesteria* been documented from New Zealand and Australia (Rublee et al. 2002), but most recently, from European waters (Jacobsen et al. 2002). Such findings suggest an organism of cosmopolitan distributions but with the extent of its distribution still to be further elucidated. Some of the factors that are important in the development of a toxic *Pfiesteria* outbreak are: enrichment of nutrients; presence of high density of, preferably, large schools of oily fish; and shallow, warm, brackish water (Burkholder et al. 2001).

The documentation of *Pfiesteria* worldwide now raises several important questions that are relevant for this programme including:

- to what extent is *Pfiesteria* toxic in waters outside the U.S.?
- are similar environmental factors related to *Pfiesteria* prevalence worldwide?
- to what extent are European waters in which *Pfiesteria* is found susceptible to fish kills?





Source: J. Burkholder.

Readiness of the Community to Undertake this Programme

There are many reasons why this is the appropriate time to undertake this programme of bilateral research. Our communities recognise the need to develop and test hypotheses, apply more rigor in field studies and in experimental design, and evaluate basic concepts through comparative ecological surveys. Research in HABs, as in many fields of geo- and biological sciences, has advanced tremendously in recent years through the introduction of new methodologies and technologies. These technologies now allow us to address questions – and pose solutions – that were previously not possible. Furthermore, advances in methodologies and in our understanding of HAB dynamics have come from both Europe and the US, and there are many future gains to be advanced from the sharing of this knowledge. From identification of species and their rapid enumeration, to our ability to monitor physical dynamics of properties on scales relevant to organismal dynamics and to model these processes, the advancements have been large, in part due to the national and multi-national ECOHAB and EUROHAB programmes and other efforts from related fields. These efforts can now best be advanced through international collaborative studies.

Positive identification and enumeration of specific algal species in discrete field samples collected over large temporal and spatial scales is a labour-intensive but necessary process for the characterisation of HABs. New tools in molecular biology and, in particular, the use of molecular probes for rapid species identification has permitted real-time measurements to be made in a manner not previously possible.

Similarly, autonomous observing systems have evolved to sophisticated networks in order to understand physical dynamics of the complex ocean. In the US, examples are the NorthEast Observing System (NEOS) and the Southeast Coastal Ocean Observing System (SEA-COOS), comprising a host of smaller component systems (Glenn et al. 2000a, 2000b). In Europe, examples are Seawatch (1991-1995) and the Poseidon Programme in the Mediterranean Sea. These systems are emerging at the same time that we are coming to realise that temporal coverage and spatial resolution are crucial for unlocking the intricacies of bloom dynamics. Autonomous observing systems have two primary and related purposes: supporting forecasting models through data assimilation and supporting research that leads to greater accuracy in these forecasts. For HABs, this means both the direct detection of blooms or toxins and the detection (and recognition) of the antecedent physical, chemical, and biological conditions that lead to blooms. The introduction of cycling profilers in coastal observing systems represents another example of new operational instrumentation that is applicable for the study of bloom dynamics. The availability of biological and chemical sensors for autonomous, *in situ* measurements of nutrients, several individual HAB species, chlorophyll-*a*, dissolved oxygen, turbulence, and the acoustic detection of fish, has greatly expanded our resolution capabilities.

Figure 7.

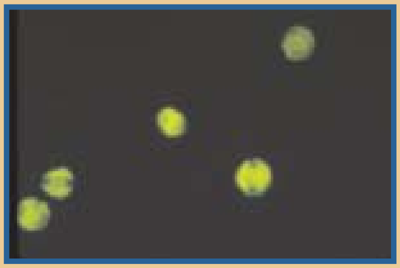
Automated moorings such as this one used in the Chesapeake Bay Observing System can be equipped with sensors to continuously monitor a range of physical, chemical, and biological parameters.

New methods for retrospective detection of organisms have also been developed. These techniques are now allowing us to examine past events, dating back hundreds or thousands of years. Particularly promising are techniques and approaches developed from the emerging field of micropaleontology, or the use of microfossils as indicators of environmental change in the sedimentary record. These represent new applications of well-established methods used in geology.

Molecular probes: Tools for rapid and accurate identification and enumeration of HAB species

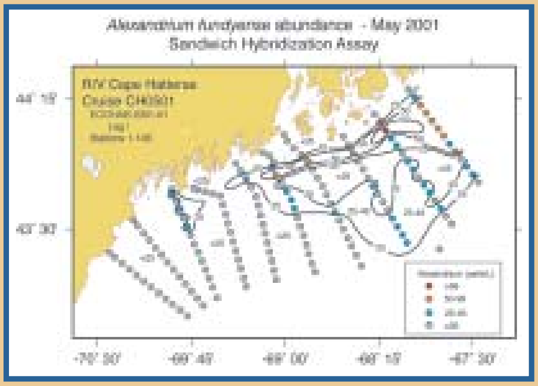
For many years, plankton biologists have been unable to collect data on the distribution and abundance of organisms of interest at temporal and spatial scales that correspond to those possible for chemists and physicists. For the latter, continuous or semi-continuous measurements are possible during cruises or from fixed mooring platforms, allowing high resolution temporal and spatial mapping of the physical and chemical environment. Until recently, this discrepancy between biological *versus* physical or chemical data resolution capabilities has been particularly constraining in studies of HAB dynamics because of the need to obtain data on individual algal species rather than for a bulk community.

Considerable effort has been devoted over the past few years to the development of molecular probes and probe-based assays for HAB species. These are typically either antibody or nucleic acid probes that bind to specific molecules at the cell surface or within the cytoplasm of target cells. The figure to the right shows a plankton sample labelled with a species-specific nucleic acid probe for *Alexandrium fundyense*. The probe binds to unique ribosomal RNA sequences and this binding is then visualised by coupling the probe to a fluorescent molecule that allows easy identification and enumeration of the target cells. Species identification is greatly facilitated and cells can be enumerated rapidly at low power under the microscope.



Alexandrium fundyense **cells labelled with a species-specific oligonucleotide probe that binds to ribosomal RNA within the cell. The labelling is visualised using a fluorescent molecule coupled to the probe. Source: B. Keafer.**

Probe technologies have recently been taken far beyond the level of labelling individual cells for microscopic identification and now permit automated or semi-automated, high-throughput analysis of samples. For example, the sandwich hybridisation assay (SHA) has been used in near real-time mode to map the distribution and abundance of toxic *A. fundyense* cells during large-scale survey cruises in the Gulf of Maine. The figure below shows the cell distribution of this toxic species determined in this manner. These data were obtained on board during a cruise using two SHA processors running 24 hours a day. These technical developments now make it possible to plan and execute large-scale field programmes in which critical biological data can be collected at temporal and spatial scales comparable to those possible for physical or chemical parameters, giving the HAB community the ability to resolve key elements of population dynamics within the context of a complex physical environment.

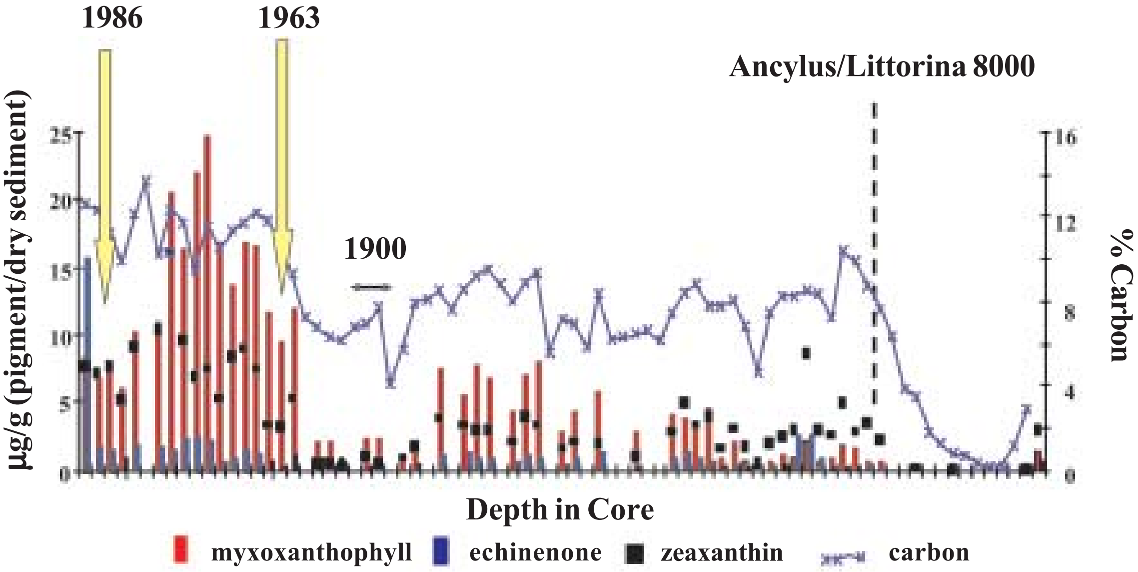


Distribution of *A. fundyense* mapped in near real-time mode using a sandwich hybridisation assay format on automated processors. At the completion of each transect, maps of *Alexandrium* distribution along that transect were available for immediate analysis and interpretation in the context of simultaneous physical and chemical measurements. Source: B. Keafer.

The main groups of species responsible for HABs, diatoms and dinoflagellates, have some species that produce microfossils that can be used in tracing the history of HABs in relation to environmental change. For example, fossil diatoms have been examined to ascertain the history of eutrophication in Chesapeake Bay, while dinoflagellate cysts have been used to examine eutrophication, marine pollution, and climate variability in relation to HABs in coastal waters of Scandinavia. These methods are ready to be applied now on the scale of larger, international research efforts, to determine past responses of HABs to various forms of environmental change (on the scale of tens/few hundreds of years) as a sound basis for estimating and predicting the effects of future global change. For example, through the quantification of cyanobacterial pigments accumulated in different sediment layers in the Baltic Sea over a 7000 year period, it was possible to track that blooms of this HAB group more than doubled from 1963 on (Poutanen and Nikkilä 2001). Application in other systems across the two continents offers excellent opportunities for identification of similar HAB forcing functions.

Figure 8.

Distribution of specific cyanobacterial pigments and percent carbon in sediment from the Gotland Deep, Baltic Sea Proper as a function of depth in a core. The core depth correlates with a time scale of about 10000 years. About 8000 years ago, there was a transition from the freshwater Ancylus Lake to the brackish Litorina Sea. In the mid-1960s, the frequency of blooms increased dramatically.



Source: Redrawn from Poutanen and Nikkilä 2001.

Models have also advanced. Models can be used to: 1) test hypotheses concerning bloom dynamics underlying observations; 2) diagnose dynamics from data; 3) design field sampling programmes; and 4) make predictions concerning HAB dynamics. There is much to be gained from EU-US collaboration in the area of modelling, since the level of model development and application for different HAB species and physical habitats differs for different systems. Approaches, algorithms, and experience are ready to be shared to accelerate progress in this rapidly advancing area of HAB research.

Thus, the scales of the approaches available now match the scales of the HAB phenomena, and new tools are available for addressing questions more comprehensively than has been previously possible. From intracellular responses to variable nutrients, light, temperature, and salinity to population shifts that accompany seasonal to decadal changes in the surrounding environment, tools from both the EU and the US can be applied to collect similar data sets with identical approaches to ensure data comparability. There is much we can learn from each other.

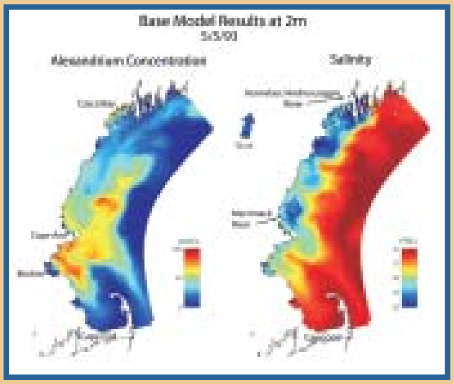
Modelling of harmful algal blooms

Early models of HABs were used to test simple hypotheses of dynamics underlying a variety of observations. The interaction of swimming behaviour and water flows due to the passage of internal waves, for example, was shown to be responsible for the formation of dense bands of dinoflagellates that propagated onshore during blooms. Other models pointed out the potential importance of grazing pressure or sudden changes in phytoplankton growth rate in initiating dense algal blooms. The predictions of such models can be, and often have been, tested in the field. Even when the field and lab tests lead to the rejection of the model, the results usually lend further insight into the processes controlling HABs.

Models are now being used as platforms for the synthesis of diverse types of data (physical, meteorological, topographic, biological, physiological, photochemical, biogeochemical, etc.). These syntheses can then be explored numerically to understand the contribution of various processes to the observations. Techniques such as adjoint data assimilation allow quantitative, statistical inferences to be drawn concerning dynamics that were not measured, or were difficult or impossible to measure. Various types of other field data (measurements of wind, insolation, currents, temperature, chlorophyll fluorescence, etc.) are continuously incorporated into model simulations, much as weather observations are incorporated into weather models. These models can then be run forward in time to provide short-term forecasts of bloom dynamics, particularly bloom transport, in response to external forcings. While initial studies will require substantial field programmes to generate sufficient data to test model forecast skill with and without data assimilation, ultimately such models may become operational tools for management purposes.

Model simulations serve as a continuous space/time representation of reality. These models can be sub-sampled in the same manner as a field programme, with limited spatial and temporal resolution. Comparison between the original and sub-sampled fields then provides a means of understanding the limitations of a given sampling strategy.

While models have been applied to HABs around the world, one well-studied/modelled bloom is *Alexandrium fundyense* in the Gulf of Maine. The intimate interaction of laboratory experiments, field sampling, and models has helped to generate a fundamental understanding of the dynamics underlying growth, transport, and landfall of the toxic blooms. Models are being used to test hypotheses concerning bloom initiation and demise, and to explore the utility of the sampling programme in generating statistically meaningful data.



Results from a prognostic model of *Alexandrium* in the Gulf of Maine. The left panel shows predicted cell concentrations a month after the start of the model run. The right panel shows the salinity structure, including the coastal buoyant plume that tends to advect the cells alongshore. The plume and entrained cells are strongly influenced by wind and topography. Models such as this can be used to diagnose the importance of physical and biological dynamics to the observed and predicted cell concentrations, to design sampling programmes, and to infer rates based on statistical comparisons of models and data. Source: C. Stock.

Physical-biological coupled models are not the only approach. A "fuzzy logic" model has been developed for the North Sea (http://www.HABES.net). Other models, such as box models, or N-P-Z (Nutrient-Phytoplankton-Zooplankton) have been applied to HAB systems to yield insight into the role of nutrients, or the outcome of competitor species with different nutrient kinetics (Stickney et al. 1999; Zhang et al. 2002). For example, the population dynamics of toxic *Pfiesteria* have been differentiated from non-inducible strains of *Pfiesteria* using such models (Zhang et al. 2002). Further applications of such models are needed in both the EU and US for other HABs.

Educational Opportunities

The proposed EU-US Scientific Initiative on HABs will provide unique educational and training opportunities for both communities. For example, the critical problem of declining phytoplankton systematic expertise in the US research community (OEUVRE 1998) could be partially alleviated by joint phytoplankton training courses, incorporating classical and molecular techniques. Developing technologies such as *in situ* measurements, real-time biosensors, and remote sensing can advance far more rapidly when such technologies are tested and calibrated in comparable ecosystems, or on apparently similar species in different regions. In some cases, methodologies are being developed in only one or two laboratories worldwide, and opportunities to learn such techniques may require training by the developing laboratory. For example, some micropaleontological methods have only recently been developed in Europe.

A high level of collaboration between the EU and US researchers is essential to the success of this proposed programme. Participants will be encouraged to plan for collaborative exchanges as part of research proposals using existing funding mechanisms. In addition, simplified, supported investigator and post-doctoral exchange (expanding existing programmes such as the EU Human Capital and Mobility Programme and the NSF's International Program activities) would be huge steps forward in further fostering this collaborative effort.

Finally, one of the unique aspects of a collaborative HAB programme is the potential opportunity for staff development. Environmental managers and policy makers in both regions have technologies and experiences to share that could be of scientific and economic benefit to other regions developing management strategies.

Intersection with Other National/International Programmes

The proposed EU-US Scientific Initiative on HABs shares some common goals with several other international collaborative programmes. However, those programmes cannot replace the effort proposed here: the EU-US joint programme is uniquely poised to study the physical, chemical, and biological processes associated with HAB dynamics, and to apply appropriate models toward their prediction. None of the related programmes focus on algal species dynamics within physical and/or geochemical contexts. Co-operation with other international programmes will be developed to the extent possible, through shared meetings, and joint research, while recognizing the ultimate goals of each of these programs.

The **Global Ocean Observing System (GOOS)** shares important technologies in long-term continuous monitoring of environmental conditions. Through shared platforms, shared data, and predictive capabilities, GOOS is a natural partner for many of the planned objectives for the proposed EU-US HAB programme.

The **OCEANS** project is developing as a focal point for the study of carbon biogeochemistry and oceans. Many of the processes and fluxes that are of interest to carbon cycling are also of interest to the development of HAB populations.

The **GLOBEC** Program is focused on investigating the productivity of zooplankton and fish in marine environments. As changes in community dynamics, particularly the grazing community, are considered to be important in HAB population dynamics, data derived from the GLOBEC Program will be relevant to many aspects of the proposed EU-US HAB programme.

Two US programmes are also related. The NSF **Biocomplexity in the Environment Program** has many objectives related to human impacts, biogeochemistry, and technology development, as they impact the richness and diversity of biological systems. Furthermore, the **Oceans and Human Health** initiative is aimed at furthering our knowledge of the human health impacts of HABs and pathogens from the oceans.

In summary, the strengths of the proposed EU-US collaborative programme on HABs include:

- **Each community has established regional research programmes (EUROHAB, ECOHAB)**
- **The scientific questions are of mutual concern with mutual benefits to be derived**
- **New research tools have advanced significantly and can be applied**
- **Unique educational and training opportunities are provided**
- **The programme intersects with many other research priorities and will thus involve the larger scientific community**

This is the next phase in multi-disciplinary, collaborative HAB research in addressing complex ecological problems inherent to these unique events.

Recommendations for Future Research Implementation

This document is the first planning document for the proposed EU-US Scientific Initiative on HABs and is intended to announce and outline the exciting opportunities provided to the wider scientific community.

Plans are to communicate the programme through several commonly accessed websites, such as those maintained by the European Commission (http://europa.eu.int/comm/research/index_en.html) and the Woods Hole National HAB office (http://www.whoi.edu/redtide/). In addition, discussions will be presented at national and international scientific meetings through posters, printed materials, or "town meetings". This should allow initial implementation of the programme in the 2003-2004 timeframe. Additional workshops, international meetings, and symposia will be developed as necessary to implement and co-ordinate research activities.

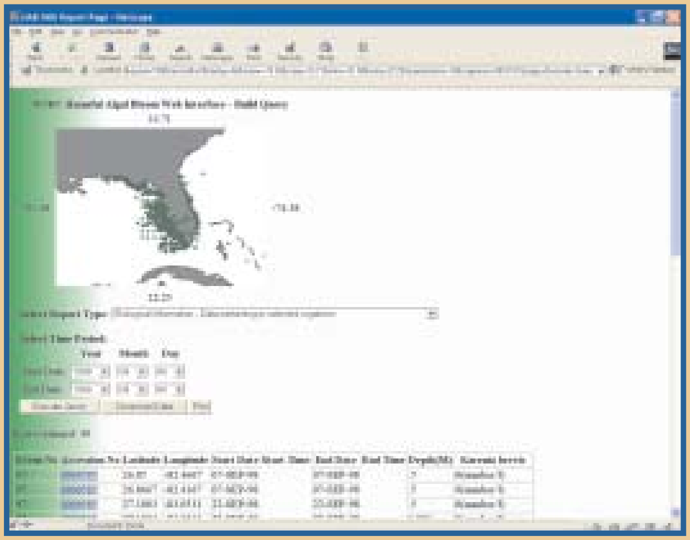
Discussions are underway at the EC and at the NSF to plan implementation. From research to co-ordination of research activities, the EU-US communities perceive several issues that require resolution:

- Co-ordination of announcements of calls for proposals and joint evaluation of proposals. Proposals must be considered within the same time frame to ensure effective collaboration.
- Joint opportunities for ship time applications. Greater flexibility must be available for funding joint cruises.
- Joint and co-ordinated access to remote sensing and other databases. There are some data that are more accessible within each of the partners than between them.

The ability to share data sets and to create, share, and analyse a wide range of environmental data types will be absolutely essential to this proposed programme. There has been a modest start on organising special purpose HAB data sets, but this effort will need to be vastly expanded to incorporate the range of environmental data available to EU and US researchers. With the development of new technologies for studying bloom or species dynamics and their incorporation as part of coastal observatories, the communities will have the potential to collect a vast amount of environmental data. Agencies such as NSF have anticipated this need and plan for ambitious

HAB data and data management

The collection of environmental data to investigate the initiation, occurrence, and demise of phytoplankton blooms is relevant to researchers and resource managers focusing on bloom events as well the general scientific community interested in defining mechanisms responsible for bloom formation and dissipation. Data describing the physical and chemical mechanisms for bloom transport and initiation (e.g., wind/current speed and direction, river discharge, precipitation, temperature, salinity, nutrients, etc.) in addition to biological measurements pertaining to species composition and abundance are key to understanding the underlying mechanisms fostering, or alternatively, preventing bloom expression. Given the reality that environmental issues of local importance, such as HABs, are not confined to legal jurisdictions or the missions of any one government, international collaboration is necessary for understanding these phenomena.



Approaches for archiving and distributing environmental data are now available. Considerable experience in data management and retrieval mechanisms has been gained in other international collaborative programs. For general dissemination of originators' data sets, a flat file system such as that used by GLOBEC and JGOFS is sufficient. In this model, ASCII text files are submitted to an identified hub for distribution to all investigators in the programme (Groman and Wiebe 1997). However, correlations between various parameters are often difficult to produce from a flat file system, as data from different principal investigators are not always compatible. For instance, the data may need to be converted to standard units, in order for any analysis to be meaningful. Once a central repository has been established, the development of a relational database from the flat files may prove more fruitful. A relational database allows a user to narrow down their search for data to particular parameters, locations, time periods, etc. Two relational databases for HAB information have been developed to date, the United States National HAB Data Management System (see figure above; http://www.nodc.noaa.gov/col/projects/habs/index.html) for HAB specific field data, and the IOC's HAEDAT database (http://ioc.unesco.org/hab/data3.htm#1) which stores information pertaining to harmful algal events. From a relational database structure, visual products (e.g., time series plots, geo-referenced maps, etc.) can be developed which help to communicate study results to the public and/or provide needed products to resource managers. Specific examples include the use of integrated data sets in detecting and forecasting blooms (e.g., the United States HABSOS pilot project) and the development of decadal maps of harmful algal events (http://www.ifremer.fr/envlit/documentation/dossiers/ciem/aindex.htm).

programmes to provide the needed cyber-infrastructure. Parallel efforts have also begun in the EU, for example, under the auspices of the Scientific Committee on Oceanic Research (SCOR). For implementation of this proposed programme, data management efforts must ensure equal accessibility and compatibility.

The strength of the proposed EU-US Scientific Initiative is that it builds on studies underway in both the US and the EU. The communities are prepared to share research material, tools, data, cultures, probes, and model code. Opportunities await to be exploited in terms of joint experiments in different regions using the same techniques.

III. Proposed Collaborative Initiative

Overarching Hypothesis and Objectives

The proposed collaborative EU-US Scientific Initiative on HABs builds on the recognition that within the EU and US, comparable systems and comparable species driven by similar factors are found, as are systems in which the relative impacts of particular forcing functions differ, leading to HABs of varying duration, toxicity, or extent.

More formally stated, the overarching hypothesis for this proposed programme is:

Varying forcing functions, including physical dynamics, climate change, nutrient loading and other anthropogenic influences, and reductions or changes in the grazing community, select for different functional groups of HABs in several distinct oceanographic systems. This selection, and the resulting bloom and population dynamics of those groups, are a consequence of these multiple forcings and the physiological, behavioural, and trophodynamic interactions of the HAB taxa.

In the following sections of this document, several major issues are described that have a high probability of yielding new insights in HAB dynamics because of the comparative approach.

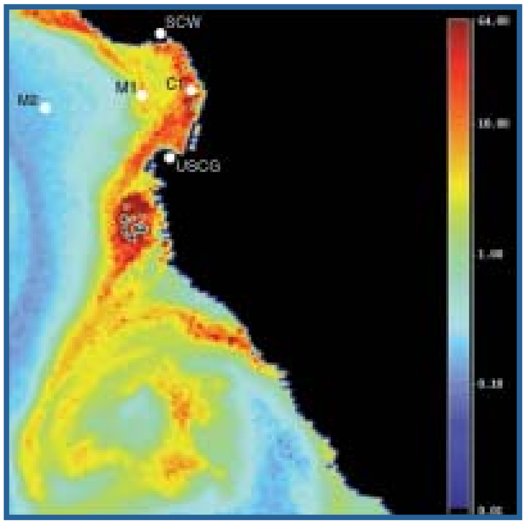
Two broad hydrographic regimes have been identified as example systems: open coastal or basin-scale systems, and enclosed or semi-enclosed systems. While many exceptions exist, open coastal systems are more commonly subject to toxic outbreaks, whereas enclosed or semi-enclosed systems are more commonly subject to high biomass blooms. Several unique objectives for these system types and several cross-cutting objectives have been identified.

Within each of these two general regimes, the types of species that develop are a function of the organisms' abilities to accommodate variable light and nutrient regimes, and to adjust to the hydrographic regime. For example, in one approach (Smayda and Reynolds 2001), three primary adaptive strategies, termed C-S-R strategies, are suggested. In chemically-disturbed (i.e. nutrient enriched) regions, the predominant blooms species are typically invasive – C- strategies – colonist species. In oligotrophic, highly-stratified water masses, S-strategies species predominate. R-strategies are mixing-drift adapted and disturbance-tolerant species that occur in and tolerate the shear/stress forces of physically-disturbed water masses and coastal currents. Identifying common HAB expressions to these regimes across the diverse pelagic habitats of the open coastal and semi-enclosed basins between the two continents provides extremely fertile areas for collaborative research.

The scientific community will ultimately determine the focus of this programme through submission of proposals within this framework and through their peer evaluation based on merit criteria.

Figure 9.

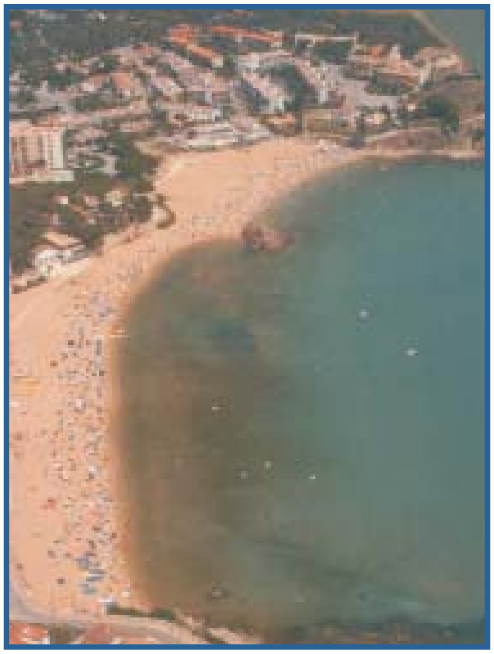
Upwelling-derived bloom off southern California in May, 1998. The upwelling of nutrients and subsequent alongshore transport resulted in *Pseudo-nitzschia* blooms, with domoic acid-producing *P. australis* leading to sea lion, sea otter, and bird deaths for the region.



Source: Scholin et al. 2000.

Figure 10.

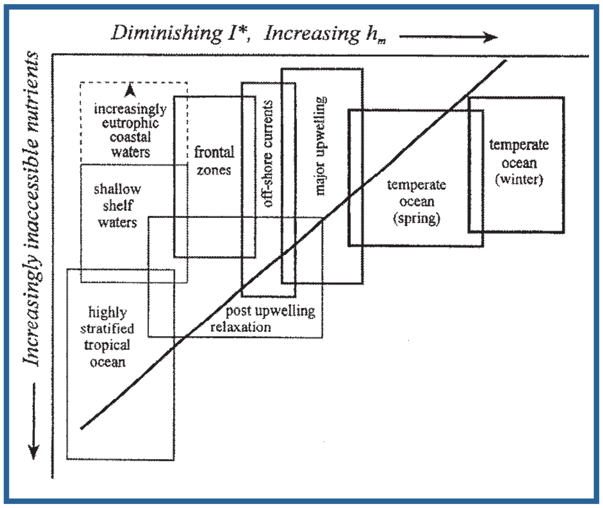
A bloom of *Alexandrium taylori* in La Fosca, a small bay on the Catalan coast, Spain. The Catalan coast is undergoing extensive development with runoff leading to elevated nutrient loads into the semi-enclosed harbours. Circulation within these basins ensures recurrent blooms and increasing problems for this Spanish tourist centre.



Source: ACA (Catalan Water Agency).

Figure 11.

Marine pelagial habitats as a function of light and nutrient fields (Smayda and Reynolds 2001). These habitats select for HAB species, functional groups, or life forms and reflect the abilities of the species to grow as physics or behaviour alter vertical distributions and growth potential in all hydrographic regimes.



Source: Smayda and Reynolds 2001.

IV. Studies in Open Coastal or Basin-Scale Systems

General System Description

In the context of the comparative ecosystems approach, open coastal and basin-scale systems, in general, are those more likely to be controlled by meso- to large scale physical processes than are enclosed or semi-enclosed systems. Thus, understanding the dynamics of HABs in these dynamic systems may require a special focus on bio-physical coupling processes. These may include biological mechanisms that allow a species to survive and proliferate within these systems (e.g., resting cell formation or vertical migration), physical dynamics that lead to local accumulation or concentration of populations (e.g., eddies and/or stratified, thin layers), as well as advective processes that may transport blooms and cause harmful effects distant from where the blooms initially develop.

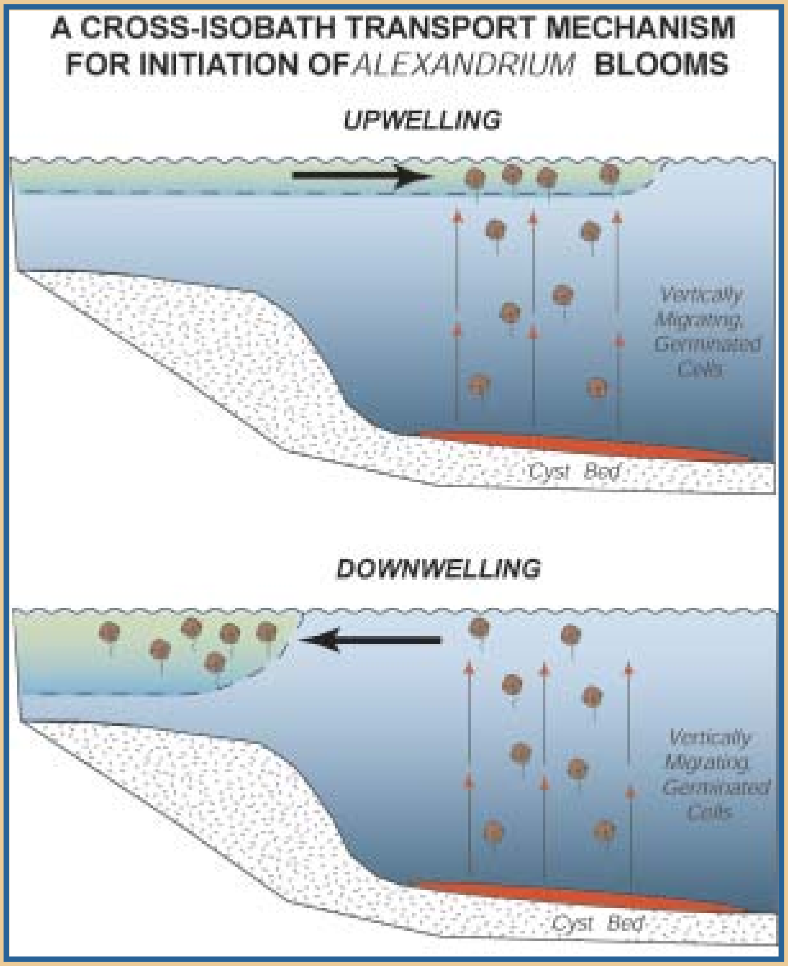
Open coastal regions impacted by HABs include narrow, steep, upwelling-dominated regions along eastern boundary currents such as the west coast of the United States and the Atlantic coast of Spain and Portugal, and regions where upwelling is not dominant, such as the broad, shallow North Sea region (including Skagerrak and Kattegat), the buoyancy-driven Norwegian Coastal Current, and the Louisiana-Texas coastal current.

Although currents and water properties may frequently be similar across relatively large distances (100s of kilometres), mesoscale ocean circulation features such as eddies occur frequently and may be critical for plankton dynamics such as bloom initiation, retention, and transport. For example, blooms of *Chattonella* have been trapped in mesoscale eddies preventing further advection along the Norwegian coast and limiting the effects of HAB events. Other features are also important. Convergence at fronts associated with upwelling (e.g., Spain; Prego 1992), or with river plumes, may increase plankton density or subduct blooms beneath the surface. In the Spanish rias, wind-driven circulation may resuspend cysts from the sediment, while fronts contribute to dense accumulation of cells. Density differences in regional water masses may cause sub-surface advection of blooms from one region to another, such as the circulation in the Skagerrak region where surface water from the Jutland region may occur subsurface along the coast of southern Norway. In other situations, frontal jets may increase the alongshore transport of harmful blooms and cause inshore blooms or be diverted offshore due to prominent coastal headlands, indicating the importance of coastal features in enhancing or reducing HABs and their impacts. Tidal fronts, formed at the abutment of stratified offshore water and tidally-mixed inshore waters, have been shown to be sites of dense accumulations of HABs (Pingree et al. 1975).

For coasts along eastern boundary currents, nutrients are supplied primarily via upwelling from nutrient-rich deeper ocean layers. These regions are dominated by a strong seasonal cycle, punctuated by episodic nutrient infusion as along-shelf wind stress strengthens, weakens, or reverses direction. In many other coastal current systems not characterised by upwelling, the early spring bloom is supplied with nutrients through winter mixing with deeper layers. After the seasonal development of stratification, nutrient delivery in these coastal areas continues through river and fjord input as well as localised tidal and wind-driven mixing.

Interactions between organism behaviour and physics in *Alexandrium* blooms

During field and modelling studies of *Alexandrium fundyense* bloom dynamics in the Gulf of Maine, a number of important physical and biological mechanisms have been highlighted that are critical to toxic bloom initiation and development. One relates to the manner in which dormant *Alexandrium* cysts germinating in bottom sediments far from shore are able to contribute to the blooms in nearshore waters (and in particular, in a coastally-trapped, buoyant, coastal current; Franks and Anderson 1992). Mapping surveys of bottom sediments revealed a large cyst "seedbed" located offshore of Casco and Penobscot Bays in waters 150 metres deep. These deep cysts are as much as 20X more abundant than the cysts in shallow waters, so the question arose as to whether they played any role in bloom initiation, and if so, how, given their distance offshore. Direct measurements of cyst germination fluxes were not possible (highlighting an important area for future research), but it was possible to explore germination inputs using laboratory-derived data on *A. fundyense* cysts in the germination module of a coupled physical/biological model of the region. Careful inspection of the model simulations revealed a previously unrecognised entrainment mechanism resulting from a combination of organism behaviour and the wind-driven response of a surface-trapped plume of low salinity water originating from riverine sources (McGillicuddy et al. submitted ms.). During upwelling-favourable winds, the plume thins vertically and extends offshore, overlying the cyst seedbeds. *Alexandrium* cells arising from germinated cysts swim towards the light, enter the thin surface layer, and are then transported back towards shore with downwelling-favourable winds. This is but one of several instances in which organism behaviour interacts with the physical environment in ways that are critical to bloom development.



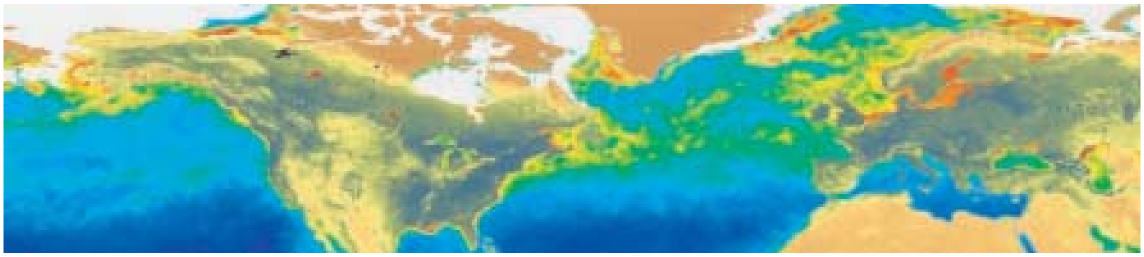
Source: D. Anderson and B. Keafer.

Physical processes operating in conjunction with bloom dynamics may also lead to accumulations of HABs in "retention zones". Physical circulations that create these zones may isolate waters with unique chemical, biological, and physical characteristics, or allow modification of those waters through changes in stratification, nutrient concentrations, and ecosystem structure. These properties, along with the residence time of the retention zones, determine the cell concentration (and thus the potential toxicity for adjacent areas) as well as the potential for density-dependent dynamics (sexual exchange, toxin accumulation, grazer deterrence) within the retention zone. Transport from these zones to other regions along the coast can lead to sudden onset of HAB toxicity, unrelated to local growth processes. Retention zones in different coastal areas must thus be identified, their physical and biological dynamics (exchange rates, growth rates) quantified and compared to non-retentive areas, and their importance to bloom dynamics assessed.

In hydrographically-dynamic systems, the interaction of HAB life histories with physical transport is a fundamental aspect of bloom initiation: a HAB species' inoculum must reach the waters in which it ultimately grows since, in a dynamic coastal system, the location of the seed source may not be coincident with the bloom region. The transport pathways for newly-excysted organisms in coastal blooms present some interesting contrasts across geographic regions and dominant physical forcings. The importance of cyst seedbeds to bloom initiation remains largely unquantified on both sides of the Atlantic. Likewise, the depth to which cysts germinate in the sediments, their ability to "escape" the overlying sand, silt, and clay particles of the bottom that impede them as they endeavour to swim upward, and the extent to which cysts and spores are resuspended into the water column as an alternative mode for germination and inoculation, all remain important unknowns that can now be investigated.

Figure 12.

SeaWIFS image of the high pigment concentrations in the EU and US. Many of these high pigment regions also experience HAB events.



Source: Modified from NASA SeaWiFS: http://seawifs.gsfc.nasa.gov.

Thus, a key research issue for open coastal or basin-scale systems is:

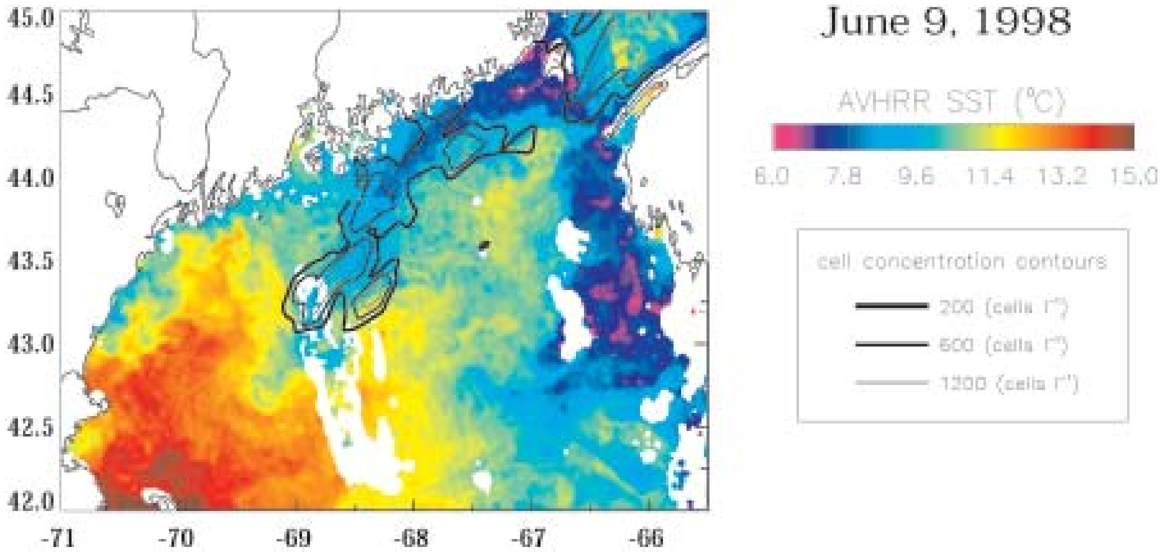
What are the relative roles of physics and biology in determining HAB bloom dynamics?

Example Comparative Studies

Dinoflagellates within the *Alexandrium* genus offer abundant opportunities for comparative studies between the US and the EU, as they bloom in the US and Europe in regions with wide and narrow shelves, with episodic and seasonal upwelling, and with deep and shallow cyst beds. Alongshore transport is fundamental to the local formation of blooms of *Alexandrium* in the Gulf of Maine (Figure 13) and *Gymnodinium* in the Galician rias of Spain. Certain similarities between the hydrography, meteorology, and patterns of PSP in California and northwest Spain are noteworthy. In both areas, the dominant hydrographic feature is coastal upwelling, driven by persistent northerly 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). Toxicity also tends to increase far faster than is possible from localised, *in situ* growth of the causative dinoflagellates. Comparative studies developed for understanding the linkage between large-scale physical forcing and the pattern of PSP are required.

Figure 13.

Satellite image of sea surface temperature (colours) with contours of *Alexandrium fundyense* cell concentrations (black lines), showing the association of the bloom population with the Eastern Maine coastal current (EMCC) in the Gulf of Maine. *Alexandrium* cells do not grow well in the cold, well-mixed portions of the EMCC (dark blue), but growth is possible when the waters warm and stratify. The alongshore and offshore transport of *Alexandrium* cells in this system covers several hundred kilometres and is critical to an understanding of the patterns of PSP in the region (Townsend et al. 2001).



Source: R. Luerssen and A. Thomas.

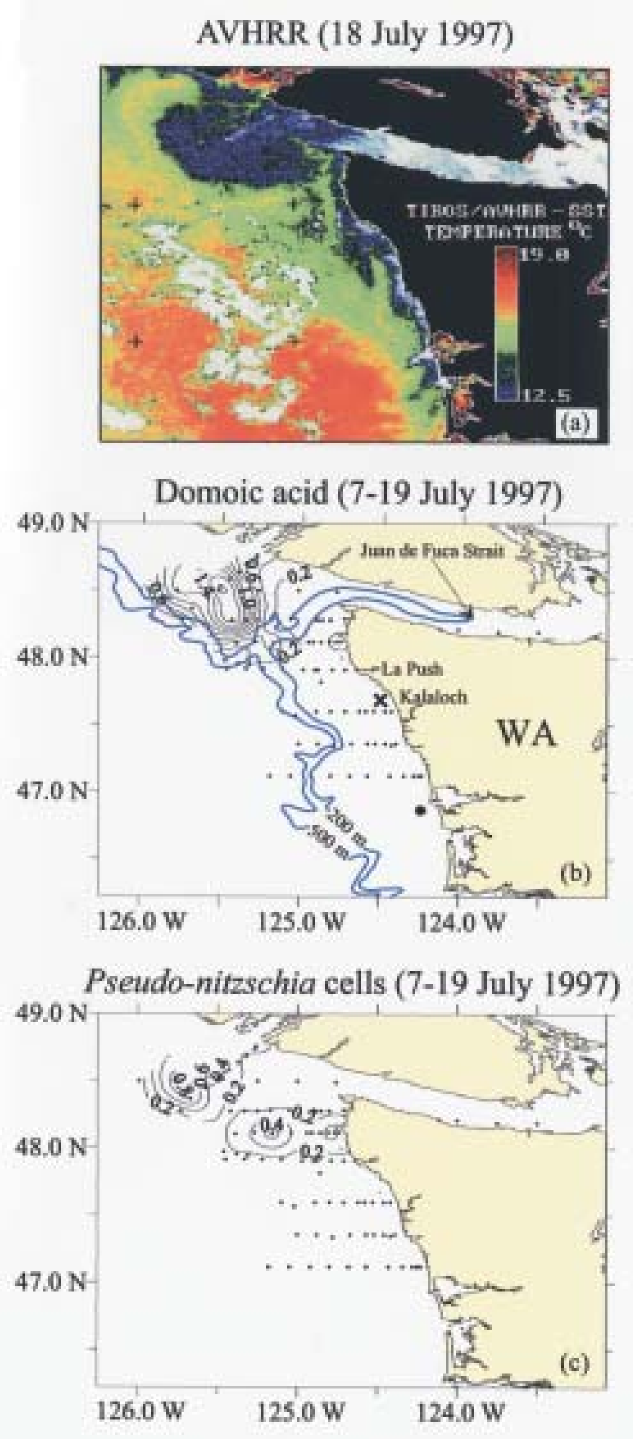
The potential importance of retention zones is recognised in the domoic acid-producing diatom *Pseudo-nitzschia*. As shown in Figure 14, along the US Pacific Northwest coast, the Juan de Fuca Eddy is hypothesised to serve as a refuge or accumulation zone for *Pseudo-nitzschia* cells that eventually can cause toxicity along the coast several hundred kilometres away. Studies of *Pseudo-nitzschia* in European waters, such as along the Irish coast, can provide evidence of alternative mechanisms through which this species initiates blooms in other habitats. The reasons these retention zones are different with respect to HAB species represents a fertile area for future study.

Once a bloom is initiated, physical processes controlling bloom transport are of paramount importance. Coastal currents driven by wind, buoyancy, or remote forcings can transport blooms hundreds or even thousands of kilometres along the coast, often from one management area to another. Understanding the physical dynamics underlying these transport pathways is essential to effective management and mitigation of HAB effects. For example, *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. Similarly, *K. mikimotoi* is transported in coastal currents along the northwest European continental shelf.

Processes at much smaller scales within the large scale features are equally important to potential HAB expression. The study of small-scale patchiness of planktonic organisms requires emerging technologies, currently being developed both in the US and Europe. The thin-layer fine

Figure 14.

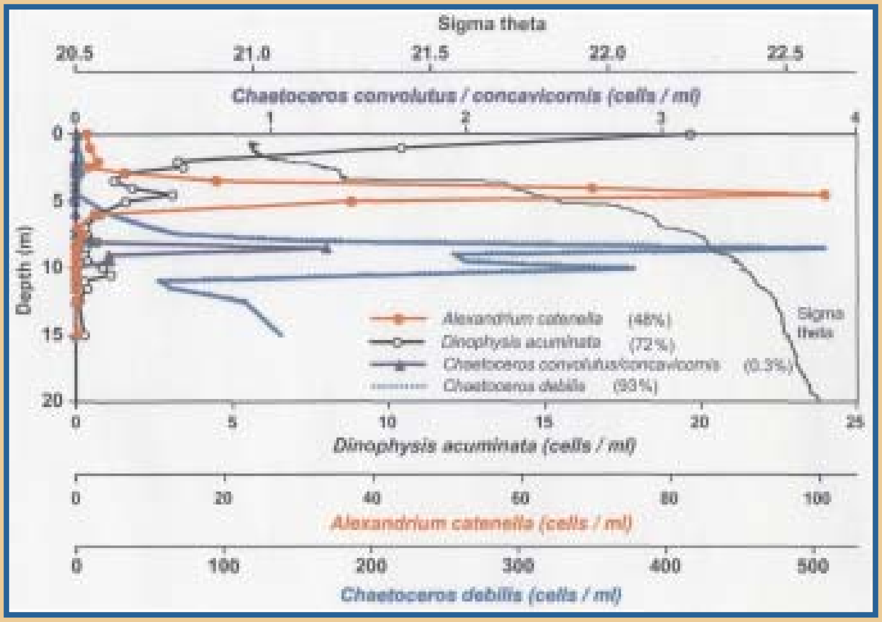
Sea surface temperature (AVHRR) imagery, domoic acid (micrograms per L), and *Pseudo nitzschia* concentrations (millions of cells per L) in the Juan de Fuca eddy region off the Washington State coast (modified from Trainer et al. 2002).



spatial scale sampling technologies developed in the US Thin Layers Program (e.g., Donaghay et al. submitted) complement the efforts on-going in Europe (e.g., Marcaillou et al. 2000) and provide platforms for potential expanded capabilities through probe and toxin detection additions.

Aggregation of HABs in thin layers

It is now recognized that HABs frequently occur in thin layers – dense, subsurface aggregations of cells (< 1m) that are often associated with density discontinuities. Elucidation of the mechanisms important in layer formation and their role in bloom dynamics and toxin development is essential to our understanding of many bloom events. Key questions include: What are the physical mechanisms allowing the establishment and duration of these structures? How are toxic populations delivered to the coast via these layers? What are the physical processes controlling dispersal? These questions are related to sub-grid formulations (formulations of viscosity, advection of limit layers, pycnocline layering) and thus represent a difficult challenge for physicists from both theoretical and modelling perspectives. In terms of biology, these layers obviously provide an adequate niche for the HAB species and detailed studies would therefore allow us to better understand the adaptive strategies involved, such as the mixotrophic potential of the HAB species. Thin layers are quite difficult to study, however, as most instruments are not suited for such fine resolution and many measurement methods will disrupt the very structure being sampled. Furthermore, thin layer investigations require a range of expertise from physics to instrumentation and ecology, given the diversity of processes involved. This is an obvious area where an effective collaboration among a community of highly skilled workers using specialised methods is needed, and this is best supplied through international co-operation. Such collaborations may build on expertise developed by those studying thin layers of *Pseudo-nitzschia* and *Alexandrium* in the East Sound of Washington, (Donaghay et al. submitted) or of *Dinophysis* species off the Brittany coast, France (Marcaillou et al. 2000). There is an obvious need for comparison and calibration of the varied types of instrumentation. This can only be achieved through multi-national workshops and cruises.



Thin layers of harmful algae observed in East Sound, WA in August 1997 overlain on vertical density structure and the vertical distribution of *Chaetoceros debilis. Alexandrium catenella* and *Dinophysis acuminata* were the dominant net plankton at the depth of their thin layer (making up 72% and 48% of the net plankton, respectively). In contrast, the thin layer of *Chaetoceros convolutus/concavicornis* occurred at the same depth as the much more abundant *C. debilis* (making up 0.3% and 93% of the net plankton, respectively). Note that while the concentrations of *C. convolutus/concavicornis* are low, they are just below the 2 cell/ml level reported to cause problems in fish. Source: Donaghay et al. (submitted).

V. Studies in Enclosed or Semi-Enclosed Systems

General System Description

Enclosed and semi-enclosed coastal systems tend to retain materials introduced from land or from the adjacent ocean. Ranging in scale from the Gulf of Mexico/ Mediterranean/Baltic Seas, to large estuaries such as the Chesapeake Bay, to lagoons and small harbours, they share a susceptibility to bloom phenomena not only through their relatively shallow depths and restrictive circulations, but to pulsed delivery of fresh water and nutrients from land runoff and atmospheric deposition. In enclosed and semi-enclosed systems the driving forces behind the initiation and success of a specific HAB species are a combination of physical, meteorological, chemical, and the intrinsic biological characteristics of the algae themselves. The most important physical process enabling species to survive is the stability of the water column. The introduction of buoyant fresh water stratifies the system, isolating the depths from vertical exchange and the replenishment of oxygen, and creates convergent circulation features such as fronts that may actively contribute to bloom formation. In addition, freshwater delivery sets up seaward gradients (salinity, nutrients), and thereby, a progression of habitats within which varying species subsist, falter, or thrive.

The retentive nature of enclosed and semi-enclosed coastal systems arises from more than the confining coastal boundaries. Sills, shoals, and banks restrict communication with the open ocean and produce long residence times in the deeper reaches of estuaries, fjords, or embayments protected by such features. The Baltic Sea, an area subject to massive cyanobacteria blooms (Figure 15), represents an extreme in this respect, with episodic deep-water renewal events occurring on decadal scales. The classic estuarine two-layer flow driven by freshwater runoff is often the most effective mode of exchange, especially in systems such as partially-mixed estuaries, where the strength of the circulation can be an order of magnitude greater than the entering rivers. On short time scales, however, wind often dominates, driving strong flows within the system and vigorous exchange with the adjacent ocean. This exchange occurs both through direct wind-driven currents and also through wind-driven water-level differences between the enclosed basin and the adjacent ocean. These same winds can force upwelling in the adjacent ocean which, in turn, creates gravity-current exchanges and overturn in the semi-enclosed basin. Wind also acts to regulate these exchanges through modification

Figure 15.

Massive high biomass cyanobacteria blooms are frequent in the Baltic Sea.

Source: K. Konnonen.

of coastal currents in the vicinity of entrances. In smaller estuaries, lagoons, and harbours, this exchange can occur as a rapid density-driven overturn much like the two-layer transient flow that occurs after the opening of a lock in a sea-level canal. Further, in these smaller and shallower systems, the regular rise and fall of the tide is often the dominant mode of exchange. All of these features have a direct effect on HAB development, persistence, and dissipation.

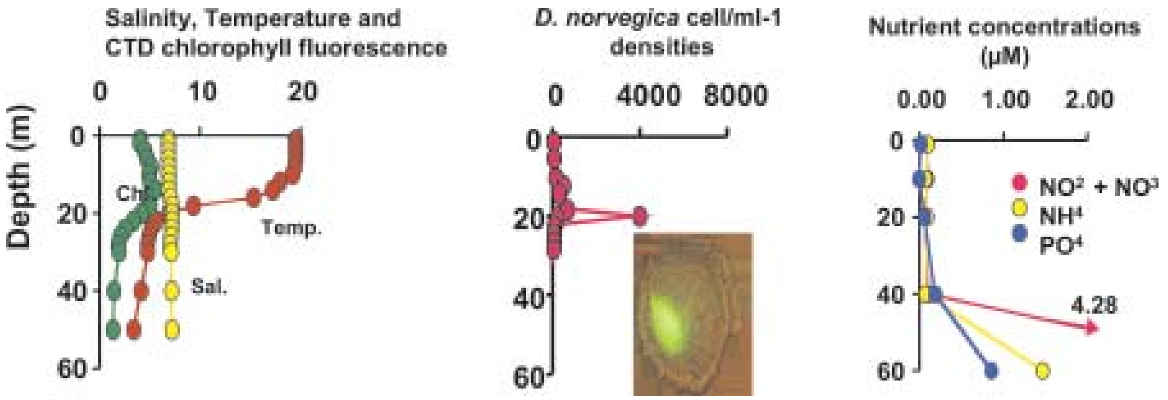
Pulsed inputs of buoyant water from rivers and dense water from the adjacent shelf also foster the development of convergent features that may serve to accumulate plankton and other water-borne materials. In smaller systems, these features may result from stratified flow interaction with the topography, such as the turbidity maximum zone, topographically locked fronts, or hydraulic controls. In larger systems, such as the Baltic Sea, the rotation of the earth acts to retain buoyant coastal currents along the coast, or to sustain frontal structures. Owing to its large scale, the Baltic comprises a weak estuarine circulation with an energetic mesoscale circulation (coastal jets, upwelling, eddies, fronts) which controls the exchange between the coastal zone and deeper basins. Thus, the Baltic has some features of both a semi-enclosed and an open coastal system.

The benthos in these basins is very important and is a unique regulator for harmful algae expressions in some environments but not others. For example, in two larger semi-enclosed basins of the US and EU, the Chesapeake Bay and the Baltic Sea, respectively, summer productivity is governed by recycled nutrients from sub-pycnocline and benthic sediments. In the Baltic Sea, phosphorus introduced from below supports blooms of *Aphanizomenon* and *Nodularia* while in the Chesapeake Bay, either short-duration diatom increases are noted or longer-lasting dinoflagellate blooms occur in response to the introduced nutrient pulses.

Fine scale aggregation, e.g., thin layers, might also ensure success of a species, and, ultimately, seed populations for bloom expression in stratified semi-enclosed basins. For example, *Dinophysis norvegica* can grow and persist in the Baltic Sea thermocline at 20 metres during the summer months, reaching more than 100 cells per ml, similar to thin layers of the same organism in East Sound, Washington (P. Donoghay, personal communication). In the Baltic Sea, *Dinophysis* spp. can attain growth rates of up to 0.4 per day during calm conditions. Photosynthesis provides carbon to sustain growth rates only up to 0.1 per day at these depths. A plausible explanation for the higher growth rates than can be sustained on photosynthesis alone is the ingestion of prey or other substrates accumulating at the thermocline (Figure 16).

Figure 16.

Accumulation of *Dinophysis norvegica* cells in a thin layer at ca 20 metre depth, with temperature, salinity, chlorophyll fluorescence and nutrient profiles in the Baltic Sea Proper during July 14-15, 1999.



Source: Redrawn from Gisselson et al. 2002.

Stratified, enclosed basins also produce nutrient conditions favouring competitive strategies that increase likely exposure to pools of limiting nutrients. Hence, the ability to move to nutrient sources is critical to harmful algae success. Flagellated harmful algae taxa, including dinoflagellates, rhaphidophytes, prymnesiophytes, etc., can migrate through stratified water columns filling internal nutrient pools during a portion of the day to meet requirements for the remainder of the day, and thereby out-competing neighbours with no migration capacity. Other harmful algae, the cyanobacteria, control buoyancy through regulation of gas vesicle content and cellular carbohydrate reserves produced in diurnal photosynthesis, again permitting vertical segregation in the water column and greater growth potential than taxa incapable of regulating access to light and nutrients. Forces and physiology controlling these intra-specific responses can only be expanded through examination across many systems.

Increased nutrient inputs to enclosed and nearshore ecosystems have resulted in widespread coastal eutrophication throughout Europe and the US (Rabalais and Nixon 2002; Seitzinger et al. 2002). The sources of these nutrients are largely associated with anthropogenic activities. Population growth and development and the production of food (crop and animal production systems) result in dramatic alteration of the landscape as well as large sewage inputs and increased runoff from the land. In addition, large increases in the production of fish and shellfish from aquaculture operations can also result in increased nutrient loading, as these systems require intensive additions of feed, only a small percentage of which is incorporated in food biomass (Naylor et al. 1998; Pitta et al. 1999; Burford and Longmore 2001). It has been suggested that undigested food pellets given to salmon pens in Scotland may lead to increased ammonium concentrations which ultimately help to support *Pseudo-nitzschia* blooms (Bolch et al. 2002). The production and consumption of energy also results in increased atmospheric inputs from NOx emissions which can then lead to increased nitrogen deposition (Paerl et al. 2002). The eutrophication of enclosed and semi-enclosed areas and its relationship to HAB development cannot be understood without an integrated approach in which land-use, river runoff, and atmospheric deposition are considered.

Innovative syntheses of nitrogen, phosphorus, and silica availability, in conjunction with species distributions, have been used to make compelling arguments for the role of coastal eutrophication in the proliferation of some HAB species (Smayda 1989, 1990). However, there is still considerable uncertainty in our predictive ability to quantitatively relate nutrient inputs to HABs. There are a number of reasons for this, including the fact that the focus has often been on the relationship of HABs with inorganic nutrient input. There is increasing evidence that the composition of nutrients, including the organic forms, as well as the ratio of their availability, may play an important role in HAB species development (Granéli et al. 1999; Anderson et al. 2002). Outbreaks of *Prorocentrum minimum, Aureococcus anophagefferens,* and *Pfiesteria piscicida* in Chesapeake Bay have all been correlated with organic nutrient input (Glibert et al. 2001). For example, organic nutrients are important to the nutrition of several HAB species (e.g., Granéli et al. 1985; Berg et al. 1997; Carlsson et al. 1998) via organic nutrient uptake or particle ingestion. Direct uptake of organic nitrogen, as urea, could be favoured from runoff associated with the increasing use of organic fertilizers in many crop systems and these substrates are not usually included in classic nutrient flux models (Granéli and Moreira 1990; Smil 2001; Anderson et al. 2002). Organic nutrients may also lead to the proliferation of heterotrophs, which may, in turn, stimulate development of heterotrophic or mixotrophic HAB species feeding on these prey (Granéli and Granéli 1999).

Thus, a key research issue in enclosed and semi-enclosed systems is:

What is the role of eutrophication and how do the inputs, quality, and fluxes of nutrients relate to HAB development and proliferation?

Example Comparative Studies

One of the striking features in the comparison of HAB outbreaks in enclosed and semi-enclosed systems of the US and the EU is the broad overlap in the key functional groups (and species); however, there are sharp contrasts in the intensity of occurrence (Table 2).

Table 2. Changes in HAB functional groups common to the Baltic Sea/Danish Strait/North Sea system (Europe) and Chesapeake Bay/Louisiana estuaries (US) over an estuarine salinity gradient.

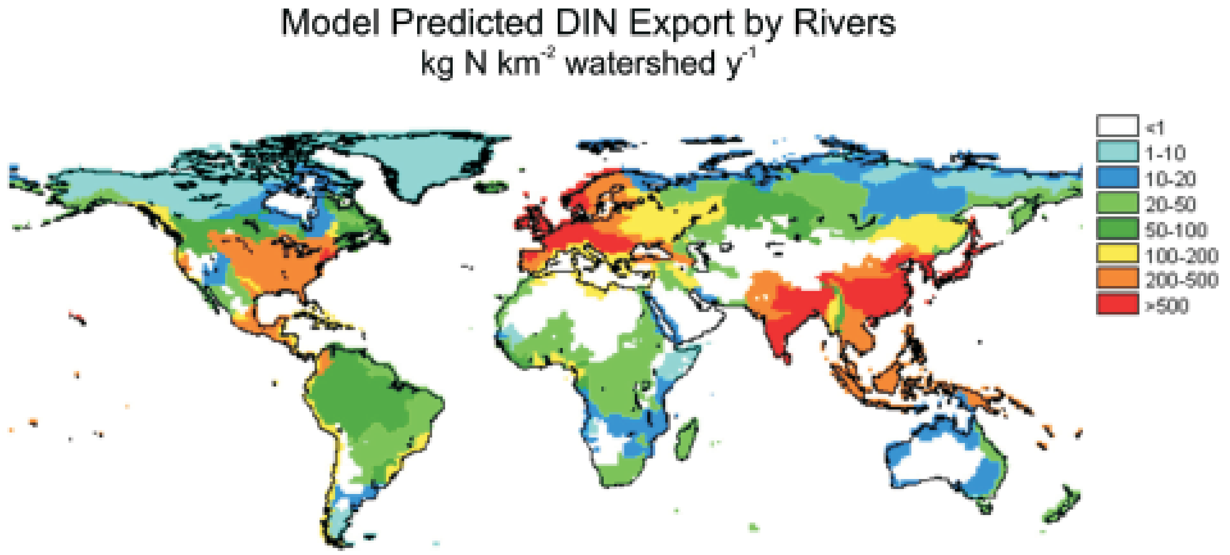
Salinity	**HAB Functional Group/Genus**	**Status in the US**	**Status in EU**
Low	Colonial cyanobacteria		
	Microcystis	High biomass toxic blooms	High biomass toxic blooms
	Anabaena	High biomass toxic blooms	High biomass toxic blooms
	Aphanizomenon	No blooms	High biomass non-toxic blooms
	Nodularia	No blooms	High biomass toxic blooms
	Small dinoflagellates		
	Prorocentrum sp.	Frequent toxic blooms	Common, no blooms
	Heterocapsa triquetra	Frequent toxic blooms	Occasional blooms
	H. rotundata	Frequent toxic blooms	Common, no blooms
	Pfiesteria	Toxic blooms	No blooms
	Mesodinium rubrum	High biomass blooms	Common, no blooms
	Fish killing flagellates		
	Chrysochromulina	Not known	Toxic blooms
	Prymnesium	Not known	Toxic blooms
	Chattonella	Toxic blooms	
	Fibrocapsa	Toxic blooms	
	Diatoms		
	Pseudo-nitzschia	Toxic blooms	Present but no blooms
High	*Phaeocystis*	Occasional high biomass blooms	Regular high biomass blooms
	Large dinoflagellates		
	Ceratium spp.	Occasional high biomass blooms	Occasional high biomass blooms

For example, colonial cyanobacteria cause harmful algae blooms in both regions, in eutrophic coastal waters most influenced by freshwater inflow. Several species are common in both domains, but the toxic *Nodularia spumigena*, the most conspicuous HAB species in the Baltic Proper, is not found in the US. Dinoflagellates/flagellates and ciliates discolour the water and include *Prorocentrum minimum* and *Mesodinium rubrum*, causing frequent blooms in Chesapeake Bay (high biomass, toxic and high biomass non-toxic, respectively) and are regular members of the plankton community in the Baltic Sea, also forming blooms without harmful effects. Similarly, *Heterocapsa triquetra* and *H. rotundata* cause mahogany tides in Chesapeake Bay and do occur in most parts of the Baltic Sea with no harmful impact.

A recently-developed global model (Figure 17) of nutrient inputs to coastal systems as a function of land use in watersheds indicates that European land discharge to coastal systems on average 5-10 times more nitrogen (per hectare) to coastal systems than estimated for the US (Seitzinger and Kroeze 1998). This is likely a result of more intensive and longer land use in Europe than in the US as there have been over 1000 years of land manipulation in the European countries compared to a modest 200 years of intensive land modification in the US. The higher contributions, loads/hectare, in the EU is intriguing considering the apparently increasing frequencies and duration of HAB events off Northern Europe and several Mediterranean countries *versus* relatively few anthropogenically-supported blooms in US waters. These differences might suggest that as the US ages, loads per unit land surface might follow the same pattern as in Europe, leading to the increasing HAB frequencies so common to Europe today. Contrasts between similarly-impacted and differentially-impacted enclosed and semi-enclosed systems are warranted.

Figure 17.

Inorganic nitrogen export (kg N km^{-2} watershed $year^{-1}$) from watersheds to coastal systems.

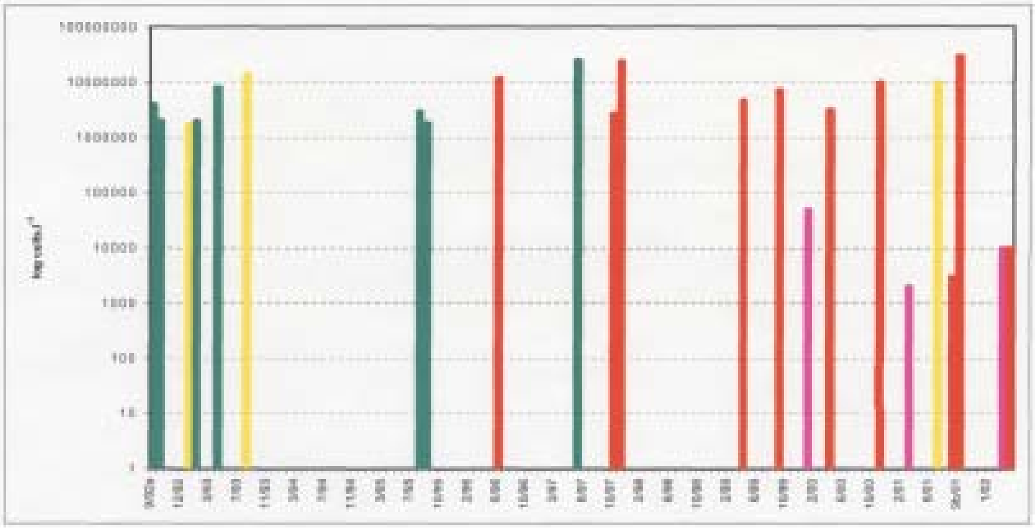


Source: Seitzinger and Kroeze 1998.

Altered nutrient loads have been associated with increasing abundance of *Pseudo-nitzschia* in the northern Gulf of Mexico since the mid 1950s (Parsons and Dortch 2002). During the same period of time, nitrogen loads have doubled, while silica availability has decreased substantially (Turner and Rabalais 1991). Besides differences in total areal loads, some coastal systems in the EU are phosphorus-limited (e.g., Mediterranean Sea) compared to many regions of the US coast which are mostly nitrogen-limited. Some shifts in nitrogen to phosphorus limitation have resulted from management intervention, such as implementation of sewage treatment, and their examination may yield predictive models for future management strategies. For example, in the Northern Aegean Sea, phytoplankton populations were mostly diatom-dominated until about 1996 when decreased ratios of nitrogen to phosphorus (N:P) developed following changes in sewage treatment and increases in phosphorus loading. These depressed ratios were subsequently correlated with increased dinoflagellate blooms, including *Dinophysis* (Figure 18).

Figure 18.

Exceptional phytoplankton blooms in Thermaikos Gulf, N. Aegean Sea (E. Mediterranean). Green columns: Diatom blooms (among them: *Thalassiosira* spp., *Skeletonema costatum, Rhizosolenia* spp., *Leptocylindrus minimum, Lithodesmium undulatum* etc.); Red columns: dinoflagellates (among them: *Prorocentrum* spp., *Gymnodinium* spp., *Scripsiella trochoidea*, etc.); Pink columns: toxic events caused by the dinoflagellate *Dinophysis acuminata*; and Yellow columns: other flagellates (among them: *Phaeocystis* sp.).



Source: Moncheva et al. 2001, and Pagou, unpub. data.

Relatedly, in the western and northern Adriatic, a shift from predominantly red tide blooms to more frequent mucilaginous blooms (Figure 19) occurred in the late 1980s coincident with phosphorus removal from detergents and expansion of sewage treatment plants (Figure 20; Sellner and Fonda Umani 1999); however, cause and effect remain to be determined as mucilaginous events were observed over 200 years ago. These patterns hold important lessons for US regions, and demonstrate that alterations in effluents and nutrient inputs have a high potential for altering phytoplankton communities. A robust test of the nutrient ratio hypothesis requires many more comparisons across systems.

Figure 19.

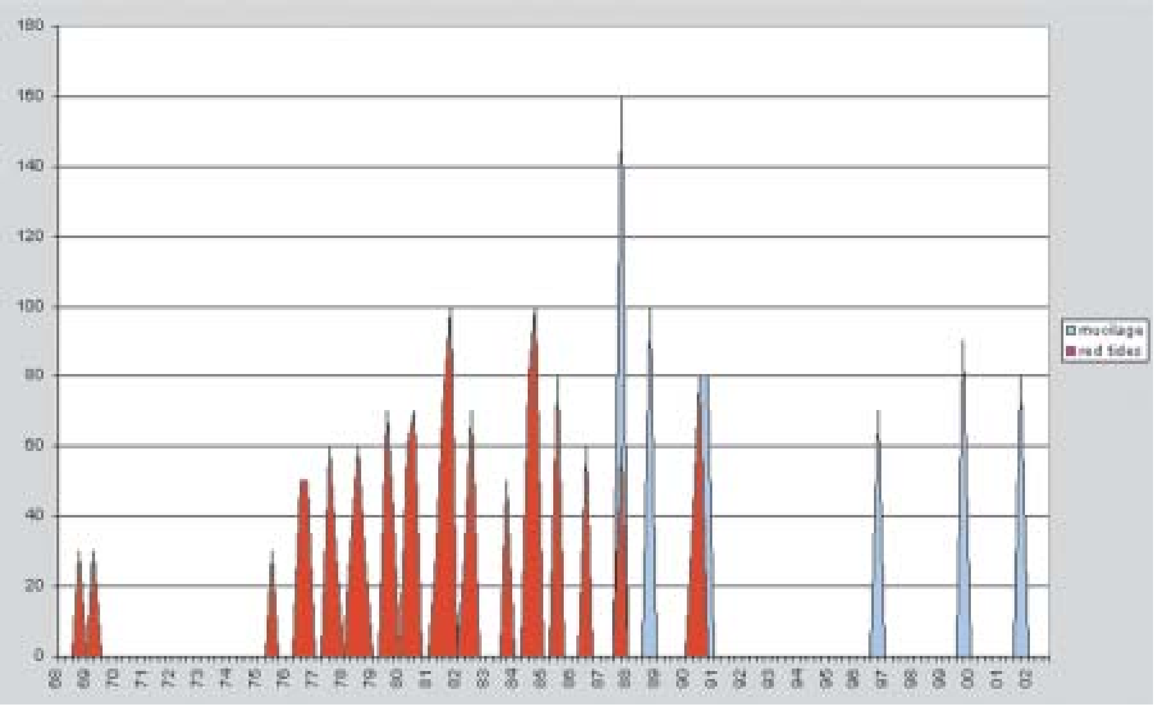
Mucilaginous aggregate in Adriatic.

Source: S. Fonda Umani.

Although not generally considered to be toxic, one of the high biomass HAB species that has been shown to develop following events that lead to runoff and increased nutrient delivery is *Prorocentrum minimum*. This species can develop to high standing stocks and result in harmful impacts on benthic habitat, including hypoxia/anoxia, as well as on shellfish, depending on their life stage. *P. minimum* is one of many mixotrophic species and will grow when organic nutrients are supplied (Li et al. 1996; Heil 1996; Carlsson et al. 1998; Glibert et al. 2001). Humic and fulvic acids from Swedish rivers increased *P. minimum* intracellular nitrogen pools, cell numbers, and growth rates relative to cultures free of the natural organics (Granéli et al. 1985). In tributaries of Chesapeake Bay, *P. minimum* also appears to grow and develop into massive blooms (chlorophyll levels exceeding 500 µg l^{-1} in some cases). These blooms have been associated with declines in submerged grasses and benthic habitat (Gallegos and Jordan 2002) and have been proven to be toxic to shellfish under

Figure 20.

Long-term record (1968-2002) of red tides (red) and mucilage (blue) events in the North Adriatic. After 1987, the system shifted from dinoflagellate-dominated coastal blooms to open water mucilage events.

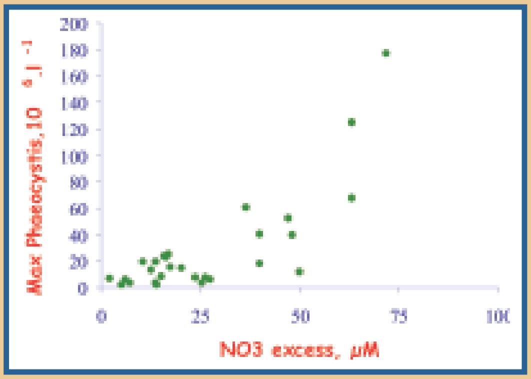


Source: S. Fonda Umani.

some growth conditions (Wikfors and Smolowitz 1999). These blooms, like those in Sweden and many other regions in the world, appear to intensify and expand in response to delivery of nutrients from rainfall events, and in particular organic nitrogen forms (Glibert et al. 2001). In this sense, stimulation of the bloom by rapid delivery of an organic nutrient source is similar to the findings from Sweden (Carlsson et al. 1999). Through comparative regional studies, further research could investigate whether similar factors are, indeed, stimulating these blooms. Comparisons of the physical dynamics of the regions, quantification of nutrient delivery and the trophodynamic composition of the plankton at the time of nutrient inputs, and the detrimental impacts of these blooms will be extremely valuable in developing predictive capabilities. In addition, comparison of strains will yield insight into comparative physiology, including the ability of different strains to develop toxins.

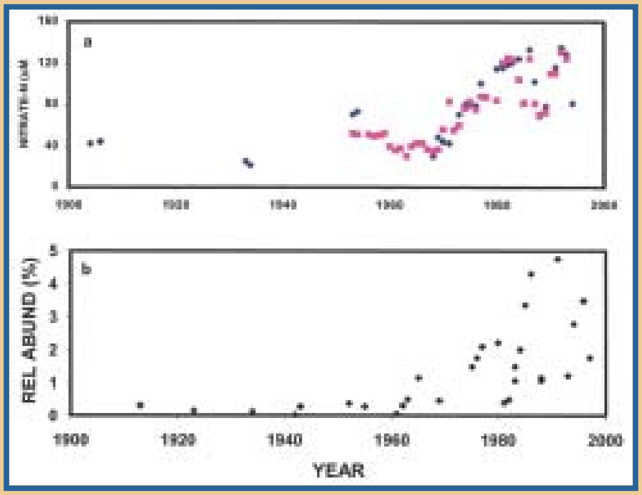
Nitrate predicts HAB outbreaks in the EU and the US

Beaches covered with foam and viscous waters moving in and out over the shores with the advance and retreat of each wave are recurrent events in Belgium waters typified by the colonial prymnesiophycean alga *Phaeocystis*. The mucilage-rich colonies of non-motile cells are common to northern European waters as a result of changing nutrient loads and ratios in the major rivers of the region. Diatoms bloom in early spring sustained by the winter stock of dissolved silicate and phosphate, but the nitrate over-enriched river waters in late April-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 to this alga in Europe, *Phaeocystis* has a limited range in the US, occurring for short periods in the Gulf of Maine and Cape Cod Bay. Blooms are less frequent and less expansive, but can dominate surface biomass for the region on occasion.



Relationship between maximum *Phaeocystis* colony cells and nitrate excess in the Eastern Channel and Southern Bight of the North Sea for the last decade. Source: Lancelot 1995.

In the Northern Gulf of Mexico, *Pseudo-nitzschia pseudodelicatissima* is the dominant *Pseudo-nitzschia* species and is of concern because of its ability to produce domoic acid (Dortch et al. 1997). Similar to the case of *Phaeocystis* in Europe, an increase in the enrichment of nitrate is highly correlated with the increase in abundance of this species in the sedimentary record.



Increase in nitrate loading (upper panel) and increase in *Pseudo-nitzschia* in the sedimentary record (lower panel) over the past few decades. Source: Redrawn from Turner and Rabalais (1991) and Parsons and Dortch (2002).

The proposed EU-US programme provides an opportunity for comparative studies that would lead to better understanding of changing riverine loads and impacts on expansion and accumulation of these and other species in the US and EU.

VI. Cross-Cutting Issues

Several issues related to HABs in both EU and US waters are not specific to habitat or ecosystem type. These issues are of equal concern across all ecosystems. Examples below are not intended to be comprehensive, but rather illustrative of where a collaborative effort would be beneficial.

How does genetic diversity and toxicity of HAB species vary in relation to their biogeography?

Rationale

Increasing evidence indicates that the distribution of HAB species is changing dramatically throughout US and European waters. Some species are expanding their geographic range; in other instances, new toxic species are being identified that were previously considered harmless. Moreover, the same species can sometimes have widely different impacts in the two regions – the same species can be toxic in one location and non-toxic in another. Underlying these observations is the realisation that morphological species identifications sometimes do not provide the resolution needed to explain differences among HAB events. In many cases, what was formerly considered a single species is in fact a mixture of genetically-similar strains of that species. Considerable genetic diversity has now been documented within a single species in a region and evidence indicates that only some of these genotypes bloom under a given set of environmental conditions. Morphologically, all cells might look like exactly the same species, but genetic differences abound, and environmental selection is acting on those differences to select one genotype over others.

Genetic diversity may reflect temporal variability in species ranges as well as population variability within a species over a given geographic range. Most research has focused on environmental regulation of HAB toxicity and geographic range. Improved molecular and analytical chemistry techniques now allow a comparable focus on the role of genetic diversity in determining species attributes in different locales and in reconstructing dispersal pathways of species at multiple spatial scales. HAB science has thus entered a new era of genetic discovery. The tools and background knowledge are now in place to allow a number of important issues to be addressed at a level of detail that was heretofore impossible.

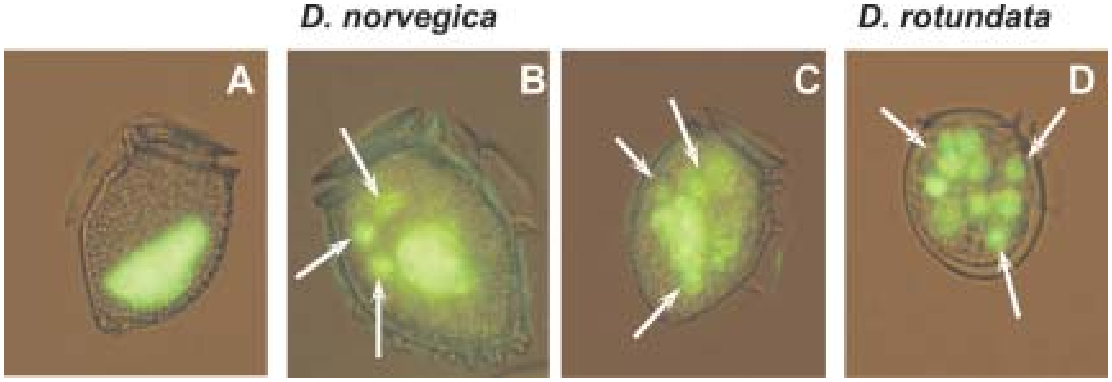
Example Comparative Studies

There are several examples from within and between systems in the EU and the US where similar HAB species occur, but differ in their ability to form high-density blooms or in their ability to form toxins. For example, the toxic dinoflagellate *Dinophysis* spp. are observed up to hundreds of thousands of cells per litre in 1-2 metre layers about 20 metre depth in the Baltic Sea (Gisselson et al. 2002), but generally reach levels of 100 to maximum levels of 40,000 cells per litre in most other European waters. In contrast, these taxa do occur in the polyhaline waters of the Chesapeake Bay and its sub-estuaries (Marshall et al. 2002) as well as coastal waters of the Gulf of Maine, but generally at much more modest levels. The toxic European populations often contaminate mussels leading to potential human health concerns whereas US population of *Dinophysis* spp. result in undetectable or very low toxicities. Reasons for these differences remain unresolved and could reflect genotypic heterogeneity or alternatively differential toxin synthesis in response to low and high nutrients, respectively, of the European and US systems.

Another important example is that of *Pseudo-nitzschia* spp. These species are found throughout Europe and the US, yet toxic outbreaks occur only in certain regions. These diatoms are common components of the phytoplankton assemblage and within the last 15 years, many species within the genus have been recognised as producing the toxin domoic acid; additional toxic species may still be unrecognised. As with *Dinophysis* spp., some species of *Pseudo-nitzschia* are commonly reported as toxic in one region but not in another. 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. In contrast, *P. australis* can be non-toxic off the US 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 provides a series of natural experiments to determine the extent to which toxin variability reflects environmental forcings as opposed to genetic and physiological differences. Are there environmental factors common to either European or US waters that enhance toxicity or are only certain genotypes capable of producing toxin?

Figure 21.

D. norvegica cells without food vacuoles (A) and cells containing food vacuoles (arrows) (B - C), *D. rotundata* with vacuoles (D=heterotroph).



Source: E. Granéli.

The change in genetic diversity through time in comparative systems is also an important question. It was recently found, for example, in the Gulf of Naples during a *Pseudo-nitzschia delicatissima* bloom that a striking amount of genetic diversity existed in the population of this species at the beginning of a bloom, but only a few genotypes were 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.

Genetic analysis will be critical also in the resolution of dispersal issues. There are many examples of apparent introductions of HAB species through human activities (e.g., McMinn et al. 2001; Lilly et al. 2002) and genetic analysis may help in identifying the potential relationship between globally-distributed, but potentially-transported, species. As with other aspects of HAB science, these studies can build from a significant base of data and experience. In particular, sequence databases for a number of genetic markers now exist for most of the HAB species complexes, derived from analysis of globally-distributed isolates (e.g., Scholin and Anderson 1994). New isolates can be quickly sequenced and compared against these databases to determine if they represent new variants or are close relatives of populations elsewhere. In the case of the recent discovery of *Alexandrium catenella* in Thau Lagoon in France, sequence analysis demonstrated that the closest relatives to the Thau isolates were from Asia, and thus the recent appearance of this species in the lagoon likely reflects accidental introduction to the Mediterranean via ballast water (Lilly et al. 2002).

To what extent is HAB distribution and extent related to climate variability and/or climate change?

Rationale

Climate ultimately controls the fundamental parameters regulating algal growth, from water temperature to nutrients, and from precipitation and runoff to light. Climate change and climate variability can be expected to result in changes in species composition, trophic structure, and function of marine ecosystems. Climate change is the long-term alteration in global or regional weather due to increasing concentrations of greenhouse gases and aerosols that have altered the radiation balance of the Earth. Climate variability, on the other hand, is the natural variation in the impact of solar variation on climate, including the periodic El Niño Southern Oscillation (ENSO) phenomenon, the North Atlantic Oscillation (NAO), or the Pacific Decadal Oscillation (PDO).

Current ecological paradigm suggest that an ecosystem does not exist in a unique, stable equilibrium state, but rather can easily be shifted to a new state by non-linear responses to physical forcings, such as those associated with climate change or variability. The ensemble biological responses are non-linear, complex mixtures of physiology, behaviour, life history, and physical redistribution. A major question is whether changes in climate will result in altered marine ecosystems that favour harmful algal species and increase probabilities of harmful events. A second question is whether, once an ecosystem shift has occurred, it can either revert to its previous state or to a new state with decreased representation of HAB species.

The proximity of enclosed and semi-enclosed systems to land increases their susceptibility to alteration in rainfall and river discharge due to climate variability. With increasing river discharge, more low salinity taxa, including freshwater bloom-forming cyanobacteria, may be carried further seaward, leading to potential exposure of new regions to toxin-producing cyanobacterial blooms. Additionally, buoyant plumes could extend much further off the coast, selecting for migrating taxa such as dinoflagellates which recur in these coastal features (e.g., Sellner and Fonda Umani 1999). For those systems with declining river discharge, more stenohaline taxa would potentially move further up estuaries, thereby exposing larger portions of upper basins to more saline HAB taxa, such as *Dinophysis*, *Karenia*, and *Alexandrium*.

With increases in water temperature, combined with alterations in hydrographic regimes, new niches for organisms may become available. For example, *G. catenatum* from northern Spain extended up to the N.E. North Sea during the Medieval Warm Period approximately 1000 years ago, but was forced southward again by the Little Ice Age about 300 YBP. In the US, mean winter water temperatures in Narragansett Bay increased 3°C between 1959-1998 and were accompanied by major changes in bloom species and timing (Borkman and Smayda, in review).

The list of possible effects on HAB species from climate change and climate variability is long, and many cannot be studied directly due to the long time scales involved. Some are amenable to experimentation, however, and others can be addressed by careful examination of long-term datasets. Multi-decadal time series are available for several sites in the US (e.g., San Diego, California, and Narragansett Bay, Rhode Island) and in the EU (e.g., Helgoland, Germany, and Flødevigen, Norway). These sites are also biogeographically-sensitive boundaries between colder-water/warmer-water species. It is precisely at such sentinel locations where the effects of climate change are expected to become evident in the form of species range retractions and expansions, and in altered bloom dynamics. Comparative ecosystem interrogations of such data sets – analysing the coupling between species behaviour and changes in water mass temperature and climate-driven winds, rainfall, and runoff patterns – will be valuable in establishing evidence of climate change as a factor in the global expansion of HABs.

Example Comparative Studies

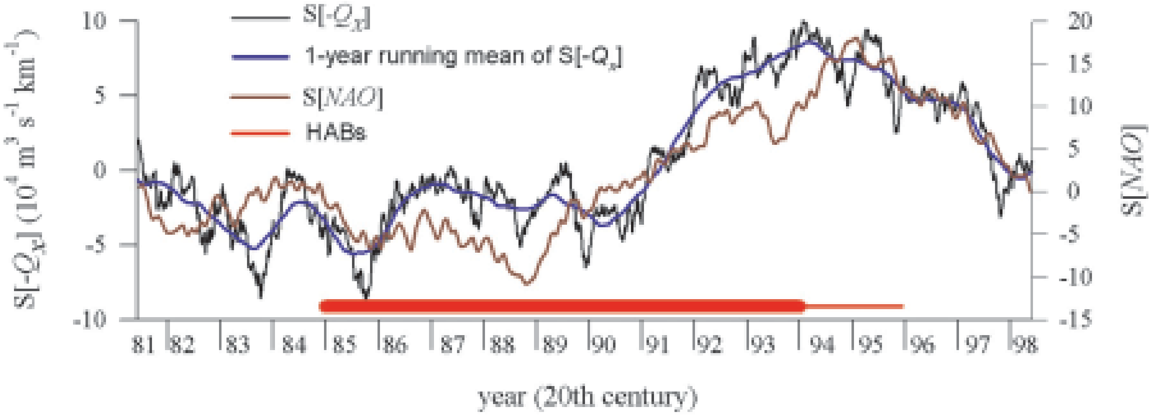
Major changes in ecosystem structure and function in response to inter-annual oscillations, such as those related to ENSO, or longer-term cycles, such as the NAO and PDO, have been documented in several systems. For example, in the tropical North Pacific Ocean, the abundance and biogeochemical importance of the nitrogen-fixing cyanobacterium *Trichodesmium* (Karl et al. 1997) dramatically increased as a consequence of increased stratification associated with an El Niño event. Another of the most striking examples comes from the northern Iberian Peninsula where the abundance of *Gymnodinium catenatum* was shown to correlate with changes in the NAO index (Figure 22). Although the underlying mechanism is not fully understood, this example suggests that examining long-term patterns of HAB ecosystems in context of climate change or variability will be fruitful. In the context of this proposed EU-US programme, a parallel examination of PSP records from the western Atlantic might reveal either similar or inverse relationships that could greatly increase our understanding of the effects of these sustained, large-scale weather patterns. These examples illustrate that climatic patterns do affect ecosystem structure and suggest that similar relationships could exist between climate change and alterations that lead to harmful events.

The potential relationship on the US west coast between PDO or ENSO and frequency and magnitude of toxic events, both for PSP with *Alexandrium* species and ASP from *Pseudo-nitzschia,* is also of interest. Patterns or relationships revealed in these studies will be of great value for those affected by these toxic species in the EU and elsewhere, even out of the context of climate change or variability.

Semi-enclosed systems often act as sediment/particle traps and therefore are ideal systems for assessing floristic changes through geologic time from buried particles. Hence, these systems lend themselves to applications of micropaleontology for retrospective assessment of these relationships more so than open coastal systems. Micropaleontology uses fossil cells and dinoflagellate cysts from cored sediments as indicators of climate change and HABs. Such approaches are now being developed and applied in Norway, the Chesapeake Bay, as well as the Gulf of Mexico, and provide ideal reservoirs for comparative explorations of climate-induced shifts in HAB flora.

Figure 22.

Possible long-term relationship between climate variability and PSP events caused by *Gymnodinium catenatum* in the Galician Ría Baixas (NW Iberian Peninsula). S[-Qx] and S[NAO] are de-seasonalised cumulative sums of offshore Ekman transport (-Qx) and the North Atlantic Oscillation index (NAO) over the period 1981-98. The straight red line indicates years of detection of *Gymnodinium catenatum* association with (thick line) or absence from (thin line) the detection of PSP toxins in shellfish. A positive trend in S[NAO] indicates transition to upwelling-favourable periods. A negative trend in S[NAO] indicates transition to downwelling-favourable periods. PSP outbreaks caused by *Gymnodinium catenatum* were more frequent and intense during the transition period (1980s to 1990s) from downwelling- to upwelling-favourable conditions.

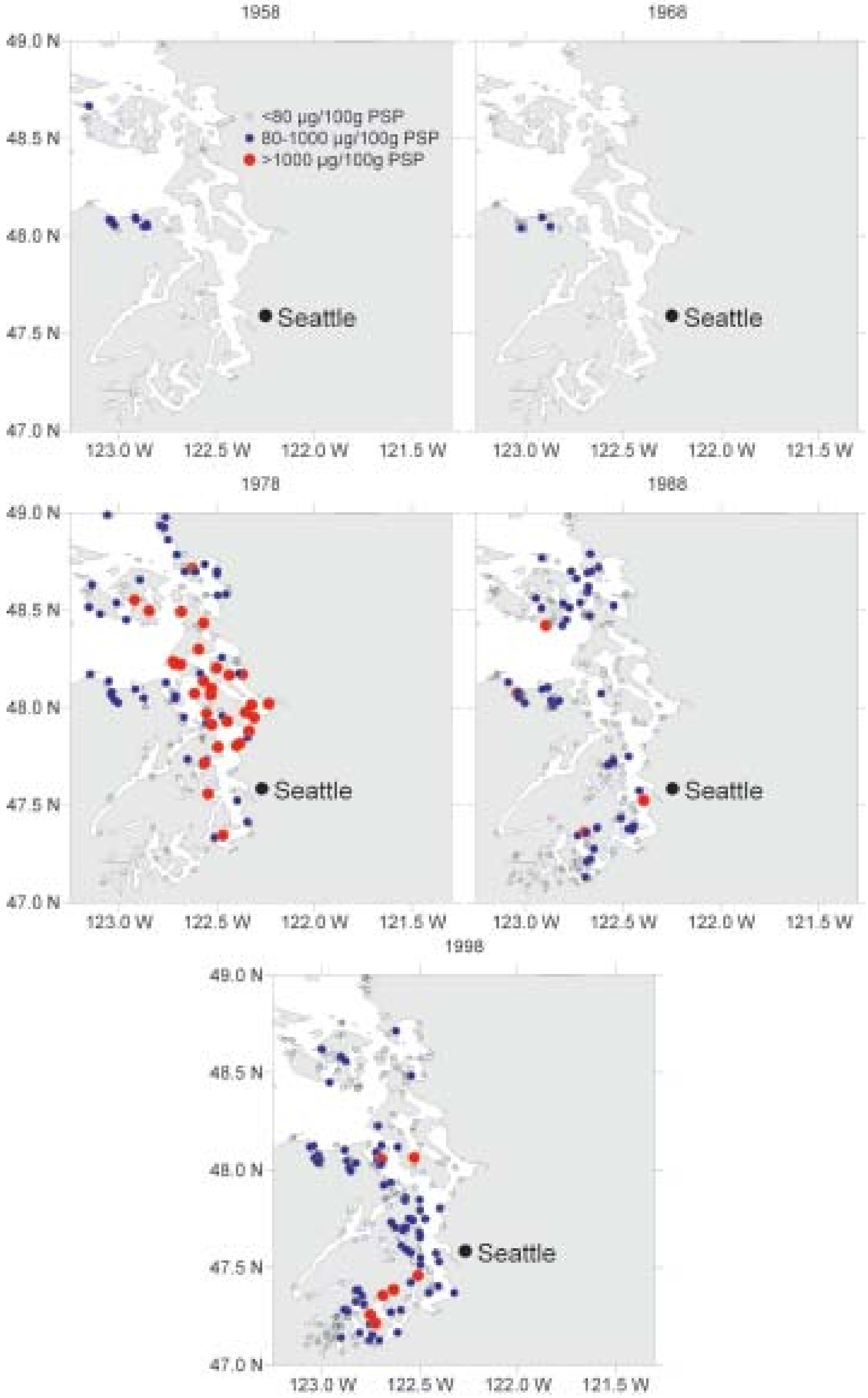


Source: F.G. Figueiras and B. Reguera, modified from Alvarez-Salgado et al. 2003.

In other areas, long-term data sets are extremely valuable for evaluating potential links between climate change, variability, and HABs. In the Iberian rias, it has been suggested that increases in HAB outbreaks have been related to long-term changes in wind-induced upwelling intensity (Fraga and Bakun 1993). Phytoplankton composition in these and other upwelling systems might verify that this regional observation is a global, climate-driven response. The reported increase in PSP in the Pacific Northwest over the last decades also indicates the importance of long-term data sets. First recognised as a cause of illness and death in the 1940s, PSP levels have been monitored regularly since then (Figure 23). The extent to which climate change or variability is associated with the southward spreading of PSP is a question that could be resolved through retrospective analyses of extensive monitoring and climate data.

Figure 23.

PSP toxin levels at monitoring sites in Puget Sound, Washington, over the decades. Data are shown for 1958, 1968, 1978, 1988, 1998.



Source: NWFSC Marine Biotoxin Program.

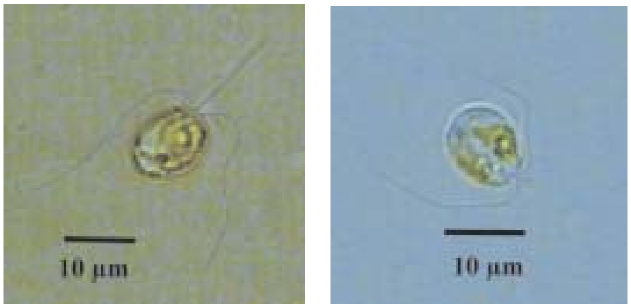
What ecosystem structures or trophic interactions favour accumulations of HABs?

Rationale

HAB species do not appear to have higher intrinsic growth rates than other phytoplankton. Embedded in the physical and nutrient regimes described above, the expression of a harmful alga in any enclosed or semi-enclosed basin is dependent on a suite of biological characteristics of the ecosystem and the harmful alga. Therefore, not only are the physiology and behaviour of the harmful algae important in bloom development and persistence but top-down controls, whether pelagial or benthic, exert tremendous influence on bloom expression. The ability of an HAB species to build up population size under specific conditions is therefore related to reduction in mortality rates.

Figure 24.

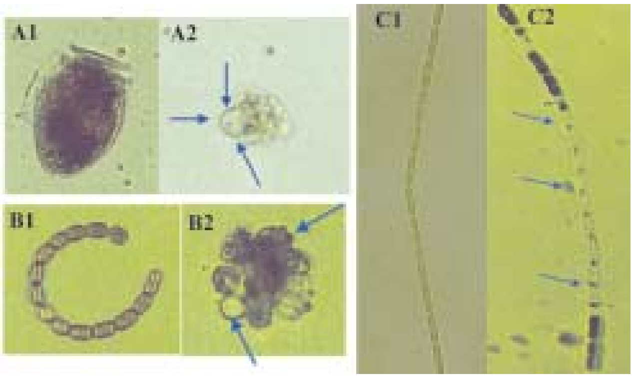
Chrysochromulina polylepis (left) and *Prymnesium parvum* (right).



Source: C. Esplund.

Figure 25.

Cells of *Dinophysis acuminata* (A), *Anabaena circinalis* (B) and *Pseudoanabaena* sp. (C) with additions of media (Controls: A1, B1 and C1) and *P. parvum* filtrates (A2, B2 and C2).



Source: C. Legrand.

Very little is known about grazing inhibition. For some taxa, specific toxins produced by HABs can confer protection against specific grazers; decreasing mortality rate by just 10% can suffice to significantly increase accumulation rates. Some near mono-specific blooms of the Haptophyte *Chrysochromulina* sp., *Prymnesium* sp., and the Raphidophytes *Chattonella* spp. and *Fibrocapsa* spp. have been favoured through reduced grazing mortality from toxin production in the HAB species. Where HAB species co-evolve with their grazers, development of mechanisms to cope with the toxins as part of the continuing predator-prey interaction can be expected (Haley and Dam 2002). Toxic species introduced to a “new” ecosystem may have even lower mortality rates as ambient grazers may not have evolved defences to the toxin; hence the harmful species may enjoy greater competitive advantage over native species and perhaps alter community structure in undesirable ways. Further, toxins can be either broken down or removed away from the target sites in which case they can be defecated, or alternately, passed up the food chain with disastrous effects on higher trophic levels.

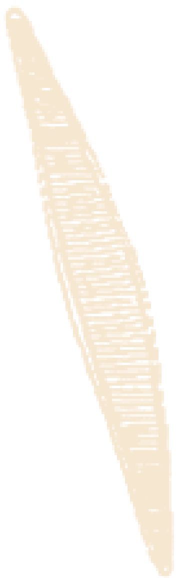
The biological control and fate of HABs are controlled by competition, parasites, pathogens, and bacteria, as well as through grazing, sedimentation, and viral lysis. There are fundamental differences in these factors within and between functional groups, and within and between the US and the EU. For example, in the San Francisco Bay, California, benthic suspension feeders rapidly consumed sedimenting blooms of *Ceratium* with no harmful effects (Cloern 1996). In contrast, huge *Ceratium* blooms in the Skagerrak and Kattegat (Granéli et al. 1989) and off the US coast of New Jersey (Malone 1976) have been shown to sink and decompose, causing anoxia over huge areas (4000 km^2 of the Baltic Sea), as sufficient benthic suspension-feeding communities were not present to remove the sedimented population.

Often, removal mechanisms are also related to complex life cycles. This is one of the important areas for HAB research and is also critical to understand for modelling efforts. Unique life strategies can facilitate HAB success; maintaining low numbers of viable cells in the water column during non-optimal conditions increases the likelihood for population recovery when the environment changes.

Very little is known – in either EU or US waters – on how pathogens are involved in promoting or decreasing the size of HAB outbreaks. During drift studies in the North Sea, Granéli et al. (2003) has shown that the loss rate imposed by infection of the parasite *Parvilucifera* sp. on *Dinophysis norvegica* was equal or higher than the growth rate of the host. Other studies indicate the importance of other taxa (lytic bacteria, viruses, and fungi) and processes (autolysis) in mortality, and comparisons across systems will be important for bringing new expertise to these questions.

Example Comparative Studies

Recent experiments indicate that there are latitudinal differences in feeding and reproduction of copepods exposed to toxic *Alexandrium* spp. (Colin and Dam 2002). Are there cross-Atlantic differences as well? The influence of toxin production as a defence mechanism must be studied in different environments in order to understand the relative role of this strategy in forming ecosystem structure. Similarly, Stoecker et al. (2002) have demonstrated different rates of potential grazing on *Pfiesteria* when grown under different toxic conditions. The highly toxic *Pfiesteria* were avoided as prey by the microzooplankton community, whereas the least toxic forms were readily consumed. The discovery of *Pfiesteria* in Norwegian and other European waters (Jacobsen et al. 2002) raises questions about whether grazing control is similar; no toxic outbreaks of *Pfiesteria* have been documented in Europe.



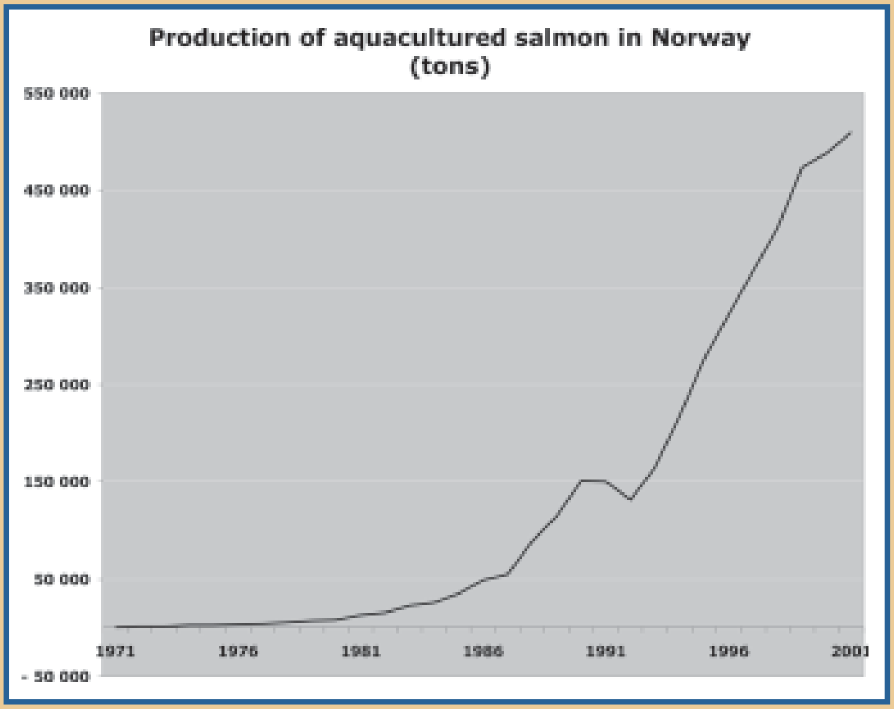
Impact of HAB on the fisheries aquaculture in Norway

Up to the 1970s, harmful algae blooms were not considered a major threat to the marine or coastal environment. Single episodic events of mussel toxicity and mortality of wild biota were recorded along the Norwegian coast, but these episodes did not attract wide public attention or lead to any management actions. Through the 1970s, several fish farms were established along the coast. Since 1980, the production of the Norwegian aquaculture industry has grown significantly from a few thousand tons to ~500,000 tons of salmon and trout in 2001, being the world largest exporter of Atlantic salmon.

In 1981, a large harmful algal bloom of the dinoflagellate *Gyrodinium aureolum* caused significant mortality of farmed salmon and economic losses to fish farmers. The bloom created much public awareness and both the fish farming industry and the authorities acknowledged that harmful algae could be a threat to activities in Norwegian coastal waters. New blooms of *Gyrodinium* followed, and during the 1980s, other phytoplankton species bloomed and caused problems: *Dinophysis* spp. in 1984; *Chrysochromulina polylepis* in 1988; recurrent blooms of *Prymnesium* since 1989; *Chrysochromulina leadbeateri* in 1991; and *Chattonella* in 1998, 2000, and 2001.

The toxic algae bloom of *Chrysocromulina polylepis* in 1988 lasted for 3 weeks and caused severe losses of ~10M Euro to the Norwegian aquaculture industry. Based on the decisions supported by the various environmental observations during the 1988 event, 115 aquaculture sites were towed away from the toxic bloom area. These plants represented fish values of ~150M Euro.

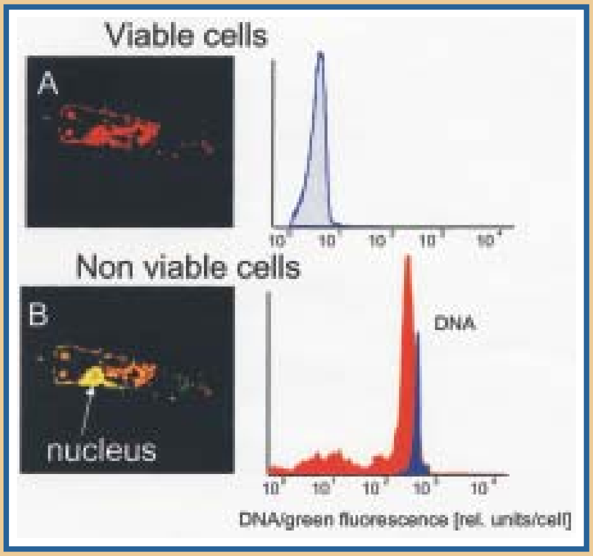
In 1998, around 350 tons of aquaculture salmon died – mainly mature fish representing a value of ~1.2M Euro, with more severe losses in 2001, thereby inducing public discussion whether aquaculture activities were viable in this region of Norway.



Source: L. Pettersson, modified from data from Norwegian Directorate of Fisheries/Statistics.

HABs imply that MORTALITY is lower than growth

Trophic dynamics in the pelagic and benthic environments govern the accumulation of biomass in many species, including harmful algae. Whereas accumulation from new growth requires nutrients and other factors to support biomass, accumulation of dividing or non-dividing cells can also represent a release from grazing pressure. If persistent, estimates of non-dividing cell numbers can provide critically needed information required for estimating bloom longevity, and therefore impact.



Flow cytometric detection of cell viability. Source: M. Veldhuis.

Major loss terms for growing phytoplankton taxa include grazing and mortality associated with parasites, bacteria, viruses, and autolysis. Grazing by larger mesozooplankton species, such as copepods, is often minimal and masked by ingestion by protozoa, rotifers, and other members of the microheterotrophic community including several mixotrophic bloom-forming species.

Inherent to all grazing by these potential consumers is the role of grazing inhibitors, whether toxins or alleopathic compounds, or alternatively, morphological characters of the prey items that might reduce losses to the consumers. Little work has been conducted on grazing deterrents, yet isolated studies from both the EU and US suggest that production of grazing inhibitors may be more common than has been suspected. From erratic swimming *Favella* exposed to toxic *Alexandrium* species (Hansen 1989) to suppressed copepod feeding when exposed to toxic dinoflagellates (Huntley et al. 1986) or domoic acid, HAB species may posses an arsenal of retardants to limit mortality in the presence of their grazers.

The roles of parasites, bacteria, viruses, and self-regulating lytic processes in HABs remain enigmatic, yet increasingly referenced as mortality agents in the marine environment. Parasitic dinoflagellates (Coats et al. 1996; Granéli et al. 2003) frequent inshore and coastal HAB species in EU and US waters, and their role in limiting biomass accumulation remains to be determined. Chytrids infect *Ceratia* and diatoms in both areas. Species-specific lytic bacteria have been identified for Raphidophytes and *K. brevis*. Lysis of HAB species from viruses has been suggested for some taxa, e.g., cyanobacteria.

The roles of these potential growth-limiting agents, and the HAB defences to combat them in HAB development and persistence remain largely unexplored. With emerging methods for studying subcellular processes, the EU and US communities face tremendously-expanded opportunities in community understanding through this cross-basin programme.

VII. Summary of Benefits of the Proposed Programme

The impacts of HABs on public health and local and regional economics are severe and increasing along all coasts of the EU and the US.

The EU and US have remarkably similar environments and species, with some species expressing similar patterns in both (e.g., some species are always toxic in both, such as *Alexandrium*) while others show dramatically unique characteristics (e.g., toxic *Dinophysis* in the EU and apparently minimally toxic *Dinophysis* in the US). There are obvious collaborations that should immediately prove fruitful to two communities in research and management.

Productive research on several taxa would be a huge benefit to the global community. The effects of increasing nutrient loads, altered N:P, and the impact of organic nutrients on HAB development can be readily addressed across systems. The EU has higher loads/hectare and generally lower N:P signals in land contributions than seen in the US and a longer history of these conditions. Is the US on a path towards these conditions and therefore ultimately an expression of the same HABs? Some toxic cyanobacteria of the EU, such as in the Baltic (*Nodularia*), are not seen in the US, yet conditions in several of our coastal systems are not unlike those of the stratified Baltic Sea. Why hasn't this taxon been established on the western side of the Atlantic? The EU and US research communities have also explored organic contributions and HAB responses. Are there some species in both systems that are more successful in organic-rich waters than others? Do the recent expressions of *Aureococcus anophagefferens*, *Prorocentrum minimum*, *Pfiesteria*, and *Chattonella* in the US have counterparts in the EU such as *Prymnesium* and *Chrysochromulina*? Are there genomes within these morphologically-distinct taxa that are functionally similar to permit responses to organic enrichment?

Certain physical features of coastal and enclosed systems are also features of the two regions, e.g., fronts and thin layers, and often support HABs. How do these features select for the HABs found and is the physical-biological activity of the features transferable from one side of the Atlantic to the other? At another level, disturbance is common to systems in both areas as well. There are global forces operating over long time scales (i.e., climate change, even eutrophication) where long-term data sets and micropaleontology from both sides of the Atlantic could be used to identify taxonomic responses to system change. Mid-range weather changes, such as El Niño, PDO, and NAO, also have demonstrated responses in the EU and US. Are the responses more predictable from comparison of the responses in the two areas? Short-term system changes due to localised events such as riverflow, local winds, or rainfall/storms also drive HAB expression in both systems. Are there generalities to be derived that can explain HAB responses in both geographic areas?

Both communities have innovative, state-of-the-art tools that are being applied in HAB research with great success. The application of this new instrumentation (*in situ* monitoring, flow cytometry, confocal laser microscopy and other methods) and a vast array of other molecular techniques (molecular genetics and cell-surface antibodies) has improved our knowledge of the dynamics of HABs tremendously in the past decade and if applied in cross-basin studies, consistent data could be generated for potential identification of similar or different HAB responses to similar or unique environmental conditions. In addition, the variety of genetic tools permits detailed classification of most HABs using a rapidly-increasing global gene bank.

The proposed EU-US Scientific Initiative on HABs offers excellent opportunities to rapidly advance our science and expand educational and training opportunities. At all scales of research, from cellular to system-wide, information on HABs will be broadened considerably, and students and researchers will be exposed to new skills and techniques. Expansion of community knowledge will stimulate new research and exploration of possibilities. The rapid advancement in knowledge provided by community rather than individual interactions and collaborations on a common basin flora is the most important benefit in implementing this proposed programme.

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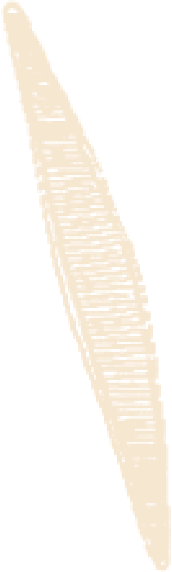

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