

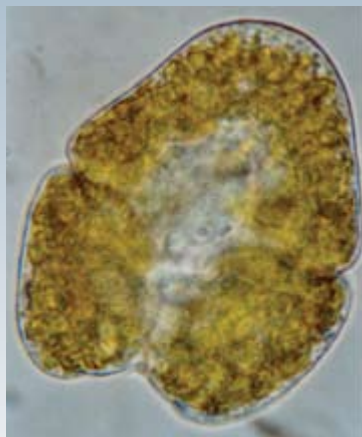
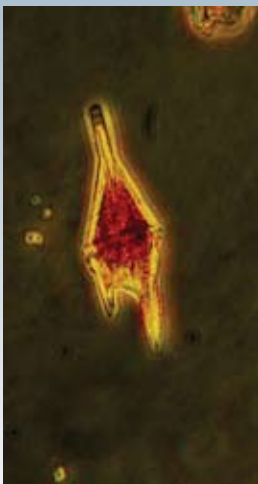


GEOHAB

Global Ecology and Oceanography of
Harmful Algal Blooms



HABs in Eutrophic Systems



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This report is also available on the web at:

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GEOHAB

GLOBAL ECOLOGY & OCEANOGRAPHY OF HARMFUL ALGAL BLOOMS

HABs in Eutrophic Systems

SPONSORED BY THE SCIENTIFIC COMMITTEE ON OCEANIC RESEARCH (SCOR)
AND THE INTERGOVERNMENTAL OCEANOGRAPHIC COMMISSION (IOC) OF UNESCO

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Based on contributions by participants of the 2005 *GEOHAB Open Science Meeting on HABs and Eutrophication*, and the GEOHAB Scientific Steering Committee

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MAY 2006

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Executive Summary



HARMFUL ALGAL BLOOMS WERE RESPONSIBLE FOR LARGE FISH KILLS IN AQUACULTURE FACILITIES IN THE EAST CHINA SEA IN SUMMER 2005. PHOTO: J. LI.

Nutrient enrichment of both land and water is a result of increased human population growth and many associated activities for food and energy production, and discharge of associated sewage and waste. The end result of nutrient loading to inland and coastal waters is often an increase in algal biomass, frequently dominated by one or more species or species groups; this process is eutrophication. An important consequence of eutrophication is the increased prevalence of harmful algal blooms (HABs) that develop high biomass, cause fish kills, intoxicate seafood, result in oxygen depletion, and alter trophic interactions. Nutrient enrichment can stimulate HABs not only directly by stimulation of growth and biomass, but indirectly in subtle, but nevertheless significant, ways through alterations in food web and ecosystem dynamics. The interactions of these alterations on HAB proliferation are only beginning to be understood.

World-wide, strong relationships have been observed between increases in nutrient loading and proliferations of specific types of HABs. In some locales, HABs have increased in response to alterations in the type of nutrient, not only major nutrient forms such as nitrogen and phosphorus, but changes in the chemical form of these nutrients. Organic, not just inorganic, nutrient loading is increasing world-wide and has been correlated with many blooms of both dinoflagellates and cyanobacteria. Advancements in our understanding of the physiology of these organisms has yielded important insights as to why these algal classes respond so favourably to these nutrients.

Increased nutrient loading from human activities is considered to be one of the reasons that HABs have been expanding in frequency, duration, and harmful properties world-wide.



Although we have good quantitative estimates of many sources and forms of nutrient loads, the transformation processes of these nutrients and how they are affected by landscape changes, food web alterations, and climatic variations are not well understood. It is imperative to learn how present trends in nutrient loading relate to algal blooms in general, as well as how they promote the development of particular species. The key to this knowledge is an understanding of the ecology and oceanography of HABs at regional and global scales.

The Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) Programme is an international network of scientists and projects, under the auspices of the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO. It has as its fundamental goal an improved understanding of HAB population dynamics through the integration of biological, chemical, and physical studies and application of advanced observational tools and modelling. This report focuses on one of the overarching questions of GEOHAB: **To what extent does increased eutrophication influence the occurrence of HABs and their harmful effects?**

This document also serves as an initial road map for the development of a Core Research Project within the GEOHAB framework on **HABs in Eutrophic Systems**. The overall strategy of GEOHAB is to apply the comparative approach, to undertake research that is interdisciplinary and international in scope to encompass the global issues of HAB events, and to benefit from the skill and experience of investigators world-wide. The research questions and priorities identified herein were developed through community interaction at an Open Science Meeting held in Baltimore Maryland, USA, in March 2005.

This document outlines the justification, the priorities for study, and some of the new approaches that may be brought to bear in studying the relationships between HABs and eutrophication. The key questions identified here include:

SHELLFISH AND FINFISH MORTALITY DUE TO HABs RESULTS IN LARGE ECONOMIC LOSSES AS WELL AS LOSS OF PRODUCT FOR CONSUMPTION. PHOTOS LEFT TO RIGHT: NRC OF CANADA, AND P. GLIBERT.

- Are there clusters or specific types of HAB species that are indicative of global nutrient increases?
- To what extent do residence time and other physical processes impact the relationship between nutrient loading and HAB proliferation?
- How do feedbacks and interactions between nutrients and the planktonic, microbial food webs impact HABs and their detrimental effects?
- Do anthropogenic alterations of the food web, including overfishing and aquaculture activities, synergistically interact with nutrients to favour HABs?
- How do anthropogenic changes in land use, agricultural use of fertiliser, NO_x emissions from vehicles, and global changes in land cover affect the delivery of nutrients to coastal waters and the resulting incidence of HABs? How do the stoichiometry and quality of these nutrient sources regulate the biological responses favouring HABs?
- Do climate change and climate variability have impacts on ecosystems that augment the impacts of eutrophication in the formation of HABs?

Research on these major priority areas in eutrophication and its associated effects on HABs is welcome within the GEOHAB framework. The understanding of this important issue, and ultimately the management of nutrient loads and improved prediction and management of HABs, will require attention from the global community of scientists.

1. Introduction



NOCTILUCA BLOOM, HOOD CANAL, WASHINGTON, USA, SUMMER 2005.
PHOTO: W. PALSSON, WDFW.



BROCHURE FOR GEOHAB OPEN SCIENCE MEETING ON HABs AND EUTROPHICATION, 7-10 MARCH 2005.

GEOHAB, the Global Ecology and Oceanography of Harmful Algal Blooms Programme, sponsored by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO, is an international programme to foster and promote co-operative research directed toward improving the prediction of harmful algal bloom (HAB) events. GEOHAB has recognized the impacts of HABs throughout all waters of the world, but has emphasized events in marine and brackish waters because of the global significance of these problems and the need for collaborative, international studies to address them.

HABs have been associated with fish and shellfish kills, human health impacts, and ecosystem damage throughout the world. Concurrent with escalating influences of human activities on coastal ecosystems, the environmental and economic impacts of HABs and consequent challenges for coastal zone management have increased in recent years. The relationship between HABs and the increasing nutrient enrichment of many of the world's coastal and estuarine environments is of particular concern. Increasing nutrient loading to coastal and enclosed or estuarine environments is a result of agricultural, aquacultural, animal operations, and industrial and sewage effluents. The relationship between nutrient (both inorganic and organic) loading and alteration in nutrient supply ratios and many HABs is now recognized, but much remains to be understood.

GEOHAB is an international programme directed toward improving the prediction of harmful algal bloom events.



This report is based on the *GEOHAB Open Science Meeting on HABs and Eutrophication* and held from 7-10 March 2005 in Baltimore, Maryland, USA. The programme and participants lists are found in Appendices I and II. This meeting, the third in a series of Open Science Meetings, brought together international experts to review the state of knowledge with respect to our understanding of the role of eutrophication in the proliferation of HABs world-wide and take the initial steps toward designing research on comparative systems and species to address this critical global issue.

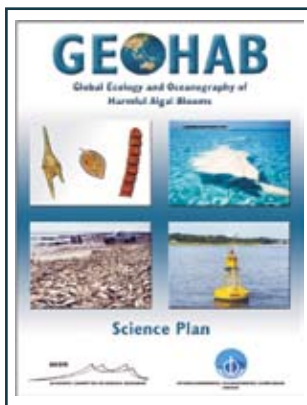
HABs in Eutrophic Systems is designed as one of the Core Research Projects in the GEOHAB Science and Implementation Plans (www.geohab.info). The research described herein provides a guide for this Core Research Project. It will serve as a nucleus for continued planning and will be augmented as research is funded, results are obtained, and new questions are formulated. This document also serves as an invitation to individuals who could not participate in the *GEOHAB Open Science Meeting on HABs and Eutrophication*.

The members of the Organising Committee for the *GEOHAB Open Science Meeting on HABs and Eutrophication* wish to thank the individuals who participated in this meeting, as it is those people who contributed so substantially to the ideas presented herein. Special thanks are also given to John Cullen for his contributions to GEOHAB during its early stages, and to members of the past and present GEOHAB Scientific Steering Committee (SSC, Appendix III). The contributors to this report wish to thank all those who contributed illustrations and who carefully reviewed drafts of this report, especially Raphael Kudela, Dennis McGillicuddy, Bob Howarth, Greg Doucette, Alan Lewitus, Sue Banahan, and Rob Magnien. The Organising Committee also thanks Ed Urban, Elizabeth Gross and Phyllis Steiner, SCOR; Judy Kleindinst, Woods Hole Oceanographic Institution; Jane

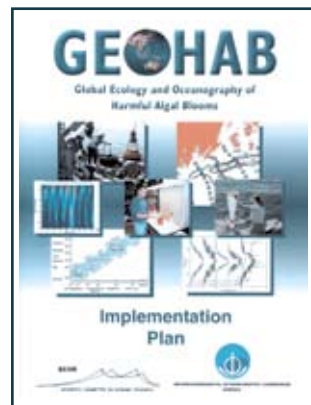
HARMFUL ALGAL BLOOMS OCCUR IN ALL COLORS, REFLECTING THE MULTITUDE OF SPECIES RESPONSIBLE FOR THESE EVENTS WORLD-WIDE (LEFT TO RIGHT: LA JOLLA, CA USA; CAMBRIDGE, MD USA; SOUTH AFRICA) PHOTOS (LEFT TO RIGHT): P. FRANKS, P. GLIBERT, AND G. PITCHER.

Hawkey, Darlene Windsor and Ji Li, University of Maryland Center for Environmental Science; and Kevin Sellner and Dan Gustafson, Chesapeake Research Consortium, for assistance with meeting preparation. The GEOHAB SSC and the Conference Organising Committees are grateful for the financial support for the conference provided by the National Oceanic and Atmospheric Administration-National Ocean Service, the US National Science Foundation-Division of Ocean Sciences, University of Maryland Center for Environmental Science, US National Office for Marine Biotoxins and Harmful Algal Blooms, Maryland Department of Natural Resources, Chesapeake Research Consortium, YSI Environmental, and Gallaudet University.

2. Development of the GEOHAB Programme and Its Study of HABs in Eutrophic Systems



GEOHAB SCIENCE PLAN,
PUBLISHED 2001



GEOHAB IMPLEMENTATION PLAN,
PUBLISHED 2003.

The Mission and Scientific Goal of GEOHAB

The mission of GEOHAB is to foster international co-operative research on HABs in ecosystem types sharing common features, comparing the key species involved, and the oceanographic processes that influence their population dynamics.

The scientific goal of GEOHAB is to improve prediction of HABs by determining the ecological and oceanographic mechanisms underlying their population dynamics, integrating biological, chemical, and physical studies supported by enhanced observational and modelling systems.

The Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) Programme was initiated under the auspices of the Scientific Committee on Oceanic Research (SCOR) of the International Council for Science (ICSU) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO.

The first GEOHAB planning meeting was held in Havreholm, Denmark in 1998, and a Scientific Steering Committee (SSC) was formed in 1999. In 2001, the *GEOHAB Science Plan* (GEOHAB 2001) was published, outlining the mission, goals, and scientific objectives of the programme. In 2003, the *GEOHAB Implementation Plan* (GEOHAB 2003) was published, representing an invitation for the community to collaborate on the objectives of GEOHAB.

GEOHAB is an international programme to co-ordinate and build upon related national, regional, and international efforts in HAB research. The GEOHAB Programme assists in bringing together investigators from different disciplines and countries to exchange technologies, concepts and findings. This takes the form of workshops and meetings, as in the case of the Baltimore meeting on HABs and Eutrophication, or more specific teams of collaborating scientists. GEOHAB is not a funding programme per se, but instead will facilitate those activities that require cooperation among nations and among scientists working in comparative ecosystems.

The central feature of the GEOHAB Programme implementation is Core Research, of which **HABs in Eutrophic Systems** is one priority area. Core Research is comparative, interdisciplinary, international and directly addresses the overall goals of GEOHAB as outlined in the *Science Plan*. As stated in the

The overall strategy of GEOHAB is to apply the comparative approach.



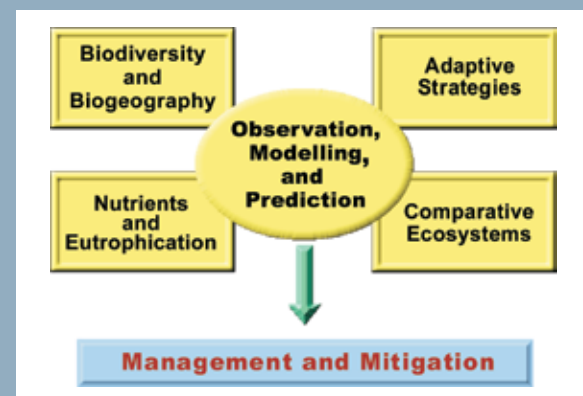
Implementation Plan, Core Research comprises oceanographic field studies conducted in, and application of models to, comparable ecosystems, supported by identification of relevant organisms, and measurements of physical, chemical, and biological processes that control their population dynamics.

The overall strategy of GEOHAB is to apply the comparative approach. The comparative method assembles the separate realisations needed for scientific inference by recognising naturally-occurring patterns, and temporal and spatial variations in existing conditions and phenomena (Anderson et al. 2005a, GEOHAB 2005). Understanding the responses of harmful algae to the increasing nutrient load of comparative ecosystems of the world's coastal zones will assist in prediction of future patterns as well.

Development of a Core Research Project in GEOHAB is based upon the premise that a comprehensive understanding of the population dynamics of HABs requires the integration of oceanographic studies with the application of models of comparable ecosystem types. Such comparisons will assist in a:

- definition of common characteristics, including the groupings of harmful species from similar habitat types and identification of functional groups;
- determination of the primary physiological, genetic or behavioural processes that regulate cellular growth and toxicity;
- identification of the important physical and chemical influences over appropriate temporal and spatial scales; and
- development and validation of technologies for detailed and extensive monitoring; establishment of real-time observation platforms.

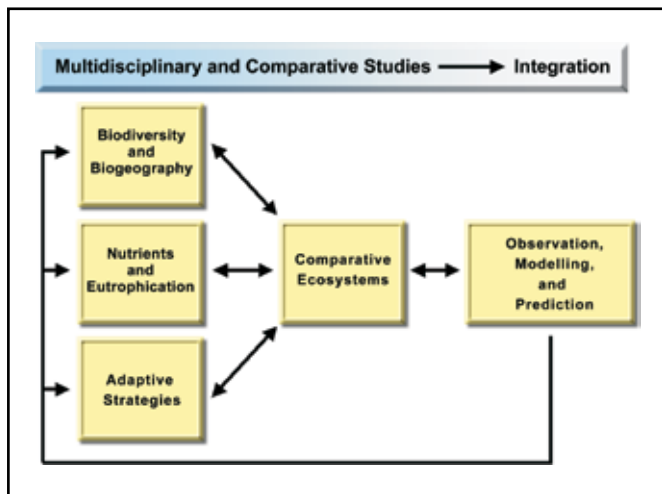
HARMFUL ALGAL BLOOMS AFFECT BOTH NEARSHORE AND OFFSHORE WATERS (LEFT TO RIGHT: SWEDEN; HONSHU, JAPAN; BALTIC SEA). PHOTOS: G. ANEER, Y. FUKUYO, AND K. KONONEN.



The GEOHAB Science Plan

The *GEOHAB Science Plan* outlines five Programme Elements that serve as a guide to establish the research priorities. These elements and their overarching questions include:

- **Biodiversity and Biogeography.** What are the factors that determine the changing distributions of HAB species, their genetic variability, and the biodiversity of associated communities?
- **Nutrients and Eutrophication.** To what extent does increased eutrophication influence the occurrence of HABs and their harmful effects?
- **Adaptive Strategies.** What are the unique adaptations of HAB species and how do they help to explain their proliferations or harmful effects?
- **Comparative Ecosystems.** To what extent do HAB species, their population dynamics, and community interactions respond similarly under comparable ecosystems?
- **Observation, Modelling, and Prediction.** How can we improve the detection and prediction of HABs by developing capabilities in observation and modelling?



THE INTEGRATION OF FINDINGS FROM THE INDIVIDUAL PROGRAMME ELEMENTS DESCRIBED IN THE *GEOHAB SCIENCE PLAN* IS REQUIRED TO ACHIEVE NOT ONLY AN UNDERSTANDING OF HAB ORGANISMS AND ASSOCIATED EVENTS, BUT ALSO TO DEVELOP PREDICTIVE CAPABILITIES. SOURCE: GEOHAB 2001.

Core research on **HABs in Eutrophic Systems** directly addresses Programme Element 2, Nutrients and Eutrophication, of the *Science Plan*. As outlined therein, the overall objective of the Nutrients and Eutrophication Programme Element is to determine the significance of eutrophication and nutrient transformation pathways to HAB population dynamics.

The identified specific objectives of the Nutrients and Eutrophication Programme Element of GEOHAB include:

- determine the composition and relative importance to HABs of different nutrient inputs associated with human activities and natural processes;
- determine the physiological responses of HAB and non-HAB species to specific nutrient inputs;
- determine the effects of varying nutrient inputs on the harmful properties of HABs; and
- determine the role of nutrient cycling processes in HAB development.

Smaller in scope, but nonetheless equally important to the success of GEOHAB, are Targeted Research Studies. Targeted Research Studies address individual objectives outlined in the *Science Plan* (GEOHAB 2001). Development of specific models, or comparative laboratory investigations of particular HAB species or species groups, may be investigations that fall under the realm of Targeted Research Studies.

This document outlines the justification, the priorities for study, and the approaches to be taken, in studying the relationship between HABs and eutrophication. Research on **HABs in Eutrophic Systems** will require the multi-dimensional approaches of a Core Research Project, combined with focused or targeted research, which may address specific needs related to individual species, systems, or model development. In the following sections, a general synopsis of the current state of understanding with respect to the role of eutrophication in HABs is provided, followed by an identification of the major research priorities, and finally a roadmap for addressing these research needs. Research on these major priority areas in eutrophication and its associated effects on HABs is welcome within the GEOHAB framework (GEOHAB 2003).

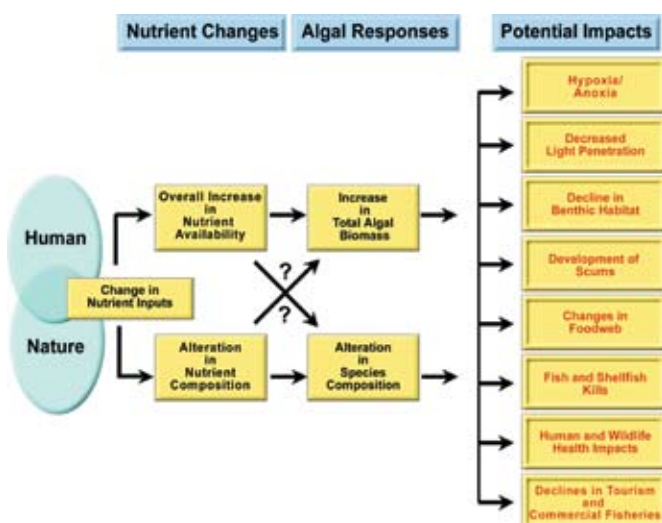


KARENIA MIKIMOTOI BLOOM IN EAST CHINA SEA, SUMMER 2005. PHOTO: J. LI.

3. General Understanding of HABs and Eutrophication: A Synopsis



MASSIVE BLOOMS OF THE DINOFLAGELLATE *PROROCENTRUM MINIMUM* DEVELOP ANNUALLY IN THE CHESAPEAKE BAY, USA. PHOTO: P. GLIBERT.

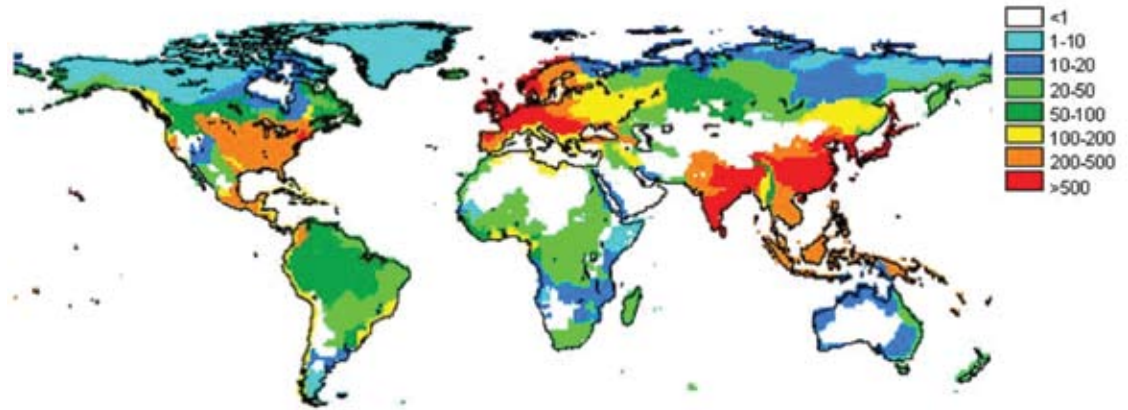


NUTRIENT CHANGES, ALGAL RESPONSES, AND ECOSYSTEM IMPACTS ARE LINKED AT MANY LEVELS. SOURCE: GEOHAB 2001.

Much has been written in recent years concerning the relationship between HABs and eutrophication (e.g., Smayda 1990, Hallegraeff 1993, Riegman 1995, Richardson and Jørgensen 1996, Anderson et al. 2002, Glibert et al. 2005), but much uncertainty remains with respect to the process of eutrophication and how it impacts the propensity for specific blooms. Although it may seem reasonable to assume a causal relationship between human activities and an expansion of HAB events, the underlying mechanisms are not well known. It is imperative to learn how present trends in pollution and nutrient loading relate to algal blooms in general, as well as how they may promote the development of particular species. The key to this knowledge is an understanding of the ecology and oceanography of HABs at both regional and global scales. Highlights of current general understanding are provided herein. This is not intended to be a comprehensive review, but rather a synopsis of where progress has been made and where significant questions still remain. By highlighting the critical issues, the justification for the Core Research Project on **HABs in Eutrophic Systems** will become apparent.

“Eutrophication is the process of increased organic enrichment of an ecosystem, generally through increased nutrient inputs.”

Nixon 1995



Eutrophication and Its Global Effects

“Eutrophication” has been defined in various ways (e.g., Nixon 1995, Richardson and Jørgensen 1996). Central to all definitions is the concept that the enrichment of water by nutrients causes an accelerated growth of algae and higher forms of plant life, which leads to an undesirable disturbance in the balance of organisms present in the water and to the quality of the water concerned. The result of eutrophication is often an increase in total algal biomass, frequently dominated by one or more species or groups. Such blooms may have deleterious effects including overgrowth and shading of seaweeds and sea grasses, oxygen depletion of the water from algal respiration or decay of algal biomass, suffocation of fish, direct toxic effects on fish and shellfish, suffocation of fish from stimulation of gill mucus production, and mechanical interference with filter feeding by fish and bivalve mollusks. Deleterious effects on the benthos may also be considerable. Of additional concern with the development of high-biomass algal blooms is the poor transfer of energy to higher trophic levels, as many bloom species are not efficiently grazed, resulting in decreased transfer of carbon and other nutrients to fish stocks when they replace desirable algal species. For example, some HAB species secrete allelopathic substances that inhibit co-occurring species (Pratt 1966, Gentien and Arzul 1990), and suppression of grazing occurs above a threshold concentration of the HAB species (Tracey 1988). Recently, it has also been shown that an increase in the production of allelochemicals occurs when some HAB species are subjected to unbalanced nitrogen or phosphorus conditions, which in turn are directly caused by eutrophication (Granéli and Johansson 2003, Fistarol et al. 2005a).

Eutrophication of both inland and coastal waters is a result of human population growth and the production of food (agriculture, animal operations, and aquaculture) and energy, and is considered one of the largest pollution problems globally (Howarth et al. 2002a, 2005). Population growth and increased food production result in major changes to the landscape, in turn increasing sewage discharges and runoff from farmed and populated lands. In addition to population growth, eutrophication arises from the large increases in the use of chemical fertilisers that began in the 1950s

MODEL-PREDICTED EXPORT OF DISSOLVED INORGANIC NITROGEN FROM WATERSHEDS TO COASTAL SYSTEMS ($\text{kg N km}^{-2} \text{WATERSHED}^{-1} \text{YEAR}^{-1}$).
SOURCE: SEITZINGER AND KROZE 1998.

and which are projected to continue to escalate in the coming decades (Smil 2001, Galloway et al. 2004, Glibert et al. 2006). Both nitrogen and phosphorus are of concern in eutrophication (NRC 2000, Howarth and Marino 2006), but nitrogen has received far more attention because it often limits primary production in estuaries and coastal waters, and because the global application of nitrogen from synthetic fertilisers is far greater than that of phosphorus (Wassman and Olli 2005). Furthermore, for many regions where phosphorus limitation has developed, it may be the result of excess nitrogen loading. Phosphorus loading, however, is often cited as the major cause of HABs in freshwaters (Oliver and Ganf 2000) where nitrogen-fixers often dominate.

Nutrients can stimulate or enhance the impact of toxic or harmful species in several ways (Anderson et al. 2002). At the simplest level, harmful phytoplankton may increase in abundance due to nutrient enrichment, but remain in the same relative fraction of the total phytoplankton biomass. Even though non-HAB species are stimulated proportionately, a modest increase in the abundance of a HAB species can cause it to become noticeable because of its toxic or harmful effects. A more frequent response to nutrient enrichment occurs when a species or group of species begins to dominate under the altered nutrient regime. In deeper freshwater, estuarine, and coastal marine systems, phytoplankton dominate the algal flora. In contrast, macroalgae and benthic microalgae often dominate many shallow lakes and poorly flushed estuaries, lagoons, and upper embayments, as well as coral reefs and rocky intertidal/subtidal habitats (Harlin 1993). In surface waters across the entire salinity gradient, there are many examples of overgrowth and high-biomass blooms by phytoplankton, benthic microalgae (especially epiphytes), and macroalgae. In many cases, the responding dominant species are not toxic and, in fact, are beneficial to coastal productivity until they exceed the assimilative capacity of the system, after which hypoxia and other adverse effects occur. When that threshold is reached, seemingly harmless species can have negative impacts.



ABOVE: LARGE BLOOMS OF *KARENIA BREVIS* OCCURRED IN FLORIDA, USA DURING 2005, RESULTING IN LARGE FISH KILLS. PHOTOS: C. HEIL.

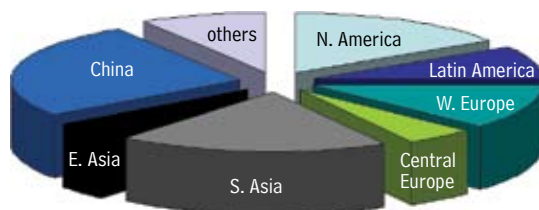
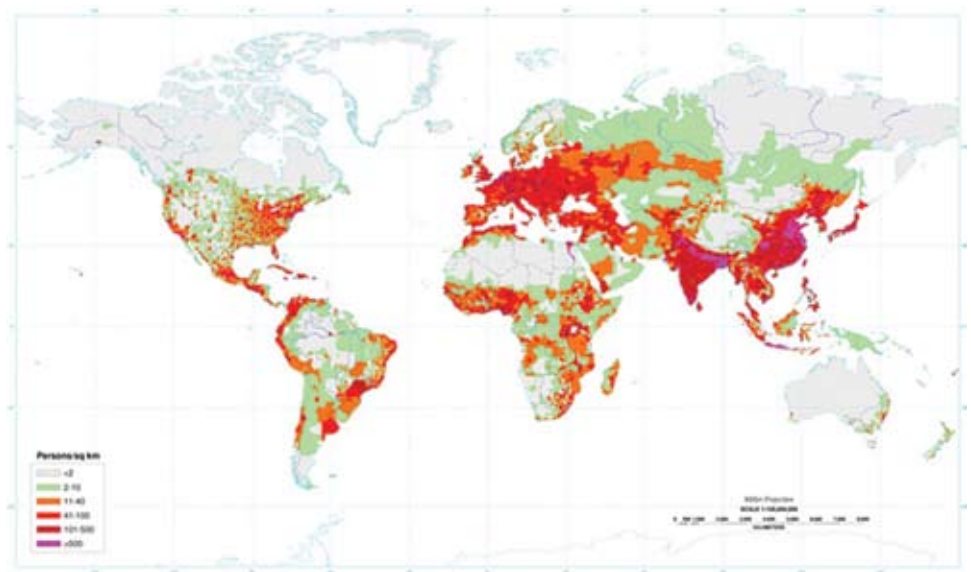
BELOW: LARGE BLOOMS OF *KARENIA MIKIMOTOI* OCCURRED IN EAST CHINA SEA IN SUMMER 2005, RESULTING IN KILLS OF BOTH WILD AND FARMED FISH. PHOTOS: J. LI.



Increases in high-biomass phytoplankton blooms have been reported from the South China Sea (Qi et al. 1993), the Black Sea (Bodeanu and Ruta 1998), Hong Kong (Lam and Ho 1989), and many other locations, typically in parallel with the nutrient enrichment of coastal waters. In Chesapeake Bay, USA, high phytoplankton biomass is typically observed in the spring, associated with high riverine nutrient inputs (Glibert et al. 1995, Malone et al. 1996). These large spring blooms eventually settle to the bottom, where heterotrophic bacteria process a major fraction of the organic material. This can result in depletion of oxygen as temperatures warm (Malone et al. 1986, Shiah and Ducklow 1994), leading to hypoxia and mortalities of benthic organisms (e.g., Boynton et al. 1982, Malone et al. 1983, Fisher et al. 1988, 1992, Glibert et al. 1995). As another example, spring eutrophication from the nitrogen loading of the Mississippi and Atchafalaya rivers to the Gulf of Mexico has resulted in enhanced phytoplankton production and the development of hypoxia in the

Gulf of Mexico, a so-called “dead zone” that has altered benthic food web dynamics and fish habitat substantially (Turner and Rabalais 1994, Craig and Crowder 2005).

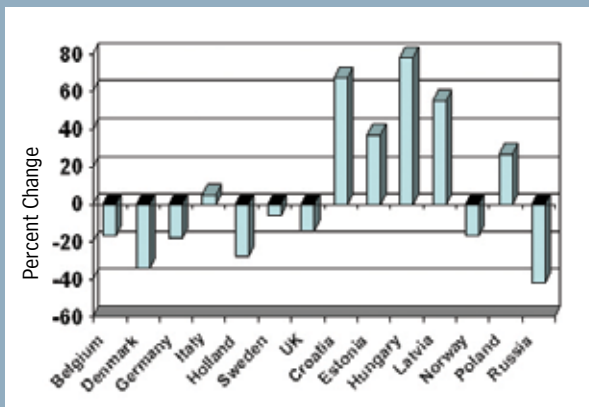
Although eutrophication is occurring globally, nutrient export is not evenly distributed (Seitzinger et al. 2002a, 2005a, Howarth et al. 2005, Glibert et al. 2006). Inorganic nitrogen export to coastal waters is estimated to be highest from European and Asian lands, although significant discharge also occurs from the United States and other parts of the world (Seitzinger and Kroeze 1998). Furthermore, the rate of nutrient export to coastal waters has increased dramatically in recent years in some parts of the world. For example, China, which used less than 5 million metric tonnes of nitrogen fertiliser annually in the 1970s, now uses more than 20 million metric tonnes per year, representing 25% of global nitrogen fertiliser consumption (Glibert et al. 2005), leading to significantly increased nitrogen pollution of its coastal waters.



CONTRIBUTION BY GLOBAL REGION TO THE CONSUMPTION OF THE WORLD'S ANNUAL CURRENT USE OF 85 MILLION TONNES OF NITROGEN. DATA FROM THE INTERNATIONAL FERTILIZER INDUSTRY. SOURCE: GLIBERT ET AL. 2005.

WHERE PEOPLE LIVE ON THE PLANET EARTH, 2003. SOURCE: NATIONAL RESOURCES CONSERVATION SERVICE, USDA.

The world's human population is expected to continue to increase by 1-2% per year (Cohen 2003), and eutrophication and its effects, including HABs, hypoxia, fish kills, and loss of habitat are expected to increase in many parts of the world. Most of these increases are expected to occur in areas that are already affected by HABs.



Projections of percent change in nitrogen fertiliser use for the three decades from 1990 to 2020 for some countries. Plotted from data provided in Cofala et al. 2001.

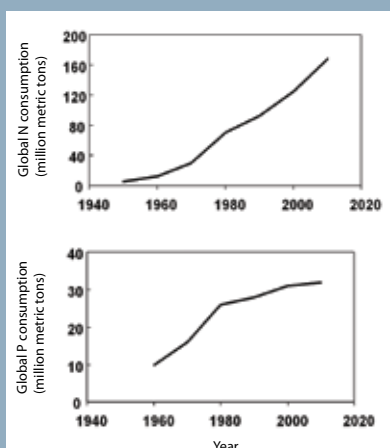


FROM (ABOVE) SEWAGE DISCHARGE (PHOTO: A. KANA), TO IMPACTS OF ATMOSPHERIC EMISSIONS, TO INTENSIVE AQUACULTURE DEVELOPMENT (PHOTO: P. GLIBERT) AND ANIMAL PRODUCTION FACILITIES, TO (BELOW) RUNOFF FROM APPLIED FERTILISER AND MANURES (PHOTO: WWW. KUHNKNIGHT.COM), THE ANTHROPOGENIC SOURCES OF NUTRIENTS ARE MANY.



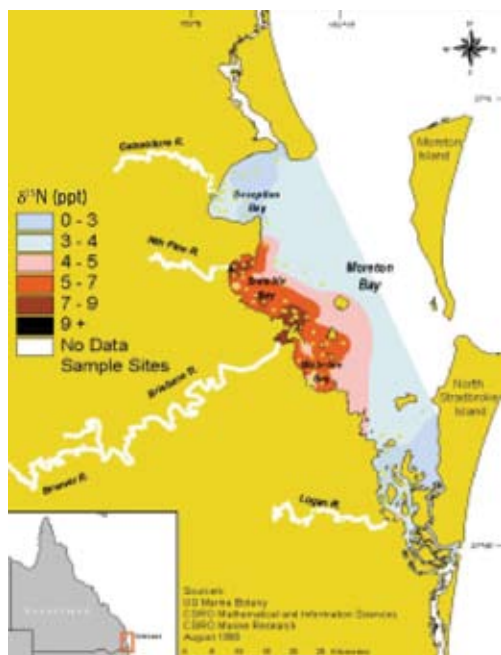
Global Use of Fertilisers

The change in global consumption of nitrogen and phosphorus synthetic fertilisers over the past several decades (from International Fertilizer Industry 2005). Projections through 2010 are based on an annual increase of 3% (Glibert and Burkholder 2006).



Sources of Nutrient Inputs

A broad range of anthropogenic activities result in significant alteration of nutrient cycling of coastal environments. Fertiliser application on land remains a major contributor to nonpoint nutrient pollution, and this source is still increasing at an alarming rate in many geographic regions (Vitousek et al. 1997). Groundwater has also been identified as an important source of nutrients to receiving surface waters. Human population growth and agricultural practices have increased nutrient loadings to groundwater, and this has the potential to affect algal growth in adjacent rivers, lakes, estuaries, and coastal zones. On local to global scales, one of the most rapidly increasing sources of nutrients to both fresh waters and the coastal zone is the atmosphere. Atmospheric inputs are important not only because of their magnitude, but because the mix of atmospheric nutrients – like other nutrient sources – can stimulate some phytoplankton species disproportionately over others. Atmospheric deposition of nitrogen comes from both fossil fuel combustion and from volatilization from agriculture and its magnitude is likely to be underestimated in many cases, since gaseous dry nitrogen deposition is seldom measured (Galloway et al. 2004, Howarth et al. 2002a, 2005). Blooms in the Yellow Sea of China, which have escalated in frequency over the past several decades, have been related to atmospheric deposition in addition to direct nutrient runoff (Zhang 1994). It is estimated that a typical rain event over the Yellow Sea may supply sufficient nitrogen, phosphorus, and silicon to account for 50-100% of the primary production of a HAB event (Zhang 1994). Aquaculture ponds and cage culture systems represent another source of nutrients, provided as feed or fertiliser and by the biological transformations occurring in these high-biomass systems. It has been suggested that these enriched systems may promote the growth of harmful species not previously detected in the source water (Anderson 1989, Hallegraeff 1993).

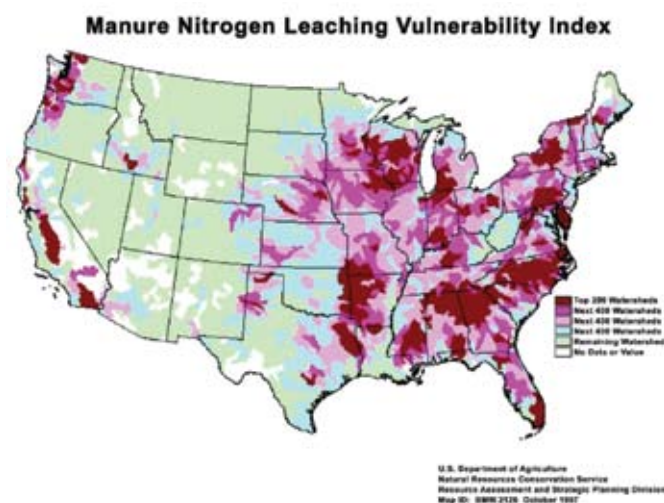


SEWAGE PLUME MAP AS INDICATED BY $\delta^{15}\text{N}$ SIGNATURES OF MACROALGAE DEPLOYED FOR 4 DAYS IN MARCH, 1998. DISTINCT SEWAGE PLUME (HIGH $\delta^{15}\text{N}$ VALUES) WAS EVIDENT AT THE MOUTH OF THE BRISBANE RIVER, AUSTRALIA. SOURCE: DENNISON AND ABAL 1999.

Strong positive relationships have been reported between increasing human population and the intensity of HAB outbreaks (Lam and Ho 1989, Trainer et al. 2003). For example, in Tolo Harbour, Hong Kong, human population within the watershed grew 6-fold between 1976 and 1986, during which the number of red tide events increased 8-fold (Lam and Ho 1989). In Puget Sound of Washington State, USA, where consistent shellfish monitoring has been carried out for decades, a strong positive relationship between the frequency of one algal toxin, paralytic shellfish toxin (PST), and the growth in human population has recently been reported (Trainer et al. 2003).

However, the impacts of differing anthropogenic activities are not necessarily the same. For example, nutrient delivery associated with sewage may bear little similarity in quantity or composition to that associated with inputs from agriculture, aquaculture, or dredging operations. In turn, nutrients from these sources may also differ in quantity and composition from those associated with natural delivery mechanisms such as groundwater flow and atmospheric deposition, recognising that these sources may also be affected by human activities. The challenge that remains is understanding the conditions under which specific nutrient forms, or specific nutrient sources, may impart an advantage to certain HAB species and thus lead to their proliferation.

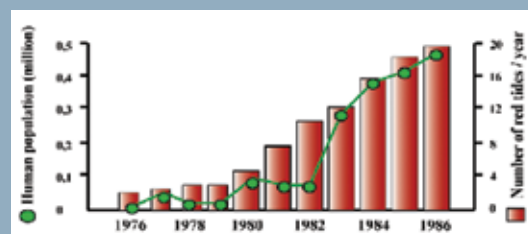
Moreover, impacts of upwelling, storms, monsoons, and/or tsunamis may also be sources of nutrient delivery that have to be distinguished from those above. Therefore, it is of critical importance to distinguish the impacts of various activities on HAB development, and how these impacts may differ from natural mechanisms based on which nutrients are delivered to the coastal zone.



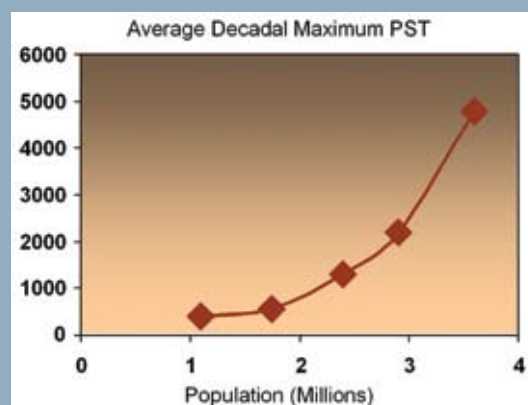
ANIMAL MANURES ARE A COMMONLY APPLIED FERTILISER. THIS MAP SHOWS THOSE WATERSHEDS MOST SUSCEPTIBLE TO LEACHING OF MANURE NITROGEN TO COASTAL AND ESTUARINE WATERS. MANURES ARE ONE SOURCE OF NUTRIENTS THAT HAVE INCREASED SUBSTANTIALLY IN RECENT YEARS. SOURCE: US DEPARTMENT OF AGRICULTURE.

Increasing HAB Occurrences

Increasing HAB occurrences in the Tolo Harbour, Hong Kong, concomitant with the increase in human population in the region. Redrawn by Granéli from Lam and Ho 1989.



The relationship between population growth (in millions) and the average decadal maximum paralytic shellfish toxin in Puget Sound, Washington State, USA. Replotted from Trainer et al. 2003.



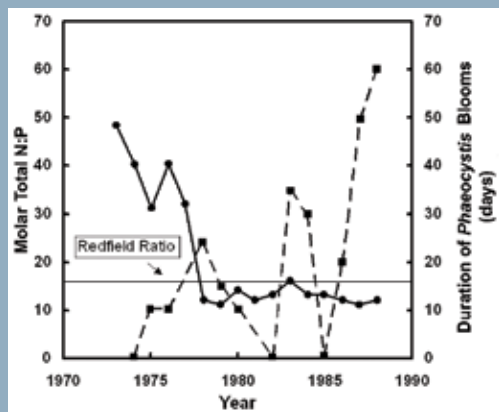


HIGH-BIOMASS BLOOM IN TOLO HARBOUR, HONG KONG, RESULTING IN DISCOLORED WATER, HYPOXIA, AND TOXICITY OF FISH AND SHELLFISH. PHOTO: M. DICKMAN.

Foams of *Phaeocystis* may be caused by the exudation of protein-rich foams by the algae. Photo by V. Rousseau, courtesy of the EUOHAB Science Initiative, 1999.



The change in N:P ratio is related to *Phaeocystis* blooms in Dutch coastal waters. From Anderson et al. 2002, based on Riegman 1995.



The Importance of Nutrient Quality

Many factors affect phytoplankton species composition and bloom development, and among these is the composition of the nutrient pool – the forms of the nutrients supplied, as well as the relative abundance of the major nutrient elements. Efforts to understand the relationships between nutrient loading and algal blooms have largely focused on total nutrient loads and altered nutrient ratios that result from selected nutrient addition or removal. Alterations in the composition of nutrient loads have been correlated with shifts from diatom-dominated to flagellate-dominated algal assemblages (Smayda 1990). For example, the number of red tide events in Chinese coastal waters increased sharply from 1970 to 1993, due in large part to altered nitrogen-to-phosphorus ratios from increasing use of synthetic fertilisers and increasing atmospheric emissions and deposition of pollutants.

Perhaps the clearest demonstration of the effect of altered nutrient supply ratios involves the stimulation of non-diatom species following increases in the availability of nitrogen or phosphorus relative to silicate. A prominent example of the importance of nutrient supply ratios in determining phytoplankton species composition is seen with the foam-producing prymnesiophyte *Phaeocystis pouchetii*. A 23-year time series off the German coast of the Baltic Sea documents the general enrichment of these coastal waters with nitrogen and phosphate, and a 4-fold increase in the N:Si and P:Si ratios (Radach et al. 1990). This was accompanied by a decrease in the diatom community and an increase in the occurrence of *Phaeocystis* blooms. A similar time series of alterations in the N:Si ratio has also been documented for Narragansett Bay, USA, in which a decreased ratio of diatoms to flagellates, and increased abundance of HAB species such as *Heterosigma akashiwo*, corresponded with an increase in the N:Si ratio due to excess nitrogen loading from the early to late 1980s (Smayda and Borkman, in press).

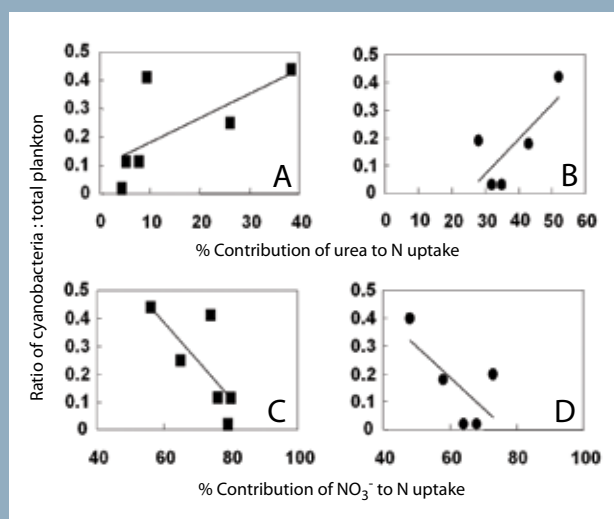


MICROCYSTIS BLOOM ON THE LOWER ST. JOHNS RIVER, FLORIDA, 2005.
 PHOTO: B. YATES, WWW.CYPIX.NET.

Many freshwater systems, and freshwater end members of estuarine systems as well, have seen a shift in phytoplankton species composition towards bloom-forming cyanobacteria, including toxic species such as *Microcystis aeruginosa*, as phosphorus loads have increased in these systems (Oliver and Ganf 2000). In tributaries of Chesapeake Bay, USA, blooms of *M. aeruginosa* in 2003 and 2004 were up to 4 times higher than a decade earlier (P. Tango, unpub. data).

Although phytoplankton have long been known to use organic nutrients in addition to inorganic nutrients (Flynn and Butler 1986, Antia et al. 1991), increasingly it has become recognised that they do so under natural conditions. Some species use organic nutrients for their sole nutritional requirements, others to supplement their use of inorganic nutrients, while still others may use organic compounds for their carbon demands as well (e.g., Granéli et al. 1997, 1999, Stoecker 1999). An increased understanding of the bioavailability of anthropogenically derived organic compounds has also developed in recent years. The chemical composition of dissolved organic matter exported from agricultural watersheds is not known, but up to 50% of this material can be taken up directly or indirectly by estuarine plankton communities (Seitzinger et al. 2002b). The chemical composition, bioavailability, and effects of dissolved organic matter on coastal plankton communities vary depending on its source, the plankton community composition, and the season (Bronk 2002). Organic nutrients have been shown to be important in the development of blooms of various HAB species, in particular cyanobacteria and dinoflagellates (e.g., Paerl 1988, Glibert et al. 2001) and the importance of this phenomenon is beginning to be documented around the world (e.g., Granéli et al. 1985, 1999, Berman 1997, 2001, Berg et al. 2003). A recent study found that in Florida Bay and on the southwest Florida continental shelf, the cyanobacterial fraction of the algal community was positively correlated with the fraction of nitrogen taken up as urea, and negatively correlated with the fraction of nitrogen taken up from the inorganic source, nitrate (Glibert et al. 2004). Other studies have shown that some cyanobacteria

The relationship between the percent contribution of urea to total N uptake by the algal community and the fraction of that community that was cyanobacteria for Florida Bay (panel A) and for the southwest Florida continental shelf (panel B), and the relationships between percent contribution of NO_3^- to total uptake (panels C and D) for the same sites. From Glibert and Heil (2005).



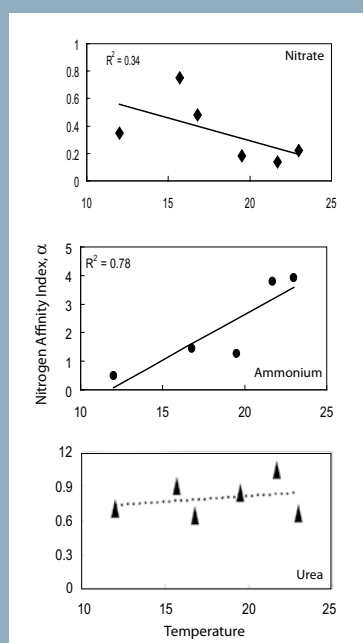
grow faster on urea than on other nitrogen sources (Berman and Chava 1999, Mulholland et al. 1999). World-wide use of urea has increased in recent decades, such that urea now represents >50% of all global nitrogen fertiliser use (Glibert et al. 2006).

“It may be that as eutrophication progresses through its various stages, changes in life-form conditions occur which determine which life-form type of phytoplankter will predominate.”

Ted Smayda (2005) p. 96



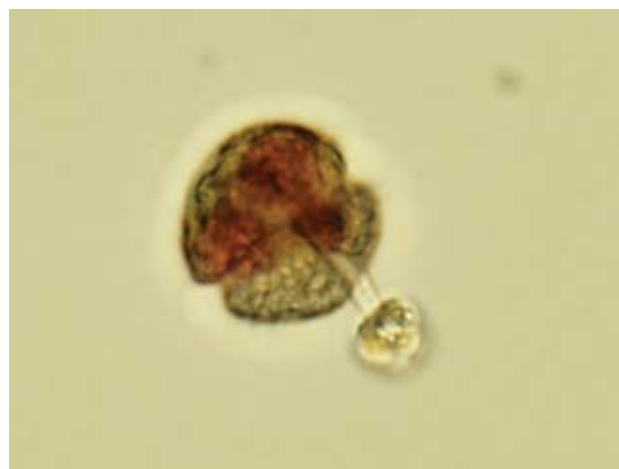
Prorocentrum minimum blooms in the tributaries of Chesapeake Bay, USA, have been related to nutrient input. The extent to which this bloom depends on different forms of nitrogen is highly dependent on temperature (Fan et al. 2003). Photo: P. Glibert.



Complexity of Responses of HABs to Nutrients

The complexity of the relationship between HABs and eutrophication is beginning to be appreciated (Smayda 1989, Anderson et al. 2002, Glibert and Burkholder 2006). The ecosystem response to nutrient enrichment, or eutrophication, is a continual process rather than a static condition or a trophic state (Cloern 2001, Smayda 2005). Nutrient availability must be matched with the preferences of the cells and their physiological conditions, and with the physical and trophic structure of the water column at the time of nutrient delivery. A recent conceptual framework of HAB dinoflagellates has been developed. This is based on distinctive morphological and habitat preferences, ranging from invasive species that dominate in habitats with enriched nutrient loading to those that thrive in more oligotrophic, stratified systems (Smayda and Reynolds 2001). Large blooms of *Prorocentrum minimum*, found in many regions affected by anthropogenic nutrient inputs, are an example of a species that thrives in habitats with enriched nutrient loading (Heil et al. 2005). In contrast, *Karenia brevis* and *K. mikimotoi* bloom in open coastal waters, aggregate in fronts, and are transported by coastal currents (Dahl and Tangen 1993, Walsh et al. 2001).

Nutritional mechanisms are complex. In addition to direct uptake by autotrophs, other pathways of nutrient acquisition must be recognized. Indeed, some species, such as the ichthyotoxic dinoflagellate *Pfiesteria piscicida* are not autotrophs at all, and instead, rely virtually exclusively on grazing for their nutrition. In the case of *Pfiesteria*, nutrition is provided through a combination of consumption of bacteria and other small algae, as well as bits of epidermal tissue of fish (Burkholder and Glasgow 1997, Lewitus et al. 1999). Such modes of nutrition complicate our ability to model and predict biomass development based solely on nutrient loadings. Several cyanobacterial species (e.g., *Trichodesmium*, *Anabaena*, *Nodularia*, *Aphanizomenon*) are also capable of fixing nitrogen and may therefore form massive blooms in circumstances where the growth of other phytoplankton is limited by nitrogen.



MANY BLOOM-FORMING FLAGELLATES HAVE PHAGOTROPHIC CAPABILITIES - THE ABILITY TO ENGULF AND INGEST PARTICULATE MATERIAL FOR NUTRITIONAL PURPOSES, SUCH AS THIS *PFISTERIA* CELL FEEDING ON A CRYPTOMONAD CELL. PHOTO: M. PARROW.

Thus, while there have been many advances in our understanding of nutrient uptake pathways by various species, these pathways and preferences are complex. It is increasingly recognized that certain species or groups of species have nutritional requirements and preferences, and therefore may be favoured when the environment is altered in such a way as to increase the relative availability of the preferred source.

In addition to species-specific responses and nutrient uptake requirements, the geographic range and biomass of algae are affected by physical controls and the behaviour of the harmful algal species. Long-distance transport of organisms (e.g., Franks and Anderson 1992), accumulation of biomass in response to water flows, buoyancy regulation, and swimming behaviour (Kamykowski 1995), and maintenance of suitable environmental conditions (including temperature, salinity, stratification, irradiance, and nutrient supply; Whittedge 1993) are critical to understanding the ecosystem response to nutrient loads.

Of additional consideration are the trophic interactions controlling the growth and accumulation of algal biomass. Changes in food web structure attributable to over-fishing, habitat degradation, invasive species, and other factors also interact with nutrient loading to increase susceptibility of a system to HABs. When algae are released from predation due to alterations in the grazing community, they may proliferate in eutrophic environments due to the abundance of nutrients (Merrell and Stoecker 1998, Stibor et al. 2004, Vadstein et al. 2004). Changes in food web structure affect grazing pressure through trophic cascading (Gismervik et al. 1996, Park and Marshall 2000, Turner et al. 2001); thus, changes at any level of the cascade may ultimately impact the grazing on the algae.

One area that is especially poorly understood is the extent to which, and the mechanisms whereby, nutrient enrichment may lead to the development of HAB species that are toxin producers. Although eutrophication may be associated with increasing numbers of high-biomass blooms or other HAB events, the specific

relationships leading to increased frequency of toxin producers, and the increased production of toxin within these organisms are often poorly characterized. As many toxins are considered to be secondary metabolites, their production will depend on the physiological condition of the cells (Flynn and Flynn 1995, Granéli et al. 1998, Granéli and Flynn 2006). Differences in toxin production may therefore be related to changes in growth rate or the growth conditions of an organism. For *Pseudo-nitzschia*, for example, more domoic acid is produced under silica or phosphorus limitation than under nitrogen limitation, likely due to the fact that domoic acid is a nitrogen-rich molecule (Bates et al. 1989, 1991). Furthermore, when adapted to its nitrogen source, *Pseudo-nitzschia* appears to produce more domoic acid when grown on urea than on other nitrogen sources (Armstrong and Kudela 2003). Growth on urea is also known to change the toxin content and composition in the genus *Alexandrium* (Dyhrman and Anderson 2003). These studies underscore the importance of nutrient source as well as physiological condition in toxin production by HAB species.

Another area that is starting to gain attention is how some HAB species increase production not only of toxins but also of allelochemicals, particularly under conditions of nitrogen or phosphorus deficiency. These allelochemicals enable such species to utilize the “scarce” nutrient resources by inhibiting and/or killing their competitors (other algae) and even their grazers (Granéli and Johansson 2003a, Tillmann 2003, Fistarol et al. 2005). In such situations, the effects of these allelochemicals are enhanced even further, as the other algae are debilitated by nutrient depletion (Fistarol et al. 2005). Monospecific blooms are often found for such species with the capability of producing potent allelochemicals, as in the case of *Prymnesium parvum* (Granéli and Johansson 2003b, Granéli and Hansen 2006).



As a further, more fundamental complication, different strains within the same species often respond to nutrients differently. A common misunderstanding is that the characteristics of one strain, maintained for years under highly artificial laboratory conditions, are representative of all strains of that species in the natural environment. This assumption overlooks the fact that for nearly all algal species studied, different strains within the same species generally have shown marked differences in fundamental traits such as growth characteristics, toxicity, bloom-forming behaviour and responses to nutrients and other environmental conditions (Cembella et al. 1987, Wood and Leatham 1992, Anderson et al. 1994, Burkholder et al. 2001, 2005, Burkholder and Glibert 2006). In the case of the cyanobacterium *Microcystis aeruginosa*, high levels of nitrogen and phosphorus were found to favour the growth of toxic strains over non-toxic strains (Vezie et al. 2002). There is much yet to be understood with respect to the response of individual species to nutrient loading, and how changes in both quantity and quality of nutrient loading, in conjunction with the physical and trophodynamic state of the receiving waters, may lead to HABs. It is therefore important to study the growth and behaviour characteristics of strains of a particular species from a number of globally-distributed locations and to do so under natural nutrient concentrations and to collect data adequate for the support of modelling (Flynn 2005b).

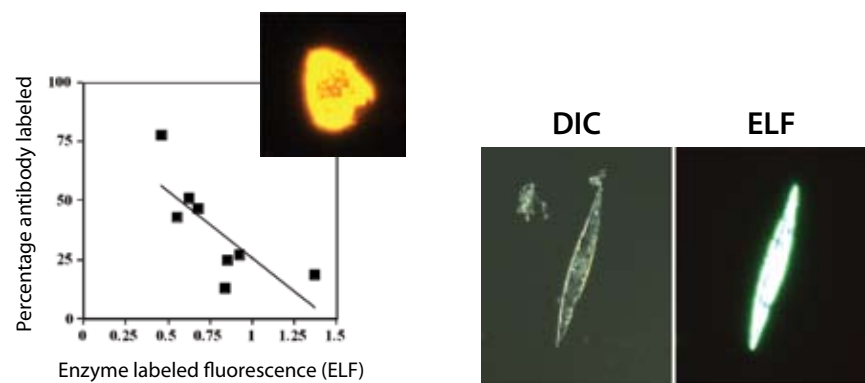
AUTONOMOUS INSTRUMENTATION IS PERMITTING ACQUISITION OF A RANGE OF DATA, INCLUDING NUTRIENT CONCENTRATIONS, BEFORE, DURING, AND AFTER BLOOMS, ADVANCING OUR UNDERSTANDING OF THE DYNAMIC RELATIONSHIPS BETWEEN NUTRIENTS AND HAB OUTBREAKS. PHOTOS LEFT TO RIGHT: W. BOICOURT AND M. TRICE.

Advancing the Study of HABs and Eutrophication Through New Techniques

The potential for advances in understanding of the impacts of nutrient pollution on, and relating eutrophication to, HABs and their proliferation is large. New and better tools are providing methodologies for addressing questions related to the complexities of the nutrient pool, the time and space scales on which nutrients are delivered, and algal nutrition. Only a few tools are illustrated here.

A classic dilemma in assessing whether, and, to what extent, nutrients are stimulatory to a given HAB is that the reporting and sampling of bloom events typically occurs after the HAB has developed. By that time, many nutrients are consumed, leading to the potentially erroneous conclusion that nutrients are unavailable and therefore unimportant. Traditional approaches for collecting information on nutrient distributions, such as weekly or bimonthly sampling, are also inadequate to detect the short-lived nutrient pulses that often follow meteorological events. Development of in situ nutrient monitors has provided a means to begin resolving the all-important antecedent conditions and to provide sufficient resolution of the temporal scale of bloom events. Use of these types of in situ instruments in conjunction with other remote methods for resolving additional environmental characteristics (Babin et al. 2005) may yield the resolution necessary to define the ephemeral changes in nutrients that can be significant to phytoplankton cells.

The HAB research field has led the oceanographic community in species detection. Advances in molecular approaches are also allowing, for some species, the resolution of the response of an individual population within a mixed species assemblage. For



LEFT: PERCENTAGE ANTIBODY LABELED. RIGHT: CELL-SPECIFIC DETECTION OF ENZYME ACTIVITY: ENZYME LABELED FLUORESCENCE (ELF) DETECTS ALKALINE PHOSPHATASE ACTIVITY IN A FIELD SAMPLE FROM THE OREGON COAST. SOURCE AND PHOTOS: S. DYHRMAN.

example, major advances in marine microbial genomics, such as the sequencing of *Thalassiosira pseudonanna* (Armbrust et al. 2004, Doney et al. 2004) are providing insight into the genetic capacity of selected algal models. In recognition of its significance, the Joint Genomic Institute (<http://www.jgi.doe.gov>) is now sequencing the *Aureococcus anophagefferens* genome (~32Mb). The availability of this first full HAB genome will allow researchers an unprecedented ability to assess physiological potential in this species, and to examine the genome for clues as to how this model organism uses nutrients and what makes it so successful in certain coastal systems. These genomic advances are driving technology development, and as the cost of sequencing becomes affordable, there are an increasing number of studies that are examining transcriptional processes in key organisms (Lidie et al. 2005). Tools such as quantitative polymerase chain reaction (PCR) and microarray chip technology are becoming available, and these approaches will increasingly allow scientists to assay (at the level of gene transcription) how different HAB species respond to changes in their exogenous nutrient environment. Additional advances in protein detection and characterisation will help to further define how HAB species respond to eutrophication. For instance, we can now track the phosphorus physiology of *Prorocentrum minimum* using antibody probes for a phosphorus-regulated protein (Dyhrman and Palenik 2001). The HAB science community is now poised to bring the full potential of these exciting advances to the study of HABs and eutrophication.

Furthermore, flow cytometry, a methodology for rapidly measuring intrinsic or applied (stained) optical characteristics of individual cells, has been used to study the occurrence, abundance, physiology, and diversity of aquatic microorganisms for the past two decades. This technology has been increasingly applied to the study of HAB species, for example, to generally enumerate and specifically identify harmful algal cells in cultures (Shumway and Cucci 1987, Vrieling et al. 1997) and natural samples (Costas and Lopez-Rodas 1996, Becker et al. 2002). This tool also has recently advanced our understanding of HABs and their relation to nutrients and for tracking changes in the complex structure of aquatic microbial communities (including viruses, pathogenic

bacteria, and harmful algae) as related to seasonal cycles, nutrients, or bloom age (e.g., Li and Dickie 2001, Jacquet et al. 2002). Such studies, including recent in situ flow cytometric investigations of phytoplankton assemblages, are providing valuable insights about biological factors (e.g., infection, competition, grazing) that influence the occurrence and distribution of HABs. Recently, the cell-sorting capacity of some flow cytometers has been applied, as well, to assess modes of nutrition by HAB species (Parrow and Burkholder 2003).

Knowledge is also advancing about the chemical composition of the nutrient environment in which HABs may thrive. The chemical composition of the dissolved organic nitrogen pool has long been recognised to be complex, consisting of a mixture of multiple compounds (Bronk 2002). Electrospray ionisation mass spectrometry is a tool now allowing greater characterisation than has been possible in the past. In contrast to past methodologies for studying the organic matter pool – which were mostly limited to bulk analysis of total carbon or nitrogen, analyses of a few individual compounds (e.g. urea, amino acids, specific proteins), or compound classes that account for a small percent of total dissolved organic matter (e.g., total carbohydrates, total proteins; Bronk 2002) – electrospray ionisation mass spectrometry allows for the examination of a large suite of individual compounds in natural mixes of dissolved organic matter. This technique also provides molecular weight information of ionisable compounds (in the form of a mass-to-charge ratio, m/z , which equals molecular weight for singly charged compounds), and a measure of concentration as ion abundance (Seitzinger et al. 2005b). As more researchers use this type of instrument, compound libraries will be developed, allowing characterisation of individual compounds, and comparison among patterns in use of specific compounds in comparable ecosystems and by comparable species in different environments.

“A subtle, but pervasive, achievement of biological oceanography is that modelling has become a mainstream activity; it permeates so much of our work that graduate students in the discipline assume it is integral to biological oceanography. Modelling was at one time an esoteric craft practiced by a gifted few; now it is the norm. Today’s biological oceanography graduate student is more likely to have a model than a microscope.”

Richard T. Barber and Anna K. Hilting (2000), p. 19

Modelling HABs and Eutrophication

Fundamental research on HABs must be guided by and validated with observations of phytoplankton dynamics in nature. To determine why HABs occur, it is necessary to describe the temporal and spatial developments of the target species in specific ecosystems. This requires observation and modelling of the physical-chemical-biological interactions that support the specific life strategies of HAB species in relation to other members of the plankton community. Consequently, measurements of physical and chemical properties and processes, along with quantitative detection and characterisation of the plankton, must be made within a spatial and temporal framework that is appropriate for characterising bloom dynamics. It is also critically important to parametrise the environmental conditions leading up to a bloom event, and not just those associated with the terminal phases of a bloom and its subsequent decline.

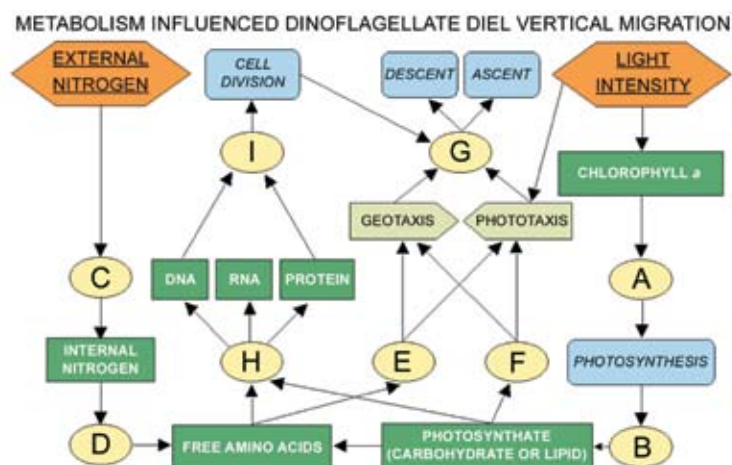
Effective interaction between observationalists and modellers is essential (Flynn 2005b). It is typical that within models, the more complex the description is of the physical environment, the less complex the description is of the biology. Similarly, the more complex the biology, the less complex is the model of the physics. An example of model hierarchy illustrates this.

Zero-dimensional models are useful for describing complex biological interactions, but with reduced physics. These models can provide test-beds to develop and check parametrisations of chemical-biological processes such as nutrient uptake, growth, grazing or production of toxins. They are appropriate for detailed descriptions of processes within the cell (e.g., interaction of the internal nutrient pools and regulation of toxin production; Flynn 1998). For advanced HAB models, processes such as these can be incorporated into dynamic models of nutrient assimilation, photosynthesis and pigment synthesis as they influence growth kinetics or toxin production (e.g., John and Flynn 2002, Flynn 2005b). Such formulations are necessary to link nutrient assimilation and growth processes with variable nutrient quotas,

cell pigments, and bio-optical signatures of phytoplankton (Schofield et al. 1999).

Further complexity can be provided through one-dimensional water column models that allow the inclusion of additional processes, such as mixing, sinking and buoyancy, nutrient uptake, and benthic-pelagic coupling in a vertically structured environment (light, salinity, temperature, nutrients). Simulations can be related directly to experiments in mesocosms and to observations in the field, if advection is not too important. Moreover, water column models can be run with very high vertical resolution to study processes in thin layers (Donaghay and Osborn 1997). Extension to two-dimensional models is useful for examining the physical-chemical-biological interactions that influence the distributions and population dynamics of phytoplankton, for example, in coastal fronts (Franks 1997). With the recognition that light and nutrient history play a major role in cell growth and metabolism (e.g., Flynn 2002), the use of Lagrangian ensemble approaches (Woods and Barkmann 1993, Anderson et al. 2005) may be necessary to unravel the population dynamics of HABs in nature.

Three-dimensional, physical-chemical-biological coupled models are required to simulate the population dynamics of HABs comprehensively in an oceanographic context. Given the scales of biological and physical variability in response to the local forcing and far-field effects, three-dimensional models must have the flexibility to allow different resolutions. Owing to their modular model structure, three-dimensional circulation models can be used for problems with different complexity of the corresponding biological processes. Examples of a simplified biological approach include the study of drifting cells that spread in response to wind-driven circulation or populations that accumulate at fronts. More complex models with physiological components, including dynamics of growth, chemical composition, and nutrient assimilation allow, in principle, comprehensive explorations of the physical, chemical, and biological interactions that determine population dynamics. These models can study the roles of sinking, buoyancy, advection, shear flows, and small-scale turbulence. So, in



addition to accounting for the physiology of algal growth and toxin production, we need to determine the rules that govern behaviour (e.g., vertical migration and variable sinking rates) and the links between behaviour and physiology (Cullen and MacIntyre 1998, Kamykowski et al. 1999).

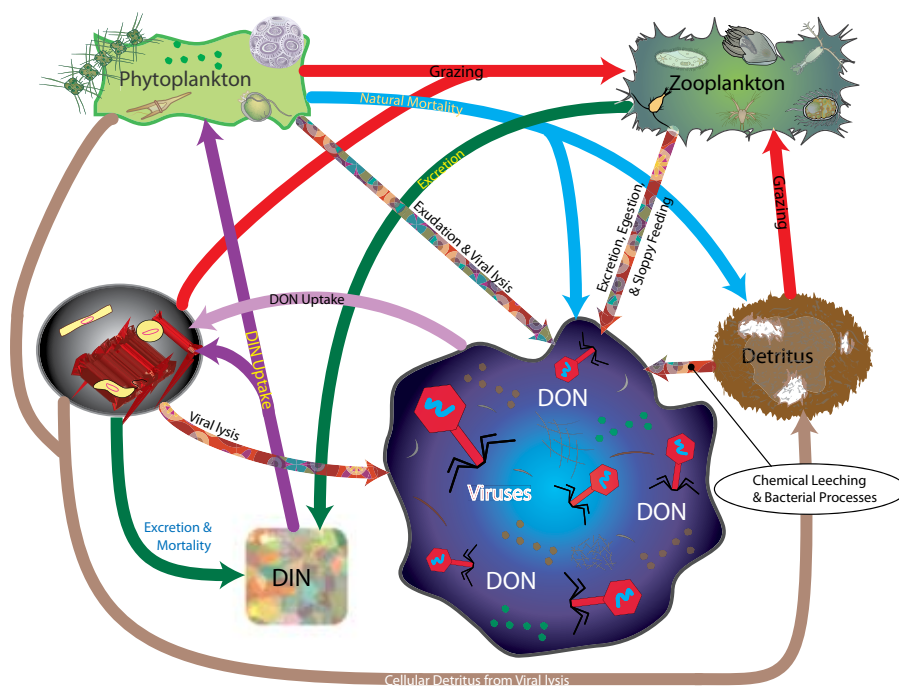
Indeed, many models could be argued as having serious flaws in their biological structure (Flynn 2005a, b). While experimental research tends to highlight differences among systems, modelers tend to try to identify unifying themes. While simplicity is the goal for all modelling efforts, the extent and means by which this is achieved is controversial. Many physical and biological oceanographers claim that model components are oversimplified. The main problem is that while physics is an exact science, biology is not; we simply know too little about the functioning of HAB ecosystems. As a consequence, biological models often rely on outdated biological knowledge. Some important biological processes are often not considered at all, for example, use of dissolved organic matter (DOM), allelopathy, mixotrophy, and prey selectivity related to nutrient status.

Effective interactions between observationalists and modellers will depend on easy interactive access for the non-specialist to modelling tools, including the component models. In turn, the interaction of observations and modelling also requires effective means for visualisation and development of interactive capabilities. Predictions of HAB-specific coupled models will be improved by well designed monitoring and use of data assimilation techniques to integrate real-time and near-real time data into a running model. Data assimilation can thus provide better now-cast predictions of conditions during process studies. These predictions are useful for adaptive sampling, and they address a principal goal of GEOHAB, the early warning and prediction of HABs.

THE COMPLEXITIES OF MODELLING POPULATION DYNAMICS ARE ILLUSTRATED HERE FOR A SPECIES THAT UNDERGOES VERTICAL MIGRATION. THE FUNCTIONS (CIRCLED LETTERS) THAT MUST BE PARAMETRISED IN THIS MODEL INCLUDE ENVIRONMENTAL FORCING, PHYSIOLOGICAL RATE PROCESSES, BIOCHEMICAL POOL CONCENTRATIONS, CELL DIVISION, AND BEHAVIOUR. SOURCE: GEOHAB 2001, MODIFIED FROM KAMYKOWSKI ET AL. 1999.

While much progress has been made, there are a number of critical issues with respect to collection of data that impede our progress to model HAB occurrence. These include (1) the range of data types, (2) the frequency of measurement, and (3) the units of measurement. While the importance of the first two are widely recognized in experimental studies, the third is not. The consequence of failings in any of these three areas is that most experimental studies (laboratory and field) are of little or no use in the development of models (Flynn 2005b). In the same way that experiments should be designed at the outset to yield data amenable to statistical analysis, so they should also generate data suitable for the support of modelling efforts. To highlight one particular problem in this regard, the routine measurement of HAB abundance using chlorophyll *in vivo* fluorescence gives data of poor value to modellers, as the chlorophyll:carbon (Chl:C) ratio changes with nutrient status and irradiance (including self shading as the bloom develops), and the ratio between the fluorescence signal and chlorophyll also varies with nutrient status (Kruskopf and Flynn 2006). Further, the use of chlorophyll as a biomass indicator for organisms with a high mixotrophic ability is arguably illogical. For example, the dynamics of *Pfiesteria piscicida* could not be modelled as a function of chlorophyll as it does not contain chlorophyll, other than that which it has eaten. Indeed, for many physiological processes, expressing the relationship as a function of chlorophyll versus carbon yields vastly different relationships.

The problem of parametrising HAB biomass is also not resolved by identification of individual species. To describe and model population dynamics, distributions of the target organisms must be determined at the species level; other members of the

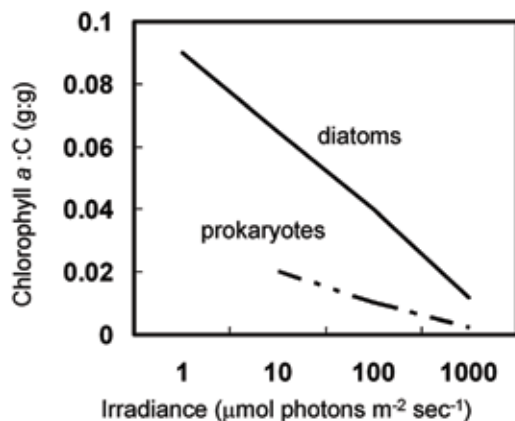


A SCHEMATIC DIAGRAM OF A NITROGEN-BASED MODEL OF MIXED-LAYER PLANKTON AND NITROGEN CYCLING SHOWING THE FLOW OF NITROGEN AMONG COMPARTMENTS. SOURCE: D. KELLER, R. HOOD, AND THE INTEGRATION AND APPLICATION NETWORK, UNIVERSITY OF MARYLAND CENTER FOR ENVIRONMENTAL SCIENCE, [WWW.IAN.UMCES.EDU](http://www.ian.umces.edu).

community should be identified and quantified as taxonomic or functional groups. This analysis is traditionally done through visual microscopic examination, a slow and tedious process that is poorly suited for research on the dynamics of HABs. Simply, resources are often inadequate to obtain and analyse enough samples to describe adequately the distributions of species in space and time. Also, some species are extremely difficult (e.g., within the genus *Alexandrium*) or impossible (e.g., *Pseudo-nitzschia*) to distinguish with light microscopy alone. These constraints also hamper efforts for routine monitoring. Automated methods are needed and several approaches are being pursued, including antibody probes (Shapiro et al. 1989, Anderson et al. 2005b), nucleotide probes (Scholin et al. 1999, Anderson et al. 2005b), and other assay mechanisms such as quantitative PCR (e.g., Coyne et al. 2006) that can be adapted for use in semi-automated bulk-sample analysis or single-cell analysis using flow cytometry, depending on the approach. In the meantime, bio-optical oceanographers continue efforts to extract information on species composition of phytoplankton from measurements of ocean colour and other optical properties of surface waters (Stuart et al. 1998, Ciotti et al. 1999, Schofield et al. 1999, Kirkpatrick et al. 2000). Even where it is possible to monitor specific algal groups, however, it must be recognised that presence alone does not confer the potential for a toxic or noxious bloom event. To describe and understand ecological controls on the activities and effects of HABs in nature, physiological status and toxicity of the algae must be determined along with identification and quantification. Fortunately, labelling and detection methods similar to those for identifying species can be used to assess biochemical or physiological properties such as the presence of a toxin (Lawrence and Cembella 1999), enzyme activity (González-Gil et al. 1998), and photosynthetic capability (Olson et al. 1996).

Inherently, all models involve some form of simplification because it is not feasible to include every organism or every species – and the interactions among them – explicitly. Many models aggregate the biological components and abstract them into functional groups or compartments. Such functional groups may represent, for example, the main roles of production (e.g., phytoplankton), consumption (e.g., zooplankton, fish) and decomposition (e.g., bacteria). Functional group models are commonly used to simulate phytoplankton and nutrient cycling, but are frequently extended to include zooplankton, detritus, and the microbial loop. There is an optimal balance between model detail and performance (Fulton et al. 2003). Too much complexity leads to uncertainty (particularly in parameter definition) and problems in interpretation of the models' dynamics and predictions; too little complexity and the models cannot reproduce realistic behaviour. However, a meta-analysis of data for process-oriented planktonic ecosystem models (based on 153 studies published between 1990 and 2002) indicates that increasing complexity does not improve the fit with data (Arhonditsis and Brett 2004, Anderson 2005). Ultimately, the selection of model complexity should be driven by questions being asked of the system under study, but limitations on the complexity may arise from the data available. Much of the research supporting our phenomenological understanding of HAB species physiology is inadequate for the parametrisation of models. Research is required to seek a more rational determination of model complexity to address the problems under consideration (Moll and Radach 2003). This must also be considered when submodels are lifted from one modelling system and applied to a new modelling system – the original caveats in the design and use may well be ignored.

In the context of HABs, the development of planktonic models with a stronger physiological basis are required if we are to obtain more accurate simulations. The key stages in defining the structure of an ecological model are to concentrate the degree of resolution or representation to the main target species and to make increasing simplifications or decrease the resolution both up and down from the target level (de Young et al. 2004).



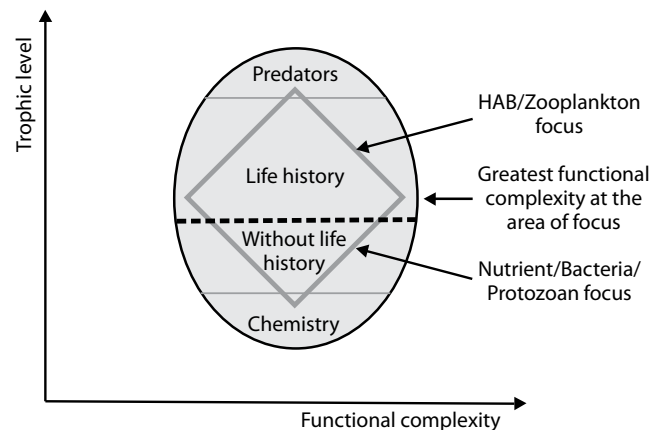
GENERAL TREND IN THE VARIATIONS IN THE CHLOROPHYLL A : C RATIO FOR PROKARYOTES AND FOR DIATOMS AS A FUNCTION OF THE IRRADIANCE AT WHICH THEY WERE GROWN. REVISED AND REDRAWN FROM MACINTYRE AND CULLEN 2005.

To model HABs, we need to consider representing the target species explicitly, possibly including the key stages of its life history and its links to the environment. For the HABs that are mixotrophs, such an approach may be more difficult, as the HAB may serve as both primary producer and consumer. Modelling mixotrophy is probably one of the most challenging activities in plankton modelling.

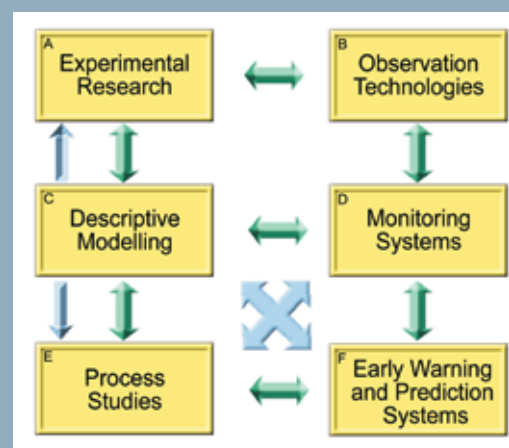
An important aspect of modelling data is that it allows an expert user to infer from it aspects of the system that the model is not able to simulate directly. In the same way that a weather forecaster interprets information about pressure and moisture fields from a numerical weather prediction model to infer what the weather will be, a marine environmental forecaster may be able to take information from a numerical ecosystem prediction model to predict aspects of the ecosystem not directly simulated. For example, we know that HAB events often coincide with distorted nitrate:phosphate ratios and low turbulence, and that toxin production often occurs when the phytoplankton are nutrient stressed. Currently, we cannot make species-specific simulations of HABs but we can simulate these indicators. In principle, we can combine information from hydrodynamic and ecosystem models to provide probability-based risk maps of HAB occurrence.

A generic modelling system may facilitate comparative studies, by providing a consistent modelling framework that can be applied in all regions. This framework needs to be modular to allow simulations of differing complexity according to the task at hand. Crucial to this is a consistent model evaluation procedure on a number of levels (temporal, spatial, and functional) and the generation of error statistics. Our current lack of physiologically robust species-specific HAB models implies that forecasting of a species-specific HAB event is probably not consistently achievable in the short term. Although modelling has evolved enormously

The Rhomboidal Modelling Approach

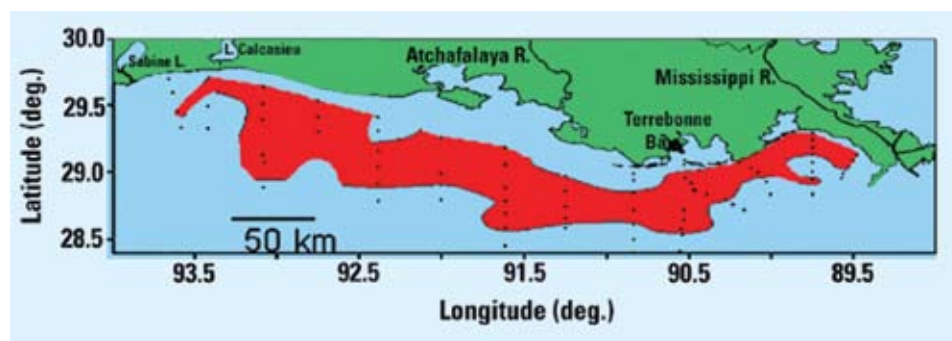


SCHEMATIC ILLUSTRATING THE RELATIONSHIP BETWEEN TROPHIC LEVEL AND FUNCTIONAL COMPLEXITY. THE RHOMBOID ILLUSTRATES THE REGION OF PRIMARY FOCUS FOR HAB MODELS. REVISED FROM DE YOUNG ET AL. 2004.



Modelling is intricately linked with observation and experimentation, and both models and predictive systems will be improved as new analytical approaches aid experimental research, and new monitoring systems yield data on time and space scales appropriate for the processes of interest.

as a discipline and as an integrated activity throughout all of oceanography and ecology (e.g., Barber and Hilting 2000), if our understanding of events surrounding the development of HABs is to be judged by our ability to simulate their occurrence, then there is much work to be done. The development of a new generation of physiologically robust HAB models will require better synergy among modellers, observational approaches, and experimentalists.



Toward a Consensus on Eutrophication and HAB Proliferation

In developing the recommendations and priorities for study in the area of HABs and eutrophication, it is recognized that there are fundamental processes, trends, principles, and relationships that are broadly accepted. GEOHAB will build on these, and will use these in guiding the development of Core Research.

Several recent documents are highlighted here to illustrate the community consensus on the role of eutrophication in HAB proliferation. Each of these efforts highlighted here was developed with community involvement. While it is impossible to encapsulate all of the debate and discussion that occurred in developing these consensus documents, nor to fully represent all such documents emerging around the world, these examples illustrate the breadth of issues on which there is broad agreement. These documents also consistently underscore the fact that an ecosystem approach will be required to fully understand the relationships between HABs and eutrophication.

With the role of eutrophication in the development of many HABs now well recognised and affirmed by various scientific and policy groups, the specific questions for further advancement can now be posed, and Core Research can be developed.

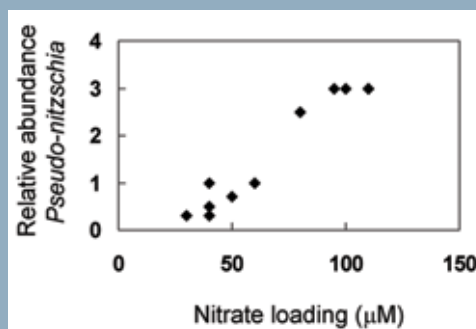


In 1999, the US National Center for Coastal Ocean Science completed an assessment of estuarine eutrophication (Bricker et al. 1999). This assessment, which will be updated in 2006, was based on results of a survey conducted over the years 1992-1997 on nutrient inputs, population projections, and land uses. It included more than 138 estuaries, representing more than 90% of the estuarine surface area of the United States. Among the key findings were:

THE "DEAD ZONE" (RED AREA) OF THE GULF OF MEXICO. SOURCE: N. RABALAIS, LUMCON.

Gulf of Mexico, USA

Hypoxia in the Gulf of Mexico, USA, is the result of nitrogen loading from the Mississippi River which drains significant agricultural lands. This nitrogen leads to large algal blooms, which, in turn, sink to the bottom and decay. The hypoxic zone in this region in the late 1990s was twice the extent that it was in the late 1980s. One HAB species, *Pseudo-nitzschia*, has been found to be increasing in this region in direct proportion to the increasing nitrogen loads in the Gulf of Mississippi.



The average abundance (%) of the diatom *Pseudo-nitzschia* in the sedimentary record as a function of the nitrate loading in the northern Gulf of Mexico. Redrawn from Turner and Rabalais 1991 and Parsons et al. 2002.

- symptoms of eutrophication are prevalent in US estuaries;
- human influence on the expression of eutrophic conditions is substantial; and
- impairment to estuarine resources, and fisheries in particular, is high.



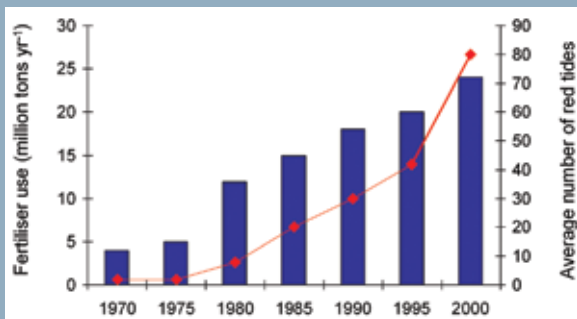
SEDIMENTS AND PHYTOPLANKTON BLOOM, MOUTH OF THE YANGTZE, EAST CHINA SEA . PHOTO: NASA VISIBLE EARTH, VISIBLEEARTH.NASA.GOV.



LARGE RED TIDES WERE VISIBLE IN THE EAST CHINA SEA, 2005. PHOTO: J. LI.

China

The average number of harmful blooms (red line), in addition to their areal extent and duration along the east coast of China have escalated in the past two decades coincident with the increasing use of synthetic fertiliser (blue bars).



Redrawn from Anderson et al. 2002 and Zhou 2005.

In March 2002, the International Council for the Exploration of the Sea (ICES) convened a workshop in The Hague, The Netherlands, on the linkage between eutrophication and its effects on phytoplankton. Consensus was reached on the following points:

- There is evidence that anthropogenic nutrient supply to coastal waters is leading to altered phytoplankton dynamics.
- While the underlying factors (mechanisms) and ecological principles (e.g., dose-yield responses) apply universally, the outcome of the collective phytoplankton response to nutrient loading is often site-specific; functional group responses are more predictable than species-level responses.
- Useful models (for management purposes) of the effects of nutrification on phytoplankton mass balances and functional group responses are attainable.
- Many knowledge and technical gaps exists, among which are the need for field observations to be carried out on time and space scales that match processes, ecophysiological data in support of models, and better understanding of the relationships between food web alterations and nutrient enrichment.



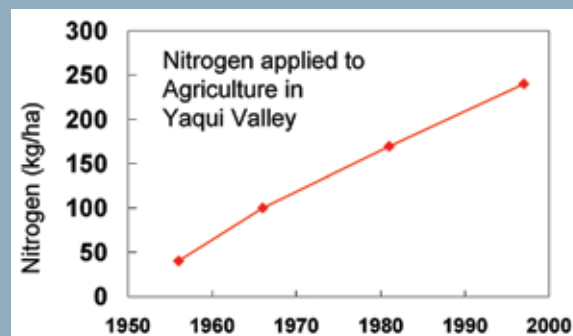
In January 2003, the US Environmental Protection Agency sponsored a scientific “roundtable” with the objective of developing a scientific consensus on the role of eutrophication and HABs. Approximately 25 scientists from the US were in attendance. Based on keynote presentations and discussion, the following statements were unanimously adopted:

- Degraded water quality from increased nutrient pollution promotes the development and persistence of many HABs and is one reason for their expansion in the US and the world.
- The composition – not just the total quantity – of the nutrient pool impacts HABs.
- High-biomass blooms must have exogenous nutrients to be sustained.
- Both chronic and episodic nutrient delivery promote HAB development.
- Recently developed tools and techniques are already improving the detection of some HABs, and emerging technologies are rapidly advancing toward operational status for the prediction of HABs and their toxins.
- Experimental studies are critical to further the understanding of the role of nutrients on HAB expression, and will strengthen prediction and mitigation of HABs.
- Management of nutrient inputs to the watershed can lead to significant reduction in HABs.

PHYTOPLANKTON BLOOM IN GULF OF CALIFORNIA. PHOTO: NASA VISIBLE EARTH, VISIBLEEARTH.NASA.GOV.

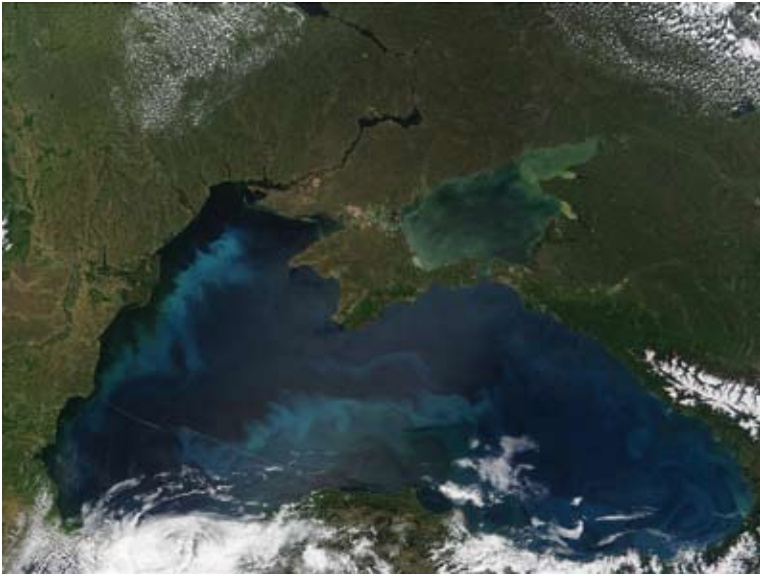
Gulf of California, USA

Runoff from agricultural regions has recently been associated with massive blooms in the Gulf of California. These blooms were found to occur within days of fertiliser applications (Beman et al. 2005). Total nitrogen loads from these applications are sufficient to support these massive blooms. For example, urea concentrations can exceed $40 \mu\text{Mol N L}^{-1}$ following fertilisation (Glibert et al. 2006).



Source: International Maize and Wheat Improvement Center (CIMMYT database).

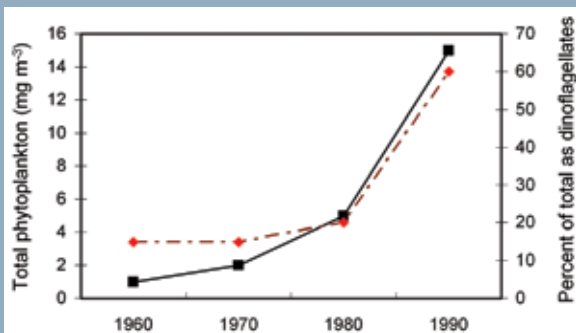
In 2004, the Study Group to Review Ecological Quality Objectives for Eutrophication (SGEUT) convened by ICES evaluated the linkage between eutrophication and HABs in European coastal waters (Aertebjerg and Smayda 2004). The SGEUT report emphasised the complexity of the relationship between HABs and eutrophication by affirming that HABs are an ecosystem-regulated response and not the result of simple, linear responses to nutrients, being also influenced by microbial and grazer communities and physical oceanographic conditions.



PHYTOPLANKTON BLOOM IN THE BLACK SEA. PHOTO: NASA VISIBLE EARTH, VISIBLEEARTH.NASA.GOV.

Black Sea

Phytoplankton blooms in the Black Sea in the mid-1990s increased to levels more than 20-fold higher than were observed in the 1960s. These increases were especially apparent during the rapid escalation of nitrogen and phosphorus loading during the 1980s. Dinoflagellate abundance increased 4-fold over this period, while diatom abundance decreased.



Modified and redrawn from Oguz 2005.

In October 2004, the 3rd International Nitrogen Conference was held in Nanjing, China with an aim toward understanding the “impacts of population growth and economic development on the nitrogen cycle: consequences and mitigation at local, regional, and global scales”. The participants of the conference affirmed, among other statements, that:

“...in many parts of the world, significant amounts of reactive nitrogen are lost to the environments in agricultural and industrial production and fossil fuel combustion. This has

lead to disturbances in the nitrogen cycle, and has increased the probability of nitrogen-induced problems, such as pollution of freshwater, terrestrial and coastal ecosystems, decreasing biodiversity, and changing climate, and poses a threat to human health.”



In 2005, the European Environmental Agency reported that “Eutrophication...is still one of the

major environmental problems across Europe” (www.eea.eu.int, Report No. 7/2005). Eutrophication affects waters from inland water bodies such as groundwater, rivers and lakes, to transitional and coastal waters and ecosystems in open seas. They further affirmed that:

- runoff from agricultural activities is the main source of nitrogen pollution and nitrogen loads parallel the surplus of nitrogen applied to large agricultural catchments;
- households and industry are the major sources of phosphorus pollution; and
- discharges from nitrogen and phosphorus are showing declines based on measured to reduce these inputs, but have been larger for phosphorus with reduced point sources.

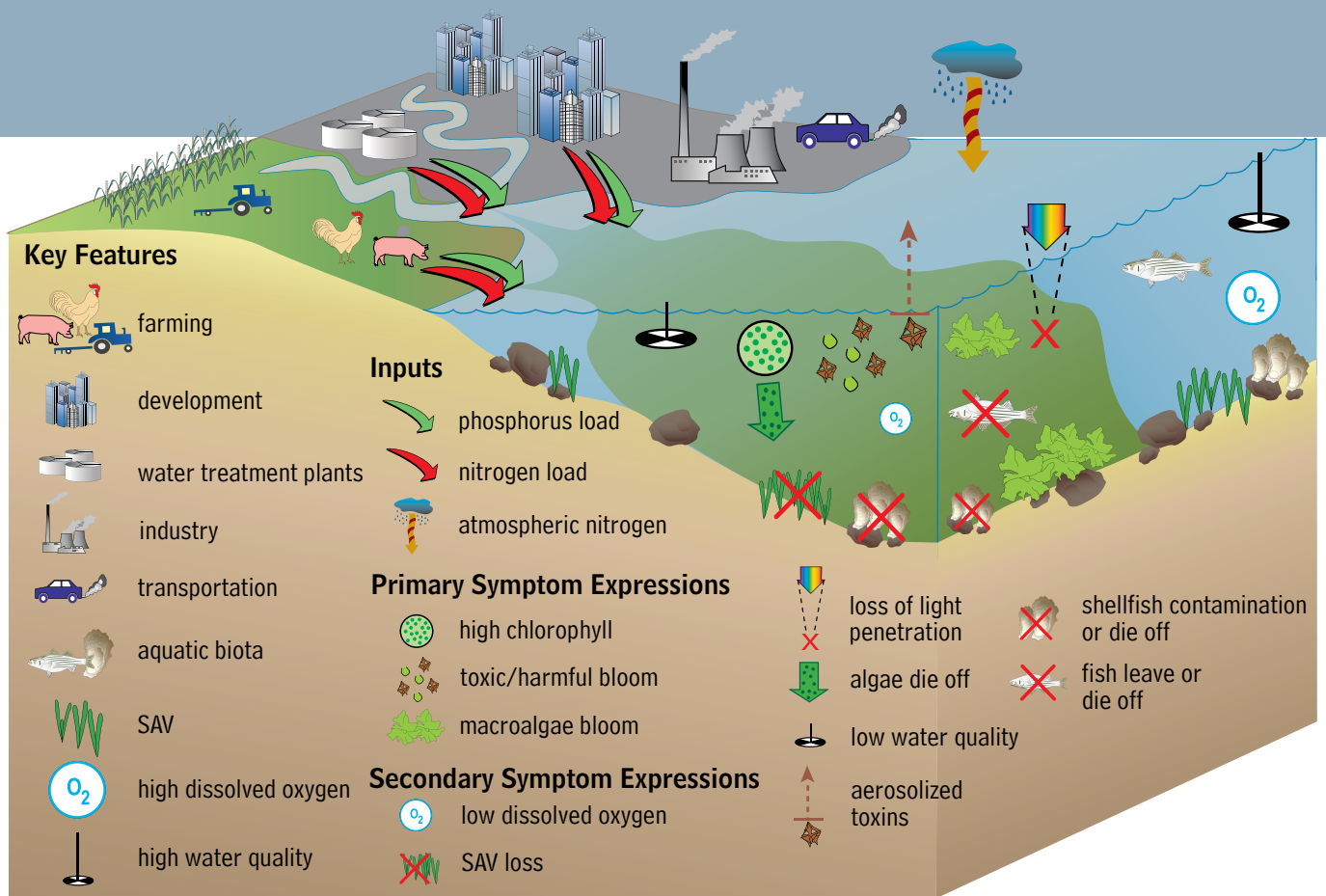
4. Priorities and Challenges for Understanding the Relationship Between HABs and Eutrophication



BALTIC SEA CYANOBACTERIA BLOOM. PHOTO: K. KONONEN.

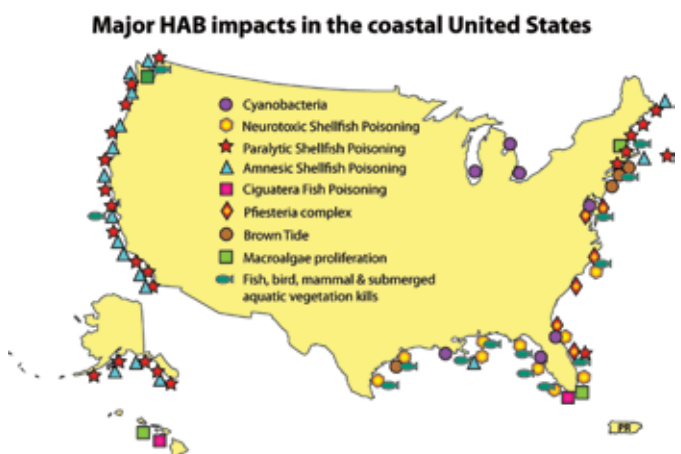
For many years, research on HABs was undertaken in response to specific events, and conducted in localised areas where specific problems occurred. Over the past decade, enormous strides have been made internationally in linking the global community of scientists to better understand the factors that lead to specific blooms, their population dynamics, and their impacts, and to do so in a comparative framework where research questions are similar. In some cases, comparative studies have shown that similar processes are controlling blooms in similar ways. In other studies, apparently similar species occur in various parts of the world, but they differ in growth dynamics or expression of harmful attributes.

Of relevance to the focus on the role of eutrophication in HAB proliferation, a comparative approach is highly beneficial in the ability to compare gradients of responses. For example, discharge from land in Europe and Asia appears to be significantly higher than in much of the rest of the world. These higher loads may potentially hold the key to understanding some of the dynamics of differential HAB occurrences. A specific example is that of the colonial prymnesiophyte *Phaeocystis*, which is thought to have proliferated in the North Sea as a result of changing nutrient loads and ratios from the major rivers of the region have been modified (Lancelot et al. 1987, 2005). In contrast, however, blooms of *Phaeocystis* have only a limited range in the United States, localised primarily in the Gulf of Maine and Cape Cod Bay, and are of significantly smaller scale and duration (Anderson et al. 2005a). Does this difference reflect lower nutrient loads or different nutrient ratios, differences in species or strains of *Phaeocystis*, or other ecological factors?

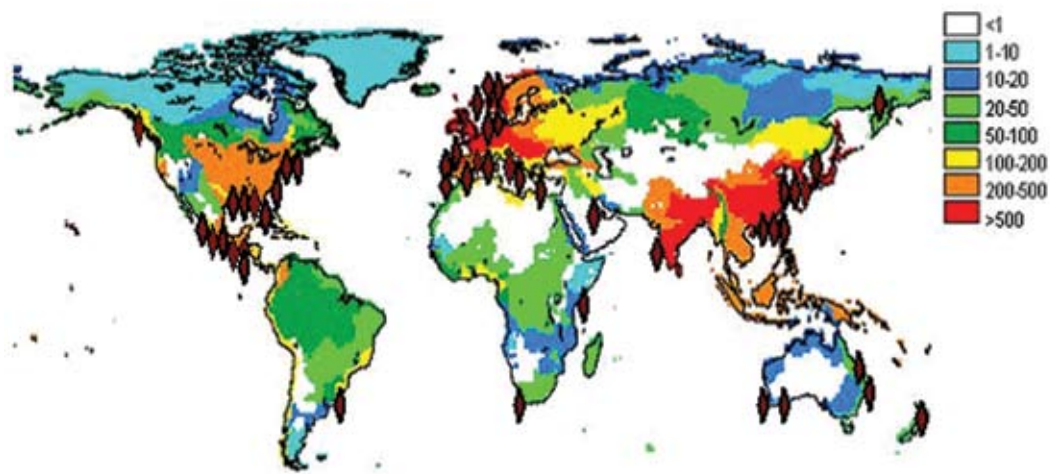


Highlighted in this chapter are the key questions that can and should be studied on an international comparative basis. Examples are provided of detailed research questions in comparative systems. In most cases, suitable sites and suitable comparative studies are numerous; thus, the identified questions and systems are representative but not a comprehensive review. This section concludes by outlining several specific, but tractable, challenges that should also be addressed with high priority.

CONCEPTUAL DIAGRAM OF THE PROCESS OF EUTROPHICATION. SOURCE: THE INTEGRATION AND APPLICATION NETWORK, UNIVERSITY OF MARYLAND CENTER FOR ENVIRONMENTAL SCIENCE, WWW.IAN.UMCES.EDU.



VIRTUALLY EVERY COAST IN THE UNITED STATES IS NOW IMPACTED BY HABs, AND THE SAME IS TRUE THROUGHOUT MUCH OF THE WORLD. SOURCE: D. ANDERSON, WHOI NATIONAL OFFICE FOR MARINE BIOTOXINS AND HARMFUL ALGAL BLOOMS.



Key questions to be addressed in the understanding the ecology and oceanography of HABs in eutrophic systems

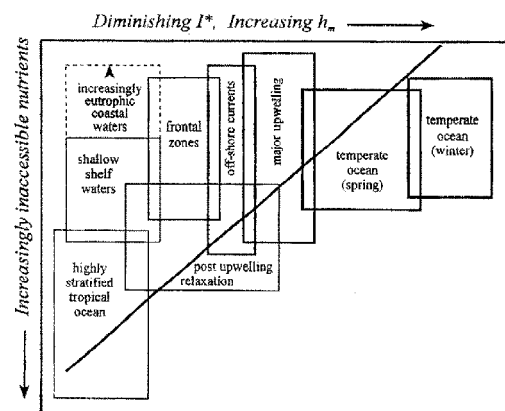
QUESTION 1

Are there clusters or specific types of HAB species that are indicative of global nutrient increases?

One of the important objectives of comparative studies on HABs is to understand commonalities that drive plankton community structure. The concept of “functional groups” provides a basis for simplification in order to improve our predictive ability relative to the dynamics of the system. The term “functional group” (or “life form”) is operationally defined to mean “a non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors” (Gitay and Noble 1997). The organisms within a functional group share one or more adaptations to those environmental conditions (Margalef 1978).

Smayda and Reynolds (2001) have provided a conceptual model for classifying HAB dinoflagellates by functional group. They identified nine distinct and diverse habitat types in which dinoflagellates may bloom. Associated with each habitat type are dinoflagellates life forms that ordinate on a habitat template along onshore-offshore gradients of decreasing nutrients, reduced mixing, and deepening of the euphotic zone. Several of these functional groups are associated with nutrient-rich or eutrophic waters. For example, dinoflagellate genera, such as *Prorocentrum*, *Phaeocystis*, *Heterocapsa*, *Scrippsiella*, *Cochlodinium*, *Heterosigma* and others, have adaptations making them suitable for thriving in nutrient-rich waters. Increasing evidence suggests that some of these species also may be increasing in their global extent.

GLOBAL DISTRIBUTION OF *PROROCENTRUM MINIMUM* IS SHOWN (RED DIAMONDS) SUPERIMPOSED ON THE GLOBAL EXPORT MAP OF N FROM RIVERS (FROM SEITZINGER AND KROEZE 1998). THE HIGHEST DENSITY OF OBSERVATIONS OF THIS SPECIES OCCURS IN REGIONS WHERE GLOBAL DIN EXPORT IS PREDICTED TO BE HIGH. REPLOTTED FROM HEIL ET AL. 2005 AND GLIBERT AND BURKHOLDER 2006.



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.

A similar classification based on functionality has been developed for freshwater phytoplankton (Reynolds et al. 2002). This conceptual model is based on tolerances and sensitivities to a range of physical and nutrient conditions. Some nitrogen-fixing cyanobacteria species capable of forming blooms, such as *Cylindrospermopsis raciborskii*, are able to tolerate low nitrogen conditions, while others, such as *Microcystis*, appear to favour eutrophic conditions. Such a framework provides a context for comparative studies of species. Similar matrices will also need to be developed for other HAB species.



A BLOOM OF THE DINOFLAGELLATE *LINGULODINIUM POLYEDRA* RESULTED IN A VISIBLE RED TIDE OFF SOUTHERN CALIFORNIA, USA, SUMMER 2005. PHOTO: S. OH.

Altered nutrient loads have been associated with increasing abundance of *Pseudo-nitzschia* in the northern Gulf of Mexico since the 1950s (Parsons et al. 2002). During the same period of time, nitrogen loads have doubled, while silica availability has decreased substantially (Turner and Rabalais 1991). This relationship has also been observed in European waters, where long-term increases in nitrate loading parallel the increase in abundance of this genus in the sedimentary record. Relatedly, in the western and northern Adriatic Sea, a shift from predominantly red tide blooms to more frequent mucilaginous blooms occurred in the 1980s coincident with phosphorus removal from detergents and expansion of sewage treatment plants (Sellner and Fonda-Umani 1999); however, cause and effect remain to be determined as mucilaginous events were also recorded in the region more than 200 years ago.

One of the high-biomass HAB species that has been shown to increase in abundance following events that lead to runoff and increased nutrient delivery is *Prorocentrum minimum* (Heil et al. 2005). 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. Blooms of this species have been observed in tropical, subtropical, and temperate regions (Heil et al. 2005). *P. minimum* is one of many mixotrophic species and will grow well when organic nutrients are supplied (Li et al. 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 natural organics (Granéli et al. 1985). In tributaries of Chesapeake Bay, USA, *P. minimum* also appears to grow and develop into massive blooms that have been associated with declines in submerged grasses and benthic habitat (Gallegos and Jordan 2002), and have proven to be toxic under some growth conditions (Wikfors 2005). These blooms have increased in magnitude with the eutrophication of the Chesapeake Bay, and cell counts are now commonly more than an order of magnitude higher than recorded just two decades ago. These blooms, like those in Sweden and many other regions of the world, appear to intensify and expand in response to delivery of nutrients from rainfall events, and in particular, from organic nitrogen delivery (Glibert et

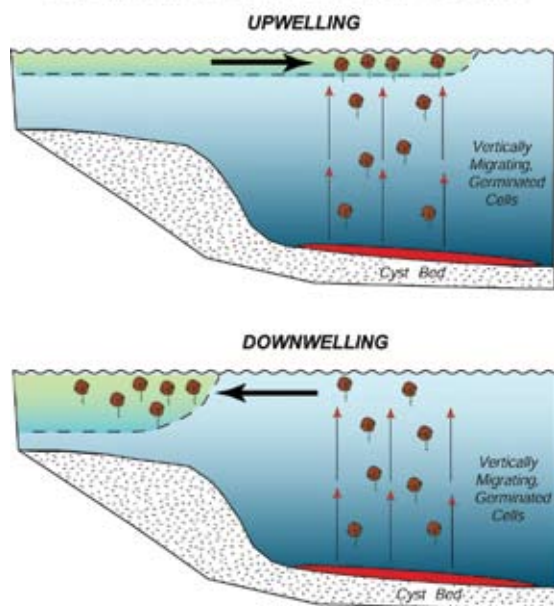
al. 2001, Heil et al. 2005). Through comparative studies it should be possible to ascertain whether these similar factors are indeed stimulating these blooms, and whether these blooms are increasing in frequency globally.

Comparisons of the physical dynamics of the regions, quantification of nutrient delivery and the trophic dynamic 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 produce toxins in response to certain environmental factors. Suitable models are needed to explore the interactions between nutrient status, physiological ability, and other factors leading to changes in biomass.

Examples of Relevant Detailed Questions

1. Can functional groups of HABs be defined that are favoured within eutrophic systems?
2. Are there specific adaptive strategies used by HABs in nutrient-altered systems?
3. Can the nutritional strategies of different HAB species be used to predict their responses to eutrophication?
4. How does intraspecific variability (strain differences) in response to eutrophication control HAB development and impacts?

A CROSS-ISOBATH TRANSPORT MECHANISM FOR INITIATION OF ALEXANDRIUM BLOOMS



PHYSICAL ENVIRONMENTS INTERACT WITH ORGANISM BEHAVIOUR IN BLOOM INITIATION, AS SHOWN HERE FOR *ALEXANDRIUM* BLOOMS. DURING UPWELLING-FAVOURABLE WINDS, THE PLUME THINS VERTICALLY AND EXTENDS OFFSHORE, OVERLYING THE CYSTS SEEDBEDS. *ALEXANDRIUM* CELLS ARISING FROM THE CYSTS SWIM TO THE SURFACE AND ARE TRANSPORTED ALONG THE COAST WITH DOWNWELLING-FAVOURABLE WINDS. SOURCE: MCGILLICUDDY ET AL. 2003.

QUESTION 2

To what extent do residence time and other physical processes impact the relationship between nutrient loading and HAB proliferation?

One of the difficulties in linking nutrient loading to HABs is the multiplicity of factors contributing to HAB species responses to nutrient loading. An understanding of the physical dynamics of blooms in relation to nutrient dynamics will help lead to an understanding of how bloom dynamics may differ when nutrient loads are similar but physical controls are different.

Physical processes are important at every stage of bloom dynamics. The initiation of a bloom requires successful recruitment of a population into a water mass. This may result from excystment of resting cells during a restricted set of suitable conditions (e.g., *Alexandrium* in the Gulf of Maine; Anderson 1998), transport of cells from a source region where blooms are already established, or response to unusual climatic or hydrographic conditions (e.g., *Pyrodinium bahamense* in the Indo-West Pacific; Maclean 1989).

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

population's range and biomass are affected by physical controls such as long-distance transport (e.g., Franks and Anderson 1992), accumulation of biomass in response to water flows and swimming behaviour (Kamykowski 1974), and the maintenance of suitable environmental conditions (including temperature and salinity, stratification, irradiance, and nutrient supply; Whitledge 1993).

Physical processes that are likely to influence the population dynamics of HAB species operate over a broad range of spatial and temporal scales. Large-scale circulation affects the distribution of water masses and biogeographical boundaries. Many examples may be found of the influence of mesoscale circulation on HAB population dynamics. Eddies from the deep ocean can, for example, impinge on slope and shelf regions, affecting the transfer of algae and nutrients across the shelf break. This type of transport may be involved in the delivery of the Florida red tide organism *Karenia brevis* to nearshore waters from an offshore zone of initiation (Steidinger et al. 1998). Although eddies are difficult to resolve through sampling at sea, they can usually be detected through remote sensing of temperature, sea-surface height, or ocean colour. Understanding of the main features of circulation is often sufficient to devise models that may be used to guide decision-makers on the movement and development of HABs, although such predictions are still mostly rudimentary.

Processes at intermediate scales result in the formation of convergence zones, fronts, and upwelling. The retentive nature of some semi-enclosed coastal systems, such as estuaries and fjords, can produce long residence times leading to prolonged suitable periods for cells to thrive (Cembella et al. 2005). The importance of fronts in bloom development, including HABs, is now recognised and included in some modelling efforts (Franks 1992). A linkage has been demonstrated, for example, between tidally generated fronts and the sites of massive blooms of the toxic dinoflagellate *Gyrodinium aureolum* (= *Karenia mikimotoi*) in the North Sea (Holligan 1979). The typical pattern is that of a high surface concentration of cells at the frontal convergence, contiguous with a subsurface chlorophyll maximum that follows the sloping interface



between the two water masses beneath the stratified side of the front. The signature of the chlorophyll maximum, sometimes visible as a “red tide”, may be 1-30 km wide. Chlorophyll concentrations are generally lower and much more uniform on the well-mixed side of the front. The significance of this differential biomass accumulation is best understood when movement of the front and its associated cells brings toxic dinoflagellate populations into contact with fish and other susceptible resources, resulting in massive mortalities. This is an example where physical-biological coupling results in biomass accumulation, and larger-scale advective mechanisms interact synergistically in a way that results in harmful effects.

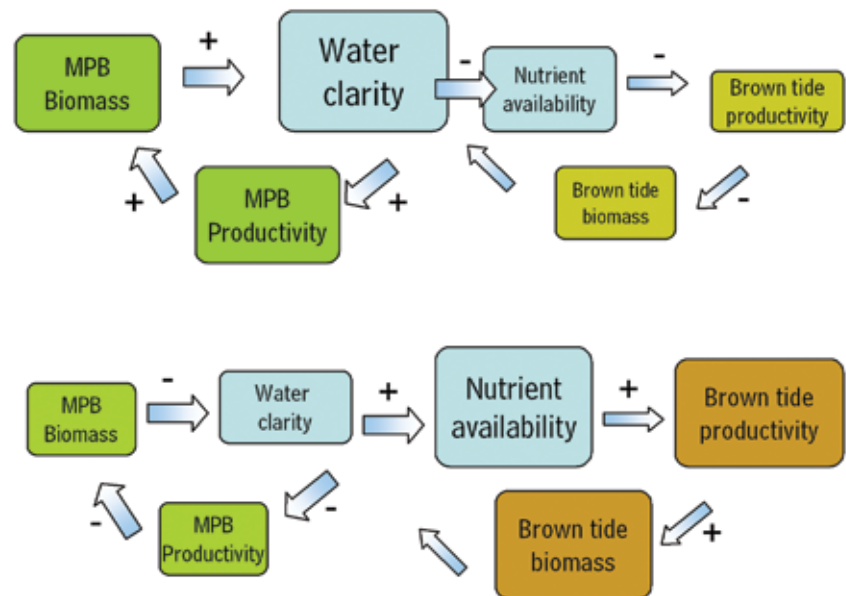
The importance of small-scale physical processes in HAB development is observed in the layering of the physical, chemical, and biological environment in stratified coastal systems. Off the French coast, for example, a thin layer of dinoflagellates, including the HAB species *Dinophysis* cf. *acuminata*, has been observed in the region of the thermocline (Gentien et al. 1995, 2005). The same pattern is found for *Dinophysis norvegica* in the Baltic Sea, where a 1-2 m thick layer with up to 80 000 cells⁻¹ is usually situated between 20-25 m depth, where light is less than 1% (Gisselsson et al. 2002). Several HAB species are well known for their ability to form these thin, subsurface layers of uncertain cause and unknown persistence, at scales as small as 10 cm in the vertical and 10-1000 km in the horizontal (Gisselsson et al. 2002). One explanation is that these layers result from the stretching of horizontal inhomogeneities by the vertical shear of horizontal currents. This produces an environment potentially favouring motile organisms that can maintain their position in this layer or organisms able to regulate their buoyancy. Any comprehensive study of HABs, including studies focussing on nutrient controls, should incorporate an understanding of the physical conditions that can lead to cell aggregation and dispersion.

**LEFT: *DINOPHYSIS ACUMINATA*. PHOTO: [WWW.SDN-WEB.DE](http://www.sdn-web.de).
RIGHT: *DINOPHYSIS* BLOOM IN COASTAL NORWAY. PHOTO:
HAVFORSKNINGSINSTITUTTET, INSTITUTE OF MARINE RESEARCH, WWW.ALGEINFO.IMR.NO.**

The need to understand physical dynamics has further importance in understanding the relationship with nutrients. For example, the responses of phytoplankton to fluctuating light (due to swimming behaviour and turbulence) are not the same as responses to the average exposure. There is cause to suspect that synergistic events may promote toxicity above that which would be expected from knowledge of the impact of individual processes (Flynn 2002). Similarly, for nutrient uptake, the kinetics of uptake measured under steady-state conditions may not apply when cells are exposed to highly variable nutrient environments, whether from changes in vertical nutrient structure or from exposure to ephemeral patches of nutrients (e.g., Goldman and Glibert 1983). Thus, there are many needs for understanding the relationships between physical environments and the physiological responses of the cells. Comparisons among similar species in different hydrographic regimes, as well as comparisons across species in similar hydrographic regimes, will be useful in this regard.

Examples of Relevant Detailed Questions

1. Do residence time and physical processes impact the likelihood for different species to bloom under eutrophic conditions in different ways or at different stages in the life cycle?
2. What are the physical factors that contribute to the persistence of high-biomass blooms in eutrophic systems?
3. To what extent do systems with the same indigenous species and nutrient load develop similar blooms when physical processes differ?
4. How do physical processes control the physiological responses of different species to light and nutrients?



QUESTION 3

How do feedbacks and interactions between nutrients and the planktonic, microbial food webs impact HABs and their detrimental effects?

CONCEPTUAL RELATIONSHIPS BETWEEN MICROPHYTOBENTHOS (MPB) AND BLOOMS OF *AUREOCOCCLUS ANOPHAGEFFERENS* (BROWN TIDE). NOTE IN THE UPPER PANEL, A BENTHIC DOMINATED STATE WILL LEAD TO LOW BROWN TIDE BIOMASS, WHILE IN THE LOWER PANEL, PELAGIC NUTRIENT- ENRICHMENT CAN LEAD TO HIGH BROWN TIDE BIOMASS. MODIFIED AND REDRAWN FROM MACINTYRE ET AL. 2005.

Nutrient enrichment can stimulate HABs not only directly by their support of increased biomass, but indirectly, in more subtle but significant ways over the long term – for example, by increasing hypoxia that, in turn, eliminates filter-feeding shellfish that would have consumed HABs but that can no longer survive in the habitat (Burkholder 2001, Glibert et al. 2005, Smayda 2005). Similarly, impacts of nutrients may be removed in time and space from the nutrient source as nutrients are consumed, recycled, and transformed, leading to complex – and often indirect – interactions between nutrients and HABs (Glibert and Burkholder 2006). In addition, bacterial interactions are often of critical importance in the development of toxins within some HAB species, and these interactions may occur differently under varying nutrient regimes.

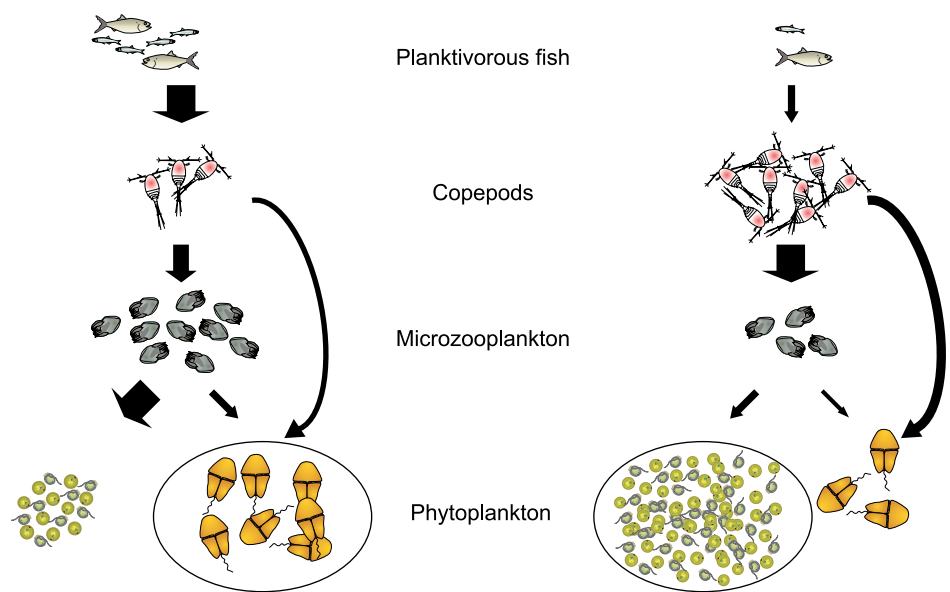
Harmful algae do not exist in isolation in natural ecosystems, and are influenced by interactions between individual cells of the same and other members of the planktonic community. Food-web interactions have a profound effect on the population dynamics of HAB species. Processes such as competition and grazing can affect the net growth rates of algae in nature. On the other hand, grazing may also increase nutrient regeneration, thus altering the availability of some nutrient forms for the algae to consume (Glibert 1998, Mitra and Flynn 2006).

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

et al. 2004a). Unique microbial communities are often associated with nutrient-rich systems, affecting internal nutrient cycling.

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

The effects of nutrient inputs on HABs are not always direct; there are indirect pathways by which nutrients can influence the development of HABs. For example, nutrients may be consumed and/or transformed from one form to another, thereby increasing their bioavailability for HAB species. On a seasonal scale, in estuarine systems such as the Chesapeake Bay, USA, nutrient input in the spring is delivered largely in the form of nitrate and is rapidly assimilated by diatoms which, in turn, sink and decompose. Subsequently, during the warmer summer months, nitrogen is released via sediment processes in the form of ammonium, which then supports an assemblage dominated by flagellates, including dinoflagellates (Malone 1992, Glibert et al. 1995). The shallow, brackish Baltic Sea is characterised by efficient cycling of phosphorus, coupled with effective removal of nitrogen, leading to a prevalence of a low N:P ratio. These conditions are especially favourable for nitrogen-fixing cyanobacteria. Furthermore, cyanobacteria are favoured in conditions where anoxia in the bottom layer leads to a release of chemically bound phosphorus



from sediments; release of phosphorus from this reservoir may prolong the harmful consequences of anthropogenic loading for years or decades after reductions in phosphorus input into the system (Carmen and Wulff 1989).

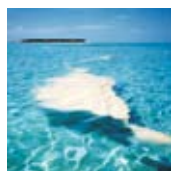
On shorter time scales, nutrients may be taken up by a particular species in one form and released in another form by the same organism or by its grazer. The cyanobacterium *Trichodesmium*, which forms massive blooms in tropical and subtropical waters, derives its nitrogen via the fixation of N_2 . However, much of this nitrogen is rapidly released as ammonium and dissolved organic nitrogen (Karl et al. 1992, Glibert and Bronk 1994, Glibert and O'Neil 1999). This released nitrogen is therefore available to support the growth of other microbial populations that cannot otherwise derive their required nitrogen in nutrient-impovertished waters. Numerous consortial associations involving other nitrogen-fixing cyanobacterial bloom taxa (*Anabaena*, *Aphanizomenon*, *Nodularia*) and bacterial epiphytes have been shown to lead to enhanced growth of cyanobacterial "hosts" (Paerl 1988, Paerl and Pinckney 1996). Relationships between nutrient inputs, and the

CONCEPTUAL DIAGRAM OF TOP-DOWN CONTROL AND EFFECT OF TROPHIC CASCADES ON SMALL AND LARGE CELL-SIZE PHYTOPLANKTON. ON THE LEFT, PROLIFERATION OF BAITFISH RESULTING FROM OVER-FISHING OF TOP PREDATORS LEADS TO BLOOMS OF LARGE DINOFLAGELLATES (CIRCLED). ALTERNATIVELY, ON THE RIGHT, REMOVAL OF SMALL FISH CAN LEAD TO BLOOMS OF SMALL PHYTOPLANKTON (CIRCLED) SUCH AS BROWN TIDE. SOURCE: D. STOECKER AND THE INTEGRATION AND APPLICATION NETWORK, UNIVERSITY OF MARYLAND CENTER FOR ENVIRONMENTAL SCIENCE, WWW.IAN.UMCES.EDU.

various processes by which nutrients are recycled and transformed are important for understanding HAB growth strategies.

It is highly likely that a combination of increases in nutrient resources and relaxation in grazing together contribute to both the frequency and intensity of HAB events. Eutrophication alters top-down control as well as providing bottom-up nutrient support for blooms. Top-down control of microzooplankton is particularly important as predation on the microzooplankton community may release HAB species from grazing control. Trophic cascades, alterations in benthic-pelagic coupling, and interactions between all components of the microbial communities need to be better understood on comparative bases.

Comparison of the ambient nutrient concentration inside and outside a dense surface bloom of *Trichodesmium* (see photo). Dinoflagellates were significantly more abundant in the plankton community inside than outside, while diatoms were more abundant outside than inside the bloom. From Glibert and O'Neil 1999.



TRICHODESMIUM BLOOM. PHOTO: P. GLIBERT.

	Inside Bloom	Outside Bloom
NH_4 (μM)	7.0	1.4
PO_4 (μM)	1.2	0.2
DON (μM)	10.3	6.9
Dinoflagellates	74%	54%
Diatoms	26%	46%

Examples of Relevant Detailed Questions

1. What are the roles of bacteria and viruses in growth dynamics and impacts of HAB species in eutrophic environments?
2. What is the impact of eutrophication on the quality of zooplankton food and how does that affect grazing activity?
3. Do HABs uniquely alter trophic interactions through their toxin production?
4. To what extent do bacterial interactions with HABs lead to toxin production that is greater in eutrophic waters?
5. How does eutrophication impact the production of allelopathic chemicals?



THIS FISH FARM IN THE EAST CHINA SEA WAS SEVERELY IMPACTED BY HABs IN 2005. PHOTO: J. LI.

QUESTION 4

Do anthropogenic alterations of the food web, including overfishing and aquaculture activities, synergistically interact with nutrients to favour HABs?

Global changes in trophic structure of nearshore habitats are occurring coincident with global changes in nutrient loading. Altered grazing structure, for example, has occurred from both overfishing, as well as from the intensification of aquaculture activities throughout the world. The dramatic decrease of important commercial fisheries in many parts of the world may interact synergistically to promote HABs. Studies in both lake and estuarine waters have shown that reductions in large piscivorous fish leads to a trophic cascade, whereby an increase in the smaller piscivorous fish is subsequently noted, which then exerts strong predation control on zooplankton, thereby reducing their biomass and thus increasing the biomass of phytoplankton (Andersson et al. 1978, Carpenter et al. 1985). In the Black Sea, for example, over-fishing has led to a virtual disappearance of the large commercial fish, and as a consequence there has been a dramatic increase in the predatory ctenophore *Mnemiopsis leidyi*, a disruption of the pelagic food web, and increases in HABs (Daskalov 2002, Lancelot et al. 2002, Kideys et al. 2005). Similarly, in Narragansett Bay, USA, recent evidence suggests that HABs have increased as *M. leidyi* has become more abundant in that system, also decreasing the zooplankton consumers of these HABs (Sullivan et al. 2001).

The synergistic impact of trophic cascades and nutrient loading has recently been shown by Granéli and Turner (2002). They observed, in mesocosms experiments, that by manipulating the food web through the introduction of jellyfish, phytoplankton biomass increased without supplemental nutrients. On the other hand, when nutrients were also added, the biomass of phytoplankton, and in particular, the biomass of HAB species, increased significantly.



IN THE EARLY 1980s, THE RAINBOW JELLY, *MNEMIOPSIS LEIDYI*, WAS ACCIDENTALLY INTRODUCED VIA THE BALLAST WATER OF SHIPS TO THE BLACK SEA WHERE IT HAD A CATASTROPHIC EFFECT ON THE ENTIRE ECOSYSTEM. PHOTO: L. KLISSUROV, BLACK SEA PHOTO GALLERY.

While control of phytoplankton through zooplankton grazing has been studied for a long time, there are still important gaps in our knowledge that seriously hinder our ability to model the interaction correctly (Mitra and Flynn 2005). In particular, there are insufficient data for the grazing of phytoplankton of different nutritional status; not only does this affect our understanding of the grazing of non-HAB species (Jones and Flynn 2005), but this issue is likely to be of even greater importance when considering the palatability of HAB species whose toxicity varies with nutrient availability. Hence, it is now becoming increasingly recognized that many HAB species are not efficiently grazed. Morphological features, poor nutritional quality, as well as intracellular or extracellular toxins or other bioactive compounds, may act as feeding deterrents (Verity and Smetacek 1996, Turner and Tester 1997). A variable susceptibility of toxic algae to grazers is considered to reflect varying toxin levels, depending on algal growth condition (Turner and Tester 1997, Turner et al. 1998). Furthermore, increasing as well as decreasing inhibition of zooplankton feeding by HAB species has been observed under both nitrogen and phosphorus limitation (Nielsen et al. 1990, Granéli and Johansson 2003a). Thus, the nutrient state of the algae may be of critical importance in controlling their susceptibility to grazing. Corroborating these findings is the fact that for many HAB species the toxicity increases when they are grown under nutrient-unbalanced conditions (Granéli et al. 1998). The idea that changes in higher levels of the food web facilitate the success of HAB species by decreasing their grazers, and, through alterations of the nutrient pool, further decrease their susceptibility to grazing by altering their toxin content, requires much more study.

Grazing control of HABs can also depend on the population density of the harmful algae, as demonstrated for the brown tides in Narragansett Bay, USA, where suppression of grazing occurs above a threshold concentration (Tracey 1988). A threshold effect may also occur if the daily production of new harmful cells



THESE AQUACULTURE FACILITIES IN KUWAIT HAVE OFTEN BEEN IMPACTED BY HABs. PHOTO: P. GLIBERT.

becomes large enough to saturate the ingestion response of the grazers and the ability of grazers to increase their populations. In that case, population growth can accelerate dramatically – if sufficient nutrients are available to support growth (Donaghay 1988). There is, however, little quantitative information on how the nature of the grazer response influences the timing, magnitude, and duration of HABs, and for those studies where such information is available, almost nothing is known about whether these responses would change under altered nutrient regimes. Model parametrisation of these effects is thus in very early stages of development. However, initial modelling studies suggest that the links between nutrient status, toxicity, poor grazing, removal of non-HAB species, and establishment of many HABs may be driven by a positive feedback loop (Mitra and Flynn 2006).

The structure of grazing communities also has been altered significantly through the development of large aquaculture facilities. An example of the association between fish farming operations and HABs comes from Norway. Up to the 1970s, harmful algal blooms were not considered a major threat to the marine or coastal environment of Norway. Single episodic events of mussel toxicity and mortality of wild biota were recorded along the Norwegian coast, but these episodes did not attract any wide public attention or lead to any management actions. Through the 1970s, several fish farms were established along the coast, and since 1980, the production of the Norwegian aquaculture industry grew significantly from a few thousand tonnes to ~500,000 tonnes of salmon and trout in 2001, and Norway's emergence as the world's largest exporter of Atlantic salmon. In parallel with this development, HABs emerged as a significant problem. In 1981, a large bloom of the dinoflagellate *Gyrodinium aureolum* caused significant mortality of farmed salmon and economic losses to fish farmers. New blooms of *Gyrodinium* followed, and during the 1980s, other phytoplankton species bloomed to cause additional problems, including *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. It is, of course, incorrect to attribute these outbreaks solely to nutrient inputs from fish farms, but some linkage seems probable.

Enrichment of nutrients from aquaculture activities has also been associated with outbreaks of pathogens that synergistically interact with HABs to alter fish health. For example, in Kuwait, a recent massive fish mortality event, attributed to an outbreak of the pathogenic bacterium *Streptococcus agalactiae* was also functionally related to an outbreak of PSP-producing dinoflagellates (Evans et al. 2002, Glibert et al. 2002). It was suggested that as massive numbers of fish died, nutrient release led to conditions favourable for the dinoflagellate outbreak.

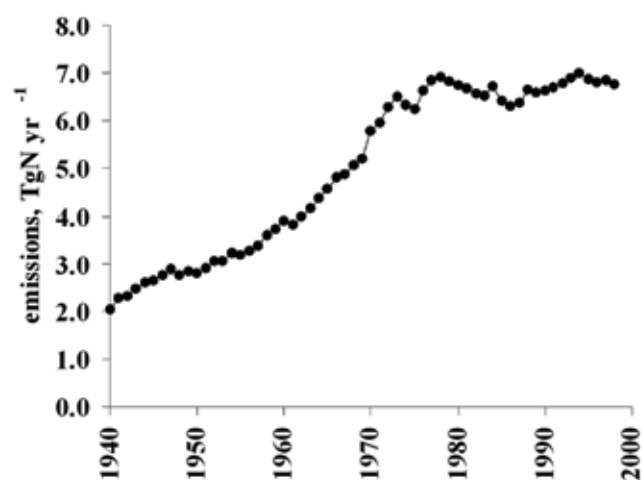
There is much that can be learned from comparative systems where major alterations of food webs have occurred through over-fishing or over-stocking. As new markets and regions are developing intensive aquaculture operations, there are also opportunities for gaining knowledge regarding the potential for increased HAB proliferation from comparisons with long-established regions.

Examples of Relevant Detailed Questions

1. Under what conditions does overfishing lead to trophic cascades that may synergistically interact with nutrient availability to promote HABs?
2. Does nutrient loading uniquely alter HAB toxin production leading to grazing alterations?
3. Is nutrient enrichment associated with both fish farming and shellfish farming, from feed additives and nutrient regeneration, correlated with HAB proliferation, and are there unique species that develop under specific aquaculture nutrient regimes?



MORE AND MORE VEHICLES, AS WELL AS VEHICLES WITH POOR GAS ECONOMY, ARE CONTRIBUTING TO NO_x EMISSIONS. PHOTO: P. GLIBERT.

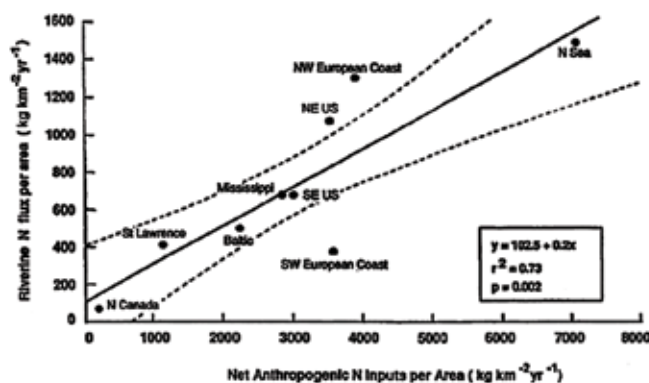


CHANGE IN US ATMOSPHERIC NO_x EMISSIONS FROM 1940 TO 2000. SOURCE: HOWARTH ET AL. 2002B.

QUESTION 5

How do anthropogenic changes in land use, agricultural use of fertiliser, NO_x emissions from vehicles, and global changes in land cover affect the delivery of nutrients to coastal waters and the resulting incidence of HABs?

As described earlier in this report, human activities have altered the nutrient regimes of coastal waters tremendously, primarily as a result of increased applications of synthetic fertilisers. Population growth and development, and the production of food (crop and animal production systems) result in dramatic alteration of the landscape as well as large sewage inputs, and increased runoff from land. Increased nutrient inputs to enclosed and nearshore ecosystems have resulted in widespread coastal eutrophication throughout Europe, Asia, and the United States. The production and consumption of energy also results in increased atmospheric inputs from NO_x emissions, which can then lead to increased nitrogen deposition. In freshwater reservoirs, increased primary production has been correlated with the proportion of increased agricultural land in the watershed (Knoll et al. 2003). Comparisons of nutrients delivered from pristine, urban or agricultural land uses are sorely needed. Similarly, little is known about comparative nutrient loading from systems undergoing rapid deforestation and/or rapid urbanisation. Of the nitrogen that humans put into the landscape, much is also denitrified. A better understanding of the fluxes from land to the atmosphere from denitrification, how they change with climatic variations, and how they may be altered as landscape is altered, is fundamentally important to our understanding of nutrient delivery to coastal waters (Howarth et al. 2006).



THE RELATIONSHIP BETWEEN HUMAN INPUTS OF N AND RIVERINE N EXPORT FOR MAJOR RIVERINE AND COASTAL REGIONS OF THE NORTH ATLANTIC OCEAN. SOURCE: HOWARTH ET AL. 1996.



MAN-MADE CANALS RESTRICT FLOW, REDUCE CIRCULATION, AND INCREASE SUSCEPTIBILITY OF THESE SYSTEMS TO BLOOMS FROM ELEVATED NUTRIENT LOADS. PHOTO: WWW.WENEEDAVACATION.COM.



IN FLORIDA, USA, SOME WATER FLOW IS UNDER GATED CONTROL. THERE ARE ONGOING RESTORATION EFFORTS TO RETURN TO SURFACE FLOW, POTENTIALLY ALTERING THE FORMS AND AMOUNTS OF NUTRIENTS TO BE DELIVERED TO THE COAST. PHOTO: EVERGLADES/FLORIDA BAY WATERSHED MANAGEMENT, WWW.SFWMD.GOV.

Large-scale human alteration of coastlines or inland waters also need to be assessed for their effect on nutrient enrichment and supply. For example, semi-enclosed harbours and extensive housing developments along artificial canals are now commonplace world-wide, from the Catalan coast of Spain to the east coasts of the United States and Australia. Reduced circulation within these harbours has been associated with recurrent blooms. In South Carolina, USA, numerous types of HABs have been frequently observed in coastal detention ponds used for stormwater control in housing developments and golf courses (Lewitus et al. 2003). These brackish, shallow, low-flow environments are depositional sites for nonpoint source pollutants, primarily fertiliser nutrients from intensive landscape maintenance and turf management. Because these ponds exchange with tidal creeks, they are sources for HAB dispersion into adjacent estuaries.

Major engineering projects are also projected to have impacts on nutrient delivery and booms. Estimates, for example, of the potential eutrophication impact of the Three Gorges Dam Project of the Changjiang (Yangtze) River, China, suggest that the nitrogen to phosphorus ratio may be significantly altered so as to yield a shift in ecosystem structure and the development of anoxia (Zhang et al. 1999). The impending restoration of surface water flow through the Everglades in Florida, USA, a project of decadal time scale, is expected to have major impacts on nutrient delivery to Florida Bay. Understanding the impact of varying nutrient quality as well as quantity is important in understanding the type of phytoplankton bloom that may develop (e.g., cyanobacteria vs. diatom; Glibert et al. 2004). Alternatively or additionally, some fundamental change in seagrass processes and the entire benthic community may be diverting recycled nutrients from sediment pools to the overlying water column, fueling phytoplankton growth.



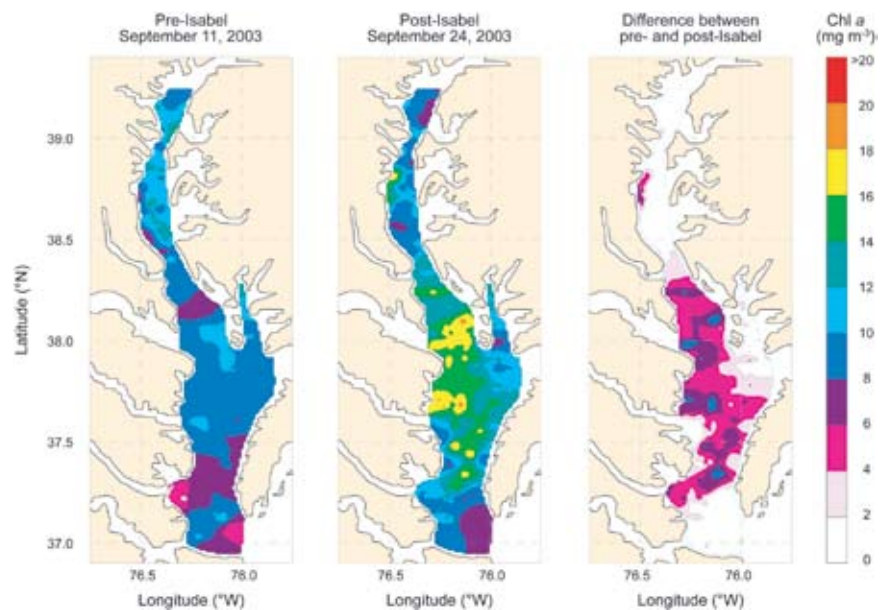
IN CHINA, THE THREE GORGES DAM ON THE YANGTZE RIVER, SCHEDULED FOR COMPLETION BY 2009, WILL BE THE LARGEST HYDROELECTRIC DAM IN THE WORLD. IT WILL SIGNIFICANTLY ALTER THE DOWNSTREAM FLOW OF NUTRIENTS. PHOTO: WWW.AFTERDREAMS.COM.

Spatially explicit, empirical models have previously been developed to quantify global nutrient export to the coastal zone as a function of watershed characteristics (Dumont et al. 2005, Harrison et al. 2005, Seitzinger et al. 2005a). Such models take into account watershed characteristics including freshwater runoff, land use, atmospheric deposition, human population, fertiliser use, and animal production among other factors. These types of models need to be coupled with long-term records of HAB occurrences.

Finally, the relationships between nutrient delivery via the range of mechanisms described above and HAB development also must be understood in terms of the physics of the water body receiving the nutrients. Equivalent nutrient inputs to different systems may have differential effects on HAB development due to differences in ecosystem structure and function.

Examples of Relevant Detailed Questions

1. To what extent do similar land-use patterns lead to similar nutrient discharges (in quantity and quality) and similar HAB outbreaks?
2. Can long-term trends in nutrient loadings be correlated with changes in HAB bloom patterns and dynamics?
3. What is the likelihood for long-term ecosystem restoration projects to alter nutrient delivery in such a way as to increase or decrease the frequency of HAB outbreaks?
4. How do nutrient transformation processes such as denitrification vary with changes in nutrient loading to the land and other landscape changes, and how do these processes affect nutrient availability for HABs?



QUESTION 6

Do climate change and climate variability have impacts on ecosystems that augment the impacts of eutrophication in the formation of HABs?

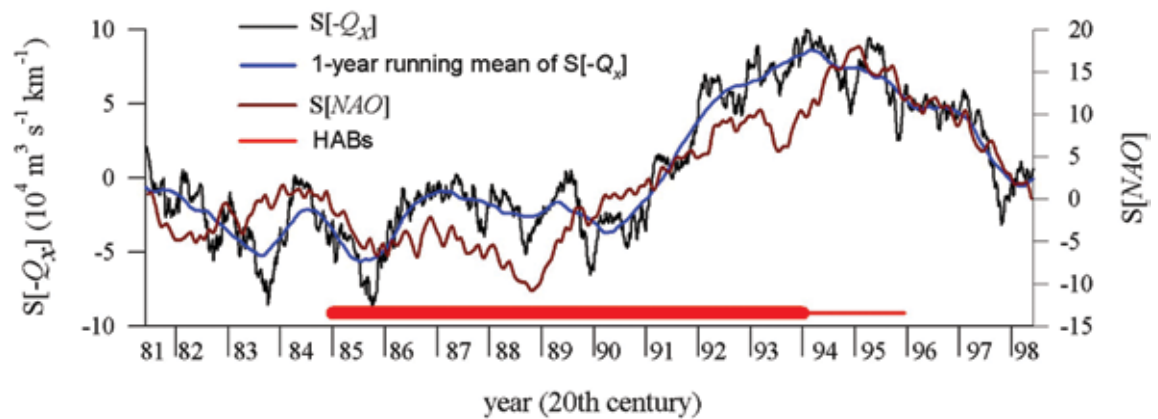
In order to assess the extent to which nutrients and/or eutrophication may be an important causative factor of specific blooms, the role of interacting or confounding factors must also be considered. Climate ultimately controls the fundamental parameters relating to algal growth, from water temperature to nutrients, and from precipitation and runoff to light. Climate change and climate variability can cause changes in species composition, trophic structure, and function of marine ecosystems. Climate change is the long-term alteration in global and/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 periodic El Niño-Southern Oscillation (ENSO) phenomenon, the North Atlantic Oscillation (NAO), and the Pacific Decadal Oscillation (PDO).

Nutrient supply is linked to freshwater input (e.g., Caraco 1995, Vitousek et al. 1997) that, in turn, is driven by regional climate variability (Najjar 1999, Miller et al. 2005, Burkholder et al. 2006, Howarth et al. 2006). Freshwater input determines, to a large extent, the spring chlorophyll *a* maximum in systems such as Chesapeake Bay, USA, by delivering nutrients (Harding 1994, Malone et al. 1996, Kemp et al. 2005). Freshwater input also plays a role in the physical transport of phytoplankton species, such as the HAB species *Prorocentrum minimum* (Tyler and Seliger 1978), blooms of which have been shown world-wide to be associated with freshwater inputs and associated nutrients (Silva 1985, Granéli and Moreira 1990, Stonik 1995, Grzebyk and Berland 1996,

SHORT-TERM NUTRIENT LOADING, SUCH AS OCCURRED FOLLOWING HURRICANE ISABEL WHICH STRUCK THE CHESAPEAKE BAY REGION, USA, IN 2003, LED TO LARGE ALGAL BLOOMS WITHIN DAYS. SOURCE: D. MILLER ET AL. 2006.

Glibert et al. 2001, Springer et al. 2005). Inter-annual variability is also important, however, affecting the timing of freshwater flow, residence times, and the magnitude and timing of blooms, including HABs. In the case of brown tide in the Peconic Estuary, USA, for example, a paucity of inorganic nitrogen addition via groundwater during dry years has been shown to stimulate the growth of the brown tide organism, *Aureococcus anophagefferens* (LaRoche et al. 1997, Nuzzi and Waters 2004) which can utilize DON resulting from the partial mineralisation of the previous year's algal growth or from the same year's spring bloom (Gobler and Sañudo-Wilhelmy 2001). Major climatological events, such as strong storms or hurricanes, also affect estuarine conditions during short time periods. As examples, Hurricane Isabel in 2003 caused a large phytoplankton bloom to develop in Chesapeake Bay, USA, within days (Miller et al. 2005), as did Hurricanes Charley and Wilma off the Florida coast (Heil et al., unpub. data).

As climate warms, one predicted scenario is for alteration in rainfall, leading to increased riverine discharge. Such an increase may lead to lowered salinity, increased abundance of taxa that proliferate in lower salinity waters, including freshwater bloom-forming cyanobacteria. With increased discharge, such species may also 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 (Sellner and Fonda-Umani 1999). Alternatively, for systems with declining riverine discharge, more stenohaline taxa could potentially move further up estuaries, thereby exposing larger portions of upper basins to more saline HAB taxa such as *Dinophysis*, *Karenia*, and *Alexandrium*.



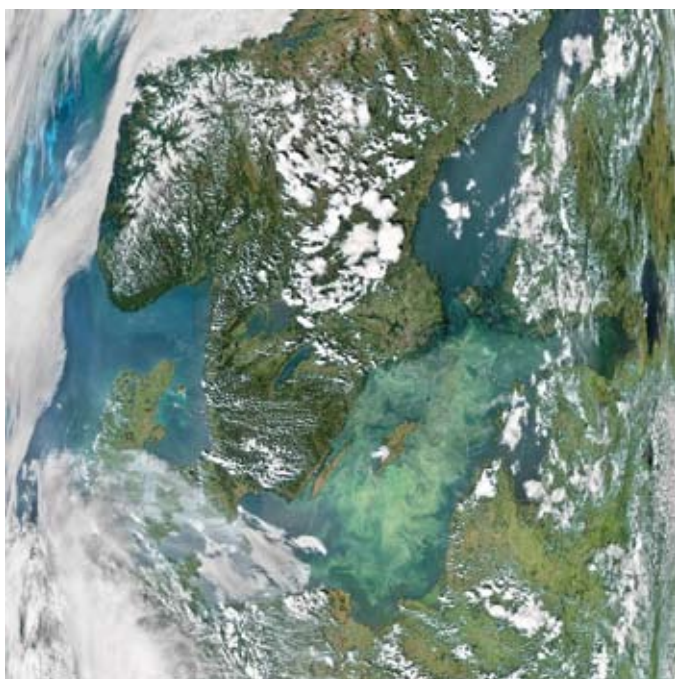
The current ecological paradigm suggests that an ecosystem does not exist in a unique, stable equilibrium state, but rather can easily be shifted to a new state by non-linear responses to physical forcings, such as those associated with climate change or variability. Biological responses are non-linear, complex mixtures of physiology, behaviour, life history, and physical redistribution. A major question is whether changes in climate synergistically interact with changes in nutrient loads to lead to increased frequency of HABs.

Climate changes are also resulting in global variations in temperature. While average global changes may be relatively small, effects of climate warming vary widely by region. Temperature is a fundamental regulator of physiological processes, affecting the activity of specific enzymes and the cues for various life cycle events, such as excystment. Temperature also regulates abundance and activity of predators. The extent to which these physiological controls and synergistic relationships with other components of the food web are regulated by temperature, is far from understood. One example of such interactions is that of *Heterocapsa triquetra*, which blooms during winter in North Carolina, USA (Litaker and Tester 2005). On a physiological level, *H. triquetra* is favoured under conditions of warm temperatures and high light. Yet, due to temperature control on its grazer, it tends to bloom at cooler temperatures when grazers are kept in check. If winters become warmer, the timing of such blooms may be altered.

POSSIBLE LONG-TERM RELATIONSHIP BETWEEN CLIMATE VARIABILITY AND PARALYTIC SHELLFISH POISONING EVENTS CAUSED BY *GYMNODINIUM CATENATUM* IN THE GALICIAN RIA BAIXAS (NW IBERIAN PENINSULA). $S[-Q_x]$ AND $S[NAO]$ ARE DE-SEASONALISED CUMULATIVE SUMS OF OFFSHORE EKMAN TRANSPORT ($-Q_x$) AND THE NORTH ATLANTIC OSCILLATION INDEX (NAO) OVER THE PERIOD 1981-1998. THE STRAIGHT RED LINE INDICATES YEARS OF DETECTION OF *G. 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 *G. CATENATUM* WERE MORE FREQUENT AND INTENSE DURING THE TRANSITION PERIOD (1980s TO 1990s) FROM DOWNWELLING- TO UPWELLING-FAVOURABLE CONDITIONS. SOURCE: ALVAREZ-SALGADO ET AL. 2003.

Examples of Relevant Detailed Questions

1. What are the chemical parameters that are likely to change due to climate and how might they impact HAB proliferation?
2. How do either small or large changes in temperature impact cellular physiology favouring HABs?
3. Do ENSO and other large-scale physical forcings have impacts on HABs?
4. How do climate variability and changes impact river flow and the associated transport of nutrients leading to HABs?



A BALTIC SEA BLOOM, POSSIBLY *NODULARIA*, JULY 2005. PHOTO: J. DESCLOITRES, MODIS LRRT, NASA GSFC.

Specific Challenges for Further Advancement

Much progress has been made over the past several years in many aspects of HAB bloom ecology and dynamics. In some cases, the linkages between cell physiology and toxicity have become clear. Progress has also been made in understanding the influences of physical process and other environmental parameters integral to harmful algal expression. Yet, many fundamental physiological processes remain unmeasured for most species. New methods of cell detection are becoming more readily available, and progress has been made in the identification of some genes involved in toxin production. Further understanding has been gained of the roles of nutrients, both inorganic and organic, in bloom development. Similarly, the roles of viruses and bacteria are better understood for some HABs. Yet, the understanding of the interactions of HABs with grazers, the sublethal effects of HABs on community dynamics, and the application of these data in developing predictive models is only just beginning.

Accurate and timely identification of harmful species is of fundamental importance to all aspects of HAB research and management. Historically, species have been delineated on the basis of morphological, ultrastructure, and life-stage features visible in the light and electron microscopes, as well as by pigment content. Increasingly, organisms are being compared and identified on the basis of molecular markers such as cell surface proteins, lipids, DNA sequences, and toxins. These same markers are serving as a basis for rapid assays designed to detect and quantify species specifically. With this progress has come an increasing demand for identifying organisms using traditional techniques so that comparative studies and new findings regarding species diversity, biogeography, and toxicology can be placed in an appropriate historical context.

Significant advances in cellular physiology of harmful microalgae have been made in the past decade with regard to nutrient regulation of toxin synthesis and assimilation of dissolved organic nutrients. However, critical information required for model development – such as photosynthesis-irradiance relationships, rates of nutrient uptake, and excretion of organic matter – is not available for most species. Studies of growth rates as a function of temperature, irradiance, nutrients, and their ratios, are rare. Most harmful species employ swimming or buoyancy-regulation strategies influenced by irradiance and nutrients, in addition to ambient temperature and salinity, and these factors influence population growth and community structure in ways that we do not yet fully understand. The growth rate of many HABs in nature largely remains unknown. Collectively, our lack of fundamental knowledge concerning the basic physiology and behaviour of most HAB species impedes our ability to develop predictive models that will ultimately aid many aspects of basic research and management.

Natural resource managers and public health officials need better tools to forecast imminent HAB events so that management strategies can be implemented effectively. Forecasting capabilities can be enhanced by improving and expanding remote-sensing technologies, such as offshore instrument moorings and satellite sensing, and this information will permit monitoring of the environmental conditions that could lead to HAB formation and decline and for the tracking of HABs as they transit through a region. Time-series analyses of existing databases for phytoplankton communities and environmental variables such as macro- or micro-nutrients, where available, are required. Retrospective analyses of historical data and information may provide important insights. In some cases, the sediments may hold important historical information. Land-use data, such as may be available from maps and geographic information systems may yield trends in nutrient loadings to the landscape. Where such data are lacking, long-term consistent monitoring programmes must be initiated in key regions where human influences are either known or are anticipated to increase. Moored instrumentation packages – including nutrient, plankton, and optical sensors – are needed



THE DARK AREAS NEAR THE SHORELINE SHOW A RED TIDE BLOOM, *KARENIA BREVIS*, ALONG THE SW COASTLINE OF FLORIDA, MARCH 2002. PHOTO: J. DESCLOITRES, MODIS LRRT, NASA GSFC .

to resolve the temporal relationships between nutrient inputs and shifts in plankton composition. Shipboard observations and field programmes would be helpful in resolving spatial differences and in the collection of samples for which sensors are not currently available.

The vast complexity of the interactions between HABs and their environment dictates that we think in terms of integrative models to address the problem in a way that our mental computing capability cannot (Noble 2002). Mechanistic ecosystem models are widely used in marine research. Models should be constructed at an appropriate level of complexity to address the hypothesis being tested and the data available to support it. However, in reality, we often lack the appropriate data to support such developments. Additionally, we should bear in mind that a well-constructed model that fails can be more informative than one that succeeds. A good model should be descriptive (represent the available data), integrative (demonstrate how elements interact), and explanatory (provide biological insight). Conceptual models of biological systems are common. They are commonly used as management tools for predicting eutrophication (e.g., Moll and Radach 2003, Tett et al. 2003), to understand ecosystem processes (e.g., ecosystem dynamics, Allen et al. 2004; response to climate change, Taylor et al. 2002) and to predict biotic responses (e.g., Besiktepe et al. 2003). Conceptual models can be viewed as having two complimentary roles. The first is a heuristic role, whereby they are used to corroborate a hypothesis, illuminate areas of further study, and identify where further empirical data are required. The second role is as predictive tools, whereby the models are used to aid marine resource management and to assess the impact of humans on the marine ecosystem.

The establishment of a robust modelling approach for simulating HAB dynamics in eutrophic environments requires the following future work:

- the definition of functional groups to describe HABs and further development and refinement of conceptual process models; crucial to this process is the definition of life histories and hence, stage-structured models; equally critical is knowledge of the interaction between HABs and non-HABs (with which they compete for common nutrients) and their predators;
- bioinformatics to acquire, archive, and interpret data;
- the construction, parametrisation, validation, and evaluation of appropriate mathematical and numerical models;
- integration of HAB models into generic coupled hydrodynamic ecosystem models for comparative studies; and
- data assimilation to improve model parameters and forecasts, and to quantify model errors.

While the ultimate goal is to develop whole ecosystem models, much is to be gained by construction and testing of models as an aid to our understanding of the biological processes underpinning HAB formation and demise. The basis for many biological models has failed to keep pace with our understanding of plankton biology (Flynn 2005). The undertaking of experiments to investigate these interactions should not be trivialised; neither should funding bodies dismiss such needs because they “have been done before”. Integrated studies of experimental research and modelling are few and far between, and few data sets from previously conducted experimental studies are adequate for the task.

5. Moving Forward in the Study of HABs in Eutrophic Systems



A CYANOBACTERIAL (BLUE-GREEN ALGAE) BLOOM ON THE SHALLOW LAKE, LAKE TAIHU, JIANGSU PROVINCE, CHINA. PHOTO: W. WURTSBAUGH, WWW.ASLO.ORG/PHOTOPOST/.



WHOLE LAKE AND EXPERIMENTAL MESOCOSM STUDIES HAVE BEEN USEFUL IN UNDERSTANDING THE IMPACTS OF NUTRIENTS ON BOTH PHYSIOLOGICAL AND ECOSYSTEM LEVELS. PHOTO: D. SCHINDLER.

In accordance with the GEOHAB strategy, the approach of the Core Research Project on **HABs in Eutrophic Systems** will be comparative from the cellular to the ecosystem level. Research that is interdisciplinary – focussing on biological, chemical, and physical processes – will be fostered. Research will be multifaceted as the problems relating to eutrophication are complex, and interactions and processes occur on a broad range of scales. Finally, research will be international in scope to encompass the global issues of HAB events and to benefit from the skill and expertise gained by HAB investigators world-wide.

Although GEOHAB is primarily built upon a coalescence of projects at many levels, the Core Research Project will also seek, through national funding mechanisms, to conduct a series of experiments and observations that directly address the key questions outlined in Chapter 4. Where possible, these efforts will capitalize on existing platforms, programmes, or ongoing studies. Research on the major priority areas identified herein is welcome within the GEOHAB framework. The understanding of this important issue, and ultimately the management of nutrient loads and improved prediction and management of HABs will require the global community of scientists.

Applying the GEOHAB Approach

Global population is rapidly increasing and concurrent changes in land use and coastal nutrient loading have been well established for many regions of the world. Critical to our long-term understanding is the need for continuous monitoring and observation, to document changes as they are occurring, and to understand the processes of change. There is a need for a global

The GEOHAB Core Research Project on HABs in Eutrophic Systems will seek to implement a range of comparative and interdisciplinary approaches.



MESOCOSM STUDIES HAVE PROVEN TO BE AN EFFECTIVE TOOL IN UNDERSTANDING POPULATION AND COMMUNITY RESPONSES TO NUTRIENT PERTURBATIONS. LEFT: MESOCOSM STUDIES IN CHINA. PHOTO: J. LI. RIGHT: MESOCOSM STUDIES IN LONG ISLAND, NY, USA. PHOTO: T. KANA.

network of sites that are deemed sensitive to nutrient alteration and eutrophication. In the United States, numerous sites now have more than a decade of data on which to build an understanding of the relationships among population change, climate change, and trends in nutrient quantity and composition. In Europe, numerous sites have been designated for continuous monitoring for benthic biodiversity and long-term phytoplankton records are known for the Scandinavian, Norwegian, British, Irish, French, Iberian, and Adriatic coasts. Japan has a long history of harmful algal records while China is rapidly expanding its coastal monitoring and HAB-specific activities. The value of long-term records is fundamental in understanding relationships between anthropogenic change, climate change, and HABs. In a manner analogous to the establishment of oceanic long-term sites such as the JGOFS HOT (Hawaii Ocean Time-series) and BATS (Bermuda Atlantic Time Series Study) sites, long-term sites for measuring nutrient loading and HABs must be maintained. Recognising the value of these long-term records is the first step in bringing comparative observational and modelling approaches together.

Natural experiments are being undertaken on a broad scale that will impact the expression of eutrophication in several parts of the world and may be deserving of special research attention. For example, Florida Bay, USA, receives freshwater flow from the Everglades, but currently this flow results from managed discharge rather than from natural hydrological conditions (Rudnick et al. 1991). Long-term management plans for the southern Florida area call for restoration of the natural flow conditions within the Everglades. Thus, key questions of concern to both scientists and managers are to what extent do nutrients originating from the Everglades contribute to eutrophication and HABs in Florida Bay and how will they change with altered flow conditions? Similarly, major engineering projects are being undertaken to alter the flow of the Yangtze River in China, where diversion of water will

Summary of Key Research Considerations

- Long-term monitoring, beyond a decade, may be required to observe trends in population, climate, and nutrient loading.
- Research must be integrated with new understanding in agricultural practices, aquacultural practices, atmospheric emissions and deposition, and human demography.
- Ecosystem characteristics such as hydrography, residence time, stratification, and trophic interactions will impact the expression of eutrophication and HABs.
- Multiple observational, experimental, and modelling approaches will be required to advance the study of HABs in relation to eutrophication.

cause major changes in nutrient loading to receiving waters. These regions are of key interest because the existing conditions are well characterised and thus, the impacts of hydrological diversion can be quantified.

The value of integrated experimental studies also must be underscored. Such approaches have led to enormous advances in our understanding of nutrient limitation. For example, whole-lake manipulations yielded tremendous insights into the differential regulation of N and P limitation in freshwater systems. Much was learned regarding the regulation of primary production by iron in the IronEx and SoFex experiments (de Baar et al. 2005), in which large patches of the ocean were fertilised with iron and the responses of the plankton community observed over days to weeks. Such approaches are beneficial in understanding HAB responses, both on a physiological level and also on a whole ecosystem level. Large-system perturbations, include nutrient additions in organic form, may provide the key to understanding how systems may respond as land use and nutrient loadings are altered.

To elevate research on HABs and eutrophication to a level consistent with the GEOHAB approach of comparative, international, multifaceted, and interdisciplinary studies, the Core Research Project on **HABs in Eutrophic Systems** will aim to undertake one or more large-scale experimental studies that will provide opportunities for researchers from around the world to participate. Such studies will be developed with considerable discussion within the broader community. These experimental studies will augment smaller-scale studies that will be linked through data sharing and smaller-scale comparative studies. Thus, the GEOHAB Core Research Project on **HABs in Eutrophic Systems** will seek to implement a range of approaches. The key questions identified in Chapter 4 will require different experimental, observational, and modelling methodologies.



THE PAST SEVERAL DECADES HAVE WITNESSED LARGE CHANGES IN TERRESTRIAL AND AQUATIC NITROGEN AND PHOSPHORUS, PRIMARILY DUE TO HUMAN ACTIVITIES SUCH AS INTENSIVE AGRICULTURE. PHOTO: J. HAWKEY.

Co-ordination of Activities

An important aspect of international activities like GEOHAB is the sharing of scarce resources among participating nations. Such sharing makes possible research activities of a scale and breadth that are not otherwise feasible, and therefore enable the comparison of ecosystems of a similar (or contrasting) type in different parts of the world. The CRP for **HABs in Eutrophic Systems** will promote the application of additional resources – in terms of scientific expertise, sampling platforms, and equipment – to the key research questions identified in this document. GEOHAB has already initiated the sharing of expertise and development of an international research community on the topic of **HABs and Eutrophic Systems** by supporting the *Open Science Meeting* in 2005.

GEOHAB Core Research Projects (CRPs) will be co-ordinated by the GEOHAB Scientific Steering Committee (SSC) through the establishment of separate sub-committees for each CRP composed of SSC members and leaders of the CRP activities. The sub-committees will primarily work by correspondence, but may meet on an opportunistic basis and when identified resources allow for meetings to address major planning and co-ordination issues. The sub-committees will work with the GEOHAB SSC and International Programme Office to encourage scientific networking.

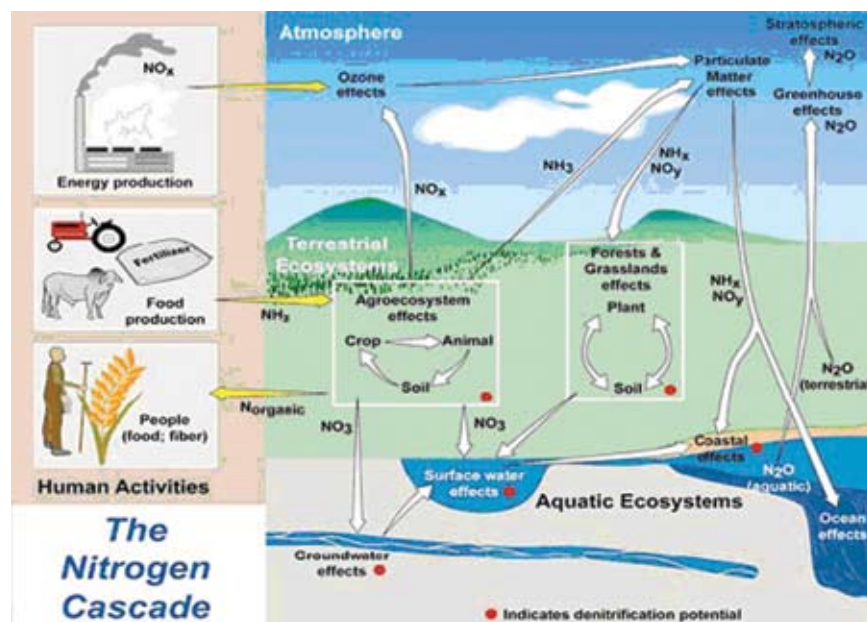
GEOHAB will identify, and draw the attention of responsible bodies to, opportunities for co-ordination of resources that will add value to ongoing and planned research. Individuals involved in studying the key questions outlined herein will be responsible for developing plans relating to the sharing of expertise and equipment and how they will contribute to the continued co-ordination of the Core Research.

GEOHAB and the CRP sub-committee will encourage the publication of results from Core Research in relevant peer-reviewed scientific journals, with appropriate reference to the relationship of the research to management issues as well as the GEOHAB goals. GEOHAB will also seek to aid researchers in the dissemination of research results and programme status more broadly to the world-wide community of managers and scientists interested in HABs through publication of articles in *Harmful Algae News*, the GEOHAB Web site, and other opportunities as become available. Each CRP sub-committee will also be responsible for disseminating announcements of meetings, symposia, or other special events, and is encouraged to form appropriate linkages and communications with the research and management communities of the impacted/studied areas.

Data Management and Data Sharing

The collective value of data is greater than its dispersed value, and comparative research requires effective data sharing among scientists working in different regions; therefore, data management and data exchange are important components of GEOHAB CRPs. The development of an appropriate data management plan is a fundamental and critical activity upon which the ultimate success of GEOHAB will depend, and the GEOHAB SSC is working with other related international marine research projects to develop basic guidelines for data management and sharing (see www.jhu.edu/scor/DataMgmt.htm). Each CRP will need to develop its own specific plans, conforming with the principles adopted by GEOHAB.

GEOHAB will use a decentralized data management and distribution system with a centralized metadata index, as the programme develops. Each CRP will create an inventory of data and data products. Each GEOHAB CRP will address the long-term archival of observational data and data products to ensure a lasting contribution to marine science.



Protocols and Quality Control

The CRP on **HABs in Eutrophic Systems** will require measurement of a broad suite of parameters that may differ depending on the key question being addressed. Where possible, well-defined, internationally agreed methods will be adopted. Regardless, to ensure quality control, the protocols used for data collections will be fully documented in information files (metadata) accompanying data sets. Where necessary, the GEOHAB SSC will initiate Framework Activities that lead to development of protocols or methods, or their intercalibration, to ensure that comparisons across systems can be accomplished.

Capacity Building

GEOHAB encourages a “training through research” approach that offers opportunities for student participation and instruction in marine research relevant to HABs. Exchange of post-doctoral fellows and senior scientists are equally important for the CRPs. Training activities that would benefit GEOHAB research will be organised by the GEOHAB SSC and proposals for specific training activities can be submitted for endorsement as GEOHAB activities.

Modelling Activities

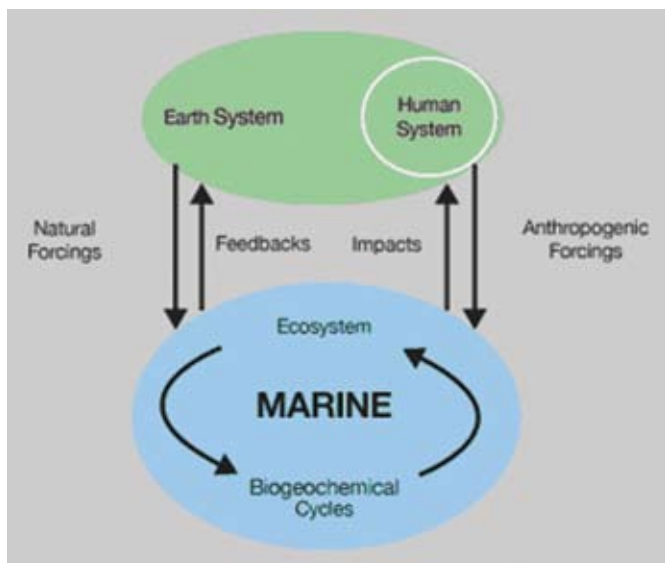
As described more fully in Chapter 3 of this report, the GEOHAB CRP on **HABs in Eutrophic Systems** will require application of a range of modelling approaches. The CRP on **HABs in Eutrophic Systems** should interact with the GEOHAB Modelling Subcommittee to compare models, to participate in model inter-comparison exercises, and share approaches. Modelling within **HABs in Eutrophic Systems** must also recognise the importance of global nutrient, climate, and population models in addition to models of population dynamics of HABs per se.

THE INTERNATIONAL NITROGEN INITIATIVE IS INTERESTED IN UNDERSTANDING ALL ASPECTS OF THE IMPACTS OF GLOBAL INCREASES IN THE USES OF ANTHROPOGENIC NITROGEN (WWW.INITROGEN.ORG). SOURCE: GALLOWAY ET AL 2003.

Interaction with Other International Programmes and Projects

GEOHAB exists in the context of several large international programmes and projects that study aspects of global change and eutrophication that could be relevant to the CRP on **HABs in Eutrophic Systems**. Some examples include:

- The Land-Ocean Interactions in the Coastal Zone (LOICZ) project has compiled information about the supply of macro-nutrients from the land to the ocean, information that could be useful in studying the relationships between nutrient supply, type, and ratios and HABs.
- The International Nitrogen Initiative (INI), under the auspices of the Scientific Committee on Problems of the Environment (SCOPE) and the International Geosphere-Biosphere Programme (IGBP), is a global effort to optimize nitrogen's beneficial role in sustainable food production and to minimize nitrogen's negative effects on human health and the environment. As part of its objectives, knowledge of the flows of nitrogen and the related problems in several targeted regions of the globe are being developed with a goal of minimizing the negative effects of human health and the environment. This information is relevant in characterising and defining nitrogen-based eutrophication.
- The Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) project is being developed with a goal of providing a comprehensive understanding of, and accurate predictive capacity for, ocean biological and chemical responses to accelerating global change and the consequent effects on the Earth System and human society. Planned observation and process studies related to the effects of nutrient inputs to coastal areas are relevant to HABs.



THE **IMBER** PROJECT IS DESIGNED TO STUDY THE IMPACTS OF ANTHROPOGENIC AND CLIMATIC CHANGE EFFECTS ON BIOGEOCHEMICAL PROCESSES IN THE OCEAN (**IMBER 2005**).

- The Climate Variability and Prediction (CLIVAR) project is studying how climate oscillations, such as ENSO and NAO, operate and are expressed in the ocean and atmosphere. Interactions between climate change and eutrophication are identified as one of the key questions of interest to **HABs in Eutrophic Systems**.
- The Global Ocean Observing System (GOOS) is a programme for sustained, co-ordinated international observations of the ocean and a platform for the generation of oceanographic products and services. **HABs in Eutrophic Systems** recognises that traditional approaches for detecting nutrient concentrations are often inadequate to resolve short-term pulses of nutrient loading that may precede HAB outbreaks. As new technologies in nutrient monitoring and cell detection move into operational status, the interactions between GOOS and **HABs in Eutrophic Systems** will become strengthened.
- The Global Ocean Ecosystem Dynamics (GLOBEC) project is focussed on understanding the relationship between physical processes and zooplankton in the support of marine fisheries. Activities of this project will be of direct relevance to **HABs in Eutrophic Systems** in determining the interactions “top down” and “bottom up” factors in controlling HABs.

In summary, with the aid of co-ordination facilitated by the CRP committee and the GEOHAB SSC as a whole, the activities of core research of **HABs in Eutrophic Systems** will strive to undertake studies that directly address the key questions identified and to become integrated with many projects at many levels, in order to advance and communicate scientific understanding of the role of eutrophication in the global proliferation of HABs. GEOHAB invites all relevant contributions to this effort.



WORLD-WIDE, FISHING, SHELLFISHING, AND SWIMMING AREAS ARE FREQUENTLY CLOSED DUE TO HARMFUL ALGAE. PHOTOS (CLOCKWISE FROM TOP LEFT): US FISH AND WILDLIFE, NEW JERSEY FIELD OFFICE; P. GLIBERT; CANADA DEPT. OF FISHERIES AND OCEAN; AND K. WHITING-GRANT, MAINE SEA GRANT.

References

- Aertebjerg, G. and T.J. Smayda. 2004. *Report of the Study Group to Review Ecological Quality Objectives for Eutrophication*. ICES Advisory Committee on Ecosystems. ICES CM 2004/ACE:04 Ref. ACME, C.E., 47 pp.
- Allen, J.I., J.R. Siddorn, J.C. Blackford, and F.J. Gilbert. 2004. Turbulence as a control on the microbial loop in a temperate seasonally stratified marine system model. *J. Sea Res.* 52:1-20.
- Alvarez-Salgado, X.A., F.G. Figueiras, F.F. Pérez, S. Groom, E. Nogueira, A. Borges, L. Chou, C.G. Castro, G. Moncoiffe, A.F. Rios, A.E.J. Miller, M. Frankignoulle, G. Savidge, and R. Wollast. 2003. The Portugal Coastal Counter Current off NW Spain: New insights on its biogeochemical variability. *Progr. Oceanogr.* 56:281-321.
- Anderson, D.M. 1989. Toxic algal blooms and red tides: A global perspective. In T. Okaichi, D.M. Anderson, and T. Nemoto (eds.), *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier Science, pp. 11-16.
- Anderson, D.M. 1998. Physiology and bloom dynamics of toxic *Alexandrium* species, with emphasis on life cycle transitions. In D.M. Anderson, A.D. Cembella, and G.M. Hallegraeff (eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer-Verlag, Berlin, Heidelberg, NATO ASI Series Vol. G 41:29-48.
- Anderson, D.M., P.M. Glibert, and J.M. Burkholder. 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25:704-726.
- Anderson, D.M., D.M. Kulis, G.J. Doucette, J.C. Gallagher, and E. Balech. 1994. Biogeography of toxic dinoflagellates in the genus *Alexandrium* from the northeastern United States and Canada. *Mar. Biol.* 120:467-478.
- Anderson, D.M., D.M. Kulis, B.A. Keafer, K.E. Gribble, R. Marin, and C.A. Scholin. 2005b. Identification and enumeration of *Alexandrium* spp. from the Gulf of Maine using molecular probes. *Deep-Sea Res II* 52:2467-2490.
- Anderson, D.M., G.C. Pitcher, and M. Estrada. 2005a. The comparative "systems" approach to HAB research. *Oceanography* 18(2):148-157.
- Anderson, T.R. 2005. Plankton functional type modelling: Running before we can walk? *J. Plank. Res.* 27:1073-1081.
- Andersson, G., H. Berggren, G. Gronberg, and C. Gelin. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia* 59:9-15.
- Antia, N.J., P.J. Harrison, and L. Oliveria. 1991. The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology. *Phycologia* 30:1-89.
- Arhonditsis, G.B. and M.T. Brett. 2004. Evaluation of the current state of mechanistic aquatic biogeochemical modeling. *Mar. Ecol. Progr. Ser.* 271:13-26.
- Armbrust, E.V., J.A. Berges, C. Bowler, B.R. Green, D. Martinez, N.H. Putnam, S. Zhou, A.E. Allen, K.E. Apt, M. Bechner, M.A. Brzezinski, B.K. Chaal, A. Chiovitti, A.K. Davis, M.S. Demarest, J.C. Detter, T. Glavina, D. Goodstein, M.Z. Hadi, U. Hellsten, M. Hildebrand, B.D. Jenkins, J. Jurka, V.V. Kapitonov, Nils Kröger, W.W.Y. Lau, T.W. Lane, F.W. Larimer, J.C. Lippmeier, S. Lucas, M. Medina, A. Montsant, M. Obornik, M.S. Parker, B. Palenik, G.J. Pazour, P.M. Richardson, T.A. Rynearson, M.A. Saito, D.C. Schwartz, K. Thamatrakoln, K. Valentin, A. Vardi, F.P. Wilkerson, and D.S. Rokhsar. 2004. The genome of the diatom *Thalassiosira pseudonana*: Ecology, evolution and metabolism. *Science* 306:79-86.
- Armstrong, M.D. and R. Kudela. 2003. *Nitrogenous Preference of Toxic Pseudo-nitzschia spp. from Enrichment Experiments Conducted in Iron Replete and Iron Deplete Regions in Central California*. Second Symposium on Harmful Algae in the US, Woods Hole, MA, Dec. 2003 (abstract only).
- Babin, M., J.J. Cullen, C.S. Roesler, P.L. Donaghay, G.J. Doucette, M. Kahru, M.R. Lewis, C.A. Scholin, M.E. Sieracki, and H.M. Sosik. 2005. New approaches and technologies for observing harmful algal blooms. *Oceanography* 18(2):210-227.

- Barber, R.T. and A.K. Hilting. 2000. Achievements in biological oceanography. In Ocean Studies Board, National Research Council (ed.), *50 Years of Ocean Discovery: National Science Foundation 1950–2000*. National Academy Press, Washington, D.C., pp. 11–21.
- Bates, S.S., C.J. Bird, A.S.W. de Freitas, R. Foxall, M. Gilgan, L.A. Hanic, G.R. Johnson, A.W. McCulloch, P. Odesne, R. Pocklington, M.A. Quilliam, P.G. Sim, J.C. Smith, D.V. Subba Rao, E.C.D. Todd, J.A. Walker, and J.L.C. Wright. 1989. Pennate diatom *Nitzschia pungens* as the primary source of domoic acid, a toxin in shellfish from eastern Prince Edward Island, Canada. *Can. J. Fish. Aquat. Sci.* 46:1203–1215.
- Bates, S.S., A.S.W. de Freitas, J.E. Milley, R. Pocklington, M.A. Quilliam, J.C. Smith, and J. Worms. 1991. Controls on domoic acid production by the diatom *Nitzschia pungens* f. *multiseries* in culture: Nutrients and irradiance. *Can. J. Fish. Aquat. Sci.* 48:1136–1144.
- Bates, S.S., D.J. Douglas, G.J. Doucette, and C. Leger. 1995. Enhancement of domoic acid production by reintroducing bacteria to axenic cultures of the diatom *Pseudo-nitzschia multiseries*. *Nat. Toxins* 3:428–435.
- Becker, A., A. Meister, and C. Wilhelm. 2002. Flow cytometric discrimination of various phycobilin-containing phytoplankton groups in a hypereutrophic reservoir. *Cytometry* 48:45–57.
- Beman, J.M., K.R. Arrigo, and P.A. Matson. 2005. Agricultural runoff fuels large phytoplankton blooms in the vulnerable areas of the ocean. *Nature* 434:211–214.
- Berg G.M., M. Balode, I. Purina, S. Bekere, C. Bechemin, and S.Y. Maestrini. 2003. Plankton community composition in relation to availability and uptake of oxidized and reduced nitrogen. *Aq. Microb. Ecol.* 30:263–274.
- Berman, T. 1997. Dissolved organic nitrogen utilization by an *Aphanizomenon* bloom in Lake Kinneret. *J. Plank. Res.* 19:577–586.
- Berman, T. 2001. The role of DON and the effect of N:P ratios on occurrence of cyanobacterial blooms: Implications from the outgrowth of *Aphanizomenon* in Lake Kinneret. *Limnol. Oceanogr.* 46:443–447.
- Berman, T. and S. Chava. 1999. Algal growth on organic compounds as nitrogen sources. *J. Plank. Res.* 21:1423–1437.
- Besiktepe, S.T., P.F.J. Lermusiaux, and A.R. Robinson. 2003. Coupled physical and biogeochemical data driven simulations of Massachusetts Bay in late summer: Real-time and post-cruise data assimilation. *J. Mar. Syst.* 40–41:171–212.
- Bodeanu, N. and G. Ruta. 1998. Development of the planktonic algae in the Romanian Black Sea sector in 1981–1996. In B. Reguera, J. Blanco, M.L. Fernandez, and T. Wyatt (eds.), *Harmful Algae*. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Paris, pp. 188–191.
- Boynton, W.R., W.M. Kemp, and C.W. Keefe. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In V. S. Kennedy (ed.), *Estuarine Comparisons*. Academic Press, NY, pp. 69–90.
- Bricker, S.B., C.G. Clement, D.E. Pirhalla, S.P. Orlando, and D.T.G. Farrow. 1999. *National Estuarine Eutrophication Assessment: Effects of Nutrient Enrichment in the Nation's Estuaries*. NOAA, National Ocean Service, Special Projects Office and the National Centers for Coastal Ocean Service, Silver Spring, MD, 71 pp.
- Bronk, D.A. 2002. Dynamics of dissolved organic nitrogen. In D.A. Hansell and C.A. Carlson (eds.), *Biogeochemistry of Marine Dissolved Organic Matter*. Elsevier, New York, NY, pp. 153–247.
- Burkholder, J.M. 2001. Beyond algal blooms, oxygen deficits and fish kills: Chronic, long-term impacts of nutrient pollution on aquatic ecosystems. In L. Bendell-Young and P. Gallagher (eds.), *Waters in Peril*. Kluwer Academic Publishers, Norwell, MA, pp. 103–126.
- Burkholder, J.M., Dickey, D.A., Kinder, C., Reed, R.E., Mallin, M.A., Melia, G., McIver, M.R., Cahoon, L.B., Brownie, C., Deamer, N., Springer, J., Glasgow, H., Toms, D., Smith, J., 2006. Comprehensive trend analysis of nutrients and related variables in a large eutrophic estuary: A decadal study of anthropogenic and climatic influences. *Limnol. Oceanogr.* 51:463–487.

- Burkholder, J.M. and H.B. Glasgow, Jr. 1997. *Pfiesteria piscicida* and other *Pfiesteria*-like dinoflagellates: Behavior, impacts, and environmental controls. *Limnol. Oceanogr.* 42:1052-1075.
- Burkholder, J.M., H.B. Glasgow, and N.J. Deamer-Melia. 2001. Overview and present status of the toxic *Pfiesteria* complex. *Phycologia* 40:186-214.
- Burkholder, J.M. and P.M. Glibert. 2006. Intraspecific variability: An important consideration in forming generalisations about toxigenic algal species. *S. Africa J. Mar. Sci.* In press.
- Burkholder, J.M., A.S. Gordon, P.D. Moeller, J.M. Law, K.J. Coyne, A.J. Lewitus, J.S. Ramsdell, H.G. Marshall, N.J. Deamer, S.C. Cary, J.W. Kempton, S.L. Morton, and P.A. Rublee. 2005. Demonstration of toxicity to fish and mammalian cells to *Pfiesteria* species: Comparison of assay methods and multiple strains. *Proc. Nat. Acad. Sci. (U.S.A.)* 102:3471-3476.
- Caraco, N.F. 1995. Influence of human populations on P transfers to aquatic systems: A regional scale study using large rivers. In H. Tiessen (ed.), *Phosphorus in the Global Environment*. SCOPE 54. John Wiley & Sons Ltd., New York, NY, pp. 235-247.
- Carlsson, P., H. Edling, and C. Bechemin. 1998. Interactions between a marine dinoflagellate (*Alexandrium catenella*) and a bacterial community utilizing riverine humic substances. *Aquat. Microb. Ecol.* 16:65-80.
- Carman, R. and F. Wulff. 1989. Adsorption capacity of phosphorus in Baltic Sea sediments. *Estuar. Coast. Shelf Sci.* 29:447-456.
- Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634-639.
- Cembella, A.D., D.A. Ibarra, J. Diogene, and E. Dahl. 2005. Harmful algal blooms and their assessment in fjords and coastal embayments. *Oceanography* 18(2):158-171.
- Cembella, A.D., J.J. Sullivan, G.L. Boyer, F.J.R. Taylor, and R.J. Anderson. 1987. Variation in paralytic shellfish toxin composition within the *Protogonyaulax tamarensis/catenella* species complex, red tide dinoflagellates. *Biochem. Syst. Ecol.* 15:171-186.
- Ciotti, Á.M., J.J. Cullen, and M.R. Lewis. 1999. A semi-analytical model of the influence of phytoplankton community structure on the relationship between light attenuation and ocean color. *J. Geophys. Res.* 104:1559-1578.
- Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210:223-253.
- Cofala, J., C. Heyes, Z. Klimont, M. Amann, D.W. Pearce, and A. Howarth. 2001. *Technical Report on Acidification, Eutrophication and Tropospheric Ozone in Europe: An Integrated Economic and Environmental Assessment*. RIVM report 481505014 under contract with the Environmental Directorate-general of the European Commission. 93 pp.
- Cohen, J.E. 2003. Human population: The next half century. *Science* 302:1172-1175.
- Costas, E. and V. Lopez-Rodas. 1996. Enumeration and separation of the toxic dinoflagellates *Alexandrium minutum* from natural samples using immunological procedures with blocking antibodies. *J. Exp. Mar. Biol. Ecol.* 198:81-87.
- Coyne, K.J., S.M. Handy, E. Demir, E.B. Whereat, D.A. Hutchins, K.J. Portune, M.A. Doblin, and S.C. Cary. 2006. Improved quantitative real-time PCR assays for enumeration of harmful algal species in field samples using an exogenous DNA reference standard. *Limnol. Oceanogr.:Methods* 3:381-391.
- Craig, J.K. and L.B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Mar. Ecol. Prog. Ser.* 294:79-94.
- Cullen, J.J. and J.G. MacIntyre. 1998. Behavior, physiology and the niche of depth regulating phytoplankton. In D.M. Anderson, A.D. Cembella, and G.M. Hallegraeff (eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer-Verlag Berlin Heidelberg, NATO ASI Series Vol. G 41:559-579.
- Dahl, E. and K. Tangen. 1993. 25 years experience with *Gyrodinium aureolum* in Norwegian waters. In T. J. Smayda and Y. Shimizu (eds.), *Toxic Phytoplankton Blooms in the Sea*. Elsevier, NY, pp. 15-21.
- Daskalov, G.M. 2002. Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.* 225: 53-63.
- De Baar, H.J.W., P.W. Boyd, K.H. Coale, M.R. Landry, A. Tsuda, P. Assmy, D.C.E. Bakker, Y. Bozec, R.T. Barber, M.A. Brzezinski, K.O. Buessler, M. Boye, P.L. Croot, F. Gervais, M.Y. Gorbunov, P.J. Harrison, W.T. Hiscock, P. Laan, C. Lancelot, C.S. Law, M. Lavasseur, A. Marchetti, F.J. Millero, J. Nishioka, Y. Nojiri, T. van Oijen, U. Riebesell, M.J.A. Rijkenberg, H. Saito, S. Takeda, K.R. Timmermans, M.J.W. Veldhuis, A.M. Waite, and C.S. Wong. 2005. Synthesis of iron fertilization experiments: From the iron age in the age of enlightenment. *J. Geophys. Res.-Oceans* 110 (C9): Art No. C09S16.

- Dennison, W.C. and E. Abal. 1999. *Moreton Bay Study: A Scientific Basis for the Healthy Waterways Campaign*. South East Queensland Regional Water Quality Management Strategy, Brisbane, Australia.
- de Young, B., M. Heath, F. Werner, F. Chai, B. Megrey, and P. Monfray. 2004. Challenges of modeling ocean basin ecosystems. *Science* 304:1463-1466.
- Donaghay, P.L. 1988. The role of temporal scales of acclimation, food quality and trophic dominance in controlling the evolution of copepod feeding behaviour. *Bull. Mar. Sci.* 43:469-485.
- Donaghay, P. and T.R. Osborn. 1997. Toward a theory of biological-physical control of harmful algal bloom dynamics and impacts. *Limnol. Oceanogr.* 42(5, part 2):1283-1296.
- Doney, S.C., M.R. Abbott, J.J. Cullen, D.M. Karl, and L. Rothstein. 2004. From genes to ecosystems: the ocean's new frontier. *Front. Ecol. Environ* 2(9):457-466.
- Dumont, E., J.H. Harrison, C. Kroeze, E.J. Bakker, and S.P. Seitzinger. 2005. Global distribution and sources of dissolved inorganic nitrogen export to the coastal zone: Results from a spatially explicit, global model. *Global Biogeochem. Cycles* 19(4):GB4S02.
- Dyhrman, S. and D.M. Anderson. 2003. Urease activity in cultures and field populations of the toxic dinoflagellate *Alexandrium*. *Limnol. Oceanogr.* 48:647-655.
- Dyhrman, S.T. and B. Palenik. 2001. A single-cell immunoassay for phosphate stress in the dinoflagellate *Prorocentrum minimum* (Dinophyceae). *J. Phycol.* 37:400-410.
- EUROHAB. 1999. European Initiative on Harmful Algal Blooms (EUROHAB): Harmful Algal Blooms in European Marine and Brackish Waters, E. Granéli, G.A. Codd, B. Dale, E. Lipiatou, S.Y. Maestrini, and H. Rosenthal (eds.). European Commission, Directorate General Science Research and Development, 93 pp.
- Evans, J.J., P.H. Klesius, P.M. Glibert, C.A. Shoemaker, M.A. Al-Sarawi, J.H. Landsberg, R.D. Duremdaz, A. Al-Marzouk, and S. Al-Zenki. 2002. Characterization of beta-hemolytic Group B *Streptococcus agalactiae* in cultured gilthead seabream, *Sparus auratus* (L.) and wild mullet, *Liza klunzingeri* (Day), in Kuwait. *J. Fish Diseases* 25:505-513.
- Fan, C., P.M. Glibert, J. Alexander, and M.W. Lomas. 2003. Characterization of urease activity in three marine phytoplankton species. *Mar. Biol.* 142:949-958.
- Fisher, T.R., L. Harding, D.W. Stanley, and L.G. Ward. 1988. Phytoplankton, nutrients, and turbidity in the Chesapeake, Delaware, and Hudson estuaries. *Estuar. Coastal Shelf Sci.* 27:61-93.
- Fisher, T.R., E.R. Peele, J.W. Ammerman, and L.W. Harding. 1992. Nutrient limitation of phytoplankton in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 82:51-63.
- Fistarol, G.O., C. Legrand, and E. Granéli. 2005. Allelopathic effect on a nutrient-limited phytoplankton species. *Aquat. Microb. Ecol.* 41:153-161.
- Fistarol, G.O., C. Legrand, C. Rengefors, and E. Granéli. 2004a. Temporary cyst formation in phytoplankton: A response to allelopathic competitors? *Environ. Microbiol.* 6(8):791-798.
- Fistarol, G.O., C. Legrand, E. Selander, C. Hummert, W. Stolte, and E. Granéli, E. 2004b. Allelopathy in *Alexandrium* spp.: Effect on a natural plankton community and on algal monocultures. *Aquat. Microbial Ecol.* 35:45-56.
- Flynn, K.J. 1998. Physiology of toxic microalgae with special emphasis on toxin production; construction of dynamic models. In B. Reguera, J. Blanco, L. Fernandez, and T. Wyatt (eds.), *Harmful Algal Blooms*. Intergovernmental Oceanographic Commission of UNESCO, pp. 315-320.
- Flynn, K.J. 2002. Toxin production in migrating dinoflagellates: A modelling study of PSP-producing *Alexandrium*. *Harmful Algae* 1:147-155.
- Flynn, K.J. 2005a. Modelling marine phytoplankton growth under eutrophic conditions. *J. Sea Res.* 54:92-103.
- Flynn, K.J. 2005b. Castles built on sand: Dysfunctional plankton models and the failure of the biology-modelling interface. *J. Plank. Res.* In press.
- Flynn, K.J. and I. Butler. 1986. Nitrogen sources for the growth of marine microalgae: Role of dissolved free amino acids. *Mar. Ecol. Prog. Ser.* 34:281-304.

- Flynn, K.J. and K. Flynn. 1995. Dinoflagellate physiology: Nutrient stress and toxicity. In P. Lassus, G. Arzul, E. Erard, P. Gentien, and C. Marcaillou (eds.), *Harmful Marine Algal Blooms*. Lavoisier Science Publishers, Paris, pp. 541-550.
- Franks, P.J.S. 1992. Sink or swim: Accumulation of biomass at fronts. *Mar. Ecol. Prog. Ser.* 82:1-12.
- Franks, P.J.S. 1997. Spatial patterns in dense algal blooms. *Limnol. Oceanogr.* 42:1297-1305.
- Franks, P.J.S. and D.M. Anderson. 1992. Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. *Mar. Biol.* 116:153-164.
- Fulton, E.A., J.S. Paslow, A.D.M. Smith, and C.R. Johnson. 2003. Effect of complexity on marine ecosystem models. *Mar. Ecol. Prog. Ser.* 253:1-16.
- Fuhrman, J.A. and C.A. Suttle. 1993. Viruses in marine planktonic systems. *Oceanography* 6:50-62.
- Gallegos, C.L. and T.E. Jordan. 2002. Impact of the spring 2000 phytoplankton bloom in Chesapeake Bay on optical properties and light penetration in the Rhode River, Maryland. *Estuaries* 25:508-518.
- Galloway, J.N., F.N. Dentener, D.G. Capone, E.W. Boyer, R.W. Howarth, S.P. Seitzinger, G.P. Asner, C. Cleveland, P.A. Green, E. Holland, D.M. Karl, A. Michaels, J.H. Porter, A. Townsend, and C. Vorosmarty. 2004. Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70:153-226.
- Gentien, P. and G. Arzul. 1990. Exotoxin production by *Gyrodinium cf. aureolum* (Dinophyceae). *J. Mar. Biol. Assoc.* 70(3):571-581.
- Gentien, P., P. Donaghay, H. Yamazaki, R. Raine, B. Reguera, and T. Osborn. 2005. Harmful algal blooms in stratified environments. *Oceanography* 18(2):172-183.
- Gentien, P., M. Lunven, M. Lehaitre, and J.L. Duvent. 1995. In situ depth profiling of particles sizes. *Deep-Sea Res.* 42:1297-1312.
- GEOHAB. 2001. *Global Ecology and Oceanography of Harmful Algal Blooms, Science Plan*, P. Glibert and G. Pitcher, (eds.). SCOR and IOC, Baltimore and Paris, 86 pp.
- GEOHAB. 2003. *Global Ecology and Oceanography of Harmful Algal Blooms, Implementation Plan*, P. Gentien, G. Pitcher, A. Cembella, and P. Glibert, (eds.). SCOR and IOC, Baltimore and Paris, 36 pp.
- GEOHAB. 2005. *Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Upwelling Systems*, G. Pitcher, T. Moita, V. Trainer, R. Kudela, F. Figueiras, and T. Probyn, (eds.). IOC and SCOR, Paris and Baltimore, 88 pp.
- Gismervik, I., T. Anderson, and O. Vadstein. 1996. Pelagic food webs and eutrophication of coastal waters: Impact of grazers on algal communities. *Mar. Poll. Bull.* 33:22-35.
- Gisselson, L.-Å., P. Carlsson, E. Granéli, and J. Pallon. 2002. *Dinophysis* blooms in the deep euphotic zone of the Baltic Sea: Do they grow in the dark? *Harmful Algae* 1:401-418.
- Gitay, H. and I.R. Noble. 1997. What are functional types and how should we seek them? In T.M. Smith, H.H. Shugart, and F.I. Woodward (eds.), *Plant Functional Types: Their Relevance to Functional Properties and Global Change*. Cambridge University Press, Cambridge, United Kingdom, pp. 3-19.
- Glibert, P.M. 1998. Interactions of top-down and bottom-up control in planktonic nitrogen cycling. *Hydrobiologia* 363:1-12.
- Glibert, P.M. and D.A. Bronk. 1994. Release of dissolved organic nitrogen by marine diazotrophic cyanobacteria, *Trichodesmium* spp. *Appl. Environ. Microbiol.* 60:3996-4000.
- Glibert, P.M., and J.M. Burkholder. 2006. The complex relationships between increasing fertilization of the earth, coastal eutrophication and proliferation of harmful algal blooms. In E. Granéli and J. Turner (eds.), *Ecology of Harmful Algae*. Springer-Verlag, Berlin/Heidelberg. In press.
- Glibert, P.M., D.J. Conley, T.R. Fisher, L.W. Harding, Jr., and T.C. Malone. 1995. Dynamics of the 1990 winter/spring bloom in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 122:27-43.
- Glibert, P.M., J. Harrison, C. Heil, and S. Seitzinger. 2006. Escalating worldwide use of urea – a global change contributing to coastal eutrophication. *Biogeochemistry* 77:441-463.
- Glibert, P.M. and C. Heil. 2005. Use of urea fertilisers and the implications for aquatic harmful algal blooms. In Z. Zhu, K. Minami, and G. Xing (eds.), *3rd International Nitrogen Conference Contributed Papers*, Science Press USA, Inc, Beijing, pp. 539-544.

- Glibert, P.M., C.A. Heil, D. Hollander, M. Revilla, A. Hoare, J. Alexander, and S. Murasko. 2004. Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay. *Mar. Ecol. Progr. Ser.* 280:73-83.
- Glibert, P.M., J. Landsberg, J. Evans, M.A. Al-Sarawi, M. Faraj, M.A. Al-Jarallah, A. Haywood, S. Ibrahim, P. Klesius, C. Powell, and C. Shoemaker. 2002. A fish kill of massive proportion in Kuwait Bay, Arabian Gulf, 2001: The roles of infectious bacteria, harmful algae, and eutrophication. *Harmful Algae* 12:1-17.
- Glibert, P.M., R. Magnien, M.W. Lomas, J. Alexander, C. Fan, E. Haramoto, M. Trice, and T.M. Kana. 2001. Harmful algal blooms in the Chesapeake and Coastal Bays of Maryland, USA: Comparison of 1997, 1998, and 1999 events. *Estuaries* 24:875-883.
- Glibert, P.M. and J.M. O'Neil. 1999. Dissolved organic nitrogen release and amino acid oxidase activity by *Trichodesmium* spp. In L. Charpy and A.W.D. Larkum (eds.), *Marine Cyanobacteria*. Monaco Musée Océanographique, Bulletin de l'Institut Océanographique, Monaco, pp. 265-271.
- Glibert, P.M., S. Seitzinger, C.A. Heil, J.M. Burkholder, M.W. Parrow, L.A. Codispoti, and V. Kelly. 2005. The role of eutrophication in the global proliferation of harmful algal blooms. *Oceanography* 18(2):198-209.
- Gobler, C.J. and S.A. Sañudo-Wilhelmy. 2001. Temporal variability of groundwater seepage and brown tide blooms in a Long Island embayment. *Mar. Ecol. Progr. Ser.* 217:299-309.
- Goldman, J.C. and P.M. Glibert. 1983. Kinetics of inorganic nitrogen uptake. In Carpenter, E.J. and Capone, D.G. (eds.), *Nitrogen in the Marine Environment*. Academic Press, NY, pp. 233-274.
- González-Gil, S., B.A. Keafer, R.V.M. Jovine, and D.M. Anderson. 1998. Detection and quantification of alkaline phosphatase in single cells of phosphorus-limited marine phytoplankton. *Mar. Ecol. Progr. Ser.* 164:31-35.
- Granéli, E. 2005. Eutrophication and harmful algal blooms. In P. Wassmann and K. Olli (eds.), *Drainage basin nutrient inputs and eutrophication: An integrated approach*. University of Tromsø, Norway, pp. 99-112.
- Granéli, E., D.M. Anderson, P. Carlsson, and S.Y. Maestrini. 1997. Light and dark carbon uptake by *Dinophysis* species in comparison to other photosynthetic and heterotrophic dinoflagellates. *Aquat. Microb. Ecol.* 13:177-186.
- Granéli, E., P. Carlsson, P. Tester, J.T. Turner, C. Bechemin, R. Dawson, and F. Azam. 1999. Effects of N:P:Si ratios and zooplankton grazing on phytoplankton communities in the northern Adriatic Sea. I. Nutrients, phytoplankton, biomass, and polysaccharide production. *Aq. Microb. Ecol.* 18:37-54.
- Granéli, E., L. Edler, D. Gedziorowska, and U. Nyman. 1985. Influence of humic and fulvic acids on *Prorocentrum minimum* (Pav.) J. Schiller. In D.M. Anderson, A.W. White, and D.G. Baden (eds.), *Toxic Dinoflagellates*. Elsevier Science Publishing Co., North-Holland, pp. 201-206.
- Granéli, E. and K.J. Flynn. 2006. Chemical and physical factors influencing toxin content in harmful algae. In E. Granéli and J.T. Turner (eds.), *Ecology of Harmful Algae*. Springer-Verlag, Berlin/Heidelberg. In press.
- Granéli, E. and P.J. Hansen. 2006. Allelopathy in harmful algae: A mechanism to compete for resources? In E. Granéli and J.T. Turner (eds.), *Ecology of Harmful Algae*. Springer-Verlag, Berlin/Heidelberg. In press.
- Granéli E. and N. Johansson N. 2003a. Increase in the production of allelopathic substances by *Prymnesium parvum* cells grown under N- or P-deficient conditions. *Harmful Algae* 2:135-145.
- Granéli, E. and N. Johansson. 2003b. Effects of the toxic haptophyte *Prymnesium parvum* on the survival and feeding of a ciliate: The influence of different nutrient conditions. *Mar. Ecol. Progr. Ser.* 254:49-56.
- Granéli, E., N. Johansson, and R. Panosso. 1998. Cellular toxin contents in relation to nutrient conditions for different groups of phycotoxins. In B. Reguera, J. Blanco, M.L. Fernández, and T. Wyatt, (eds.), *Harmful Algae*. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, pp. 321-324.
- Granéli, E. and M.O. Moreira. 1990. Effects of river water of different origin on the growth of marine dinoflagellates and diatoms in laboratory cultures. *J. Exp. Mar. Ecol.* 136:89-106.
- Granéli, E. and J.T. Turner. 2002. "Top-down" regulation in ctenophore - copepod - ciliate - diatom - phytoflagellate communities in coastal waters: A mesocosm study. *Mar. Ecol. Progr. Ser.* 239:57-68.
- Grzebyk, D. and B. Berland. 1996. Influences of temperature, salinity and irradiance on growth of *Prorocentrum minimum* (Dinophyceae) from the Mediterranean Sea. *J. Plankt. Res.* 18:1837-1849.

- Hagy, J.D., W.R. Boynton, C.W. Keefe, and K.V. Wood. 2002. Hypoxia in Chesapeake Bay, 1950-2001: Long-term change in relation to nutrient loading and river flow. *Estuaries* 27:634-658.
- Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32:79-99.
- Harding, L.W., Jr. 1994. Long-term trends in the distribution of phytoplankton in Chesapeake Bay: Roles of light, nutrients and streamflow. *Mar. Ecol. Prog. Ser.* 104:267-291.
- Harlin, M.M. 1993. Changes in major plant groups following nutrient enrichment. In A.J. McComb (ed.), *Eutrophic Shallow Estuaries and Lagoons*. CRC Press, Inc., Boca Raton, FL, pp. 173-187.
- Harrison, J.H., N.F. Caraco, and S.P. Seitzinger. 2005. Global patterns and sources of dissolved organic matter export to the coastal zone: Results from a spatially explicit, global model. *Global Biogeochem. Cycles* 19(4):GBS406.
- Heil, C.A., P.M. Glibert, and C. Fan. 2005. *Prorocentrum minimum* (Pavillard) Schiller – A review of a harmful algal bloom species of growing worldwide importance. *Harmful Algae* 4:449-470.
- Holligan, P.M. 1979. Dinoflagellate blooms associated with tidal fronts around the British Isles. In D.L. Taylor and H.H. Seliger (eds.), *Toxic Dinoflagellate Blooms*. Elsevier North Holland, NY, pp. 249-256.
- Howarth, R.W., G. Billen, D. Swaney, A. Townsend, N. Jaworski, K. Lajtha, J.A. Downing, R. Elmgren, N. Caraco, T. Jordan, F. Beredse, J. Freney, V. Kueyarov, P. Murdoch, and Z. Zhao-Liang. 1996. Riverine inputs of nitrogen to the North Atlantic Ocean: Fluxes and human influences. *Biogeochemistry* 35:75-139.
- Howarth, R.W., E.W. Boyer, R. Marino, D. Swaney, N. Jaworski, and C. Goodale. 2006. The influence of climate on average nitrogen export from large watersheds in the northeastern United States. *Biogeochemistry*. In press.
- Howarth, R.W., E.W. Boyer, W.J. Pabich, and J.N. Galloway. 2002b. Nitrogen use in the United States from 1961-2000 and potential future trends. *Ambio* 31:88-96.
- Howarth, R.W. and R. Marino. 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: Evolving views over 3 decades. *Limnol. Oceanogr.* 51:364-376.
- Howarth, R.W., K. Ramakrishna, E. Choi, R. Elmgren, L. Martinelli, A. Mendoza, W. Moomaw, C. Palm, R. Boy, M. Scholes, and Z. Zhao-Liang. 2005. Nutrient management, responses assessment. In: *Ecosystems and Human Well-Being, Volume 3, Policy Responses, the Millennium Ecosystem Assessment*. Island Press, Washington DC, pp. 295-311.
- Howarth, R.W., A. Sharpley, and D. Walker. 2002a. Sources of nutrient pollution to coastal waters in the United States: Implications for achieving coastal water quality goals. *Estuaries* 25:656-676.
- Humborg, C., D.J. Conley, L. Rahm, F. Wulff, A. Cociasu, and V. Ittekkot. 2000. Silica retention in river basins: far reaching effects on biogeochemistry and aquatic food webs. *Ambio* 29:45-50.
- Integrated Marine Biogeochemistry and Ecosystem Research (IMBER). 2005. *Science Plan and Implementation Strategy*. IGBP Report No. 52, IGBP Secretariat, Stockholm, Sweden. 76 pp.
- International Fertilizer Industry 2005. www.fertilizer.org/ifa/statistics.
- Jacquet, S., L. Prieur, C. Avois-Jacquet, J.-F. Lennon, and D. Vaultot. 2002. Short-timescale variability of picophytoplankton abundance and cellular parameters in surface waters of the Alboran Sea (western Mediterranean). *J. Plank. Res.* 24:633-651.
- Jang, M.H., K. Ha, G.-J. Joo, and N. Takamura. 2003. Toxin production of cyanobacteria is increased by exposure to zooplankton. *Freshwater Biol.* 48:1540-1550.
- John, E.H. and K.J. Flynn. 2002. Modelling changes in paralytic shellfish toxin content of dinoflagellates in response to nitrogen and phosphorus supply. *Mar. Ecol. Prog. Ser.* 225:147-160.
- Jones, R.H. and K.J. Flynn. 2005. Nutritional status and diet composition affect the value of diatoms as copepod prey. *Science* 307:1457-1459.
- Kamykowski, D. 1974. Possible interactions between phytoplankton and semidiurnal internal tides. *J. Mar. Res.* 32:67-89.
- Kamykowski, D. 1995. Trajectories of autotrophic marine dinoflagellates. *J. Phycol.* 31:200-208.

- Kamykowski, D., J.E. Milligan, R.E. Reed, and W. Liu. 1999. Geotaxis/phototaxis and biochemical patterns in *Heterocapsa illdefina* (Dinophyceae) during vertical migrations. *J. Phycol.* 35:1397-1403.
- Karl, D., R. Letelier, D.V. Hebel, D.F. Bird, and C.D. Winn. 1992. *Trichodesmium* blooms and new nitrogen in the North Pacific Gyre. In E.J. Carpenter, D.G. Capone, and J.G. Reuter (eds.), *Marine Pelagic Cyanobacteria: Trichodesmium and Other Diazotrophs*. Kluwer Academic Publishers, Netherlands, pp. 219-238.
- Kemp, W.M., W.R. Boynton, J.E. Adolf, D.F. Boesch, W.C. Boicourt, G. Brush, J.C. Cornwell, T.R. Fisher, P.M. Glibert, J.D. Hagy, L.W. Harding, E.D. Houde, D.G. Kimmel, W.D. Miller, R.I.E. Newell, M. R. Roman, E.M. Smith, and J.C. Stevenson. 2005. Eutrophication in Chesapeake Bay: Historical trends and ecological interactions. *Mar. Ecol. Prog. Ser.* 303:1-29.
- Kideys, A.E., A. Roohi, S. Bagheri, G. Finenko, and L. Kamburska. 2005. Impacts of invasive ctenophores on the fisheries of the Black Sea and Caspian Sea. *Oceanography* 18(2):76-85.
- Kirkpatrick, G., D.F. Millie, M.A. Moline, and O. Schofield. 2000. Optical discrimination of a phytoplankton species in natural mixed populations. *Limnol. Oceanogr.* 45:467-471.
- Knoll, L.B., M.J. Vanni, and W.H. Renwick. 2003. Phytoplankton primary production and photosynthetic parameters in reservoirs along a gradient of watershed land use. *Limnol. Oceanogr.* 48:608-617.
- Kruskopf, M. and K.J. Flynn. 2006. Chl content and fluorescence response cannot be used to gauge reliably phytoplankton biomass, nutrient status or growth rate. *New Phytologist* 169:525-536.
- Lam, C.W.Y. and K.C. Ho. 1989. Red tides in Tolo Harbour, Hong Kong. In T. Okaichi, D.M. Anderson, and T. Nemoto (eds.), *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier Science, pp. 49-52.
- Lancelot, C., G. Billen, A. Sournia, T. Weisse, F. Colijn, M.J.W. Veldhuis, A. Davies, and P. Wassmann. 1987. *Phaeocystis* blooms and nutrient enrichment in the continental coastal zones of the North Sea. *Ambio* 16:38-46.
- Lancelot, C., J.M. Martin, N. Panin, and Y. Zaitsev. 2002. The North-western Black Sea: A pilot site to understand the complex interaction between human activities and the coastal environment. *Estuar. Coastal Shelf Sci.* 54:279-283.
- Lancelot, C., Y. Spitz, N. Gypens, K. Ruddick, S. Becquevort, V. Rousseau, G. Lacroix, and G. Billin. 2005. Modelling diatom and *Phaeocystis* blooms and nutrient cycles in the Southern Bight of the North Sea: The MIRO model. *Mar. Ecol. Prog. Ser.* 289:63-78.
- LaRoche, J., R. Nuzzi, R. Waters, K. Wyman, P.G. Falkowski, and D.W.R. Wallace. 1997. Brown tide blooms in Long Island's coastal waters linked to variability in groundwater flow. *Global Change Biol.* 3:397-410.
- Lawrence, J.E. and A.D. Cembella. 1999. An immunolabeling technique for the localisation of diarrhetic shellfish toxins in individual microalgae. *Phycologia* 38:60-65.
- Lewitus, A.J., L.B. Schmidt, L.J. Mason, J.W. Kempton, S.B. Wilde, J.L. Wolny, K.C. Hayes, S.N. Hymel, C.J. Keppler, and A.H. Ringwood. 2003. Harmful algal blooms in South Carolina residential and golf course ponds. *Pop. Environ.* 24:387-413.
- Lewitus, A.J., B.M. Willis, K.C. Hayes, J.M. Burkholder, H.B. Glasgow, Jr., P.M. Glibert, and M.K. Burke. 1999. Mixotrophy and nitrogen uptake by *Pfiesteria piscicida* (Dinophyceae). *J. Phycol.* 35:1430-1437.
- Li, A., D.K. Stoecker, D.W. Coats, and E.J. Adam. 1996. Ingestion of fluorescently labeled and phycoerythrin-containing prey by mixotrophic dinoflagellates. *Aquat. Microb. Ecol.* 10:139-147.
- Li, W.K.W. and P.M. Dickie. 2001. Monitoring phytoplankton, bacterioplankton and virioplankton in a coastal inlet (Bedford Basin) by flow cytometry. *Cytometry* 44:236-246.
- Lidie, K.L., J.C. Ryan, M. Barbier, and F.M. Van Dolah. 2005. Gene expression in the Florida red tide dinoflagellate *Karenia brevis*: analysis of an expressed sequence tag (EST) library and development of a DNA microarray. *Mar. Biotech.* In press.
- Litaker, R.W. and P.A. Tester. 2005. Abiotic and biotic factors controlling a nutrient driven dinoflagellate bloom and likely responses to increased eutrophication. *GEOHAB Open Science Meeting on HABs and Eutrophication*, Baltimore, MD (abstract only).
- MacIntyre, H. and J.J. Cullen. 2005. Using cultures to investigate the physiological ecology of microalgae. In R.A. Anderson (ed.), *Algal Culturing Techniques*. Elsevier Academic Press. Hong Kong, pp. 287-326.
- MacIntyre, H.L., M.W. Lomas, J. Cornwell, D.J. Suggett, C.J. Gobler, E.W. Koch, and T.M. Kana. 2005. Mediation of benthic-pelagic coupling by microphytobenthos: and energy- and material-based model for initiation of blooms of *Aureococcus anophagefferens*. *Harmful Algae* 3: 403-438.

- Maclean, J.L. 1989. Indo-Pacific red tides, 1985-1988. *Mar. Pollution Bull.* 20:304-310.
- Malone, T.C. 1992. Effects of water column processes on dissolved oxygen, nutrients, phytoplankton and zooplankton. In D.E. Smith, M. Leffler, and G. Mackiernan (eds.), *Oxygen Dynamics in the Chesapeake Bay: A Synthesis of Research*. Maryland Sea Grant College Publication No. UM-SG-TS-92-01, College Park, MD, pp. 61-112.
- Malone, T.C., D.J. Conley, T.R. Fisher, P.M. Glibert, L.W. Harding, and K.G. Sellner. 1996. Scales of nutrient-limited phytoplankton productivity in Chesapeake Bay. *Estuaries* 19:371-385.
- Malone, T.C., P.G. Falkowski, T.S. Hopkins, G.T. Rowe, and T.E. Whitledge. 1983. Mesoscale response of diatom populations to wind events in the plume of the Hudson River. *Deep-Sea Res.* 30:149-170.
- Malone, T.C., W.M. Kemp, H.W. Ducklow, W.R. Boynton, J.H. Tuttle, and R.B. Jonas. 1986. Lateral variability in the production and fate of phytoplankton in a partially stratified estuary. *Mar. Ecol. Prog. Ser.* 32:149-160.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta* 1:493-509.
- McGillicuddy, D.J., R.P. Signell, C.A. Stock, B.A. Keafer, D.M. Keller, R.D. Hetland, and D.M. Anderson. 2003. A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine. *J. Plank. Res.* 25:1131-1138.
- Merrell, J.R. and D.K. Stoecker. 1998. Differential grazing on protozoan microplankton by developmental stages of the calenoid copepod *Eurytemora affinis* Poppe. *J. Plank. Res.* 20:289-304.
- Miller, W.D., L.W. Harding, and J.E. Adolf. 2005. The influence of Hurricane Isabel on Chesapeake Bay phytoplankton dynamics. In K.G. Sellner (ed.), *Hurricane Isabel in Perspective*. Chesapeake Research Consortium Publication 05-160, Edgewater, MD.
- Miller, W.D., L.W. Harding, Jr., and J.E. Adolf. 2006. Hurricane Isabel generated an unusual fall bloom in Chesapeake Bay. *Geophys. Res. Lett.* 33, L06612, doi:10.1029/2005GL025658.
- Mitra, A. and K.J. Flynn. 2005. Predator-prey interactions: Is "ecological stoichiometry" sufficient when good food goes bad? *J. Plank. Res.* 27: 393-399.
- Mitra, A. and K.J. Flynn. 2006. Promotion of harmful algal blooms by zooplankton predatory activity. *Biol. Lett.* Doi:10.1098/rsbl.2006.0447.
- Moll, A. and G. Radach. 2003. Review of three-dimensional ecological modelling related to the North Sea shelf system - Part 1: Models and their results. *Progr. Oceanogr.* 57(2):175-217.
- Mulholland M.R., K. Ohki, and D.G. Capone. 1999. Nitrogen utilization and metabolism relative to patterns of N₂ fixation in cultures of *Trichodesmium* NIBB1967. *J. Phycol.* 35:977-988.
- Najjar, R.G. 1999. The water balance of the Susquehanna River basin and its response to climate change. *J. Hydrology* 219:7-19.
- National Research Council (NRC). 2000. *Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution*. National Academies Press, Washington, DC.
- Nielsen, T.G., T. Kjørbo, and P.K. Bjørnsen. 1990. Effects of a *Chrysochromulina polylepis* subsurface bloom on the planktonic community. *Mar. Ecol. Prog. Ser.* 62:21-35.
- Nixon, S.W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia* 41:199-219.
- Noble, D. 2002. The rise of computational biology. *Nature Rev. Mol. Cell Biol.* 3:460-463.
- Nuzzi, R. and R.M. Waters. 2004. Long-term perspective on the dynamics of brown tide blooms in Long Island coastal waters. *Harmful Algae* 3:279-294.
- Oguz, T. 2005. Long-term impacts of anthropogenic forcing on the Black Sea ecosystem. *Oceanography* 18(2):112-121.
- Oliver, R.L. and G.C. Ganf. 2000. Freshwater blooms. In B.A. Whitton and M. Potts (ed.), *The Ecology of Cyanobacteria*. Kluwer Academic Publishers, pp. 149-194.
- Olson, R.J., A.M. Chekalyuk, and H.M. Sosik. 1996. Phytoplankton photosynthetic characteristics from fluorescence induction assays of individual cells. *Limnol. Oceanogr.* 41:1253-1263.
- Paerl, H.W. 1988. Nuisance phytoplankton in coastal, estuarine and inland waters. *Limnol. Oceanogr.* 33:823-847.

- Paerl, H.W. and D.F. Millie. 1996. Physiological ecology of toxic cyanobacteria. *Phycologia* 35:160-167.
- Paerl, H.W. and J.L. Pinckney. 1996. Microbial consortia: Their role in aquatic production and biogeochemical cycling. *Microbiol. Ecol.* 31:225-247.
- Park, G.S. and H.G. Marshall. 2000. Estuarine relationships between zooplankton community structure and trophic gradients. *J. Plankt. Res.* 22:121-135.
- Parrow, M.W. and J.M. Burkholder. 2004. The sexual life cycles of *Pfiesteria piscicida* and cryptoperidiniopsoids (Dinophyceae). *J. Phycol.* 40:664-673.
- Parsons, M.L., Q. Dortch, and R.E. Turner. 2002. Sedimentological evidence of an increase in *Pseudo-nitzschia* (Bacillariophyceae) abundance in response to coastal eutrophication. *Limnol. Oceanogr.* 47:551-558.
- Pratt, D.M. 1966. Competition between *Skeletonema costatum* and *Olisthodiscus luteus* in Narragansett Bay and in culture. *Limnol. Oceanogr.* 11:447-445.
- Qi, Y.Z., Z. Zhang, Y. Hong, S. Lu, C. Zhu, and Y. Li. 1993. Occurrence of red tides on the coasts of China. In T. Smayda and Y. Shimizu (eds.), *Toxic Phytoplankton Blooms in the Sea*. Elsevier Science Publishers, B.V. Amsterdam, pp. 43-46.
- Radach, G., J. Berg, and E. Hagmeier. 1990. Long-term changes of the annual cycles of meteorological, hydrographic nutrient and phytoplankton time series at Helgoland and at LV Elbe 1 in the German Bight. *Cont. Shelf Res.* 10:305-328.
- Reynolds, C.S., V.L.M. Huszar, C. Kruk, L. Naseill-Flores, and S. Melo. 2002. Toward a functional classification of the freshwater phytoplankton. *J. Plank. Res.* 24:417-428.
- Richardson, K. and B.B. Jørgensen. 1996. Eutrophication: Definition, history and effects. In B.B. Jørgensen and K. Richardson (eds.), *Eutrophication in Coastal Marine Ecosystems. Coastal and Estuarine Studies, Volume 52*. American Geophysical Union, Washington, DC, pp. 1-19.
- Riegman, R. 1995. Nutrient-related selection mechanisms in marine phytoplankton communities and the impact of eutrophication on the planktonic food web. *Water Sci. Technol.* 32(4):63-75.
- Schofield, O., J. Grzyski, W.P. Bissett, G.J. Kirkpatrick, D.F. Millie, M. Moline, and C.S. Roesler. 1999. Optical monitoring and forecasting systems for harmful algal blooms: Possibility or pipe dream? *J. Phycol.* 35:1476-1496.
- Scholin, C.A., R. Marin III, P.E. Miller, G.J. Doucette, C.L. Powell, P. Haydock, J. Howard, and J. Ray. 1999. DNA probes and a receptor-binding assay for detection of *Pseudo-nitzschia* (Bacillariophyceae) species and domoic acid activity in cultured natural samples. *J. Phycol.* 35:1356-1367.
- Seitzinger, S.P., J.A. Harrison, E. Dumont, A.H.W. Beusen, and A.F. Bouwman. 2005a. Sources and delivery of carbon, nitrogen and phosphorous to the coastal zone: An overview of global nutrient export from watersheds (NEWS) models and their application. *Global Biogeochem. Cycles* 19:GB4S09.
- Seitzinger, S.P., H. Hartnett, R. Lauck, M. Mazurek, T. Minegishi, G. Spyres, and R. Styles. 2005b. Molecular level chemical characterization and bioavailability of dissolved organic matter in streamwater using ESI mass spectrometry. *Limnol. Oceanogr.* 50(1):1-12.
- Seitzinger, S.P. and C. Kroeze. 1998. Global distribution of nitrous oxide production and N inputs in freshwater and coastal marine ecosystems. *Global Biogeochem. Cycl.* 12: 93-113.
- Seitzinger, S.P., C. Kroeze, A.F. Bouwman, N. Caraco, F. Dentener, and R.V. Styles. 2002a. Global patterns of dissolved inorganic and particulate nitrogen inputs to coastal systems: Recent conditions and future projections. *Estuaries* 25:640-655.
- Seitzinger, S.P., R.W. Sanders, and R.V. Styles. 2002b. Bioavailability of DON from natural and anthropogenic sources to estuarine plankton. *Limnol. Oceanogr.* 47:353-366.
- Sellner K.G. and S. Fonda-Umani. 1999. Dinoflagellate blooms and mucilage production. In T.C. Malone, A. Malej, L.W. Harding Jr, N. Smolaka, and R.E. Turner (eds.), *Ecosystems at the Land-Sea Margin: Drainage Basin to Coastal Sea*. Coastal Estuarine Studies 55, American Geophysical Union, Washington, DC, pp. 173-206.
- Shapiro, L.P., L. Campbell, and E.M. Haugen. 1989. Immunochemical recognition of phytoplankton species. *Mar. Ecol. Prog. Ser.* 57:219-224.

- Shiah, F-K. and H.W. Ducklow. 1994. Temperature regulation of heterotrophic bacterioplankton abundance, production, and specific growth rate in Chesapeake Bay. *Limnol. Oceanogr.* 39:1243-1258.
- Shumway, S.E and T.L.Cucci. 1987. The effects of the toxic dinoflagellate *Protogonyaulax tamarensis* on the feeding and behaviour of bivalve molluscs. *Aq. Toxicology.* 10:19-27.
- Silva, E.S. 1985. Ecological factors related to *Prorocentrum minimum* blooms in Obidos Lagoon (Portugal). In D.M. Anderson, A. White, and D. Baden, (eds.), *Toxic Dinoflagellates*. Elsevier, NY, pp. 251-256.
- Smayda, T.J., 1989. Primary production and the global epidemic of phytoplankton blooms in the sea: A linkage? In E.M. Cosper, V.M. Bricelj, and E.J. Carpenter, (eds.), *Novel Phytoplankton Blooms*. Coastal and Estuarine Studies No. 35, Springer-Verlag, NY, pp. 449-484.
- Smayda, T.J. 1990. Novel and nuisance phytoplankton blooms in the sea: Evidence for a global epidemic. In E. Granéli, B. Sundström, L. Edler, and D.M. Anderson (eds.), *Toxic Marine Phytoplankton*. Elsevier Science Publishing, New York, pp. 29-40.
- Smayda, T.J. 2005. Eutrophication and phytoplankton. In P. Wassmann and K. Olli (eds.), *Drainage Basin Nutrient Inputs and Eutrophication: An Integrated Approach*. University of Tromsø, Norway, www.ut.ee/~olli/eutr/, pp. 89-98.
- Smayda, T.J. and D.G. Borkman. 2006. Nutrient and plankton gradients in Narragansett Bay. In B. Costa-Pierce, A. Colt, and A. Desbonnet (eds.), *Ecosystem-based Management of a Southern New England Estuary: A Case Study of Narragansett Bay*. Springer, New York . In press.
- Smayda, T.J. and C.S. Reynolds. 2001. Community assembly in marine phytoplankton: Application of recent models to harmful dinoflagellate blooms. *J. Plankton Res.* 23:447-461.
- Smil, V. 2001. *Enriching the Earth: Fritz Haber, Carl Bosch, and the Transformation of World Food*. The MIT Press, Cambridge, MA.
- Springer, J.J., J.M. Burkholder, H.B. Glasgow, P.M. Glibert, and R.E. Reed. 2005. Use of a real-time monitoring network (RTRM) and shipboard sampling to characterize a dinoflagellate bloom in the Neuse Estuary, North Carolina, U.S.A. *Harmful Algae* 4:553-574.
- Steidinger, K.A., G.A. Vargo, P.A. Tester, and C.R. Tomas. 1998. Bloom dynamics and physiology of *Gymnodinium breve* with emphasis on the Gulf of Mexico. In D.M. Anderson, A.D. Cembella, and G.M. Hallegraeff (eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer-Verlag, Berlin, Heidelberg, NATO ASI Series Vol. G 41:133-153.
- Stibor H., O. Vadstein, S. Diehl, A. Glezlichter, T. Hansen, F. Hantzsche, A. Katechalis, K. Loseth, C. Peters, W. Roederer, M. Sandow, L. Sundt-Hansen, and Y Olsen. 2004. Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. *Ecol. Lett.* 7:321-328.
- Stoecker, D.K. 1999. Mixotrophy among dinoflagellates. *J. Eukaryot. Microbiol.* 46:397-401.
- Stonik, I.V., 1995. A potentially toxic dinoflagellate, *Prorocentrum minimum*, in Amurskii Bay of the Sea of Japan. *Russ. J. Mar. Biol.* 20:314-320.
- Stuart, V., S. Sathyendranath, T. Platt, H. Maass, and B.D. Irwin. 1998. Pigments and species composition of natural phytoplankton populations: Effect on the absorption spectra. *J. Plankton Res.* 20:187-217.
- Sullivan, B.K., D. Van Keuren, and M. Clancy. 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. *Hydrobiologia* 451:113-120.
- Taylor, A.H., J.I. Allen, and P.A. Clark. 2002. Extraction of a weak climatic signal by an ecosystem. *Nature* 416:629-632.
- Tett, P., G. Gilpin, H. Svendsen, C.P. Erlnadsson, U. Larsson, S. Kratzer, E. Fouilland, C. Janzen, J.Y. Lee, C. Grenz, A. Newton, J.G. Ferrier, T. Fernandez, and S. Scory. 2003. Eutrophication and some European waters of restricted exchange. *Cont. Shelf Res.* 23:1635-1671.
- Tillmann, U. 2003. Kill and eat your predator: A winning strategy of the planktonic flagellate *Prymnesium parvum*. *Aq. Microb. Ecol.* 32:73-84.
- Tracey, G.A. 1988. Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 "brown tide" in Narragansett Bay, Rhode Island. *Mar. Ecol. Prog. Ser.* 50:73-81.
- Trainer, V., B-T.L. Eberhart, J.C. Wekell, N.G. Adams, L. Hanson, F. Cox, and J. Dowell. 2003. Paralytic shellfish toxins in Puget Sound, Washington. *J. Shellfish Res.* 22:213-223.

- Turner, J.T., A. Ianora, A. Miralto, M. Laabir, and F. Esposito. 2001. Decoupling of copepod grazing rates, fecundity and egg-hatching success on mixed and alternating diatom and dinoflagellate diets. *Mar. Ecol. Prog. Ser.* 220:187-199.
- Turner, J.T. and P.A. Tester. 1997. Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. *Limnol. Oceanogr.* 42:1203-1214.
- Turner, J.T., P.A. Tester, and P.J. Hansen. 1998. Interactions between toxic marine phytoplankton and metazoan and protistan grazers. In D.M. Anderson, A.D. Cembella and G.M. Hallegraeff (eds.), *Physiological Ecology of Harmful Algal Blooms*. NATO ASI Series G: Ecological Sciences, 41:453-474.
- Turner, R.E. and N.N. Rabalais. 1991. Changes in Mississippi River water quality this century and implications for coastal food webs. *BioScience* 41(3):140-147.
- Turner, R.E. and N. Rabalais. 1994. Coastal eutrophication near the Mississippi river delta. *Nature* 368:619-621.
- Turner, J.T., P.A. Tester, and P.J. Hansen. 1998. Interactions between toxic marine phytoplankton and metazoan and protistan grazers. In D.M. Anderson, A.D. Cembella, and G.M. Hallegraeff (eds.), *Physiological Ecology of Harmful Algal Blooms*. NATO ASI Series G: Ecological Sciences, Vol. 41. Springer-Verlag, Berlin, pp. 453-474.
- Tyler, M.A. and H.H. Seliger. 1978. Annual subsurface transport of a red tide dinoflagellate to its bloom area: Water circulation patterns and organism distributions in the Chesapeake Bay. *Limnol. Oceanogr.* 23:227-246.
- Vadstein O., H. Stibor, B. Lippert, K. Loseth, W. Roederer, L. Sundt-Hansen, and Y. Olsen. 2004. Moderate increase in the biomass of omnivorous copepods may ease grazing control of planktonic algae. *Mar. Ecol. Prog. Ser.* 270:199-207.
- Verity, P.G. and V. Smetacek. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.* 130:277-293.
- Vezie, C., J. Rapala, J. Vaitoma, J. Seitsonen, and K. Sivonen. 2002. Effect of nitrogen and phosphorus on growth of toxic and nontoxic *Microcystis* strains and on intracellular microcystin concentrations. *Microbial Ecol.* 43:443-454.
- Vitousek, P.M., J. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger, and G.D. Tilman. 1997. Human alteration of the global nitrogen cycle: Causes and consequences. *Ecol. Appl.* 7:737-750.
- Vrieling E.G., W.H. van de Poll, G. Vriezekolk, and W.W.C. Gieskes. 1997. Immuno-flow cytometric detection of the ichthyotoxic dinoflagellates *Gyrodinium aureolum* and *Gymnodinium nagasakiense*: Independence of physiological state. *J. Sea Res.* 37:91-100.
- Walsh, J.J., B. Penta, D.A. Dieterle, and W.P. Bissett. 2001. Predictive ecological modeling of harmful algal blooms. *Human Ecol. Risk Assess.* 7:1369-1383.
- Wassmann, P. and K. Olli (eds.). 2006. *Drainage Basin Nutrient Inputs and Eutrophication: An Integrated Approach*. University of Tromsø, Norway, www.ut.ee/~olli/eutr/. 325 pp.
- Whitledge, T.E. 1993. The nutrient and hydrographic conditions prevailing in Laguna Madre, Texas before and during a brown tide event. In T.J. Smayda and Y. Shimizu (eds.), *Toxic Phytoplankton Blooms in the Sea*. Elsevier Science Publishers, B.V. Amsterdam, pp. 711-716.
- Wikfors, G.H. 2005. A review and new analysis of trophic interactions between *Prorocentrum minimum* and clams, scallops, and oysters. *Harmful Algae* 4:585-592.
- Wood, A.M. and T. Leatham. 1992. The species concept in phytoplankton ecology. *J. Phycol.* 28:723-729.
- Woods, J. and W. Barkmann. 1993. The plankton multiplier – positive feedback in the greenhouse. *J. Plank. Res.* 15:1053-1074.
- Zhang, J. 1994. Atmospheric wet depositions of nutrient elements: Correlations with harmful biological blooms in the Northwest Pacific coastal zones. *Ambio* 23:464-468.
- Zhang, J., Z.F. Zhang, S.M. Liu, Y. Wu, H. Xiong, and H.T. Chen. 1999. Human impacts on the large world rivers: Would the Changjiang (Yangtze) River be an illustration? *Global Biogeochem. Cycles* 13:1099-1105.
- Zhou, M. 2005. Which is the trigger factor to the outbreak of large scale *Prorocentrum* bloom in the East China Sea? *GEOHAB Open Science Meeting on HABs and Eutrophication*, Baltimore, MD (abstract only).

APPENDIX I: GEOHAB OPEN SCIENCE MEETING ON HABs AND EUTROPHICATION, MARCH 2005

Programme

Monday, March 7, 2005

SESSION 1

TRENDS IN EUTROPHICATION AND HABs

(Session Chair: Patricia M. Glibert)

- 9:15- 9:45 Opening Remarks – Patricia M. Glibert (USA)
9:45 - 10:25 Nitrogen pollution: sources, trends, and effects globally and regionally – Robert Howarth (USA)
10:25-11:00 COFFEE BREAK
11:00-11:30 National and global trends in HABs – Donald Anderson (USA)
11:30-12:00 Multidecadal changes in the diatom: Flagellate ratio and Si:N and Si:P ratios in Narragansett Bay, and influence of Si:N supply ratios on diatom species competition – Ted Smayda (USA) and D. Borkman
12:00-13:30 LUNCH

SESSION 2

PHYSIOLOGY AND ECOLOGY OF HABs WITH RESPECT TO NUTRIENTS

(Session Chairs: Edna Granéli and Cindy Heil)

- 13:30-14:10 The role of nutrient conditions on toxicity, allelopathy, and mixotrophy in HABs – Edna Granéli (Sweden)
14:10-14:30 Nitrogen uptake by the toxigenic diatom *Pseudo-nitzschia australis* – William Cochlan (USA), J. Herndon, N.C. Ladizinsky and R.M. Kudela.
14:30-14:50 Urea-ammonium-nitrate interactions in Thau lagoon (Southern France): Relationships with *Alexandrium catenella* blooms – Yves Collos (France), A. Vaquer, M. Laabir, E. Abadie, T. Laugier, and A. Pastoureaud
14:50-15:15 BREAK
15:15- 15:35 A role for anthropogenically derived nitrogen in the formation of harmful algal blooms along the US west coast – Raphael Kudela (USA), M. Armstrong, W. Cochlan, and J. Herndon
15:35- 15:55 Nitrogen preference of the fish-killing flagellate *Chattonella* cf. *verruculosa* – Carmelo Tomas (USA)
15:55- 16:15 Intraspecific variability in the nutritional ecology of harmful algae – JoAnn Burkholder (USA)
16:15 -16:45 The effects of macro- and micro-nutrient limitation on karlotoxin production by *Karlodinium micrum* strains – Jason Adolf (USA), T. Bachvaroff, G.F. Reidel, and A. R. Place
16:45- 17:05 Effect of N:P supply ratio on biochemical composition and toxicity in dinoflagellate *Alexandrium tamarense* – Ai Murata (Japan), S. C. Y. Leong, Y. Nagashima, and S. Taguchi
17:05-17:30 Open discussion
17:30- 19:30 Poster Session One (see page 68)
(Hosted by the University of Maryland Center for Environmental Science, the Chesapeake Research Consortium, and the Maryland Department of Natural Resources)

Tuesday, March 8, 2005

SESSION 3

THE GEOHAB PROGRAMME AND OTHER INITIATIVES

(Session Chair: Donald Anderson)

- 8:30-8:45 Introduction to the GEOHAB Programme – Grant Pitcher (S. Africa)
8:45-9:05 Introduction to IOC and SCOR – Henrik Enevoldsen (IOC) and Ed Urban (SCOR)
9:05-9:35 NOAA extramural HAB research: Present and future – Quay Dortch (USA), S. Banahan, and M. Suddleson
9:35-9:55 Perspectives of the US Ocean Commission and the Pew Oceans Commission – Donald Boesch (USA)
9:55-10:20 COFFEE BREAK

SESSION 4

COMPARATIVE STUDIES AND INTERNATIONAL PROGRAMMES ON HABs IN EUTROPHIC AREAS

(Session Chairs: Mingjiang Zhou and Lars Edler)

- 10:20-11:00 The Chinese HAB Programme: CEOHAB – Mingjiang Zhou (China)
11:00-11:40 Do the coastal eutrophication and warming cause widespread and persistent *Cochlodinium polykroides* blooms in Korean waters? – HakGyoon Kim (Korea), C-K. Lee, W-A. Lim, S-Y. Kim, and H-G. Jin
11:40-12:20 Influence of monsoons and oceanographic processes on red tides in Hong Kong waters – Kedong Yin (Hong Kong China)
12:20-14:00 LUNCH
14:00-14:40 Harmful algae and eutrophication in the Baltic Sea Area – Lars Edler (Sweden)
14:40-15:00 Oceanographic and environmental assessment of Kuwait's waters in relevance to algal blooms – Faiza Al-Yamani (Kuwait), W.A. Ismail, K.S. Al-Rifaie, and A. Lennox

15:00-15:20	HABs in Western Australia: Expressions of eutrophication in a southern climate – Malcolm Robb (Australia), T. Reitsema, W. Hosja, and A. Begum
15:20-15:45	BREAK
15:45-16:05	An integrated approach to predicting harmful algal blooms: Phytoplankton physiology, nutrient dynamics and their application in an ecosystem model – Paul Armstrong (Australia), P.A. Thompson, C.J.S. Bolch, S.I. Blackburn, J.P. Parslow, M. Herzfeld and K. Wild-Allen
16:05-16:25	Comparative analysis of the relationships between nutrient cycling and phytoplankton community composition in two eutrophied subtropical estuaries: Florida Bay, USA, and Moreton Bay, Australia – Cynthia Heil (USA), P.M. Glibert, J. O’Neil, W.C. Dennison, D. Hollander, J. Greenwood, M. O’Donohue, S. Costanzo, M. Revilla, J. Alexander, A. Hoare, and S. Murasko
16:25-16:45	Linkages between land-based nutrient discharges and harmful macroalgal blooms: Comparative studies on coral reefs of southeast Florida and Jamaica – Brian Lapointe (USA), B. Bedford, P.J. Barile, C. Hanson, and L. Getten
16:45-17:30	Open discussion

Wednesday, March 9, 2005

SESSION 5 MACRONUTRIENT INTERACTIONS WITH OTHER FACTORS CONTROLLING HABs

	(Session Chair: Ted Smayda)
8:30-8:50	How does eutrophication affect the role of grazers in harmful algal bloom dynamics? – Edward Buskey (USA)
8:50-9:10	Freshwater flow and nutrients: effects on top-down control of bloom-forming dinoflagellates? – Diane Stoecker (USA), M.L. Reaugh, A.E. Thessen, D.E. Gustafson, M.R. Roman, and W.C. Boicourt
9:10-9:30	A conceptual model for ecosystem disruptive algal blooms: The interactive roles of eutrophication, algal toxicity, and limitation by nutrients and light – William Sunda (USA) and R. Hardison
9:30- 9:50	Abiotic and biotic factors controlling a nutrient driven dinoflagellate bloom and likely responses to increased eutrophication – R. Wayne Litaker (USA) and P.A. Tester
9:50- 10:20	COFFEE BREAK
10:20-10:40	Brackish stormwater detention ponds as promoters of HABs and eutrophication along the South Carolina coast – Alan Lewitus (USA), M.K. Burke, L. J. Mason, K. N. Bunker, S.R. Drescher, and W.H.J. Strosnider
10:40-11:00	Iron induced development pathway of HABs community and its consequence on mitigation of eutrophication – Jun Sun (China), Y. Feng, and P. Sun.
11:00- 11:20	The synergy of iron, copper and the toxicity of diatoms – Mark Wells (USA), C. G. Trick, W.P. Cochlan, P. Hughes, and N. C. Ladizinsky

SESSION 6 NEW CHALLENGES AND METHODOLOGIES

	(Session Chair: Marc Suddleson)
11:20-11:50	Implementing the coastal module of the Global Ocean Observing System (GOOS): Toward rapid detection and timely predictions of harmful algal blooms – Thomas Malone (USA)
11:50-12:30	New approaches and technologies for observing harmful algal blooms – Marcel Babin (France)
12:30-14:00	LUNCH
SESSION 6	(continued)
	(Session Chair: Marcel Babin)
14:00-14:20	Application of the environmental sample processor (ESP) for remote detection of harmful algae and toxins they produce – Chris Scholin and Greg Doucette (USA)
14:20-14:40	Autonomous nutrient monitoring and water sampling as tools for studying HABs: Progress and prospects- Lou Codispoti (USA), V. Kelly, P. Glibert, and J. Alexander
14:40-15:00	New technologies for monitoring and assessing harmful algal blooms and water quality in Chesapeake Bay, Maryland – Christopher Heyer (USA), T. M.Trice, P. J. Tango, B.Michael, L.Codispoti, V. Kelly
15:00-15:30	BREAK
15:30-15:50	Diagnostic indicators of HAB nutritional physiology – Sonia Dyhrman (USA)
15:50-16:10	New approaches to understanding the role of dissolved organic matter in HAB dynamics – Sybil Seitzinger (USA), P. M. Glibert, J.P. Simjouw, and R. Sipler
16:10-16:40	Open discussion
16:45-18:45	Poster Session Two (see page 69)

Thursday, March 10, 2005

SESSION 7 MODELLING OF NUTRIENTS AND HABS

(Session Chairs: J. Icarus Allen and Kevin Flynn)

- 8:30- 9:10 Eutrophication and HAB models for the NW European continental shelf – J. Icarus Allen (UK), F. Gilbert, J. Holt, M. Holt, R. Proctor, and J. Siddorn
- 9:10- 9:50 Garbage in, Garbage out? Problems in experimental design and modelling of HAB ecology – Kevin Flynn (Wales)
- 9:50- 10:10 COFFEE BREAK
- 10:10- 10:40 Assessing the validation of a preliminary *Karlodinium micrum* nowcast model system in Chesapeake Bay and its tributaries: a framework for HAB nowcasts and forecasts – Peter Tango (USA), C.W. Brown, T.F. Gross, D.L. Ramers, R.R. Hood, and B.D. Michael
- 10:40- 11:00 Modelling *Pfiesteria* life cycle attributes and population dynamics – Raleigh Hood (USA), X. Zhang and J.T. Anderson
- 11:00-11:30 Open discussion of modelling

SESSION 8 GEOHAB IMPLEMENTATION

(Session Chair: Grant Pitcher)

- 11:30-11:45 Charge to working groups – Patricia Glibert and Grant Pitcher
- 11:45-12:45 First break-out groups meet
- 12:45-14:15 LUNCH
- 14:15-14:45 Reports of first break-out groups
- 14:45-16:00 Second break-out groups meet
- 16:00-16:15 BREAK
- 16:15-16:45 Reports of second break-out groups
- 16:45 Final wrap-up
- 17:00 Adjourn

Monday, March 7, 2005

POSTER SESSION ONE

1. Phytoplankton indices of eutrophication in UK coastal waters – R.J. Gowen, D.K. Mills, M. Best, M.J. Devlin, M. Edwards, J. Foden, S.J. Painting, R. Park, C. Reid, and P. Tett
2. Eutrophication and harmful algal blooms in the Swan River estuary, Western Australia – J. John
3. The research of the eutrophication status of East China Sea – X.-L. Wang, X.-Y. Shi, and C.-S. Zhang
4. Coastal nutrification following the passage of Hurricane Charley and its relation to a subsequent *Karenia brevis* bloom on the West Florida Shelf – M.B. Neely, C.A. Heil, and G.A. Vargo
5. The effect of nutrient concentration at different growth stages on hemolytic ability of three clones of the ichthyotoxic flagellate *Prymnesium parvum* from blooms in the United States – M. Clouse and C. Tomas
6. Strain Variation in *Karlodinium micrum* toxin production – T. Bachvaroff, J.E. Adolf, and A.R. Place
7. Fatty acids and growth in the heterotrophic dinoflagellates *Pfiesteria* Spp. and PLOs – L.W. Haas, V. Foster, L. Ott, W.K. Vogelbein, K.S. Reece, J.D. Shields, and P. Mason
8. The influence of dissolved copper on the production of domoic acid by toxigenic species of *Pseudo-nitzschia* in Monterey Bay, California – N.C. Ladizinsky, G.J. Smith, K.H. Coale, and W.P. Cochlan
9. Toxin levels in the benthic cyanobacterium *Lyngbya majuscula* in relation to tissue nutrient content and bloom intensity – J.M. O'Neil, S. Albert, N. Osborne, and G. Shaw
10. The potential role of increased nutrient inputs to higher incidences of ciguatera in Hawaii – M.L. Parsons
11. Nutrient regulation of toxin production: Comparison of hemolytic activity of *Amphidinium carterae* and *Amphidinium klebsii* – L.A. Zimmermann and C.R. Tomas
12. Nitrate uptake kinetics of the toxic dinoflagellate *Alexandrium tamarense* in response to nitrate supply mode – S.C.Y. Leong, M. Maekawa, and S. Taguchi
13. Bioavailability of dissolved organic phosphorus compounds to typical harmful dinoflagellate *Prorocentrum donghaiense* Lu – B. Huang, L. Ou, H. Hong, H. Luo, and D. Wang
14. Dissolved organic matter concentration and characteristics during *Aureococcus anophagefferens* blooms in 2002 and 2003: A comparison – J.-P. Simjouw, E.C. Minor, and M.R. Mulholland
15. The role of natural DOM sources in *Prorocentrum minimum* growth dynamics – R. Sipler, S.P. Seitzinger, and P.M. Glibert
16. Urea utilisation by harmful algal species in the Chesapeake Bay, Maryland, USA – C.M. Solomon and P. M. Glibert
17. A comparison of nutrient effects on the growth of *Chattonella subsalsa* and *Heterosigma akashiwo* (Raphidophyceae) isolated from the Inland Bays, Delaware (U.S.A) – Y. Zhang and D.A. Hutchins
18. The assessment of brown tide blooms caused by the alga, *Aureococcus anophagefferens* and related environmental factors in coastal waters of New Jersey (2000-2002) – M. Downes Gastrich, R. Lathrop, S. Haag, M.P. Weinstein, M. Danko, D.A. Caron, and R. Schaffner
19. Harmful algae in Suffolk County (N.Y., USA) estuaries: A 30 year history – R. Nuzzi
20. Organic nutrients and brown tide in Maryland Coastal Bays – C. Wazniak

Wednesday, March 9, 2005
POSTER SESSION TWO

1. Top down control and demise of a nutrient driven dinoflagellate bloom – P.A. Tester and R.W. Litaker
2. Modelling the contribution of prey deselection in the formation of harmful algal blooms – A. Mitra and K.J. Flynn
3. Raphidophyte systematics and rapid identification: Sequence analyses and real time PCR Assays – H.A. Bowers, C. Tomas, J.W. Kempton, S. Goto, A.J. Lewitus, and D.W. Oldach.
4. Geographic distribution of *Pfesteria* spp. and environmental factors – H. Zhang and S. Lin
5. Improved accuracy of quantitative real-time PCR of HAB species in environmental water samples using an exogenous DNA internal standard – K.J. Coyne, S.M. Handy, E. Demir, K.J. Portune, Y. Zhang, M.A. Doblin, D.A. Hutchins, and S.C. Cary
6. Harmful phytoplankton indicator species applied to eutrophication assessments of Scottish coastal waters supporting aquaculture – M.J. Gubbins, P.J. Sammes, and I.M. Davies.
7. Monitoring toxic phytoplankton and shellfish in support of eutrophication assessments for Scottish coastal waters – M.J. Gubbins, E.A. Smith, M. Grieve, and E. Bresnan
8. History of HAB monitoring in Maryland tidewaters: Monitoring, response, nowcasting and forecasting – P.J. Tango, B. Michael, D. Goshorn, R. Magnien, C. Heyer, T.M. Trice, W. Butler, C. Wazniak, R. Karrh, S. Bowen, R. Lacouture, H. Bowers, D. Oldach, C. Luckett, C. Poukish, D. Matuzsak, J. Ryan, H. Lynch, C. Brown, R. Hood, T. Gross, and D. Ramers
9. An autonomous urea monitor for studying HABs – V. Kelly, L.A. Codispoti, P. Glibert, and J. Alexander
10. Applications of an in situ water quality monitoring platform (MARVIN) for HAB research: A comparison of data collected in the St. Johns and Caloosahatchee River systems in Florida – J. Rueter, M.B. Neely, B. Bendis, R. Pigg, K. Steidinger, and C. Heil
11. Relationships between nitrogen loading and concentrations of nitrogen and chlorophyll in coastal embayments – E.H. Dettmann, L.B. Mason, A. Erhunse, and K.M. Henry
12. Modeled *Karenia brevis* bloom initiation and subsequent accumulation in the vicinity of a coastal nutrient front – G.S. Janowitz and D. Kamykowski
13. Ecosystem modelling of the NW European shelf seas towards the forecasting of harmful algal blooms – J.R. Siddorn, J.I. Allen, and M. Holt
14. Environmental and behavioural influences on *Karenia brevis*' nitrate uptake: A bloom initiation scenario – G. Sinclair, D. Kamykowski, E. Milligan, and B. Schaeffer
15. A behaving drifter for simulating transport of mobile HAB organisms in nature – T.G. Wolcott, D. Kamykowski, and G. Janowitz
16. Potential roles of *Prorocentrum minimum* to Chesapeake Bay dissolved oxygen and oyster dynamics – E. Brownlee, S. Sellner, and K.G. Sellner
17. Volunteer HAB monitoring provides a "First Watch" for resource managers and researchers in the Delaware Inland Bays, USA – E. Whereat and M. Farestad
18. Problems with ballast water exchange as a means of controlling movement of harmful algal species throughout the world – C.E. Orano-Dawson, R. Dawson, and D.A. Wright

APPENDIX II: *GEOHAB OPEN SCIENCE MEETING ON HABs AND EUTROPHICATION*, MARCH 2005

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APPENDIX III: GLOBAL ECOLOGY AND OCEANOGRAPHY OF HARMFUL ALGAL BLOOMS

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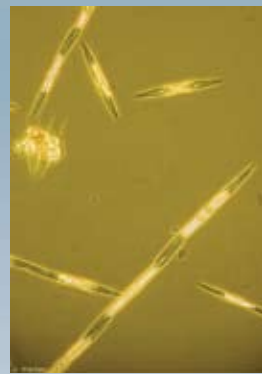
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