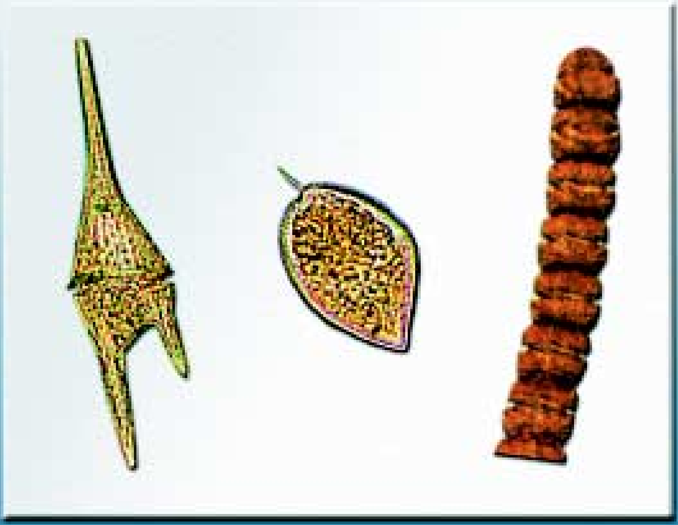
GEOHAB

Global Ecology and Oceanography of Harmful Algal Blooms



Science Plan

SCOR

SCIENTIFIC COMMITTEE ON OCEANIC RESEARCH

INTERGOVERNMENTAL OCEANOGRAPHIC COMMISSION
UNESCO

GEOHAB

Global Ecology and Oceanography of Harmful Algal Blooms

Science Plan

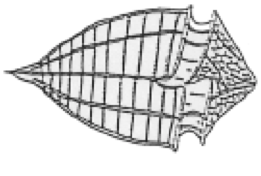
An International Programme Sponsored by the
Scientific Committee on Oceanic Research (SCOR) and the
Intergovernmental Oceanographic Commission (UNESCO)

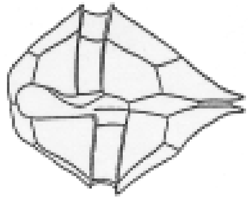
Edited by: Patricia M. Glibert and Grant Pitcher

With the assistance of: Allan Cembella, John Cullen, and Yasuwo Fukuyo

Based on contributions by the GEOHAB Scientific Steering Committee:
Patrick Gentien, Yasuwo Fukuyo, Donald M. Anderson, Susan Blackburn, Allan Cembella, John Cullen, Malte Elbrächter, Henrik Enevoldsen, Marta Estrada, Wolfgang Fennel, Patricia M. Glibert, Elizabeth Gross, Kaisa Kononen, Nestor Lagos, Thomas Osborn, Grant Pitcher, Arturo P. Sierra-Beltrán, Steve Thorpe, Edward R. Urban, Jr., Jing Zhang, and Adriana Zingone

April 2001





This report may be cited as: GEOHAB, 2001. *Global Ecology and Oceanography of Harmful Algal Blooms, Science Plan*. P. Glibert and G. Pitcher (eds). SCOR and IOC, Baltimore and Paris. 87 pp.

Science Plan

This document describes a Science Plan reviewed and approved by the Scientific Commission on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of the U.N. Education, Scientific, and Cultural Organisation (UNESCO)

This document is GEOHAB Report #1. Copies may be obtained from:

Edward R. Urban, Jr.
Executive Director, SCOR
Department of Earth and Planetary Sciences
The Johns Hopkins University
Baltimore, MD 21218 U.S.A.
Tel: +1-410-516-4070
Fax: +1-410-516-4019
E-mail: scor@jhu.edu

Henrik Enevoldsen
Project Coordinator
IOC Science and Communication Centre on Harmful Algae
Botanical Institute, University of Copenhagen
Øster Farimagsgade 2D
DK-1353 Copenhagen K, Denmark
Tel: +45 33 13 44 46
Fax: +45 33 13 44 47
E-mail: hab@bot.ku.dk

This report is also available on the web at:
http://www.jhu.edu/~scor
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Cover photos. Examples of causative organisms of harmful algal blooms, their impacts, and new approaches that are required to understand their population dynamics. Upper left hand panel - vegetative cells of *Ceratium furca*, *Prorocentrum micans*, and *Gymnodinium catenatum*. Upper right hand photo - surface accumulation of *Trichodesmium* off the Great Barrier Reef, Australia. Lower left hand panel - fish kill caused by *P. micans* and *C. furca* on the west coast of South Africa. Lower right hand panel - remote observing system for continuous monitoring. Photos by Y. Fukuyo, P. Glibert, and W. Boicourt.

Back cover. Representative HAB species (upper photos), and mass mortality event by a red tide of *Cochlodinium polykrikoides*. Photos by Y. Fukuyo.

Published by SCOR and IOC, Baltimore and Paris, 2001.

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PREFACE

The last two decades have been marked by a new appreciation of the serious impacts of the marine phenomena we now call harmful algal blooms (HABs). These occurrences of toxic or harmful microalgae represent a significant and seemingly expanding threat to human health, fishery resources, and marine ecosystems throughout the world. Many causes, both natural and anthropogenic, may be responsible for this dramatic expansion in HAB effects; it is likely that human activities are making the problems worse through increased nutrient inputs to coastal areas, transportation and discharge of ballast water, and other factors.

Given that HAB problems may be expanding and that they have many causes, both natural and human assisted, what can be done about them in a practical sense? What information is needed for efficient management of affected marine ecosystems that simultaneously protects public and ecosystem health, encourages and supports aquaculture development, and contributes to policy decisions on coastal zone issues such as wastewater disposal, aquaculture development, and dredging? What research and monitoring should be conducted to determine the extent to which human activities are making the HAB problem worse and what steps should be taken to minimize further impacts? The answers to these important practical questions, of course, require scientific investigation. Single investigators and some national programmes are now conducting research and focused monitoring to answer such questions. To date, however, international co-ordination of individual and national research efforts has largely been absent.

The clear need for a co-ordinated international scientific programme on the ecology and oceanography of HABs prompted the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) to form a partnership to develop such a programme. The first step in this process was an international workshop sponsored by SCOR and IOC, which took place in Havreholm, Denmark on October 13-17, 1998. Thirty-seven scientists from twenty countries participated in the workshop, chaired by Professor John Cullen. That workshop report is available on the SCOR Website at www.jhu.edu/~scor.

As a result of the Havreholm meeting and report, and emerging activities on harmful algal blooms in a number of nations, SCOR and IOC formed a Scientific Steering Committee (SSC) for a new programme on the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB). The GEOHAB SSC worked diligently in 2000 to produce the GEOHAB Science Plan presented here. The plan was reviewed and approved by SCOR at SCOR’s General Meeting in October 2000.

With publication of this Science Plan, the GEOHAB SSC begins a new phase of its activity. This document will be used as the basis for a detailed plan for carrying out the proposed science over the next decade. As the SSC develops the GEOHAB Implementation Plan, comments from the broader international community of scientists who study HABs will be solicited. It will also be crucial to involve scientists who study other oceanographic factors that affect HABs, such as physical, chemical, and biological conditions in ocean areas where blooms occur. An important aspect of the Implementation Plan will be to describe how national programmes can co-ordinate to meet GEOHAB objectives and to plan for multinational research activities that will transcend national efforts and make comparative studies possible.

We are grateful for the support for this project provided by the Maj and Tor Nessling Foundation (Finland), the U.S. National Aeronautics and Space Administration, the U.S. National Oceanic and Atmospheric Administration, and the U.S. National Science Foundation*. We wish to thank the GEOHAB SSC for their hard work and diligence in completing this Science Plan so quickly. We particularly appreciate guidance from Patrick Gentien (SSC Chair) and Yasuwo Fukuyo (SSC Vice-Chair) for guiding the process, and Patricia Glibert for co-ordinating the formatting and printing of the Science Plan. SSC members Patricia Glibert, Grant Pitcher, Allan Cembella, John Cullen, and Yasuwo Fukuyo formed an editorial team that met several times to refine the report. Mark Trice and Jane Hawkey at the Horn Point Laboratory, University of Maryland Center for Environmental Science, and A.P. van Dalsen at Marine and Coastal Management in Cape Town, South Africa, helped the SSC by assisting with graphics and layout of the Science Plan, and their efforts are greatly appreciated. Final thanks are due to Elizabeth Gross, former Executive Director of SCOR for her many efforts on behalf of GEOHAB and the HAB community.

On behalf of the sponsors:

Edward R. Urban Jr.

Henrik Enevoldsen, IOC

Edward R. Urban, Jr., SCOR

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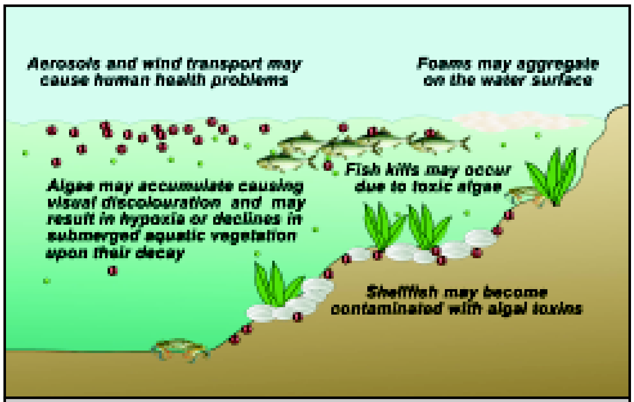
* This document is based on work partially supported by the U.S. National Science Foundation under Grant No. 0003700. Any opinions, findings, and conclusions or recommendations expressed in this document are those of the authors and do not necessarily reflect the views of the U.S. National Science Foundation.

EXECUTIVE SUMMARY

Proliferations of algae in marine or brackish waters can cause massive fish kills, contaminate seafood with toxins, and alter ecosystems in ways that humans perceive as harmful. The scientific community refers to these events with a generic term, "Harmful Algal Blooms" (HABs), while recognising that some species cause toxic effects even at low cell densities, and that not all HAB species are technically "algae". A broad classification of HAB species distinguishes two groups: the toxin producers, which can contaminate seafood or kill fish, and the high-biomass producers, which can cause anoxia and indiscriminate mortalities of marine life after reaching dense concentrations. Some HAB species have characteristics of both groups.



The impacts of HABs are numerous, and the effects may be felt by many components of the ecosystem.

Although HABs were present long before human activities began to impact coastal ecosystems, a survey of affected regions and of economic losses and human poisonings throughout the world demonstrates clearly that there has been a dramatic increase in the impacts of HABs over the last few decades. The HAB problem is now widespread and serious. Harmful effects attributed to HABs extend well beyond impacts on human health and direct economic losses. When HABs contaminate or destroy coastal resources, the livelihoods of local residents are threatened and the sustenance of human populations is compromised. Clearly, there is a pressing need to develop effective responses to the threat of HABs through management and mitigation. This requires knowledge of the ecological and oceanographic factors that control the distributions and population dynamics of HAB species.

A great deal is known about harmful algae and HABs, but our ability to describe the factors controlling the dynamics of individual species is limited by critical gaps in understanding the physiological, behavioural, and morphological characteristics of algae (including HAB species), and how these interact with environmental conditions to promote the selection for one species over another.

Successful research to date shows that the key to explaining HAB phenomena is to identify and quantify special adaptations of HAB species that lead to their selection in particular hydrodynamic and ecological conditions.

Thus, **the central challenge before us is to understand the critical features and mechanisms underlying the population dynamics of HAB species in a variety of oceanographic regimes**. This understanding can be used as a basis for monitoring and predicting the occurrence, movement, toxicity, and environmental effects of HABs. In turn, monitoring and prediction are essential for management and mitigation of HABs.

Because HAB species are found in marine and brackish-water ecosystems worldwide, the central research problem can be addressed comprehensively and effectively only through international, interdisciplinary, and comparative research on the dynamics of HABs. Progress depends on advancement

Effects of HABs include the development of high biomass “red tides”, as shown by this *Noctiluca* bloom in New South Wales, Australia.

through targeted studies and technological innovation in biology, ecology, chemical and physical oceanography, modelling, and ocean observation.

The SCOR-IOC Programme on the **Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB)** was thus established to address the need for broad-based advancement in the understanding of HABs. The scientific goal of GEOHAB will be approached by addressing research questions such as:

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 observation and modelling systems.

1. What are the factors that determine the changing distribution of HAB species, their genetic variability, and the biodiversity of associated communities?

2. To what extent does increased eutrophication influence the occurrences of HABs and their harmful effects?

3. What are the unique adaptations of HAB species and how do they help to explain their proliferation or harmful effects?

4. To what extent do HAB species, their population dynamics, and community interactions respond similarly under comparable ecosystem types?

The following Programme Elements have been identified as the key areas of research for GEOHAB studies.

Programme Element 1: Biodiversity and Biogeography

Knowledge of the present geographic distribution of HAB species and of the long-term fluctuations in species composition is essential in explaining novel and recurrent HAB events and the extent to which HABs are spreading globally.

The overall objective of this Programme Element is to determine the relationships among distributions of HAB species, biodiversity, and environmental change.

Programme Element 2: Nutrients and Eutrophication

Concurrent with escalating human activities in coastal ecosystems, the environmental and economic impacts of HABs have increased in recent decades. The relationships between nutrient loading and increased frequency of both algal blooms and toxic algae are not well known.

The overall objective of this Programme Element is to determine the significance of eutrophication and nutrient transformation pathways to HAB population dynamics.

Programme Element 3: Adaptive Strategies

Each species has adaptive characteristics that define its niche, that is, the suite of ecological factors that determine its distribution and activities. By characterising the adaptations of different HAB species, it should be possible to describe patterns of species abundance as functions of hydrographic processes, nutrient distributions, and community interactions.

The overall objective of this Programme Element is to define the particular characteristics and adaptations of HAB species that determine when and where they occur and produce harmful effects.

Programme Element 4: Comparative Ecosystems

Critical processes controlling HABs can be identified by comparing the dynamics of harmful algae and related species across ecosystems, grouped according to their hydrographic and chemical regimes and their biology.

The overall objective of this Programme Element is to identify mechanisms underlying HAB population and community dynamics across ecosystem types through comparative studies.

Programme Element 5: Observation, Modelling, and Prediction

Fundamental research on HABs must be guided by, and validated with, observations of phytoplankton dynamics in nature. Modelling supports specific tasks and synthesises findings, leading to predictions of HABs. Effective detection and prediction of HABs are needed to manage and mitigate their effects.

The overall objective of this Programme Element is to improve the detection and prediction of HABs by developing capabilities in observation and modelling.

GEOHAB Approach

GEOHAB will foster scientific advancement in the understanding of HABs by encouraging and co-ordinating fundamental scientific research – multi-faceted, international, and interdisciplinary, maintaining an ecological and oceanographic context. International, co-operative research on comparative ecosystems will be encouraged, as will targeted studies on organisms, processes, and methods, including new observational technologies, that are needed to understand and resolve influences of environmental factors (both natural and anthropogenic) on distributions and trends in HABs. GEOHAB is not a funding programme, but rather a mechanism to facilitate those activities that require co-operation among nations, such as the development of methodologies, and the co-sponsorship of cruise or research activities.

GEOHAB Benefits

Many benefits will accrue from GEOHAB. Better methodologies will be developed for predicting HABs, their toxicity, and other deleterious effects. A better understanding of the physical and environmental mechanisms underlying a diverse array of HABs will be developed. GEOHAB projects will also contribute to improving global observation systems that are required to resolve influences of environmental factors (anthropogenic and climate-related) on distributions and trends in HABs. Strong links between GEOHAB and other international efforts, such as the Global Ocean Observing System (GOOS) will therefore be forged. Through additional links to national and international agencies responsible for protecting coastal resources and public health, the knowledge gained from GEOHAB will be used to develop capabilities for more effective management and mitigation of HAB problems.

INTRODUCTION: The Global Problem of Harmful Algal Blooms

The Nature of HABs

Marine planktonic algae form the basis of the marine food chain and, owing to their sheer number and the huge size of the world ocean, they are responsible for the bulk of global primary production. When oceanographic conditions are suitable, they show significant population increases known as blooms. Sometimes proliferations of these microalgae cause fish kills, contaminate seafood with toxins, cause serious human health problems, or alter ecosystems in other ways that humans perceive as harmful.

Public concern over HAB events is growing, as evidenced by headlines such as these that have appeared in newspapers throughout the world.

The scientific community refers to these events with the generic term "Harmful Algal Blooms" (HABs); sometimes they are popularly called "red tides", but this is a misnomer. The term "Harmful Algal Bloom" is not at all precise, and "algae" and "phytoplankton" are colloquial terms. A wide range of organisms is involved, including dinoflagellates, other flagellates, cyanobacteria, diatoms, and other phytoplankton. Not all harmful algal events involve the development of significant accumulations of biomass. Many HAB species are harmful at very low densities. HABs include events caused by the proliferation of benthic microalgae that produce toxins transferred through the food chain.

A broad classification of HABs distinguishes two major groups of causative organisms: those that produce toxins, which can contaminate seafood or kill fish even when their cell density is low, and those that do not produce toxins, but which cause other deleterious impacts, e.g. the consumption of oxygen as blooms decay, the production of scums, or the reduction of habitat for fish or shellfish.

As with all phytoplankton blooms, the proliferation of harmful algal species results from a combination of physical, chemical, and biological mechanisms and interactions, many of which remain poorly understood. Although HABs are often linked to the increased input of nutrients to coastal ecosystems as a consequence of human activities, many harmful events occur in areas where human activities or pollution are not considered to be contributing factors.

HABs have been linked to numerous fish kill events. In this 1994 fish kill in St. Helena Bay on the west coast of South Africa, the HAB species *Prorocentrum micans* and *Ceratium furca* were the causative organisms. Low oxygen and the subsequent generation of hydrogen sulfide were responsible for the mortality.

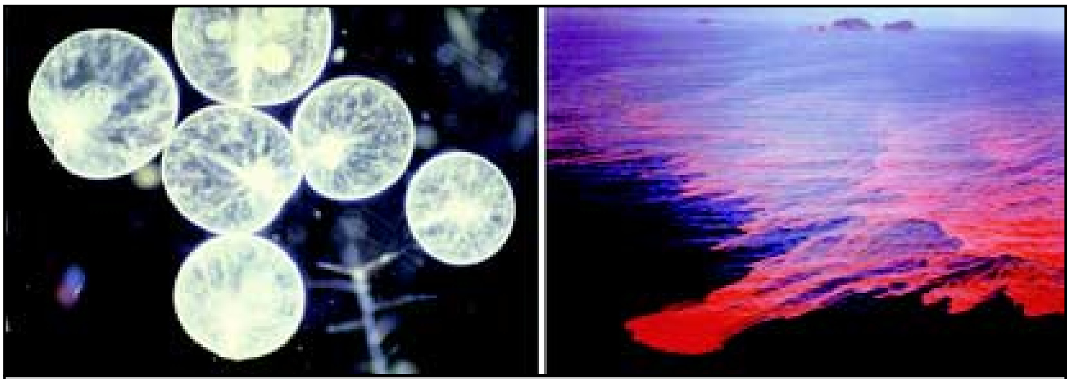
Consequences of HABs

Toxic and harmful blooms cause negative impacts and economic losses in many parts of the world. The consequences and mechanisms of impact of harmful blooms vary depending on the species involved. Broadly speaking, there are four categories of deleterious effects, including risks to human health, loss of natural or cultured seafood resources, impairment of tourism and recreational activities, and damages to non-commercial marine resources and wildlife (Table 1). Each species or event exerts predominantly one type of impact, but many blooms have negative consequences in more than one category.

While specific economic losses can be estimated from damage to fisheries or aquaculture, the total economic impact of HABs is not easily assessed owing to the range of sectors of society impacted. Apart from direct economic losses associated with human intoxications, fish kills, loss of market share, and declines in tourism, there are other serious human costs associated with the collapse of fishing communities, as well as cascading economic effects that are virtually incalculable. Furthermore, data on losses by the seafood industry are not always released to the public and in many cases losses are never well quantified. When HABs contaminate or destroy coastal resources, the functioning of ecosystems may be impaired, and the livelihood and food supply of local communities threatened.

Human Health Issues

Of major concern are the marine and brackish-water HAB species that cause public health impacts due to the production of toxins. The most toxic species are recorded among dinoflagellates, such as *Pyrodinium bahamense* var. *compressum* and several species of the genus *Alexandrium*, which can have dramatic effects at barely detectable concentrations (10^2-10^3 cells l^{-1}). A number of diatoms and cyanobacteria also produce neurotoxins that can endanger human health. People can be poisoned when they consume fish and shellfish that have accumulated phytoplankton toxins filtered from the water (Shumway et al. 1995). Toxicity to humans is also caused by the consumption of gastropods and crabs, as well as of certain fish species that have accumulated algal toxins via the food chain (Lewis et al. 1995). Examples of toxic syndromes caused by HABs include ciguatera fish poisoning, and paralytic, diarrhetic, neurotoxic, azaspiracid and amnesic shellfish poisoning (PSP, DSP, NSP, AZP, and ASP) associated mostly with shellfish consumption. Of additional concern are the respiratory problems linked to the onshore transport of toxins in aerosols under particular wind and wave conditions (Baden 1983). Allergy-like reactions in humans, such as skin irritations, have also been reported in some coastal areas as a result of cyanobacterial blooms (Carmichael 1997).

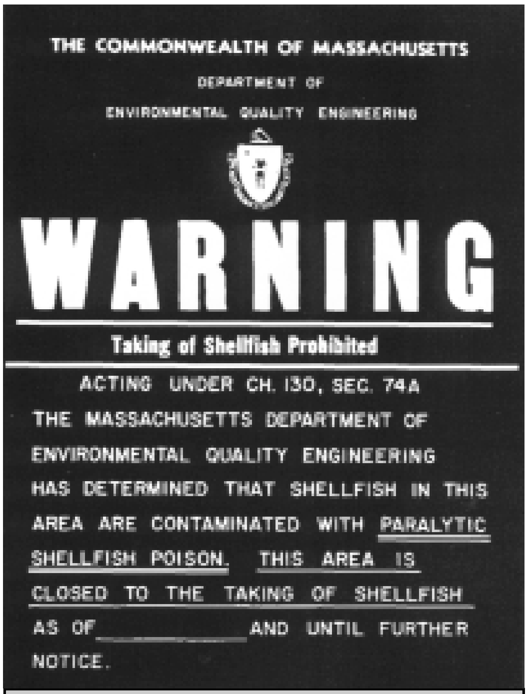


Red tides, causing visible water discolouration such as those produced by *Noctiluca* blooms, may be noxious because of unpleasant odours and anoxic effects.

Table 1. Some deleterious effects caused by harmful algae in coastal and brackish waters (modified from Zingone and Enevoldsen 2000). Note that a single event may have several negative consequences.

EFFECT	**EXAMPLES OF CAUSATIVE ORGANISMS**	
Human health		
Paralytic shellfish poisoning (PSP)	Dinoflagellates	*Alexandrium* spp., *Pyrodinium bahamense* var. *compressum*, *Gymnodinium catenatum*
	Cyanobacteria	*Anabaena circinalis*
Diarrhetic shellfish poisoning (DSP)	Dinoflagellates	*Dinophysis* spp., *Prorocentrum* spp.
Neurotoxic shellfish poisoning (NSP)	Dinoflagellates	*Gymnodinium breve*
Amnesic shellfish poisoning (ASP)	Diatoms	*Pseudo-nitzschia* spp., *Nitzschia navis-varingica*
Azaspiracid shellfish poisoning (AZP)	unknown	unknown
Ciguatera fish poisoning (CFP)	Dinoflagellates	*Gambierdiscus toxicus*
Respiratory problems and skin irritation, neurological effects	Dinoflagellates	*Gymnodinium breve, Pfiesteria piscicida*
	Cyanobacteria	*Nodularia spumigena*
Hepatotoxicity	Cyanobacteria	*Microcystis aeruginosa, Nodularia spumigena*
Natural and cultured marine resources		
Haemolytic, hepatotoxic, osmoregulatory effects, and other unspecified toxicity	Dinoflagellates	*Gymnodinium* spp., *Cochlodinium polykrikoides, Pfiesteria piscicida, Gonyaulax* spp.
	Raphidophytes	*Heterosigma akashiwo*, *Chattonella* spp., *Fibrocapsa japonica*
	Prymnesiophytes	*Chrysochromulina* spp. *Phaeocystis pouchetii, Prymnesium* spp.
	Cyanobacteria	*Microcystis aeruginosa, Nodularia* spp.
Negative effects on feeding behaviour	Pelagophytes	*Aureococcus anophagefferens*
Hypoxia, anoxia	Dinoflagellates	*Prorocentrum micans, Ceratium furca*
Mechanical damage	Diatoms	*Chaetoceros* spp.
Gill clogging and necrosis	Prymnesiophytes	*Phaeocystis* spp.
Tourism and recreational activities		
Production of foam, mucilage, discolouration, repellent odour	Dinoflagellates	*Noctiluca scintillans, Prorocentrum* spp.
	Prymnesiophytes	*Phaeocystis* spp.
	Diatoms	*Cylindrotheca closterium*
	Cyanobacteria	*Nodularia spumigena, Aphanizomenon flos-aquae, Microcystis aeruginosa, Lyngbya* spp.
Marine ecosystem impacts		
Hypoxia, anoxia	Dinoflagellates	*Noctiluca scintillans, Heterocapsa triquetra*
	Diatoms	*Skeletonema costatum*
	Prymnesiophytes	*Phaeocystis* spp.
Negative effects on feeding behaviour	Pelagophytes	*Aureococcus anophagefferens, Aureoumbra lagunensis*
Reduction of water clarity	Dinoflagellates	*Prorocentrum minimum*
Toxicity to marine wild fauna	Dinoflagellates	*Gymnodinium breve, Alexandrium* spp.
	Diatoms	*Pseudo-nitzschia australis*

There are ongoing efforts to revise the nomenclature of many HAB species, including recent changes to the taxonomy of some unarmoured dinoflagellates (Daugbjerg et al. 2000). For consistency, we have retained the most commonly used and widely accepted names at the time this document was prepared.



THE COMMONWEALTH OF MASSACHUSETTS
DEPARTMENT OF
ENVIRONMENTAL QUALITY ENGINEERING

WARNING

Taking of Shellfish Prohibited

ACTING UNDER CH. 130, SEC. 74A
THE MASSACHUSETTS DEPARTMENT OF
ENVIRONMENTAL QUALITY ENGINEERING
HAS DETERMINED THAT SHELLFISH IN THIS
AREA ARE CONTAMINATED WITH PARALYTIC
SHELLFISH POISON. THIS AREA IS
CLOSED TO THE TAKING OF SHELLFISH
AS OF ____________ AND UNTIL FURTHER
NOTICE.

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

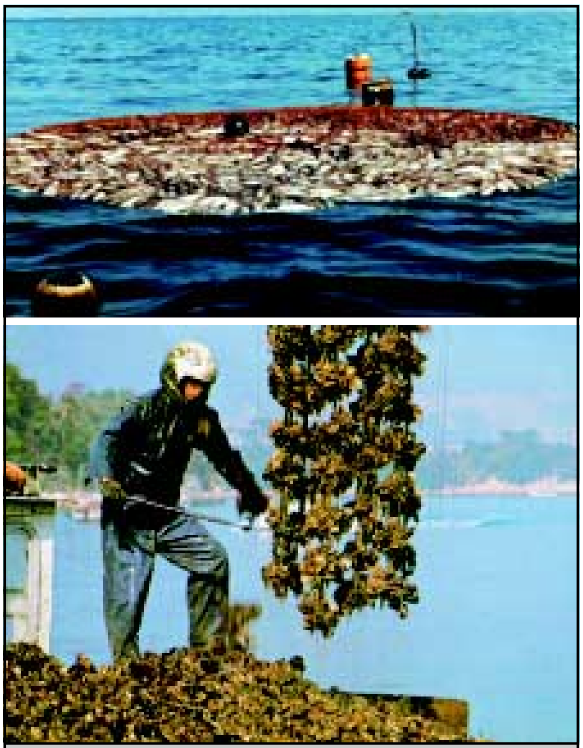
The list of toxic algal species and related syndromes has increased in recent years as have human activities within the coastal zone. Intensive monitoring operations have been set in place in many countries of the world to protect human health; however, many areas are presently not adequately controlled. About 2000 cases of human poisoning have been reported worldwide, and fatal events are estimated to exceed several hundred cases. The number of actual cases is surely underestimated owing to incorrect diagnoses, especially in isolated locations and when gastro-intestinal symptoms are involved. In addition to their direct impact on human health, toxic algae exert a negative effect on the exploitation of marine resources that are contaminated, causing incalculable economic damage to the seafood industry. As an example, in 1917, the harvest of wild shellfish in Alaska produced 5 million pounds of product. Today, this industry is virtually non-existent as a consequence of persistent contamination by PSP (Neve and Reichardt 1984).

Natural and Cultured Marine Resources

While toxic algae indirectly impinge on use of marine resources, other HAB events can directly affect wild and cultivated fish and invertebrates that are valuable seafood. This generally occurs through the production of specific toxins, but damages due to mechanical clogging, lesions of the gills, and anoxia are also well documented.

Both natural fish stocks and farmed fish stocks have experienced massive mortalities (Rensel 1995), which are caused by ichthyotoxic species such as the raphidophytes *Heterosigma akashiwo* and *Chattonella* spp., a number of dinoflagellates, and some prasinophytes. A bloom of *Chrysochromulina polylepis* in May-June 1988 in the Kattegat and Skagerrak area (North Sea) caused the death of 900 hundred tons of fish, including cod, salmon, and trout. *Heterocapsa circularisquama* has caused massive kills of cultured shellfish since 1988 in Japan. In summer 1997, anoxic conditions that accompanied bloom decay of non-toxic dinoflagellates caused the stranding of 2000 tons of rock lobster at Elands Bay (South Africa), with an estimated loss of 50 million U.S. dollars. This was the worst of a long-term series of anoxic episodes that are recurrent in the area (Pitcher and Cockcroft 1998). Brown tides produced by *Aureococcus anophagefferens* in bays of the midwestern Atlantic coast of the U.S.A. led to mortalities, recruitment failure, and growth inhibition of commercially important, suspension-feeding bivalves, including blue mussels and bay scallops (Bricelj and Lonsdale 1997).

In Japan and many other countries where aquaculture operations are in place, noxious blooms of dinoflagellates and raphidophytes kill finfish and shellfish, resulting in losses of millions of U.S. dollars per year. As the demand for farmed species has increased, it is likely that the economic impact of HAB events on the aquaculture industry will continue to grow.



Finfish and shellfish mortality in aquaculture due to HABs results in large economic losses as well as loss of product for consumption.

Tourism and Recreational Activities

Blooms of algae may have significant negative effects on tourism and on the recreational uses of coastal areas. Tourism and recreation depend on relatively high water quality, free from visible scums or mats, noxious smells, or skin irritants. Many coastal areas worldwide are affected by such blooms, with a range of visual and human effects. For example, discoloured water and mucilage, caused by a variety of non-toxic species, are recurrent on the Mediterranean coast and often coincident with the tourist season, while in the Baltic Sea, massive blooms of cyanobacteria are found during the warmest months and often prevent the recreational use of the sea.

Marine Ecosystem Impacts

Attempts to quantify the economic value of natural marine ecosystems are recent (Costanza et al. 1997). It is nevertheless clear that losses of non-commercial marine resources may also have severe consequences.

High biomass, non-toxic blooms of HAB species can have significant deleterious effects on entire ecosystems. One such ecosystem effect is the damage to seagrass or coral reef communities following a reduction in light penetration and anoxia. Severe light attenuation by brown tides results in significant reductions in the photosynthetic capacity and leaf biomass of eelgrass beds, leading to the loss of nursery habitat for numerous fish and shellfish. Oxygen depletion following the degradation of non-toxic blooms can kill not only commercially important species, but also other animals and plants.

In addition to their effects on human health and seafood, toxins can move through an ecosystem in a manner similar to the flow of carbon or nutrients, and thus the impacts can be far-reaching. Negative influences on viability, fecundity, recruitment, and growth are just beginning to be recognised. Marine mammals such as whales, dolphins, sea lions and manatees, have all suffered morbidity and mortalities as a result of exposure to HAB toxins transferred through the food web (Scholin et al. 2000). Mass mortalities of seabirds, including brown pelicans and cormorants, have also been linked to blooms of diatoms whose toxins were transferred via consumption of contaminated planktivorous fish (Work et al. 1993).

Mortalities of domestic fauna can occur when blooms of toxic algae occur in fresh, brackish, or marine waters. Photo by W. Carmichael.

The Apparent Global Increase of HABs

> “The sea in many places here is cover’d with a kind of brown scum ..”
>
> Captain James Cook,
> 28 August, 1770

Harmful algal blooms are natural phenomena that have occurred throughout recorded history. For example, references to what were most likely outbreaks of HABs are documented in Captain James Cook’s journal, 1770, upon arrival off the Great Barrier Reef, Australia, and also in documents from Captain George Vancouver’s voyage to British Columbia in 1793 in an area now known as Poison Cove. Indeed, Vancouver noted that local native tribes considered it taboo to eat shellfish when the seawater became phosphorescent. This phenomenon was later shown to be associated with some toxic dinoflagellate blooms. In the Baltic Sea, paleoecological records have revealed the presence of cyanobacterial blooms more than 8000 years ago (Bianchi et al. 2000).

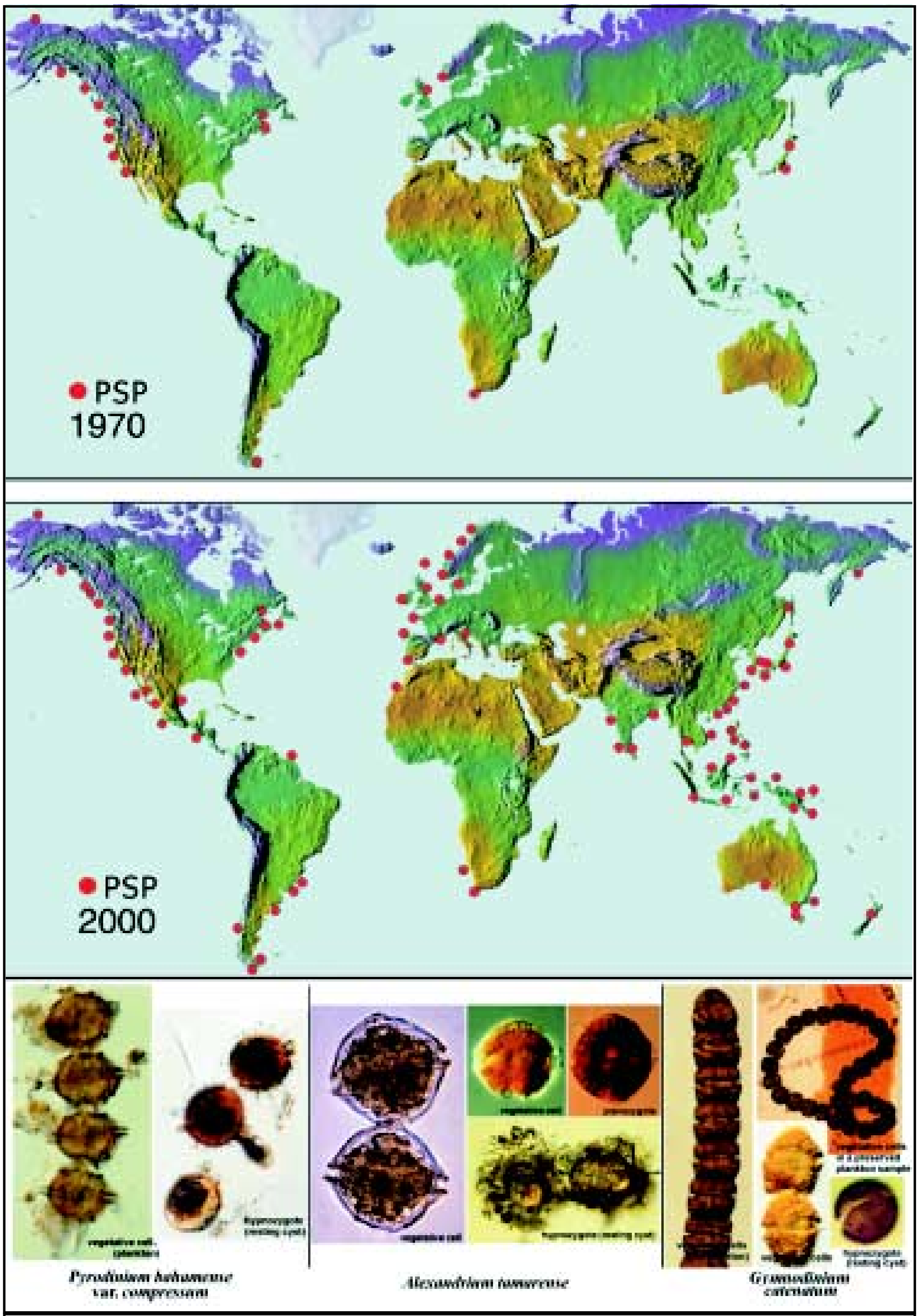
Trichodesmium blooms are common on the Great Barrier Reef, Australia. Similar blooms were likely seen by Capt. James Cook. Such blooms are unpleasant for tourists visiting the Great Barrier Reef today. Photo by P. Glibert.

It is now thought that HABs may be increasing worldwide (Anderson 1989, Smayda 1990, Hallegraeff 1993). Several reasons have been suggested for the apparent increase in frequency, in distribution or severity, such as:

- Species dispersal through currents, storms, or other natural mechanisms
- Nutrient enrichment of coastal waters by human activities, leading to the selection for, and proliferation of, harmful algae
- Increased aquaculture operations, which can reveal the presence of previously unknown HAB species
- Transport and dispersal of HAB species via ballast water or shellfish seeding activities
- Long-term climatic changes
- Improved scientific methodology and monitoring activities leading to the detection of new species, toxins, or toxic events

The current lack of appropriate data prevents the resolution of long-term trends in HABs in many regions, but few would argue that the impacts of these blooms are increasing and represent a serious constraint to the sustainable development of marine resources.

The global problem of HABs is serious and much larger than was previously recognised. Given the significant social and ecosystem impacts from HABs, a global research programme is clearly needed. If HABs are increasing due to human activities, then the need for such a research programme is even more urgent.



Paralytic shellfish poisoning (PSP) is a toxin syndrome caused by consumption of seafood contaminated by certain HAB species. The above maps show the cumulative global increase in the recorded distribution of the causative organisms and the confirmed appearance of PSP toxins in shellfish at levels above the regulatory limit for human consumption.

An International Programme on the Global Ecology and Oceanography of Harmful Algal Blooms: GEOHAB

Emergence of the GEOHAB Programme

Research on HABs emerged as a discipline in its own right at the First International Conference on Toxic Dinoflagellate Blooms, held in Boston, Massachusetts, U.S.A. in 1974. Since then, the field has expanded rapidly as concerns about HABs have increased, and in 2000 over 500 scientists from approximately 50 countries attended the Ninth International Conference on Harmful Algal Blooms in Tasmania, Australia.

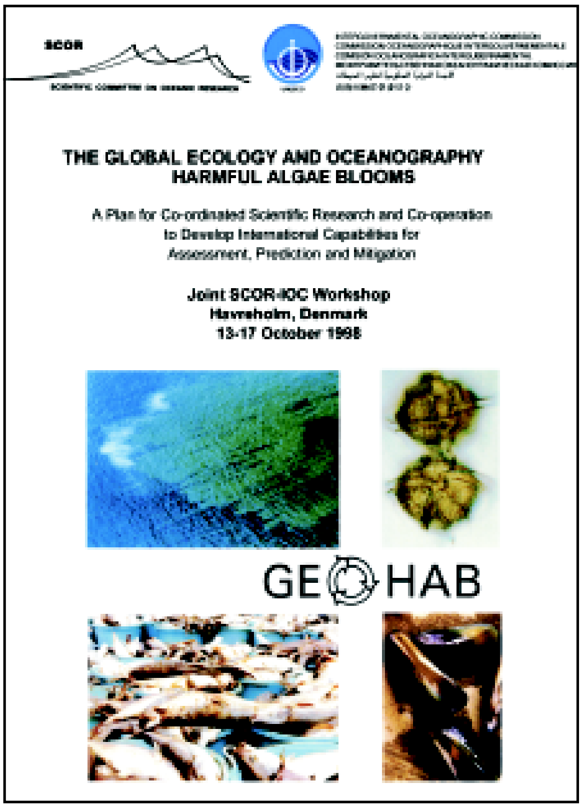
The proceedings of the Fourth International Conference on Harmful Marine Phytoplankton stated “that some human activities may be involved in increasing the intensity and global distribution of blooms,” and recommended “that international research efforts be undertaken to evaluate the possibility of global expansion of algal blooms and man’s involvement in this phenomenon”. Subsequently, a number of national and international initiatives were undertaken to study and manage HABs and their linkages to environmental change, consistent with the global nature of the phenomenon.

This increased awareness resulted in the Member States of the Intergovernmental Oceanographic Commission (IOC) requesting the establishment of an international programme on HABs. The IOC Harmful Algal Bloom Programme was first formulated at a workshop jointly sponsored by the Scientific Committee on Oceanic Research (SCOR) in Rhode Island in October 1991. The Intergovernmental Panel on Harmful Algal Blooms (IPHAB) was established in 1992 with the overall programme goal “to foster the effective management of, and scientific research on, harmful algal blooms in order to understand their causes, predict their occurrences and mitigate their effects.”

At the same time, the International Council for the Exploration of the Sea (ICES) and the IOC established a joint Working Group on Harmful Algal Bloom Dynamics. A working group on the Physiological Ecology of HABs was also established by SCOR and the IOC, which recommended that there should be an international programme emphasising the oceanography and ecology of HABs.

At its Fourth Session, IPHAB decided to work towards the development of an international science agenda on the ecology and oceanography of HABs and sought assistance from SCOR in this effort. The strengths of IOC and SCOR lent themselves to a natural partnership between these organisations in the development of a new international science programme on the ecology and oceanography of HABs.

SCOR and IOC convened a workshop in October 1998 at which scientists from a broad



SCOR

THE GLOBAL ECOLOGY AND OCEANOGRAPHY
HARMFUL ALGAE BLOOMS

A Plan for Co-ordinated Scientific Research and Co-operation
to Develop International Capabilities for
Assessment, Prediction and Mitigation

Joint SCOR-IOC Workshop
Havreholm, Denmark
13-17 October 1998

GEOHAB

range of biological, chemical, and physical disciplines discussed the state of understanding of HABs globally, and identified the requirements for a co-ordinated, interdisciplinary international research programme. They recommended that SCOR and IOC undertake a joint effort on the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) and the recommendation was accepted and approved.

The GEOHAB Mission

Acknowledging that the HAB problem is global, but recognising that insufficient efforts have been directed toward studying the biological, chemical, and physical factors that regulate HAB dynamics and impacts, the SCOR/IOC GEOHAB Programme has as its **mission** 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 GEOHAB Goal

To achieve the mission of GEOHAB, the overall scientific **goal** 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 observation and modelling systems.*

The GEOHAB Strategy:
A Comparative Approach

The approach of the GEOHAB Programme is ***comparative***, from the cellular to the ecosystem level. This approach is based on the view that the ecology and oceanography of HABs can best be understood through the study of causative organisms and affected systems in relation to comparable species and systems. The GEOHAB strategy is also to identify the particular adaptations of HAB species and to study processes at multiple temporal and spatial scales. Important physical processes occur on scales ranging from those controlling turbulence to internal waves, eddies, and currents, while important biological processes occur at subcellular and cellular levels as well as at the population, community, and ecosystem levels.

The approach of GEOHAB is to apply multiple techniques to fully understand the biological, chemical, and physical factors regulating HAB dynamics and impacts. Field studies are essential, as are laboratory and mesocosm studies. Modelling the population dynamics (Table 2) will be critical in every aspect of these studies. Improved global observation systems will be required to resolve influences of environmental factors (anthropogenic and climate-related) on the distributions and trends in HABs.

Therefore, the GEOHAB Programme fosters research that is ***interdisciplinary***, focusing on the important interactions among biological, chemical, and physical processes. GEOHAB research must also be ***multifaceted*** as the problems are complex and interactions and processes occur on a broad range of scales. Finally, GEOHAB research should be ***international*** in scope to encompass the global issues of HAB events and benefit from skill and experience gained by HAB investigators worldwide.

Table 2. Modelling of population dynamics.

A robust mathematical equation for the local number of organisms per unit volume can be written in the following form:

$$\frac{\partial n}{\partial t} = \mu n - mn - \nabla\cdot(n\bar{v}) - \nabla\cdot(n\bar{u})$$

$\frac{\partial n}{\partial t}$ is the time rate of change of the state variable n, the number of cells of a particular HAB species per unit volume. Population dynamics is defined as the change of n in space and time.

μn represents growth by cell division. The growth rate is determined by intrinsic genetic factors, as well as by environmental factors, such as nutritional and light history, turbulence, temperature, and salinity.

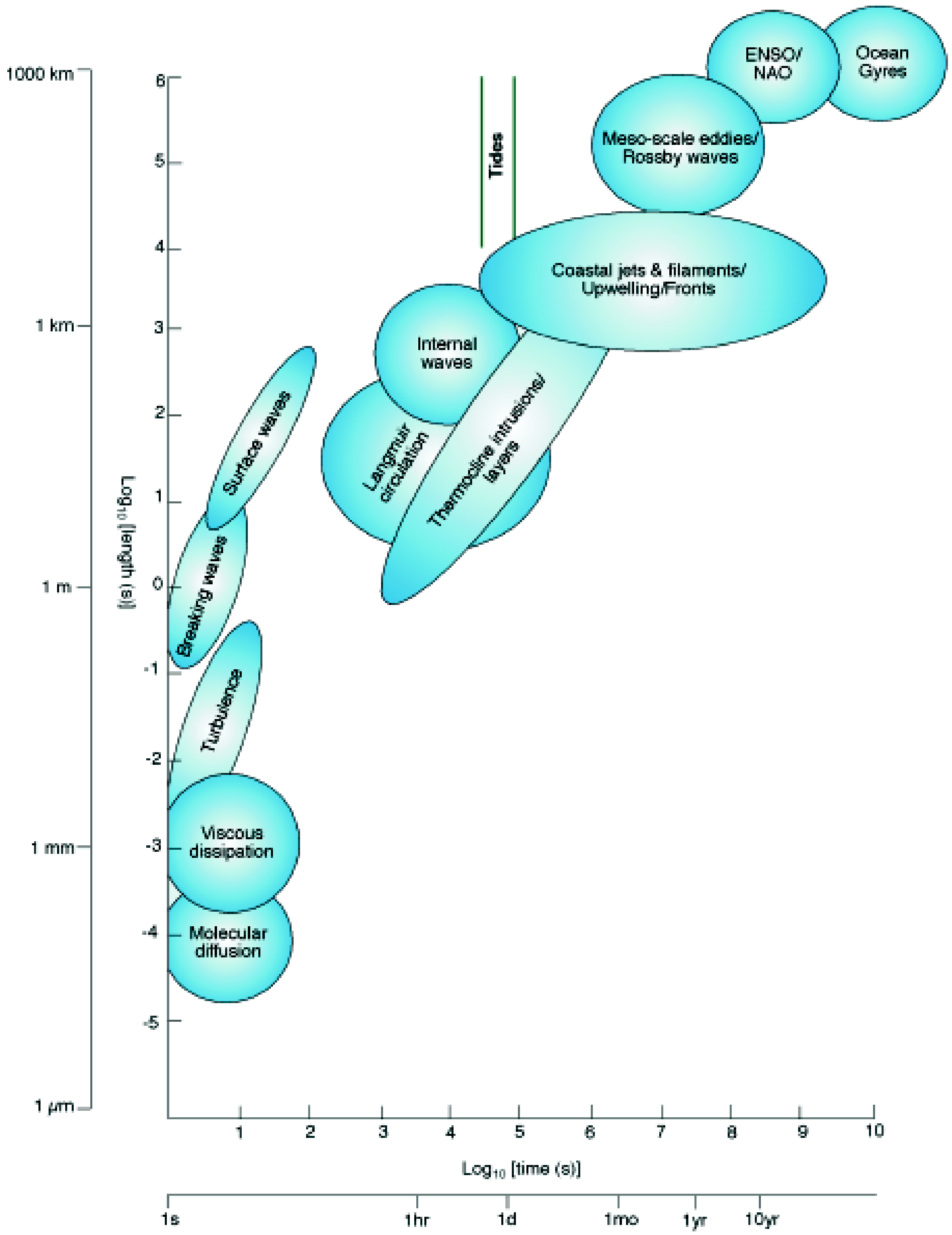
mn is the direct loss of organisms through mortality. This term includes processes such as grazing, mechanical damage, and death from infections by viruses or other pathogens.

$\nabla\cdot(n\bar{u})$ includes the three-dimensional, time-variable transport of cells by the water flow, for example, mean circulation, tidal currents, wind drift, and turbulence (often identified as turbulent diffusion). “Disappearance” of blooms due to offshore flow would appear in this term.

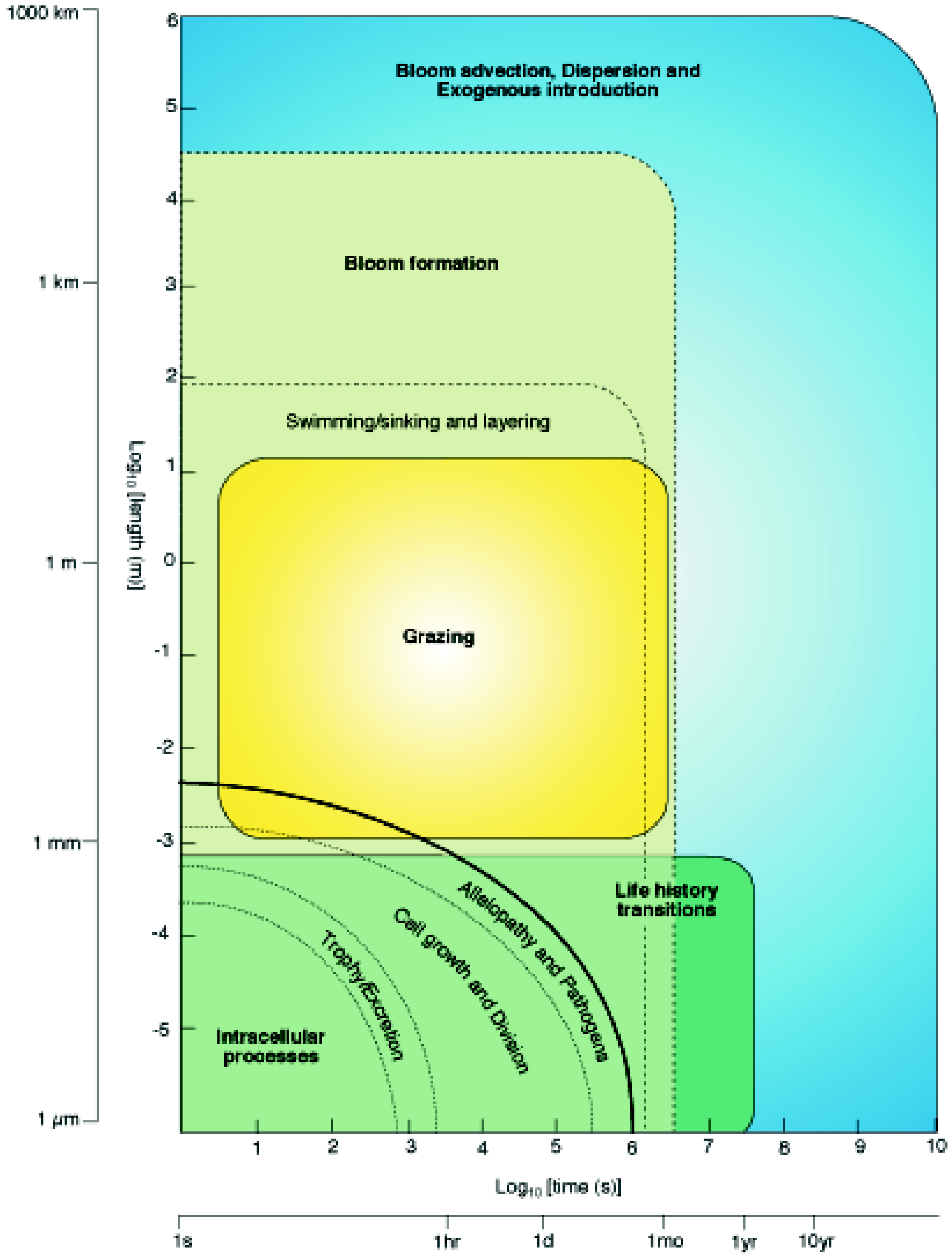
$\nabla\cdot(n\bar{v})$ is the motion of organisms relative to the water, described as velocity, $\bar{v}$. This term includes swimming, sinking, or rising due to buoyancy, and slippage, relative to the local flow that arises for a variety of reasons such as size and shape.

In general, there is a set of state variables, n_i , corresponding to different species, and a corresponding set of equations governing many direct and coupled biological, chemical, and physical processes. Environmental processes affect the population dynamics in several of the terms of this equation, while the coupled processes cover a broad range of temporal and spatial scales, with many non-linearities. A major challenge is to understand the processes to a level of detail that allows a simplified mathematical formulation (parameterisation) and that still reproduces the salient features of HAB population dynamics.

Studies on population dynamics of HABs will lead to a better understanding of events such as cyanobacterial blooms in the Baltic Sea.



For some HABs, the physical-biological interactions are dominated by physical processes such as large-scale advection and transport phenomena in coastal ecosystems. In other cases, biological factors such as swimming and aggregation behaviour are the dominant processes affecting the distribution of a HAB



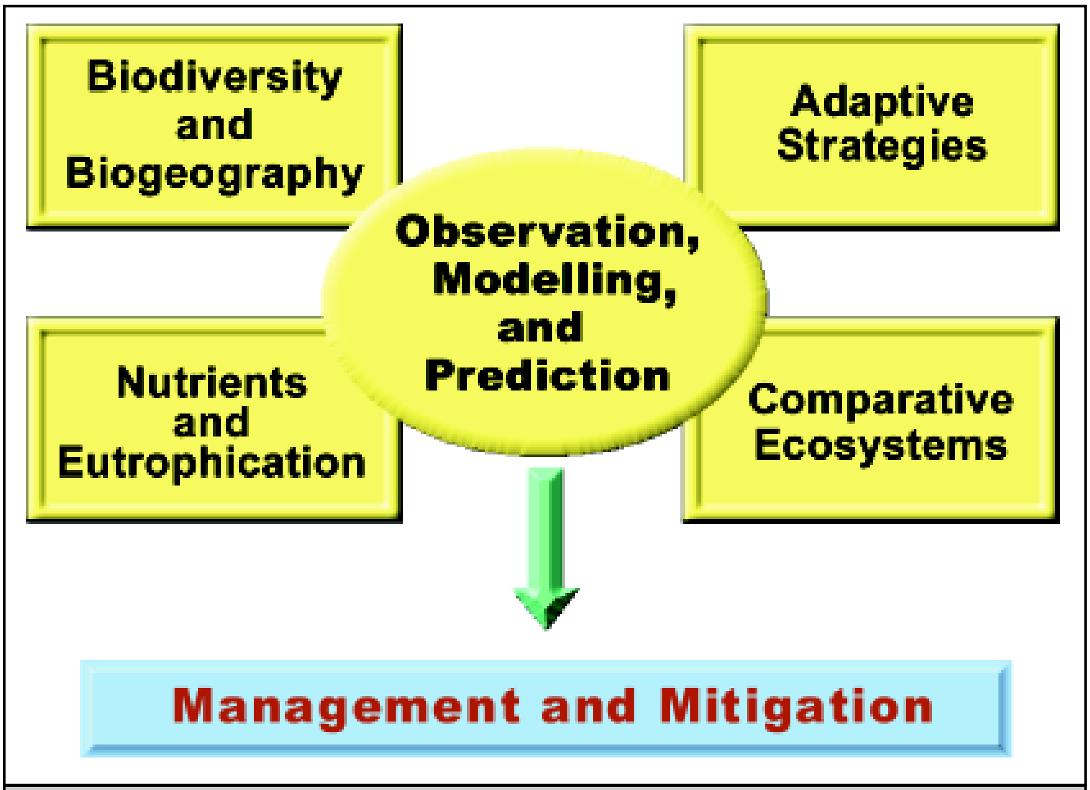
species. For these reasons, physical and biological processes must be considered from a multi-disciplinary perspective and not in isolation.

Organisation and Priorities of the GEOHAB Programme

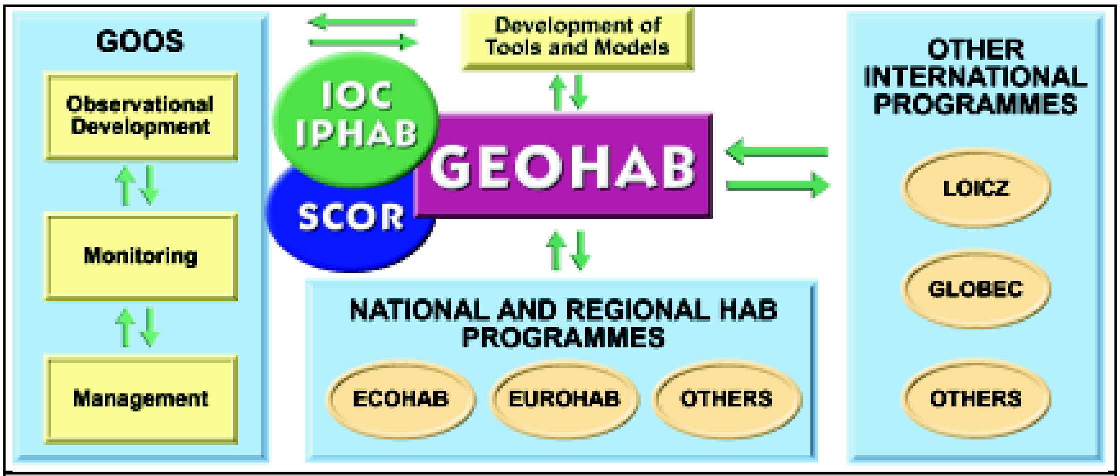
GEOHAB is an international programme to co-ordinate and build upon related national, regional, and international efforts in HAB research. The GEOHAB Programme will assist in bringing together investigators from different disciplines and countries to exchange technologies, concepts, and findings. This may take the form of formal or informal workshops, working groups, and collaborating teams of investigators. GEOHAB is not a research-funding programme per se, but instead will facilitate those activities that require co-operation among nations. This might include the development and sharing of methodologies; efficient use of major resources, such as research vessels; and co-ordination and standardisation of data management, making feasible the integration of results and a global synthesis. GEOHAB projects will be funded by a variety of national and international sources; the programme will therefore be a coalescence of projects at many levels, from large, multi-investigator, multi-national field investigations, to co-ordinated laboratory studies on specific processes or methods.

GEOHAB has defined five Programme Elements that serve as a framework to guide priorities and research. These include: *Biodiversity and Biogeography; Nutrients and Eutrophication; Adaptive Strategies; Comparative Ecosystems; and Observation, Modelling, and Prediction.*

Research and technical advances will be encouraged in several ways. For example, major field programmes such as those envisioned under *Comparative Ecosystems* will be expected to include observation and modelling components, incorporating characterisation of the sites with measurements and models prior to and during process studies. In addition, targeted research, such as that conducted within the *Adaptive Strategies* or *Nutrients and Eutrophication* components, will



While the Programme Elements of GEOHAB are individually described and justified, the goals of GEOHAB will only be advanced through the linkages between the Programme Elements.



GEOHAB will co-operate and co-ordinate with relevant national, regional, and international programmes.

be directed toward addressing gaps in our abilities to observe or model properties and processes. The resulting technical achievements will be incorporated rapidly into research programmes, and observation and modelling systems. Through the development of in situ and remote sensing techniques and the creation of networks of laboratories to monitor, collate, and disseminate data, the priorities of GEOHAB will be advanced in the form of more effective monitoring systems, risk assessment, and improved forecasts of the timing, magnitude, and effects of HABs.

Links Between GEOHAB and Other International Activities

Three international programmes with scientific interests that overlap with those of GEOHAB are the Land-Ocean Interactions in the Coastal Zone (LOICZ), Global Ocean Ecosystem Dynamics (GLOBEC), and the Global Ocean Observing System (GOOS) programmes. The first two are part of the International Geosphere-Biosphere Programme (IGBP).

The major goals of LOICZ are the quantification of fluxes of nutrients and water from coastal drainage basins to estuaries and the coastal ocean, and of nutrient budgets for coastal ecosystems. The complementary goals of GEOHAB include quantifying the effects of anthropogenic nutrient enrichment on the population dynamics of HABs.

GLOBEC emphasises the roles of physical processes and zooplankton in the trophic dynamics of food webs that support marine fisheries. The focus of GEOHAB is on the dynamics of HABs that have significant effects on the trophic dynamics linking nutrients and phytoplankton productivity to zooplankton and fisheries.

Clearly, co-ordination with LOICZ and GLOBEC must be a high priority for GEOHAB. Co-ordination will include the design and implementation of research projects and the exchange of data and information to achieve the related objectives of both programmes. National programmes will, of course, be integral to the activities of GEOHAB.

The Global Ocean Observing System (GOOS) is designed to monitor the oceans and develop sufficient understanding of environmental change to achieve the goals of sustainable development and integrated management of the marine environment and its natural resources. GOOS has been charged with promoting the development of observation systems that will improve documentation and prediction of the effects of human activities and climate change on marine ecosystems and the living resources they support.

The knowledge and tools generated by GEOHAB will benefit the coastal component of GOOS in the form of more effective operational monitoring systems, data-based risk assessment, and improved forecasts of the timing, magnitude, and effects of HABs. In turn, it is expected that GOOS will encourage the implementation and development of sustained observing systems required to document HAB trends, evaluate the efficacy of management actions (HAB mitigation), and define those areas that require additional research.

The Benefits of GEOHAB

A better understanding and quantification of the factors that regulate the dynamics of HABs in the context of physical and chemical forcing, ecosystem dynamics, and human influences will be used to improve strategies for monitoring, prediction, and mitigation of HABs. Through links to national agencies and international organisations responsible for protecting coastal resources and public health, the knowledge gained from GEOHAB will be used to develop international capabilities for more effective management and mitigation of HAB problems. Linking basic scientific research directly to societal needs should result in an effective contribution of science to the protection of the intrinsic and economic value of coastal marine ecosystems.

Massive cyanobacterial blooms in the Baltic Sea are common in the summer months. Understanding the factors leading to these and other HAB events, and ultimately improving prediction of such HABs, is the aim of GEOHAB.

PROGRAMME ELEMENT 1: Biodiversity and Biogeography

INTRODUCTION

On a global basis, there is evidence of changes in the distribution of harmful species, with new records in areas previously unaffected by these phenomena (Anderson 1989, Smayda 1990, Hallegraeff 1993). Increased interaction with the coastal zone and greater awareness of the problems caused by microalgae have contributed to more effective detection of harmful species. On the other hand, several alternative scenarios could account for the appearance of previously unrecorded species in a new area. These include the introduction of non-indigenous harmful species, followed by possible acclimation and genetic adaptation to attain and maintain HAB status. Also, differential stimulation of population growth of a previously unrecorded or rare species following environmental change may result in the emergence of the harmful species as a dominant organism. Finally, the appearance of new HAB events in previously unaffected areas may be a consequence of the manifestation of noxious traits in strains formerly thought to be benign.

> ***Biodiversity** is defined as the collection of genomes, species, and ecosystems occurring in a geographically-defined region.*
>
> ***Committee on Biological Diversity in Marine Systems***

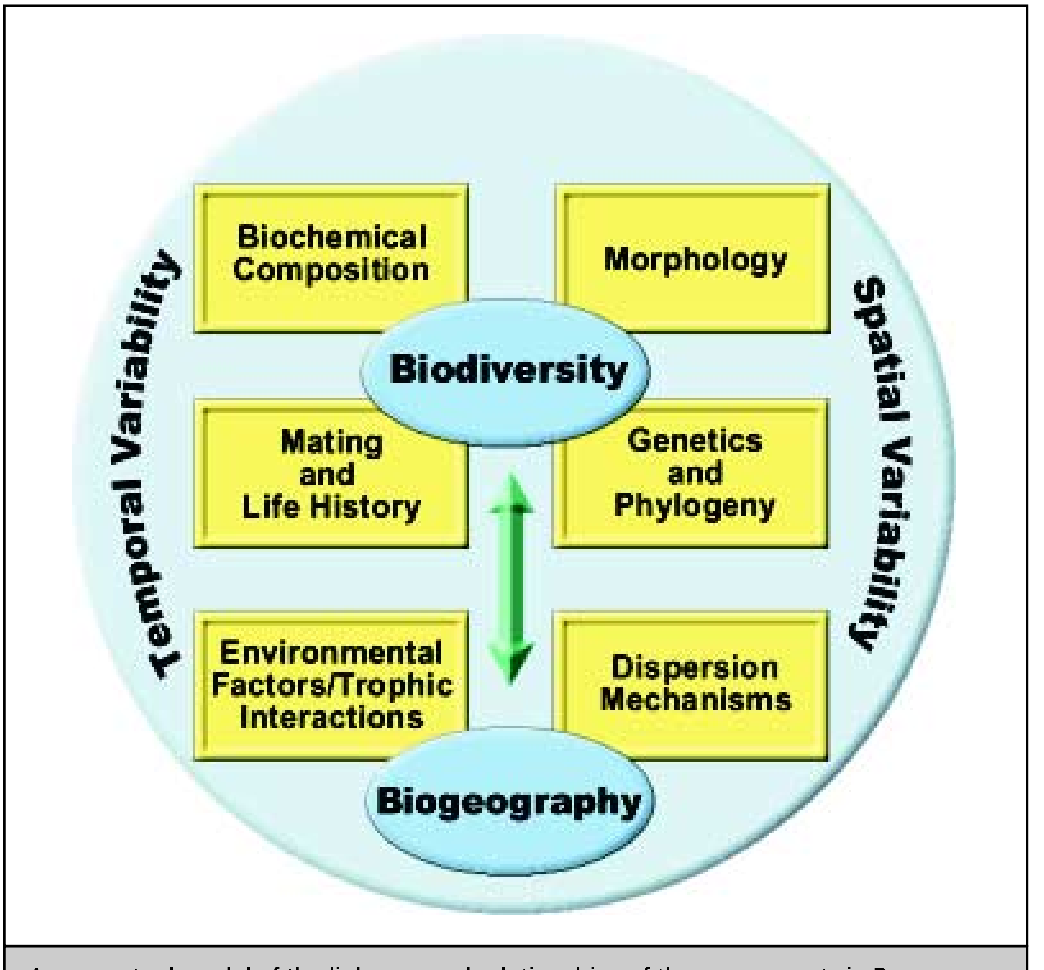
Many harmful species can form resting stages or enter quiescent phases that allow their survival in the dark. Ballast water discharge is one mechanism by which these species may be introduced to new regions.

Knowledge of the present geographic distribution of HAB species and of the long-term fluctuations in species composition are essential for distinguishing novel and recurrent HAB events, and for evaluating the global spreading hypothesis (Anderson 1989, Smayda 1990, Hallegraeff 1993). Within the context of HAB research and management, several biodiversity issues need to be addressed. These include determination of the number of distinct taxa to be classified (taxonomic diversity), and determination of the variation in primary gene sequences and expressed gene products (genetic diversity). Patterns of variation and changes in biodiversity should be assessed at scales spanning the genetic structure of populations or blooms of a single species, to relationships among populations, to the general diversity of phytoplankton populations in areas prone to HAB events. A high degree of genetic variability is typically associated with phenotypic characteristics such as growth rates, environmental tolerance, and, in the case of harmful species, cell toxicity. The use of molecular techniques – including nucleic acid sequencing and genotyping – offers much promise in identifying genetic variations over their geographic range. Molecular data can also be employed to evaluate hypotheses regarding the introduction of HAB taxa into new environments. Detailed knowledge of the genetic characteristics of a species across a wide spatial scale may provide valuable information regarding mechanisms of adaptation and dispersal, allowing tracking and possible prediction of expansion or patterns of recession.

In the framework of the international co-operation fostered by GEOHAB, the overall result expected from this investigation is a detailed analysis of biodiversity at various taxonomic and genetic levels, as they relate to both static geographic and dynamic climatological, oceanographic, and anthropogenic features. In this context, patterns and trends in the distribution of species endangering human welfare and ecosystem health will become clearer and the response of harmful species to natural and human-induced changes thus become more predictable. Studies of HAB species distributions and biodiversity will also provide an indication of chronic problems related to shifts in species dominance and environmental vulnerability to the introduction of foreign harmful species.

In summary, this Programme Element aims to address the following research question:

> *What are the factors that determine the changing distribution of HAB species, their genetic variability, and the biodiversity of the associated communities?*



A conceptual model of the linkages and relationships of the components in Programme Element 1. These various components of biogeography and biodiversity must be studied over a wide range of temporal and spatial scales and compared for different ecosystems.

OVERALL OBJECTIVE

To determine the relationships among distributions of HAB species, biodiversity, and environmental change

THE STRATEGY

GEOHAB will foster co-ordinated and comparative studies on changing distributions and biodiversity of HAB taxa. The development and application of appropriate technologies for species discrimination and assessment of genetic variation should be accomplished through the exchange of cultured material and natural samples collected from all regions of the world. Through the standardisation of methods, species distribution and biodiversity can be compared among different ecosystems. GEOHAB will facilitate the interpretation of genetic variability of harmful species at the level of discrete local populations and ultimately on a global scale.

A summary of the objectives and types of tasks that might be addressed under this Programme Element, as well as the anticipated outcomes, is provided in Figure 1.1.

Specific Objective #1

Assess the genetic variability of HAB species in relation to their toxicity, population dynamics, and biogeography

Rationale

A suite of methods has been developed for assessing the phylogenetic relatedness among species, for recognising intraspecific genetic diversity, and for complementing the morphological characterisation of harmful and other species. For example, molecular techniques coupled with morphological observations have allowed for discrimination of toxic and non-toxic specimens of the diatom *Pseudo-nitzschia* at the species level (Hasle 1995, Manhart et al. 1995), and have revealed the existence of new species in the haptophyte genus *Phaeocystis*, which had been considered monospecific (Medlin et al. 1994, Zingone et al. 1999). On the other hand, research on some species of the dinoflagellate genera *Alexandrium* and *Gymnodinium* has demonstrated high genetic variability within species, often with a high sequence similarity among selected strains of different morphospecies from the same geographical area (Scholin and Anderson 1996, Bolch et al. 1999).

Many HAB species have a high degree of genetic variability that is not always morphologically expressed. Nevertheless, within certain species there may be morphologically stable and geographically disjunct varieties. For example, *Pyrodinium bahamense* var. *compressum* produces long chains of apically compressed cells, whereas var. *bahamense* occurs as short chains or individual cells that are roughly isodiametrical. Note that the spiny cyst form of this species does not resemble the vegetative cell of either variety, and that spine length and overall morphology are subject to environmental influences.

There are many examples of how variation in ecophysiological characteristics reflects an underlying genetic variability (Brand 1989). The existence of both toxic and non-toxic

Figure 1.1 Summary of Programme Element 1: Biodiversity and Biogeography.

OVERALL OBJECTIVE Programme Element 1: To determine the relationships among distributions of HAB species, biodiversity, and environmental change

1
Assess the genetic variability of HAB species in relation to their toxicity, population dynamics, and biogeography

- Characterise HAB species using morphology, molecular genetics, biochemical composition, and other cellular properties
- Develop diagnostic tools for the discrimination of HAB taxa at various taxonomic levels
- Evaluate the population genetics of HAB species over the annual cycle
- Assess the relatedness of different strains of HAB species at different locations

2
Determine the changes in the biogeographical range of HAB species caused by natural mechanisms or human activities

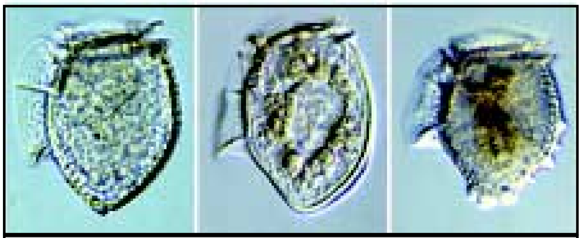
- Conduct global biogeographic analyses of key HAB taxa
- Examine the distributional pattern of HAB species in the water column, benthic habitats, and the sedimentary record
- Evaluate the potential for survival and growth of a HAB species from a given area in other geographical regions
- Evaluate whether HAB species have been introduced into new regions by natural or anthropogenic processes

3
Determine changes in microalgal species composition and diversity in response to environmental change

- Characterise the biodiversity of the microalgal community, including HAB organisms, in different ecosystems
- Identify shifts in species succession and microalgal diversity over seasonal time-scales in environments subject to HAB events
- Define possible links between changes in biodiversity and environmental factors on a multi-annual time-scale, including hindcasting from historical data

OUTPUTS
- New tools for detecting harmful and potentially harmful organisms
- Comprehensive inventories of harmful species at local, regional, and global scales
- Foundation for assessing the importance of human-assisted dispersal of HAB organisms
- Quantitative assessment of historical relationships between climate variability, human activities, and HABs

strains within a single species, and even among isolates originating from the same locality or bloom event, is an extreme demonstration of genetic variability within a species (Scholin and Anderson 1993, Anderson et al. 1994, Cembella and Destombe 1996). In addition, mating compatibility (Destombe and Cembella 1990) may also vary within a single species.



Taxonomic identification of certain HAB species using morphological characteristics is complicated by the high degree of variation expressed among and within populations. For example, the cells of *Dinophysis* shown here vary with respect to pigmentation, thecal ornamentation, length of the list ("wing"), and general cell shape, yet they belong to the same species.

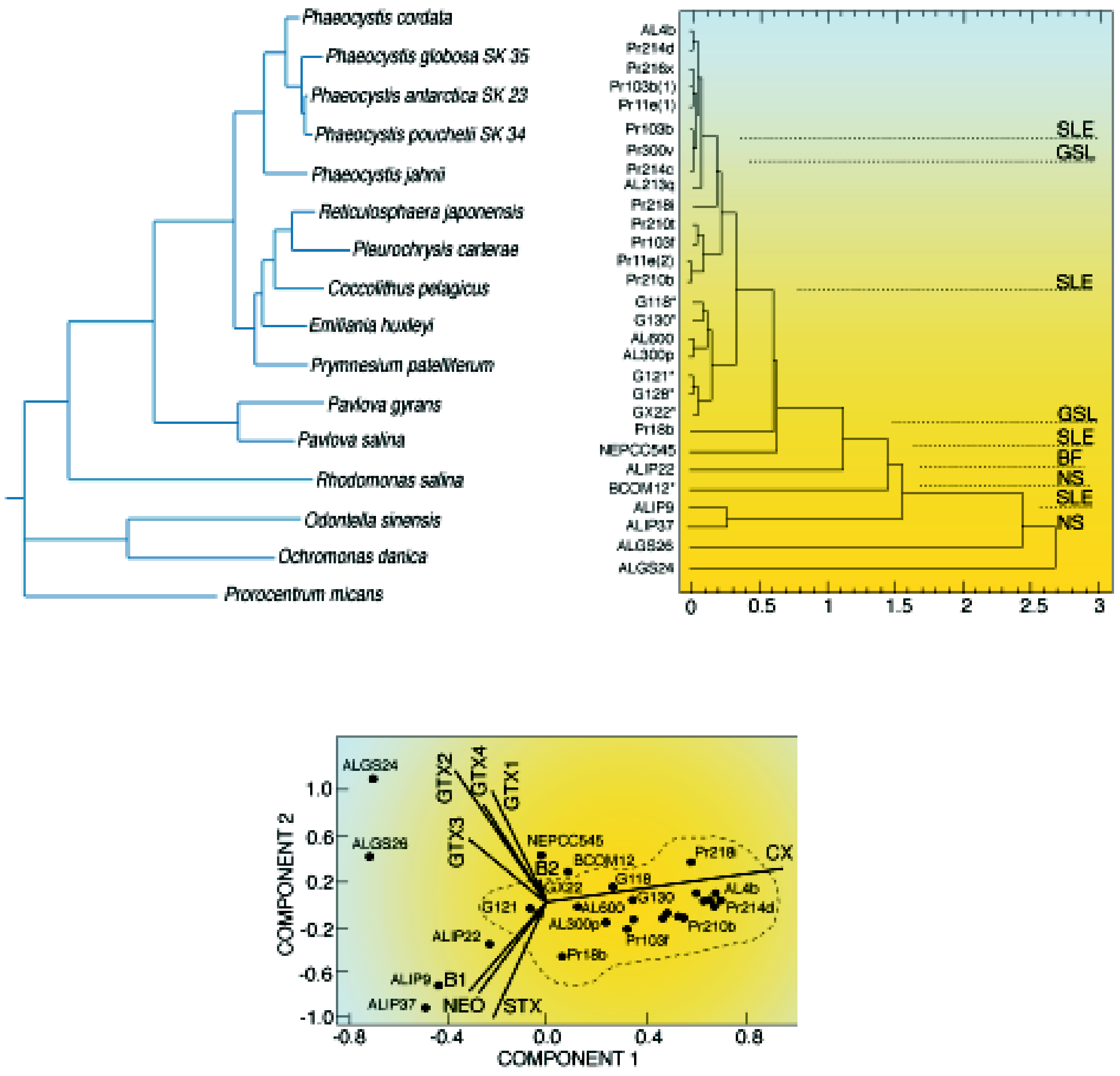
Isolates of the same species obtained at diverse localities have shown a great deal of variability in their ecophysiological characteristics; examples include *Gymnodinium catenatum* from Spain, Japan, and Australia (Hallegraeff and Fraga 1998) and *Pseudo-nitzschia* obtained from diverse localities worldwide (Bates et al. 1998). Intraspecific variability influences many types of physiological responses that are relevant to ecological success and the harm caused by a species in different environments and under different conditions. Much of this variation may have adaptive significance in terms of population dynamics. It is particularly important to know the extent to which intraspecific variability is related to genetic differences as regulated by environmental variables.

The assessment of genetic variability within a single species along a biogeographic gradient, and among different populations in the same area, represents the baseline for the characterisation of harmful organisms and for the definition of the functional role of biodiversity. At a local scale, the degree of genetic variability for a given species is a proxy for its capability to adapt and thrive under different environmental conditions. As an example, the annual alternation of blooms of different strains of a species could explain why some species persist for longer periods than others. Cyst maturation in *Alexandrium tamarense* populations from shallow coastal lagoons and offshore cyst beds of the Gulf of Maine has been shown to be regulated by environmental conditions or by an endogenous clock, respectively (Anderson and Keafer 1987). On the regional to global scale, genetic analyses could account for different bloom dynamics and reveal the presence of cryptic species or species complexes within a single morpho-species. This kind of information is necessary for the development of models of bloom dynamics of single species in different ecosystems. Finally, knowledge of the genetic structure of a species over its distributional range provides the basis for the reconstruction of pathways of spreading and colonisation into new areas.

Among chain-forming HAB species, such as *Gymnodinium catenatum*, chain length is a function of both genetic and environmental factors. Chain-forming isolates from natural populations often lose the ability to form long chains and atypical cells of distorted morphology may be produced after many generations in culture.

Example Tasks

- Characterise HAB species using morphology, molecular genetics, biochemical composition, and other cellular properties



For ease of understanding biogeographical, taxonomic and phylogenetic relationships among HAB taxa, the data are often presented as a cluster diagram or multi-dimensional ordination. In cluster diagrams or "trees" the relatedness may be shown quantitatively according to principles of numerical techniques (similarity in diagnostic traits) or phylogenetic analysis, by inferring shared derived characteristics (cladistics). Often the branch lengths are used to indicate "genetic distance" between taxa. The upper left panel shows the relatedness among prymnesiophytes based on small sub-unit ribosomal RNA sequences using the distantly related dinoflagellate *Prorocentrum* as an "outgroup" to root the tree (from Zingone et al. 1999). In the upper right panel, the tree represents the genetic distance (X-axis scale) among cultured isolates and natural populations of *Alexandrium* from eastern Canada (GSL= Gulf of St. Lawrence; SLE = St. Lawrence estuary; BF=Bay of Fundy; NS = Nova Scotia) based on similarity in PSP toxin composition (from Cembella and Destombe 1996). An alternative representation of the same toxin data set shows the application of principal components analysis, an ordination method in multi-dimensional space, with axes indicating the principal toxin components. The encircled points represent populations from the St. Lawrence ecosystem.

- Develop diagnostic tools for the discrimination of HAB taxa at various taxonomic levels

- Evaluate the population genetics of HAB species over the annual cycle

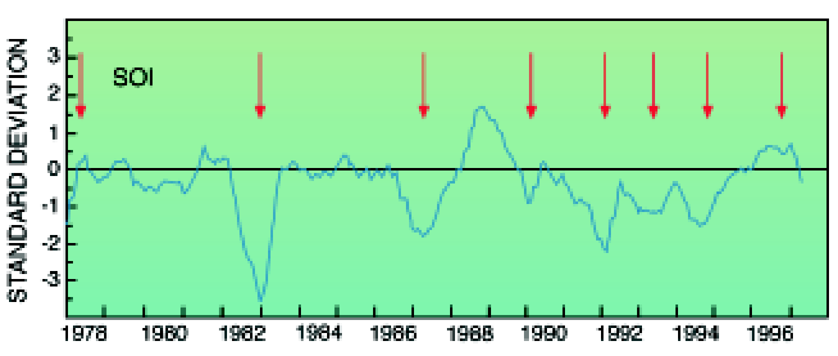
- Assess the relatedness of different strains of HAB species at different locations

Specific Objective #2

Determine the changes in the biogeographical range of HAB species caused by natural mechanisms or human activities

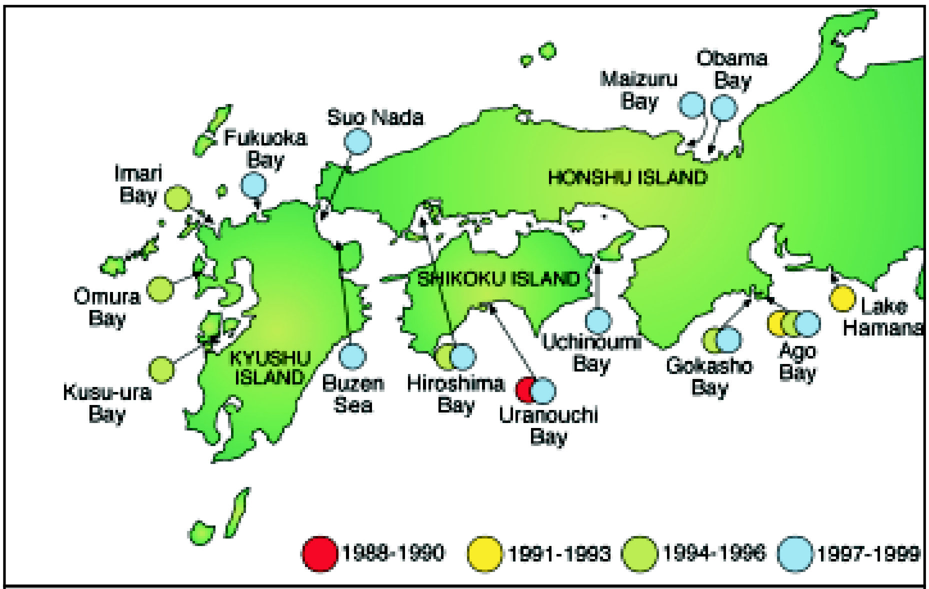
Rationale

HAB organisms may be categorised into two broad groups based on their biogeographical distribution. Certain species may have a rather circumscribed distribution within very narrow environmental constraints. For example, species such as *Pyrodinium bahamense* are restricted to tropical and subtropical regions in the Pacific Ocean and Caribbean Sea (Hallegraeff and Maclean 1989), while species such as *Alexandrium catenella* are found only in temperate waters at mid- to high latitudes. Other species, including the benthic dinoflagellate *Prorocentrum lima* and the raphidophyte *Heterosigma akashiwo*, have a rather cosmopolitan distribution, from temperate to tropical waters.



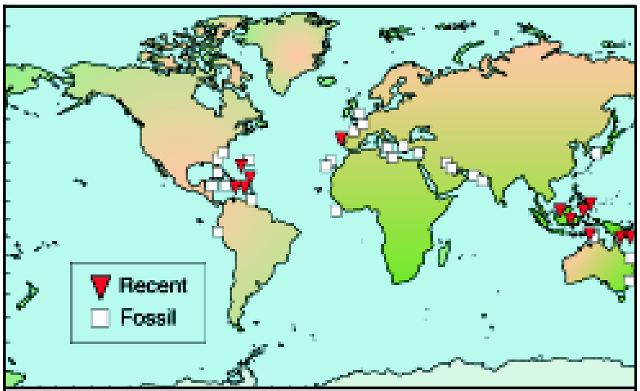
The El Niño - Southern Oscillation (ENSO) is the result of a cyclic warming and cooling of the surface ocean of the central and eastern Pacific. This region of the ocean is normally colder than its equatorial location would suggest, mainly due to the influence of north-easterly trade winds; however, during periods when this cold water influence diminishes, solar heating of the tropical Pacific results in an El Niño event. Several attempts have been made to link the appearance and biogeographical extent of specific HAB events, particularly in the tropics, to El Niño, but the data are inconclusive and reasons for this correlation (even if apparent) are inconclusive. In this figure, the coincidence of ENSO events and major toxic red tides of *Pyrodinium bahamense* (1978-1997) are shown for the western Pacific (from Usup and Azanza 1998). Arrows indicate specific occurrences in the Philippines and Malaysia. The Southern Oscillation Index (SOI) is a measure of the difference between sea level pressure between Darwin and Tahiti caused by this cyclic warming and cooling of the eastern and central Pacific - negative SOI values indicate "ocean warming" associated with ENSO.

Climatic shifts have resulted in long-term sustained changes to oceanographic features and other environmental conditions. For example, after the last ice age, the opening of the Bering Strait connected the North Pacific and North Atlantic Oceans. This condition would have permitted the invasion of many planktonic species from one ocean to the other, perhaps accounting for the cosmopolitan distribution of most of the extant taxa. Comparative studies of the geographical distribution of HAB species in relation to the environment should provide a probabilistic model of the likelihood of spreading or invading another ecosystem. For example, current knowledge on the restricted distribution of *Pyrodinium bahamense* within tropical and subtropical waters suggests that this species is unlikely to establish viable populations in waters with low temperatures and salinities. The same rationale suggests that *Alexandrium catenella* would probably not be viable in tropical waters owing to its low tolerance for sustained high temperatures. In the few cases in which HAB species are able to produce a resting stage, which may be fossilised (such as *Gymnodinium catenatum*, *Pyrodinium bahamense*), cyst records may provide valuable insight into paleo-climatological events and related fluctuations in species dominance, as well as evidence of the global spreading or recession of a given species.



Changes in the biogeographical distribution of previously described and novel HAB species have resulted in ecological devastation and massive losses of fisheries and aquaculture resources in many areas of the world. For example, the recently described dinoflagellate *Heterocapsa circularisquama* first appeared in Japan in 1988. Since then, blooms of this species have spread rapidly to other areas of the Japanese coast, with massive blooms (>10^6 cells L^{-1}) causing heavy damage to shellfish aquaculture, particularly in western Japan (from Matsuyama 1999). It is still unclear if *H. circularisquama* is endemic to Japan or whether it was introduced from tropical regions through transfer of shellfish stock or via advection in the prevailing northward currents.

Human activities, such as the discharge of ballast from ships and the transport of live aquaculture stock, have almost certainly resulted in the introduction of alien species, including those responsible for HABs, into other regions. For example, the dinoflagellate *Heterocapsa circularisquama* is thought to have been introduced from tropical or sub-tropical waters through transfer of stocks of juvenile oysters, and to have spread within Japan in subsequent years by movement of oyster spat to other locations. The only well-documented case of human-assisted transfer of a harmful species is the introduction of *Gymnodinium catenatum* to Tasmania, probably via ballast water discharge (McMinn et al. 1997).



Several HAB species produce resting stages and cysts that sink in the water column. The analysis of these stages in the sediments can provide insights into the distribution of the species integrated over time and space. For species producing fossilisable stages, such as some dinoflagellates and cyanobacteria, the analysis of fossil sediments may allow the reconstruction of their past geographic range. As an example, *Pyrodinium bahamense* is presently restricted to coastal waters of the tropics and subtropics, but fossil records dating back to the Pleistocene, show that the species range reached higher latitudes in both hemispheres in the past (Matsuoka 1989), possibly under different climatic conditions. Recently, a live cyst has been found off Portugal (Amorim and Dale 1998). Is this the first indication of a new range expansion for this species?

Knowledge of the distribution of different genotypes over the geographic range of harmful species is a powerful tool to reconstruct its pathways of dispersal to new areas. In addition, mechanisms whereby invading species are introduced and can become established in new areas should be well understood in order to mitigate the potential spreading of harmful species.

Example Tasks

- Conduct global biogeographic analyses of key HAB taxa
- Examine the distributional pattern of HAB species in the water column, benthic habitats, and the sedimentary record
- Evaluate the potential for survival and growth of a HAB species from a given area in other geographical regions
- Evaluate whether HAB species have been introduced into new regions by natural or anthropogenic processes

Specific Objective #3

Determine changes in microalgal species composition and diversity in response to environmental change

Rationale

Phytoplankton distributions in coastal and shelf waters are characterised by a high degree of variability over a wide range of scales. Compositional shifts, changes in dominant species, and the emergence of previously unrecorded or rare species are well known phenomena. These shifts in biodiversity are particularly important when they involve harmful algae, thereby affecting human activities. In some cases, the emergence of harmful events in new areas may be associated with an increase in the abundance of the causative species. For example, *Chrysochromulina polylepis* and *Chrysochromulina leadbeateri* were sporadic and rare components of the local microflora in Scandinavian waters prior to their respective massive blooms in 1988 and 1991 (Moestrup 1994). The biodiversity of endemic phytoplankton populations is insufficiently known, therefore it is difficult to ascertain whether a previously unrecorded HAB organism has been introduced or whether it has merely escaped detection in the past owing to inadequate sampling. This could be the case with the diatom *Pseudo-nitzschia australis*, which has been known to occur in the Gulf of California since 1985 (Hernández-Becerril 1998), but has only recently been associated with the production of domoic acid. In most cases, it is not possible to trace the historical abundance of the species prior to harmful events owing to the absence of appropriate time-series data. Consequently, it is difficult to determine if recent toxicity is a result of an increase in the abundance of established populations, environmental influences on toxicity, or the introduction of a toxic strain.

Seasonal changes in species composition are driven by such factors as annually recurrent patterns of light, water column structure, and nutrient availability. However, high interannual variability is often recorded in the initiation, duration, and species composition of seasonal blooms that may include harmful species in an unpredictable fashion. As an example, blooms of *Gymnodinium catenatum* in Tasmanian waters (Hallegraeff et al. 1995) and of *Aureococcus anophagefferens* along the eastern coast of U.S.A. (Bricelj and Lonsdale 1997), show high interannual and seasonal variability. In contrast, annual toxic blooms of *Alexandrium ostenfeldii* and *Alexandium tamarense* along the eastern coast of Nova Scotia, Canada are remarkably predictable (Cembella et al. 1998). In Laguna Madre, Texas, a bloom of *Aureoumbra lagunensis* persisted for seven years, demonstrating the long-term persistence of a harmful species following a shift in environmental and weather conditions (DeYoe and Suttle 1994).

Changes in populations, including HAB species, have often been associated with local interannual meteorological variations, as well as with large-scale climatic fluctuations. Examples include the periodicity of blooms of *Pyrodinium bahamense* var. *compressum* in southeast Asia (Maclean 1989) and the recent blooms of fish-killing species in Hong Kong (Yin et al. 1999), both of which showed a relationship with the El Niño - Southern Oscillation. Blooms of the cyanobacterium *Trichodesmium,* in several areas of the North Pacific subtropical gyre, also followed an ENSO event, in 1992 (Karl et al. 1997). In the Gullmar Fjord in Sweden, the presence of toxic phytoplankton blooms has been related to phase changes in the North Atlantic Oscillation (NAO) (Belgrano et al. 1999).

The different driving forces determining long-term plankton variability may interact in a poorly discernible fashion, either by enhancing or dampening the respective effects. One of the most ambitious research goals of GEOHAB is to ascertain to what extent population changes resulting in increased HAB activity are caused by natural variability and/or human activities.

Example Tasks

- Characterise the biodiversity of the microalgal community, including HAB organisms, in different ecosystems
- Identify shifts in species succession and microalgal diversity over seasonal time-scales in environments subject to HAB events
- Define possible links between changes in biodiversity and environmental factors on a multi-annual time-scale, including hindcasting from historical data

Episodic meteorological events, such as Hurricane Floyd which hit the east coast of the United States in 1999, can result in major changes in the ecosystem through the delivery of freshwater, sediments, or nutrients, all of which can lead to changes in species composition. Photo by United States Geological Survey.

OUTPUTS

The results of this Programme Element should lead to:

- New tools for detecting harmful and potentially harmful organisms
- Comprehensive inventories of harmful species at local, regional, and global scales
- Foundation for assessing the importance of human-assisted dispersal of HAB organisms
- Quantitative assessment of historical relationships between climate variability, human activities, and HABs

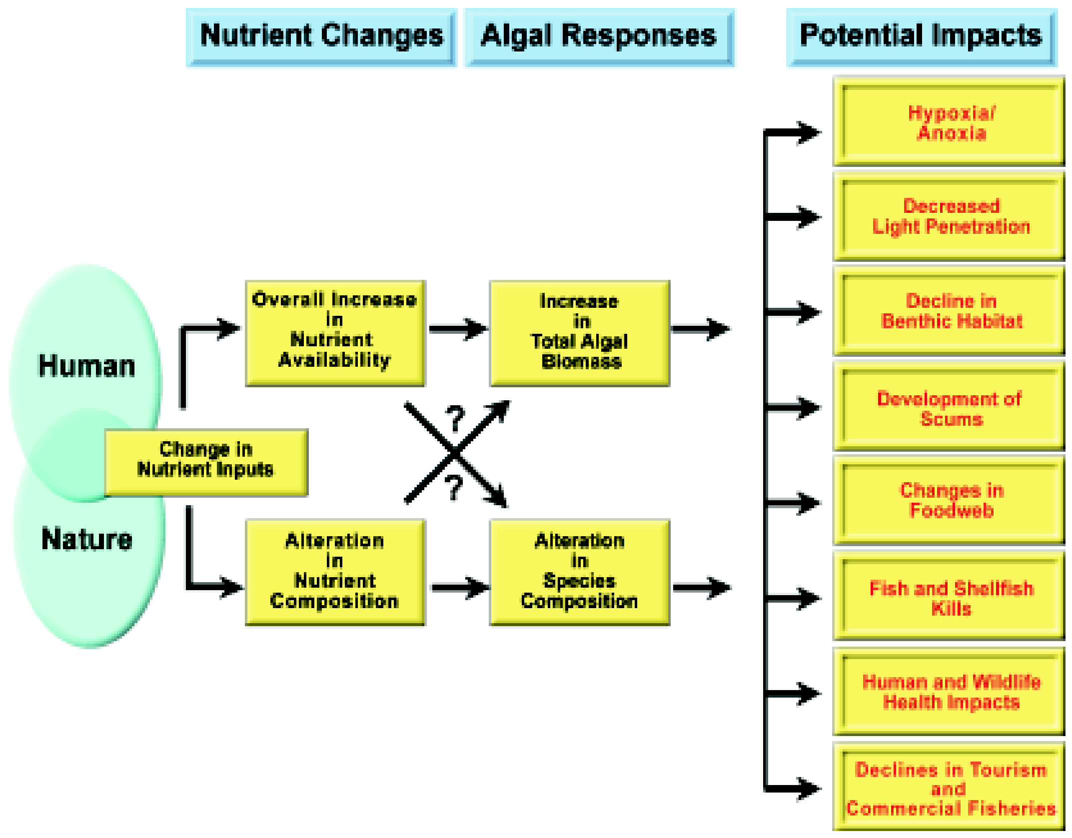
PROGRAMME ELEMENT 2: Nutrients and Eutrophication

INTRODUCTION

Concurrent with escalating influences of human activities on coastal ecosystems, the environmental and economic impacts of HABs have increased in recent years. Of particular concern is the potential relationship between HABs and the growing eutrophication of coastal waters. This linkage has often been suggested (Smayda 1990, Riegman 1995, Richardson and Jørgensen 1996) as coastal waters receive large quantities of nutrients from agricultural, industrial, and sewage effluents. Although it may seem reasonable to assume a causal relationship between human activities and an expansion of HAB events, the underlying mechanisms are not known. It is imperative to know how present trends in pollution and 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 both regional and global scales.

> ***Eutrophication*** *is the process of increased organic enrichment of an ecosystem, generally through increased nutrient inputs.*
>
> ***Nixon 1995***

The sources of nutrients that may stimulate blooms are many, from sewage to atmospheric and groundwater inputs, to agricultural and aquaculture runoff and effluent. It has been estimated that the flux of phosphorus to the



Schematic representation of potential links between nutrient inputs, algal responses, and the expression of HAB effects.

oceans has increased 3-fold compared to pre-industrial, pre-agricultural levels, while the flux of nitrogen has increased even more dramatically (Smil 2001). For example, the flux of nitrogen to the rivers of the North Sea has increased 10-fold during this period, and human activity is thought to have increased the nitrogen inputs to the northeastern United States by 6-8 fold (Boynton et al. 1995, Howarth 1998).

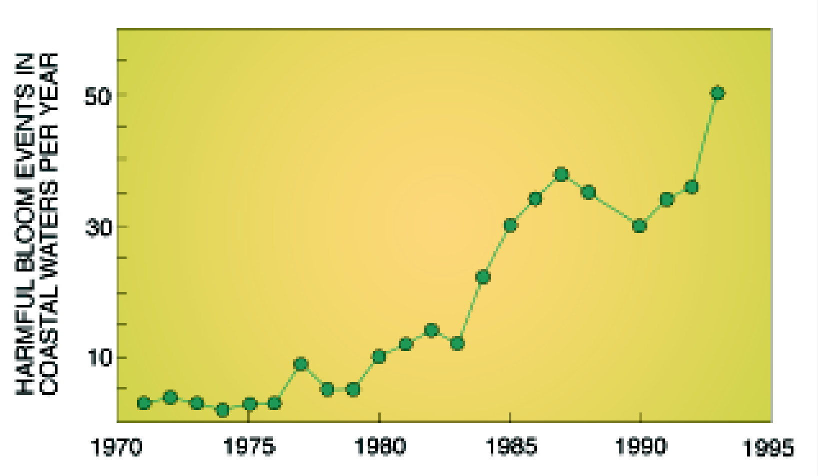
The responses of ecosystems to nutrient loading are variable. For example, the effects of nutrient loading on phytoplankton depend on the extent to which growth rates or net biomass yield are limited by the supply of ambient nutrients (Malone et al. 1996). Thus, in some cases the response may be an increase in growth rate or turnover of one or more species, while in other cases the response may be an overall increase in algal biomass. Effects are also dependent on the time scale of the nutrient addition; responses of phytoplankton to variable nutrient supply may range from hours to days when the growth rate is nutrient limited, to weeks when standing crops of phytoplankton are limited by nutrients (Caperon et al. 1971).

The result of eutrophication is often an increase in total algal biomass, due to the development of one or more species or groups. Increases in high biomass blooms in parallel with increased nutrient enrichment have been reported for the South China Sea (Qi et al, 1993), the Black Sea (Bodeanu and Ruta 1998), Hong Kong (Lam and Ho 1989), among many other locations. Such blooms may have deleterious effects including overgrowth and shading of seaweeds, oxygen depletion of the water from the decay of algal biomass, suffocation of fish from stimulation of gill mucus production, and mechanical interference with filter feeding. 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 blooms are not efficiently grazed, resulting in decreased transfer of carbon and other nutrients to fish stocks. 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).

The extent and the mechanisms whereby nutrient enrichment may lead to the development of toxin producing HAB species is poorly understood. Although eutrophication may be associated with an increasing number of high-biomass blooms and other HAB events,

From Hong Kong (left) to the tributaries of the Chesapeake Bay, U.S.A. (right), high biomass blooms result in discoloured water, hypoxia, and toxicity of fish and shellfish. Through the efforts of GEOHAB, a greater understanding of the roles of environmental factors, such as nutrient loading, and anthropogenic influences in bloom development will be obtained, and better prediction and mitigation strategies can be developed. Photos by M. Dickman and P. Glibert.

the specific relationships leading to the increased frequency of toxin-producers, or the increased production of toxin within these organisms are often poorly characterised. Therefore, the means to mitigate impacts of eutrophication on toxic HABs are not known and have been the subject of much controversy and debate.



Outbreaks of harmful algal blooms in Chinese coastal waters increased 10-fold from 1975 to 1993 (redrawn from Zhang 1994).

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 assemblages (Smayda 1997). A 23-year time series off the German coast documents the general enrichment of coastal waters with nitrogen and phosphorus, and a resulting shift in the relative nutrient composition. This shift was accompanied by a 10-fold increase in flagellates and a concomitant decrease in diatoms (Radach et al. 1990). In Tolo Harbour, Hong Kong, the human population within the watershed grew 6-fold between 1976 and 1986, during which time the number of red tide events increased 8-fold (Lam and Ho 1989). The underlying mechanism is presumed to be increased nutrient loading from population growth. Similarly, the number of red tide events in Chinese coastal waters increased sharply from 1975 to 1993, due largely to altered nitrogen to phosphorus ratios from increasing atmospheric emissions and deposition of pollutants (Zhang 1994).

In addition to nutrient uptake requirements, the geographic range and biomass of algal populations are affected by several other factors. These include physical forcings, nutrient supply, the physiology and behaviour of algal species, and the trophodynamics, all of which interact to determine the timing, location, and biomass of a bloom, which in turn determines the harmful consequences. Yet, these relationships are far from understood.

In summary, this Programme Element aims to address the following research question:

To what extent does increased eutrophication influence the occurrences of HABs and their harmful effects?

OVERALL OBJECTIVE

To determine the significance of eutrophication and nutrient transformation pathways to HAB population dynamics

THE STRATEGY

GEOHAB will foster robust quantitative approaches to distinguish direct effects of eutrophication from climate-related influences on HABs. To fully resolve direct impacts of anthropogenic nutrient inputs on HABs, it will be necessary to understand the effects of nutrients in a regional and a global context. By addressing the effects of nutrients on HAB development on scales ranging from cellular regulation to regional comparative systems, GEOHAB will strengthen the theoretical basis of issues related to nutrient regulation of species diversity in planktonic ecosystems.

A summary of the objectives and types of tasks that might be addressed under this Programme Element, as well as the anticipated outcomes, is provided in Figure 2.1.

Specific Objective #1

Determine the composition and relative importance to HABs of different nutrient inputs associated with human activities and natural processes

Rationale

A broad range of anthropogenic activities may result in significant alteration of nutrient cycling in coastal environments. However, the impacts of differing anthropogenic activities are not necessarily the same. For example, wastewater contributes roughly 70% of the nitrogen inputs to Long Island Sound, largely from the sewage of New York City. Similarly, sewage is responsible for up to 80% of the nitrogen delivered to Kaneohe Bay, Hawaii, and Narragansett Bay, Rhode Island (Nixon and Pilson 1983, National Research Council 1993). Yet, non-point sources of nutrients, such as agricultural operations, fossil-fuel combustion, and animal feeding operations may be of greater concern for coastal eutrophication and for HABs. Nutrient input from agricultural runoff can vary in quantity, influenced by rain and other environmental effects, and it can also differ in composition, based on the form of fertiliser in use. A dramatic trend in world fertiliser production is the increased proportion of urea, now representing up to 40% of all fertiliser produced (Constant and Sheldrick 1992).

Groundwater may be an important nutrient source to some coastal zones, and has been linked to HABs. However, such linkages are often complex and difficult to prove conclusively. In the Long Island bays of New York, it has been suggested that reduced rainfall decreases the input of dissolved inorganic nitrogen, which in turn leads to an increase in dissolved organic nitrogen and stimulates the growth of *Aureococcus anophagefferens* (LaRoche et al. 1997). This study further suggests that there can be a significant time lag between the human activities that enrich the groundwater and the HAB impact; in this case, the brown tides of today may reflect increases in development and fertiliser applications of 10 to 20 years ago.

Atmospheric nutrient input is one of the most rapidly increasing sources of nutrients to the coastal zone. Current estimates suggest that from 20-40% of nitrogen inputs are ultimately derived from atmospheric sources, from industrial, urban, or agricultural sources (Duce 1986, Fisher and Oppenheimer 1991, Paerl 1995, 1997). Experimental manipulations have demonstrated that nutrients carried in rainwater may disproportionately stimulate phytoplankton more than the addition of a single nitrogen source (Paerl 1997). 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 has been suggested 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 and cage culture systems represent another source of nutrients, due to the high additions of fertilizer or feed, or to the intensive biological transformations that occur in these systems. Nutrients released from aquaculture sites may impact a region 3-9 times the size of the aquaculture zone (Sakamoto 1986). Depending on whether such a site is well flushed or quiescent, the effect on plankton productivity and species development will vary (Wu et al. 1994, Romdhane et al. 1998).

Figure 2.1 Summary of Programme Element 2: Nutrients and Eutrophication.

OVERALL OBJECTIVE Programme Element 2: To determine the significance of eutrophication and nutrient transformation pathways to HAB population dynamics

1 *Determine the composition and relative importance to HABs of different nutrient inputs associated with human activities and natural processes*	• Conduct retrospective analyses of the temporal and spatial extent of HAB occurrences associated with nutrient loading • Determine the relative importance of nutrient loading from human activities and natural processes to HAB events • Compare HAB events in diverse regimes under varying conditions of eutrophication
2 *Determine the physiological responses of HAB and non-HAB species to specific nutrient inputs*	• Assess the importance of different nutritional strategies among HAB species and in comparison to non-HAB species • Quantify the nutrient uptake and growth kinetics for HAB species in relation to competing organisms • Determine the conditions under which a HAB species may adopt alternative nutritional strategies
3 *Determine the effects of varying nutrient inputs on the harmful properties of HABs*	• Measure toxin production in HAB species in culture at different stages of growth and under different nutritional conditions • Determine the nutrient-dependent factors that regulate toxin synthesis • Determine the role of nutrient supply in the production of noxious foams and scums
4 *Determine the role of nutrient cycling processes in HAB development*	• Determine nutrient transformation and regeneration processes in relation to HABs • Assess the functional relationships between HAB species and the co-occurring non-HAB organisms, in terms of nutrient pathways and fluxes

OUTPUTS
- Guidance for development of policies related to eutrophication and HABs
- Improved basis for establishing site selection criteria for aquaculture operations
- Quantitative baseline information for integrated coastal management

The impacts of nutrients from all sources, and their potential to lead disproportionately to a HAB event will depend on whether the HAB species is present in the assemblage and the composition of the nutrient pool, as well as the physics of the water body receiving the nutrients. Equivalent nutrient inputs to different systems may have differential effects on HAB development due to difference in ecosystem structure and function.

Example Tasks

- Conduct retrospective analyses of the temporal and spatial extent of HAB occurrences associated with nutrient loading
- Determine the relative importance of nutrient loading from human activities and natural processes to HAB events
- Compare HAB events in diverse regimes under varying conditions of eutrophication

Specific Objective #2

Determine the physiological responses of HAB and non-HAB species to specific nutrient inputs

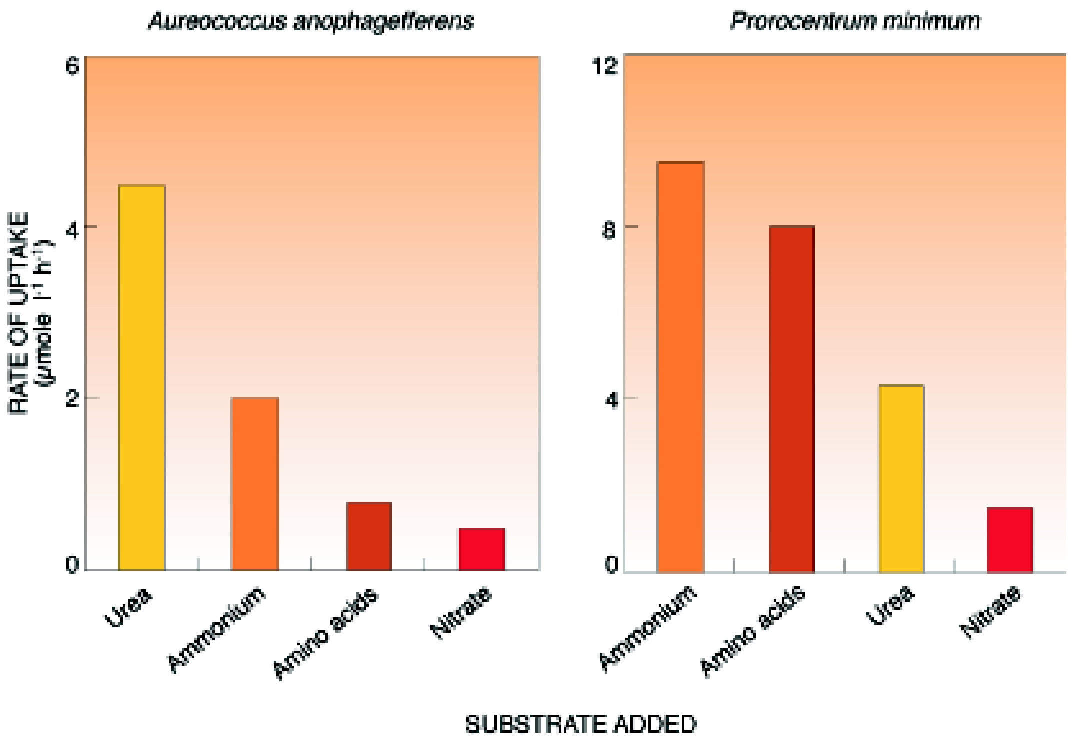
Rationale

Nutrient limitation of phytoplankton growth is a fundamental factor that restricts the accumulation of biomass and may determine the outcome of competition among species in mixed assemblages. Nutrients can stimulate or enhance the impact of toxic or harmful species in several ways. 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 (that is, all species are affected equally by the enrichment). Alternatively, there may be a selective enrichment of the HAB species by nutrient enrichment. It is increasingly recognised that certain species or groups of species have nutritional requirements or preferences, and therefore may be favoured when the environment is altered in such a way as to increase the relative availability of the preferred nutrient source.

This concept is often expressed as the nutrient ratio hypothesis (Tilman 1977, Smayda 1990, 1997), which argues that human activities have altered nutrient ratios in such a way as to favour harmful or toxic forms. For example, diatoms, the vast majority of which are harmless, require silicon in their cell walls, whereas other phytoplankton do not. Since silicon is not abundant in sewage effluent or agricultural wastewater runoff, but nitrogen and phosphorus are, the N:Si or P:Si ratios in coastal waters have increased in regions receiving sewage effluent. In theory, diatom growth will cease when Si supplies are depleted, but other phytoplankton can continue to proliferate. Red tides of Tolo Harbour in Hong Kong exemplify this effect. From 1976 to 1989, there was an 8-fold increase in dinoflagellate-dominated red tides coincident with a 6-fold increase in human population, a 2.5-fold increase in nitrogen and phosphorus loading (Lam and Ho 1989).

It was further demonstrated for Tolo Harbour that when N:P ratios fell below ~10:1, dinoflagellates such as *Prorocentrum micans*, *P. sigmoides*, and *P. triestrium*, increased in abundance (Hodgkiss 2001). In a similar manner, blooms of *Gymnodinium mikimotoi* in Tunisian aquaculture lagoons have been shown to increase when the N:P ratio declines seasonally (Romdhane et al. 1998).

There are other types of human development that can also affect nutrient ratios. The building of dams may decrease the availability of silicate to coastal waters (Zhang et al. 1999). In the development of the massive Three Gorges Dam in the upstream region of the Changjiang (Yangtze River), the potential for eutrophication and ecosystem changes due to alterations in the N:Si or N:P ratios have been greatly debated (Zhang et al. 1999).



Measurements of the rate of uptake of nutrients have proven to be insightful in determining nutritional preferences of HAB species. In this example, the rates of nitrogen uptake were determined using ^{15}N tracer techniques for two different bloom populations. The *Aureococcus anophagefferens* bloom occurred off Long Island, New York, while *the Prorocentrum minimum* bloom occurred in Chesapeake Bay, Maryland, U.S.A. Both species exhibited rapid rates of uptake in short-term incubations, and exhibited preferences for ammonium, urea, and amino acids over nitrate (adapted from Berg et al. 1997, and Glibert and Fan, unpublished data).

Some phytoplankton species, including HAB species, may preferentially use organic sources over inorganic sources of nutrients when both are supplied, suggesting that their growth may be promoted when organic sources are abundant (Cembella et al. 1984, Taylor and Pollinger 1987, Berg et al. 1997). For example, *Aureococcus anophagefferens* has been shown to preferentially use organic nitrogen over nitrate (Lomas et al. 1996, Berg et al. 1997). Such a nutritional preference may be an important factor regulating the dynamics of this species and co-occurring organisms. Furthermore, some phytoplankton species, including HAB species, may rely on mixotrophy to supplement their carbon or nitrogen requirements, providing an additional adaptive mechanism to survive and proliferate under conditions unfavourable for the growth of other algae (Sanders and Porter 1988, Stoecker 1999). Indeed, the ichthyotoxic dinoflagellate *Pfiesteria piscicida* is not an autotroph, and consumes fragments of epidermal tissue and blood cells from affected fish as well as bacteria and other small algal cells (Burkholder and Glasgow 1997, Lewitus et al. 1999).

Several cyanobacterial species (e.g., *Trichodesmium*, *Anabaena*, *Nodularia*, *Aphanizomenon*) are capable of fixing molecular nitrogen and may therefore form massive blooms in circumstances where the growth of other phytoplankton is limited by nitrogen.

While there have been many advances in our understanding of nutrient uptake pathways for many species, these pathways and preferences are complex. Many HAB species share similar nutrient preferences or uptake mechanisms with non-HAB species. The challenge is to understand under what conditions specific nutrient preferences may impart an advantage to HAB species.

Example Tasks

- Assess the importance of different nutritional strategies among HAB species and in comparison to non-HAB species
- Quantify the nutrient uptake and growth kinetics for HAB species in relation to competing organisms
- Determine the conditions under which a HAB species may adopt alternative nutritional strategies

Specific Objective #3

Determine the effects of varying nutrient inputs on the harmful properties of HABs

Rationale

While relatively few organisms have been examined, the available data suggest that the amounts and forms of toxins produced within certain HAB species may vary with physiological status, including nutritional state. Cellular toxin content of species from a variety of taxonomic groups varies dramatically during nutrient starvation in culture. For example, the abundance of saxitoxins in *Alexandrium* species can vary by more than an order of magnitude depending on whether phosphorus or nitrogen is limiting (e.g., Hall 1982, Boyer et al. 1987, Anderson et al. 1990). Likewise, domoic acid production in *Pseudo-nitzschia* species varies with silicate availability (Bates et al. 1991, Bates and Douglas 1993), and *Chysochromulina polylepis,* the prymnesiophyte responsible for massive fish and invertebrate mortalities in Sweden and Norway in 1987, has been shown to be more toxic when phosphorus is limiting (Edvardsen et al. 1990, Granéli et al. 1993). Nutrient enrichment may also stimulate toxin production. It has been shown in the laboratory, for example, that urea may stimulate toxin production in *Gymnodinium breve* (Shimizu et al. 1995). Combined nitrogen has also been shown to enhance *Microcystis* and *Anabaena* toxicity. Clearly, the effects of nutrient availability on toxicity have major implications with respect to our efforts to understand the manner in which HABs are influenced by, and, in turn, impact the environment.

As toxins are secondary metabolites, their production will depend on the physiological condition of the cells (Flynn and Flynn 1995). Differences in toxin production may therefore be related to changes in the growth rate or the stage of growth of an organism. Production of algal toxins can also be modulated by co-occurring bacteria (Bates et al. 1995) and in some cases, bacteria themselves may represent autonomous sources of phycotoxins (Kodama et al. 1988, Doucette and Trick 1995).

The relationship between nutrient availability and the development of other potentially harmful effects of algae, such as the production of mucilage, foams, and scums, is not well elucidated. Blooms of *Phaeocystis* spp., which recur in the Barents Sea, Norwegian fjords, and along the coast of the North Sea, are well known for depositing thick layers of odorous foam on the beaches (Lancelot et al. 1987). The foams are caused by the exudation of protein-rich compounds by the algae, which are then whipped into foams by wave action (Richardson 1997). *Phaecystis* blooms typically follow spring diatom blooms and appear to develop mucilagenous colonies when nitrate is the dominant source (Lancelot 1995). The negative impacts of the blooms and foams, including the clogging of fish gills and visible nuisance to beach visitors and fishermen, warrants considerable more effort on understanding the relationship between nutrient availability and these events.

A high biomass bloom of the prymnesiophyte *Phaeocystis pouchetii* on the Belgian coast. Photo by V. Rousseau, courtesy of Eurohab Science Initiative, 1998.

Example Tasks

- Measure toxin production in HAB species in culture at different stages of growth and under different nutritional conditions
- Determine the nutrient-dependent factors that regulate toxin synthesis
- Determine the role of nutrient supply in the production of noxious foams and scums

Specific Objective #4

Determine the role of nutrient cycling processes in HAB development

Rationale

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, U.S.A., nutrient input in the spring is 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 serves to support 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 the sediments. The 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 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 impoverished 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 various processes by which nutrients are recycled and transformed are critical for understanding HAB growth strategies.

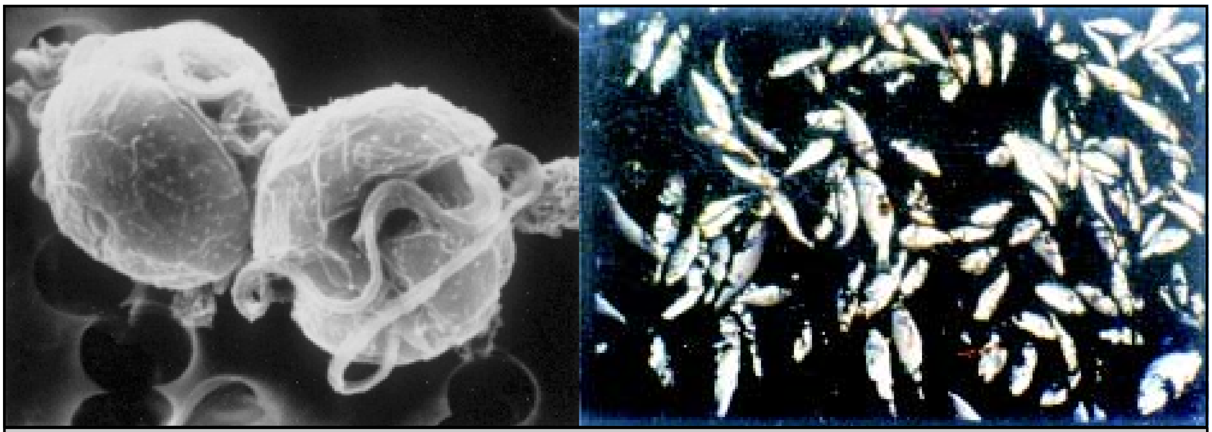
Example Tasks

- Determine nutrient transformation and regeneration processes in relation to HABs
- Assess the functional relationships between HAB species and the co-occurring non-HAB organisms, in terms of nutrient pathways and fluxes

OUTPUTS

The results of this Programme Element should lead to:

- Guidance for development of policies related to eutrophication and HABs
- Improved basis for establishing site selection criteria for aquaculture operations
- Quantitative baseline information for integrated coastal management



Among the toxic dinoflagellates, *Pfiesteria piscicida* and related species have been implicated as causative agents of some major fish kills along the east coast of the United States. Although nutritional stimuli influencing *P. piscicida* are complex, there are strong indications that this organism may thrive in systems that are impacted by eutrophication, particularly estuaries and tributaries receiving runoff and/or aerial deposition from agricultural and intensive animal operations.
Photos by C. Hobbs and J. Burkholder.

PROGRAMME ELEMENT 3: Adaptive Strategies

INTRODUCTION

HAB species are diverse with respect to their morphology, phylogeny, life history transitions, growth requirements, capacity for production of toxins and other bio-active compounds, and their intraspecific and interspecific interactions. Each species has a different combination of characteristics that defines its ecological niche, that is, the suite of factors that determines its distribution and activities. Although variations in species-specific characteristics are well described for many HAB organisms, the basis for intraspecific variability is poorly understood. Further research is needed to determine the relative contribution of genetic components versus expressed characteristics (phenotype) to this observed variability.

Adaptations are heritable traits that confer a selective advantage upon those individuals in the population capable of expressing them. As for all species, it can be assumed that many characteristics of harmful algae evolved and are maintained by natural selection and are thus adaptive. Adaptations are expressed at different scales, influencing processes at the level of the cell, colony, whole population, and community. Nevertheless, it must be recognised that not all variation is adaptive, in the sense that it necessarily provides a selective advantage. For example, morphological variations, such as changes in cell shape, size, and the production of spines, microfilaments, and horns in many phytoplankton species are often considered to be adaptations. But true adaptations are notoriously difficult to discriminate from short term phenotypic consequences of environmental perturbation. The challenge is to define unique adaptations of HAB species that account for their survival and persistence, and in some instances, their dominance during bloom events. By understanding the adaptations of different HAB species, it should be possible to describe and predict patterns of species abundance and harmful effects as functions of hydrographic processes, nutrient distributions, and community interactions. Improved generalisations about the causes and consequences of HABs would be particularly useful in management and mitigation of their effects.

It might be argued that once the physiological characteristics of a single species are well described, it should be possible to predict its presence and abundance, based on some knowledge of the environmental conditions. A corresponding view is that a given species will have maximum growth potential in conditions where environmental parameters – such as light, temperature, nutrient concentrations, or turbulence – are optimal for vegetative growth. However, the response of organisms in natural ecosystems is much more complicated; multiform life strategies, migratory behaviour, complex trophic interactions, and small-scale physical-biological interactions allow a species to exploit a spectrum of environmental conditions. By multi-faceted exploitation of ecological niches, the species may be able to survive and thrive in situations apparently far from its optimal requirements. In addition, while many classical physiological studies focus on the response of an organism to a single parameter, physical, chemical, and biological parameters interact and often vary independently in nature, thereby producing non-linear effects. Clear examples are the role of small-scale turbulence on nutrient assimilation (Karp-Boss et al. 1996) and grazing (Marrasé et al. 1990) and the relationships between water mixing and photoacclimation (Lewis et al. 1984). In the context of particular ecosystems, interactions between organisms and water circulation are essential to understand transport, population confinement, and persistence of certain blooms (Anderson 1997, Hallegraeff and Fraga 1998, Garcés et al. 1999).

Information on adaptive strategies should provide the physiological bases for explaining why HAB species occur and proliferate. This can be used to address relationships between HABs and eutrophication, to complement studies of biodiversity and biogeography, to support research on population dynamics in comparable ecosystems, and to guide the construction and parameterisation of models to predict HABs. The integration of this knowledge along a broad range of temporal and spatial scales will allow the development of integrative models coupling the biology of a species with physical and chemical processes.

In summary, this Programme Element aims to address the following research question:

What are the unique adaptations of HAB species and how do they help to explain their proliferation or harmful effects?

OVERALL OBJECTIVE

Define the particular characteristics and adaptations of HAB species that determine when and where they occur and produce harmful effects

THE STRATEGY

GEOHAB will foster the application of common techniques and the development of innovative technologies to enable detection of particular cell properties. Investigations of different HAB species and different strains of a single species from ecosystems worldwide is essential to ascertain their growth characteristics, physiological properties, and persistence in specific ecosystems. GEOHAB will also encourage the establishment of reference collections of HAB species.

A summary of the objectives and types of tasks that might be addressed under this Programme Element, as well as the anticipated outcomes, is provided in Figure 3.1.

Specific Objective #1

Define the characteristics of HAB species that determine their intrinsic potential for growth and persistence

Rationale

There is considerable diversity among HAB species with respect to patterns of growth and bloom formation in natural ecosystems. There are numerous explanations for the different patterns of bloom initiation and development, many of which are the result of unique adaptations of HAB organisms. Studies of cell characteristics related to vegetative growth and life-history transitions and their response to environmental factors are therefore essential to understanding the population dynamics of HABs.

The influences of important environmental factors, such as light, temperature, and turbulence, on the physiological, behavioural, and life history processes related to the growth of harmful algae have been quantified for only a few clones of some HAB species. Nevertheless, comprehensive data on the degree of intraspecific variability are rare and the interactions of physiological, behavioural, and life history processes with key environmental factors are not well known.

There is evidence of substantial differences among populations of the same species sampled from different locations and at different times (Bolch et al. 1999, Doblin et al. 1999). It is therefore important to study growth and behavioural characteristics of strains of a particular species from a number of globally distributed locations. Understanding the effects of all these factor

Figure 3.1 Summary of Programme Element 3: Adaptive Strategies.

OVERALL OBJECTIVE Programme Element 3: Define the particular characteristics and adaptations of HAB species that determine when and where they occur and produce harmful effects

1
Define the characteristics of HAB species that determine their intrinsic potential for growth and persistence

- Determine tolerance ranges and optima for growth and toxin production in response to a suite of environmental variables
- Culture and compare growth of multiple strains of individual species under different environmental conditions
- Characterise environmental influences on life history events, including resting stages

2
Define and quantify biological-physical interactions at the scale of individual cells

- Quantify the effects of small-scale turbulence on nutrient acquisition, growth, and motility
- Assess the factors controlling vertical migration behaviour
- Define the effect of fluctuating environmental regimes on growth processes and life history events including excystment and encystment.
- Determine the functional role of size, shape, mucus production, and the formation of colonies or aggregates

3
Describe and quantify chemical and biological processes affecting species interactions

- Identify key bio-active compounds that mediate species interactions
- Assess the importance of toxin production in selective grazing
- Characterise modes of action of bio-active compounds on other organisms

4
Identify the functional role of cell properties

- Identify morphological, physiological, life-history, and behavioural characteristics that form the basis for common patterns of species in nature
- Assess the role of toxins and other bio-active compounds in determining functional groups

OUTPUTS
- Establishment of HAB strains and species within an international network of reference culture collections
- Identification of key adaptive strategies of particular HAB species
- Ecologically-based classification of different species according to their adaptations and characteristics
- Quantification, parameterisation, and prioritisation of ecophysiological processes at the cellular level for incorporation into models

Cell growth can be defined in many ways, including changes in cell number, size, volume, or mass. With respect to HAB dynamics, the following conventional definitions are commonly used:

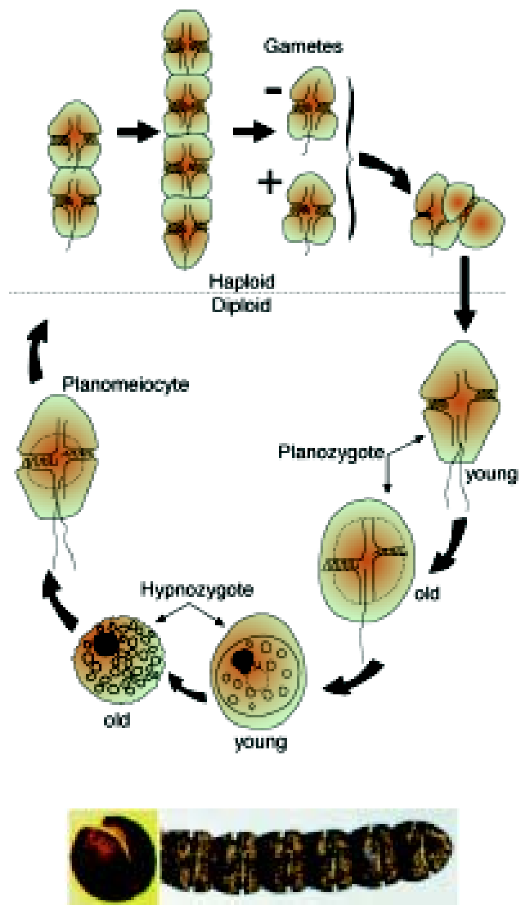
Growth rate *is the change in cell number with time. The growth rate is limited by intrinsic factors, such as the rate of DNA replication in the cell cycle, as well as by external conditions.*

Generation time *is the time required for cells to double in number (also called the "doubling time"). The time for one complete cell division cycle is called the division time. For many bloom-forming species, this typically ranges from several hours to a few days.*

Population growth rate *is the net rate of change in cell numbers in a population, usually expressed within a defined water volume under natural conditions. This parameter is estimated from the increase in cell numbers through time, and thus includes cell losses due to physical transport and biological factors such as grazing.*

Although the critical importance of resting cysts in the bloom strategies of HAB species is recognised (Anderson 1998, Imai and Itakura 1999), for most HAB species there are significant unknown elements, for example, the sexual basis for resting cyst formation (heterothallism, homothallism, mating systems), dormancy period, encystment and interactions requires the use of diverse strains of HAB species in culture under carefully controlled multi-dimensional experimental regimes.

Many HAB species have complex life histories that include different morphotypes as well as the formation of various types of resting stages. For example, in certain dinoflagellates and raphidophytes, the formation of resting stages (or cysts) with resistant walls expands the tolerance range of the species and therefore allows extension of its geographical distribution. The induction of sexuality can have important short-term consequences for the population growth. During the initiation of sexual reproduction, the generation time increases dramatically as the asexual (vegetative) cell division rate declines, effectively to zero for those cells that become gametes. Although not all cells in a population participate in sexual reproduction, the net population growth rate may even be negative because of reduction in cell numbers through fusion of gametes and subsequent hypnozygote formation.



In the life history of a typical cyst-forming dinoflagellate, such as that depicted here for *Gymnodinium catenatum*, there is an alternation of asexual stages (vegetative cells) with sexual forms (zygotes). The fusion of gametes formed from vegetative cells results in the formation of a swimming planozygote, which subsequently loses its flagella to form a zygotic resting stage (or cyst). Both external environmental triggers (light, temperature, nutrients) and endogenous rhythms have been implicated in inducing life cycle transitions in various species. Transitions between vegetative and resting stages can influence population dynamics by determining the size of the "seed" stock or inoculum for subsequent bloom initiation.

excystment cues, and the numerical and genetic contribution of cysts to bloom dynamics. Complete descriptions of life cycles, including the definition of mating-type systems, dormancy requirements of resting stages, and the effect of environmental factors on inducing cyst production and germination are needed.

The motile asexual stage of *Chattonella antiqua*, a marine raphidophyte implicated in numerous incidents of mass mortalities of fish, may undergo sexual reproduction under unfavourable environmental conditions after bloom events. A roughly spherical haploid resting cyst is formed and persists in the sediment until excystment is triggered, typically by a change in the environmental regime, such as a shift in temperature.

One of the most common harmful consequences of blooms of *Phaeocystis* species is the nuisance caused by the dense foams produced by the colonial life-cycle stage. Although several researchers have addressed the transition between colonial and flagellated stages, many aspects of the life cycle of this species, as well as the environmental factors driving transitions among the different stages, are still hypothetical (Rousseau et al. 1994). Such stage transitions are clearly subject to strong selective pressure and environmental regulation. The challenge is to describe the life history strategies and to establish how they respond to environmental forcing in the ecosystems in which they are expressed.

Example Tasks

- Determine tolerance ranges and optima for growth and toxin production in response to a suite of environmental variables
- Culture and compare growth of multiple strains of individual species under different environmental conditions
- Characterise environmental influences on life history events, including resting stages

Reference culture collections are essential in studies of adaptive strategies of HAB species. Such collections provide genetically consistent strains that can be shared among laboratories for experiments under defined environmental conditions. Photo by T. Kana.

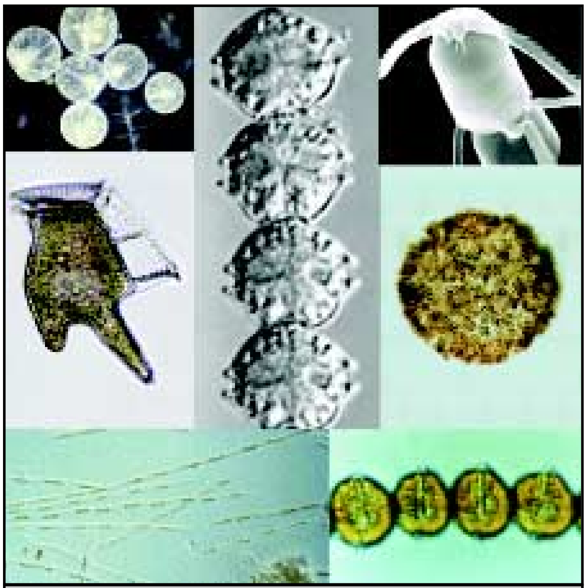
Specific Objective #2

Define and quantify biological-physical interactions at the scale of individual cells

Rationale

The mechanisms through which HAB species interact with their environment must be characterised to understand and predict their distributions and effects in natural waters.

Small-scale turbulence needs to be considered because it may have significant consequences for the growth and decline of HABs through its influence on the transport of nutrients, and by direct impairment of growth (Estrada and Berdalet 1998). Some phytoplankton, including *Alexandrium* species, are very sensitive to turbulent motion even at low levels (White 1976, Thomas et al. 1995), whereas others seem to benefit from higher levels of turbulence that enhance nutrient availability and uptake, thereby increasing the rate of cell growth and division (Kiørboe 1993). Diatoms have recently been shown to react within a few



Many morphological and physiological characteristics of HAB species may be adaptive strategies. Examples shown in this panel include: buoyancy/sinking regulation through adjustment of ion balance, gas vacuoles, colony formation, and spine production, and the use of external wings/rudders and chain formation to optimize swimming capacity.

seconds to external shear and chemical stimuli (Falciatore et al. 2000), faster than the variations in mechanical stress within small eddies under ocean conditions. The generality and ecological significance of such responses should be assessed for HAB species.

Physical processes, such as wind-mixing, convection and upwelling, can profoundly influence the irradiance field experienced by phytoplankton, and thus the conditions for photosynthesis and growth. Consequently, phytoplankton species have developed a range of physiological and behavioural adaptations for different mixing regimes, which may include vertical migration (Cullen and MacIntyre 1998). Some species are adapted to exploit fluctuating irradiance associated with rapid vertical mixing (Ibelings et al. 1994).

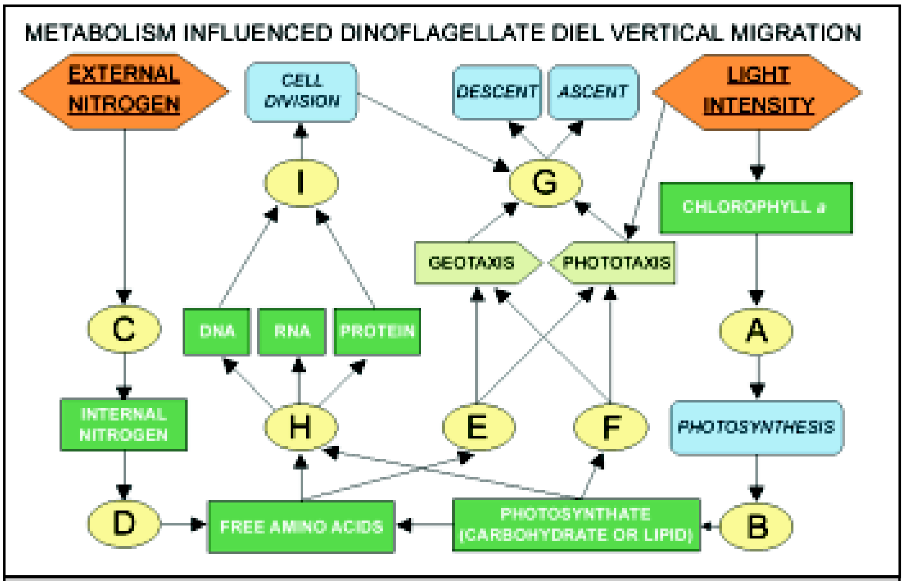
Adaptations for life in strongly stratified waters include physiologically regulated changes in buoyancy (Walsby and Reynolds 1980) and motility (Kamykowski 1995), resulting in vertical migration or the maintenance of stable subsurface layers of phytoplankton. These adaptations must be understood to explain the selection for HAB species in particular hydrographic regimes.

Physical processes strongly influence the biological responses of phytoplankton cells, but biological processes can also influence physical characteristics of the water. For those HAB species that produce dense blooms, the processes of flocculation and deflocculation may change their physical and chemical environment, as well as the spatio-temporal distribution of cells. The production and disintegration of cellular flocculations and colonies is partly a non-linear interaction of cell stickiness and turbulence (Kiørboe and Hansen 1993, Hansen et al. 1995). Flocculation, cell adhesion, and aggregation need to be better understood, as do the effects of water movement and organism motility on communication among cells and colonies, and between these organisms and their physico-chemical environment (Jenkinson and Wyatt 1992).

Research on the importance of the size and shape of organisms, including phytoplankton, has gradually progressed for several decades (such as Margalef 1978, Vernadskiy 1978, Kamenir and Khaylov 1987, Reynolds 1997). However, this work has been hampered by difficulties in assessing the contributions by soft structures, such as mucus sheaths and processes projecting from pores, as well as hard structures (such as siliceous setae) to the functional dimensions of organisms. These features, which may represent adaptations for particular hydrodynamic regimes, can also be responsible for harmful effects, such as the clogging or laceration of gills of fish. Studies of functional size and shape of HAB species and how morphological features vary in response to turbulence (as well as to other environmental influences) is thus essential to a fundamental understanding of both HAB population dynamics and the expression of harmful effects.

Example Tasks

- Quantify the effects of small-scale turbulence on nutrient acquisition, growth, and motility
- Assess the factors controlling vertical migration behaviour
- Define the effect of fluctuating environmental regimes on growth processes and life history events including excystment and encystment
- Determine the functional role of size, shape, mucus production, and the formation of colonies or aggregates



A flowchart describing the relationships between environmental forcing, physiological rate processes, biochemical pool concentrations, cell division, and behaviour for a hypothetical dinoflagellate (modified from Kamykowski et al. 1999). The circled letters refer to functions that must be defined in a detailed model.

Specific Objective #3

Describe and quantify chemical and biological processes affecting species interactions

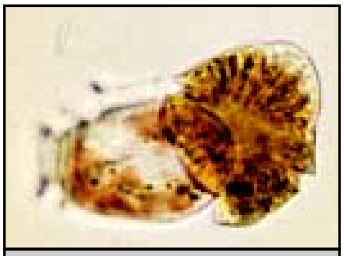
Rationale

Harmful algae do not exist in isolation in natural ecosystems and thus they are influenced by interactions between individual cells of the same and other species. Food-web interactions have a profound effect on the population dynamics of HAB species. Processes such as competition and grazing can strongly affect the net growth rates of phytoplankton in nature.

Bio-physical constraints may have a profound effect on the microenvironment surrounding cells of HAB species and their competitors and predators. For example, even a low level of mucus as produced by some harmful algae may make respiration (Jenkinson and Arzul 1998) and filter-feeding more energetically costly and slower. Mucus tends to show its most pronounced properties, such as increased polymeric viscosity and elasticity, in association with algae, with increasing effect varying with increasing phytoplankton abundance (Jenkinson and Biddanda, 1995). This is consistent with abundant organisms having a relatively greater potential to interact with each other and to change their environment to their selective advantage.

Chemical interactions (including the effects of toxins and other bio-active compounds) are little understood but they may be critical for communication within populations of HAB species, as has been hypothesised for *Alexandrium* (Wyatt and Jenkinson 1997). In addition, these substances could influence growth and the outcomes of interspecific interactions in the presence of competitors (allelochemical effects) and predators, as shown in the case of *Heterosigma akashiwo* (Pratt 1966, Tomas and Deason 1981). The production and utilisation of trace organic substances such as vitamins and chelators also represent biological processes that can strongly influence interactions among species.

The production of phycotoxins as potential anti-predator defence mechanisms is a good example of a chemically mediated interaction. Toxin production may have important implications for the maintenance and dynamics of harmful algal blooms by inhibiting grazing. To date, however, evidence that some HAB species are in fact toxic to their potential grazers such as copepods, is rather equivocal (Turner and Tester 1997). For example, whereas some authors have reported pre-ingestive rejection of toxic *Alexandrium* strains by copepods (Huntley et al. 1986), others have found that some copepods were unaffected and fed at high rates on both toxic and non-toxic *Alexandrium* cells (Teegarden and Cembella 1996). Most of these studies, however, both in the laboratory and in situ, have been carried out during the course of short-term (one day) grazing experiments. A further caveat is that the grazing responses of copepods are highly species-specific and may vary according to the state of pre-conditioning (starved versus replete individuals), the prey concentration, and the diversity of the food regime offered. Furthermore, few studies have been made to evaluate long-term effects of exposure to algal toxins, as would be the case during a HAB bloom lasting several days to weeks, when zooplankton grazers would have less choice in available prey species. Finally, the sub-lethal effects on zooplankton grazers of acute exposure to phycotoxins and consequent effects on fertility, quality and quantity of egg production, and hatching success must be investigated as a long term factor in the "top-down" control of bloom dynamics.



Many bloom-forming flagellates have phagotrophic capabilities – the ability to engulf and ingest particulate material for nutritional purposes, even, in some cases, large prey species as is shown here.

HAB species can employ different trophic strategies, including the utilisation of organic compounds (Carlsson and Granéli 1998), nitrogen fixation, and consumption of prey organisms (e.g., mixotrophy; Granéli and Carlsson 1998, Hansen 1998). These processes and the extent to which they contribute to blooms are not well known for most HAB species. However, specific trophic strategies may be crucial to proliferation of HAB species and must be investigated in the context of adaptations, effects of eutrophication, and the modelling of ecosystem processes.

Example Tasks

- Identify key bio-active compounds that mediate species interactions
- Assess the importance of toxin production in selective grazing
- Characterise modes of action of bio-active compounds on other organisms

Laboratory studies are essential to understanding adaptive strategies. Controlled experiments with cultured cells can be used to discriminate genetic factors that are truly adaptive, in that they offer a selective advantage, from short-term responses to environmental conditions. Photo by M Trice.

Specific Objective #4

Identify the functional role of cell properties

Rationale

Harmful species belong to several distinct phylogenetic groups, and therefore have different morphologies, ecophysiological requirements, and growth dynamics. Ecological diversity is evident even at the intraspecific level. For example, *Heterosigma akashiwo* is able to thrive in many different environmental conditions (see Smayda 1998 for a review), and different bloom mechanisms have been suggested for *Gymnodinium catenatum* in Tasmanian and Atlantic Spanish waters, respectively (Hallegraeff and Fraga 1998).

Nevertheless, convergent morphological, physiological and ecological traits are also common among harmful species, despite considerable phylogenetic distances. To reduce the natural complexity and facilitate the development of conceptual and numerical models of HAB dynamics, it is desirable to recognise, among HAB species, common patterns of response to environmental factors. These common patterns may be based on similarities in morphological, ecophysiological (such as life strategies, trophic characteristics), or behavioural (such as swimming, migration) adaptations. In this context, functional groups can be recognised as sets of organisms sharing a particular suite of adaptations.

*What are "**life-forms**" or "**functional groups**"?*

*"... '**life-forms**'... can be conceived as the expression of adaptation syndromes of organisms to certain recurrent patterns of selective factors. I have chosen as principal factors those related to the supply of external energy, i.e., supply of nutrients and decaying turbulence." (Margalef 1978).*

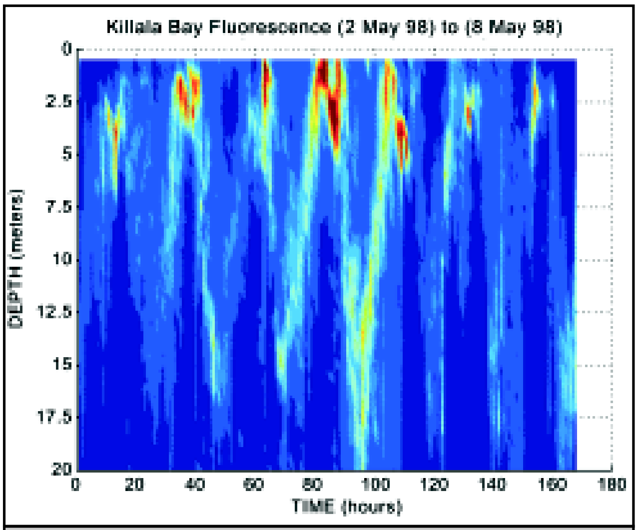
*"**Functional groups** are groupings of species based on physiology, morphology, life history, or other traits relevant to controls on an ecosystem process..." (Hooper and Vitousek 1997).*

*"... a **functional group** is a non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors... a functional group is the basis for a context-specific simplification of the real world to deal with predictions of the dynamics of the systems or any of their components..." (Gitay and Noble 1997).*

The aim of the specific objective considered here is complementary to the aspect of the large-scale ecosystem studies that focuses on the identification of groups of species commonly co-occurring in nature. The species constituting these recurrent groups can be considered as examples of ecological convergence; their study can help to identify the cellular properties forming the basis for their common distributional patterns.

Efforts to interpret the ecological implications of morphological or other phenotypic phytoplankton characteristics have been reviewed by Sournia (1982), Elbrächter (1984), Fogg (1991), and Kiørboe (1993), among others. However, while some cellular properties (such as size) have well described ecological implications (e.g., faster sinking for larger organisms), the significance of many other features is unknown.

The range of morphological variability exhibited among HAB species is impressive. Some species occur as single cells whereas others may form colonies, including large aggregates formed by mucilage production. Chain formation in flagellated HAB species has been shown to enhance swimming speed (Fraga et al. 1989). Cells



Time-depth fluorescence showing diel vertical migration of the toxic dinoflagellate *Gymnodinium catenatum* at Killala Bay in the Huon Estuary, Tasmania. In vivo fluorescence of chlorophyll pigment is used to track the rhythmic movement of cells in the water column. From CSIRO Marine Research.

may be non-motile and only passively subject to dispersion, flagellated and thus capable of swimming, or non-motile, but able to regulate their cell buoyancy. Certain species may exhibit aspects of all of these properties at various stages of their life history.

Differences in size, shape, and surface/ volume ratio influence properties such as nutrient uptake capacities and reaction to small-scale turbulence (Karp-Boss et al. 1996). In addition, size and shape affect grazing vulnerability and the spectrum of potential grazers.

Different functional groups can be represented not only by different species, but also by different stages of the cell division or life cycle. Alternative life histories of HAB organisms create both functional diversity within a species and commonalities among species. For example, some organisms undergo asynchronous cell division, apparently independent of the photoperiod, whereas others may divide only during a narrow window of the light/dark cycle. The life history of a species may include resting stages – often but not invariably with an obligatory dormancy period before resuming vegetative reproduction (Pfiester and Anderson 1987).

Another aspect of functional groups refers to toxic properties. Species with different morphologies and phylogenetic affinities, and found in diverse habitats, may nevertheless produce a similar suite of toxins. For example, PSP toxins are found in species of the dinoflagellates *Alexandrium*, *Gymnodinium*, *Pyrodinium*, and certain strains of the cyanobacteria *Aphanizomenon* and *Anabaena* (Cembella 1998). Conversely, toxin production may vary among strains of the same species and depend upon environmental factors (such as nutrient concentration).

Example Tasks

- Identify morphological, physiological, life-history, and behavioural characteristics that form the basis for common patterns of species in nature
- Assess the role of toxins and other bio-active compounds in determining functional groups

OUTPUTS

The results of this Programme Element should lead to:

- Establishment of HAB strains and species within an international network of reference culture collections
- Identification of key adaptive strategies of particular HAB species
- Ecologically-based classification of different species according to their adaptations and characteristics
- Quantification, parameterisation, and prioritisation of ecophysiological processes at the cellular level for incorporation into models

PROGRAMME ELEMENT 4: Comparative Ecosystems

INTRODUCTION

HABs occur in pelagic and benthic ecosystems, and these can often be classified operationally, according to their physical and chemical characteristics and their particular biology. Comparative approaches have a long tradition in ecology but have been relatively underused in aquatic sciences (Cole et al. 1991). There is a need therefore to develop marine ecosystem typologies and to then classify marine ecosystems into these similar types for the purposes of comparison.

Comparisons of ecosystems allow the synthesis of knowledge and data needed to group HABs from similar habitat types and to distinguish the mechanisms controlling their population dynamics. The adaptive strategies of key HAB species will also be better understood in the context of particular ecosystem types or particular processes.

Having identified characteristic marine ecosystem types and having classified ecosystems, understanding the response of HABs to perturbation or change within these systems (both natural, such as climate variability, and anthropogenic, such as eutrophication) is important. Similar ecosystems should respond in broadly similar ways, therefore the identification of early warning indicators of system changes within and across ecosystem types will greatly help prediction and possible mitigation of the effects of change on the incidence of HABs. It will also permit extension of predicted responses to similar but less well studied ecosystems. Identification of divergences from predicted responses will also be informative.

In summary, this Programme Element aims to address the following research question:

To what extent do HAB species, their population dynamics, and community interactions respond similarly under comparable ecosystem types?

OVERALL OBJECTIVE

To identify mechanisms underlying HAB population and community dynamics across ecosystem types through comparative studies

THE STRATEGY

GEOHAB will foster similar field investigations in comparable ecosystems from different regions, accompanied by the exchange of technology and data. Classification of systems based on physical, chemical, and biological regimes will be possible through GEOHAB. Through such a comparative approach, the identification of the critical processes controlling HABs in different hydrographic, chemical, and biological regimes will be possible.

A summary of the objectives and types of tasks that might be addressed under this Programme Element, as well as the anticipated outcomes, is provided in Figure 4.1.

Figure 4.1 Summary of Programme Element 4: Comparative Ecosystems.

OVERALL OBJECTIVE Programme Element 4: To identify mechanisms underlying HAB population and community dynamics across ecosystem types through comparative studies

1
Quantify the response of HAB species to environmental factors in natural ecosystems

- Develop methods for in situ estimation of physiological rates of HAB species
- Incorporate studies of resting stage dynamics into field investigations
- Parameterise the vertical migration and buoyancy regulation of HAB species in natural ecosystems

2
Identify and quantify the effects of physical processes on accumulation and transport of harmful algae

- Characterise the hydrodynamic processes of particular ecosystems and prioritise their effects on HAB dynamics
- Identify and quantify the specific suite of biological features associated with HABs in particular hydrographic regimes
- Measure key biological variables at spatial and temporal scales consistent with those of the physical variables

3
Identify and quantify the community interactions influencing HAB dynamics

- Determine the effects of bioactive compounds within natural communities on HAB dynamics
- Determine the importance of density-dependent processes in HABs
- Quantify the effects of microbial pathogens on HABs
- Determine the role of grazing control in HAB dynamics

4
Define functional groups in communities containing HAB species

- Determine groups of co-occurring taxa or assemblages within given ecosystem types
- Establish the distribution of functional groups and their relationship to environmental factors
- Identify common morphological, physiological, and life-history features within HAB species and define the environmental characteristics that support these specific features

OUTPUTS

- Identification of common physiological and behavioural characteristics of HAB species in given ecosystem types
- Quantitative descriptions of the effects of physical forcing on bloom dynamics
- Bases for developing management and mitigation strategies tailored to the characteristics of particular organisms

Example ecosystem types, as defined by their bathymetry, hydrography, nutrient status, productivity, and trophic structure:

- *Upwelling systems, such as those off the coast of Portugal and Spain, Peru, Mazatlan in Mexico, the west coast of the United States, Australia, Japan, West Africa, and Southern Africa.*
- *Estuaries, fjords, and coastal embayment systems, as in the United States, Canada, Australia, southeast Asia, Philippines, Mexico, Scandinavia, and Chile.*
- *Thin-layer producing systems along most coasts, including the Atlantic coast of France, Sweden, California, and in East Sound, Washington.*
- *Coastal lagoon systems such as in the United States, Mexico, Brazil, and France.*
- *Shelf systems affected by basin-wide oceanic gyres and coastal alongshore currents such as off the northwestern European coast, the Gulf of Mexico and Gulf of Maine in the United States, and off the coast of southeastern India.*
- *Systems strongly influenced by eutrophication, such as in Hong Kong, Black Sea, Baltic Sea, Adriatic Sea, Seto Inland Sea of Japan, and the mid-Atlantic regions of the United States.*
- *Brackish or hypersaline water systems such as the Baltic Sea, St. Lawrence, Dead Sea, and Salton Sea.*
- *Benthic systems associated with ciguatera in the tropics or DSP in temperate waters.*

The above list is not intended to be comprehensive or exclusive, and these systems are offered only as examples of the types of ecosystems that could be studied and compared within GEOHAB. Upper right photo by F. Kristo.

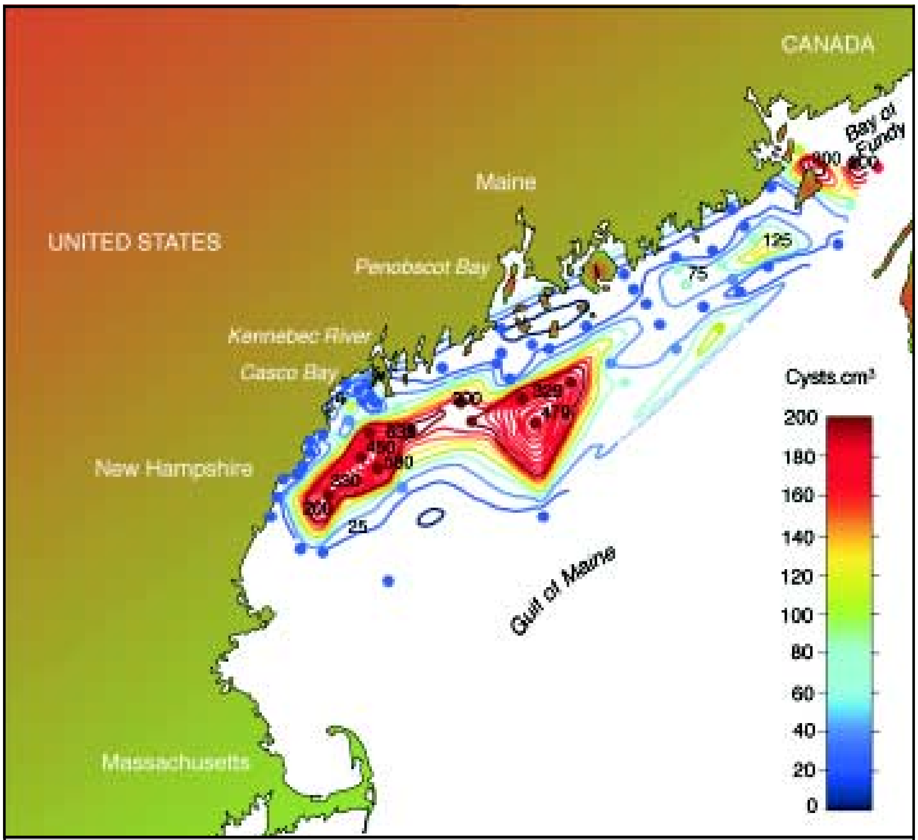
Specific Objective #1

Quantify the response of HAB species to environmental factors in natural ecosystems

Rationale

Studies of species responses at the ecosystem level are essential to understanding the population dynamics of HABs. The specific growth rate of a species is determined by many metabolic processes, including photosynthesis, and nutrient uptake and assimilation, all of which are under genetic control. The net population growth of a species is controlled by external environmental factors, including physical transport, grazing, and other community interactions. An important step in the investigation of HABs should therefore be a series of studies that characterize the response of populations to the physical, chemical, and biological characteristics of the natural environment.

For example, turbulence has significant consequences for the growth and decline of HABs by influencing the transport of nutrients, the mixing of phytoplankton through gradients of light, and by direct impairment of growth. Many HAB species are motile, and under certain environmental conditions their swimming behavior or buoyancy may result in the formation of high-density patches (e.g., Franks 1992, Cullen and MacIntyre 1998, Kamykowski et al. 1998). Diel vertical movement by motile cells in a stratified environment undoubtedly has functional significance, maximizing encounter frequencies for sexual reproduction, minimizing grazing losses, and allowing cells to optimize nutrient acquisition at depth and light-dependent photosynthetic reactions near the surface. Some cyanobacterial species are able to regulate their vertical positioning in the water column by synthesis and collapse of gas vesicles and by accumulation of photosynthetic "ballast." The challenge is to identify which conditions will cause a particular species to bloom or conversely to cause its strategy to fail.



The distribution of *Alexandrium tamarense* cysts in the nearshore waters of the Gulf of Maine. Two distinct seedbeds are evident in the offshore waters. These are thought to play an important role in the timing and location of bloom development for this toxic dinoflagellate, but new methods and approaches are needed to quantify this input. (Source: D.M. Anderson, unpublished data)

Another survival and growth strategy that should be explored involves the benthic resting stages of many HAB species. These cysts or spores provide a recurrent seed source or inoculum for planktonic populations. The capacity to form resting stages may be a critical factor in determining not only the geographic distribution of species, but also their cellular abundance over time (Anderson and Wall 1978, Anderson 1998, Imai et al. 1998). Therefore, it is important to establish the role of various environmental factors in regulating resting stage formation and germination, and to quantify these processes.

These are a few examples of the many physiological, behavioural, and life history processes of HAB species that interact with environmental factors. Population studies should allow the identification of the common mechanisms and processes that underlie the dynamics of HAB species occurring within particular ecosystem types.

Example Tasks

- Develop methods for in situ estimation of physiological rates of HAB species
- Incorporate studies of resting stage dynamics into field investigations
- Parameterise the vertical migration and buoyancy regulation of HAB species in natural ecosystems

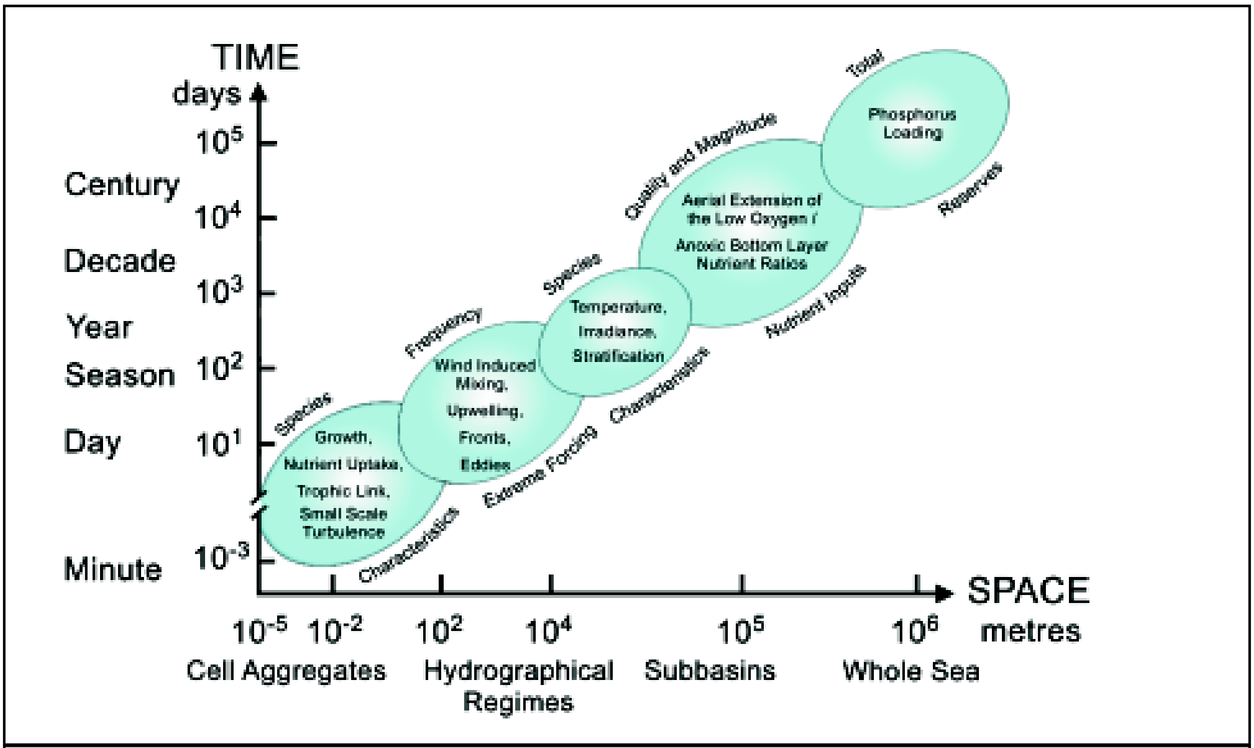
Specific Objective #2

Identify and quantify the effects of physical processes on accumulation and transport of harmful algae

Rationale

The geographic range, persistence, and intensity of HABs are determined by both physical and biological factors. For example, 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 (such as *Alexandrium* in the Gulf of Maine; Anderson and Keafer 1987); transport of cells from a source region where blooms are already established (such as *Gymnodinium catenatum* in northwest Spain; Fraga et al. 1988), and exploitation of unusual climatic or hydrographic conditions (such as *Pyrodinium bahamense* in the Indo-West Pacific; Maclean 1989). Once a population is established, its range and biomass are affected by physical controls such as the transport and accumulation of biomass in response to water flows (such as Franks and Anderson 1992), by the swimming behaviour of organisms (Kamykowski 1974, Cullen and Horrigan 1981) and by the maintenance of suitable environmental conditions (including temperature and salinity, stratification, irradiance, and nutrient supply; Whitledge, 1993). Thus, physical forcings, nutrient supply, and the behaviour of organisms all interact to determine the timing, location, and ultimate biomass achieved by the bloom, as well as its impacts.

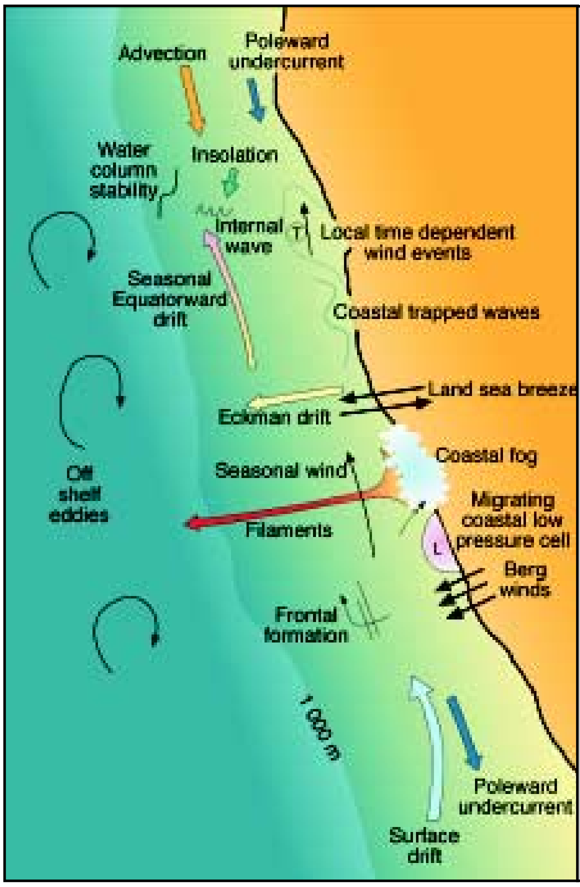
Physical processes that are likely to influence the population dynamics of HAB species are operative over a broad range of spatial and temporal scales. Large-scale, mean circulation affects the distribution of water masses and biogeographical boundaries. The understanding of the main features of mean circulation is sufficient to devise models of the circulation of many estuaries, coastal currents, and upwelling areas. Time-dependent, atmospherically and tidally-forced models are available for many geographic regions (such as the North Sea, Baltic, Bay of Biscay, Gulf of Maine and Gulf of Mexico) and may be used to predict the movement and development of HABs, although considerable uncertainty remain, however, in forecasting their dispersion. Many examples of the influence of mesoscale circulation on HAB population dynamics may be found. 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 *Gymnodinium breve* 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 satellite remote sensing of temperature, sea-surface height, or ocean colour.



The processes regulating cyanobacterial blooms in the Baltic have been identified at the scales depicted above (Kononen and Leppänen 1997).

Processes at intermediate scales result in the formation of convergence zones, fronts, and upwelling. There are many examples of the importance of fronts in phytoplankton bloom dynamics, and several prominent studies involve HAB species (Franks 1992). For example, a linkage has been demonstrated between tidally generated fronts and the sites of massive blooms of the toxic dinoflagellate *Gymnodinium mikimotoi* (= *Gyrodinium aureolum*) in the North Sea (Holligan 1979). The pattern generally seen is 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 surface 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 *G. mikimotoi* populations into contact with fish and other susceptible resources, resulting in massive mortalities. This is an example where small-scale physical-biological coupling results in biomass accumulation, and larger-scale advective mechanisms cause the biomass to become harmful.

The rias of northwest Spain are a group of oceanic bays noted for their prolific production of blue mussels. Here, PSP toxicity is not primarily due to the in situ growth of toxic cells, but rather to the transport and introduction of blooms that originate elsewhere. Similar meteorology, hydrography, and patterns of PSP are found in the California and Benguela current systems. A comparative approach may therefore aid in developing a fundamental understanding of the linkage between large-scale forcings and the pattern of PSP toxicity.



A schematic representation of the complex array of physical processes affecting the shelf zone of the Benguela upwelling system (Shannon et al. 1990), a region prone to HABs. Wind is a dominant factor at all spatial scales, having a direct influence on large-scale currents, local upwelling and frontal dynamics, and the dynamics of the surface mixed layer. Consequently, the formation of red tides has been closely linked to the prevailing winds of the Benguela (Pitcher et al. 1998). The seasonal development of subsurface dinoflagellate blooms is associated with increased stratification during the upwelling season, which depends in a fairly predictable way on the wind and insolation. The dinoflagellate populations appear as a surface bloom in the region of the upwelling front, which is displaced from the coast during the active phase of upwelling. Red tides form and impact on the coast following relaxation of upwelling and the onshore movement of the upwelling front, as cross-shelf currents become weaker and directed onshore. During these periods of decreased wind stress, net poleward surface flow is responsible for the southward propagation of red tides.

The importance of small-scale physical processes in HAB development is observed in the layering of the physical, chemical, and biological influences 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 proximity of the thermocline (Gentien et al. 1995). Several HAB species are known to form thin, subsurface layers of uncertain cause and unknown persistence, at scales as small as 10 cm in the vertical and as large as 10 km in the horizontal dimension. One simple kinematic explanation is that these layers result from the stretching of horizontal inhomogeneities by the vertical shear of horizontal currents. This produces an environment potentially favouring motile organisms that can maintain their position in this layer. Resolution of the biological, physical, and chemical mechanisms underlying these aggregations should be an important area of GEOHAB investigation.

Tidal- and wave-induced currents generate turbulence in the bottom boundary layer. One key element of this interaction involves the benthic resting stages of many HAB species, which serve to re-colonise the water column. The magnitude and timing of the contribution of motile cells through cyst germination, and the physical, chemical, or biological mechanisms that influence that process are major unknowns in HAB dynamics (Anderson 1998). Although cyst germination is of great importance to the bloom dynamics of many HAB species, it is still not known whether the germination that occurs is gradual and predominantly from the surface sediments, or is episodic and dominated by the resuspension of sediments following erosion of deeper sediment layers.

The above represent some well established examples of the effects of physical processes on the distribution of harmful algae. There are, however, many examples where the physical processes common to particular ecosystems are poorly characterised and understood and therefore their influence on HAB species remains uncertain. Comparative studies provide an opportunity to ascertain and describe the physical processes common to particular ecosystem types and to evaluate the importance of these processes to the distribution of HABs within those ecosystems.

Example Tasks

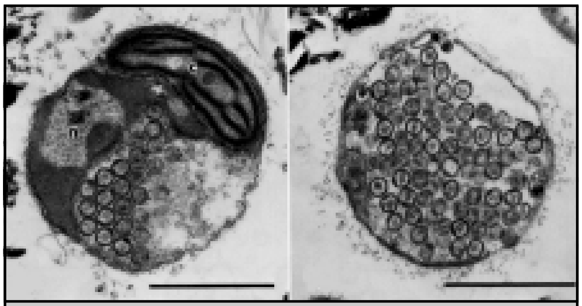
- Characterize the hydrodynamic processes of particular ecosystems and prioritise their effects on HAB dynamics
- Identify and quantify the specific suite of biological features associated with HABs in particular hydrographic regimes
- Measure key biological variables at spatial and temporal scales consistent with those of the physical variables

Specific Objective #3

Identify and quantify the community interactions influencing HAB dynamics

Rationale

The growth and accumulation of the cells that cause HABs, is, in many cases, a consequence of the interaction of those cells with other members of the planktonic community. For example, viruses are now known to have significant impacts on the dynamics of marine communities and some viruses have been found to infect algae and have been implicated in the demise of red or brown tide blooms (Fuhrman and Suttle 1993).



Viruses may dramatically influence planktonic communities. In the above figure, cells of *Aureococcus anophagefferens* from Narragansett Bay are shown infected with polyhedral virus particles (from Sieburth et al. 1988). Similarly, Nagasaki et al. (1994a,b) linked the collapse of a red tide bloom of *Heterosigma* to the appearance of virus particles within algal cells.

Similarly, recent research suggests that bacteria could play an important role in controlling HABs and regulating their impacts, including their toxicity. An intriguing example is the bacterium responsible for the decline of *Gymnodinium mikimotoi* blooms (Ishida et al. 1997). A bacterial strain isolated at the end of a *G. mikimotoi* bloom was found to exhibit strong and very specific algicidal activity against this dinoflagellate species. Bacteria may also interact with HABs in a positive manner by stimulating their growth. 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 is not known, and represents an important line of inquiry.

Interactions also occur between HAB species and other algae. For example, it has long been argued that production of allelopathic exudates allows some harmful species to outcompete co-occurring phytoplankton (Pratt 1966, Smayda 1998). Some HAB species that form thin subsurface or surface layers of cells at extraordinary densities (Gentien et al. 1995, Smayda 1998) may do so because this allows them to change the ambient water chemistry and light penetration in a manner that deters grazing or that inhibits co-occurring algal species. These ecological strategies are appealing, but there are few direct investigations of these mechanisms or their effects on the plankton community. Quantification of these effects in the context of HAB population dynamics is virtually non-existent.

A vast number of toxins and other biologically active compounds are produced by HAB species. These compounds are generally classified as secondary metabolites because they are not directly involved in the pathways of primary metabolism. Their functional significance and eco-evolutionary roles are usually unknown. Field observations suggest that some compounds produced by HAB species serve to reduce grazing losses. Fish and zooplankton avoid dense concentrations of certain HAB species (Fiedler 1982), and laboratory studies indicate that toxic species are rejected by at least some predators or grazers either by pre-ingestive selection or after ingestion of a threshold dosage of toxic cells (Ives 1987, Teegarden and Cembella 1996). Reductions in grazer abundance can also play a key role in bloom development. This might result from physical factors or behavioural strategies, which lead to spatial separation of harmful algal species and grazers. Local reductions in grazer abundances may also be in direct response to the HAB (that is, avoidance or mortality induced by the HAB), or in response to the effects of past HAB events on grazer populations. In those cases where grazers are abundant, grazing control may still not be exerted because toxins or small prey size reduce the ability of the grazers to ingest the HAB species. The response of zooplankton and other grazers to toxic algae is often species-specific in terms of behavioural responses and toxin susceptibility (Huntley et al. 1986, Uye and Takamatsu 1990). It is therefore necessary to conduct studies of community interactions on a location- or HAB-specific basis.

Grazing control of HABs can also depend on the population density of the harmful alga, as demonstrated for the brown tides in Narragansett Bay, U.S.A., where suppression of grazing occurs above a threshold concentration of the alga (Tracey 1988). A threshold effect may also occur if the daily production of new harmful cells 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 (Donaghay 1988). A breakdown of grazing control has been implicated in the brown tides in Narragansett Bay (Tracey 1988) and in Texas (Buskey and Stockwell 1993) and removal or loss of the grazer population has been reported to precede or accompany bloom development (Montagna et al. 1993). There is, however, little quantitative information on how the nature of the grazer response influences the timing, magnitude, and duration of HABs. Model parameterisation of these effects is thus not yet possible.

Moving to higher trophic levels, zooplankton impaired by ingesting harmful algae may be more susceptible to predation, and thus may become an important vector for transferring toxins in the pelagic food-web. Alternatively, zooplankton fecal pellets may also be important sources of toxin to benthic communities. Herbivorous fish can accumulate and transfer toxins, and even cause mass mortalities of the marine birds that consume them (Work et al. 1993). Mortality of marine mammals linked to trophic transfer of HAB toxins has also been reported (Geraci et al. 1989). During their food-web transfers, toxins may be bio-accumulated, excreted, degraded, or structurally modified, as in the case of enzymatic bio-transformation of PSP toxins in some bivalve molluscs (Cembella et al. 1993). In order to understand the effects of HAB species on the marine food web, the pathways by which toxins are transferred and transformed and the differential susceptibility of marine organisms to these toxins must be determined.

Example Tasks

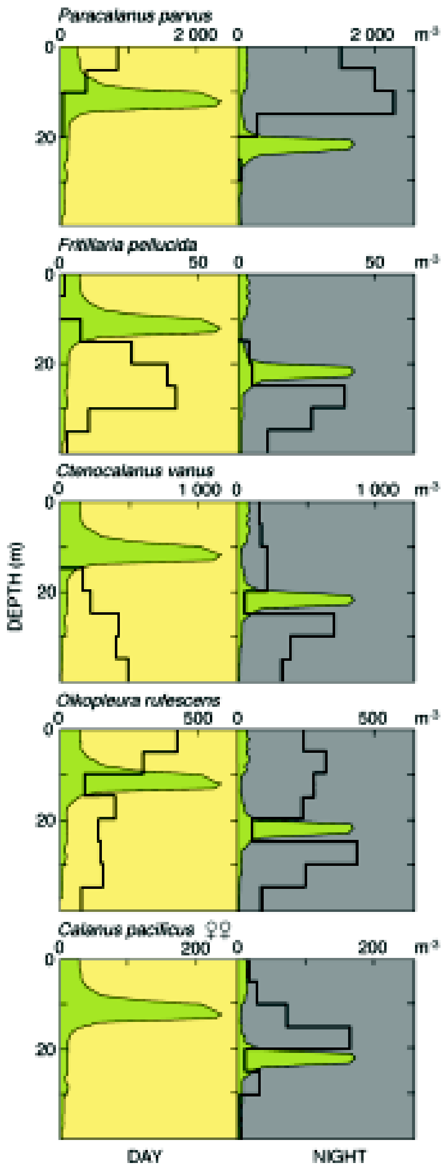
- Determine the effects of bioactive compounds within natural communities on HAB dynamics
- Determine the importance of density-dependent processes in HABs
- Quantify the effects of microbial pathogens on HABs
- Determine the role of grazing control in HAB dynamics

Specific Objective #4

Define functional groups in communities containing HAB species

Rationale

The composition of microalgal communities including HAB species varies strongly in space and time and reflects two fundamental selection features, notably life-form and species-specific selection. As has been recognized for terrestrial ecosystems (Gitay and Noble 1997), it is not feasible to develop models for every species and ecosystem. Reynolds (1997) pointed out that the dominance of the better adapted species in a strongly selective environment is a probability, not a mechanistic certainty. Therefore, precise community composition may, in practice, be impossible to predict. Recent modelling has shown that competitive interactions may generate oscillations and chaotic behaviour of



The extent to which grazing can control HABs depends upon the abundance of grazers, their ability to ingest the harmful algal species, and the effects of the HAB species on the grazers. Some copepods and other macrozooplankton reduce their grazing when they encounter dense blooms of some toxic dinoflagellates, perhaps as a result of impaired motor control and elevated heart rates (Sykes and Huntley 1987). These mechanisms provide an explanation of the vertical distribution of a dense layer of *Gymnodinium splendens* (chlorophyll *a*) and various zooplankton species in southern Californian coastal waters (Fiedler 1982). The distributions suggest active avoidance of the subsurface bloom by macrozooplankton. The observed lower rate of feeding by herbivores within the layer indicated a further reduction in grazing pressure on this dinoflagellate population. These behavioural responses may help explain the formation and persistence of dinoflagellate blooms.

species abundances and allow the persistence of a great diversity of competitors, even in a well-mixed environment with only a few limiting resources (Huissman and Weissing 1999). The formulation of functional groups provides a basis for simplification in order to improve predictive ability relative to the dynamics of the system.

Some functional classifications of phytoplankton are based on empirically obvious morphological or physiological traits. Margalef (1978) devised a conceptual model in which functional groups of phytoplankton were interpreted as adaptations to a turbulent environment and were plotted against axes representing nutrient availability and the intensity of turbulence. In this context, the typical phytoplankton succession, from fast-growing diatoms to motile dinoflagellates, is driven by seasonal changes leading from a well mixed, nutrient-rich water column to a nutrient-poor, stratified environment. This model was later redesigned (Margalef et al. 1979) to include a "red tide sequence" as a parallel trajectory to the typical succession, in an environment in which a relatively high nutrient concentration was associated with relatively low turbulence. Along similar lines, Reynolds and Smayda (1998) proposed a triangular habitat template, in which successional changes and external forcing, such as storms or seasonal mixing, were represented in different axes. Cullen and MacIntyre (1998) reconsidered Margalef's (1978) model emphasizing physiological and biochemical adaptations that could be experimentally quantified. These models have been useful in providing a general conceptual framework. However, little is known of the functional significance of many morphological, physiological, or behavioural features of phytoplankton (Sournia 1982, Elbrächter 1984, Fogg 1991, Kiørboe 1993, Kamykowski et al. 1998) and even less is known for benthic microalgae. Progress in the interpretation of the ecological implications of these phytoplankton characteristics and their role as adaptive strategies will have to be based both on field studies and studies at the cellular level.

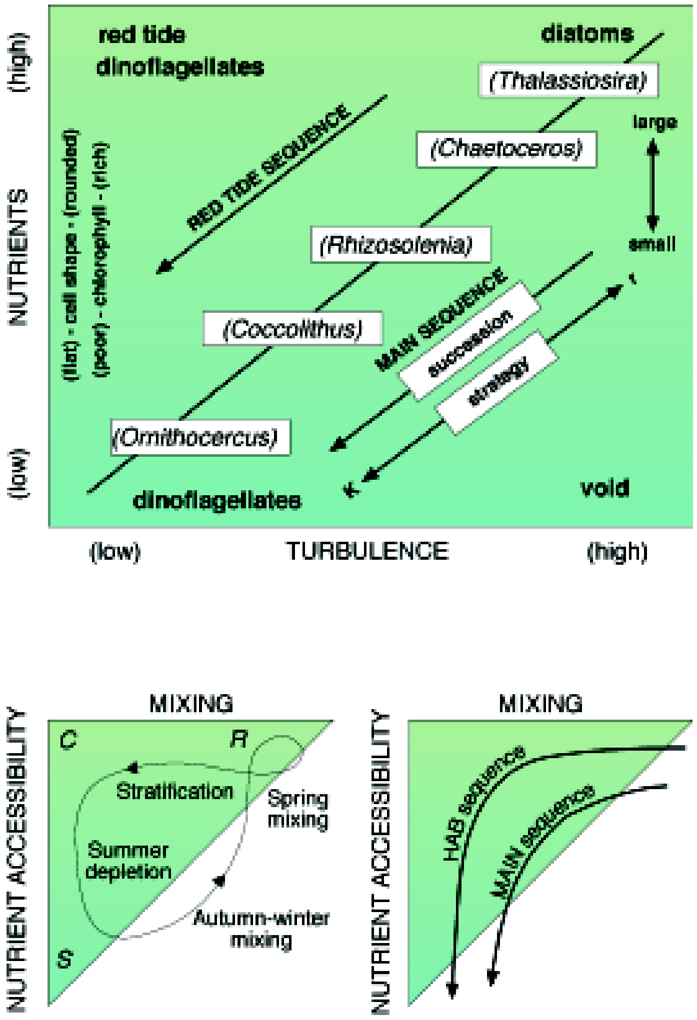
Example Tasks

- Determine groups of co-occurring taxa or assemblages within given ecosystem types
- Establish the distribution of functional groups and their relationship to environmental factors
- Identify common morphological, physiological, and life-history features within HAB species and define the environmental characteristics that support these specific features

OUTPUTS

The results of this Programme Element should lead to:

- Identification of common physiological and behavioural characteristics of HAB species in given ecosystem types
- Quantitative descriptions of the effects of physical forcing on bloom dynamics
- Bases for developing management and mitigation strategies tailored to the characteristics of particular organisms



The conceptual model of Margalef (above - modified from Margalef, 1978; see also Margalef et al. 1979) places phytoplankton life-forms in an ecological space defined by nutrient concentration, as related to specific growth rate (*r*, with dimension t^{-1}) and an expression of turbulence (coefficient of vertical eddy diffusivity). Red tides appear along a path parallel to that of the typical phytoplankton succession, but in situations of increased nutrient availability relative to turbulence intensity. The letters *r* and *K* are commonly used in the logistic growth equation to indicate, respectively, specific growth rate and environmental carrying capacity. In the figure, they refer to a classification of phytoplankton into *r*-strategists, species with high specific growth rates (*r*), which tend to dominate initial succession stages, and *K*-strategists, species with higher potential for survival, which tend to dominate in late phases of the succession.

The position of phytoplankton communities as trajectories in the ecological matrix of Reynolds (bottom left) is defined by nutrient availability (which decreases along with phytoplankton succession) and external forcing (mixing intensity). C, S and R indicate the position of appropriately adapted taxa (C = competitor, S = stress tolerant and R = disturbance-tolerant, ruderal or “rubbish-loving”). Amplification of the top left hand corner of the previous figure (bottom right), shows the typical successional sequence and the HAB sequence which, with more nutrients available, selects for algae with stronger competitor-strategist characteristics (modified from Reynolds and Smayda 1998).

PROGRAMME ELEMENT 5: Observation, Modelling, and Prediction

INTRODUCTION

To describe, understand, and predict the population dynamics and environmental effects of harmful algae, it is necessary to characterise distributions of HAB species and other components of their communities in relation to the environmental factors that ultimately control bloom dynamics. This requires specialised and highly resolving measurements to observe and describe the biological, chemical, and physical interactions that determine the population dynamics of individual species in natural communities. Equally important are synoptic and long-term measurements of biological, chemical, and physical variability as related to HABs in the context of regional processes. Such co-ordinated observation programmes (that is, monitoring systems) are central to the development and evaluation of early warning and prediction systems. Ultimately, effective monitoring is needed to support decision-making for the protection and management of coastal resources.

Models are effective tools for describing the complex relationships among physical, chemical, and biological variability in ecosystems. They can range from quantitative descriptions of physiological processes as functions of temperature, light, and nutrient concentration, to empirical predictions of HABs (such as, blooms will occur after major runoff events), to detailed numerical forecasts based on simulations of algal growth and behaviour as influenced by local hydrodynamics. Models help to develop an understanding of the processes that determine the population dynamics of HABs, and they are extremely useful in the construction and testing of hypotheses. Prediction of HABs is a goal, but success will be limited at first. Even inaccurate predictions are useful in revealing incompletely described factors that are important in the dynamics of HABs. Ultimately, the development, evaluation, and utility of predictive models depend on the availability of appropriate observations, that is, those that can be related directly to the models.

Progress in observing, modelling, and predicting HABs depends on innovation, co-ordination and focus. New instruments and sensing systems for characterising variability in coastal ecosystems are being developed at a rapid pace. However, their application in the detection, study, and prediction of HABs is only beginning, and some crucial capabilities, such as the means to detect single species in situ, are still in the development stage. In turn, models of marine ecosystem dynamics are becoming increasingly effective at describing ecological interactions and the influence of physics on the dynamics of plankton. A focus on HABs, with close interaction among biologists, oceanographers, and modellers, is needed to further the objectives of GEOHAB. Consequently, improvements in observation and modelling in support of detection, understanding, and prediction of HABs are central aims of GEOHAB.

OVERALL OBJECTIVE

> *To improve the detection and prediction of HABs by developing capabilities in observation and modelling*

THE STRATEGY

GEOHAB will foster the development of new observation technologies and models to support fundamental research on HABs, improve monitoring, and develop predictive capabilities. Because capabilities in coastal observation and modelling are advancing rapidly on many fronts, co-ordination and co-operation among the different elements of the GEOHAB programme is essential. The intention is to ensure rapid and effective integration of new knowledge, technical capabilities, and data across disciplines and regions.

A summary of the objectives and types of tasks that might be addressed under this Programme Element, as well as the anticipated outcomes is provided in Figure 5.1.

Specific Objective #1

Develop capabilities to observe HAB organisms in situ, their properties, and the processes that influence them

Rationale

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-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. One important objective, seldom if ever attained in HAB research, is to match the scales and specificity of observations with those of the models that describe environmental influences on phytoplankton dynamics. Thus, GEOHAB will encourage the development of novel observation systems that characterise physical, chemical, and biological variability on appropriate scales. The scales need to be defined through observation and modelling.

To describe population dynamics, distributions of the target organisms must be determined at the species level; other members of the 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 inadequate to obtain and analyse enough samples to describe adequately the distributions of species in space and time. Also, some species are extremely difficult (such as, within the genus *Alexandrium*) or impossible (such as, *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) and nucleotide probes (Scholin et al. 1999), which can be adapted for use in semi-automated bulk-sample analysis and single-cell analysis using microscopy or flow cytometry. Meanwhile, 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).

Identification of individual species in situ is not enough. To describe and understand ecological controls on the activities and effects of harmful algae in nature, physiological status and toxicity of harmful 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

Figure 5.1 Summary of Programme Element 5: Observation, Modelling, and Prediction.

OVERALL OBJECTIVE Programme Element 5: To improve the detection and prediction of HABs by developing capabilities in observation and modelling

1 *Develop capabilities to observe HAB organisms in situ, their properties, and the processes that influence them*	• Develop techniques and sensors for simultaneous measurements of the distributions of phytoplankton, predators, and physical and chemical parameters • Develop methods for rapid identification of HAB species • Develop assays of physiological status and toxicity at the cellular level in natural samples
2 *Develop models to describe and quantify the biological, chemical, and physical processes related to HABs*	• Develop models of physiological processes of HAB species • Develop theoretical descriptions of HABs as community phenomena, including responses to perturbations • Conduct coupled physical-chemical-biological simulations, guided and tested by comparisons with observations • Support the design of field and monitoring programmes by results of simulations
3 *Develop and evaluate systems for long-term monitoring of HAB species*	• Develop new automated systems for monitoring HABs • Establish test sites for development and evaluation of systems for monitoring phytoplankton (including HAB species) in situ and with remote sensing • Help to develop procedures for international integration and management of data from monitoring programmes
4 *Develop capabilities for describing and predicting HABs with empirical models*	• Conduct retrospective analysis leading to empirical predictive models • Test and refine the predictive models through monitoring and analysis
5 *Develop capabilities in real-time observation and prediction of HABs*	• Develop comprehensive observation and prediction systems at selected sites • Use real-time data assimilation in predictive models

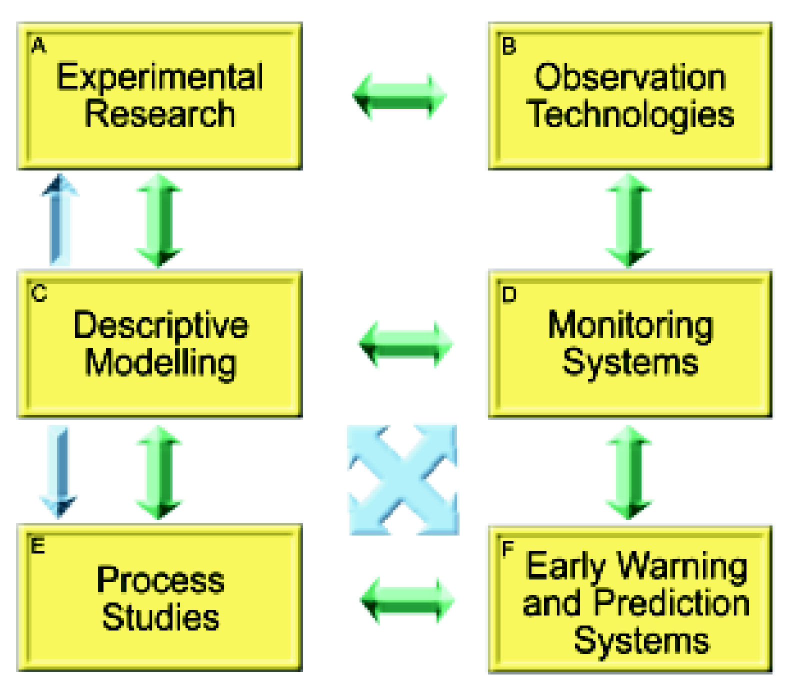
OUTPUTS

- New instrument systems and analytical techniques to support fundamental research on HABs
- Models to describe the coupling of physical, chemical, and biological processes important to HABs
- Advanced systems for monitoring HABs and environmental processes in coastal waters
- Prototype early warning and prediction systems for HABs

(Olson et al. 1996). GEOHAB will encourage development of these analytical methods to address key questions concerning environmental influences on physiological processes.

For HAB research, the long-term goal is automated identification of species in situ, and assessment of their physiological and biochemical properties. Considering that flow cytometers are being adapted for deployment in the ocean (Dubelaar et al. 1998), and new optical instruments are being introduced regularly (Sieracki et al. 1998, Weidemann et al. 1998, Kirkpatrick et al. 2000), this goal is worth pursuing, if only for target species of particular interest.

Many of the new observational capabilities required for GEOHAB are being developed as part of research programmes throughout the world, without strong ties to HAB research. Co-ordination of efforts and additional emphasis on HABs will provide great benefits. GEOHAB will therefore encourage direct linkages between the HAB studies outlined in previous sections and research on new observation systems and approaches, within GEOHAB and with other programmes.



Observation and modelling will be improved by pursuing specific objectives in three complementary contexts: fundamental research (i.e., experimental research, modelling and process studies), monitoring, and prediction. There are many links between these objectives: When new analytical approaches, such as nucleotide probes or active fluorescence techniques, are introduced through experimental research, observation technologies useful for HAB research can be developed (A→B). In turn, observation technologies, such as flow cytometry, can be used in many new ways for experiments (B→A). Process studies, often complemented by experimental research in the laboratory (and vice-versa), guide descriptive modelling (A,E→C), which in turn provides a framework for constructing and testing hypotheses through observation and experimentation (C→A,E). Monitoring systems require appropriate observation technologies (B→D) and interpretations (e.g., of ocean colour algorithms), which are developed and validated through experimentation and modelling (A,E→C→D). Simulation models are useful in the design of monitoring systems (C→D). Results from monitoring programmes are important for the design and implementation of process studies and in the testing and refinement of models (D→E,C). Also, deployment in a monitoring system is a rigorous test of an observation technology, important in product improvement (D→B). Through data assimilation techniques or the development of empirical models, monitoring systems can be used for early warning and prediction (C,D→F). Data assimilation models provide now-casts, that is, statistical interpolations and extrapolations of available data, which are excellent products for monitoring programmes (F→D) and for directing detailed process studies (F→E). Continuous comparison of predictions with observations provides the means for improving descriptive and forecast models (F→C).

Example Tasks

- Develop techniques and sensors for simultaneous measurements of the distributions of phytoplankton, predators, and physical and chemical parameters
- Develop methods for rapid identification of HAB species
- Develop assays of physiological status and toxicity at the cellular level in natural samples

Specific Objective #2

Develop models to describe and quantify the biological, chemical, and physical processes related to HABs

Rationale

Modelling is a cross-cutting activity that supports specific tasks and synthesises the findings of all Programme Elements. GEOHAB will foster the development of a new generation of models adaptable to HABs. The process will be characterised by close interdisciplinary interaction of experimentalists and modellers, to develop a qualitative and quantitative understanding of HABs in a variable physical environment.

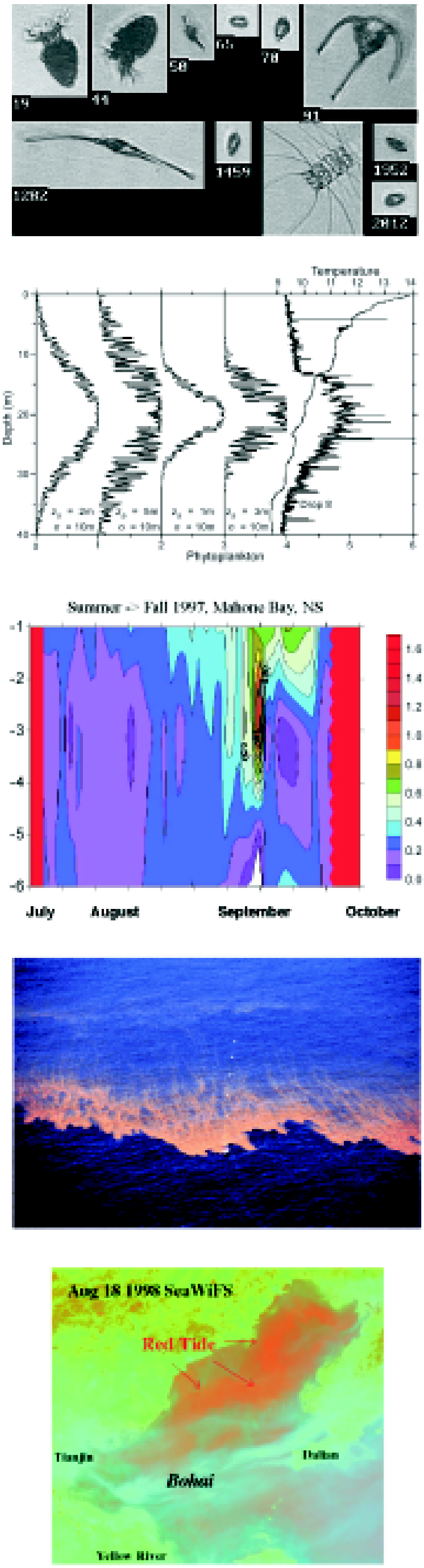
Generally, a range of processes acting on different scales must be integrated to simulate ecosystem processes, including the development of HABs and the effects of harmful algae, such as toxicity or the formation of noxious scums or foams. For the development of models it is always necessary to reduce complexity by isolating the most important processes. This involves, for example, reducing the number of biological state variables to a minimum and the parameterisation of sub-grid processes, that is, those that are not explicitly resolved. Consequently, the simulation of ecosystems depends on a hierarchy of models describing physiological processes, vegetative growth, and life history transitions of phytoplankton, complemented by models of community interactions; all of which are influenced by environmental factors such as light, temperature, salinity, and nutrient supply as described by models of the physical and chemical environment.

Advanced three-dimensional circulation models coupled with models of chemical and biological processes allow simulations of the responses of systems to physical (such as irradiation, wind, freshwater runoff) and chemical (nutrient input from rivers, atmosphere) forcing. These simulations capture the thermodynamics (T,S), the advection (circulation, fronts and eddies) and the turbulent diffusion due to small-scale processes in response to meteorological forcing, and they include interactions within the food web. Ecologically important physical processes can therefore be described in a realistic manner. The principal challenge now is to incorporate more realistic descriptions of biological and chemical processes into these physical models through the translation of experimental results and observations into model equations. This requires effective, two-way flows of information between biologists and modellers. The resulting coupled models promote understanding of problems that depend on the interaction of physics and biology, that is, effects that cannot be explained by biology or physics alone. Model simulations can be very helpful in the development and testing of hypotheses and in the design of laboratory experiments and sampling programmes for process studies. Experimental simulations of different scenarios can also help to identify the specific adaptations that favour blooms of the harmful species.

Coupled models can be used to predict HABs. Prediction is evaluated by comparison with observations, so a temporal and spatial correspondence between observations and models, which minimises the differences between them, is an important goal. With increasing refinement of the models, their predictive potential will be enhanced. Accurate prediction is essential for effective early warning and mitigation. Although this may be a distant goal, much can be learned about ecological dynamics from comparisons of predictions with observations. Even if the accuracy of predictions compared with observations is initially poor, the lessons will be used to improve subsequent models.

Example Tasks

- Develop models of physiological processes of HAB species
- Develop theoretical descriptions of HABs as community phenomena, including responses to perturbations
- Conduct coupled physical-chemical-biological simulations, guided and tested by comparisons with observations
- Support the design of field and monitoring programmes by results of simulations



Advances in observation technologies make it possible to characterise distributions of HAB organisms, members of their communities, and physical/chemical properties on a broad range of scales. Members of the microplankton >20 µm are automatically detected using a flowCAM (top) which has the potential to provide continuous information on abundance of HAB organisms and community structure (from the Bigelow Laboratory flowCAM web page; see Sieracki et al. 1998). Thin layers of phytoplankton can be formed by physical processes that are modelled in the centre-left panel and compared with high resolution measurements (fluorescence trace “Drop 8”) from T.J. Cowles (Franks 1995). The seasonal progression of phytoplankton abundance is resolved vertically using a buoy that measures attenuation of solar irradiance at 490 nm (lower left; $K_d(490)$, m^{-1}; Cullen et al. 1997). Aircraft can assess distributions of phytoplankton on scales from meters to tens of kilometres, using photography or imaging radiometry (photo from Franks 1997). For synoptic views of conditions on the regional- to basin-scale, there is no substitute for satellite sensors, such as SeaWiFS, which obtained the image of chlorophyll from ocean colour during a red tide in the Bohai (from CCAR/HKUST, Hong Kong).

Specific Objective #3

Develop and evaluate systems for long-term monitoring of HAB species

Rationale

Harmful algal blooms are episodic and patchy, so observations of algal distributions in relation to physical and chemical properties should be both continuous and synoptic. Although this ideal is unachievable, a new generation of oceanographic instruments can provide continuous measurements of many physical, chemical, and biological properties from autonomous moorings, in vertical profile and along ship tracks. Also, remote sensing from aircraft and satellites can provide synoptic views of coastal processes when conditions allow.

Monitoring systems can play a key role in describing multi-scale variability that influences coastal ecosystems and hence the population dynamics of HABs. For example, long-term monitoring documents ecological variability over a large range of temporal scales; several long time-series have demonstrated dramatic changes in ecosystems forced by climatic shifts that are now appreciated to have far-reaching effects (McGowan et al. 1998, Karl 1999). In the context of HABs, long-term records on regional scales are essential to distinguish local anthropogenic effects (e.g., from eutrophication) from changes related to climate variability, such as the El Niño - Southern Oscillation phenomenon. Monitoring also serves the important role of detecting rare or transient events. So, if analysed carefully, data from well designed monitoring and modelling systems could contribute effectively to early warning and prediction of algal blooms. Monitoring data are also of great value for verification and refinement of models.

Discrete sampling for microscopic enumeration of plankton, determination of chemical constituents (e.g., toxicity, nutrients) or molecular characterisation, and perhaps detailed vertical sampling at selected sites, will always be part of monitoring programmes. Temporal and spatial variability in these discrete measurements is often difficult to interpret. Continuous and synoptic records from a monitoring programme, reconciled through now-cast models with results of discrete sampling as discussed below, can

Advanced monitoring systems. Automated moorings can be equipped with sensors to monitor continuously the temperature and salinity of the water column, depth-resolved currents, and meteorological conditions. Passive optical sensors can measure ocean colour and the attenuation of sunlight with depth. The corresponding optical properties, spectral reflectance and attenuation, can be related to the constituents of the water, including phytoplankton and dense HABs, both at the surface and in layers. Other optical instruments with their own light sources, such as fluorometers and absorption-attenuation meters, show great promise for autonomous characterisation of phytoplankton and environmental conditions in coastal waters. Ocean observation moorings, pictured here, have been deployed in several locations, such as the Chesapeake Bay, Maryland, of the United States. Photo courtesy of CBOS.

provide the environmental context for interpretation of detailed, but intermittent sampling. For example, now-casts could describe the temporal relationship between a set of discrete samples and an episodic event such as an upwelling pulse or an algal bloom.

Development of autonomous monitoring systems has begun (Johnsen et al. 1997, Glenn et al. 2000). However, costs for instruments are relatively high, some of the measurements (such as ocean colour) are difficult to interpret or to correct for interference, and instruments deployed in the water are subject to fouling and disturbance. Nevertheless, the development of coastal observation systems is strongly justified, as demonstrated by the establishment of the Coastal Ocean Observations Panel (COOP; Malone and Cole 2000). HABs are an ecologically prominent component of coastal variability, and regional processes must be understood to describe their seasonal and interannual variability. Close co-ordination between HAB research and international efforts to develop coastal monitoring systems is important to GEOHAB and to the broader community that will rely on coastal monitoring for protection and management of coastal resources. In order to understand the dynamics of HABs in a global context, it is also essential to integrate and manage data from a broad range of monitoring sources, including conventional sampling programmes, in situ systems, and remote sensing.

Example Tasks

- Develop new automated systems for monitoring HABs
- Establish test sites for development and evaluation of systems for monitoring phytoplankton (including HAB species) in situ and with remote sensing
- Help to develop procedures for international integration and management of data from monitoring programmes

In situ nutrient analysers will increasingly be used for monitoring nutrient loading. Upon laboratory calibration, they can be deployed for periods of weeks to months. Photo by M. Trice.

Specific Objective #4

Develop capabilities for describing and predicting HABs with empirical models

Rationale

Monitoring programmes alone are very useful for describing and understanding the dynamics of HABs, but they provide limited means for advance warning of blooms or harmful effects. Predictions of HABs are needed, whatever the source of information. For example, important decisions relevant to mitigating the effects of harmful blooms must rely on empirical or conceptual models relating algal population dynamics to environmental forcing, such as climate variability (e.g., El Niño) versus human influences, such as nutrient loading. A great deal of work has been done addressing the influences of nutrient loading on algal blooms, but many uncertainties persist. Given that large amounts of data have been collected but not analysed in the context of HABs, opportunities exist for retrospective studies relating HABs to environmental forcing, including human activities. Studies of the sediment record can also provide much information on the occurrence of phytoplankton, including HAB species, relative to environmental factors. Evaluation of the conclusions and implicit predictions of these studies can only be improved if observation systems are upgraded so that more data can be acquired with improved temporal and spatial resolution.

Although GEOHAB will encourage the development of new autonomous observation systems and modelling approaches, it is well recognised that throughout the world great quantities of relevant data will be collected through established procedures and analysed using a variety of approaches leading to empirical or conceptual models. Capabilities for empirical predictions will be enhanced by co-ordination in the collection and analysis of data and through international co-operation in the sharing of data and development of models. Comparison of predictions with new observations is crucial. In co-operation with COOP, GEOHAB will encourage these activities.

Example Tasks

- Conduct retrospective analysis leading to empirical predictive models

- Test and refine the predictive models through monitoring and analysis

Specific Objective #5

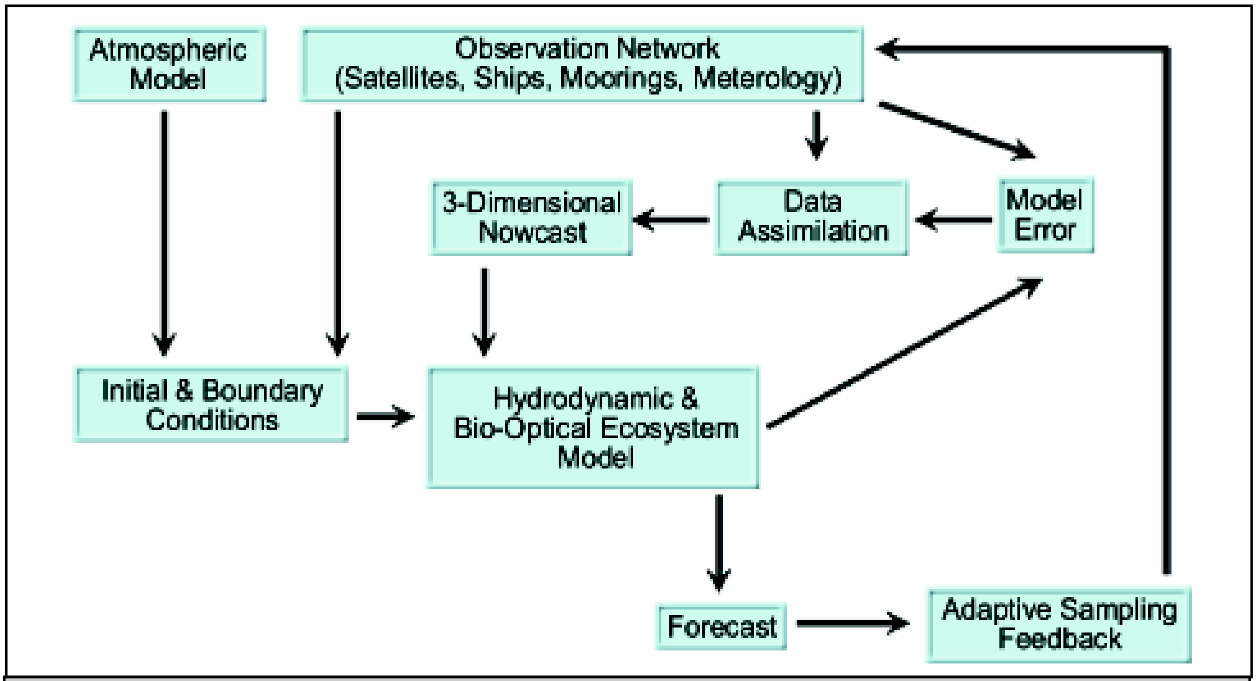
Develop capabilities in real-time observation and prediction of HABs

Rationale

Empirical models that explain HABs are needed. However, automated forecast systems for HABs are an ultimate goal. Real-time observation and prediction systems could guide traditional monitoring programmes and provide a proactive means for responding to HABs. Also, predictive models can guide fundamental research because they are based on knowledge about HABs that is tested directly by comparison of forecast with observations.

Forecasting systems will require near real-time observation capabilities linked directly to hydrodynamic/biological models. These observation-prediction networks must detect and forecast over ecologically relevant scales, so they should utilise remote sensing and in situ observation systems. To improve the quality of forecasts, adaptive sampling by ships and autonomous vehicles can be initiated to collect detailed data (such as species composition, detailed vertical structure) in specific regions within the forecast grid. Conversely, the now-casts and forecasts provide an unprecedented opportunity for biologists to devise sampling strategies to characterise episodic events, which can play a disproportionately large role in structuring phytoplankton communities and are poorly sampled using traditional protocols. Therefore, real-time observation and prediction systems will be critical in studying the population dynamics of HABs.

The scientific field of ocean forecasting has advanced rapidly through the use of data assimilation methods adopted from the meteorology community. Assimilation of data into oceanographic models is accomplished through a variety of methods (Walstad and McGillicuddy 2000). Coastal ocean forecasting networks generally work in a recursive mode: the data-assimilative model provides a now-cast that is moved forward in time 2-4 days by a circulation model driven by surface-boundary forcing from a weather prediction system. During the forecast cycle, additional field data are assimilated to constrain the model dynamics to provide improved now-casts for the next set of forecasts. Several coupled physical-biological models have been



Schematic for a now-cast/forecast system that includes adaptive sampling of events poorly resolved by monitoring activities. From Schofield et al. 1999, modified from Glenn et al. 1999.

constructed with data assimilative methods (Ishizaka 1990, Fasham and Evans 1995, Lawson et al. 1995, Matear 1995) providing a blueprint for future data assimilative models of HAB events.

Although recent advances in instrumentation and data assimilative modelling provide the components necessary for building algal forecasting systems (Schofield et al. 1999), numerous hurdles must be overcome before we can expect to predict HAB events effectively. Many of the needs for development of HAB forecasting systems have already been identified in this Science Plan: they represent the knowledge and capabilities we require to describe the population dynamics of harmful algae. Real-time observation and prediction of HABs can therefore be pursued by co-ordinating the acquisition of new knowledge, the development and establishment of observation systems, and the integration of models with data in forecasting efforts.

Example Tasks

- Develop comprehensive observation and prediction systems at selected sites
- Use real-time data assimilation in predictive models

OUTPUTS

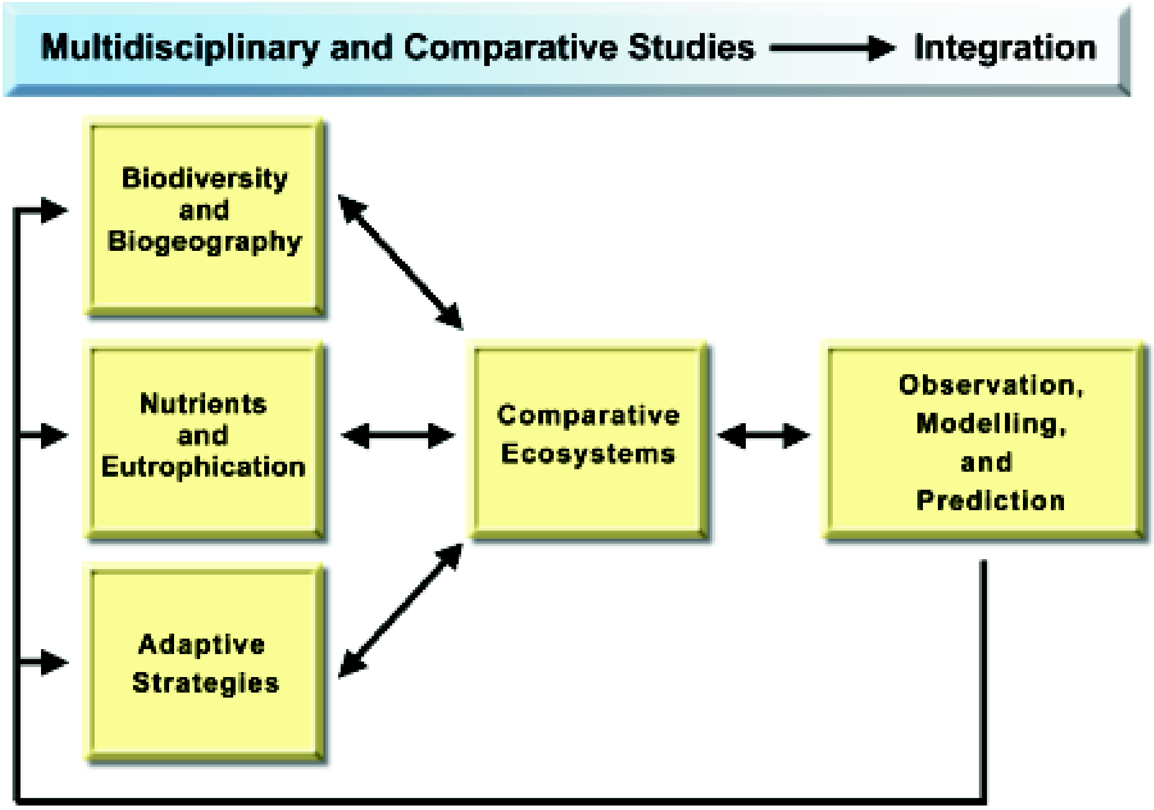
The results of this Programme Element should lead to:

- New instrument systems and analytical techniques to support fundamental research on HABs
- Models to describe the coupling of physical, chemical, and biological processes important to HABs
- Advanced systems for monitoring HABs and environmental processes in coastal waters
- Prototype early warning and prediction systems for HABs

LINKAGES AMONG PROGRAMME ELEMENTS

The scientific goal of GEOHAB is to improve prediction of HABs by determining the ecological and oceanographic mechanisms underlying their population dynamics. Understanding, and ultimately predicting, HABs will require the broad range of observations described in the individual Programme Elements as well as co-ordination among those elements. Although many activities and objectives have been presented independently for each element, these must ultimately be linked and integrated to achieve the understanding required.

Programme Element 5, *Observation, Modelling, and Prediction*, establishes the framework for prediction based on observation and modelling. Modelling will be based on HAB biomass and population dynamics. Parameterisation of processes such as growth, mortality, and turbulent dispersion will require information from each of the Programme Elements, as will model validation. For example, Programme Element 1, *Biodiversity and Biogeography*, will contribute to prediction by documenting the present and historical distribution of key HAB species and their life cycle stages. Biodiversity studies will address the genetic variability within local, regional, and global populations of those species. This is necessary because growth or mortality rates determined for a single strain of a species may not apply to all strains of that species even within a region. Similarly, physiological, behavioural, or rate data obtained for a species in one area may not be



The integration of findings from the individual Programme Elements described in this Science Plan is required to achieve not only an understanding of HAB organisms and associated events, but also to develop predictive capabilities.

applicable to the same species from another region. Programme Element 2, *Nutrients and Eutrophication*, will contribute the rate data and cycling parameters specific for nutrients, again recognizing the differential response of the range of HAB species. The potential importance of anthropogenic nutrient loading in the development of both high biomass and toxic blooms will also be addressed. Programme Element 3, *Adaptive Strategies*, seeks to reduce the genetic and physiological complexities studied in the first two Programme Elements by identifying functional groups of species that interact with the environment in similar ways. For example, species that undergo diel vertical migration will exploit stratified waters characterized by consistent light and temperature regimes, whereas non-motile species are better suited to turbulent regimes. Nitrogen-fixing species may thrive in waters where other species cannot because of a shortage of dissolved inorganic nitrogen. Behavioural and physiological adaptations can thus account for the survival and persistence of certain HAB species or functional groups in particular ecosystem types. Programme Element 4, *Comparable Ecosystems*, integrates the findings of biodiversity, nutritional, and eutrophication effects, and adaptive strategies by examining, through field studies in different hydrographic and ecological systems, the physical, chemical, and biological characteristics of the environment. Improved understanding of HAB population dynamics, and ultimately, improved predictions of HAB events within particular ecosystem types, clearly requires the integration of knowledge derived from the five Programme Elements.

In summary, GEOHAB is a combined experimental, observational, and modelling programme, using current and innovative technologies in a multidisciplinary approach consistent with the multiple scales and oceanographic complexity of HAB phenomena.

Red tide caused by *Gymnodinium mikimotoi* in the commercial and fishing port of Tanabe Bay, on the Pacific coast of Honshu, Japan. Red tides such as this can cause devasting impacts on ecosystems and on aquaculture industries. In this photo, the small white areas off the island are fish-culture cages which experienced stress from this red tide. Photo by Y. Fukuyo.

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GEOHAB SCIENTIFIC STEERING COMMITTEE

Patrick Gentien, Chair
Institut Français de Recherche pour l'Exploitation de la Mer
CREMA-CNRS/IFREMER
BP5 - 17137 L'Houmeau, France
Tel: +33-(0)5-46500630
Fax: +33-(0)5-46500660
E-mail: pgentien@ifremer.fr

Yasuwo Fukuyo, Vice-Chair
Asian Natural Environmental Science Center
The University of Tokyo
Yayoi 1-1-1, Bunkyo-ku, Tokyo 113-8657 Japan
Tel: +81-3-5841-2782
Fax: +81-3-5841-8040
E-mail: ufukuyo@mail.ecc.u-tokyo.ac.jp

Donald M. Anderson
Biology Department
Mail Stop 32, Redfield 332
Woods Hole Oceanographic Institution
Woods Hole MA 02543-1049 U.S.A.
Tel: +1-508-289-2351
Fax: +1-508-457-2027
E-Mail: danderson@whoi.edu

Marcel Babin
Laboratoire d'Océanographie de Villefranche
Université Pierre et Marie Curie / CNRS
Quai de la Darse, B.P. 8
06238 Villefranche-sur-Mer Cedex
France
Tel: +33-4-93-76-37-12
Fax: +33-4-93-76-37-39
E-mail: marcel@obs-vlfr.fr

Susan Blackburn
CSIRO Microalgae Research Centre
CSIRO Marine Research
GPO Box 1538 Hobart, Tasmania 7001 Australia
Tel: +61-3-62325307
Fax: +61-3-62325090
E-mail: susan.blackburn@marine.csiro.au

Allan Cembella
Institute for Marine Biosciences
National Research Council
1411 Oxford Street
Halifax, Nova Scotia B3H 3Z1, Canada
Tel: +1-902-426-4735
Fax: +1-902-426-9413
E-mail: Allan.Cembella@nrc.ca

John Cullen
(1999-2000)
Department of Oceanography
Dalhousie University
Halifax, Nova Scotia, Canada B3H 4J1
Tel: 902-494-6667
Fax: 902-494-3877
E-mail: John.Cullen@dal.ca

Malte Elbrächter
(1999-2000)
Deutsches Zentrum für Marine Biodiversität
Forschungs-Institut Senckenberg
Wattenmeerstation Sylt
Hafenstrasse 43
D-25992 List/Sylt, Germany
E-mail: melbraechter@awi-bremerhaven.de

Henrik Enevoldsen *
Project Coordinator
IOC Science and Communication Centre on Harmful Algae
Botanical Institute, University of Copenhagen
Øster Farimagsgade 2D
DK-1353 Copenhagen K, Denmark
Tel: +45 33 13 44 46
Fax: +45 33 13 44 47
E-mail: hab@bot.ku.dk

Marta Estrada
Institut de Ciències del Mar CSIC
Paseo Joan de Borbó s/n
Barcelona 08039, Spain
Tel: +34-93-2216416
Fax: +34-93-2217340
E-mail: marta@icm.csic.es

Wolfgang Fennel
Institut für Ostseeforschung Warnemuende
an der Universitaet Rostock
18119 Rostock, Germany
Tel: +49 381 5197 110
Fax: +49 381 5197 480
E-mail: wolfgang.fennel@io-warnemuende.de

Patricia M. Glibert
Horn Point Laboratory
University of Maryland Center for Environmental Science
P. O. Box 775, Cambridge MD 21613, U.S.A.
Tel: +1-410-221-8422
Fax: +1-410-221-8490
E-mail: glibert@hpl.umces.edu

Elizabeth Gross *
(1999-2000)
Department of Earth and Planetary Sciences
The Johns Hopkins University
Baltimore, MD 21218 U.S.A.
Tel: +1-410-516-4070
Fax: +1-410-516-4019
E-mail: scor@jhu.edu

Kaisa Kononen
Maj and Tor Nessling Foundation
Fredrikinkatu 20 B 16
Fin-00120 Helsinki, Finland
Tel: +358-9-43426611
Fax: +358-9-43425555
E-mail: Kaisa.Kononen@nessling.fi

Nestor Lagos
Departamento de Fisiologia y Biofisica
Faculdad de Medicina
Universidad de Chile
Independencia 1027, Casilla 70005
Santiago, Chile
Tel: +56-2-678 6309
Fax: +56-2-777 6916
E-mail: nlagos@machi.med.uchile.cl

Thomas Osborn
Department of Earth and Planetary Sciences
The Johns Hopkins University
Baltimore, MD 21218 U.S.A.
Tel: +1-410-516-7519
Fax: +1-410-516-7933
E-mail: osborn@jhu.edu

Grant Pitcher
Marine and Coastal Management
Private Bag X2, Rogge Bay 8012
Cape Town, South Africa
Tel: +27 21 402-3345
Fax: +27 21 439-9345
E-mail: gpitcher@sfri2.wcape.gov.za

Arturo P. Sierra-Beltrán
Marine Pathology Unit. CIBNOR
A.P. 128 La Paz, 23000
Mexico
Tel: +52 112 53 633 ext 3809
Fax: +52 112 53 625
E-mail: asierra@cibnor.mx

Steve Thorpe
School of Ocean and Earth Science
Southampton Oceanography Centre
European Way, Southampton SO14 3ZH
United Kingdom
Tel: +44-1248-490-210
Fax: +44-1248-716-367
E-mail: sxt@soc.soton.ac.uk

Edward R Urban, Jr. *
Executive Director, SCOR
Department of Earth and Planetary Sciences
The Johns Hopkins University
Baltimore, MD 21218 U.S.A.
Tel: +1-410-516-4070
Fax: +1-410-516-4019
E-mail: scor@jhu.edu

Jing Zhang
State Key Laboratory of Estuarine and Coastal Research
East China Normal University
3663 Zhongshan Road North
Shanghai 200062, China
Tel: +86-21-62233009
Fax: +86-21-62546441
E-mail: jzhang@sklec.ecnu.edu.cn

Adriana Zingone *
Stazione Zoologica ‘A. Dohrn’
Villa Comunale
80121 Napoli, Italy
Tel: +39 081 5833295
Fax: +39 081 7641355
E-mail: zingone@alpha.szn.it

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* Ex-Officio Members

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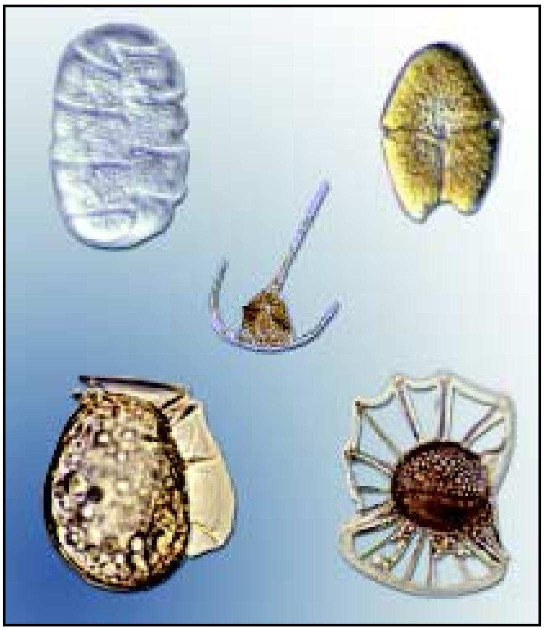

Harmful Algal Blooms (HABs) are the cause of massive fish kills, shellfish contamination, human health problems, and detrimental effects on marine and coastal ecosystems. HABs are caused by a variety of species, some of which are toxic and some of which cause indirect harm to the environment. The key to better prediction of these events, and ultimately their mitigation, is an understanding of the ecology and oceanography of their population dynamics. The GEOHAB (**G**lobal **E**cology and **O**ceanography of **H**armful **A**lgal **B**looms) Programme is aimed toward fostering international co-operative research on HABs in a range of ecosystems, and toward developing and applying innovative technologies in support of their detection and prediction.

Mass mortality of flat-fish by a red tide of *Cochlodinium polykrikoides*.