ELSEVIER

Ocean & Coastal Management 43 (2000) 725–748

Ocean & Coastal Management

www.elsevier.com/locate/ocecoaman

The diversity of harmful algal blooms: a challenge for science and management

Adriana Zingone[a],*, Henrik Oksfeldt Enevoldsen[b]

[a] *Stazione Zoologica 'A. Dohrn', Villa Comunale, 80121, Naples, Italy*
[b] *IOC Science and Communication Centre on Harmful Algae, Botanical Institute, University of Copenhagen, Oster Farimagsgade 2D, 1353 Copenhagen K, Denmark*

Abstract

A broad spectrum of events come under the category of harmful algal blooms (HABs), the common denominator being a negative impact on human activities. Harmful algal blooms involve a wide diversity of organisms, bloom dynamics, and mechanisms of impact. Here we review the effects of natural and man-induced environmental fluctuations on the frequency and apparent spreading of these phenomena. This article highlights the need for interdisciplinary research aimed at shedding light on basic mechanisms governing the occurrence and succession of microalgae in coastal seas. Information integrated from various discipline coupled with improved, sustained monitoring systems, will help predict and manage problems caused by HABs over a wide range of space and time scales. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

The need to exploit marine resources has increased with the growth of the world's population and with enhanced demographic pressure in coastal areas. Harmful phytoplankton events are a serious constraint to the sustainable development of coastal areas. This scenario calls for a co-ordinated scientific and management approach.

The term 'harmful algal blooms' (HABs) covers a heterogeneous set of events that share two characteristics: they are caused by microalgae and they have a negative impact on human activities. Despite these common features, HABs are very diverse in terms of causative organisms, dynamics of blooms and type of impact.

---

*Corresponding author.

PII: S0964-5691(00)00056-9

Numerous publications focusing on harmful algal blooms testify to the increasing interest, both scientific and practical, in these events [1–6]. We refer the reader to these publications for comprehensive descriptions of the current status of knowledge in the field. Here, we review HABs highlighting their heterogeneity and the gaps in our knowledge that impede optimal management and mitigation strategies.

2. The diversity of causative organisms

The list of microalgal species that are potentially involved in HABs comprises about 80 toxic species and about 200 noxious species out of an approximate total of 4000 marine planktonic microalgae described thus far [7]. This list has increased remarkably in recent years because of new cases of harmful events, the development of scientific research in the field, and enhanced human interactions with the coastal zone. Before the first instance of amnesic shellfish poisoning (ASP) in 1987 [8], diatoms were not thought to be toxic, while to date about 10 species are known to produce the toxic compound domoic acid. The total number of potentially harmful species is deemed to be largely underestimated [7,9], given the relatively high number of species (3 or 4) added to the list yearly. This is hardly a surprising finding, considering that several thousand phytoplankton species are still undescribed [10].

It is not an easy task to associate a known species with a harmful phenomenon, as demonstrated by the case of *Protoceratium reticulatum* (Fig. 1). This is a widely

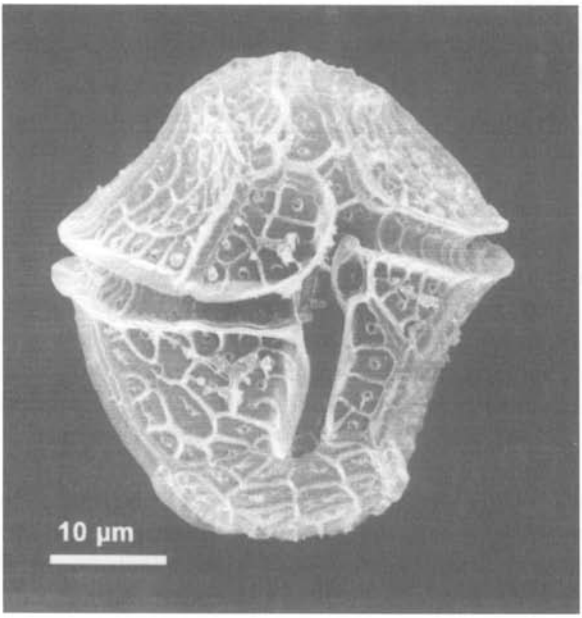

Fig. 1. *Protoceratium reticulatum.*

distributed species which in 1966 was associated with a mass white mussel death on the west coasts of South Africa [11]. At that time, the species was misidentified and subsequently redescribed as a new species, *Gonyaulax grindleyi* [12]. Similar events were subsequently observed in the same area, but the source of toxicity remained obscure. Only 20 yr later [13] was it demonstrated that *P. reticulatum* produces yessotoxin, a toxin that had been known for 10 yr.

Toxicity and other negative effects caused by harmful algae are not limited to a single algal class or to a few genera, but are distributed among several taxonomic groups. This is not surprising: in the terrestrial environment, weeds, pests and poisonous organisms belong to a wide variety of groups, from fungi to flowering plants. The variety of secondary terrestrial plant metabolites and of their ecological effects is amazing [14]. Similarly, the high taxonomical diversity of harmful algae results in a variety of toxins and relative mechanisms of action at different levels of the trophic chain. Ecological requirements and bloom dynamics also vary considerably from one species to another and, like the case of non-harmful species, even within a single species [15,16] different populations of the same species may be toxic or not, exhibit different growth rates under the same conditions and show different life strategies.

Another implication of the taxonomic diversity of HAB species is that the production of toxic substances or other offensive or disturbing features has been selected as an advantageous character more than once in the evolution of these microorganisms. However, the significance of these features in terms of increased fitness or competitive ability is not known.

From a practical viewpoint, the taxonomic diversity of HAB species complicates monitoring operations, which require a high degree of specialised expertise. The automatised detection of harmful species, e.g with specific molecular probes [17], seems an attractive approach that would increase monitoring efficiency; however, the high number of species to be targeted and their genetic diversity impede rapid progress in this field.

3. The diversity of negative effects

Broadly speaking, there are four categories of deleterious effects related to marine microalgae (Table 1):

(i) *Risks for human health*: Some algal toxins, different in structure and toxicity (Table 2), reach humans through specific vector organisms that accumulate these noxious substances in their gastrointestinal tract or body tissues. The most toxic algal species are recorded among dinoflagellates, but a number of diatoms and cyanobacteria also produce neurotoxic substances that can endanger human health (Fig. 2). These toxins induce a number of acute and chronic syndromes i.e. paralytic shellfish poisoning (PSP), diarrhoeic shellfish poisoning (DSP), neurotoxic shellfish poisoning (NSP), amnesic shellfish poisoning (ASP), and ciguatera fish poisoning (CFP), which cause a wide variety of neurological and/or gastroenteric symptoms and at times can be fatal. Toxins can accumulate in many species of bivalve molluscs

Table 1
Overview of the deleterious effects caused by harmful algae and harmful algal blooms

Effect	Examples of causative organisms	
Human health		
Paralytic shellfish poisoning (PSP)	Dinoflagellates	*Alexandrium* spp., *Pyrodinium bahamense* var. *compressum*, *Gymnodinium catenatum*
	Cyanobacteria	*Anabaena circinalis*
Diarrhetic shellfish poisoning (DSP)	Dinoflagellates	*Dinophysis* spp., *Prorocentrum* spp.
Neurotoxic shellfish poisoning (NSP)	Dinoflagellates	*Gymnodinium breve*
Amnesic shellfish poisoning (ASP)	Diatoms	*Pseudo-nitzschia* spp.
Ciguatera fish poisoning (CFP)	Dinoflagellates	*Gambierdiscus toxicus*
Allergies, respiratory problems and skin irritation	Dinoflagellates	*Gymnodinium breve*, *Pfiesteria piscicida*
	Cyanobacteria	*Nodularia spumigena*
Hepatotoxicity	Cyanobacteria	*Microcystis aeruginosa*, *Nodularia spumigena*
Natural and cultured marine resources		
Haemolytic, hepatotoxic, osmoregulatory effects and other unspecified toxicity	Dinoflagellates	*Gymnodinium* spp., *Cochlodinium polykrikoides*, *Pfiesteria piscicida*, *Gonyaulax* spp.
	Raphidophytes	*Heterosigma akashiwo*, *Fibrocapsa japonica*
	Prymnesiophytes	*Chrysochromulina* spp., *Prymnesium* spp.
	Pelagophytes	*Aureococcus anophagefferens*
	Cyanobacteria	*Microcystis aeruginosa*
Mechanical damage	Diatoms	*Chaetoceros* spp.
Gill clogging and necrosis	Prymnesiophytes	*Phaeocystis* spp.
	Diatoms	*Thalassiosira* spp.
Tourism and recreational activities		
Production of foams, mucilages, discolouration, repellent odours	Dinoflagellates	*Noctiluca scintillans*
	Prymnesiophytes	*Phaeocystis* spp.
	Diatoms	*Cylindrotheca closterium*
	Pelagophytes	Aureococcus anophagefferens
	Cyanobacteria	*Nodularia spumigena*
Marine ecosystem		
Hypoxia, anoxia	Dinoflagellatesi	*Noctiluca scintillans*, *Heterocapsa triquetra*
	Diatoms	*Skeletonema costatum*
	Prymnesiophytes	*Phaeocystis* spp.
Negative effects on feeding behaviour, reduction of water clarity	Pelagophytes	*Aureococcus anophagefferens*, *Aureoumbra lagunensis*
Toxicity to wild marine fauna	Dinoflagellates	*Gymnodinium breve*, *Alexandrium* spp.
	Diatoms	*Pseudo-nitzschia australis*

(e.g. scallops, mussels, cockles and oysters) as well as in some gastropods, crabs and fish; the characteristics of toxification and de-toxification vary remarkably from one vector to another [18]. In the case of CFP the toxin is accumulated by a number of tropical benthic fish that feed on macroalgae but also ingest harmful microalgae that colonise the macroalgal surfaces. Cyanobacteria are also hazardous for human health. These are generally fresh water organisms but may create problems in low

Table 2
Some algal toxins are extremely potent and may be several times more toxic than for example cobra venom, and more than one thousand times more toxic than cyanide. The table shows the relative toxicity to mice of some algal toxins compared with other biological toxins and with cyanide

Toxin	Source	Toxicity (fold)
Cyanide		1
Muscarin	Amanita muscaria, fungus	9
Okadaic acid	Algae, dinoflagellates (e.g. *Dinophysis* spp.)	50
Domoic acid	Algae, diatoms (*Pseudo-nitzschia* spp.)	80
Prymnesine	Algae, haptophytes (e.g. *Prymnesium parvum*)	350
Cobra toxin	Cobra snake	500
Saxitoxin	Algae, dinoflagellates (e.g. *Alexandrium* spp., *Pyrodinium bahamense*)	1 100
Ciguatoxin	Algae, dinoflagellates (*Gambierdiscus toxicus*)	22 000
Tetanus toxin	Bacterium (*Clostridium tetanii*)	100 000 000

salinity and estuarine coastal waters, where they can produce diverse neurotoxins, including PSP toxins, and such hepatotoxins as mycrocystins and nodularins. Finally, respiratory problems have been reported during blooms of *Gymnodinium breve* along the Gulf coasts of the USA.

About 2000 cases of human poisoning are reported each year [19]. However, this is probably an underestimation because many cases, particularly those involving gastrointestinal symptoms, are incorrectly diagnosed. Fatal episodes are estimated to exceed several hundred cases annually. In some areas affected by PSP, historical reports reveal that coastal populations were well aware of risks associated with eating sea-food in certain periods or under such conditions as a sea-water discoloration [20] or phosphorescence [21]. Although many affected areas are nowadays well controlled thanks to monitoring, the occurrence of toxic events in new areas and the lack of control in others pose a serious risk to human health and life. This is a potentially explosive situation given the pressing need to exploit coastal areas for food production.

(ii) *Impact on living marine resources*: Besides the cases cited above, in which harmful algae may indirectly impinge upon the exploitation of marine resources, several kinds of harmful algae may directly affect wild and cultivated fish (Fig. 3) or marine invertebrates that are valuable seafood. These events are occasionally caused by some of the species that endanger human health when accumulated in filter-feeding animals, such as *Gymnodinium breve* or *Alexandrium* spp. However, most mass mortalities of cultivated fish around the world are generally caused by such ichthyotoxic species as the raphidophytes *Heterosigma akashiwo* and *Chattonella marina*, a number of dinoflagellates and some prymnesiophytes. An alarming case in point is the bloom of *Chrysochromulina polylepis* in May–June 1988 in the Kattegat and Skagerrak area (North Sea) that caused the death of 900 tons of fish, including cod, salmon and trout. This was followed by other extensive prymnesiophyte blooms in 1991 and 1992 [9].

Harmful algae usually affect fish and other invertebrates by producing toxins, but mucilage-producing or spine-bearing algae may cause mechanical clogging or lesions

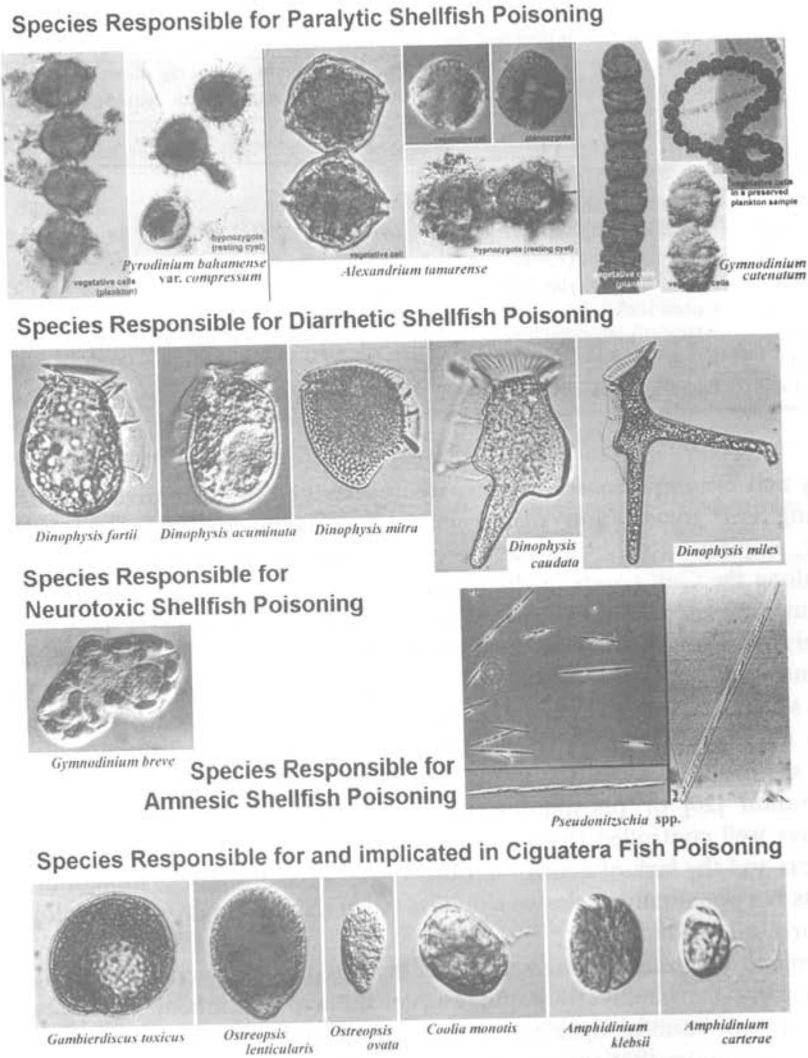

Fig. 2. The most common harmful microalgae that endanger human health.

of the gills. A reduction in oxygen and hydrogen sulphide production can also cause mass mortalities of huge proportions of commercially valuable species. In March 1994, approximately 60 tons of dead rock lobsters and 1500 tons of fish were stranded on the shores of St. Helena Bay (South Africa) consequent to the decay of a massive bloom of non-toxic algae [22]. Finally, brown tides produced by the picoplanktonic *Aureococcus anophagefferens* in bays of the midwestern Atlantic coasts of the USA led to starvation and recruitment failure in commercially valuable bay scallop populations [23].

Fig. 3. Mass mortality of flat fish in a Korean fish–farm caused by the algal species *Cochlodinium polykrikoides*. Photo by Mr. San Geun Lee, National Fisheries Research and Development Agency of Korea.

(iii) *Impact on tourism and on the recreational use of coastal areas*: A requisite for the exploitation of tourism and of the recreational resources in coastal areas is a high quality of the environment, including unaltered seawater colour, transparency, smell, etc. Algal blooms may cause intense discolorations of seawater, which earned them the name of 'red-tides', but in fact the discolorations can vary from golden brown to emerald green, from reddish to whitish (Fig. 4).

Green–brown-coloured seawater caused by the non-toxic dinoflagellate *Alexandrium taylori* is recurrent along the Mediterranean coasts of Costa Brava since 1982, in coincidence with the annual peak tourists season [24]. Repellent mucilages which are produced by several diatom species have often been reported from the Adriatic Sea [25,26], whereas thick layers of malodorous foams caused by the prymnesiophyte *Phaeocystis globosa* may accumulate along the North Sea shores [27]. Allergic reactions and even more serious disorders caused by cyanobacteria blooms are also a constraint for the recreational use of coastal areas.

(iv) *Damage to the marine ecosystem*: A number of HABs affect organisms that may have no commercial value but nonetheless are functional components of the marine ecosystem. The degradation of high biomass blooms can exhaust oxygen supplies, thus killing not only commercially important species, but also other plants

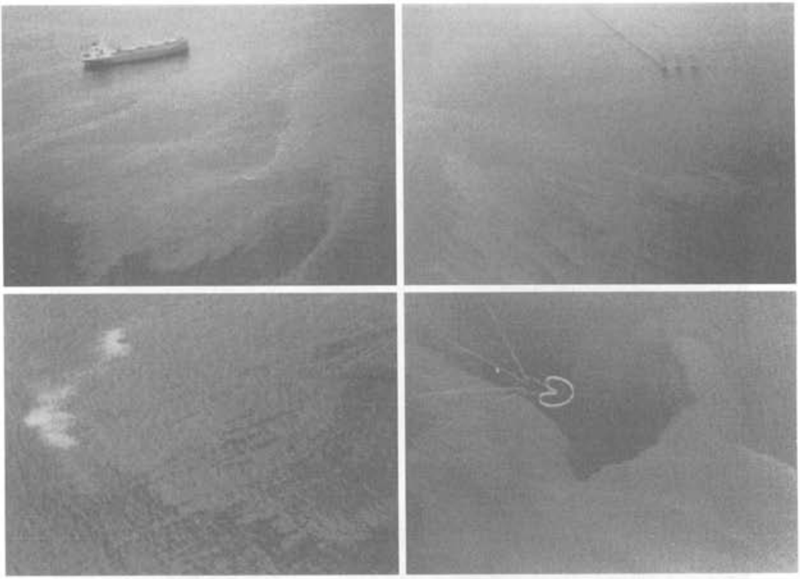

Fig. 4. Sea water discoloration caused by algal blooms in the Gulf of Thailand. Photo by Dr. Thaithaworn Lirdwitayaprasit, Department of Fisheries of Thailand.

and animals that are unable to leave the anoxic area. The co-occurrence of several conditions is required to generate these situations, i.e. non-limiting light and nutrient supplies and local physiographic and oceanographic conditions that entrap the bloom, thereby amplifying the effects of biomass degradation. Generally, anoxic events tend to recur more or less regularly at the same sites, but increased nutrient availability and reduced advection and mixing may cause these events to spread to other different sites.

Anoxia is not the only mechanism whereby HABs exert a deleterious effect on different components of the coastal ecosystem. The aforementioned brown tides of *Aureococcus anophagefferens* caused starvation and recruitment failure in a number of suspension-feeders, including bay scallops. They also reduced grazing by microzooplankton and decimated eelgrass beds through severe light attenuation [23]. In other cases, specific toxins seem to affect a single population of marine mammals, fish, birds, or other organisms. In 1987, 14 humpback whales died in Cape Cod Bay after eating Atlantic mackerel containing saxitoxin [28]. *Gymnodinium breve* has been frequently associated with mortalities of sea turtles, birds, dolphins and manatees in Florida waters [29]. In May 1998, the diatom *Pseudo-nitzschia australis* caused the death of over 400 California sea lions [30]. During this outbreak the neurotoxic domoic acid was detected in sea lion body fluids and in planktivorous fish. Taken together, these findings clearly show that the pathways of the toxins through the food web are diverse and may involve animals other than molluscs as vectors.

4. The diversity of bloom dynamics

The taxonomic diversity of HAB species suggests that each species is adapted to some set of preferred environmental conditions or, in ecological terms, to a defined niche. Conceivably, once the ecological requirements for each species are known, it would be easy to predict its occurrence [4]. One might also predict that several harmful species share a similar niche, thus leading to the identification of a few, basic, unifying bloom mechanisms and, consequently, to the construction of bloom models.

Unfortunately, the real world is more complicated. The ecophysiological requirements of most harmful species are poorly known, and laboratory studies are required to learn more about this field. However, results from laboratory studies are not sufficient to predict the succession of phytoplankton species and blooms of specific harmful organisms in the sea. Indeed, the net growth performance of a species is affected by complex interactions with other organisms, which are scarcely reproducible in laboratory experiments. These include negative interactions, such as grazing, competition, and viral infections, and a positive feedback from predator's excretion, bacterial nutrient regeneration and viral lysis. In fact, it is becoming increasingly evident that phytoplankton life strategies and their interactions with the surrounding environment may reach a degree of complexity unexpected for unicellular organisms. As a result, the capability of a species to cope with environmental conditions apparently not matching its optimal ranges is notably expanded and its occurrence is more difficult to predict.

Numerous phytoplankton species have complex life cycles, i.e. alternation of stages that differ in terms of physiology, motility, resistance to adverse conditions and life styles. Non motile, benthic resting stages (Fig. 5) are widely distributed among HAB dinoflagellates and raphidophytes, and may play a significant role in bloom initiation by inoculating seed populations when conditions are favourable. At the end of a bloom, cyst formation may represent a mechanism whereby organisms are rapidly removed from the water column so as to prepare the 'seed bank' to inoculate the next bloom [31]. Within this already complex framework, it appears that encystment rates, dormancy length, and cyst germination triggers can be species-specific and at times strain-specific. The transitions between different life stages of a species are presumably controlled by the interplay of endogenous factors with the physical and chemical environment, but the role and relative importance of these factors for different species are poorly known [32].

Regarding common mechanisms of bloom dynamics, one might expect the bloom dynamics of a cyst-forming species to differ significantly from that of an ASP-producing pennate diatom, a foam-producing *Phaeocystis* or a benthic dinoflagellate. Less obvious is the notable diversity that may exist among species with apparently homogeneous life strategies, such as cyst-forming dinoflagellates, and even within single species. *Heterosigma akashiwo*, a widely distributed fish killer, may bloom in eutrophic waters or at moderate nutrient levels, in both stratified and mixed waters, in high-salinity waters and in areas influenced by river runoff, in areas with 'natural' trophic chains as well as in places where aquaculture has altered the

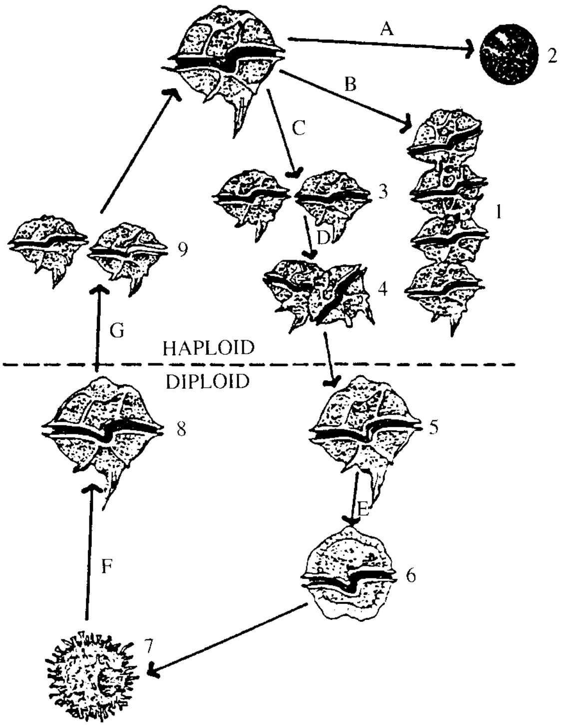

Fig. 5. The life cycle of *P. bahamense* (from Usup & Azanza [68]): (1). Vegetative cells. (2). Pellicle cyst. (3). Gametes. (4). Fusing gametes. (5). Planozygote. (6). Hypnozygote. (7). Resting cyst. (8). Planomeiocyte. (9). Products of meiosis: (A). Ecdysis. (B). Binary fission. (C). Gamete formation. (D). Gamete fusion. (E). Cyst formation. (F). Germination. (G). Meiosis.

trophodynamic balance [33]. Clearly, different ecotypes or cryptospecies must be involved in generating blooms in such diverse environments.

Gymnodinium catenatum (Fig. 6), a naked dinoflagellate responsible for PSP, is another case of a species blooming under different hydrographic conditions. In Tasmanian waters, blooms develop in estuarine waters possibly after inoculation from the extensive cyst beds present on the bottom of these areas [34]. In the Rias Bajas of Galicia, blooms have been related to the relaxation of upwelling events in the coastal North Atlantic, and to the advection of seed populations from offshore waters [35]. Not only the areas affected, but also the bloom mechanisms appear to be different, i.e. very strong biological regulation of the population through cyst germination in one case, and hydrographic control in the other.

These examples clearly demonstrate that the dynamics of harmful algal blooms cannot be elucidated by research on one or a few organisms. The diversity of harmful species at interspecific and intraspecific level is high enough to require a case focused, analytical study, which nonetheless may reveal common features, if any, for mechanisms of bloom initiation, development and termination. The examples

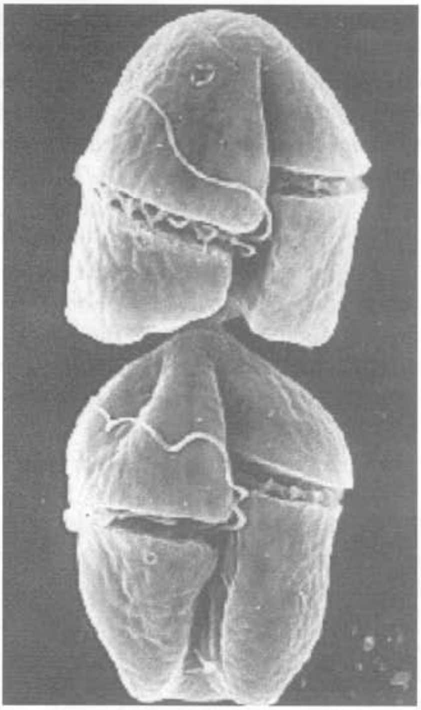

Fig. 6. *Gymnodinium catenatum.*

provided also indicate that it is difficult to define one kind of coastal area which is more prone to HABs, even when a single species is considered. This contrasts with the widespread idea that HABs prefer sheltered areas characterized by nutrient enrichment, possibly of anthropogenic origin, offering more or less prolonged periods of stratification. Indeed, HABs may occur in a variety of areas and hydrographic conditions, including upwelling regions, pristine coastal waters with moderate nutrient levels, and coastal areas affected by shelf-scale circulation.

5. HABs and biomass

The concept of high abundance is implicit in the term 'bloom', however it has a dynamic and relative meaning: a bloom is a 'significant population increase' [36], which leads to a peak. The magnitude of this peak is specific for each species and may vary considerably in space and time, being dependent on environmental conditions. In this sense, a bloom does not imply a high biomass. Nonetheless, the impact of HABs depends on the concentration of the harmful species, even the most toxic species must have a minimum cell concentration to exert the harmful effect. In fact, most harmful species are probably ubiquitous, and they become hazardous only when their concentration exceeds a certain threshold for a sufficiently long period.

At barely detectable concentrations (10^2–10^3 cells l^{-1}), some harmful species can have dramatic effects; this is the case of highly toxic species like the PSP producers *Pyrodinium bahamense* var. *compressum* and *Alexandrium tamarense*, which however may also form much denser blooms (10^6–10^7 cells l^{-1}). The DSP-producer species of the genus *Dinophysis* (Fig. 7) rarely reach concentrations higher than 10^4–10^5 cells l^{-1}, but are nevertheless dangerous at much lower concentrations. Concentrations as low as 5 cells ml^{-1} are also sufficient for some diatoms endowed with long siliceous spines, such as *Chaetoceros concavicornis* and *C. convolutus* [37], to cause fish mortalities by producing lesions in the gill tissues. Because of the difficulty in detecting low concentrations of planktonic algae, it is not always possible to pre-alert to the harmful events, especially in the case of these extremely noxious species.

On the diametrically opposed end of a scale of danger (Fig. 8) are species that are noxious only when they reach very high concentrations, as in the case of *Phaeocystis* (Fig. 9). This is a normal component of plankton blooms in temperate areas, which has recently been shown to produce a toxin that has anaesthetic properties [38]. At high concentrations *Phaeocystis* may affect fisheries [39], confer a bad taste to fish (blackberry feeding) [40], deviate the herring migration patterns [41] and in some cases produce unsightly slime and foams [27]. Also, very dense blooms of non-toxic

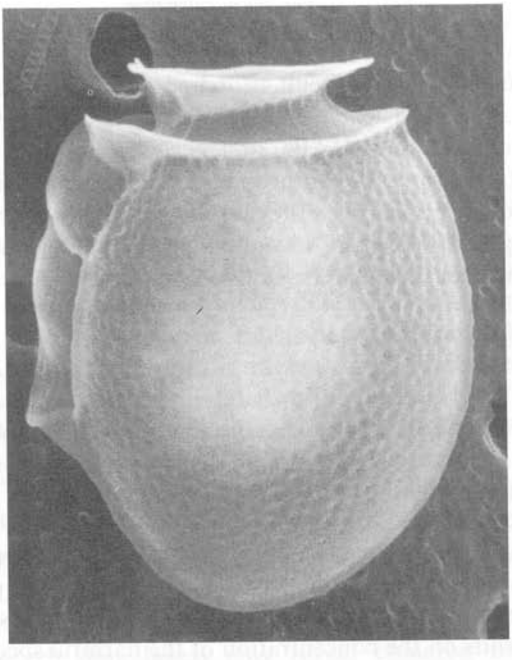

Fig. 7. *Dinophysis acuminata*.

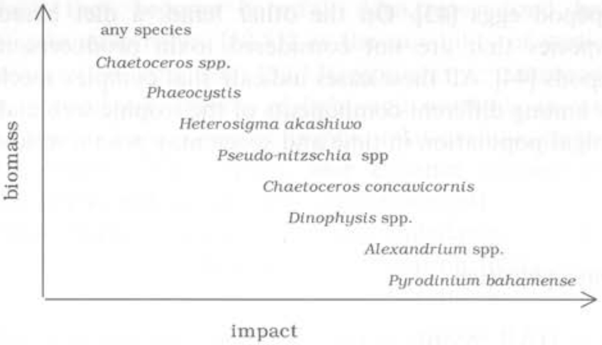

Fig. 8. Schematic representation of the impact/biomass relationships for selected HAB species. Scales for both axes are arbitrary and non-linear.

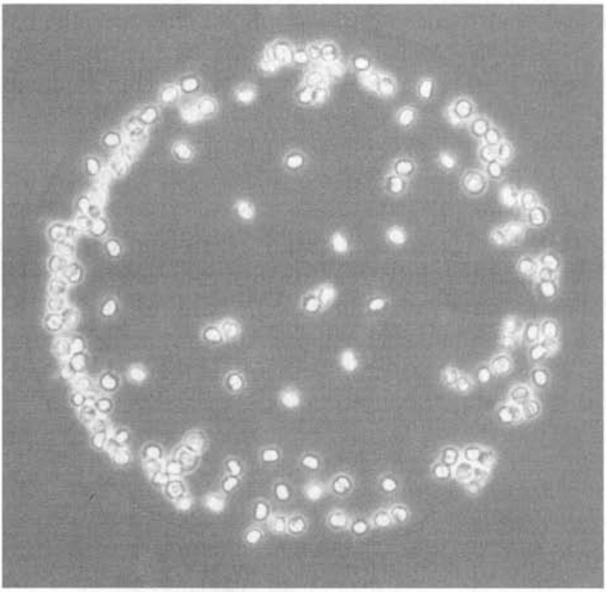

Fig. 9. A sphaerical colony of *Phaocystis* sp.

diatoms (e.g., *Coscinodiscus* spp., *Thalassiosira mala*) have caused discolorations or fish gill clogging [42].

Finally, it could be argued that any phytoplankton species can exert a negative impact when it persistently dominates phytoplankton populations: diatoms have long been considered an optimal food for copepods and identified as the primary producer of the trophic web that sustains exploitable fish species. However, it has recently been demonstrated that diatoms can produce substances that inhibit viability in copepod eggs [43]. On the other hand, a diet based exclusively on dinoflagellate species that are not considered toxin producers may lower male fertility in copepods [44]. All these cases indicate that complex mechanisms regulate the interactions among different components of the trophic web and that a lowering in diversity of algal population in time and space may pose a serious risk to coastal ecosystems.

6. HABs and eutrophication

The increase of HAB records in coastal waters around the world has often been associated with nutrients derived from anthropogenic activities [1,45]. Recently, such nutrient sources as rainfall have been implicated in the enhanced magnitude of noxious blooms [46]. Cases in point are Tolo Bay, Hong Kong [47,48] and the Seto Inland Sea, in Japan (Fig. 10) [49], where the number of visible blooms, what used to be called 'red tides', increased with eutrophication, and decreased subsequent to restoration practices that reduced nutrient inputs. However, the reduction in bloom frequency and intensity has not been paralleled by the disappearance of harmful species: recently new harmful species have been detected in Japanese waters (e.g. *Heterocapsa circularisquama*), and the lower impact of high biomass blooms has been counterbalanced by a higher impact of toxic species.

In the laboratory it is easy to demonstrate that algal growth increases with increasing nutrient availability. However, there is scarce evidence for a direct relationship between the spread of harmful events and eutrophication in the sea. High biomass blooms obviously require high nutrient levels. However, a high nutrient supply may not necessarily favour harmful species; an abundance of nutrients could stimulate the development of blooms of non-harmful opportunistic diatoms, flagellates or dinoflagellates, which could outcompete toxic species. On the other hand, species highly toxic at low concentrations, i.e. *Alexandrium* and *Dinophysis*, presumably do not depend on high nutrient concentrations to reach the

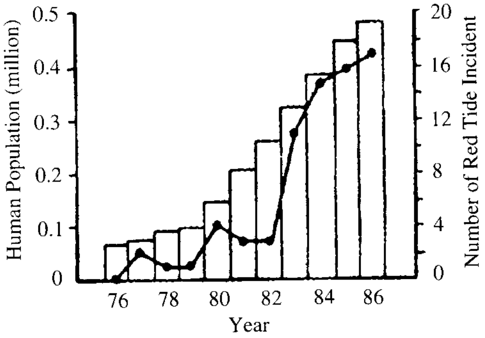

Fig. 10. Number of 'Red tides' in Tolo Harbour, Hong Kong, and human population in Hong Kong from 1976 to 1986 [48].

threshold at which they become harmful. Also, specialized behaviours, like facultative or obligate mixotrophy [50,51] or the capability of vertically migrating to nutrient-replete water column layers [52,53], represent very successful adaptations to cope with the vertical segregation of light and nutrients in stratified waters. Finally, at the ecosystem level, complex trophic relationships, including microbial interactions and excretion from grazers, may enhance nutrient availability and growth rates under apparently oligotrophic conditions [54].

Not only nutrient increase, but also nutrient imbalance, could favour certain species versus others [47,55]. Because eutrophication increases nitrogen and phosphorus inputs, the ratio of these nutrients to silicates becomes very high. This would favour non-diatom species including several harmful/toxic species [45]. In an equilibrium system, the nutrient-ratio hypothesis would hold true only when the deficient nutrient becomes limiting, not when both resources saturate the growth of the species [56]. However, in a delayed-effect scenario, nutrient imbalance would affect the development of different algal species. As an example, in a balanced system of 0.7 : 1 Si : N the consumption of silicates by diatoms would lead to a proportional consumption of dissolved N, with very little resources left for the subsequent successional stage, i.e. flagellates. Conversely, when the Si : N ratio decreases, due to increased N, diatom performance would not change but the contribution of flagellates to annual production would increase [57]. However there are cases, such as that of the Black Sea, where increased eutrophication accompanied by a reduction in silicate concentrations has led to an increase of flagellates and also of diatom blooms [5].

Regardless of the controversy about HAB–eutrophication relationships, the impact of high nutrient supplies and of massive inputs of inorganic and organic compounds in coastal systems undoubtedly merits detailed investigation. In fact, besides the above-mentioned cases of high biomass blooms leading to hypoxic or anoxic events, other negative effects of eutrophication might be worth assessing, e.g. the loss of phytoplankton diversity and shifts in the specific composition of microalgal communities. These changes could influence the fate of primary production and modify the shape of the trophic web in coastal areas, with grave consequences for fisheries and for the exploitation of natural resources. Also, this calls for an interdisciplinary and across-boundary scientific approach that includes data from the watershed to the offshore boundary and that integrates the physical, chemical and biological components of the system analysed at their matching scales of variability.

7. HABs and climatic fluctuations

It is not possible to demonstrate a worldwide increase in HABs because we are unable to detect long-term trends of algal blooms due to the lack of time series at the correct scale [58]. However, at a local scale there are numerous examples of HABs in areas where they were previously unknown. For instance, the first massive *Alexandrium* bloom along the coasts from southern Maine to Massachusetts was recorded in 1972 and has been followed by PSP outbreaks every year [15]. *Gymnodinium catenatum* was not known in Galician waters before 1976 [59] and it was found in Australian waters only after 1979 [35]. Compositional shifts, changes of dominance and sudden emergence of previously unrecorded species are well known phenomena in long-term phytoplankton dynamics. The passive introduction of species from other sites by means of natural (currents, storms) or man-mediated events (ballast waters, keels, mussel strains transport, etc.) has been implicated in variations in the geographic range of a species, which has also been supported by the absence of cyst records prior to certain dates [60].

The biodiversity of no local phytoplankton population is thoroughly known, therefore it cannot be excluded that a previously unrecorded species was already in an area, although at undetectable concentrations or confined to unsampled microlayers, or that it bloomed for a very brief period. Sediment investigations on resting cysts provide further information on planktonic organisms with benthic stages, and may lead to the detection of rare species that eluded planktonic sampling [61]. Similar investigations on fossilized resting cysts provide data on the distribution of a species over a wider time scale, which covers different hydrographic situations alternating over the geological periods in given areas. As an example, cyst investigations on sediment cores showed that microreticulate cysts attributed to the toxic species *Gymnodinium catenatum* were abundant in the Kattegat area (North Sea) at time windows that corresponded to periods of a relatively warmer climate [62]. Recently, a new non-toxic species that produces a microreticulate cyst has been described from the Kattegat area, *Gymnodinium nolleri* (Fig. 11), that is probably the same species that produced past blooms [63,64]. Even though the Scandinavian species was non-toxic, this case clearly shows the value of sediment core investigations for tracking long-term trends of specific phytoplankton blooms.

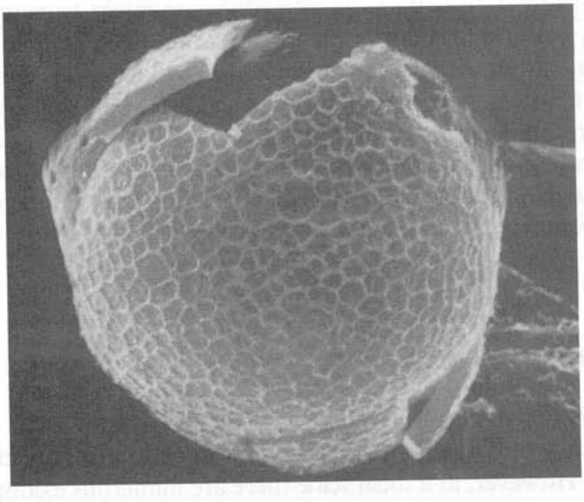

Fig. 11. The microreticulate cyst of *Gymnodinium nolleri*. Photo by Dr. Marianne Ellegaard, University of Copenhagen.

Climatic variations can also affect the spatial distribution of a species. The PSP-producer *Pyrodinium bahamense* is presently known only from tropical seas, but the geographic range of its fossil cysts is much wider and expands over temperate regions of both hemispheres (Fig. 12) [65]. Presumably, these records reflect periods of different climatic conditions, including those warmer than nowadays. In view of climatic changes, either natural or man-enhanced, which possibly lead to global warming, it could be envisioned that the distribution range of this species will tend to widen again. A recent finding of a living cyst of *P. bahamense* off the coasts of Portugal [66] supports this idea. Germination experiments are required to assess whether this is indeed the same species and to test its toxicity.

A relationship between the interannual variability of HABs and climatic variations has been suggested for several cases. The periodicity of blooms of *Pyrodinium bahamense* var. *compressum* in south-east Asia is related with El Niño Southern Oscillation (ENSO) events (Fig. 13) [67,68]. The recent outburst of fish killing species in Hong Kong [69], which caused US$ 32 million damage, has been associated with the high magnitude of El Niño in 1997–1998. A correlation between interranual variations of occurrence and climatic variability has also been hypothesized for *Gymnodinium catenatum* blooms in Australian waters [34] and for *Phaeocystis* sp. in the Atlantic [70].

Temperature variations not only directly affect the geographic range and the magnitude of certain blooms, but can also induce changes in circulation patterns, prolong stratification periods and cause variations in the physical structure of the water column that can favour particular species, including dinoflagellates and their potentially harmful representatives [69,71,72]. These effects highlight the links between long-term variations of HABs and physical oceanography, and point to the

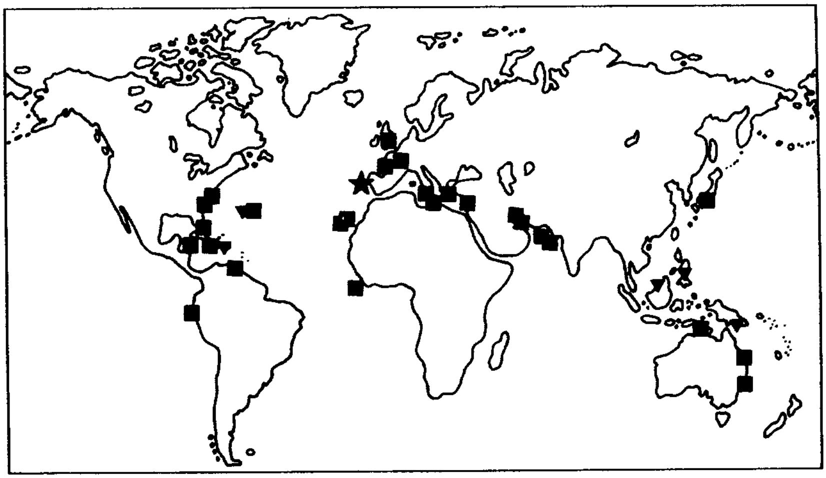

Fig. 12. Distribution of recent (triangles) and fossil (squares) *P. bahamense* cysts (redrawn from Matsuoka [65]). The star marks the recent finding of a living cyst off Portugal [66].

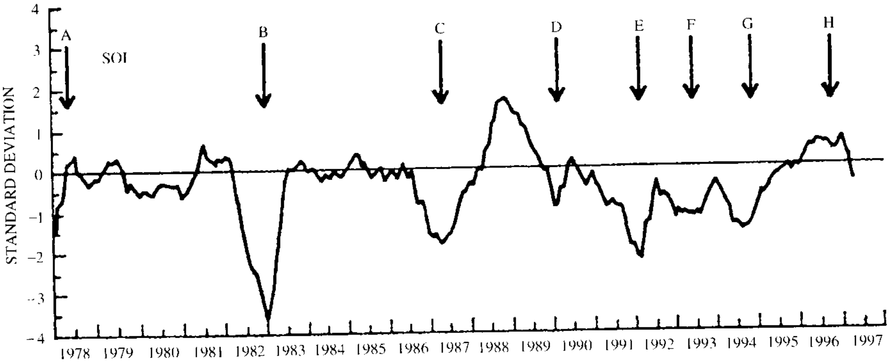

Fig. 13. The relationship between ENSO and blooms of *Pyrodinium bahamense* var. *compressum* (from [68]).

need to predict scenarios in coastal circulation and water mass distribution so as to be able to assess the risk of HABs in coastal areas.

8. Science and management perspectives

Harmful algal blooms are apparently an antithesis to the concept of 'health of the ocean'. However, we have argued that in most cases HABs do not damage marine ecosystems, nor impair their sustained biological functioning. Though extremely dangerous for human health and deleterious for the commercial exploitation of coastal areas, these blooms are natural phenomena with barely evident negative effects on coastal oceans. On the other hand, the health of the oceans and the sustainable development of coastal marine ecosystems can be endangered by human activities that reduce habitat and species diversity. This generally leads to dire consequences for the trophic web, and in some cases may divert energy entrapped by primary production towards non-exploitable living marine resources. Within this category, high biomass blooms in eutrophied areas indeed represent a menace, especially when they are associated with biodiversity loss.

The problems arising from HABs are very diverse, the causes are many and they are on the increase. Like other natural catastrophic phenomena, such as earthquakes, tsunamies and storm surges, correct management is required to mitigate the threat posed by HABs to the economic development of coastal areas and to human health. But what can be done in a practical sense? What information is needed to manage efficiently marine resources, protect public and ecosystem health, encourage and support aquaculture development, and contribute to policy decisions about coastal zone issues, such as waste and sewage disposal, aquaculture development, and dredging? Do human activities exacerbate HABs? How can this be verified, and what steps must be taken to minimise the effects of human activities?

Thus far, early warning when harmful species or toxins in sea-food reach critical concentrations is the most widely used management strategy. An early alert means that specific contingency plans can be put in action to avoid health problems and limit economic losses. The next step, as yet feasible in only a few cases, is to forecast harmful events with a lead time of 1–7 days, so as to mitigate more effectively the economic impact, e.g. harvesting mussels before they become toxic or moving fish-cages to safer depths or areas. At a long time scale, it would be necessary to assess the risk for harmful events when planning the use of coastal areas. In addition, the role of human activities in enhancing these phenomena through eutrophication, transport of harmful species and modifications of coastal areas should be thoroughly assessed. Finally, ad hoc procedures designed to prevent harmful events or to accelerate their termination are the ultimate goal for HAB management.

At present, capillary monitoring seems to be the only tool we have to protect ourselves and food resources of marine origin from the deleterious effect of HABs. To move from early alert and contingency plans to prediction and mitigation, we need basic knowledge about the distribution, species succession, long-term trends and population dynamics of HAB species. Much is known about harmful algae, yet our ability to describe the factors controlling the dynamics of individual species is limited by gaps in our knowledge about how the physiological, behavioural and morphological characteristics of algae (including HAB species) interact with environmental conditions to promote the proliferation of one species versus another. For example, we do not know enough about the environmental cues for encystment and germination, or about the interactions of life cycles with hydrography, 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 migrate vertically to exploit deep-water sources of nutrients at night, and light near the surface during the day.

The key to predicting HAB phenomena is to identify and quantify adaptations of HAB species that lead to their selection in particular hydrodynamic and ecological conditions. Thus, the central research problem and a challenge for biological oceanographers is to understand the critical features and mechanisms underlying the population dynamics of HAB species. This understanding will serve as a basis for improved monitoring and to build models that predict the occurrence, movement, toxicity, and environmental effects of harmful algal blooms. These predictions are essential for the efficient management and mitigation procedures mentioned above.

Another gap in our knowledge of phytoplankton, including potentially harmful species, are the long-term trends of occurrence and abundance of these organisms, which are related with climatic factors and with their influence on coastal hydrography. To bridge this gap, there is the need for a global network of intercalibrated observations, integrated in a multidisciplinary monitoring framework like that envisioned by the Global Ocean Observing System (GOOS). This would provide the data needed to detect trends and patterns of occurrence and distinguish the effects of natural variability from those of anthropogenic modifications of the environment.

Progress in oceanographic research should be paralleled by progress in the field of toxicology. Newly discovered toxins should be characterised, and detection and analytical methods devised in order to clarify the different types of toxins. Potential new toxin producers should also be identified. Lastly, enzymatic processes involved in the metabolism and elimination of HAB toxins from shellfish should be elucidated.

Targeted studies and technological innovations are essential to improve our understanding of HABs. For example, we need better tools for the detection and monitoring of harmful algae and their biologically active products, more sensitive approaches with which to study the nutrition of planktonic protists, integrated techniques to be able to observe physical, chemical, and biological variability on the scales relevant to physical forcing, improved representations of the physical processes that influence HAB dynamics, advances in physical–biological coupled models (including data assimilation models), and more effective observation systems for the detection and characterisation of phytoplankton community dynamics (including HABs). Rapid advances in bio-technology and instrumentation with which to measure physical and bio-optical variability in the sea, together with more sensitive and selective methods for chemical analysis and improvements in computational abilities, will ensure rapid progress if efforts are well focussed and co-ordinated.

Recently, three initiatives have addressed the question of HAB research and have pinpointed the most pressing research issues for the next decade in the field of oceanography. The first was the formulation of a USA national research plan, ECOHAB. The second is an international initiative by IOC and SCOR devoted to the Global Ecology and Oceanography of Harmful Algal Blooms, (GEOHAB).

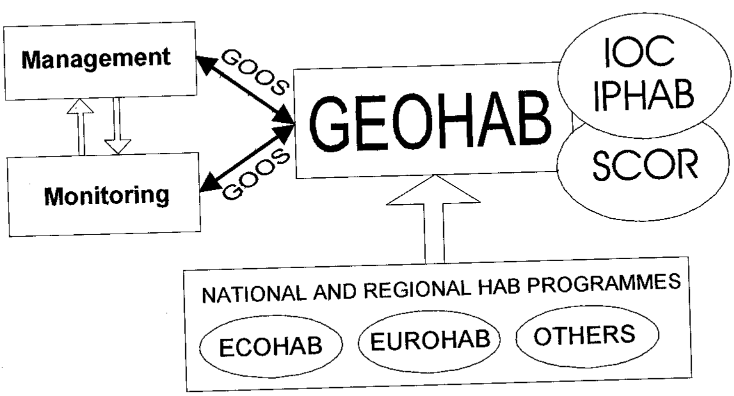

Fig. 14. The relationships between national and international scientific initiatives concerning harmful algal blooms: GEOHAB and its two mother organizations SCOR and the IOC; the linkage to the Intergovernmental Panel on HAB (IPHAB) as the intergovernmental mechanism; the linkage of national HAB research to the GEOHAB Programme; and how GOOS will be an important vehicle to convey the scientific results of GEOHAB to user groups and to the improvement of operational monitoring of HABs. Links with other international science programmes are also present e.g. for establishing ecosystem models.

Lastly, the European Commision sponsored a European initiative on harmful algal blooms (EUROHAB) (Fig. 14). These integrated, multidisciplinary, across-boundaries initiatives will lead to 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. This in turn will result in more effective management and mitigation of the effects of HABs, thus safeguarding the intrinsic and commercial value of coastal marine ecosystems.

References

[1] Hallegraeff GM. A review of harmful algal blooms and their apparent global increase. Phycologia 1993;32:79–99.

[2] Hallegraeff GM, Anderson DM. Cembella AD, editors. Manual on harmful marine microalgae. In: IOC manuals and guides, vol. 33. Paris: I. O. Commission UNESCO, 33 1995. p. 551.

[3] Anderson DM, Garrison DJ. The ecology and oceanography of harmful algal blooms. Limnology and Oceanography 1997;42:1009–305.

[4] Richardson K. Harmful or exceptional phytoplankton blooms in the marine ecosystem. Advances in Marine Biology 1997;31:301–85.

[5] Wyatt T. Harmful algae, marine blooms, and simple population models. Nature and Resources 1998;34:40–51.

[6] Anderson DM, Cembella AD, Hallegraeff GM, editors. Physiological ecology of harmful algal blooms. In: Series G: ecological sciences, vol. 41. Berlin: Springer-Verlag, 1998. p. 662.

[7] Sournia A. Red tide and toxic marine phytoplankton of the world ocean: an inquiry into biodiversity. In: Lassus P, Arzul G, Erard E, Gentien P, Marcaillou C, editors. Harmful marine algal blooms. Paris: Lavoisier, Intercept Ltd, 1995. p. 103–12.

[8] Bates SS, Bird CJ, Freitas ASWD, Foxall R, Gilgan MW, Hanic LA, Johnson JE, McCulloch AW, Odense P, Pocklington R, Quilliam MA, Sim PG, Smith JC, Rao DVS, Todd ECD, Walter JA, Wright JLC. Pennate diatom *Nitzschia pungens* as the primary source of domoic acid, a toxin in shellfish from eastern Prince Edward Island, Canada. Canadian Journal of Fisheries and Aquatic Sciences 1989;46:1203–15.

[9] Moestrup Ø. Economic aspects: 'blooms', nuisance species, and toxins. In: Green JC, Leadbeater BSC, editors. The haptophyte algae, vol. 51. Oxford: Clarendon Press, 1994. p. 265–85.

[10] Andersen RA. Diversity of eukaryotic algae. Biodiversity and Conservation 1992;1:267–92.

[11] Grindley JR, Nel E. Mussel poisoning and shellfish mortality on the West Coast of Africa. South African Journal of Science 1968;64:420–2.

[12] Reinecke P. *Gonyaulax grindleyi* sp. nov.: a dinoflagellate causing a red tide at Elands Bay, Cape Province, in December 1966. South African Journal of Botany 1967;33:157–60.

[13] Satake M, MacKenzie L, Yasumoto T. Identification of *Protoceratium reticulatum* as the biogenetic origin of yessotoxin. Natural Toxins 1997;5:164–7.

[14] Rosenthal GS, Berenbaum MR. Herbivores. Their interactions with secondary plant metabolites. I: The chemical partecipants, 2nd ed. San Diego: Academic Press, 1991. p. 468.

[15] Anderson DM. Bloom dynamics of toxic *Alexandrium* species in the northwestern US. Limnology and Oceanography 1997;42:1009–22.

[16] Gallagher JC. Genetic variation in harmful algal bloom species: an evolutionary ecology approach. In: Anderson DM, Cembella AD, Hallegraeff GM, editors. Physiological ecology of harmful algal blooms. Berlin: Springer, 1998. p. 225–42.

[17] Scholin CA, Anderson DM. Detection and quantification of HAB species using antibody and DNA probes: progress to date and future research objectives. In: Reguera B, Blanco J, Fernandez ML, Wyatt T, editors. Harmful algae. Santiago de Compostela: Xunta De Galicia and Intergovernmental Oceanographic Commission of UNESCO, 1998. p. 253–7.

[18] Shumway SE, Egmond HPv, Hurst JW, Bean LL. Management of shellfish resources. In: Hallegraeff GM, Andeson DM, Cembella AD, editors. Manual on harmful marine microalgae, vol. 33. Paris: UNESCO, 1995. p. 433–74.

[19] Hallegraeff GM. Harmful algal blooms: a global overview. In: Hallegraeff GM, Andeson DM, Cembella AD, editors. Manual on harmful marine microalgae, vol. 33. Paris: UNESCO, 1995. p. 1–22.

[20] Margalef R. Red tide and ciguatera as successful ways in the evolution and survival of an admirable old phylum. In: Reguera B, Blanco J, Fernandez ML, Wyatt T, editors. Harmful algae. Santiago De Compostela, Spain: Xunta de Galicia and IOC, 1998. p. 3–7.

[21] Dale B, Yentsch CM. Red tide and paralytic shellfish poisoning. Oceanus 1978;21:41–9.

[22] Matthews SG, Pitcher GC. Worst recorded marine mortality on the South African coast. In: Yasumoto T, Oshima Y, Fukuyo Y, editors. Harmful and toxic algal blooms. Sendai: UNESCO, Sendai Kyodo Printer, 1996. p. 89–92.

[23] Cosper EM, Bricelj VM, Carpenter EJ, editors. Novel phytoplankton blooms. In: Coastal and estuarine studies, vol. 35. Berlin: Springer 1989. p. 799.

[24] Garcés E, Masó M, Camp J. A recurrent and localized dinoflagellate bloom in a Mediterranean beach. Journal of Plankton Research 1999;21:2373–91.

[25] Degobbis D, Umani SF, Franco P, Malej A, Precali R, Smodlaka N. Changes in the northern Adriatic ecosystem and the hypertrophic appearance of gelatinous aggregates. Science of the Total Environment 1995;165:43–58.

[26] Cataletto B, Feoli E, Umani SF, Monti M, Pecchiar I. Analyses of the relationship between mucous aggregates and phytoplankton communities in the Gulf of Trieste (Northern Adriatic Sea) by multivariate techniques. P.S.Z.N.I: Marine Ecology 1995;17:291–308.

[27] Lancelot C. The mucilage phenomenon in the continental coastal waters of the North Sea. Science of the Total Environment 1995;165:83–102.

[28] Geraci JR, Anderson DM, Timperi RJ, Aubin DJS, Early GA, Prescott JH, Mayo CA. Humpback whales (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxin. Canadian Journal of Fisheries and Aquatic Sciences 1989;46:1895–8.

[29] Landsberg JH, Steidinger KA. A historical review of *Gymnodinium breve* red tides implicated in mass mortalities of the manatee (*Thrichechus manatus latirostris*) in Florida, USA. In: Reguera B, Blanco J, Fernandez ML, Wyatt T, editors. Harmful algae. Santiago De Compostela, Spain: Xunta de Galicia & IOC 1998. p. 97–103.

[30] Scholin CA, Gulland F, Doucette GJ, Benson S, Busman M, Chavez FP, Cordaro J, DeLong R, Vogetaere AD, Harvey J, Haulena M, Lefebvre K, Lipscomb T, Loscutoff S, Lowenstine LJ, Marin R III, Miller PE, McLellan WA, Moeller PDR, Powell CL, Rowles T, Silvagni P, Silver M, Spraker T, Trainer V, Dolah FMV. Mortality of sea lions along the central California coast linked to a toxic diatom bloom. Nature 2000;403:80–4.

[31] Wyatt T, Jenkinson IR. Notes on *Alexandrium population* dynamics. Journal of Plankton Research 1997;19:551–75.

[32] Anderson DM. Physiology and bloom dynamics of toxic *Alexandrium* species, with emphasis on life cycle transitions. In: Anderson DM, Cembella AD, Hallegraeff GM, editors. Physiological ecology of harmful algal blooms, vol. G41. Berlin: Springer, 1998. p. 29–48.

[33] Smayda TJ. Ecophysiology and bloom dynamics of *Heterosigma akashiwo* (Raphidophyceae). In: Anderson DM, Cembella AD, Hallegraeff GM, editors. Physiological ecology of harmful algal blooms, vol. 41. Berlin: Springer, 1998. p. 113–32.

[34] Hallegraeff GM, McCausland MA, Brown RK. Early warning of toxic dinoflagellate blooms of *Gymnodinium catenatum* in southern Tasmanian waters. Journal of Plankton Research 1995;17:1163–76.

[35] Hallegraeff GM, Fraga S. Bloom dynamics of the toxic dinoflagellate *Gymnodinium catenatum*, with emphasis on Tasmanian and Spanish coastal waters. In: Anderson DM, Cembella AD, Hallegraeff GM, editors. Physiological ecology of harmful algal blooms, vol. 41. Berlin: Springer, 1998. p. 59–80.

[36] Smayda TJ. What is a bloom? A commentary. Limnology and Oceanography 1997;42:1132–6.

[37] Yang CZ, Albright LJ. Effects of the harmful diatom *Chaetoceros concavicornis* on respiration of rainbow trout *Oncorhynchus mykiss*. Diseases of Aquatic Organisms 1992;14:105–14.

[38] Stabell OB, Aanesen RT, Eilertsen HC. Toxic peculiarities of the marine alga *Phaeocystis pouchetii* detected by in vivo and in vitro bioassay methods. Aquatic Toxicology 1999;44:279–88.

[39] Hurley DE. The 'Nelson Slime'. Observations on past occurrences. New Zealand Oceanography Institution Oceanographic Summary 1982;20:1–11.

[40] Levasseur M, Keller MD, Bonneau E, D'Amours D, Bellows WK. Oceanographic basis of a DMS-related Atlantic cod (*Gadus morhua*) fishery problem: blackberry feed. Canadian Journal of Fisheries and Aquatic Sciences 1994;51:881–9.

[41] Savage RE. The influence of *Phaeocystis* on the migration of the herring. Fisheries Investigations 1930;12:5–14.

[42] Hasle GR, Fryxell GA. Taxonomy of diatoms. In: Hallegraeff GM, Anderson DM, Cembella AD, editors. Manual on harmful marine microalgae, vol. 33. Paris: France UNESCO, 1995. p. 339–64.

[43] Miralto A, Barone G, Romano G, Poulet SA, Ianora A, Russo GL, Buttino I, Mazzarella G, Laabir M, Cabrini M, Giacobbe MG. The insidious effect of diatoms on copepod reproduction. Nature 1999;402:173–6.

[44] Ianora A, Miralto A, Buttino I, Romano G, Poulet S. First evidence of some dinoflagellates reducing male copepod fertilization capacity. Limnology and Oceanography 1999;44:147–53.

[45] Smayda TJ. Primary production and the global epidemic of phytoplankton blooms in the sea: a linkage? In: Cosper EM, Bricelj VM, Carpenter EJ, editors. Novel phytoplankton blooms, vol. 35. Berlin: Springer, 1989. p. 449–83.

[46] Paerl HW, Whitall DR. Anthropogenically-derived atmospheric nitrogen deposition, marine eutrophication and harmful algal bloom expansion : is there a link? Ambio 1999;29:307–11.

[47] Hodgkiss IJ, Ho KC. Are changes in N:P ratios in coastal waters the key to increased red tide blooms? Hydrobiologia 1997;352:141–7.

[48] Lam CWY, Ho KC. Red tides in Tolo harbour, Hong Kong. In: Okaiki T, Anderson DM, Nemoto T, editors. Red tides: biology, environmental science and toxicology. New York: Elsevier, 1989. p. 49–52.

[49] Okaiki T. Red tide problems in the Seto Inland sea, Japan. In: Okaiki T, Anderson DM, Nemoto T, editors. Red tides: biology, environmental science and toxicology. New York: Elsevier, 1989. p. 137–42.

[50] Stoecker DK. Mixotrophy among dinoflagellates. Journal of Eukaryotic Microbiology. 1999;46: 397–401.

[51] Granéli E, Carlsson P. The ecological significance of phagotrophy in photosynthetic flagellates. In: Anderson DM, Cembella AD, Hallegraeff GM, editors. Physiological ecology of harmful algal blooms, vol. 41. Berlin: Springer, 1998. p. 539–57.

[52] Hasle GR. Phototactic vertical migration in marine dinoflagellates. Oikos 1950;2:162–75.

[53] Villarino ML, Figueiras FG, Jones KJ, Alvarez-Salgado XA, Richard J, Edwards A. Evidence of in situ diel vertical migration of a red-tide microplankton species in Ria de Vigo (NW Spain). Marine Biology 1995;123:607–17.

[54] Goldman JC, McCarthy JJ, Peavey DG. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature 1979;279:210–5.

[55] Bulgakov NG, Levich AP. The nitrogen: phosphorus ratio as a factor regulating phytoplankton community structure. Archiv für Hydrobiologie 1999;146:3–22.

[56] Reynolds CS. Non-determinism to probability, or N:P in the community ecology of phytoplankton. Archiv für Hydrobiologie 1999;146:23–35.

[57] Sommer U. A comment on the proper use of nutrient ratios in microalgal ecology. Archiv für Hydrobiologie 1999;146:55–64.

[58] Wyatt T. Global spreading, time series, models and monitoring. In: Lassus P, Arzul G, Erard E, Gentien P, Marcaillou C, editors. Harmful marine algal blooms, vol. 19. Paris: Lavoisier, Intercept Ltd, 1995. p. 755–64.

[59] Estrada M, Sanchez FJ, Fraga S. *Gymnodinium catenatum* (Graham) en las rias gallegas (NO de España). Investigacion Pesquera 1984;48:31–40.

[60] McMinn A, Hallegraeff GH, Thomson P, Jenkinson AV, Heijnis H. Cyst and radionuclide evidence for the recent introduction of the toxic dinoflagellate *Gymnodinium catenatum* into Tasmanian waters. Marine Ecology Progress Series 1997;161:165–72.

[61] Montresor M, Zingone A, Sarno D. Dinoflagellate cyst production at a coastal Mediterranean site. Journal of Plankton Research 1998;20:2291–312.

[62] Thorsen TA, Dale B. Climatically influenced distribution of *Gymnodinium catenatum* during the past 2000 years in coastal sediments of southern Norway. Plaeogeography, Palaeoclimatology, Palaeoecology 1998;143:159–77.

[63] Ellegaard M, Oshima Y. *Gymnodinium nolleri* Ellegaard et Moestrup sp. ined. (Dinophyceae) from Danish waters, a new species producing *Gymnodinium catenatum*-like cysts: molecular and toxicological comparisons with Australian and Spanish strains of *Gymnodinium catenatum*. Phycologia 1998;37:369–78.

[64] Ellegaard M, Kulis DM, Anderson DM. Cysts of the Danish *Gymnodinium nolleri* Ellegaard et Moestrup sp. ined. (Dinophyceae): studies on encystment, excystment and toxicity. Journal of Plankton Research 1998;20:1743–55.

[65] Matsuoka K. Morphological features of the cyst of *Pyrodinium bahamense* var. *compressum*. In: Hallegraeff GM, Maclean JL, editors. Biology, epidemiology and management of pyrodinium red tides. ICLARM Conference Proceedings, vol. 21 1989. p. 219–29.

[66] Amorim A, Dale B. Distribution of cysts from toxic or potentially toxic dinoflagellates along the Portuguese coast. In: Reguera B, Blanco J, Fernandez ML, Wyatt T, editors. Harmful algae. Santiago De Compostela, Spain: Xunta de Galicia & IOC, 1998. p. 64–5.

[67] Maclean JL. Indo–Pacific red tides, 1985–1988. Marine Pollution Bulletin 1989;20:304–10.

[68] Usup G, Azanza RV. Physiology and bloom dynamics of the tropical dinoflagellate *Pyrodinium bahamense*. In: Anderson DM, Cembella AD, Hallegraeff GM, editors. Physiological ecology of harmful algal blooms, vol. G41. Berlin: Springer, 1998. p. 81–94.

[69] Yin K, Harrison PJ, Chen J, Huang W, Qian P-Y. Red tides during spring 1998 in Hong Kong: is El Niño responsible? Marine Ecology Progress Series 1999;187:289–94.

[70] Owens NJP, Cook D, Colebrook M, Hunt H, Reid PC. Long term trends in the occurrence of *Phaeocystis* sp. in the north-east Atlantic. Journal of the Marine Biological Association U.K. 1989;69:813–21.

[71] Fraga S, Sanchez FJ. Toxic and potentially toxic dinoflagellates found in the Galician Rias (NW Spain). In: Anderson DM, White AW, Baden DG, editors. Toxic dinoflagellates. Amsterdam: Elsevier, 1985. p. 51–4.

[72] Tester PA, Geesey ME, Vukovich FM. *Gymnodinium breve* and global warming: what are the possibilities? In: Smayda TJ, Shimizu Y, editors. Phytoplankton blooms in the sea. Amsterdam: Elsevier, 1993. p. 67–72.