GEOHAB REPORT #0

GEOHAB: Global Ecology and Oceanography of Harmful Algal Blooms

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

Report from a Joint IOC / SCOR Workshop Havreholm, Denmark 13 - 17 October 1998

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Preface

The last two decades have been marked by an extraordinary expansion in the nature and extent of the marine phenomenon we now call "harmful algal blooms." These occurrences of toxic or harmful microalgae represent a significant and expanding threat to human health and fisheries resources throughout the world. There are many reasons, both natural and anthropogenic, for this dramatic expansion in HAB problems; there is, however, no doubt that human activities are making the problems worse.

Given that HAB problems are 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 to efficiently manage affected marine resources, protect public and ecosystem health, encourage and support aquaculture development, and contribute to policy decisions on coastal zone issues, such as waste or sewage disposal, aquaculture development, or dredging? If human activities are making the HAB problem worse, how can that be verified, and what steps should be taken to minimise further impacts? The answers to these important practical questions, of course, require scientific investigation. To date, however, there is little international co-ordination in the realm of scientific research.

A number of international organisations and agencies have established programmes or working groups focused on specific aspects of HABs and their impacts. Of these the IOC HAB Programme provides a general framework for international co-operation and the SCOR-IOC Working Group on the Physiological Ecology on Harmful Algal Blooms provided, in its final recommendations in 1997, some directions for research. A prominent gap in the various activities implemented to date is any initiative for a co-ordinated international research effort. At the national level, considerable energy and money have been devoted to detecting and characterising HAB toxins and to implementing and sustaining monitoring programs to protect public health, but insufficient effort has been directed toward studying the biological, chemical, ecological and physical factors which regulate HAB dynamics and impacts.

What is clearly needed is a co-ordinated international scientific programme on the ecology and oceanography of HABs that incorporates the full participation of numerous countries. In late 1997, the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) agreed to form a partnership to develop such a programme for the following reasons:

- Harmful algal blooms have significant and growing impacts on human health and fisheries resources throughout the world;
- Strong political and scientific leadership is needed to co-ordinate international research activities in this area (the IOC Intergovernmental Panel on HAB is in a position to provide the former, and the involvement of SCOR will help to ensure the latter, especially given the globally broad, but thinly distributed expertise);
- The ecological and oceanographic uncertainties about HABs and their impacts are significant and involve all of the oceanographic disciplines as well as numerous coastal habitats and ecosystems; and
- Considerable progress has already been achieved and a framework exists on which an international ecology and oceanography program can be based.

The first step in the process of developing this program was an international workshop sponsored by SCOR and IOC which took place near Copenhagen from 13 to 17 October 1998. Thirty-seven scientists from twenty countries participated. This report is the result of that workshop.

The HAB problem is serious and it needs immediate attention. Readers should be aware that this report was prepared in haste in order to ensure that its recommendations could be considered by the SCOR General Meeting less than two weeks after the workshop, and by the IOC Executive Council within three weeks. We recognise that it is not as comprehensive as it could have been if more time had been available. It is expected that a much more extensive GEOHAB report will be produced in the very early stages of the new international program once it is established by the sponsors. Such a document would be based on the discussions and contributions of the participants at this workshop as well as on input from the broader community that would be solicited during the early stages of GEOHAB.

We are grateful for the support provided to the workshop from the following agencies and organizations: Intergovernmental Oceanographic Commission, Maj and Tor Nessling Foundation (Finland), Scientific Committee on Oceanic Research, US National Aeronautics and Space Administration, US National Oceanic and Atmospheric Administration, and US National Science Foundation. In particular, the sponsors wish to acknowledge publicly the contribution of John Cullen in chairing the workshop and in producing this report under very severe time constraints.

On behalf of the sponsors:

Elizabeth Gross, SCOR

Henrik Enevoldsen, IOC

Message from the Chair

The five days of the GEOHAB Workshop were characterised by hard work, a clear sense of purpose, good humour, and a remarkable convergence of opinions on the needs for an international research programme on the ecology and oceanography of harmful algal blooms.

The Executive Summary, which was carefully reviewed by the participants, describes and justifies our recommendations. It can be considered an accurate representation of the workshop proceedings.

The report which follows the Executive Summary is intended to present background information and arguments in support of GEOHAB. It was prepared in ten days, based on hours of group discussions and many pages of text prepared by participants. There was insufficient time for careful copy-editing, much less for review by the participants. I regret that some important contributions by my colleagues may have been omitted or distorted. Some of the later sections, in particular, were not given the attention they deserved. We hope that a more comprehensive document, well referenced, carefully reviewed, and based on broad input in response to international consultation, will follow.

Sincere thanks are extended to the sponsors, organisers, and participants. Their insights, dedication and spirit of co-operation were essential to the success of the workshop.

John Cullen 29 October 1998

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GEOHAB: Global Ecology and Oceanography of Harmful Algal Blooms

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

EXECUTIVE SUMMARY

Proliferations of microalgae 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 Bloom" (HAB), recognising that, because a wide range of organisms is involved and some species have toxic effects at low cell densities, not all HABs are "algal" and not all occur as "blooms." A broad classification of HABs distinguishes two groups of organisms: the toxin producers, which can contaminate seafood or kill fish, and the high-biomass producers, which can cause anoxia and indiscriminate kills of marine life after reaching dense concentrations. Some HABs have characteristics of both.

Although HABs occurred long before human activities began to transform coastal ecosystems, a survey of affected regions and of economic losses and human poisonings throughout the world demonstrates very well that there has been a dramatic increase in the impacts of HABs over the last few decades and that the HAB problem is now widespread, and serious. It must be remembered, however, that the harmful effects of HABs extend well beyond direct economic losses and impacts on human health. 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 factors that control the distributions and net growth rates (i.e., the population dynamics) of HAB species.

A great deal is known about harmful algae and HABs, but our abilities to describe the factors controlling the dynamics of individual species is limited by critical gaps in knowledge about how the physiological, behavioural and morphological characteristics of algae (including HAB species) interact with environmental conditions to promote the selection for one species vs. another. For example, information about the environmental cues for encystment (formation of a resting stage) and germination, as well as the interactions of life cycles with hydrography, is generally inadequate to quantify the role of resting stages in the population dynamics of cyst-forming harmful algae. Also, it is often difficult to assess the role of nutrients and light in algal population dynamics and toxicity because some phytoplankton can migrate vertically to exploit deep sources of nutrients at night and light near the surface during the day. Further, some harmful protists can exploit several forms of nutrition (including consumption of other micro-organisms), complicating models of growth or toxicity vs. nutrient concentration. The nutritional status of harmful algae could be assessed by measuring cellular bio-chemical composition, but this is presently impractical unless the harmful algae dominate the plankton. Compounding the problems, essentially all effects of physical forcing

and nutrient supply on harmful algal populations also influence food-web/community interactions, which ultimately determine the selection for or against a particular species.

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 research problem is to understand the critical features and mechanisms underlying the population dynamics of HAB species. This understanding can be used as a basis for monitoring and predicting the occurrence, movement, toxicity, and environmental effects of harmful algal blooms. In turn, these predictions are essential for management and mitigation of HABs.

Because HABs are globally distributed and are integral parts of marine and brackish-water ecosystems, the central research problem can be addressed comprehensively and effectively only through international, interdisciplinary, and comparative research on important questions about the dynamics of HABs within their oceanographic and ecological systems. Progress depends upon advancement through targeted studies and technological innovation in biology, ecology, chemical and physical oceanography, modelling, and ocean observation.

To address the need for broad-based advancement in the understanding of HABs, we propose the establishment of GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms), a programme of scientific research. The mission of GEOHAB is to foster international cooperative research on harmful algal blooms in the context of their ecological systems and the oceanographic processes which influence them.

The scientific goal of GEOHAB is to:

Determine ecological and oceanographic mechanisms underlying the population dynamics of harmful algae, by the integration of biological and ecological studies with chemical and physical oceanography, supported by improved observation systems.

The benefits of this programme will be better methodologies for predicting the occurrence, distributions, toxicity, and environmental effects of HABs. The scientific goal of GEOHAB will be approached by addressing these major research questions:

- 1. What are the unique adaptations of HAB species that determine when and where they occur and the extent to which they produce harmful effects?
- 2. How do HAB species and their community interactions respond to environmental forcings?
- 3. What are the effects of human activities (e.g., eutrophication) and interannual and decadal climate variability (e.g., El Niño, North Atlantic Oscillation) on the occurrence of HABs?

A broad range of research is directly relevant to these questions, including: interdisciplinary process studies of HABs in comparable ecosystems; taxonomic and genetic surveys of HAB organisms from different locations, along with physiological characterisation of isolates and examination of possible dispersal mechanisms; studies of the influences of turbulence or variations in nutrient fluxes on community interactions (conducted in micro- or mesocosms, modelled, and compared with observations of natural communities); and examination of temporal and spatial trends in phytoplankton dynamics (including HABs), relative to human influence and climate variability, as inferred from existing sources and a developing Global Ocean Observing System.

Targeted studies and technological innovation are essential to the GEOHAB programme, and the list of opportunities for advancement is long indeed. For example, we need better tools for detecting harmful algae and their biologically active products, more sensitive approaches for studying the nutrition of planktonic protists, integrated techniques for observing physical, chemical, and biological variability on the scales relevant to physical forcing, improved representations of the physical processes that influence HAB dynamics, progress in physical-biological coupled models (including data assimilation models), and more effective observation systems for detecting and characterising phytoplankton community dynamics (including HABs). Rapid advances in biotechnology and instrumentation for measuring physical and bio-optical variability in the sea, along with more sensitive and selective methods for chemical analysis and stunning improvements in computational abilities, ensure that rapid progress can be made if efforts are well focused and coordinated.

It is not our intention to specify or circumscribe the research directions for GEOHAB. Rather, we recommend that SCOR and IOC organise a Scientific Steering Committee (SSC), charged with identifying the scientific issues and detailed goals and objectives for an international study of the ecology and oceanography of harmful algal blooms. GEOHAB will foster scientific advancement in the understanding of HABs by encouraging and co-ordinating fundamental scientific research — multifaceted, international, and interdisciplinary, maintaining an ecological and oceanographic context consistent with the scientific goal of the programme. International, co-operative research on comparable ecosystems would be encouraged. In addition, GEOHAB will identify targeted studies on organisms, processes, methods, and observation technologies that are needed to support the interdisciplinary research. Improved global observation systems will be required to resolve influences of environmental factors (anthropogenic and climate-related) on distributions and trends in HAB occurrence. This will be greatly facilitated through strong links between GEOHAB and the Global Ocean Observing System (GOOS).

A better understanding 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 and prediction of HABs. However, this is not the only benefit of GEOHAB. 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. This linking of 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.

GEOHAB: Global Ecology and Oceanography of Harmful Algal Blooms

1.0 The Global Problem of Harmful Algal Blooms

1.1 Definition and classification of harmful algal blooms

Marine microalgae, or phytoplankton, fuel the marine food web. In mass occurrences or blooms, they are generally beneficial to the productivity of marine ecosystems, including wild fisheries operations and aquaculture. Sometimes, however, proliferations of microalgae in marine or brackish waters cause massive fish kills, contaminate seafood with toxins, or alter ecosystems in other ways that humans perceive as harmful.

The scientific community refers to these events with the generic term, "Harmful Algal Bloom" (HAB), recognising that, because a wide range of organisms is involved and some species have toxic effects at low cell densities, not all HABs are "algal" and not all occur as "blooms." Referring to modern systematics, "algae" and "phytoplankton" are colloquial terms, not well defined or natural groupings. The only common feature of the variety of HAB organisms is that they belong to the kingdom of protists. A broad classification of HABs distinguishes two groups of organisms: the toxin producers, which can contaminate seafood or kill fish, and the high-biomass producers, which can cause anoxia and indiscriminate kills of marine life after reaching dense concentrations. Some HABs have characteristics of both.

1.2 Harmful effects

One major category of harm from HABs occurs when toxic phytoplankton are filtered from the water as food by shellfish such as clams, mussels, oysters, or scallops, which then accumulate the algal toxins to levels that are potentially lethal to humans or other consumers. The phenomenon is not new: one of the first recorded fatal cases of human poisoning after eating shellfish contaminated with algal toxins happened in 1793, when Captain George Vancouver and his crew landed in British Columbia in an area now known as Poison Cove. He noted that for local Indian tribes it was taboo to eat shellfish when the seawater became phosphorescent due to dinoflagellate blooms. On a global scale, close to 2 000 cases of human poisoning (fatal in 15 % of the cases) through fish or shellfish consumption are now reported each year. Poisoning syndromes have been given the names paralytic, diarrhetic, neurotoxic, and amnesic shellfish poisoning (PSP, DSP, NSP, and ASP) according to their various manifestations. A fifth human illness, ciguatera fish poisoning (CFP), is caused by biotoxins produced by epibenthic dinoflagellates attached to surfaces in many coral reef communities. If not controlled, the economic damage through reduced local consumption and reduced export of seafood products can be considerable.

Table 1.1. Different types of harmful algal blooms

- 1. Species which produce basically harmless water discolourations; however, under exceptional conditions in sheltered bays, blooms can grow so dense that they cause indiscriminate kills of fish and invertebrates due to oxygen depletion. Examples: dinoflagellates *Gonyaulax polygramma*, *Noctiluca scintillans*, *Scrippsiella trochoidea*, cyanobacterium *Trichodesmium erythraeum*.
- 2. Species which produce potent toxins that can find their way through the food chain to humans, causing a variety of gastrointestinal and neurological illnesses (see Table 1.2).
- 3. Species which are non-toxic to humans, but harm to fish and invertebrates (especially in intensive aquaculture systems) by damaging or clogging their gills. Examples: diatom *Chaetoceros convolutus*, dinoflagellate *Gymnodinium mikimotoi*, prymnesiophytes *Chrysochromulina polylepis, Prymnesium parvum, P. patelliferum*, raphidophytes *Heterosigma carterae*, *Chattonella antiqua*.

Table 1.2. Some types of fish and shellfish poisoning

Paralytic Shellfish Poisoning (PSP)	Diarrhetic Shellfish Poisoning (DSP)	Amnesic Shellfish Poisoning (ASP)	Neurotoxic Shellfish Poisoning (NSP)
Causative organism Alexandrium catenella Alexandrium minutum; Alexandrium tamarense; Gymnodinium catenatum; Pyrodinium bahamense	Dinophysis acuta; Dinophysis fortii; Dinophysis norvegica; Prorocentrum lima	Pseudo-nitzschia multiseries; pseudodelicatissima; australis	Gymmnodinium breve; G. cf breve (New Zealand)
Symptoms Mild Case Within 30 min: tingling sensation or numbness around lips, gradually spreading to face and neck; prickly sensation in fingertips and toes; headache, dizziness, nausea, vomiting, diarrhoea.	After 30 min to a few hrs (seldom more than 12 hrs): diarrhoea, nausea, vomiting, abdominal pain.	After 3–5 hrs: nausea, vomiting, diarrhoea, abdominal cramps.	After 3-6 hrs: chills,headache, diarrhoea; muscle weak- ness, muscle and joint pain; nausea and vomiting
Extreme Case Muscular paralysis; pronounced respiratory difficulty; death through respiratory paralysis may occur 2–24 hrs after ingestion.	Chronic exposure may promote tumor formation in the digestive system.	Decreased reaction to deep pain; dizziness, hallucinations, confusion; short-term memory loss; seizures.	Paraesthesia; altered perception of hot and cold; difficulty in breathing, double vision,trouble in talking and swallowing

A second type of harmful algal bloom has become apparent only as a result of our increased interest in intensive aquaculture systems for finfish. Some algal species can seriously damage fish gills, either mechanically or through production of haemolytic substances. While wild fish stocks have the freedom to swim away from problem areas, caged fish appear to be extremely vulnerable to such noxious algal blooms. In 1972 in Japan, a bloom of the raphidophyte flagellate *Chattonella antiqua* killed 500 million US dollars worth of caged yellowtail fish in the Seto Inland Sea. Finally, toxic

Pfiesteria-like dinoflagellates have been implicated as causative agents of major fish kills, and have been linked to serious human health impacts.

Toxic blooms cause negative impacts and economical losses in all parts of the world. Here are a few of many examples:

- In Japan, noxious blooms of dinoflagellates and raphidophytes kill finfish and shellfish in aquaculture sites. The average economic loss associated with these blooms is about one billion yen per year. Efforts to decrease nitrogen and phosphorus in the water and sediment have led to a decrease of incidents, but an increase in the number causative species. Coastal shellfish aquaculture in northern and western Japan is seriously affected by PSP and DSP toxins produced by several dinoflagellate species.
- In **Mexico**, 45% of environmental emergencies recorded in 1996 were associated with toxic algal blooms. Most of these cases occurred on the Pacific coast, with some human poisoning cases related mainly to the consumption of oysters. Toxin analyses revealed levels well above standards of the World Health Organisation. Total economical losses due to confiscation of molluses from the market and from hospital treatments were estimated roughly to be several million US\$.
- In naturally eutrophic upwelling systems on the west coast of **South Africa**, high biomass dinoflagellate blooms are often associated with anoxic events and in some instances the production of hydrogen sulphide. For many years these events have been responsible for large faunal mortalities. In the southern Benguela, a single event of this type in 1997, attributed to the decay of a massive bloom of *Ceratium furca*, was responsible for the stranding of an estimated 2000 tons of rock lobster with a value of 50 million US\$.
- Since the first record of a toxic dinoflagellate bloom in 1983 in **Philippines**, over 2000 PSP poisoning cases, leading to a total of 115 deaths, have been associated with toxic blooms. The economic losses are estimated as high as 10 million PHP for each PSP event.
- The **Scandinavian** countries bordering the Baltic Sea are affected by massive blooms of hepatotoxic cyanobacteria. Kills of domestic animals and human skin irritations are associated with these phenomena. Fish-farming in the Scandinavian coastal regions of the North Sea and the Atlantic Ocean suffer from occasional toxic blooms of haptophyte flagellates, which may cause death to a wide range of marine organisms and cause extensive economic damage to commercial fisheries.

Blooms of microalgae need not be toxic to be harmful. Dense accumulations of nontoxic bloomforming algae can generate anoxic conditions resulting in indiscriminate kills of both fish and invertebrates. The oxygen depletion can be due to high rates of respiration by the algae (at night or in dim light during the day), but more commonly it is caused by bacterial respiration during decay of the bloom. Mass occurrences of species forming mucilage, for example *Phaeocystis* in the Baltic Sea, can be a serious aesthetic and economical problem to areas used for recreation.

The economic losses associated with harmful algal events are not easily assessed due to the broad range of sectors in society which are affected. Furthermore, data on losses in the seafood industry are often not released to the public and in many cases the losses are never quantified. Apart from the direct economic losses associated with fish kills, human intoxications, loss of market shares, decline in tourism, etc., there are serious human costs associated with the collapse of local fishing communities, lack of food resources for artisanal fishers, etc. It must be remembered, then, that the harmful effects of HABs extend well beyond economic losses and direct impacts on human health. When HABs contaminate or destroy coastal resources, the functioning of coastal ecosystems is

impaired, the livelihoods and social structure of local residents are threatened, and, in fact, the sustenance of human populations is compromised.

1.3 Oceanographic and ecological systems with HABs

HABs occur in different geographic locations which, due to their particular biology, circulation, basin morphometry, and chemistry, would be classified as "systems" in an operational sense. Examples include:

- a) upwelling systems, as off the Portugal/Spain coast, Peru, Mazatlan in Mexico, Australia, Japan, West Africa-Benguela, etc.;
- b) estuaries and coastal embayment systems, as in the USA, Canada, Australia, southeast Asia, Philippines, Mexico, Scandinavia, etc.;
- c) systems strongly influenced by eutrophication, as in Hong Kong, Baltic Sea, Adriatic Sea, Japan's Seto Inland Sea, mid-Atlantic regions of the USA, etc.;
- d) thin layer systems along most coasts, including France's Atlantic coast, California, and in East Sound, Washington;
- e) coastal lagoon systems as in the USA, Mexico, Brazil, etc.; and
- f) shelf systems affected by basin-wide oceanic gyres and coastal longshore currents as the northwestern European coast, the Gulf of Mexico and Gulf of Maine in the USA, southeastern India coastline.

The great diversity of environments occupied by HABs means that there should be similar diversity in strategies for their study and in the establishment of effective monitoring, preventive and mitigation actions. However, similarities within systems of circulation, biology, chemistry, and basin morphology may permit the development of system models that might be applicable to many coastal areas. By relating physiological and behavioural characteristics of key HAB species to system models adapted for particular regions, predictions of growth and accumulation of the HAB species may be more readily obtained than by repeating an entire system model development for each coastal habitat. Thus, an international program to support the development of models describing comparable ecosystems would rapidly increase international abilities to predict and therefore mitigate local HAB impacts.

1.4 Human influences on the occurrence of HABs

Harmful algal blooms, in the strictest sense, are natural phenomena which have occurred throughout recorded history. There is also fossil evidence of mass occurrences of microalgae and associated mass mortality of marine life. Nonetheless, there is a clear trend towards an increasing frequency and distribution of such events, and thus the threats to coastal regions are clear. On a global basis, the expansion of human activities (fisheries, aquaculture, recreational use and living) in the coastal zone has been seriously affected by HABs, with significant economic and human costs.

Dramatic global increases in the impacts of HABs, and questions about human influences on the occurrence of harmful blooms have been topics for discussion at all major conferences dealing with HABs. Four explanations for the apparent increase in HABs have been proposed: increased scientific awareness of toxic species; increased utilisation of coastal waters for aquaculture; stimulation of microalgal blooms by eutrophication and/ or unusual climatic conditions; and transport of

dinoflagellate resting cysts either in ships' ballast water or associated with translocation of shellfish stocks from one area to another. Tests of alternate (but not necessarily mutually exclusive) hypotheses are difficult to conduct, in large part because data are inadequate and local awareness of HABs generally correlates with human activities in a region. Consequently, there are few, if any, clear-cut demonstrations of the influence of specific anthropogenic activities on the frequency, intensity and geographic distribution of particular HABs.

2.0 Background for the Emergence of the GEOHAB Programme

Research on HABs first emerged as a discipline in its own right at the First International Conference on Toxic Dinoflagellate Blooms which was held in Boston, USA, in 1974. Since then, the field has expanded rapidly as concerns about HABs have increased: in 1997, 464 participants from 58 countries attended the Eighth International Conference in Vigo (Galicia, Spain).

In 1989, The Fourth International Conference on Harmful Marine Phytoplankton reached a consensus "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 new international initiatives have been taken to address the world-wide problem of HABs (see Appendix 1).

Particularly relevant to GEOHAB are the Intergovernmental Oceanographic Commission (IOC), the Intergovernmental Panel on Harmful Algal Blooms (IPHAB), and the Scientific Committee on Ocean Research (SCOR). In response to the wishes of IOC and member states, a Programme Plan for the IOC Harmful Algal Bloom Programme was first formulated at an IOC-SCOR Workshop in Rhode Island, October 1991. Consequently, the Intergovernmental Panel on Harmful Algal Blooms (IPHAB) was established in 1992. At its Fourth Session, IPHAB decided to work towards the development of an international science agenda on the ecology and oceanography of HABs. Simultaneously, SCOR was requested by the United States to take similar initiative. Because SCOR has longstanding experience in the establishment and implementation of international science programmes, and since it is also an advisory body to the IOC, it was natural for the IOC to invite SCOR to take joint action in the development of the new international science programme on the ecology and oceanography of harmful algal blooms.

As described in the Preface, SCOR and IOC organised the GEOHAB workshop on which this report is based. It is hoped that a GEOHAB programme will follow, and that one of its first activities will be the preparation of a more thorough report, based on input from this initial workshop.

3.0 Scientific Background

To understand HAB phenomena, we must consider the growth, physiology, behaviour, and life history strategies of HAB organisms in the context of community interactions as influenced by human activities (e.g., eutrophication, transport of cysts in ballast water) and oceanographic processes on a very broad range of scales.

The harmful effects of algal blooms depend not just on organism density and total number, but also on the features which make them harmful – e.g. toxin content, total biomass, and the degree to which their harmful effects come in contact with sensitive targets, such as shellfish beds or aquaculture sites. The impact of HABs is thus a function of the net growth and metabolism of individual algal cells, as influenced by ecological and oceanographic processes (see "Population Dynamics"). The adaptations of HAB organisms determine which species will proliferate in a particular ecological and oceanographic regime. Thus a focus on adaptations in an ecological context is central to the understanding of HABs.

The following overview of scientific knowledge illustrates that, although a great deal is known about harmful algae and HABs, our abilities to describe the factors controlling the dynamics of individual species is limited by critical gaps in knowledge about how the adaptations of HAB species interact with environmental conditions to promote the selection for one species vs. another.

3.1 Adaptations of HAB organisms

The growth of phytoplankton reflects photosynthesis, nutrient uptake and assimilation, and numerous other metabolic processes within cells. The inherent growth characteristics of species are genetically determined, but the realisation of the growth potential is controlled by environmental factors as mediated through morphology, behaviour (broadly defined) and community interactions. Adaptations of phytoplankton, including HAB species, optimise their net growth in particular ecological systems.

There is considerable diversity among HAB species with respect to patterns of growth and bloom formation in natural systems. Some cause harm at relatively low cell densities (e.g., DSP can occur with only a few hundred *Dinophysis* cells per litre), but in other cases, population growth of HAB species results in a monospecific bloom at high densities. There are numerous explanations for the different types of growth and accumulation, and many of those explanations are rooted in the unique adaptations of the organisms involved. Some adaptations are reviewed below.

3.1.1 Life history strategies

Many HAB species have complex life histories which include different morphotypes as well as the formation of various types of resting stages. Transitions between vegetative and resting stages (excystment and encystment) can influence population dynamics by determining the size of the "seed" stock or inoculum for bloom initiation. The locations and densities of seedbeds will depend on where and how the population encysts and sinks out of the photic zone. The formation of resting stages with resistant walls widens the tolerance range of a species and therefore allows extension of its distributional range, sometimes as a result of human-assisted transport in ship's ballast.

POPULATION DYNAMICS

There is a robust mathematical equation for the local concentration of organisms per unit volume which can be written in the following form:

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

 $\frac{\partial n}{\partial t}$ is the time rate of change of n, the local concentration per unit volume of the organisms under consideration. Integration over a fixed spatial region gives the total number of organisms in the volume, while integration over the total population gives the total number regardless of volume. Population dynamics is the variability of n in space and time.

 μ n represents growth by cell division. This can be affected by endogenous rhythms, as well as by physiological and environmental factors, such as nutritional and light history, turbulence, temperature, salinity.

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

 $\nabla \cdot (n\vec{u})$ includes the three-dimensional, time-variable advection of organisms by the water flow, e.g., 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.

 $\nabla \cdot (n\vec{v})$ is the transport of organisms by their motion relative to the water, described as velocity, \vec{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.

Despite the apparent simplicity of this equation there are many direct and coupled biological, chemical and physical processes. The same environmental processes affect the population dynamics in many different terms, while the coupling covers a broad range of scales in both time and space with many non-linearities. A major challenge is to understand the processes to a level of detail that allows a mathematical statement (parameterisation) that can be incorporated into the equation for calculations. Direct calculations will always be based on simplified descriptions of the actual processes, which are much too complicated to specify exactly. A major problem is to determine what is occurring and how to represent the important details in a tractable fashion that still reproduces the salient and necessary features of HAB population dynamics.

Resting stages are considered to be the product of sexual reproduction, although sexuality has not been confirmed in all cyst-forming species. Life histories are not well described for many HAB species, but there are indications that different strategies exist even among closely related species or different populations of the same species. Laboratory studies and field observations have led to working hypotheses about the influence of cyst dynamics on blooms of some species, however these hypotheses are difficult to test rigorously in nature, largely because inadequate data are available. For other HAB species, cyst dynamics are poorly understood for lack of data on life histories *in situ*.

It is well recognised that the interaction between life history strategies and oceanographic processes determines whether a particular harmful alga can persist in a given region. To make progress, we need to know the respective roles of chemical and physical cues and their interplay with biological characteristics of organisms in the transition between different life stages in the natural environment.

3.1.2 Adaptations for acquiring nutrients and utilising light

Most HAB species depend on photosynthesis for organic carbon, and thus need light and nutrients to grow. There are many ways to characterise adaptations to different regimes of light and nutrients, but one of the most compelling is Margalef's "mandala," which shows how life-forms of phytoplankton, represented by exemplary species, correspond to different regimes of turbulence and availability of nutrients. The trends in cell size, shape, pigment content, and ecological strategy are consistent with a strong influence of nutrient availability on ecological selection.

Conventionally, the special adaptations of phytoplankton for utilisation of light and acquisition of nutrients are characterised by descriptions of photosynthesis or growth rate vs. irradiance (μ vs. E or P vs. E), and nutrient uptake vs. substrate concentration (nutrient uptake kinetics). There is some work characterising the adaptations of harmful species to irradiance, but few studies have been carried out on the nutrient uptake kinetics of HAB species. This is partly because many organisms are difficult to culture (e.g., Dinophysis spp.) or are extremely sensitive to mechanical disturbance (e.g. $Gymnodinium\ catenatum$). A further problem is the difficulty of establishing axenic cultures, which are essential for testing the uptake of organic substances not mediated by bacteria.

Even if more experimental results were available, the extrapolation of μ vs. E or nutrient uptake kinetics to field populations would be uncertain. For example, the responses of phytoplankton to fluctuating light (due to swimming behaviour and turbulence) are not the same as to the average exposure. Further, nutrient uptake kinetics are a strong function of nutritional status so that no one experimental determination of uptake parameters can apply to natural situations where nutrient supplies vary and phytoplankton acclimate to changing availability of nutrients. When it is possible to determine cellular nutrient content or bio-chemical composition, strong inferences about nutritional status can be made. However, this is not generally possible in the field, except when one species dominates plankton biomass.

Some phytoplankton, including HAB species, can move vertically between deep sources of nutrients and well-lighted surface layers, so the characterisation of light-nutrient interactions and adaptations to different hydrographic regimes has required special approaches, including experiments with enclosed water columns, investigations of the responses of phytoplankton to varying nutrient supplies, and modelling of photosynthesis during vertical migration and mixing. Progress has been made describing adaptations of some HAB species, but only a few of these adaptations have been observed in the field, largely because capabilities for appropriate sampling are lacking.

The strong potential influence of nutrient ratios (e.g., Si:N, N:P) on the selection of species is surely relevant to HAB phenomena. Experiments with mixed cultures have demonstrated influences of nutrient ratios on competitive interactions, and results are consistent with patterns of species dominance in some coastal environments subject to eutrophication. When one considers competition for nutrients in the context of differential capabilities for vertical migration, gaps in our knowledge become obvious.

Some dinoflagellate species are able to change nutritional mode from autotrophy to heterotrophy (mixotrophy), thus being able to survive and grow for long periods in complete darkness, and many species of phytoplankton have enzymatic mechanisms to derive nutrient molecules from organic substances. We do not know the relative importance of organic vs. inorganic nutritional sources, the environmental conditions that determine the switching from one nutritional mode to another, or how

mixotrophic nutrition affects toxin production. Mixotrophy is an important aspect of community interactions (discussed below), so it has indirect effects on HAB population dynamics as well. The complex life cycle of *Pfiesteria piscicida* illustrates how complicated the interactions between nutrition, life history strategies, and community interactions can be. The ability of several cyanobacterial species to fix molecular nitrogen (diazotrophy) allows them to build up huge biomasses in circumstances where other phytoplankton species are nitrogen-limited.

Better approaches and more information on light, nutrients and the growth of harmful algae are required. As discussed below, we also need to understand better the influence of nutrients and light on behaviour and the production of biologically active compounds. Also, we need to understand the roles of various nutritional sources, including mixotrophy.

3.1.3 Behavioural and morphological adaptations

The wide range of specific behavioural patterns of the vegetative stages of HAB species enables exploitation of the physico-chemical environment in different ways. Thus strong swimmers can obtain nutrients from deeper layers by vertical migration, and others can accumulate in thin layers where light and nutrients may be favourable and extracellular products can accumulate, perhaps to deter grazers. The ecological importance of these strategies have been well described for several species, but it is likely that the full stories are not yet known (e.g., the effects of nutrition on behaviour are complex) and that many other species have behavioural adaptations that in part determine their ecological success. Major uncertainties about many proposed behavioural adaptations will persist until capabilities for small-scale species-specific sampling are developed so the target species can be studied in nature.

Some species that accumulate large biomass do so in colonies which are much larger than solitary cells. Colonies can be either sphaerical (*Phaeocystis*) and gelatinous (*Microcystis*) or in the form of chains (*Alexandrium catenella*, *Gymnodinium catenatum*). Increasing size reduces the number of potential predators and increases ascent and descent velocities of buoyancy-regulating and swimming phytoplankton. Micro-zones can form in dense colonies, facilitating the utilisation of some micro-nutrients.

It is therefore important to improve our understanding of the functional morphology of phytoplankton as an indicator of adaptation to the environment. A life form or functional group consists of organisms that respond in a similar way to recurrent patterns of environmental factors due to common morphological, physiological or life history traits. Functional groups provide a basis for simplification of the real world in order to improve our predictive ability relative to the dynamics of the system. In many cases it is useful, and perhaps necessary, to consider HAB species as representatives of functional groups.

3.1.4 Production of toxins and other bio-active compounds

A vast array of toxins and other biologically active compounds is produced among various HAB species. These compounds are generally classified as secondary metabolites – they are not directly involved in the pathways of primary metabolism, and their functional significance and ecoevolutionary roles are usually unknown. Many of the major components have been isolated and structurally characterised, particularly from species of high acute toxicity, and this has been accompanied by the development of the appropriate analytical methods. Some of the hypothetical functions attributed to these biologically active substances include allelopathy (chemical defence),

intracellular nutrient reservoirs, regulation of nucleic acid synthesis, and involvement in the induction of sexuality, as pheromones.

For only a few key toxic species (e.g., *Alexandrium* and *Pseudo-nitzchia* spp.) we have rather detailed information from culture experiments on the dynamics of toxin production under varying controlled environmental regimes. Extrapolation of experimental results to natural populations is difficult, however, because of complications associated with variable nutrient supplies and the possibility of vertical movements discussed in section 3.1.2, and the difficulty in verifying laboratory results (e.g., cellular toxin content) with comparable measurements from the field.

For bio-active substances that harm marine life but do not affect common laboratory animals (such as those produced by certain ichthyotoxic species – *Chattonella*, *Heterosigma*) it has been difficult to study biological responses, and many questions remain regarding the nature of the "toxins." Consequently, although it seems likely that toxin production is an important factor in determining the population dynamics of some HAB species (by determining competitive outcomes and grazing regulation, etc.), we know little about the ecological effects of the toxins. Progress depends on acquiring appropriate tools from molecular biology, including methods for detecting toxins in individual cells from natural populations.

3.2 Physical-chemical-biological interactions

In aquatic environments, hydrodynamic processes have paramount importance in the selection of plankton, including harmful algal species, through transport of the organisms, modification of the physico-chemical environment (e.g. light and nutrients), and direct effects on algal cells and the ways in which they interact with their surroundings. Because all other planktonic organisms are influenced by hydrodynamics and the distributions of nutrients or food, HABs can be considered an expression of planktonic community dynamics, which are determined by specific physico-chemical conditions. Although physical-biological interactions (which frequently involve nutrients or other biologically important chemicals) can be considered at different scales in isolation, it is the synergistic interaction among factors operating at different scales that defines the environment governing the dynamics of species or life forms.

3.2.1 Important physical processes and scales

The following overview highlights physical processes that are likely to influence the population dynamics of HAB species over a broad range of spatial and temporal scales. The emphasis is on the degree to which current knowledge can be applied to describing key influences of hydrodynamics on HABs.

There is a good first order understanding of the main features of the mean circulation in the ocean, so it is possible to measure and model the circulation of estuaries, coastal currents, and upwelling areas. Time-dependent, atmospherically- and tidally-forced models are available for many geographic regions (e.g., the North Sea, Baltic, Bay of Biscay, Gulfs of Maine and Mexico). A wide variety of models exists for estuaries and many are used to guide environmental decision makers. Turbulent stresses and buoyancy fluxes are parameterised with a variety of schemes that are increasingly found to have shortcomings, so it is not surprising that models often have substantial uncertainty in the details of their predictions of stratification in response to variations in solar heating, evaporation and fresh water input. Because stratification is known to be a critical factor in

the selection of phytoplankton life-forms, improved models of turbulent stresses and buoyancy fluxes are needed to describe the couplings between mean circulation and HAB population dynamics.

Mesoscale eddies from the deep ocean can impinge on slope and shelf regions, affecting upwelling and the transfer of properties (including algae and nutrients) across the shelf break. These eddies perturb the circulation and can alter residence times of plankton in coastal waters. Difficult to resolve through sampling at sea, eddies are readily detected through remote sensing of temperature, sea-surface height, or ocean colour.

Processes at intermediate scales, ranging (for example) from Langmuir circulation (a few meters) to those at the Rossby radius (about 10 km at mid-latitudes), result in the formation of convergence zones, fronts, and upwelling. These processes appear to determine many of the fluxes that are most important to HABs. Offshore, cross-shelf transport, often occurs at these scales. Whilst arrays of moored current meters and thermistor chains can help determine the advective transport of water and the presence or movement of fronts, Langmuir circulation is often most apparent from the linear patterns of algal concentration; here physical and biological studies may combine to mutual benefit.

Turbulence has significant consequences for the growth and decline of HABs through its influence on the transport of nutrients, the mixing of phytoplankton through gradients of light, and the effectiveness of grazers that might consume harmful algae. Some species are very sensitive to turbulent motions while others seem to benefit from minimal turbulence which can enhance nutrient uptake, thereby increasing the rate of cell division.

Turbulence in different parts of the water column varies in space and time in response to different types of forcing:

- a) Surface Boundary Layer: The turbulence associated with breaking waves and mixed layer dynamics is of great interest to physical oceanographers, which is good because it has a strong influence on the growth and distributions of phytoplankton. The momentum and energy flow from the surface wave field into the water column are at this time largely unquantified.
- b) *Interior Turbulence/Internal Waves*: Empirical relations have been developed between the internal wave field and turbulence in stratified water columns. The role of internal wave interactions with sloping bottom topography and the subsequent mixing in the bottom boundary layer and in the interior of the fluid is largely unquantified but is needed to understand fluxes in the coastal ocean and the influences of mixing on coastal phytoplankton.
- c) Bottom Boundary Layer: The bottom boundary layer often provides much of the stress controlling coastal circulation. Tidal- and wave-induced currents generate turbulence in the bottom boundary layer, and this may affect stratification and biological distributions. Shellfish, worms and other creatures generate small scale roughness that can significantly modify turbulence characteristics of the bottom boundary layer, implying biological-physical coupling. Cyst dynamics within this boundary layer remain unresolved.

Small-scale turbulence (<1 m) is critical to direct community interactions in the plankton. It can be measured and related to some aspects of the larger scale flow (e.g., inertial currents, atmospheric cooling of the upper layer, and other current systems). To characterise small-scale turbulence for

HAB research, it would be necessary to make *in situ* measurements of turbulence and density microstructure in combination with appropriate measurements of the HAB organisms.

Layering of physical, biological and chemical species is often observed in the stratified portion of the coastal ocean. These **thin layers** (fine structure), of uncertain cause and unknown persistence, are found with scales as small as 0.1 m in the vertical and 10 km in the horizontal. One simple kinematic explanation is the stretching of horizontal inhomogeneities by the vertical shear of the horizontal current. This horizontal straining leads to subsurface thin layer formation, producing an environment potentially favouring motile organisms that can maintain their position in this layer. Consistent with vertical aggregation, concentrations of phytoplankton in thin layers are sometimes much higher than could develop in any horizontal inhomogeneity, growing on available nutrients. This scenario moves the unknowns to larger scale that will eventually be amenable to combined biological-physical modelling.

Internal waves are known to affect the distribution of HABs, and the vertical transport of nutrients. Their occurrence is generally unpredictable, but they can be detected acoustically or with arrays of simple sensors. Topographically generated/linked eddies can be persistent, thereby offering a level of predictability of their effects on the circulation, mixing, etc. in shelf seas.

3.2.2 Direct biological-physical interaction

Examples of the importance of **fronts** in phytoplankton bloom dynamics are many, and several prominent studies involve HAB species. A linkage has been demonstrated between tidally generated fronts and the sites of massive blooms of the toxic dinoflagellate *Gyrodinium aureolum* in the North Sea. The pattern generally seen is a high surface concentration of cells at the frontal convergence, contiguous with a subsurface chlorophyll maximum which follows the sloping interface between the two water masses beneath the stratified side of the front. The surface signature of the chlorophyll maximum (sometimes a visible 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. aureolum* 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 Bajas of northwest Spain are a group of oceanic bays noted for their prolific production of blue mussels. This productivity is due in large part to intermittent enrichment of the rias by nutrient-rich deep water during **upwelling**, which is driven by persistent winds from the north. Beginning in 1976, these mussels have been affected by outbreaks of PSP which are often quite sudden; toxicity can rise from undetectable to extremely high levels in a few days. PSP toxicity is linked to the relaxation of upwelling following a change in wind direction and speed. Thus, PSP outbreaks are not due to *in situ* growth of the red tide algae, but instead to the transport or delivery of blooms that originated elsewhere. Similar hydrography, meteorology, and patterns of PSP are found off California and South Africa. In all these areas: a) the dominant hydrographic feature is coastal upwelling, driven by persistent equatorward winds; b) sudden outbreaks of PSP toxicity occur, with toxicity increasing far faster than is possible from localized, *in situ* growth of the causative dinoflagellates; and c) PSP typically occurs during months when a cessation or relaxation of upwelling is common. A comparative approach may aid in developing a fundamental understanding of the linkage between large-scale physical forcings and the pattern of PSP outbreaks.

3.2.3 Nutrient Dynamics

The availability of nutrients is essential for the growth of HAB species, and nutrition affects the production of toxins. Thus, nutrient dynamics should be integral to any physical-biological model of algal population dynamics. Depending on external sources of nutrients and hydrodynamic processes that influence loss rates, the growth rates or accumulations of phytoplankton can be limited by N (like in most marine ecosystems), P (e.g., Mediterranean), Fe (high-nutrient, low-chlorophyll waters), Si (for diatoms) or co-limited by several nutrients (e.g., Baltic Sea). At the very least, potentially limiting nutrients should be considered in physical-chemical-biological models. However, nutrients often exist in different chemical forms which vary both in their biological availability and in the energetics of their assimilation. As an example, one of the most critical limiting nutrients, N, exists as ammonia, nitrate, nitrite, N₂, as well as in dissolved organic N (DON). The poorly characterised pool of DON is by far the largest in most cases, and its complexity makes its utilisation difficult to assess. Chemical speciation is also a critical issue for the availability of many micronutrients which exist in a variety of oxidation states (e.g., Fe(III) vs. Fe(II)) and in inorganic and organically complexed species. To complicate matters further, the ability to exploit different pools of nutrients differs between species and with physiological state, although many

details are unknown for HAB species. It is thus possible that seasonal variation in several pools of nutrients is a critical factor controlling algal succession, including the appearance of HAB species.

Confronted with the daunting complexity of nutrient dynamics, and considering the problems associated with parameterising nutrient utilisation by phytoplankton (section 3.1.2), one might conclude that meaningful advances are a distant dream. Fortunately, the situation is much better than that. Targeted studies on nutrient interactions for particular species, and explorations of the effects of nutrient regime on community structure, reveal much about systems in which HABs occur. Further research will contribute significantly, if the questions are relevant to the ecosystems and oceanographic regimes in which particular HABs occur.

3.2.4 HABs and eutrophication

A classic example of anthropogenic eutrophication comes from the Seto Inland Sea of Japan, where pollution increased nutrient loadings through the 1970's, during which time visible blooms more than tripled. A reduction in industrial and domestic effluents resulted in a decrease in the frequency of blooms to one third of peak levels, a level that has been sustained to this day. Measurements of Secchi depth quantified long-term declines in water transparency that also stopped when controls were imposed. Such eutrophication and remediation represents a large change in chemical influences on HAB dynamics without a large change in physical forcing.

Given the many examples of coastal eutrophication throughout the world, and the increasing frequency of HAB impacts, it might seem reasonable to assume a causal relationship. For example, in Tolo Harbour, Hong Kong, the frequency of observed blooms increased dramatically with population growth between 1976 and 1986, and species composition changed. The underlying mechanisms are presumed to be the increased nutrient loading and altered nutrient ratios from pollution that accompanied human population growth. However, rigorous testing of alternate hypotheses is difficult, because not just harmful blooms were recorded, more blooms might have been missed early in the record, and many things changed in concert with population density. Empirical assessment of the effects of eutrophication on HABs is hampered by similar problems (or worse, due to less comprehensive sampling) elsewhere in the world. One solution is better coastal monitoring. Quantitative measurements, comparable between sites and robust over time, are essential. Continuous measures of key properties, as well as synoptic assessment of spatial patterns (e.g., from satellite imagery or networks of instruments), would help greatly. Another path to understanding is through experimentation and modelling, as discussed below.

3.2.5 Dispersal of HAB species

Some HAB species show a disjunct but cosmopolitan distribution, others are confined to a particular biogeographic environment, e.g., tropical. It is not yet clear whether the apparent increase in the frequency of blooms is due to species dispersion through natural or anthropogenic means, or to an increase in the development of blooms of species already present in the area of concern. This remains as a significant gap in defining the extent of the HAB problem on a global scale.

Studies of geographic distributions are complicated by evidence of genetic heterogeneity at the level of populations of a particular species, from local to global scales. There has been only one major study of global molecular discrimination of a HAB species: for *Alexandrium*. The few other studies on HAB molecular biodiversity have been limited by the need to obtain genetic data on HAB species across their geographic range of distribution. At this time, we do not have enough knowledge to

elucidate the genetic structure of a single population or bloom of a particular species, or the relationships between populations of the same species on any relevant spatial scale. International networking and collaboration will be required in order to resolve global molecular biodiversity of HABs by acquiring detailed genetic data for many other species. The information should be crucial for resolving the mechanisms by which the geographic distributions of HAB species are maintained, and the degree to which human activities are altering them.

3.2.6 Physical-chemical forcing on larger scales

Environmental variability affects HAB on scales ranging from that of storm events to greater than a century (glacial/interglacial). In order to resolve the direct effects of anthropogenic activities (e.g., local eutrophication; transport of HAB species through ship's ballast) from natural variability (here, the term "natural" encompasses all variability in weather and climate, regardless of human influences on atmospheric processes), the temporal and spatial patterns of HABs, HAB species, and their functional groups should be related to environmental variability over scales from seasonal to decadal.

Seasonal variability of HABs is well documented for many systems. The effects of seasonal changes in physical-chemical forcing reveal much about the environmental factors that govern HAB occurrence, e.g., upwelling vs. downwelling-favourable winds and seasonal changes in temperature and light that correspond to optimal growth conditions for particular species.

On the interannual scale, there is accumulating evidence that *Pyrodinium bahamense var. compressum* red tides in the Western Pacific (1978-1998) are associated with the tail end of the El Niño phase of the ENSO (El Niño Southern Oscillation) cycle. Likewise, Central America and Mexico registered the first observation of *Pyrodinium bahamense var compressum* blooms following the 1987 ENSO event, and the blooms have recurred thereafter during every ENSO cycle. Additionally, the cooling trend associated with the increasing Southern Oscillation Index from 1991-1995 was accompanied by southward expansion of *Pseudo-nitzschia australis* from Canada, down the US Pacific coast, to the Gulf of California.

The scarce available information regarding fossil records of harmful algal cysts indicate that distributions in the past were much different from what they are now. When available, this long term (greater than a century) information can provide clues to different circulation patterns and environmental conditions of the past that are conducive to the growth of HAB species for which we have records. More recent samples will help us attempt to resolve the anthropogenic influences on such events. Effective interpretation will require information on climate variability and the biogeography of key HAB species and the suite of other indicator organisms over broad geographical and time scales. These data will allow us to establish patterns that explain the distributions of harmful algae, increased bloom occurrences, and possible introduction to other areas.

3.3 Food-web/community interactions

Harmful algal blooms occur within an ecosystem context, with multiple connections and feedbacks among predators, competitors and HAB species. Pelagic systems are characterised by a seasonal succession of algal species and their predators. The latter comprise a very heterogeneous group that ranges from nanoflagellates and various medium-sized protozoa (such as ciliates and dinoflagellates) to the larger metazooplankton, including the more familiar copepods and euphausiids. Different feeding mechanisms - some of which allow predators to feed on much larger prey - are represented

in this disparate group. Indeed, many HAB species are capable of ingesting particles (phagotrophy), and some of them can be classified as grazers. Thus, the traditional separation between "algae" and "grazers" no longer does justice to the complex trophic interactions present in the plankton.

Recent observations have shown that most phagotrophs feed selectively, with distinct preferences for certain species over others. Since the accumulation of algal cells is as much a function of mortality as it is of growth, it follows that species domination of a bloom can be due to selective adaptations for avoiding particular predators. Infection by viruses and pathogenic bacteria can also affect pelagic organisms, and mortality due to these pathogens is likely to be even more species-specific than in the case of predators. Identifying the various specific predators and pathogens of HAB species is a major challenge for future research. Clearly, recognition of predation, infection and other community interactions is essential for a comprehensive understanding of HABs.

3.3.1 Responses of food webs to eutrophication

In recent decades, many coastal areas have experienced an order of magnitude enrichment in N and P. The ecosystem response to enhanced nutrient loading is generally a build-up of dense algal blooms, often dominated by one or a few species. Such blooms can also have harmful effects such as overgrowth and shading of seaweeds, oxygen depletion of the water column from the decay of bloom biomass, fish suffocation from stimulation of gill mucus production, and mechanical interference with filter-feeding structures. Their impact on the benthos can be considerable.

Several responses of the pelagic community to nutrient enrichment can be predicted. In one scenario supported by observations, an initial enhancement of primary production causes a shift in the modulation toward top-down vs. bottom-up control. Algal species become more rigorously selected for their potential to avoid predation and infection. This mechanism promotes the dominance of algal species which may be toxic, and which contribute less to the productivity of the pelagic zone because of slow turnover. A larger proportion of the primary production remains in the algal biomass or is transported towards the sediments. This progression can be altered if a different nutrient becomes limiting. For example, if macro-nutrients are present in excess and loss rates are low, cellular uptake of available Fe can limit growth rates, thereby favouring smaller cells with greater surface-area:volume ratios.

There is also convincing evidence that shifts in macro-nutrient ratios can act as a forcing function on the entire species composition of nutrient controlled phytoplankton communities. This implies that alterations in the chemical environment might encourage the proliferation of toxic algal species which were not present before.

In shallow embayments and in areas with a completely mixed water column, the sediments may act as a sink or a source for N and P, depending on their organic carbon load and temperature. The role of the sediments as a reservoir for nutrients and algal species (i.e., cysts), the presence of allelopathic mechanisms, and the reduced turn-over rates in the phytoplankton community, will all give rise to hysteresis effects when measures are taken to improve water quality. In other words, the ecosystem will not respond as quickly to nutrient reduction as it responded to nutrient enrichment.

Mathematical models, incorporating a biological and a chemical module and implemented in a physical transport model, have yielded good predictions of the effects of reduced nutrient discharges on the performance of high-algal-biomass blooms for some regions. Nevertheless, the reliability of

these models is still restricted due to our severe lack of knowledge about mechanisms (such as allelopathy and species selection) that increase in importance during restoration of the water quality.

3.3.2 Ecological roles of toxins and other bio-active compounds

Production of toxins or other bio-active compounds (such as viscous exudates) is a wide-spread, but not universal, characteristic of HAB species. The functional roles suggested for toxins are: 1) as deterrents to grazers; 2) as allelopathic compounds that restrict the growth of co-occurring algal species; and 3) as storage products. Alternately, toxins may be secondary metabolites with no selective benefit to the producer.

Field observations suggest that some products of HAB species serve to reduce losses to grazing: fish and zooplankton avoid dense concentrations of certain HAB species, and laboratory studies indicate that toxic species are rejected by at least some predators or grazers. Defence mechanisms against specific predators can have a double advantage: grazing on the more palatable species, such as diatoms, can release nutrients that can then be used by the "protected" algae to increase their net growth rate in a nutrient-limited environment. The response of zooplankton and benthic grazers to toxic algal occurrence is often species-specific in terms of behavioural responses and toxin susceptibility. If harmful algal species are consumed, the grazers may be unaffected, impaired or killed. However, studies to date are limited to a few species and are only a beginning. They certainly have not addressed the diversity of grazer-algal relationships necessary to evaluate the role of toxins in natural populations.

Production of allelopathic compounds by toxic algae has been shown to restrict the growth of cooccurring algal species. However, these studies are limited to a few species and the role of allelopathic compounds in the development of dense algal blooms in natural environments is largely unknown.

3.3.3 Effects of HABs on community interactions

Harmful algal blooms occur within an ecosystem context, with multiple connections and feed-backs among predators, competitors and HAB species. Toxins can move through ecosystems in a manner analogous to the flow of carbon or energy, and the impacts can thus be far-reaching and significant. We are only now beginning to recognise that there can be impacts from toxic blooms in virtually all compartments of the marine food web, due to adverse effects on viability, growth, fecundity, and recruitment of other species. The scope of these effects, resulting from both chronic and acute exposure to the toxins, has become more evident in recent years, as a wide variety of animals is now known to accumulate biotoxins and act as intermediate vectors to consumers at higher trophic levels.

As described in section 3.3.1, high-biomass blooms can also have profound effects on community interactions, beyond the dramatic consequences such as anoxia and mass mortality. Strong influences of high-biomass HABs on community interactions occur even when the blooms are not directly associated with eutrophication.

3.4 Modelling

The preceding overview demonstrates that the problem of describing HAB dynamics is complex indeed. Models, which come in a variety of forms (e.g., conceptual, statistical, dynamical, diagnostic, prognostic), are the key to managing this complexity. They provide theoretical descriptions of systems by means of mathematical relationships that express the underlying processes, thereby allowing us to assess key components of the systems and the nature of their interactions, and to clarify the level of our understanding. Models can play different roles in the study of HABs, including assessing the adequacy of sampling design, allowing the synthesis of diverse types of data, aiding in the evaluation of system dynamics, and predicting the dynamical features of HABs.

3.4.1 Models that have been applied to HABs

Models have been used to study HAB processes since the 1950's. The simplest aggregate the plankton into one or two compartments to explore, for example, the influence of grazing or vertical migration on bloom dynamics. Several models have examined the effects of simple physical flows (internal waves; Langmuir circulation; two-dimensional, cross-frontal circulation) on aggregation patterns of swimming phytoplankton. The most detailed have combined three-dimensional physical flows with models of phytoplankton growth or simple ecosystem models.

Most models of HAB processes have been used to develop better understanding of the possible dynamics underlying HAB formation, and have not been tested (and may not be testable) in the field. A few have been applied to field data, but with limited success. When models do give a reasonable simulation of field data (i.e., they can reproduce well recognised patterns, even if they cannot accurately predict distributions in nature), they are powerful tools for evaluating different processes that influence the dynamics underlying bloom formation, transport and dissipation. For example, processes such as vertical migration or grazing can be deleted from the models to demonstrate how they had contributed to the observed distributions, and parameters can be varied to explore the sensitivity of the model to poorly resolved processes (e.g., growth vs. irradiance, nutrient uptake kinetics, and behavioural patterns).

Although three-dimensional physical-biological models of HABs have been developed, they remain poorly resolved spatially and poorly constrained by data. Experience with modelling and sampling (e.g., for *Alexandrium* in the Gulf of Maine) has shown that testing and forcing of physical-biological models requires observations that are spatially and temporally well-resolved. When such data are available, the techniques of data assimilation can be applied to refine further aspects of the physical and biological models, and most significantly, to give some measure of predictive ability.

3.4.2 Limitations of models

In spite of the gradual improvement in models of HABs, there are significant areas that will benefit from further work. Toxic blooms, in particular, are a phenomenon of the plankton community, not just of a single species. However, the growth and accumulation of individual harmful algal species in a mixed planktonic assemblage are exceedingly complex processes involving an array of chemical, physical, and biological interactions, and there have been almost no models examining marine HABs as a community phenomenon. Formulation of models requires resolution of the various rate processes integral to the population dynamics (e.g., input and losses due to growth, grazing, encystment, excystment, and physical advection). Many of these processes are difficult to quantify in the field because of the lack of appropriate methods and technologies, and the fact that harmful species are often only a small fraction of the biomass in natural samples.

The result is that, despite the proven utility of models in so many oceanographic disciplines, there are no predictive models of population development, transport, and toxin accumulation for any of the major harmful algal species. There is thus a clear need to develop realistic physical models for regions subject to HAB events (section 3.2.1), and to incorporate growth, behaviour and community interactions into those simulations. A variety of strategies coupling biology and physics are necessary to obviate computational limitations. The insights to be gained from modelling studies will do much to advance our general understanding of the dynamics and consequences of HABs, and the models will serve as a basis for predictions.

3.5 Bio-optical oceanography and remote sensing

In order to describe and understand the dynamics of HABs, and to test predictions of models, it is essential to characterise variability in distributions of HAB species, other components of their communities, and key aspects of the physico-chemical environment on the same scales as the factors which control bloom dynamics. Because forcing factors operate on spatial scales from centimetres to thousands of kilometres, and temporal scales from seconds to decades and longer, there is a need for measurements that can provide continuous records at fixed locations, high-resolution vertical profiles, and synoptic measurements over broad regions of coast and shelf. Many different observation technologies are needed to provide this capability, some of which have not yet been developed and many of which are not widely available or adapted for HAB studies. Specific needs for biological (species-specific and biochemical), chemical and physical sampling capabilities will be described later in this report. Recent advances in bio-optical oceanography and remote sensing can in principle satisfy many, but certainly not all, sampling requirements, so the capabilities and limitations of optical observations should be considered in an evaluation of HAB research.

3.5.1 Bio-optical measurements

Algae absorb and scatter light at visible wavelengths (400-700nm). They fluoresce in the red (685nm) when stimulated by natural or artificial sources of light, and some bioluminesce in the

green. The absorption and scattering of light by algae, other micro-organisms, particles, dissolved substances and water modify both the underwater and upwelling (reflected) light fields. The influences of algae, which are generally distinct from those of other components, can be detected and quantified by *in situ* instruments that measure absorption and scattering, as well as by a variety of fluorometers; reflected and fluoresced light can be detected by near-surface and above-water radiometers and by space-borne satellite sensors. Penetration of solar radiation, largely controlled by absorption, can be measured with subsurface detectors. Optical sensors may be installed in profiling instruments, moorings, drifters, flow-through systems on ships, and on undulators, which provide quasi-synoptic sampling. Satellites are unique in their ability to provide mesoscale synoptic coverage but are limited by cloud cover. The launch of the SeaWiFS ocean colour sensor marks the start of a series of operational ocean colour sensors. Some planned for the next decade will have greatly enhanced capabilities to observe coastal waters.

3.5.2 Capabilities and limitations

Where HABs occur at sufficient biomass, they may be detected by optical instruments, including ocean-colour sensors on satellites. Optical sensors cannot detect toxic HABs that occur as minor components of the phytoplankton, although, as with higher-biomass HABs, estimates of total pigment and information such as spectral attenuation from these sensors provide important data for biological-chemical-physical models of HABs. Well-recognised limitations of satellite remote sensing, including interference by clouds, relatively coarse spatial resolution (for coastal processes), and discrete observation periods can be overcome by deployment of *in situ* ocean-colour radiometers on moorings or drifters and by using radiometers on aircraft for surveys during events or process studies. A variety of sensors can also be deployed on ferries or other ships of opportunity. One great strength of ocean-colour measurements is that they are radiometric quantities that retain their validity for long-term and wide-ranging comparisons (e.g., for resolving influences of eutrophication or climate variability). Interpretations of the measurements may improve, but the data should never become obsolete.

Bio-optical models (algorithms) that derive the biomass of algae in terms of pigment have been particularly successful in open ocean (Case I) waters where the bio-optical signal results only from algal biomass. Coastal waters (Case II), where HABs occur, present problems since the algorithms have to discriminate the absorption and scattering of algae from the absorption and scattering of the terrigenous inputs of coloured dissolved organic matter and sediment. These problems are being addressed vigorously by the ocean-colour remote sensing community, and progress has been good.

Knowledge of radiative transfer and the optical properties of phytoplankton is sufficiently mature to state that HABs cannot be distinguished at the species level by satellite ocean colour alone. Synergy of ocean colour with other sensors e.g. sea surface temperature (SST) may provide greater insights into HAB dynamics and remote sensing. Pairing of SST and pigment information allows the identification of key HAB processes and their relationships to physical dynamics. A key contribution of space-borne sensors is their spatial coverage. SST pattern evolution alone has proven a valuable tool to evaluate the oceanographic conditions conducive to HAB onset, development and demise.

Although HAB species cannot be distinguished in ocean colour, research indicates that it may be possible to distinguish the presence of some HAB species using instruments that measure high-resolution absorption spectra of phytoplankton directly. Also, it is now possible to measure spectral fluorescence emission and excitation *in situ*. These measurements can be related to taxonomically and physiologically relevant differences in pigment composition.

A variety of *in situ* optical instruments can provide much additional information relevant to HABs. The fast repetition rate fluorometer (FRRF) directly assesses photosynthetic physiology of the phytoplankton assemblage; methods for single-cell determinations have been developed in the research setting. Interpretations of these active fluorescence measurements are developing rapidly, but more study is needed before the measurements can be related directly to the growth rate or nutrient status of HAB species *in situ*.

A principal problem with *in situ* optical systems is that they are not generally used where HABs occur, either for monitoring or research. Wider use of optical observations, particulary in less developed countries, will require the development of simpler, more affordable optical systems, with robust, widely accepted approaches for interpreting the measurements.

It can be concluded that bio-optical observation systems, including remote sensors on satellites, offer great promise for the study of HABs in an oceanographic context, even though optical methods will not be suitable for describing temporal and spatial variability of many harmful algae, particularly toxin producers. Biological interpretations of optical measurements are still imprecise, but the situation will improve through integration of optical studies with HAB research.

4.0 Background on Mitigation and Control of HABs

The ultimate goal of research and monitoring efforts on HABs and their impacts is to protect public health, fisheries resources, industry of aquaculture, ecosystem structure and function, and coastal aesthetics. This requires a fundamental understanding of the many factors that regulate the dynamics of HABs, but by itself, that knowledge does not provide sufficient protection. Mitigation strategies are needed that reduce impacts by avoiding the blooms or minimising their effects (hereafter termed *impact prevention*) or by actions targeting the bloom population (*control*).

Given the extent of the global HAB problem and the increasing use of coastal waters for food, commerce, and recreation, it seems logical that efforts would be undertaken to control the blooms or minimise their impacts, but little has been done in this regard. The need for bloom mitigation strategies is most compelling in aquaculture areas, given that such facilities are already manipulating the local habitat to produce food. Countries which "farm" the sea heavily (e.g., Korea, China, Japan) have thus invested in research on controlling blooms. Most countries, though open to ideas about mitigating the impacts of HABs, have not investigated options for bloom control.

4.1 Impact Prevention

Some effects of HABs on marine resources can be minimised by predicting the threats and taking actions to avoid them. For example: fish cages can be transported to refuge sites; fish or shellfish can be harvested early; sites for aquaculture facilities can be chosen on the basis of hydrodynamics and water quality; content and quantity of fish food can be modified; species which are less susceptible to particular HABs can be selected for aquaculture. Except for immediate responses to blooms, these strategies require conceptual or numerical models of regional bloom dynamics that must be developed and validated on the basis of local surveys and monitoring. For most regions, models are either unavailable or rudimentary.

Attempts at impact prevention have been successful in some situations, but critical gaps in our knowledge constrain the broader-scale application of these methods and the development of new

strategies. Monitoring and management systems for HABs and their toxins are not optimised for prediction or model development. Models are not presently capable of predicting the occurrence, distribution, toxicity, and environmental response of HABs, and the modes of action of some HAB toxins are not sufficiently understood to guide intervention efforts on affected fish.

EUTROPHICATION AND GREEN TIDES

A prominent example of the link between certain HABs, eutrophication and efforts to mitigate the effects is the Long Island "green tide" of the 1950s. During that time, bays on the south shore of Long Island, New York, were subject to extremely dense blooms of a small *Nannochloris* species that turned the water a vivid green colour. This not only altered the aesthetic quality of that region as a recreational area, but these blooms were also blamed for the failure of the local oyster industry. Research correlated the green tides with the local duck farm industry. The dense green tides which occurred in the 1950s diminished during the 1960s after the flushing characteristics of local waters were increased by opening a channel to the ocean and by the gradual demise of the duck farming business. Pollution control measures were also imposed on existing duck farms. There have not been any recurrences of the green tide blooms.

This green tide example highlights the connection between human pollution and HAB incidence. However, it is not possible to say how many blooms actually reflect this linkage. Clearly, before control strategies based on the reduction of nutrient inputs are implemented, the case must be proven that human pollution is in fact responsible for the proliferation of a particular HAB species. This is an obvious area for extensive field and laboratory effort. Additional research is also needed if we are to predict the shifts in community composition that are likely to accompany major changes in water quality.

4.2 Control

Prevention efforts are designed to address the impacts of blooms; control methods attempt to alter the size, composition, or duration of the blooms. Control can be categorised as either "direct" or "indirect" depending upon whether the effort targets an existing bloom or strives to reduce future blooms, such as through alteration of pollution inputs.

4.2.1 Indirect Control

Nutrients/eutrophication. HAB species require major and minor nutrients that can be supplied either naturally or through human activities, such as pollution. A case has been made that increases in pollution are linked to increases in the frequency and abundance of HABs (see section 3.2.4). It follows that a reduction in pollution would lead to a decrease in bloom frequency. However, if nutrient ratios are altered, unwelcome species might be encouraged (section 3.3.1).

Bio-manipulation. Human modification of ecosystem structure to conserve, establish or re-establish a biological structure that may prevent HABs is termed "bio-remediation". One example might be the establishment of populations of benthic filter feeders to control populations of HABs or grazers. Another might be artificial aeration to mix the water column, favouring species which thrive in well-mixed waters over those requiring stratification. The design and evaluation of bio-manipulation strategies require a fundamental understanding of associated processes, such as the grazing losses, or

the influence of water column mixing on species succession. These are important unknowns and thus represent promising research directions.

Modification of water circulation. In some semi-enclosed areas, HABs linked to either local eutrophication or restricted circulation can be minimised by changing the circulation of water masses to optimise flushing of nutrient rich water and HAB species. This again requires understanding of linkages between hydrography, nutrient loadings, and bloom dynamics, of which little is known for most HAB species.

4.2.2 Direct Control

Biological Control. Predation and mortality of HAB species are obviously critical elements of bloom dynamics, but they also represent an avenue to explore with respect to control strategies. Research on predator-prey interaction is needed both to elucidate aspects of HAB dynamics and to identify opportunities for mitigation.

Viruses, parasites, and bacteria are also promising control agents, as they can be abundant in marine systems, replicate rapidly, and sometimes are host-specific. Thus far, no field trials of bloom control using pathogens have been attempted, in large part because of uncertainties about host specificity, pathogen stability, and environmental impacts. It is clear that "microbes" of this type can have profound impacts upon HAB population dynamics, but we have little knowledge of underlying mechanisms, or of their impacts on bloom dynamics.

Physical/chemical control. Forty years ago, copper sulphate was applied to a red tide in Florida, but was deemed too expensive and non-specific. Another study screened 4,700 chemicals against Florida's red tide alga but found not one that was sufficiently potent and did not adversely affect other organisms. Thereafter, chemical control options have received little attention. One promising non-chemical strategy involves the treatment of blooms with flocculants such as clay, which scavenge particles (including algal cells) from seawater and carry them to bottom sediments. Small-and large-scale field trials near fish farms have been successful, though not well-documented. This mitigation strategy looks promising, but considerable research is needed first, especially at the ecosystem or community level. Critical unknowns include the fate and effects of sedimented cells and toxins on bottom-dwelling animals and the collateral mortality of co-occurring planktonic organisms. Decomposition of sedimented biomass and the resulting oxygen depletion are also serious concerns.

4.3 Relationship between scientific research and mitigation strategies

Clearly, there are key processes and mechanisms in HABs that are critical elements of bloom dynamics, and which are therefore logical areas to target with prevention or control strategies. An understanding of these same processes and mechanism is central to scientific research on HAB phenomena. We feel that the design and testing of specific HAB mitigation strategies is beyond the scope of an international scientific research programme. However, as the scientific research progresses, mitigation applications are likely to follow. In turn, if new mitigation strategies are proposed, relevant scientific questions will no doubt arise.

5.0 GEOHAB, an International Response to a Global Problem

Problems associated with HABs are widespread, serious, and on the increase. A great deal has been learned about harmful algae and the factors that influence their population dynamics and harmful effects, but many key questions are unanswered. To resolve these uncertainties about HABs, it is necessary to consider harmful species in an ecological context, as influenced by human activities and oceanographic processes. At the national level, considerable energy and money have been devoted to detecting and characterising HAB toxins and to implementing and sustaining monitoring programs to protect public health, but insufficient effort has been directed toward studying the biological, chemical, ecological and physical factors which regulate algal population dynamics, and thus HABs and their impacts. Many countries are strongly affected by HABs, but do not have the infrastructure and resources to conduct such interdisciplinary research on coastal processes. Consequently, there is a need for a co-ordinated international scientific program on the ecology and oceanography of HABs that incorporates the participation of numerous countries.

Participants in the Joint SCOR-IOC Workshop at Havreholm, Denmark carefully considered the needs for scientific research on HABs, and developed the following plan for a co-ordinated international scientific research programme to study the ecology and oceanography of harmful algal blooms. Although we identify key research questions and promising avenues for advancement, it is not our intention to specify the research directions for a new programme. Rather, we recommend that a programme be established so that, through international co-operation, the most effective research can be pursued.

5.1 Mission statement

To address the need for broadly-based advancement in the understanding of HABs, we propose the establishment of GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms), a programme of scientific research. Acknowledging that the HAB problem is very broad, but recognising that insufficient efforts have been directed toward studying the biological, chemical, ecological and physical factors which regulate HAB dynamics and impacts, we define the objectives of the GEOHAB programme with the following statement:

The mission of GEOHAB is to foster international co-operative research on harmful algal blooms in the context of their ecological systems and the oceanographic processes which influence them.

GEOHAB would be different from most scientific programmes. Like other international research efforts, it would encourage and develop co-ordinated, interdisciplinary, international scientific research on HABs. However, GEOHAB would be committed to working with other organizations and programmes to see that the benefits of this research get to the global community as effectively as possible.

5.2 Scientific goal

The mission statement for GEOHAB explains the kind of research that will be encouraged. The scientific goal describes what we intend to accomplish:

Determine ecological and oceanographic mechanisms underlying the population dynamics of harmful algae, by the integration of biological and ecological studies with chemical and physical oceanography, supported by improved observation systems.

Integration of different disciplinary approaches in new ways is essential to progress, so achieving that integration is included in the goal of the programme.

5.3 Major research questions

Participants at the GEOHAB workshop identified three major research questions that must be answered to describe the ecological and oceanographic mechanisms underlying the population dynamics of harmful algae. Each question is followed by a brief description of possible research directions:

1. What are the unique adaptations of HAB species that determine when and where they occur and the extent to which they produce harmful effects?

The question of unique adaptations can be addressed by documenting the life cycles of HAB species, their physiology and behaviour, and the interplay between physical processes, environmental cues and progression through their life cycles. Every species is unique, whether it causes HABs or not. Thus, it would not be enough to find the particular adaptations of certain HAB species; it would also be necessary to show, for example, that non-HAB species lack these adaptations. Interdisciplinary process studies of HABs in comparable ecosystems would be important to resolving the mechanisms underlying algal population dynamics that explain the selection for HAB species.

2. How do HAB species and their community interactions respond to environmental forcings?

It is important to know whether HAB species respond selectively (in terms of growth rate, biomass and/or the production of toxins) to environmental forcings including, but not limited to, inorganic and organic enrichment (amounts, patterns of input, qualitative effects), temperature, and changes in the abundance of large consumers in an ecosystem context (e.g., in the presence of bacteria, competitors, grazers and predators). Interdisciplinary studies of the influences of turbulence, altered trophic structure or variations in nutrient fluxes on community interactions could be conducted in micro- or mesocosms; findings would be modelled, and compared with observations of natural communities in comparable ecosystems.

3. What are the effects of human activities (e.g., eutrophication) and interannual and decadal climate variability (e.g., El Niño, North Atlantic Oscillation) on the occurrence of HABs?

Robust, quantitative approaches are required to distinguish direct anthropogenic effects from climate-related influences on HABs. To resolve spatial patterns and temporal trends as they relate to environmental forcing, it will be necessary to quantify patterns in HABs relative to phytoplankton in general, with concomitant information on physical and chemical variability, including human influences such as nutrient loading. To study possible effects of human-assisted dispersal, taxonomic and genetic surveys of HAB organisms from different locations, along with physiological characterisation of isolates, could be examined to test hypotheses about possible dispersal mechanisms. Temporal and spatial distributions of harmful algae and other phytoplankton could be examined using records in sediments (for some species), contemporary observations, and new observations from a developing Global Ocean Observing System.

5.4 The need for targeted studies and technological advancement

The relatively broad research directions outlined above are best addressed through international, cooperative, interdisciplinary research. Because there are many gaps in our knowledge about HABs, and limitations in our abilities to measure key properties or processes, targeted studies and technological innovation are essential to addressing the research questions central to GEOHAB. The list of needs, and hence of opportunities for advancement, is long indeed. Some examples follow. It is important to recognise that these directions for research are presented only to illustrate that much needs to be done; it is not our intention to specify or circumscribe the research directions for GEOHAB.

5.4.1 Adaptations of HAB organisms

The approach to *life history strategies* requires small-scale laboratory experiments on the triggering mechanisms for transitional stages (encystment/excystment), and the induction cues for sexuality. Such studies should be combined with *in situ* observations of the dynamics of resting stages, using sediment traps and other benthic sampling equipment, accompanied by measurement of the appropriate chemical and physical parameters. Combined with data on growth rates of vegetative cells, this information could be used to construct physical-biological models of population dynamics.

To improve our knowledge of swimming behaviour and other strategies for maintaining buoyancy (colony formation, production of low density metabolites), it will be important to consider how realistic interactions of light and nutrients influence swimming or buoyancy, and how such behaviour facilitates utilisation of light and nutrients. Studies in mesocosms with the appropropriate

gradients (light, temperature, salinity, nutrients) could be particularly useful. Comparisons of HAB species with other phytoplankton would be important for resolving any special adaptations of harmful algae.

Morphological characteristics of phytoplankton indicate adaptation to the environment. To interpret how changes in cell size and shape are related to genetic factors vs. to environmental conditions we need to know the stages of the life cycle and the physiological status of these species. Development of rapid identification tools (molecular probes, neural-network image analysis, etc.) will assist in the accurate identification of field specimens and will permit extrapolation from small-scale culture experiments.

Factors that influence production and cellular accumulation or excretion of biologically active compounds (including toxins) should be characterised in a fashion relevant to the population dynamics of HAB species. It will thus be necessary to compare results from carefully designed experiments on unialgal or axenic cultures to measurements in natural populations. This can be accomplished with the development of sensitive assay techniques (neuroreceptor, immunological, enzyme-based, reporter gene, etc.) and increases in the sensitivity of chemical analytical methods to be applied at the cellular level.

5.4.2 Physical-chemical-biological interactions

Research into many areas of physical oceanography related to HABs is ongoing and requires no special part in the program. However, models of physical processes for use in biological prediction could be improved considerably if some specific needs were addressed. First, a substantial database of stress and dissipation measurements is needed in order to *improve the parameterisation used in physical modelling* of circulation, advection, turbulence, and mixing on scales that are relevant for the biological distributions. Second, *simultaneous*, *coincident measurements of the distributions of phytoplankton, predators, and the appropriate physical parameters* to define the processes of algal transport, growth, and mortality are needed. For example this will involve the measurement of correlations between the local concentration (e.g., patchiness) of algae and the physical features of the flow and its stratification (e.g., eddies, turbulent dissipation, current shear, the presence of thin layers) which affect algal distributions, growth, and mortality.

To study the interactions between the *behaviour* of HAB organisms and their habitat requires the integration of multiple factors, including turbulence, stratification, geotaxis and phototaxis, and strategies of nutrient acquisition. For example, to establish the interaction between physical factors and swimming behaviour at convergences and other fronts (typical in the case of *Gymnodinium catenatum* in downwelling systems), we need to measure the current field over the slope and on the shelf, as well as estimating vertical velocities.

It is important to describe the effects of *nutrients* (concentrations and ratios) on the growth of HAB species vs. other phytoplankton, e.g., which specific nutrients are limiting for individual species in their environment. As described in sections 3.1.2 and 3.2.3, this requires analytical information on both the concentration of total dissolved nutrients and the individual pools of available chemical forms. There is also a need for robust analytical methods to assess nutrient limitation from cellular bio-chemical composition. Progress depends on the development of sensitive and selective chemical analyses (e.g., ways to measure the availability of the DON pool and of micro-nutrients), and better methods for identifying nutrient limitation in phytoplankton, particularly species-specific methods.

Sensitive immunoassays to key proteins (e.g., metallo-proteins or cytochromes) are especially promising but they need to be rigorously tested under controlled laboratory conditions with cultures.

One approach to studying nutrient dynamics is to conduct micro-nutrient and organic addition or light perturbation experiments in field water samples and to measure the response of HABs and other important members of the community to these additions. However, in these experiments, it is often impossible to separate effects on algal growth from those due to changes in grazing. The need for considering community responses is clear.

Experiments with *micro-nutrient metals* (Fe, Mn, Zn, Co) can overcome some experimental difficulties by using metal ion buffer systems to examine relationships among growth rate, cellular content, and free metal ion concentration, the parameter which is understood to control metal uptake and growth effects. In principle, these experiments can be used to estimate limitation in field situations by using emerging techniques for measuring free metal ion concentrations. Care must be taken, however, to consider important factors such as interactions with competing metals or with other nutrients. In some cases the free metal ion concentrations may not provide an accurate measure of availability, but such issues can be addressed in controlled laboratory experiments.

To define the significance of *species dispersion*, past and present, in the spread and occurrence of HABs on a global scale, it will be important to elucidate the molecular bio-diversity of HAB species and its relationship to physiological characteristics and spatial patterns. To achieve this, collaboration is needed among laboratories in many different countries in order to characterise individual strains of HAB species in cultures from populations on local and regional scales. Development and testing of appropriate techniques for these different levels of discrimination is required. This molecular typing will provide crucial data with which to define the significance of intra- and interspecific bio-diversity in bloom dynamics. Such techniques could also be used in the monitoring systems that will be required to implement regulations to ensure that human activities do not contribute to the spread of HAB species.

To observe the effects *physical-chemical forcing on larger scales*, and thus to resolve in part the relative contributions of human influences vs. natural climate variability on algal population dynamics, we need to develop a retrospective and current data base of information on HAB events and harmful species distribution, including associated organisms. Data are already being compiled; an expanded data base would include environmental information, remote sensing data, and information on anthropogenic factors such as: population increase, ballast transport, major coastal engineering activities, wars, etc. For the few known HAB species that form resistant resting cysts capable of persisting in sediments, stratigraphic evaluation of sediment cores offers potential as indicators of historic conditions. Measurements of pigments in the sediment might also yield useful information on phytoplankton communities. Multivariate analyses of distributional data might foster the development of empirical models based upon long-term climatic variation.

5.4.3 Food-web/community interactions

Assessing the role of HAB species in community interactions requires comprehensive studies of their relationships with other algae (competitors) and their predators. It will be necessary to study various properties and mechanisms such as allelopathy, grazer defences, etc. that distinguish HAB species from other algae. Explicit comparisons with non-HAB species are important to understanding the selective significance of characteristics that are advantageous to HAB species.

Key issues include: the extent of allelopathic interactions, interclonal variability and biochemical activity, including toxin transfer in food webs; the importance of spatial and temporal separation between harmful algal species and their specific predators, and the relative contribution of pelagic and benthic grazing; the role of behaviour, toxicity and cellular chemical composition (food quality) in reducing or avoiding predation controls; and the effects of mixed toxic/non-toxic assemblages on grazing control — e.g., does breakdown of grazing only occur once harmful algae become a dominant component of the phytoplankton?

To study feeding behaviour and its relation to toxins and other biologically active compounds, requires improvements in analytical methods for the detection of these trace compounds in dissolved in seawater and in samples of particulate matter in which harmful algae are a minor component. Targeted studies can be designed using simple culture systems (e.g., single predator-prey), but more realistic behavioural responses can be measured in mesocosms or in natural communities. Technologies such as flow cytometry and micro-cinematography could be useful for single-cell observations of feeding behaviour.

More laboratory studies should be conducted to examine the influence of specific pathogens and predators (viruses, bacteria, parasitoids, different protist and metazoan groups) on algal species and community interactions. This will be a major undertaking. New methods should be developed to examine these processes in the field.

Questions such as how cascading effects will ultimately have an effect on HABs (by decreasing of grazing pressure) are possible to investigate in mesocosm systems. Top predators such as planktivorous fishes, jelly-fishes, etc, may be added to tanks, bags, containing hundreds to several thousands m³ of seawater and its indigenous plankton communities (where harmful algal species are present). Nutrients might be added, if bottom-up control versus top-down control on the HABs, is to be investigated. The entire microbial food web is then quantified for some days and rates estimated (eg. specific growth rates, production, ingestion rates nutrient fluxes). Experimental control of turbulence must be carefully considered.

5.4.4 Modelling

A modelling framework is crucial to furthering our understanding of HAB dynamics. To determine reasons for HAB events in specific ecosystems, it is necessary to define the physical characteristics that support specific life strategies of successful HAB species in relation to other members of the plankton community. These physical influences are examined through coupled physical-chemicalbiological models. Appropriate data are required for construction and validation of the models. It is therefore necessary to develop sampling strategies that take into account simultaneous measurements in a spatial and temporal framework combining different platforms, using simultaneous multi-ship efforts, and in situ sampling tools, in conjunction with existing monitoring programs. Characterisation of water motion at selected scales is required to understand the response of bloom species, including use of current profilers, towed undulating systems, and remote sensing techniques in addition to standard discrete measurements. Only the synergistic combination of models and data will lead to an improvement of our predictive skills. Thus, major efforts will be required to develop a suite of data assimilation techniques to strengthen the linkage between observations and models. Improved observation systems are needed not only for process studies in support of model development, but also for both empirical analysis and models predicting regional, inter-annual, or seasonal variability.

Even the best programme of sampling and modelling will provide only an approximation of the spatial/temporal distributions of HAB populations and their communities in relation to the physical/chemical/ecological factors that influence them. That is, observations and models require varying degrees of abstraction and aggregation and thus fail to resolve all relevant features. Nested models on small-scale interactions can be used to evaluate the consequences of aggregating observations and predictions.

5.4.5 Bio-optical oceanography and remote sensing

Optical sensors show great promise for *in situ* monitoring of phytoplankton dynamics, and HABs, when they dominate the algal assemblage. Radiometric sensors on moorings, profilers or undulating instrument packages can measure ocean colour and the penetration of sunlight, to characterise components of the water (including phytoplankton) and to complement satellite imagery. Such radiometric measurements would be appropriate for a long-term global database on coastal variability, developed through Coastal GOOS. Observations of ocean colour *in situ* are also important for the development of local bio-optical algorithms that will be needed for monitoring programmes.

Instruments that measure spectral absorption, scatter and fluorescence *in situ* can provide continuous information on algal pigments with excellent spatial resolution. The potential for resolving certain taxonomic groups is good, and specialised instruments with high spectral resolution may be able to distinguish important species or functional groups.

New instruments such the fast-repetition-rate fluorometer can be used to provide a key link between laboratory physiological studies and observations of natural phytoplankton communities. More experimentation on HAB species and other phytoplankton is necessary to evaluate existing physiological interpretations of measurements from active fluorometers. Successful attempts to determine fluorescence parameters on single cells through specialised flow cytometry suggest that it may be possible to characterise physiological status of harmful vs. other phytoplankton in the same community.

Even though ocean colour is unlikely to provide adequate information to determine species composition, remote sensing can be very useful in studies of HABs. For example, remote sensing can provide the oceanographic context for areas where HABs occur. Satellite sensors can provide data to describe patterns of wind, rainfall (between 40°N to 40°S), sea-surface temperature, seasurface height (thus geostrophic currents), salinity and ocean colour, although of coarser resolution than desirable to describer HAB dynamics. These data would provide key insights into models of HAB development, in some cases providing good information on the transport of blooms. Some of the observations would be used directly in data assimilation models. New satellite sensors will have better spatial and spectral resolution for ocean colour, and thus may be even more useful.

The important research directions for bio-optical oceanography and remote sensing in support of HAB studies are thus: integration of ocean colour data with that from other sensors i.e., compound remote sensing; and continued research on the optical properties (including fluorescence responses) of algal groups, including HABs, in relation to nutritional and taxonomic status.

5.4.6 Topics related to mitigation

For impact prevention at the local level, it is necessary to develop early warning systems. These require: a) improvement and /or development of observation systems (remote sensing, moorings networks, species-specific spectral signatures, specific sensors, telemetry networks); and b) development and calibration of operational models to assess and predict risks.

Direct bloom control will not be possible without a thorough understanding of the critical "control points" of HAB population dynamics which could be exploited in mitigation strategies. One mechanism in bloom dynamics that might be exploited involves mortality of the HAB species due to natural pathogens such as viruses, bacteria, or parasites. A scientific assessment of the feasibility of biological control of this type requires investigations into HAB population dynamics, with emphasis on microbially-mediated mortality or loss factors.

Long before physical/chemical mitigation strategies (such as clay flocculation) can be applied to blooms on a large scale, we must be able to estimate the effects of the treatment on local ecosystems. Multidisciplinary studies are needed which document an ecosystem's sensitivity to these perturbations. This could be accomplished through a process study on a large-scale clay application, for example. Another potential mitigation approach might derive from assessments of the effects of environmental conditions (such as salinity, pH, light changes or stratification) on growth and toxicity of organisms.

Indirect control strategies will require considerable background information prior to implementation. Predictions of the effect of changing local hydrodynamics of an area subject to HAB outbreaks will require coupled physical/biological models that adequately represent local population dynamics and water circulation. Methods to quantify ecosystem or community impacts, and net population growth rate estimates are also needed.

Other indirect control strategies might involve bioremediation through the introduction of a beneficial species such as a bivalve which would remove the HAB cells. This should not be attempted unless there is a thorough understanding of the nature and dynamics of "top-down" control of HAB populations in a given area.

5.5 Specific recommendations

The preceding discussion of promising research directions was presented primarily to demonstrate that a broad range of targeted questions and technological advances are directly relevant to the interdisciplinary, co-operative research that GEOHAB will encourage. Only through broad consultation can the most important research directions be identified. We reiterate that is not our intention to specify or circumscribe the research directions for GEOHAB. Rather, we recommend that SCOR and IOC organise a Scientific Steering Committee (SSC), charged with identifying the scientific issues and detailed goals and objectives for an international study of the ecology and oceanography of harmful algal blooms. These issues, goals and objectives would be identified through broad consultation. Consideration of, and co-operation with, the many national and regional programmes throughout the world would be central to the efforts of GEOHAB.

The GEOHAB programme would foster scientific advancement in the understanding of HABs by encouraging and co-ordinating fundamental scientific research — multifaceted, international, and interdisciplinary, maintaining an ecological and oceanographic context consistent with the scientific goal of the programme. International, co-operative research on comparable ecosystems would be encouraged. In addition, GEOHAB would identify targeted studies on organisms, processes,

methods, and observation technologies that are needed to support the interdisciplinary research. Improved global observation systems will be required to resolve influences of environmental factors (anthropogenic and climate-related) on distributions and trends in the occurrence of HABs in the context of environmental forcing and community interactions. This will be greatly facilitated through strong links between GEOHAB and the Global Ocean Observing System (GOOS).

6.0 Deliverables and benefits

6.1 Advances in understanding and capabilities

Scientific understanding of the factors controlling HABs will be a principal benefit of GEOHAB. The focus on ecology and oceanography and the commitment to interdisciplinary research will ensure that major advances are made in the study of algal population dynamics and community interactions. In addition, through international co-operation, a much better appreciation of global patterns, including similarities and differences between comparable systems, will be acquired. All these advances will provide a much strengthened scientific framework for monitoring HABs, assessing their effects, and resolving the causes of their occurrence. It is strongly felt, however, that this program must provide more than scientific progress *per se*. The research should contribute quickly and efficiently to better strategies for management of HABs in terms of monitoring, prevention and control.

6.2 Improved capabilities for monitoring, mitigation and prediction

There is presently a widespread need for improved monitoring of HABs and their effects. In many regions, the cost vs. demonstrable benefits of available technologies is a major consideration. Research encouraged by GEOHAB will contribute significantly to the development and evaluation of monitoring techniques, thereby improving international capabilities for effective monitoring. Practically useful benefits of GEOHAB include:

- New tools for detecting and identifying HAB species (e.g. genetic probes, surface antibodies, lectins, automatons,...). These should, after proper quality control, reduce the analysis time in monitoring programmes while improving specificity.
- In some cases, the **species responsible** for toxic effects, presently unknown, may be identified. Research along those lines can only be beneficial to monitoring programs.
- Determination of the **modes of action** of toxins will allow the development of alternate toxicity tests. One can envisage development of enzymatic electrodes, cytotoxicity tests, use of synthetic membranes, etc.
- Clear understanding of HAB development scenarios will allow an **optimisation** of the sampling strategy, guaranteeing a better assessment at lower cost.
- As **optical chemical physical observation systems** are developed, along with improved biological interpretations of optical measurements, cost-effective monitoring approaches can be identified, and input can be provided into data-assimilation models.

Results from GEOHAB will also provide elementary tools for impact prevention. For example, empirical models, even if they provide little extra insight into underlying mechanisms, may be of

great help in defining the probability of a harmful event. They may encompass a wide range of approaches. A good example is the prediction of seasonal risk for PSP contamination by surveying resting cysts in the Spring.

Identification of the **controlling factors** in the dynamics of a given HAB population may guide strategies for direct action to control blooms.

As our understanding improves, our **predictive capabilities** will eventually become useful for managerial purposes. Utility can only be demonstrated by the quantitative comparison of prediction with observation, so the development of monitoring capabilities concurrent with modelling techniques, is essential.

Scientific knowledge about HABs will be especially useful if insights and suggestions are conveyed effectively to people responsible for protecting coastal resources. One avenue would be through advice, which would be disseminated and provided, with the necessary quality control, through an appropriate interface. Any plans for establishing an advisory mechanisms would have to be considered very carefully. The GEOHAB Scientific Steering Committee may wish to explore the idea. Formal advice on management (such as suggestions concerning strategies for mitigating HABs through reductions of nutrient loading) are only conceivable in the long term but, as research develops in the context of the scientific agenda, it would be useful to develop a mechanism for the exchange of between the scientific community and the operational organizations (monitoring agencies, public health, seafood safety, etc.). Links to the Global Ocean Observing System (described below) represent one avenue for **effective transfer of information**.

6.3 Links to GOOS

The Global Ocean Observing System (GOOS) was created in 1992 in response to conventions signed at the UN Conference on Environment and Development (UNCED, Rio de Janeiro, 1992) that required the establishment of "an adequate observing system 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." To this end, with support from the IOC, WMO, UNEP and ICSU, GOOS has been charged with *promoting* the development of observation systems that will improve: (i) weather forecasts and climate predictions; (ii) now-casting and forecasting for safe marine operations and the mitigation of natural hazards; and (iii) documentation and prediction of the effects of human activities and climate change on marine ecosystems and the living resources they support.

GOOS consists of two related components, a basin-scale component concerned primarily with the role of the oceans in global climate change and a coastal-scale component concerned primarily with the combined environmental effects of climate change and human activities at local to regional scales (C-GOOS). GOOS is intended to address issues that are global in scope as well as those that occur on smaller (local-regional) scales but which are globally ubiquitous and would benefit from comparative analysis or from data and information collected on larger (regional-global) scales. The charge to C-GOOS is to promote the establishment of the *integrated, multi-disciplinary observation* systems required to achieve these goals in cases requiring information on scales that are beyond the capabilities of any individual nation. Such systems must be responsive to user needs in the coastal zone. In this context the C-GOOS Panel has established the following goals: (i) determine user needs and specify data and products (deliverables) required to satisfy them; (ii) identify regions where current monitoring programs are inadequate and formulate plans to fill them; (iii) identify

inadequacies in measurement programs and develop recommendations for improvements in terms of variables measured, the scales on which they are measured, and their usefulness; and (iv) promote

- regional to global co-ordination and integration of monitoring, research and modelling;
- the design and implementation of internationally co-ordinated strategies for data acquisition, integration, synthesis and dissemination of products (deliverables);
- the implementation of regional to global networks to improve now-casting, forecasting, and prediction of environmental change; and
- training and capacity-building to enable international participation.

The priorities of C-GOOS include the design and implementation of HAB observation systems on regional to global scales and the development of *in situ* and remote sensing techniques for monitoring the effects of nutrient enrichment and the development of HABs in coastal ecosystems. This will involve the establishment of networks of coastal laboratories to monitor, collate and disseminate data and information on HABs and related environmental variables and to supply the *in situ* data needed to parameterise the optical properties and validate algorithms for determining the concentrations of chlorophyll, total suspended solids and dissolved organic matter in Case II coastal waters.

Figure goes here

The knowledge and tools generated by GEOHAB will benefit C-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 these ways, GEOHAB will help to "close the loop" in the delivery of benefits as they relate to the health of the oceans and to the economic value of coastal ecosystems. In turn, it is expected that GOOS will encourage the implementation and development of sustained observing systems required to document trends, evaluate the efficacy of management actions (mitigation), and define those areas that require additional research.

A global, long-term monitoring network in representative coastal regions will constitute a significant step forward in the attempt to understand the causes and consequences of HABs. HAB monitoring is currently carried out in several countries with the aim of minimising damages to human health and to living marine resources, as well as economic loss. However, the coverage is far from adequate in terms of the quality of the data collected (there are problems with correct identification of species to quantification of abundance and measurements of related environmental factors), duration, spatial extent, and resolution. Although this is especially true of many developing nations, these problems are global in nature. The capacity-building activities of C-GOOS are co-ordinated through the newly established GOOS Committee on Capacity Building as well as with TEMA (Training, Education and Mutual Awareness Programme of IOC), regional GOOS programs (e.g., NEAR-GOOS), GLOSS and the IOC HAB Intergovernmental Panel.

6.4 Relationship to other research programmes

The Land-Ocean Interactions in the Coastal Zone Program (LOICZ) of IGBP was established to determine at regional to global scales (1) the fluxes of material between land, sea and atmosphere through the coastal zone, the capacity of coastal systems to transfer and store particulate and dissolved matter, and the effects of changes in external forcing conditions on the structure and function of coastal ecosystems; (2) how changes in land use, climate, sea level, and human activities alter the fluxes and retention of particulate matter in the coastal zone; (3) how changes in coastal systems, including responses to varying terrestrial and oceanic inputs of organic matter and nutrients, affect the global carbon cycle and trace gas composition of the atmosphere; and (4) how responses of coastal systems to global change will affect the habitation and use by humans of coastal environments. ELOISE (European Land-Ocean Interaction Studies), the European contribution to LOICZ, consists of 29 research projects organised into three working groups: biogeochemical fluxes and cycling, ecosystem structures, and modelling and data management.

The Global Ocean Ecosystem Dynamics (GLOBEC) Program, established by SCOR and the IOC in 1991, addresses the need to "understand how changes in the global environment will affect the abundance, diversity and production of animal populations comprising a major component of the ocean's ecosystems." The GLOBEC science plan emphasises the need for basic research to quantify the dynamics of zooplankton populations in general, and the importance of predator-prey interactions (phytoplankton-zooplankton-fish) and physical forcings in particular. These goals are to be achieved by (1) building a foundation for global ecosystem models through re-examination of historical data bases, synthesis and integration; (2) conducting process studies; (3) developing predictive modelling capabilities through interdisciplinary, interactive modelling and observations; and (4) co-operating with other ocean, atmosphere, terrestrial and social global change efforts to assess the feedback effects of larger scale changes in the structure of the biosphere.

LOICZ, GLOBEC, and GEOHAB clearly have elements that are relevant to one another. 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 are major goals of LOICZ. Major goals of GEOHAB include quantifying the effects of anthropogenic nutrient enrichment and buoyancy flux on the population and toxicity 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 which have significant effects on the trophic dynamics linking nutrients and phytoplankton productivity to zooplankton and fisheries. Clearly, coordination 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 programs. National programmes will, of course, be integral to the activities of GEOHAB.

7.0 Summary: the benefits of GEOHAB

A better understanding 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 and prediction of HABs. However, this is not the only benefit of GEOHAB. 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.

8.0 Recent publications on the ecology and oceanography of HABs

Anderson, D.M., Cembella A.D. and Hallegraeff, G.M. (eds.). 1998. Physiological Ecology of Harmful Algal Blooms, NATO ASI Series vol. G 41. Springer-Verlag, Heidelburg.

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Reguera, B., J. Blanco, M.L. Fernandez and T. Wyatt (eds.) 1998. Harmful Algae. Xunta de Galicia and IOC of UNESCO Publishers.

Yasumoto, T., Y. Oshima and Y. Fukuyo (eds). 1996. Harmful and Toxic Algal Blooms, IOC of UNESCO Publisher, pp. 257-260.

Appendix 1: Detailed Background for the Emergence of the GEOHAB Programme

Research on HABs first emerged as a discipline in its own right at the First International Conference on Toxic Dinoflagellate Blooms which was held in Boston, USA, in 1974. This successful meeting was followed by a number of international conferences about every second year and expanded in scope to include a broader range of topics related to HABs. In 1989 the Fourth International Conference on Harmful Marine Phytoplankton reached a consensus "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 new international initiatives were taken to study and manage harmful algal blooms and their linkages to environmental changes in a manner consistent with the global nature of the phenomenon.

This increasing awareness of the problem resulted in the Member States of the Intergovernmental Oceanographic Commission asking for the establishment of an international framework programme on HABs. The Programme Plan for the IOC Harmful Algal Bloom Programme was first formulated at an IOC-SCOR Workshop in Rhode Island, October 1991. After the adoption of the Programme by the IOC Assembly, moves were made to develop an international Programme with an intergovernmental mechanism whereby countries could co-ordinate efforts and develop joint initiatives. Consequently the Intergovernmental Panel on Harmful Algal Blooms (IPHAB) was established in 1992. Four Sessions of IPHAB have been held so far, and the next session will be timed to well to help with the development of GEOHAB. The IPHAB is presently composed of representatives of 42 countries.

The IOC HAB Programme Plan is a comprehensive framework that includes most aspects of HAB and is composed of an Educational Element, a Scientific Element, and an Operational Element. The overall goal is: "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." Within each of the three main Elements specific priorities and objectives of the international Programme are identified. The IOC HAB Programme is implemented by the IOC and by other organizations with expertise in the various aspects of the Programme.

To date, the implementation of the HAB programme focussed on the Educational Element through organisation of training courses, and the preparation of manuals, databases, training material, etc. The implementation is primarily carried out through the two Science and Communication Centres on HAB in Copenhagen, Denmark, and Vigo, Spain, and the University of Tokyo, Japan.

The Science Element of the IOC HAB Programme includes an Ecology and Oceanography component with the goal: "To understand the population dynamics of harmful algae." This component has in particular been developed and implemented through close co-operation between the IOC, SCOR and ICES. A joint SCOR-IOC Working Group on the Physiological Ecology of Harmful Algal Blooms resulted in a successful NATO ASI which, among its results, had a list of research priorities. The ICES-IOC Working Group on Harmful Algal Bloom Dynamics has in particular focussed on biological-physical interactions. The deliberations of this group have been important in the process leading to GEOHAB. The ICES-IOC Working Group has also produced a meta-database on Harmful Algal Events (HAE-DAT) which includes decadal maps of HAB occurrences in the ICES area. The HAEDAT is intended to be expanded to global coverage.

At its Fourth Session the Intergovernmental Panel on HAB decided to work towards the development of an international science agenda on the ecology and oceanography of HABs. Simultaneously, SCOR was requested by the United States to take similar initiative. SCOR has longstanding experience in the establishment and implementation of international science programmes. As SCOR is also an advisory body to the IOC, it was natural for the IOC to invite SCOR to take joint action in the development of the new international science programme, just as SCOR and the IOC worked jointly in the development of the overall HAB Programme.

The process leading to GEOHAB is thus the natural development of a focussed science programme within the framework of the HAB Programme. GEOHAB is unique in its focus, yet it complements ongoing activities. The IPHAB provides an intergovernmental mechanism for the implementation of GEOHAB, which will be used to optimise the possibilities for national and regional participation and funding of GEOHAB projects.

Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB)

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