

Harmful or Exceptional Phytoplankton Blooms in the Marine Ecosystem

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1. INTRODUCTION

A phytoplankton (also called “microalgal” or “algal”) bloom is the rapid growth of one or more species which leads to an increase in biomass of the species. In recent years, there has been considerable popular and scientific attention directed towards “exceptional” (also called “noxious” or “nuisance”) and “harmful” phytoplankton blooms. Often, in the case of exceptional/harmful blooms, it is a single species that comes to dominate the phytoplankton community (i.e. the blooms are “monospecific”). However, when toxic algae are involved in a harmful bloom, the mere presence of the toxic alga in concentrations sufficient to elicit effects is often enough to cause the scientific community and public at large to refer to a “bloom” of that particular species. In other words, one refers to “blooms” of toxic phytoplankton on the basis of the effects observed and not necessarily because of a large biomass.

2. DEFINITIONS

Exceptional phytoplankton blooms have been defined as “those which are noticeable, particularly to the general public, directly or indirectly through their *effects* such as visible discolouration of the water, foam production, fish or invertebrate mortality or toxicity to humans” (ICES, 1984). Here, it is important to note that the list of potential “noticeable effects” of exceptional algal blooms contains effects that are caused by very different processes and which affect humans in very different ways. Some bloom-forming phytoplankton are directly harmful to humans and thus form a subset of exceptional blooms referred to as “harmful”.

Harmful phytoplankton may contain potent neurotoxins that, when they become concentrated in, for example, filter-feeding bivalves, can pose a serious public health threat. Indeed, it has been estimated (Hallegraeff, 1993) that, on a global scale, approximately 300 people die annually as a result of eating shellfish contaminated with toxic phytoplankton. Other phytoplankton species contain toxins that can induce sublethal responses in humans (diarrhoea, eye/skin irritation, breathing difficulties, etc.). Some phycotoxins appear to be carcinogenic. This, for example, is the case for some blue-green algae (cyanobacteria), which are primarily found in fresh water but which invade and can bloom in brackish waters (Falconer, 1991; Carmichael, 1992).

Other phytoplankton (*Phaeocystis* spp.) are considered to be harmful because they exude protein-rich compounds that can be whipped into a stiff foam by wave action and which, under certain hydrographic



Figure 1 *Phaeocystis* foam accumulation on the beach—eastern North Sea.
Photograph courtesy of Helene Munk Sørensen.

conditions, can accumulate along beaches and deter (paying) beach guests (Figure 1). “Red tides”, which have nothing to do with tidal action *per se* but are simply accumulations of phytoplankton so dense that the water appears to be coloured (red, green, brown, orange, etc.), can also discourage coastal visitors. Still other blooms attract public attention and earn their designation “harmful” because their occurrence in large numbers can pose an economic threat to fin- or shellfish aquaculture (see, e.g., Shumway, 1992). Mortalities of caged fish or wild fish and shellfish can occur as a result of phytoplankton blooms for a number of reasons. In some cases, there can be mechanical interaction between the phytoplankton and the gills which leads to gill damage and, ultimately, suffocation of the fish. Diatoms are often implicated in such events (Bell, 1961; Taylor *et al.*, 1985; Farrington, 1988; Rensel, 1993; Kent *et al.*, 1995; Tester and Mahoney, 1995). In some cases, anoxia and/or bacterial infection in combination with the damaged gill tissue leads to mortality of the fish (Jones and Rhodes, 1994; Tester and Mahoney, 1995). Hypoxia or anoxia resulting from the respiration or decay of dense blooms of phytoplankton can also, on its own, lead to fish or shellfish kills—especially of caged fish that are unable to swim from the affected area (Steimle and Sindermann, 1978; Taylor *et al.*, 1985). Finally, some types of

phytoplankton blooms cause fish mortality through the production of toxins. A number of toxins produced by phytoplankton that affect humans also affect fish (White, 1977; Gosselin *et al.*, 1989; Riley *et al.*, 1989; Robineau *et al.*, 1991). In addition, however, some bloom-forming phytoplankton species that have not been shown to be toxic to humans produce toxins that affect fish or other marine organisms (Moshiri *et al.*, 1978; Granmo *et al.*, 1988; Change *et al.*, 1990; Black *et al.*, 1991; Aune *et al.*, 1992; Heinig and Campbell, 1992; Eilertsen and Raa, 1994).

Thus the responses elicited by harmful phytoplankton blooms are very different. The common feature that such blooms share is that they attract public attention and that they often have public health or economic implications. No common physiological, phylogenetic or structural feature has yet been identified that distinguishes "harmful" phytoplankton species from non-harmful and the scientific basis for treating harmful phytoplankton blooms as a distinct subset of algal blooms is not obvious. Rao and Pan (1995) conducted a literature survey in which they compared photosynthetic and respiratory characteristics of some toxic and non-toxic phytoplankters in an attempt to identify physiological differences between them. They concluded that there were no differences in the characteristics examined between the toxic and non-toxic dinoflagellates studied. However, they did find that photon efficiency and maximum rates of photosynthesis were lower in the diatom *Pseudo-nitzschia pungens* f. *multiseries* when domoic acid, the toxin with which this species is associated, was produced. This, they suggest, may have been a result of the fact that domoic acid may be a product of physiologically stressed cells while at least one of the dinoflagellates considered (*Alexandrium tamarense*) is known to produce toxin during all phases of the life cycle. Such studies should serve to remind us that even within the subset of "harmful" phytoplankton that produce toxins, the differences are great and it may not be wise to expect similar responses or behaviour from these organisms.

A number of workers have argued that there has been an increase in harmful blooms in recent years (Anderson, 1989; Smayda, 1990; Hallegraeff, 1993) and it is often argued that the apparent increase in the occurrence of "harmful" blooms is linked to eutrophication.¹ Indeed, in some areas—especially those with limited water exchange such as fjords,

¹ Eutrophication as defined by Nixon (1995) = "an increase in the rate of supply of organic matter to an ecosystem". Eutrophication can occur via natural processes or as a result of human activities (cultural eutrophication). In practice, since the supply of organic matter to marine ecosystems is almost entirely the result of primary production and an increase in mineral nutrients can stimulate primary production, we equate cultural eutrophication with an increase in nutrients to a given water body resulting from human activities. When the term "eutrophication" is used in this review, it is cultural eutrophication that is referred to.

estuaries and inland seas—there does seem to be good evidence for a stimulation of the number of algal blooms occurring by eutrophication. However, the relationship between the occurrence of harmful phytoplankton blooms and environmental conditions is complicated and anthropogenic perturbation of the environment is certainly not a prerequisite for all harmful algal blooms. Thus, the occurrence of a harmful bloom may or may not have as one of its underlying causes a change in human activities or behaviour.

In Section 3 of this review, a discussion of our current state of knowledge with respect to harmful or exceptional phytoplankton blooms is presented. This section draws heavily on other recent reviews dealing with aspects of the problem of harmful phytoplankton blooms and, to the authors of these reviews, I am grateful. In the present review, particular attention is given to consideration of whether or not anthropogenic alteration of the environment may, directly or indirectly, selectively stimulate harmful phytoplankton species and the types of data required in order to be able to identify possible trends in the occurrence of harmful blooms.

Section 4 deals with the occurrence of exceptional/harmful blooms in the context of the seasonal cycles of phytoplankton bloom distribution in different latitudinal regions. In the last substantive section of the review (Section 5), the dynamics relating to the formation, maintenance and decay of exceptional/harmful blooms are discussed.

3. "HARMFUL" OR "EXCEPTIONAL" PHYTOPLANKTON BLOOMS

3.1. History

Given that exceptional/harmful algal blooms were defined above as phytoplankton blooms where the effects are noticeable and/or harmful to humans, the real history of these blooms can only begin with the records left behind by man. Indeed, it is often cited that the first written record of a harmful algal bloom (albeit in fresh water) appears in the Bible (Exodus 7: 20–21). However, there is fossil evidence that harmful algal blooms were occurring long before this. Noe-Nygaard *et al.* (1987) have suggested, on the basis of the distribution of dinoflagellate cysts and bivalve shells in fossil sediments taken from the island of Bornholm in the Baltic Sea, that toxic dinoflagellates caused mass mortalities of bivalves on several occasions dating back to about 130 million years ago (Figure 2).

Dale *et al.* (1993) have also studied the distribution of fossil dinoflagellate cysts and present evidence suggesting bloom formation by the toxic

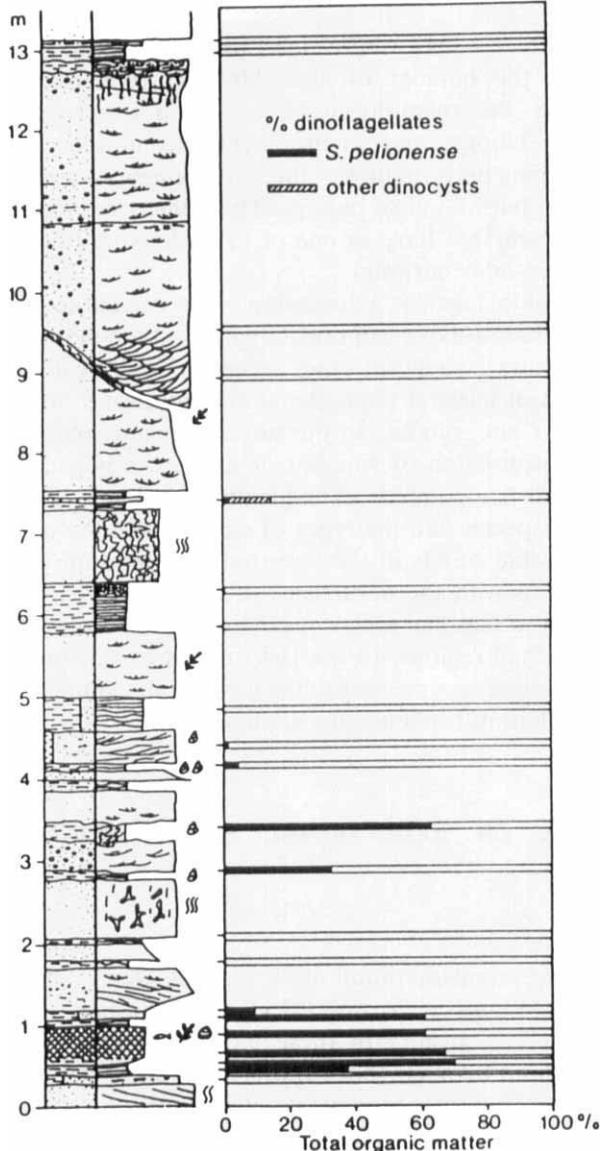


Figure 2 Sedimentological section made from a region on Bornholm, Denmark, showing the monospecific occurrences of the dinoflagellate *Sentusidium pelionense* in beds with mass occurrences of the bivalve, *Neomiodon angulata* (indicated in the drawings to the left of the bar diagram). The relative proportion of dinoflagellate cysts in relation to the total organic matter is indicated. It is not possible from such a section to establish cause and effect between the dinoflagellate blooms and mass mortalities of *Neomiodon*. However, the repeated coincidence of these events suggests that the bivalve mortalities may have been caused by the dinoflagellate blooms. (After Noe-Nygaard *et al.*, 1987.)

dinoflagellate *Gymnodinium catenatum* in the Kattegat–Skagerrak long before anthropogenic activities can have influenced these waters. The species first appeared in the region about 6000 years ago and achieved a “minor peak in production” about 4500 years ago. After that, it occurred in relatively low numbers until about 2000 years ago. During the next 1500 years, periodic blooms of the species took place. In the sediment records for the last 300 years, these workers found no evidence of this dinoflagellate. However, in a postscript to another paper (Dale and Nordberg, 1993), they indicate that living cysts of *G. catenatum* have recently been isolated from Kattegat sediments. Dale and Nordberg (1993) believe that the most important regulating factor with respect to these ancient phytoplankton blooms was climate change (the blooms appear to be associated with periods of relatively warm water) and its resultant influence on hydrographic conditions.

These forays into the fossil record emphasize two important points with respect to exceptional algal blooms: (1) the occurrence of such blooms is not only a recent phenomenon (i.e. anthropogenic perturbation of the environment is not a necessary prerequisite for all exceptional blooms) and (2) phytoplankton species are not necessarily permanent residents of a given water body. Their relative abundance within an area can vary dramatically over a relatively short time span.

The fact that harmful blooms can occur in pristine waters is further illustrated by the chronicles of a number of European explorers who report encounters with poisoned shellfish upon arriving on the shores of North America. In Canada, for example, there is still a cove known as “Poison Cove” so named by Captain George Vancouver in 1793 after an ill-fated dinner on the local bivalves (as cited in Hallegraeff, 1993).

It is not only reports of algae that are directly toxic to humans that appear in the historical literature—Pouchet described blooms of what must have been *Phaeocystis* in Norwegian waters occurring in 1882. He also recorded observing this same plankton organism at the Faeroe Islands in 1890 (cited in Moestrup, 1994). *Phaeocystis* blooms concentrated enough to clog fishing nets were recorded along the New Zealand coast (here called “Tasman Bay Slime”) as early as the 1860s (Hurley, 1982). Wyatt (1980) has suggested that a massive seal mortality event recorded off south-west Africa by Benjamin Morrell in the early 1800s may have been the result of a toxic phytoplankton bloom.

3.2. Causative Organisms

Sournia (1995) has recently conducted a survey of known marine phytoplankton species and estimated numbers of species within each

Table 1 Census of the total known number of species, number of species implicated in exceptional/harmful blooms and toxic species in the world's ocean for each class of the phytoplankton flora. (From Sournia, 1995.)

Class	Number of phytoplankton species	Number of exceptional/harmful bloom species	Number of toxic species
Chlorarachniophyceae	1	0	0
Chlorophyceae	107–122	5–6	0
Chrysophyceae	96–126	6	1
Cryptophyceae	57–73	5–8	0
Cyanophyceae	7–10	3–4	1–2
Diatomoph. Centrales	870–999	30–65	1–2
Diatomoph. Pennales	300	15–18	3–4
Dictyochophyceae	1–3	1–2	0
Dinophyceae	1514–1880	93–127	45–57
Euglenophyceae	36–37	6–8	1
Eustigmatophyceae	3	0	0
Prasinophyceae	103–136	5	0
Prymnesiophyceae	244–303	8–9	4–5
Raphidophyceae	11–12	7–9	4–6
Rhodophyceae	6	0	0
Tribophyceae	9–13	0	0
Total	3365–4024	184–267	60–78

phytoplankton class, how many of these have been implicated in the formation of exceptional or harmful blooms² and how many have been identified as being toxic. In his census (Table 1), the dinoflagellates (Dinophyceae) comprise the class which is numerically largest and it is also within this class that we find the greatest numbers of both exceptional/harmful bloom-forming and toxic species: Sournia estimates that 5.5–6.7% of the known phytoplankton species in the world's oceans (i.e. about 200 species) have been identified as causing exceptional/harmful blooms. About half of these species are dinoflagellates. Diatoms were the second most important algal class in Sournia's analysis in terms of causing exceptional/harmful blooms.

Not all exceptional/harmful blooms are toxic, of course, and Sournia has estimated that only 1.8–1.9% of the world's phytoplankton flora has so far been identified as toxic. However, he also makes the point that this value may be an underestimate as several new toxic species have become

² Sournia actually identifies organisms implicated in "red tides". However, his use of the term red tide corresponds to the definition of exceptional/harmful used here.

Table 2 Census of the number of species, exceptional/harmful bloom forming, and toxic species in the world's ocean for each order of the class *Dinophyceae* (dinoflagellates). (From Sournia, 1995.)

Order	Number of species	Number of exceptional/harmful bloom species	Number of toxic species
Actinisciales	8–11	0	0
Brachydiniales	7–8	0	0
Desmonomonadales	6	0–1	0
Dinococcales	4	0	0
Dinophysales	240–382	3–4	7–11
Dinotrichales	3	0	0
Ebriales	3	0–1	0
Gymnodiniales	512–529	31–52	9–14
Noctilucales	15–19	1	0–1
Oxyrrhinales	2	1	0
Peridiniales	656–788	46–53	21–22
Prorocentrales	30–83	11–13	7–8
Protaspidales	4–6	0–1	0
Pyrocystales	7–17	0	0
Doubtful dinoflagellates	15–17	0	0
Total	1514–1880	93–127	45–57

known in recent years. Approximately 75% of the species that have been identified as being toxic belong to the *Dinophyceae* and most of these belong to the orders Peridiniales, Gymnodiniales and Dinophysales (Table 2). Four genera (*Alexandrium*, *Dinophysis*, *Gymnodinium* and *Prorocentrum*) dominate in terms of causing toxic blooms.

Moestrup (1994) has reviewed bloom formation by phytoplankton belonging to the *Prymnesiophyceae* and concluded that only species of *Chrysosphaerulina*, *Prymnesium* and *Phaeocystis* are known to form exceptional/harmful blooms. A number of species from both *Chrysosphaerulina* and *Prymnesium* have been implicated in fish kills in both fresh and marine waters. However, the mechanism of their toxic effect is, in most cases, not well documented. Like Sournia (1995), Moestrup (1994) concludes that there is a good chance that more species will be discovered as being potentially toxic in the coming years.

Considerable attention has been given to "brown tides" occurring in recent years in Narragansett Bay and around Long Island on the east coast of the USA. The causative organism here is the chrysophyte *Aureococcus anophagefferens* (Nuzzi and Waters, 1989; Smayda and Villareal, 1989). This organism has been shown to reduce or stop filter feeding in some

shellfish (Tracey, 1988; Gallager *et al.*, 1989; Gainey and Shumway, 1991). In addition, adverse effects of blooms of this organism have been observed in field studies on a number of different organisms (Cosper *et al.*, 1987; Durbin and Durbin, 1989; Smayda and Fofonoff, 1989) although the mechanism of the interaction between *A. anophagefferens* and the various affected components of the ecosystem is not, in all cases, well documented. The southern Texas coast has also recently been plagued by "brown tides". Here, the causative organism is also a chrysophyte but somewhat larger than *A. anophagefferens*. Buskey and Stockwell (1993) have demonstrated in their field studies that micro- and mesozooplankton populations are, apparently, reduced during these blooms.

While it is clearly a relatively small percentage of the world's total phytoplankton population that has been identified as having the potential to develop exceptional/harmful blooms, Sournia (1995) makes the point that there is still a large number of species involved representing great taxonomic diversity. In view of this diversity he argues that there is "no hope of defining a single algal type or target organism for use in understanding, modeling or protection against" exceptional/harmful algal blooms.

3.3. Toxic Algal Blooms

The analytical chemistry surrounding the description and identification of the toxins associated with algal blooms is complex. In addition, the technical capabilities in terms of toxin identification have been evolving rapidly in recent years. It is not the purpose of the present review to consider the more chemical aspects of the toxins associated with algal blooms. The more chemically inclined reader is referred to the following recent works for a status of knowledge concerning the chemistry of algal toxins (WHO, 1984; Falconer, 1993; Premazzi and Volterra, 1993). For the purposes of this review, it is sufficient to consider types of "toxicity events" rather than deal with the individual toxins themselves.

3.3.1. Amnesic Shellfish Poisoning (ASP)

Amnesic shellfish poisoning gets its name from the fact that one of the symptoms of the poisoning is loss of memory. ASP was first recognized in 1987 on Prince Edward Island on the Canadian east coast when a very serious incident occurred which caused several human fatalities and over a hundred cases of acute poisoning following the consumption of blue mussels (Bates *et al.*, 1989). The cause of this poisoning was traced to a

bloom dominated by the pennate diatom, *Pseudo-nitzschia multiseries* (formerly *Pseudonitzschia pungens f. multiseries*) which produces the neurotoxin domoic acid (Bates *et al.*, 1989, 1995).

After the discovery of ASP, many countries began routine monitoring for the occurrence of domoic acid in shellfish products. Already in 1988, unacceptably high concentrations of domoic acid were found in soft-shelled clams, *Mya arenaria*, and blue mussels, *Mytilus edulis*, in the south-western Bay of Fundy (Canadian coast). Shellfish harvesting areas were closed and no incidents of poisoning were reported at this time (Haya *et al.*, 1991; Martin *et al.*, 1993).

Coastal fisheries along the North American west coast were closed in the autumn of 1991 due to the detection of domoic acid (Drum *et al.*, 1993; Langlois *et al.*, 1993; Villac *et al.*, 1993). There was also a report of poisonings by domoic acid at this time from Santa Cruz, California (Work *et al.*, 1993). In this poisoning event, no human victims were reported; however, mortalities of pelicans and cormorants were observed. Remnants of frustules from the diatom, *Pseudo-nitzschia australis* (= *Nitzschia pseudoseriata*) and high levels of domoic acid were found in the stomachs of the dead birds. A bloom of *Pseudo-nitzschia australis* was occurring at the time of the mortalities. Thus, it was possible to confirm that domoic acid production was associated with this diatom. Work *et al.* (1993) also demonstrated the presence of domoic acid in anchovies from the area of the bloom, thus identifying finfish as potential vectors of ASP.

Lundholm *et al.* (1994) have shown that the diatom *Pseudo-nitzschia seriata* also produces domoic acid at levels similar to those observed with *Pseudo-nitzschia multiseries*. This diatom is common in colder waters of the Northern Hemisphere. There is also an indication in the literature that several other common diatom species may produce domoic acid (e.g. *Fragilaria* sp.: Pauley *et al.*, 1993; *Amphora coffeaeformis*: Maranda *et al.*, 1990) so it would seem likely that other species may soon be confirmed as domoic acid producers. Thus, although ASP has only recently been recognized, the fact that the causative organisms have a wide geographic distribution (Douglas *et al.*, 1993; Hallegraeff, 1993) and that commercial finfish have the potential to harbour and transmit domoic acid poisoning suggests that there is a serious risk of ASP incidents occurring in many parts of the world's oceans.

3.3.2. Paralytic Shellfish Poisoning (PSP)

In contrast to ASP, the existence of PSP has been recognized for many centuries. It has even been claimed that the Indians along the Pacific west coast of North America practised a form of public health control by not

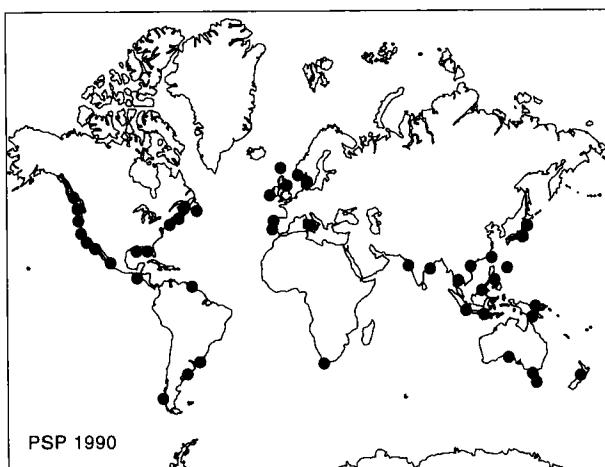


Figure 3 Known global distribution of paralytic shellfish poisoning (PSP) in 1990. (After Hallegraeff, 1993.)

harvesting shellfish in periods when there was bioluminescence in the water (many of the dinoflagellates responsible for PSP are bioluminescent; Dale and Yentsch, 1978). This form of shellfish poisoning induces muscular paralysis and, in severe cases, can lead to death through paralysis of the respiratory system. PSP is caused by one or more of about 18 different toxins which include saxitoxins, neosaxitoxins and gonyautoxins (Frémy, 1991). These toxins are often referred to collectively as "PSP toxins". The combination of toxins found in contaminated shellfish seems to depend upon the type of toxin produced by the causative phytoplankton organism as well as the storage conditions and the metabolism of the compounds in the shellfish (Kirschbaum *et al.*, 1995).

Hallegraeff (1993) reviewed the distribution of areas known in 1990 to have been affected by PSP events at one time or another (Figure 3). From his census it would appear that, with the exception of the African and parts of the South American coasts, PSP is a worldwide problem. To what degree the lack of reports of PSP in Africa and South America indicate a true absence of the potential for PSP incidents in these regions is not yet clear. Recent anecdotal evidence (Baddyr, 1992) suggests that PSP incidents have occurred along the Moroccan coast during the 1980s and 1990s. Thus it seems likely that PSP is even more widespread than Figure 3 would suggest.

Shellfish are the usual vectors of PSP to human consumers. However, crustaceans can also accumulate PSP toxins (Desbiens and Cembella, 1995). Lobsters harbour the toxins primarily in the hepatopancreas rather

than in the meat—a fact that caused the Department of Health and Welfare in Canada to recommend that no more than two lobster “tomalley” be consumed at any one meal (Todd *et al.*, 1993). Lobster larvae do not appear to be sensitive to PSP toxins but a number of fish larvae (mackerel: Robineau *et al.*, 1991; capelin and herring: Gosselin *et al.*, 1989) have been shown to be vulnerable to these toxins. PSP toxins have been found in zooplankton and the guts of dead or diseased fish in the vicinity of blooms (White, 1977). Occasionally, some PSP toxins have also been found in the muscle of affected fish and there is at least circumstantial evidence that PSP toxins may be implicated in mortalities of marine mammals (Hofman, 1989; Anderson and White, 1992).

Sublethal effects of PSP toxins on marine food webs have also been recorded. A number of studies have indicated reduced grazing rates by copepods on PSP-containing phytoplankton (Ives, 1985, 1987; Huntley *et al.*, 1986; Turriff *et al.*, 1995). In an elegant study, Hansen (1989) examined the effect of the presence of the PSP producers, *Alexandrium tamarense* and *A. fundyense*, on a tintinnid, *Favella ehrenbergii*. In this case, it was not the ingestion of the alga that affected the grazer but, rather, the presence of algal exudates in the medium. These exudates appear to affect the cell membrane and induce ciliary reversals which cause the organism to swim backwards. A similar response has been observed when *F. ehrenbergii* is presented with *Alexandrium ostenfeldii* (Hansen *et al.*, 1992).

3.3.3. Neurotoxic Shellfish Poisoning (NSP)

Blooms of the dinoflagellate *Ptychodiscus breve* (formerly *Gymnodinium breve*) have been associated with human poisonings which are characterized by neurological symptoms but no paralysis. Here again, it appears that a group of toxins are responsible for these intoxications and these are referred to collectively as “brevetoxins”. Brevetoxins are potent polyether neurotoxins (Baden, 1989; Trainer *et al.*, 1990). Two types of human poisonings are recorded: one causing paraesthesia, alternating hot and cold sensations, nausea, diarrhoea and ataxia; the other form is characterized by upper respiratory distress and/or eye irritation (WHO, 1984). NSP is a serious problem along the south-eastern coast of North America and in the Gulf of Mexico. However, the causative organism has also been recorded in other parts of the world. It was recorded for the first time in 1993 in New Zealand waters concomitant with an outbreak of respiratory problems in the local population (Smith *et al.*, 1993).

In addition to causing human poisonings, brevetoxins affect marine organisms (Riley *et al.*, 1989) and have been implicated in a number of

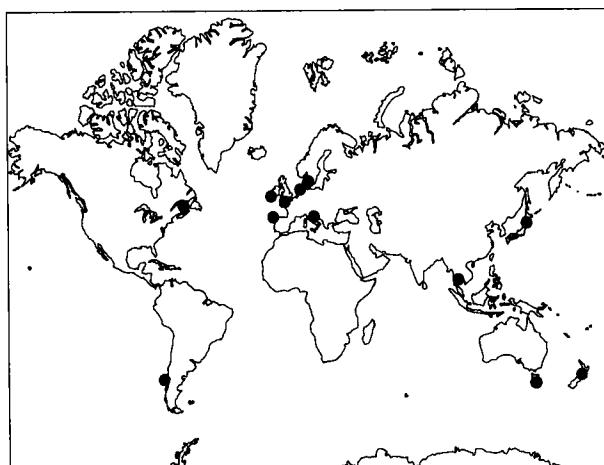


Figure 4 Known global distribution of diarrhoeic shellfish poisoning (DSP). (After Hallegraeff, 1993.)

mortality events for marine mammals. (Hofman, 1989; O'Shea *et al.*, 1991; Anderson and White, 1992). Recent studies (Shimuzu *et al.*, 1995) have suggested that toxin production by *P. breve* is increased when the organism is metabolizing heterotrophically.

3.3.4. *Diarrhoeic Shellfish Poisoning (DSP)*

DSP was first identified in Japan in 1976 (Yasumoto *et al.*, 1978). Incidents of DSP had, however, almost certainly occurred earlier when they were probably mistaken for being caused by bacterial gastrointestinal infections. The symptoms of DSP include stomach pain, nausea, vomiting and diarrhoea (WHO, 1984). No fatalities directly associated with DSP have ever been recorded. However, Suganuma *et al.* (1988) have reported that some of the toxins associated with DSP may promote the development of stomach tumours. Thus prolonged or chronic exposure to DSP toxins may have long-term negative effects on public health. The toxins implicated here are okadaic acid and derivatives and polyether lactones (WHO, 1984). A number of dinoflagellate species (Hallegraeff, 1993), especially from the genus *Dinophysis*, have been identified as producing these toxins. Again, these organisms are broadly distributed on a global scale and confirmed DSP incidents have been reported from all continents except Africa and Antarctica (Figure 4). As in the case of PSP, there is evidence that DSP may be geographically more widespread than the

scientific literature would suggest. Mendez (1992), for example, reports in a newsletter on algal blooms that DSP occurred along the Uruguayan coast during January 1992.

3.3.5. *Ciguatera*

Ciguatera poisoning has been known for centuries in subtropical and tropical areas—Captain Cook was stricken in New Caledonia in 1774—and is a growing problem in some areas. During the period 1960–84, over 24 000 cases were reported in French Polynesia alone (Hallegraeff, 1993). Ciguatera is caused by benthic dinoflagellates such as *Gambierdiscus toxicus* and, possibly, *Ostreopsis siamensis*, *Coolia monotis*, *Prorocentrum lima* and related species (Hallegraeff, 1993). The toxins are transported through the food chain and usually reach humans through the consumption of finfish.

There are chemical similarities between ciguatoxin and brevetoxins and the toxic effects of both of these types of toxin are, apparently, caused by changes in sodium ion influx in the affected organism (Baden, 1989, 1995; Trainer *et al.*, 1990). Many of the symptoms associated with ciguatera poisoning also resemble NSP and, in severe cases, death can result from circulatory collapse or respiratory failure (WHO, 1984). Ciguatoxins have also been implicated in marine mammal kills (Hofman, 1989).

3.3.6. *Cyanobacterial Toxins*

Toxic cyanobacteria (blue-green algae) blooms are most often associated with fresh waters. However, it has recently been shown that blooms of the cyanobacterium, *Trichodesmium thiebautii* occurring in the open ocean of the US Virgin Islands can be toxic (Hawser and Codd, 1992). Guo and Tester (1994) conducted toxicity tests with *Trichodesmium* sp. cells (taken from a 1992 bloom off the North American coast) on the copepod, *Acartia tonsa*. These workers demonstrated that intact cells were not toxic to *A. tonsa* but that homogenized cells were. Thus, the authors suggest that the alga contained one or more intracellular biotoxins. Brackish waters can also harbour toxic cyanobacteria blooms. Some Australian estuaries and inlets (Huber and Hamel, 1985; Lenanton *et al.*, 1985; Blackburn and Jones, 1995) and the Baltic Sea (Kononen, 1992) are examples of brackish areas where the toxic cyanobacterium, *Nodularia spumigena*, frequently forms blooms.

Other toxic cyanobacteria have also been reported to occur in the Baltic but these have apparently not been associated with bloom formation (Kononen, 1992). Nodularin, the toxin associated with *Nodularia*

spumigena, is (like some of the toxins associated with the most common freshwater blooms of toxic cyanobacteria) hepatotoxic and may promote tumours with chronic exposure (Falconer, 1991). There are a number of incidents reported in the literature of animal poisonings/mortalities with associated liver damage which have been seen in connection with blooms of *N. spumigena* (Kononen, 1992).

Some marine regions (e.g. Hawaii, USA and Okinawa, Japan) have experienced blooms of the filamentous cyanobacterium, *Lyngbya majuscula*, which has been documented to produce toxins that induce dermatitis in animals. Thus, swimmers exposed to blooms of this organism have suffered attacks of dermatitis (WHO, 1984).

While toxic cyanobacteria blooms comprise a relatively small proportion of the phytoplankton blooms occurring in the world's oceans, the fact that they occur in brackish waters means that they are often found near the mouths of rivers and in bays and inlets affected by freshwater runoff. Such regions are often heavily used by the local human population. Given the recent discovery that some cyanobacterial toxins may stimulate tumour formation (Falconer, 1991; Carmichael, 1992), it is likely that there will be increasing awareness directed towards this type of phytoplankton bloom in coming years.

3.3.7. Other Types of Toxic Blooms

In addition to the toxic bloom events that directly threaten public health, there occur each year phytoplankton blooms that elicit mortality in wild or cultured marine animals without exhibiting any adverse effects for humans. Much publicity is given to such blooms, especially when cultured stocks (i.e. aquaculture activities) are threatened, and there has been a tendency to consider the occurrence of such blooms as a recent phenomenon. In fact, reports of mortalities of wild marine organisms in association with algal blooms have appeared in the scientific literature for at least the last century:

During the last two months the inhabitants in Rhode Island witnessed the following remarkable phenomenon. The water of a considerable portion of the Bay became thick and red, emitting an odor almost intolerable to those living near by. The situation became alarming when, on the 9th and 10th of September, thousands of dead fish, crabs and shrimps were found strewn along the shores or even piled up in the windrows . . .

During the last of August, throughout September and a part of October streaks of red or 'chocolate' water were observed from near Quonset Point and Providence Island. (Mead, 1898)

As identified in Section 2, the mortalities resulting from such blooms

can have different causes or combination of causes including suffocation due to anoxia and/or gill damage and/or bacterial infection in weakened animals. However, in other cases the causative phytoplankton are known toxin producers or evoke responses in the affected organisms that suggest that toxin production is implicated.

Toxic blooms of Prymnesiophytes are frequently reported to be a problem for aquaculture facilities. For example, a massive bloom of *Chrysochromulina polylepis* in the Skagerrak/Kattegat during May–June 1988, caused havoc with salmon-raising facilities along the Swedish and Norwegian coasts (insurance companies in Norway paid out the equivalent of approximately 10 million US\$ in connection with the bloom (Moestrup, 1994). This bloom also affected wild stocks of a number of different genera (Olsgard, 1993) and, in addition to causing mortalities of mature animals, it has been shown that the presence of the phytoplankton inhibits the reproduction process in the ascidian, *Ciona intestinalis* and the mussel, *Mytilus edulis* (Granmo *et al.*, 1988). Thus, Granmo *et al.* (1988) suggested that the phytoplankton bloom may have had long-term effects in the affected area by reducing larval settlement and recruitment for these and possibly other species. Other plankton organisms were also shown to be affected by this *Chrysochromulina* bloom (Nielsen *et al.*, 1990). *Chrysochromulina leadbeateri* caused mortalities in caged salmon along the northern Norwegian coast in 1991 and two *Prymnesium* species (*P. patelliferum* and *P. parvum*) have also caused mortalities in aquaculture facilities for salmon and rainbow trout (Aune *et al.*, 1992; Meldahl *et al.*, 1995).

The raphidophyte, *Heterosigma akashiwo*, presents a serious problem for aquaculture in many parts of the world including Japan, North America, Asia and New Zealand (Haigh and Taylor, 1990; Change *et al.*, 1990; Black *et al.*, 1991; MacKenzie, 1991; Qi-Yusao *et al.*, 1993; Honjo, 1994). Affected salmon show signs of gill and intestinal pathology and death has been attributed to impairment of the gills' respiratory and osmoregulatory functions (Change *et al.*, 1990). It has been suggested that the toxic effects elicited by this organism on salmon may be brought about by the formation of toxic concentrations of oxygen radical and hydrogen peroxide (Yang and Albright, 1994).

A number of dinoflagellates are also dreaded by aquaculture operators for their toxic effects although the mechanism by which these dinoflagellates cause fish mortalities is not always well documented. An example here is *Gyrodinium aureolum* which has been recognized as a fish killer for many years (Tangen, 1977). Gill histopathology in affected fish has been reported to be similar to that observed in fish exposed to *Heterosigma* (Change *et al.*, 1990). However, there has been considerable discussion in the scientific literature as to whether or not this organism is toxic and

the nature of the toxin(s) that it may produce (see discussion in Bullock *et al.*, 1985). It is now generally accepted that toxin production by *G. aureolum* is, at least in some cases, involved in mortalities caused by this organism (Boalch, 1983; Bullock *et al.*, 1985; Heinig and Campbell, 1992).

It has also been suggested (Jenkinson, 1989, 1993) that *Gymnodinium aureolum* (and some other bloom-forming flagellates) may alter sea water characteristics through the production of extracellular organic material. This extracellular material should increase the viscosity of the medium surrounding the fish so that the energy expended in filtering water through the gills exceeds that which can be supported by the oxygen uptake. Support for the hypothesis that certain phytoplankton blooms can alter sea water characteristics is found in measurements made in the North Sea (Jenkinson and Biddanda, 1995). There is also some experimental evidence (Jenkinson, unpublished data) that the presence of certain phytoplankton in the medium decreases the rate at which fish are capable of filtering water over the gills. Thus, the mechanism(s) by which phytoplankton blooms may lead to fish mortalities are not always straightforward and, in some cases, several factors may be involved.

A new toxic dinoflagellate (*Pfiesteria piscicida*; Steidinger *et al.* 1996 (dubbed the "phantom" dinoflagellate) has recently been described (Burkholder *et al.*, 1992). This dinoflagellate requires live finfish (or their excrement) in order to excyst and to release its potent neurotoxin. It appears to be highly lethal to both fin- and shellfish in laboratory studies and it is believed that this organism may be responsible for major fish kills. "Blooms" of this dinoflagellate appear to be very short-lived in that the organism appears in relatively large numbers during a fish kill (i.e. while the fish are dying) but within hours of the death of the fish, the dinoflagellate appears to encyst and settle into the sediments. Fish kills associated with this dinoflagellate usually last less than 3 d (Burkholder *et al.*, 1995).

3.4. Role of Bacteria in Toxin Production

As noted by Sournia (1995; see Table 1), the greatest number, by far, of identified toxic species are found within the Dinophyceae. Two provocative papers presented (Kodama, 1990; Sousa-Silva, 1990) suggested that bacteria (either intra- or extracellular) may be implicated in the production of dinoflagellate toxicity. In the wake of these papers, considerable activity has been directed towards elucidating the potential role of bacteria in the production of phytoplankton toxicity. Although it now seems clear that not all phytoplankton toxicity is the direct result of bacterial activity,

some bacteria have been identified as being capable of autonomous "phyco"toxin production (Doucette and Trick, 1995; and references contained in Doucette, 1995). In addition, there is growing evidence that bacteria or some unidentified algal-bacterial interaction(s) may play a potential role in many types of toxicity events.

Bates *et al.* (1995) examined the effects of bacteria on domoic acid production by the diatom, *Pseudo-nitzschia multiseries*. They observed a dramatic increase in domoic acid production in non-axenic cultures as compared to axenic ones (Figure 5). Furthermore, they demonstrated that toxin production was stimulated when bacteria were reintroduced to the axenic cultures. This stimulation occurred with the introduction of different types of bacteria indicating that the response observed was not specific to the presence of a single bacterium. Thus, while the presence of bacteria is not essential for the production of domoic acid by *P. multiseries*, some sort of extracellular bacterial interaction with the diatom may enhance the production of toxin. Further research is clearly needed to elucidate the nature of the relationship between bacteria and algal toxin production.

3.5. Role of Nutrient Availability in Toxin Production

As in the case of the potential influence of bacteria on toxin production, the role of nutritional status of toxin producers on the rate of toxin production is still not clear. Given the many different types of toxins produced by phytoplankton and the varying metabolic pathways involved in this toxin production, it seems likely that nutrient availability will affect different toxin producers in different ways. Certainly, the studies that have been conducted thus far on the influence of nutritional status on toxin production do not suggest a consistent relationship between nutrient availability and toxin production.

Many studies have been carried out on changes in toxin concentration throughout the life cycle or under changing nutrient/environmental conditions (Boyer *et al.*, 1987; Ogata *et al.*, 1987; Anderson *et al.*, 1990; Reguera and Oshimo, 1990; Bates *et al.*, 1991; Aikman *et al.*, 1993). Most, but not all, of the studies examining rates of toxin production or content throughout the toxin-producing organism's growth cycle suggest that toxin production varies as a function of life cycle stages. It should be noted, however, that the majority of these studies have been carried out on batch cultures. In addition, most have been limited to a description of the toxin responses observed and no attempt has been made to describe the underlying physiological mechanisms.

Anderson *et al.* (1990) examined different PSP-producing dinoflagellates

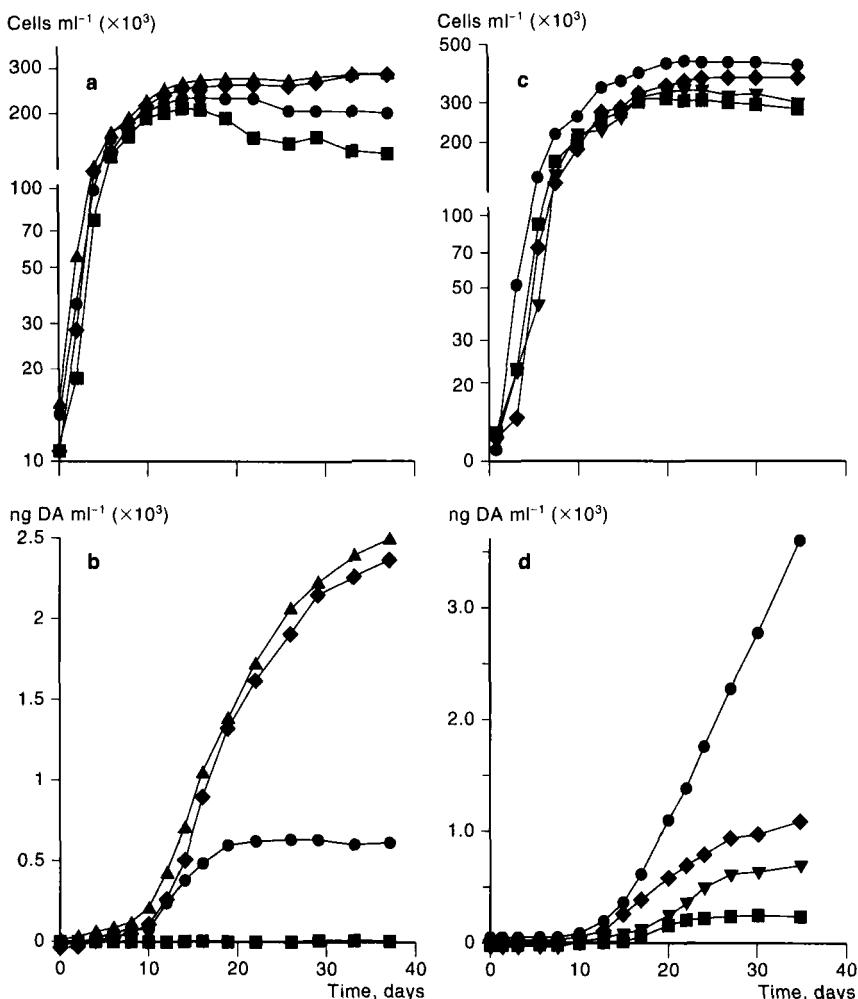


Figure 5 Cell growth and domoic acid (DA) production by two different strains of *Pseudo-nitzschia multiseries*: (a) and (c) illustrate cell numbers (based on optical density) in strains "POM" and "KP-14", respectively. ▀, Axenic and ●, non-axenic cultures; ▲, reintroduced with strain BO-2 (originally isolated from a *P. multiseries* culture); ◆, introduced bacterial strain BD-1 (originally isolated from a *P. multiseries* culture); ▽, introduced bacterial strain CH-1 (originally isolated from a *Chaetoceros* sp. culture). (b) and (d) are domoic acid (DA) measured as concentration in the whole culture. (After Bates *et al.*, 1995.)

Table 3 *Alexandrium fundyense*. Net toxin production rates (R_{tox}) in batch culture during different growth stages. Intervals define early exponential growth and late exponential/early stationary phase growth. (From Anderson *et al.*, 1990.)

Treatment	Interval (d)	R_{tox}
Control	0-4	73.5
	4-6	30.0
Low PO_4^{3-}	0-5	88.6
	5-9	160.6
Low NO_3^-	0-4	69.7
	4-5	11.7
High salinity	0-4	58.3
	4-10	31.2
Low temperature	0-11	106.8
	11-19	29.6

(*Alexandrium fundyense*, *A. tamarensis* and *A. sp.*) in both batch and semi-continuous culture. They identified differences in toxin production that were directly related to changes in growth rate associated with the various stages of the life cycle ("growth stage variability"). In addition, they were able to identify changes in toxin production related to "environmental" factors (i.e. temperature) and "nutrient" stress (Table 3). In particular, they found that phosphate limitation dramatically stimulated toxin production in *A. fundyense*. These workers suggested that the observed increase in toxic production in phosphate-stressed cells may be related to a build-up of arginine in the cells.

Other studies have also suggested an increase in toxicity for some phytoplankton species when grown under phosphate-limiting conditions (Edvardsen *et al.*, 1990; Aure and Rey, 1992) and demonstrated increased haemolytic activity of extracts from the prymnesiophyte, *Chrysochromulina polylepis*, when the organism was phosphate-stressed. This observation caused these and other workers (Maestrini and Granéli, 1991) to suggest that the high N:P ratio, which often is recorded in association with eutrophication and which was observed in the Skagerrak prior to the massive bloom of *C. polylepis* in 1988, may have stimulated the toxicity. It is worth noting here that this organism has been a component of the plankton community in the region both before and after 1988 but toxic effects have only been recorded in 1988 when an unusually high N:P ratio was reported (Maestrini and Granéli, 1991).

There is a developing awareness that the relative availability of different nutrients may also affect rates of toxin production. This may help in the search for an explanation for the physiological mechanisms behind toxin

production and in our understanding of the relationship between environmental conditions and toxic events. Flynn and Flynn (1995) point out that toxins are secondary metabolites, the production of which is dependent upon a cell's physiological condition which, in turn, is a function of nutrient status. Production of secondary metabolites may increase either at "upshock" (e.g. nutrient refeeding of starved cells) or "downshock" (e.g. nutrient deprivation). These workers also argue that the unnaturally high nitrogen concentrations relative to carbon and phosphorus found in most laboratory culture media may complicate interpretation of results of studies designed to describe the interaction between toxin synthesis and nutrient availability.

3.6. Do Human Activities Stimulate Blooms/Select for Harmful Species?

3.6.1. Has there been an Increase in Harmful Algal Blooms?

Several authors have argued that there has been a global increase in harmful phytoplankton blooms in recent decades (Anderson, 1989; Smayda, 1990; Hallegraeff, 1993) and considerable concern has been expressed with respect to the potential role that human activities may have played in this increase. Before examining the potential influence that human activities may have had on the occurrence of harmful algal blooms, the evidence for the supposed increase in such algal blooms will be considered.

Quantitative demonstration of an increase in harmful algal blooms is difficult for several reasons. First, there is a degree of subjectivity associated with the definition of harmful blooms (see Section 2). The utilization of coastal resources has been expanding in recent decades. Thus, what is "harmful" today in a region heavily exploited for aquaculture might not even have been noticed in the period prior to the development of the aquaculture industry.

Environmental monitoring programmes have also been expanding during the past decades. Many of these programmes include comprehensive monitoring of chlorophyll distributions, primary production and/or mapping of the distributions of algal species. Thus, more effort is expended in looking for algal blooms than was the case, for example, 10 or 20 years ago. This increased effort in looking for blooms may also contribute to the fact that more are apparently found.

These considerations make it difficult to deduce on the basis of an increased number of reportings that there has been a real increase in the number of potentially harmful blooms occurring on a global basis. They

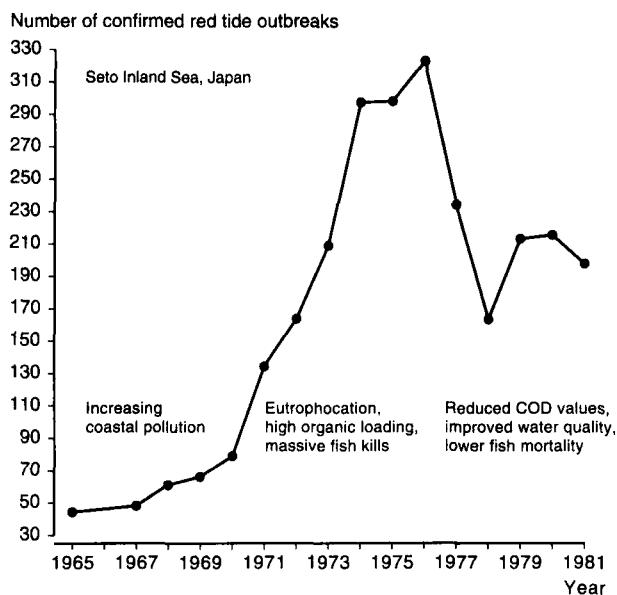


Figure 6 Trends in red tide (i.e. "exceptional" phytoplankton blooms) from 1965 to 1981 in relation to stages of environmental changes in the Seto Inland Sea. (After Prakash, 1987.)

also illustrate the problems in establishing a quantitative database that can be used to assess the development of phytoplankton blooms and possible relationships between their frequency and human activities. Nevertheless, it does seem clear that in some semi-enclosed marine areas there has been a real increase in the number of harmful algal blooms.

3.6.2. Influence of Cultural Eutrophication on the Frequency of Algal Blooms

Perhaps the most frequently cited examples of areas exhibiting an increased bloom frequency are the Seto Inland Sea, Japan (Prakash, 1987, Figure 6) and Hong Kong Harbour (Lam and Ho, 1989). For the Seto Inland Sea, there is also evidence that the observed increase is directly related to human activities in that a decrease in the number of exceptional/harmful blooms ("red tides") occurred following a reduction in chemical oxygen demand (COD) in effluents (Prakash, 1987). Thus, there would appear to be a direct link in this region between eutrophication and the frequency of algal blooms.

Similar suggestions of increases in exceptional or harmful algal blooms caused by eutrophication have been made for other marine areas (especially those with relatively slow flushing times). The Baltic Sea, the coastal North Sea and the Black Sea have all been identified as regions where such an increase in algal blooms may have occurred (references cited in Smayda, 1990). However, while it intuitively seems likely that cultural eutrophication may have influenced phytoplankton growth and species distribution in these areas, quantitative evidence of an absolute increase in harmful algal blooms for most of these areas is lacking.

Here, it is worth considering what types of data might be useful in identifying possible trends in the occurrence of exceptional/harmful algal blooms related to cultural eutrophication. The difficulties in using reports of harmful algal blooms *per se* in order to address this question have been discussed above. Other types of data that are routinely collected which pertain to phytoplankton and might, therefore, be able to provide information concerning the incidences of harmful blooms include primary production, chlorophyll (as a proxy for biomass) distributions and algal species abundance.

An International Council for the Exploration of the Seas (ICES) Working Group dealing with phytoplankton collated in 1991 a list of data time series available that might be useful for quantifying potential changes in the frequency of harmful blooms (Table 4). While this list is not meant to include all long-term data sets pertaining to phytoplankton, it does illustrate the types of data available and the typical lengths/geographic coverages of such data sets. Note that, for the most part, these data series are no more than a few decades in length. In addition, sampling frequency has not been constant throughout the duration of some of these time series.

Species abundance data potentially offer the opportunity of quantifying changes in the relative frequency of occurrence of exceptional/harmful bloom species. However, the abundance of individual species varies dramatically interannually and identification of an increase in a particular area requires that a change in the normally occurring abundance pattern can be demonstrated (Figure 7). Increases in the occurrence of individual harmful species have been identified in some regions (e.g. *Phaeocystis* at the Marsdiep (Dutch Wadden Sea): Cadée and Hegemann, 1986). However, for the most part, the time series upon which these increases have been demonstrated are not, biologically speaking, very long. Until longer data series are available, it is difficult to ascertain with any degree of certainty that the increases observed are true increases and not simply an expression of the naturally occurring changes in species abundance.

Table 4 Examples of available time series of data pertaining to phytoplankton and harmful blooms. (From ICES, 1991.)

Country	Area	Data	First year
Norway	Oslofjord	PSP	1962
	Rest of coast	PSP	1982
	All	Mortalities	1966
		<i>Gyrodinium</i>	1981
		<i>Dinophysis</i>	1984
		DSP	1984
Sweden	West coast	PSP	1982
		Phytoplankton	1989
		DSP	1984
Finland	All	Mortalities	1984
	Gulf of Finland	Phytoplankton	1968
Germany	German Bight	Phytoplankton	1962
UK	NE England	PSP	1968
France	All	PSP	1984
		Mortalities	1976
		Phytoplankton	1984
		<i>Gyrodinium</i>	1980
		DSP	1983
Spain	Galicia	PSP	1976
		Phytoplankton	1977
		<i>Dinophysis</i>	1985
		DSP	1982
Portugal	All	PSP	1986
		Phytoplankton	1987
		DSP	1987
USA	Maine	PSP	1958
	Massachusetts	PSP	1972
	California	PSP	1962
	Washington	PSP	1978
	Oregon	PSP	1980
	Florida	NSP	1978
	Florida	Mortalities	1980
	Washington	Mortalities	1989
	Narragansett Bay	Phytoplankton	1958
Canada	East coast	PSP	1942
	West coast	PSP	1950
HELCOM	Baltic Sea	Phytoplankton	1979

PSP, Paralytic shellfish poisoning; DSP, diarrhoeic shellfish poisoning; NSP, neurotoxic shellfish poisoning.

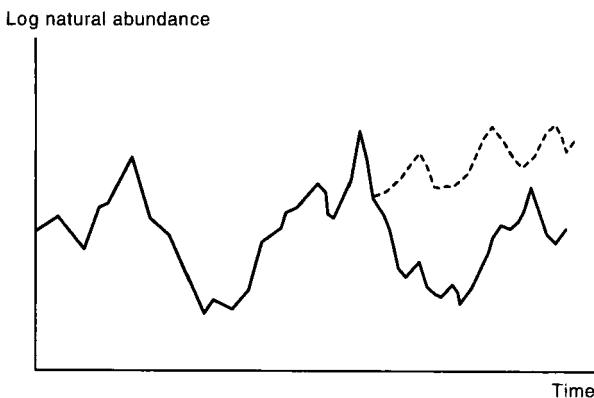


Figure 7 Hypothetical time series of mean annual abundance of a single phytoplankton species over a period of a few decades. Solid line: no overall increase in abundance of species over time. If the last third of the time series were described by the broken line, then species abundance would have increased during the period of study. The challenge in identifying whether or not there has been an increase in harmful algal blooms in recent years is to identify such changes from the naturally occurring interannual variability in phytoplankton species abundance. This requires relatively long time series that are, for the most part, lacking. (After Wyatt, 1995.)

3.6.3. Harmful Phytoplankton Species as a Subset of the Total Phytoplankton Community

If we assume that exceptional/harmful phytoplankton represent a relatively constant percentage of the total phytoplankton population, then another way in which we can investigate potential changes in the occurrence of exceptional/harmful events is to look for changes in the total phytoplankton abundance in a given area. Choosing this approach allows us to use phytoplankton biomass data (i.e. chlorophyll determined either by direct sampling or through remote sensing methods such as satellite-borne sensors) and/or primary production data. An advantage in using this type of data is that interannual variability in the primary production/algae biomass recorded is generally much less than that observed in connection with annual abundance of individual species.

This can be demonstrated by data presented in Heilmann *et al.* (1994). These workers examined biological and hydrographic characteristics of the water column during May 1988 (when the *Chrysochromulina polylepis* bloom discussed in Section 2.3.7 was underway) with similar characteristics observed in this region during the month of May in six different years distributed on either side of the bloom (Table 5). During none of the other

Table 5 Interannual variations (mean \pm SD) in characteristics derived from chlorophyll *a* ($\mu\text{g l}^{-1}$) at the surface (2 m), integrated water column chlorophyll *a* (mg m) and primary production ($\text{mg C m}^{-2} \text{d}^{-1}$) measurements for May cruises in the period 1987–93. (After Heilmann *et al.*, 1994.)

Year	Surface chlorophyll	Surf. pigm./max. pigm.*	Integrated chlorophyll	Primary production
1987	2.15 ± 0.51	0.60 ± 0.16	65 ± 7.2	908 ± 412
1988	0.58 ± 0.25	0.39 ± 0.28	19 ± 4.5	591 ± 242
1989	1.30 ± 1.04	0.79 ± 0.12	47 ± 29	—
1990	0.77 ± 0.24	0.57 ± 0.28	28 ± 9.6	699 ± 334
1991	1.29 ± 0.59	0.36 ± 0.19	29 ± 10	697 ± 355
1992	1.16 ± 0.44	0.55 ± 0.22	31 ± 4	838 ± 255
1993	0.38 ± 0.10	0.17 ± 0.09	41 ± 17	575 ± 232

* Surf. pigm./max. pigm. is concentration of chlorophyll *a* in surface (2.5 m) waters/greatest concentration of chlorophyll measured in the water column. When this value is 1, then the highest chlorophyll concentrations are found at the surface or chlorophyll is homogeneously distributed throughout the surface and the rest (or part) of the water column. The smaller this ratio, the larger the amount of chlorophyll found in a subsurface peak relative to the surface chlorophyll concentration.

Sampling in May 1988 occurred during the *Chrysochromulina polylepis* bloom in the Skagerrak-Kattegat. Note that there is no significant difference in the total primary production occurring during the *C. polylepis* bloom and in the other May studies.

six years was *C. polylepis* identified as a major component of the phytoplankton community. Despite the apparently very great differences in abundance of *C. polylepis*, no significant differences could be identified in the primary production occurring at this time during the different years. The reduced variability seen in primary production rates relative to abundances of individual species may make it possible to identify trends with shorter time series from data.

Unfortunately, there are not many long time series pertaining to marine phytoplankton primary production. This is largely due to the fact that the most sensitive method available for routine determination of primary production (^{14}C incorporation method) was first developed in the 1950s (Steemann Nielsen, 1952). As this method requires the use of radioactive material, it was some time before it found its way into routine use. Another problem with the ^{14}C incorporation method is that most laboratories have “adapted” the original method to fit their own needs and facilities. Thus, it is not certain that exactly the same measurements are being conducted by different laboratories. Indeed, there have been shown to be large interlaboratory differences in the estimates obtained for primary

production even when made on the same water sample (Richardson, 1991). Nevertheless, some primary production and/or chlorophyll data do suggest that changes have occurred in the total phytoplankton biomass or activity in certain regions. Richardson and Heilmann (1995) have considered the data concerning primary production in the Kattegat. For this region, there is no continuous long-term data set. However, this was a region extensively studied by the developer of the ^{14}C method, Steemann Nielsen (1964). Thus, there are primary production measurements from the 1950s and the period 1954–60 was especially well studied (approximately fortnightly measurements made throughout these years). One of the stations considered by Steemann Nielsen is located in the middle of an area which has been extensively studied in the late 1980s to early 1990s (Heilmann *et al.*, 1994).

Richardson and Heilmann (1995) examined, and as far as possible corrected for, the differences between the methods used during the two different periods in order to compare the magnitude of the primary production occurring in this region during the two studies. They concluded that a real increase (at least a doubling) in pelagic primary production had occurred in the Kattegat between the 1950s and the late 1980s to early 1990s. Furthermore, their analysis suggested that there was no significant difference in the measurements made during the winter (i.e. November–February) in the two studies, when light is usually limiting for phytoplankton growth (Figure 8). Considerable differences between the two studies were noted in primary production measurements made during most of the rest of the year. As the period March–October corresponds well to the period in which phytoplankton are nutrient-limited in the surface waters of the Kattegat (Richardson and Christoffersen, 1991), Richardson and Heilmann argue that the observed difference in pelagic primary production between the 1950s and the 1980 to 90s is a result of increased nutrient availability. Richardson (1996) examined the various natural and anthropogenically affected processes that might contribute to a change in nutrient availability for phytoplankton in the Kattegat and concluded that the observed increase in primary production in this region was most likely the result of eutrophication.

There are many examples of freshwater systems that respond to increased nutrient loading by increasing the total phytoplankton biomass production. The Kattegat is a marine region with limited water exchange with the open ocean and heavily influenced by freshwater input from land. Thus, it is perhaps not surprising that eutrophication effects seem to be evident here. Other studies carried out in marine waters heavily influenced by land processes have also indicated an increase in phytoplankton biomass and/or production which may be linked to eutrophication (i.e. Adriatic Sea: Justic *et al.*, 1987; Wadden Sea

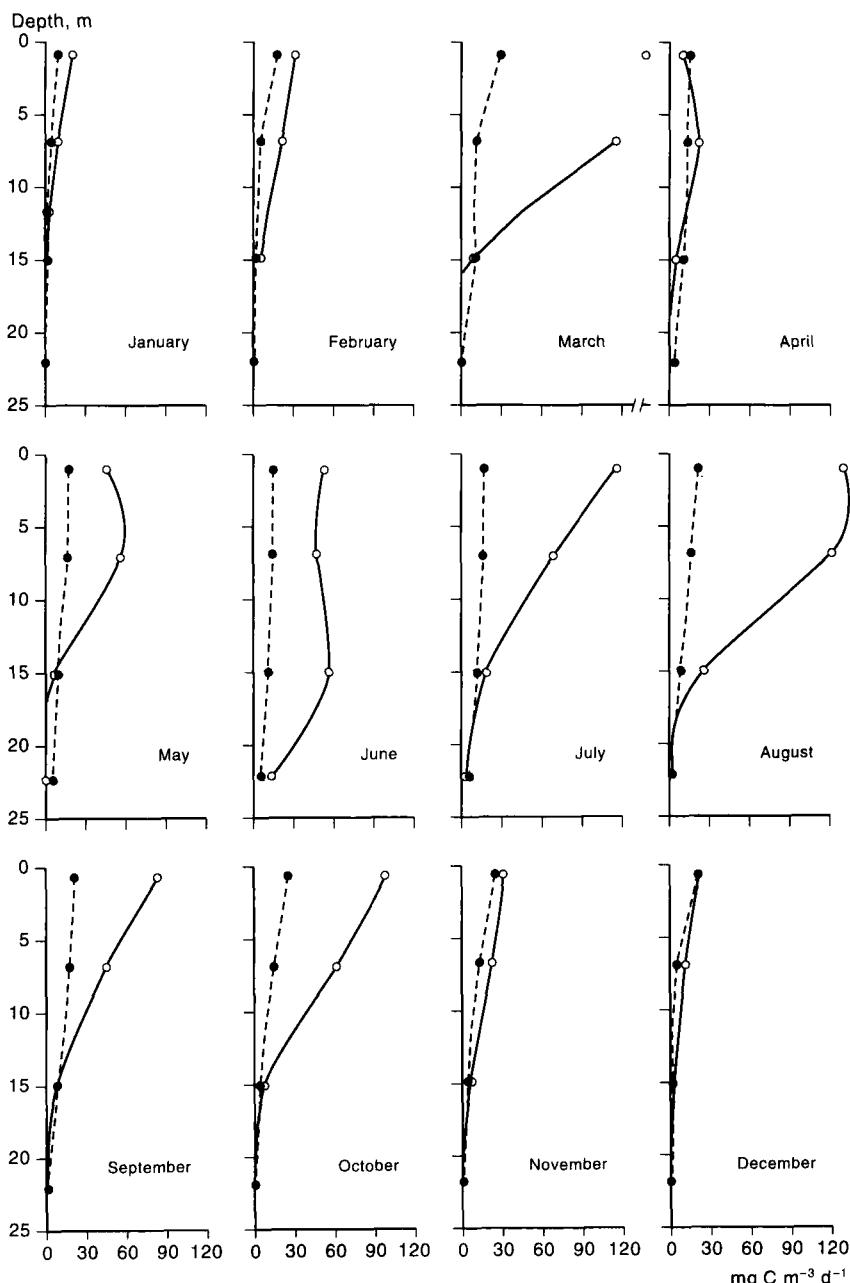


Figure 8 Average daily primary production throughout the water column for each month of the year in the period 1954–60 (●) and in the 1980s to early 1990s (○). (After Richardson and Heilmann, 1995.)

(southern North Sea): Cadée, 1986; Helgoland (south-eastern North Sea): Berg and Radach, 1985).

There does, then, appear to be evidence of an increase in total phytoplankton biomass/primary production in some marine areas which may be related to eutrophication. If exceptional/harmful bloom-forming phytoplankton species represent a constant proportion of the total phytoplankton community, then anthropogenically induced nutrient enrichment leading to an increase in total phytoplankton production will also lead to an increase in the production of these species. There is, of course, no way at present of determining whether or not the biomass of harmful species represents a relatively constant proportion of total phytoplankton biomass. However, there is no intuitive reason to suggest that the proportion of harmful phytoplankton in the total phytoplankton community is on the decrease.

3.6.4. Does Eutrophication Select for Harmful Species?

It has been suggested (Smayda, 1989, 1990) that eutrophication may actually increase the proportion of harmful species relative to the total phytoplankton biomass. The argument is based on the premise that non-diatom species are most often associated with harmful blooms and the fact that eutrophication does not increase the availability of silicon within the system. Since diatoms have an obligate requirement for silicon, eutrophication should not stimulate diatom abundance. Hence, blooms resulting from eutrophication should be comprised of non-diatom species. Circumstantial support for this argument can be drawn from a number of different regions (see review by Conley *et al.*, 1993) as well as from mesocosm experiments (Egge and Aksnes, 1992). Thus, it appears that there is the potential for a change in the availability of silicon relative to other inorganic macronutrients to alter the biomass of various phytoplankton groups relative to one another. The weakness in the argument that a species shift resulting from a change in the relative abundance of silicon will selectively stimulate the occurrence of harmful phytoplankton is that diatoms have actually been shown to be the second most implicated taxonomic group in harmful blooms. However, they are relatively unimportant in terms of toxic blooms (see Table 1). Thus, it is possible that conditions selecting for non-diatom species may increase the probability of the occurrence of toxic phytoplankton species.

Less attention has been directed towards the role that other nutrient ratios may have played in controlling relative abundance of various phytoplankton groups in relation to each other. However, changes in, for example, N : P ratios have been shown to be related to changes in

phytoplankton species succession (Egge and Heimdal, 1994). In addition, certain contaminants in the marine environment are suspected to affect phytoplankton succession (Papathanassiou *et al.*, 1994). Thus, there is the potential for human activities to alter the natural pattern of phytoplankton species succession. However, the role that this influence on species succession may have in changing the relative abundance of exceptional/harmful bloom-forming species is not yet clear.

In addition to influencing species succession *per se*, and thus potentially selecting for exceptional/harmful bloom-forming species, the stimulation of phytoplankton biomass by eutrophication may not affect all phytoplankton groups equally. In general, toxic bloom-forming species are flagellates (see above). The relative proportion of flagellate species in the phytoplankton community is not constant throughout the year. The stimulation of phytoplankton biomass through eutrophication appears to be most pronounced during periods when flagellates dominate the phytoplankton community and thus eutrophication will, in some regions, selectively stimulate flagellate biomass.

A distinct pattern in the size structure of the phytoplankton community has been identified relative to various hydrographic conditions in temperate regions (Cushing, 1989; Kiørboe, 1993). Assuming that adequate light is available for phytoplankton growth, high nutrient conditions tend to promote large cells while low nutrient conditions select for small cells. In many temperate coastal ecosystems, nutrients become mixed into the surface waters as a result of winter storm activity. In the spring, as light conditions increase, the high nutrient/high light conditions give rise to a bloom of phytoplankton dominated by large cells ("spring phytoplankton bloom"). As cells sediment out of surface waters at the end of this bloom, nutrients are transferred from the surface to deeper layers of the water column. Wind conditions are generally calmer during the summer than during the winter. Thus, except under some storm events, nutrients remain in the deep layers and the high light surface waters become nutrient depleted. Because of their greater efficiency relative to large cells in uptake of nutrients under limiting conditions (Cushing, 1989; Kiørboe, 1993), small cells are favoured under these conditions.

There is often a pattern in the size distribution of phytoplankton in surface stratified waters in temperate regions where large cells dominate in the early spring and late autumn (when the onset of winter storms again brings nutrients into the surface waters) while small cells dominate during the summer. In the Kattegat (Figure 9), the small cells observed during summer are mostly flagellates, and dinoflagellates comprise a significant proportion of these (Thomsen, 1992). This dominance during the summer months of flagellates/dinoflagellates is probably typical for surface stratified waters in temperate regions but there are exceptions. Richardson and

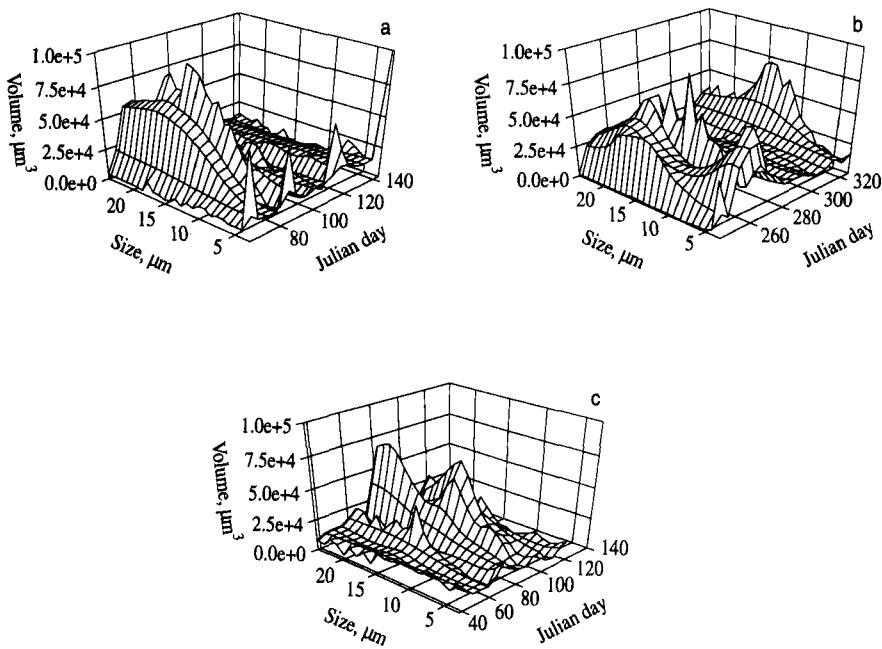


Figure 9 Particle size distribution in surface waters of the Kattegat. Total volume in a given size range (estimated spherical diameter) plotted as a function of a Julian day. (a) Spring/early summer 1994; (b) autumn 1994; (c) spring/early summer 1995. (Richardson, unpublished data.)

Heilmann (1995; see discussion above) have suggested that eutrophication resulting from human activities has led to an increase in phytoplankton production in the Kattegat throughout the annual period in which nutrients are predicted to be limiting for phytoplankton growth—a period which includes the entire summer months when flagellates dominate the phytoplankton community. Although it has been argued above that cultural eutrophication may alter the availability of silicon relative to nitrogen and phosphorus and, thus, select against diatoms, let us, for the sake of the present analysis, assume that all phytoplankton species occurring in this nutrient-limited period will be equally stimulated by the increased availability of nutrients. It can be predicted that the result of this fertilization will be an increase in the magnitude and/or duration of the spring bloom. Several authors (Cushing, 1989; Kiørboe, 1993) have pointed out that the growth rates of the herbivores capable of consuming large phytoplankton cells are slow relative to the growth rates of the algae and that there will be a relatively long lag time between the onset of an increase in growth rate in larger phytoplankton species and a build-up in

the biomass of their predators. Thus, algal biomass will accumulate (i.e. a "bloom" will develop) before the grazing community is built up. If this scenario is correct, then eutrophication effects during the spring bloom period ought to be quantifiable in terms of an increase in the magnitude/duration of the spring bloom.

On the other hand, it has been pointed out (see Kiørboe, 1993, and references therein) that there is a much closer coupling between the growth rates of smaller phytoplankton and those of their predators. It is argued that this coupling will discriminate against a build-up in biomass ("bloom") of small phytoplankton cells as grazing pressure will develop at approximately the same rate as phytoplankton biomass. Thus, it could be predicted that the increased nutrient availability associated with eutrophication should not lead to blooms of the small flagellates that dominate during the summer months but, rather, to an increase in the biomass of herbivores or to an increased rate of carbon and nutrient turnover in the pelagic community. An exception here would be in the case of small algae that, for some reason, are not easily grazed.

A number of harmful and toxic species have been identified as having inhibitory effects on potential grazers (Fiedler, 1982; Ives, 1985, 1987; Huntley *et al.*, 1986; Durbin and Durbin, 1989; Gallager *et al.*, 1989; Hansen, 1989, 1995; Hansen *et al.*, 1992; Buskey and Stockwell, 1993). In addition, herbivore distributions (Figure 10) in relation to the distribution of harmful/toxic species suggests, in some cases, avoidance of the phytoplankton by potential grazers (Nielsen *et al.*, 1990). If, as Kiørboe suggests, it is grazing pressure that controls phytoplankton biomass during the periods in which small cells dominate the phytoplankton community, then we may predict that the only blooms likely to occur during summer months in stratified temperate waters are those of "unpalatable" species. Following the same line of reasoning we used above to argue that eutrophication may increase the magnitude and/or the duration of the spring bloom, we can argue that the magnitude and/or duration of blooms of unpalatable (i.e. some toxic/harmful species) may be stimulated during the summer months by eutrophication. Thus, a consequence of eutrophication in some coastal waters may be an increase in the occurrence of biomass accumulations (i.e. "blooms") of toxic or other phytoplankton species that are not easily grazed.

Equally, anthropogenic activities that potentially influence grazing activity (such as the use of pesticides that may be generally harmful to crustaceans) may be predicted to increase the probability of blooms of phytoplankton in periods when algal biomass is controlled by grazing pressure. Following concern that nutrient enrichment occurring in connection with aquaculture activities in Loch Linnhe, Scotland, might lead to an increase in algal blooms, Ross *et al.* (1993) constructed a model to

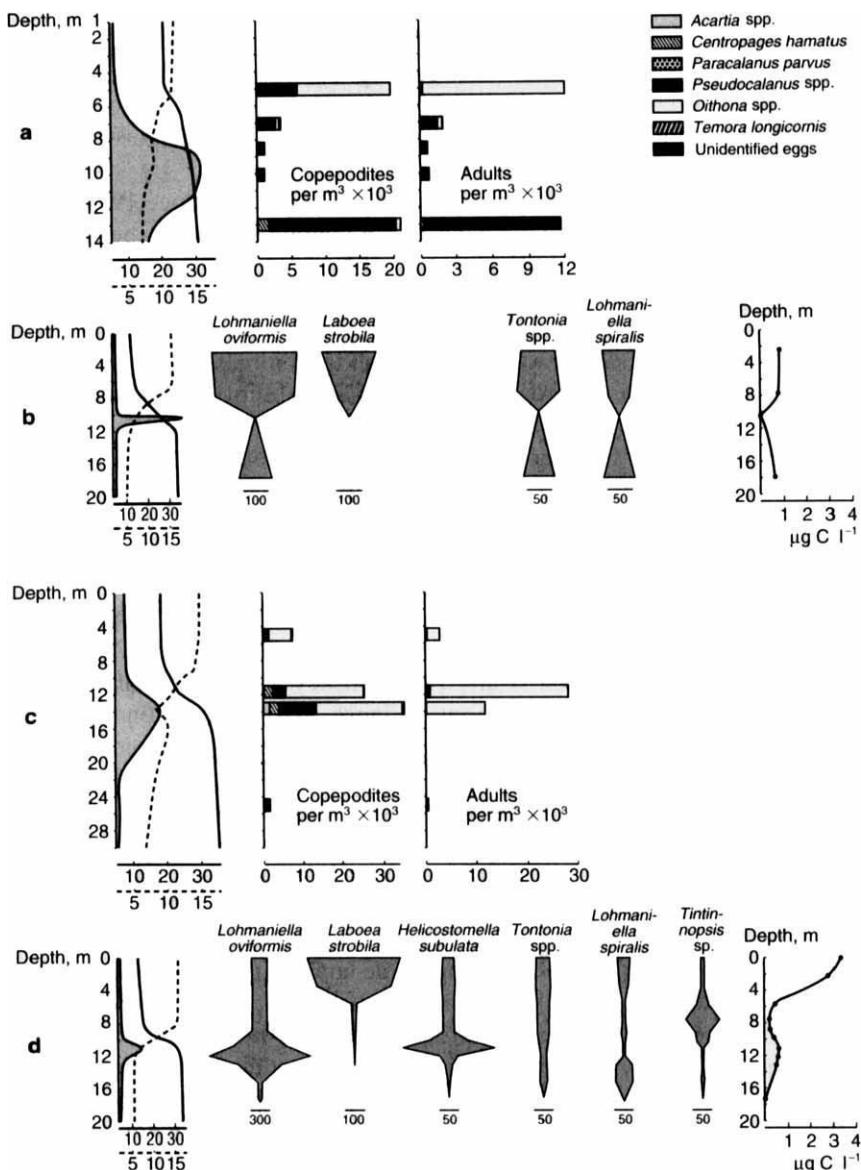


Figure 10 Vertical distribution of: (a) copepods, and (b) ciliates, in the water column at two stations examined during the 1988 *Chrysochromulina polylepis* bloom in the Skagerrak-Kattegat. At both stations, *C. polylepis* dominated the phytoplankton community (relative fluorescence (shaded area), salinity (solid line) and temperature (broken line) shown in left-hand panels). Total ciliate biomass in the water column is illustrated in the far right-hand panels of (b) and (d). When *C. polylepis* was not dominating in the phytoplankton community no avoidance at the pycnocline region was noted in copepods (c) or in ciliates (d). (After Nielsen *et al.*, 1990.)

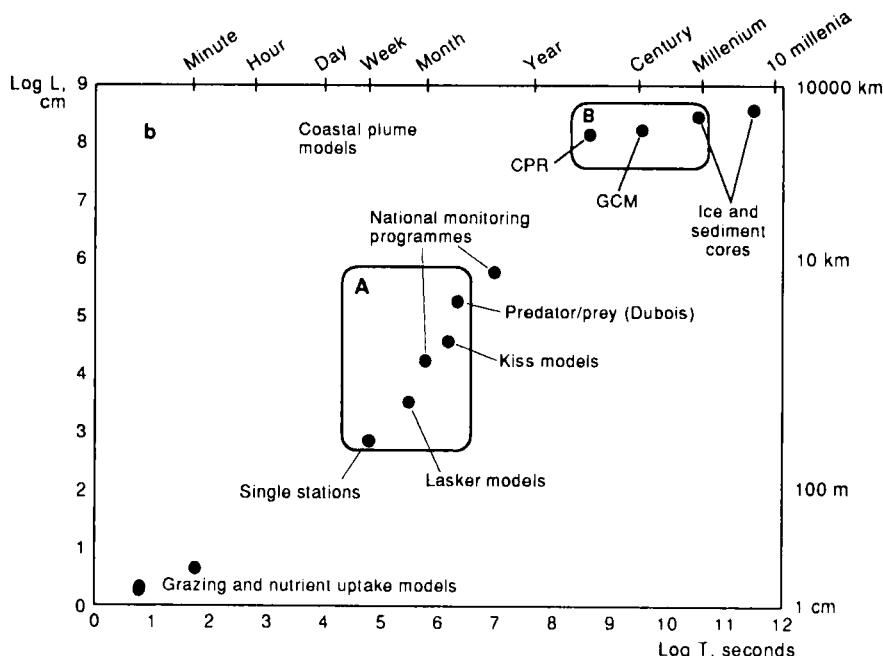
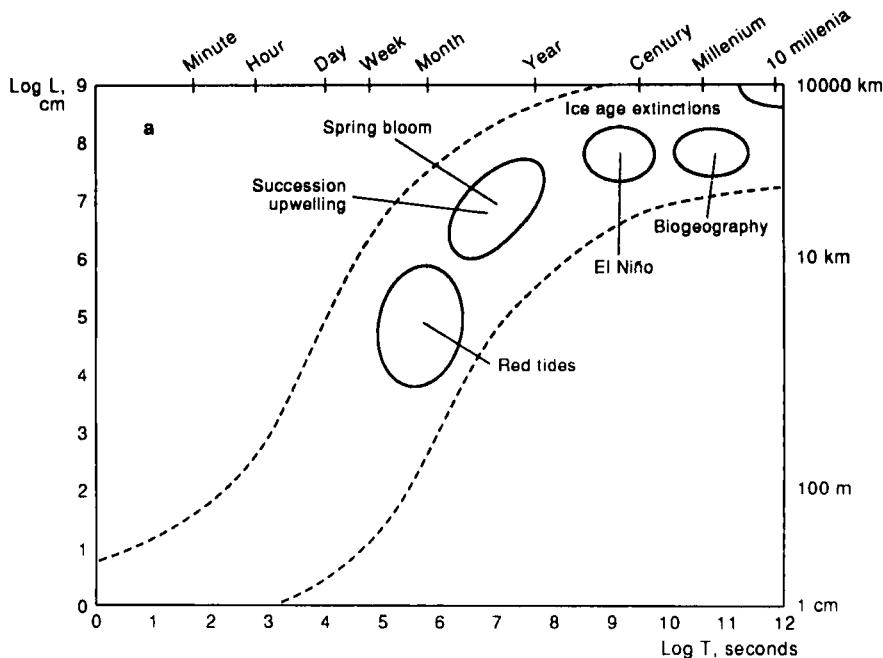
examine the interaction of aquaculture and the pelagic community. This model suggested that phytoplankton biomass in the loch is determined by grazing pressure. Thus, the authors conclude that activities interfering with zooplankton activity and/or abundance are more likely to give rise to algal blooms than the nutrient enrichment associated with the aquaculture activities. Such activities might include the use of pesticides to combat sea-lice in aquaculture facilities. In such cases, however, it seems likely that the biomass of harmful and non-harmful species alike would be stimulated.

3.6.5. *Spreading of Harmful Species*

In addition to the suggestion that human activities may have increased the number of harmful blooms occurring, several workers (Anderson, 1989; Smayda, 1989; Hallegraeff, 1993) believe there has been a global spreading of harmful species during recent years. Quantifying such a spreading is difficult for several reasons. First, the increased awareness of harmful algae in recent years often makes it impossible to determine whether a "new" siting of a harmful alga is simply the first recorded observation of a species which has always been present in the area or whether the organism has only recently entered the region. Secondly, as pointed out in the introduction, it is known that phytoplankton distributions vary naturally over time.

Wyatt (1995) has considered the types of data series that would be required in order to quantitatively address what he calls the "global spreading hypothesis" relating to harmful algae. He considers first the time and space scales relevant to harmful algal blooms and to the spreading hypothesis (i.e. biogeography) (Figure 11). He then considers the scales of the data sets which would be required to examine these phytoplankton phenomena and relates them to existing monitoring programmes and models (Figure 11b). His analysis suggests that there are data collections underway and models either developed or under development that operate at scales that are relevant to addressing questions relating to the frequency of algal blooms in restricted areas. However, for addressing questions relating to biogeography, few data sets or tools are available. Thus, he concludes that quantitative confirmation of the global spreading hypothesis is not possible at the present time.

Nevertheless, there is strong circumstantial evidence, especially from Australian waters, that several species of toxic dinoflagellates are new introductions (references reviewed by Hallegraeff, 1993). It has been shown that resting cysts of a number of toxic dinoflagellates are able to survive transport over great distances in ballast water tanks (Hallegraeff and Bolch, 1992) and Hallegraeff and Bolch (1991) estimated that one



single ballast tank contained over 300 million viable toxic dinoflagellate cysts. Thus, a likely mechanism for new introduction and transfer of harmful species has been identified. The case for this type of transfer is further strengthened by rRNA sequencing studies (Scholin and Anderson, 1991) that have shown strong similarities between *Alexandrium minutum* cultures isolated from the Spanish and Australian coasts.

Other anthropogenic vectors for the potential transport of toxic algae or their cysts have also been identified (i.e. the transfer of shellfish stocks containing phytoplankton in their digestive organs (Hallegraeff, 1993)). Thus, while quantitative demonstration of the global spreading hypothesis may not be possible on the basis of existing data, there does seem to be a potential for anthropogenic activities to increase the global distribution of harmful species.

4. EXCEPTIONAL BLOOMS IN THE CONTEXT OF SEASONAL BLOOM DEVELOPMENT

4.1. Background

It has long been realized that phytoplankton blooms are a natural phenomenon occurring within the pelagic marine ecosystem (Mills, 1989). Cushing (1959) recognized and produced a theoretical model describing the different patterns in the seasonal distribution of blooms as a function of latitude (Figure 12). This generic model is still widely accepted as a basis for understanding of bloom occurrence in different latitudinal regions and appears in most introductory textbooks on marine biology. However, there is increasing appreciation for the fact that the general patterns described are modified by different hydrographic conditions (Cushing, 1989; Richardson, 1985). Blooms are important in channelling carbon (energy) into the marine food web and it is hypothesized that the high productivity (in terms of fisheries yield) of temperate and arctic marine ecosystems compared with tropical systems may result from the more intense blooms that occur in these regions. Following this hypothesis, the occurrence of intense algal blooms may actually be a prerequisite for highly productive marine ecosystems. Intense blooms occur at temperate and polar latitudes because the

Figure 11 Stommel diagram showing spatial and temporal scales of some planktonic phenomena. (a) Space-time scales relevant to population dynamics and various modelling/monitoring programmes. (b) Time-scales relevant to the global spreading hypothesis (see text). Only the continuous plankton recorder (CPR) programme and global climate models (GCM) are identified as operating as space-time scales relevant to addressing the global spreading hypothesis. (After Wyatt, 1995.)

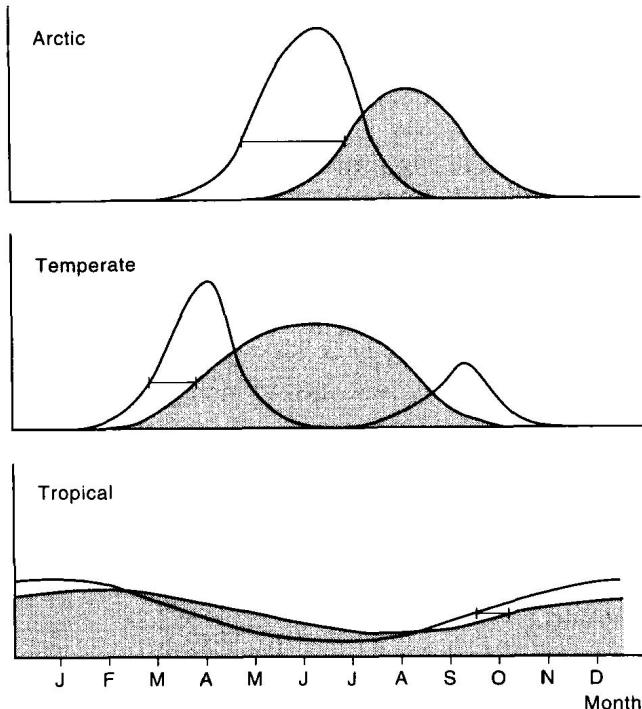


Figure 12 Seasonal variations in phytoplankton and zooplankton grazers (hatched) in different latitudinal regions. Horizontal bar indicates delay period between increases in zooplankton and phytoplankton biomasses. (After Cushing, 1959.)

hydrographic processes occurring in these regions allow phytoplankton, nutrients and light to be present simultaneously in the surface waters prior to the development of grazing populations (Gran and Braarud, 1935; Sverdrup, 1953) while the permanent stratification in tropical seas spatially separates light and nutrients.

The general mechanisms leading to the occurrence of the spring (vernial) phytoplankton blooms in temperate and arctic waters are predictable and well studied and it is not the purpose of the present chapter to consider these blooms in detail. Some consideration of vernal blooms is, however, relevant in the context of exceptional/harmful blooms both because some of the species which can occur in or immediately following vernal blooms can be harmful (i.e. *Phaeocystis*) and because sedimentation of vernal blooms can, under some conditions, lead to hypoxia or anoxia.

Following the lead of Cushing (1959), the seasonal development of phytoplankton blooms as it relates to exceptional/harmful blooms will here be considered for each latitudinal region.

4.2. Temperate Regions

4.2.1. Spring Bloom

As indicated above, the most striking non-exceptional bloom that occurs annually in temperate waters is the spring bloom. In this bloom, chlorophyll concentrations often reach levels of about two orders of magnitude greater than those observed during the dark winter months. The spring bloom in temperate regions is recognized to be important for the secondary production occurring in these regions and this bloom produces a substantial proportion of the organic material annually entering the food web (Figure 13) (for other examples, see Parsons *et al.*, 1984).

The growth rates of herbivores that are supported by relatively large phytoplankton that usually dominate during the spring bloom (Kiørboe, 1993) are temperature-dependent (Huntley and Lopez, 1992). Because of the low temperatures at the time of the spring bloom, grazing pressure is low at this time. Thus, much of the organic material produced during the spring bloom may sediment directly to the bottom rather than being degraded in the pelagic zone (Figure 14). In some cases, this sedimentation and subsequent degradation can give rise to hypoxia or anoxia which can cause mortality of benthic marine organisms (Morrison *et al.*, 1991).

While the occurrence of the spring bloom is predictable, it has long been

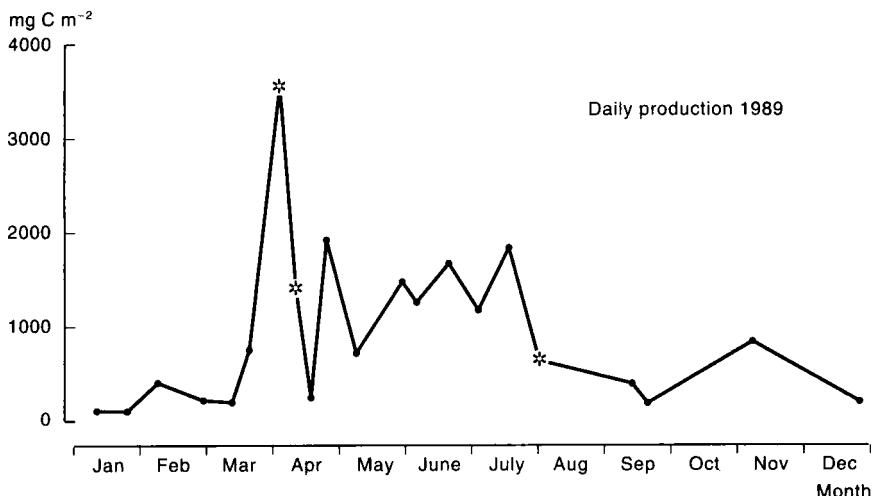


Figure 13 Annual cycle of water column primary production at a station in the southern Kattegat in 1989. Stars indicate weeks in which more than one sample was taken. For these weeks, an average of all primary production measurements is plotted. (From Richardson and Christoffersen, 1991.)

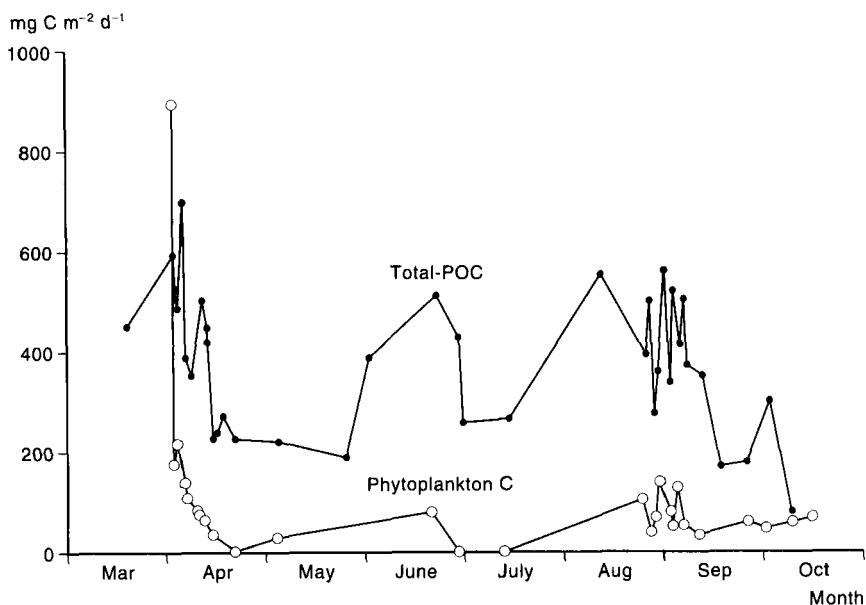


Figure 14 Sedimentation of particulate organic carbon (POC) and phytoplankton carbon at a station in the southern Kattegat during the period March–October 1989. Note that it is only during the spring bloom that substantial quantities of intact phytoplankton reach the bottom of the water column (~26 m). (After Olesen and Lundsgaard, 1992.)

recognized that its timing varies from year to year (Bigelow *et al.*, 1940). Until recently, however, there has been little interest shown in how these differences in timing of the spring bloom might affect the role of these blooms in the marine ecosystem. Townsend *et al.* (1994) hypothesized that the timing of the bloom is important for the ultimate fate of its products and, thus, is potentially critical for the survival of the organisms dependent upon the carbon flux initiated by the bloom. These workers developed a numerical simulation model to examine the effect of the temperature at the time of the bloom on the fate of the bloom products. Their results (Figure 15) indicate that differences in the timing of the bloom between years can have a very significant influence on the fate of the phytoplankton comprising the spring bloom. Using input data from a “cold” year (1974) and a “warm” year (1978) for the shallow coastal waters of the Gulf of Maine on the North American east coast, these workers compared model predictions concerning the timing and magnitude of the spring phytoplankton and its fate. During the cold year (water temperatures during the bloom 0–2°C), the phytoplankton bloom occurred about one week later than in the warm

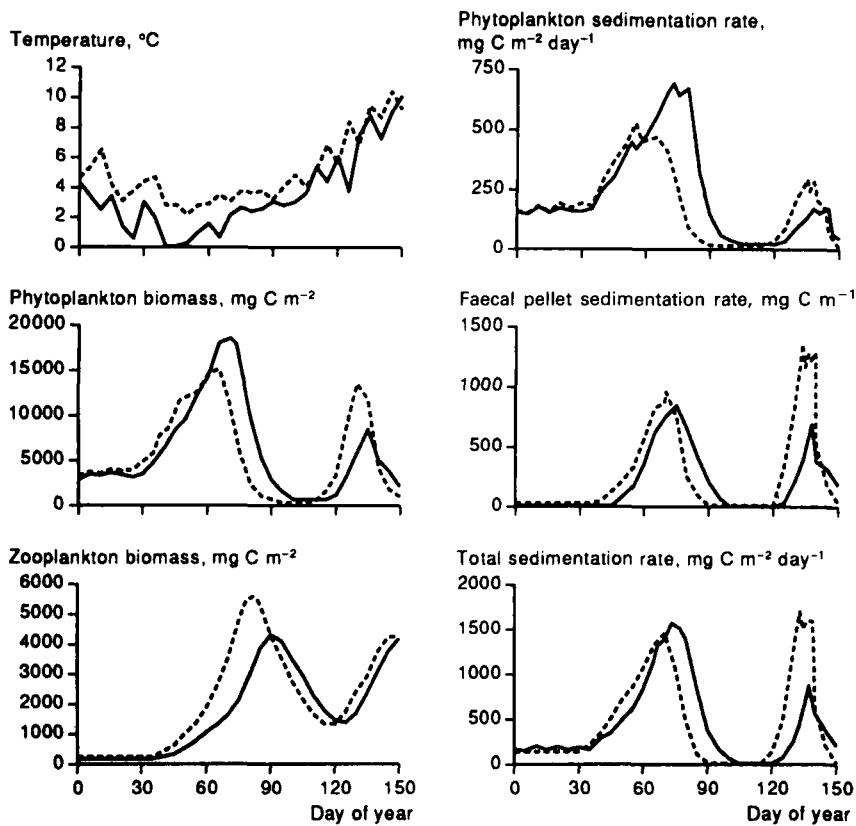


Figure 15 Results from Townsend *et al.*'s (1994) model demonstrating differences in "export" of phytoplankton carbon in "cold" (solid line) and "warm" (broken line) water spring blooms in shallow inshore waters of the Gulf of Maine. The double phytoplankton and zooplankton peaks result from the collapse of the first phytoplankton pulse due to light limitation by self-shading, followed by recovery and a second peak.

(water temperatures 2–4°C) year. In addition, the zooplankton bloom which occurs following the phytoplankton bloom was delayed by about two weeks in the cold year as opposed to the warm. Net phytoplankton production was greater during the cold year (7%) and zooplankton grazing was 11% less. As a result, Townsend *et al.*'s model indicates that about 30% more of the phytoplankton associated with the spring bloom settled to the bottom during the cold year than in the warm year.

Conventional wisdom indicates that the spring bloom in temperate offshore waters occurs as a single peak following the onset of stratification of the water column. However, another interesting result of Townsend *et*

al.'s model was the suggestion that the spring bloom may occur as a series of "pulses" rather than a single peak during some years and that stratification is not a necessary prerequisite for bloom formation. Support for the model conclusions can be found in a number of reports of field data (Townsend *et al.*, 1992; Garside and Garside, 1993). Townsend *et al.* (1994) suggest that spring bloom pulses occur in the period prior to the establishment of stratification when the wind is below a certain threshold level (and phytoplankton in surface waters are not mixed deeply in the water column). It is hypothesized that these pulses end either because of nutrient exhaustion or self-shading but that subsequent pulses may occur when the necessary conditions are again met. The "chain" of pulses that may occur in any given year will end with the pulse associated with the onset of stratification as nutrients will no longer be delivered to the high light surface waters above the pycnocline until stratification is broken down.

If the spring bloom occurs as a series of pulses in offshore temperate waters, as suggested by these workers, then the magnitude of the production occurring in association with the spring bloom(s) in some regions may be even greater than previously believed. In addition, interannual variability in weather conditions (especially in relation to wind and insolation) will be critical in determining both the magnitude of the spring bloom(s) and the fate of the bloom(s) in any given year.

This example concerning newer studies on the conditions surrounding the spring bloom emphasizes how limited our understanding of bloom dynamics actually is—even when the bloom in question is a predictable and well-known phenomenon. This is an important point to consider in light of the major national and international efforts currently underway to understand the occurrence and dynamics of *harmful* algal blooms. Perhaps it would be wiser for these programmes to focus on a better understanding of the dynamics of algal blooms, in general, rather than to focus on the distinct but very heterogeneous (see Sections 1–3) subgroup of harmful algal blooms.

4.2.2. *Summer Blooms in Offshore Surface Waters*

The traditionally accepted distribution of algal biomass in offshore surface waters of temperate regions (Figure 12) indicates that the period following the spring bloom until the autumnal breakdown of stratification is characterized by low phytoplankton biomasses. Despite these low biomasses it has become clear in recent years, with the help of satellite remote sensing (Figure 16), that huge blooms of coccolithophorids occur regularly during the summer and early autumn months in temperate and subarctic regions and it is possible that these blooms can account for a



Figure 16 Satellite (coastal zone colour scanner, CZCS) image on 6 July 1983 showing the eastern North Sea, Skagerrak, Kattegat and western Baltic Seas. The light area in the North Sea extending into the Skagerrak shows the area affected by a bloom of the coccolithophorid, *Emiliania huxleyi*. Satellite image provided by T. Aarup.

substantial proportion of the primary production occurring in some years in these regions (Holligan *et al.*, 1983, 1989; Brown and Yoder, 1994).

Coccolithophorids comprise a group within the Prymnesiophyceae which is characterized by the fact that the organisms form calcite particles intracellularly which are then extruded. Together, these extruded "coccoliths" form a "cocosphere" around the cell and it is light reflected from these coccoliths (both those in the cocospheres and those released into the water column) that produces the strong signal observed in the satellite pictures. Brown and Yoder (1994) examined satellite pictures and estimated that a spectral signal similar to those recorded in association with well-studied coccolithophorid blooms annually covered an average of $1.4 \times 10^6 \text{ km}^{-2}$ of the world's ocean area during the period 1979–85. Of these signal recordings, 71% were from subarctic latitudes. The most affected area was the subpolar North Atlantic. However, a similar spectral signal was recorded in the North Pacific and Southern Ocean, as well as off the Chilean and New Zealand coasts. There did not appear to be any indication in the spectral signal data of coccolithophorid blooms in the open equatorial waters. These workers emphasize that there is good biogeographical data to support their conclusion that the "cocco-

"lithophorid-like" spectral signal observed in temperate and subarctic latitudes actually represents coccolithophorid blooms. On the other hand, it is not known whether or not the signals observed at the lower latitudes represent coccolithophorid blooms.

Emiliania huxleyi is the most common bloom forming coccolithophorid in the North Sea where its blooms are characterized by only moderate concentrations of chlorophyll ($1\text{--}2 \mu\text{g}^{-1}$) (Holligan *et al.*, 1993b). This phytoplankton also forms blooms throughout the rest of the North Atlantic. Interestingly, although these blooms are "non-exceptional" in the sense that they are not noticeable to the general public because of their effects, they may well be considered to be "harmful" under some circumstances. This is because coccolithophorids (along with a number of other phytoplankton species including *Phaeocystis*) are known to produce dimethylsulphide (DMS).

DMS is a sulphur-containing gas that may be involved in climate regulation. A number of different phytoplankton species are implicated in DMS production. It has been suggested that most DMS producers belong to the Prymnesiophyceae or Dinophyceae (Keller *et al.*, 1989) and there is some indication that DMS production may be greatest at the late stages of a bloom (Matrai and Keller, 1993). The phytoplankton produce a precursor to DMS, dimethylsulphonium propionate (DMSP) which may be enzymatically cleaved to form DMS which is volatile (Andreae, 1990). Thus, the production of DMS will affect the sea-to-air flux of sulphur and, potentially, the geochemical sulphur cycle. As DMS is an important precursor for cloud condensation nuclei in the maritime atmosphere (Brown and Yoder, 1994), it is argued that DMS release may influence regional albedo (Charlson *et al.*, 1987). In addition, as a source of sulphur to the atmosphere, DMS may be implicated as a potential cause of "acid rain". Brown and Yoder (1994) concluded that DMS sulphur production by coccolithophorid blooms produces only a minor portion (0.03–0.07%) of the total amount of DMS sulphur (0.5–1.1 Tmol DMS-S (Tmol = 32×10^{12} mols)) produced annually on a global scale. However, there is evidence that DMS production by coccolithophorid and other phytoplankton blooms may be an important factor in determining sulphur cycling at the regional level (Holligan *et al.*, 1993a; Malin *et al.*, 1993; Brown and Yoder, 1994).

Because coccolithophorids produce calcite plates or "coccoliths", considerable interest has also been directed towards this group of phytoplankton in recent years with respect to the potential effect that they may have on oceanic carbon cycling (Fernández *et al.*, 1993; Holligan *et al.*, 1993a; Robertson *et al.*, 1994; van der Wal *et al.*, 1995). It is clear that the sedimentation of coccoliths is potentially an important mechanism for removal of carbon from the water column. However, on the basis of

theoretical chemical considerations (see discussion by Robertson *et al.*, 1994), the calcification process involved in the production of coccoliths should cause a drop in alkalinity, thus shifting the inorganic carbon equilibria in the sea water medium where a coccolithophorid bloom is underway in the direction of the dissolved gas. By affecting the partial pressure difference with respect to CO₂ in the atmosphere and in sea water, a coccolithophorid bloom may actually decrease CO₂ uptake in sea water from the atmosphere relative to when non-calcifying organisms are present.

Robertson *et al.* (1994) have, indeed, demonstrated that a coccolithophorid bloom occurring in the north-east Atlantic in 1991 apparently reduced the air-sea gradient in dissolved CO₂ by a mean of 15 µatm. These workers further estimated, by comparing measurements taken in 1990 (when few coccolithophorids were present) and those made during the 1991 bloom, that the presence of a bloom such as that observed in 1991 could reduce the uptake of atmospheric CO₂ over the spring-summer period by about 17%. Given these observations, it seems clear that knowledge of the magnitude of the occurrence of coccolithophorids in the total phytoplankton community is important in developing models to describe global carbon cycling.

These examples concerning the potential influence of coccolithophorid blooms on the geochemical cycling of sulphur and carbon illustrate that, while it is the local effects of algal blooms where and when they come in contact with human activities that attract public attention, changes in the magnitude or frequency of phytoplankton blooms may have more than local implications. Such changes may affect global geochemical cycling and, thus, climate. A better understanding of the role that phytoplankton blooms may play in the geochemical cycling processes occurring in the sea is, thus, necessary in order to predict the potential impact of global warming on climate processes and *vice versa*.

4.2.3. Subsurface Blooms in Summer Months

A further modification of the general picture of phytoplankton biomass distribution and blooms in temperate waters that has become obvious in recent years is the fact that large phytoplankton biomasses (often with peak chlorophyll concentrations similar to or greater than those recorded during the spring bloom) can occur during the late spring and summer months in association with the pycnocline (Holligan and Harbour, 1977; Pingree *et al.*, 1982; Holligan *et al.*, 1984; Richardson, 1985; Cushing, 1989; Riegman *et al.*, 1990; Kaas *et al.*, 1991; Bjørnseth *et al.*, 1993; Nielsen *et al.*, 1993b). In some cases, these large biomasses associated

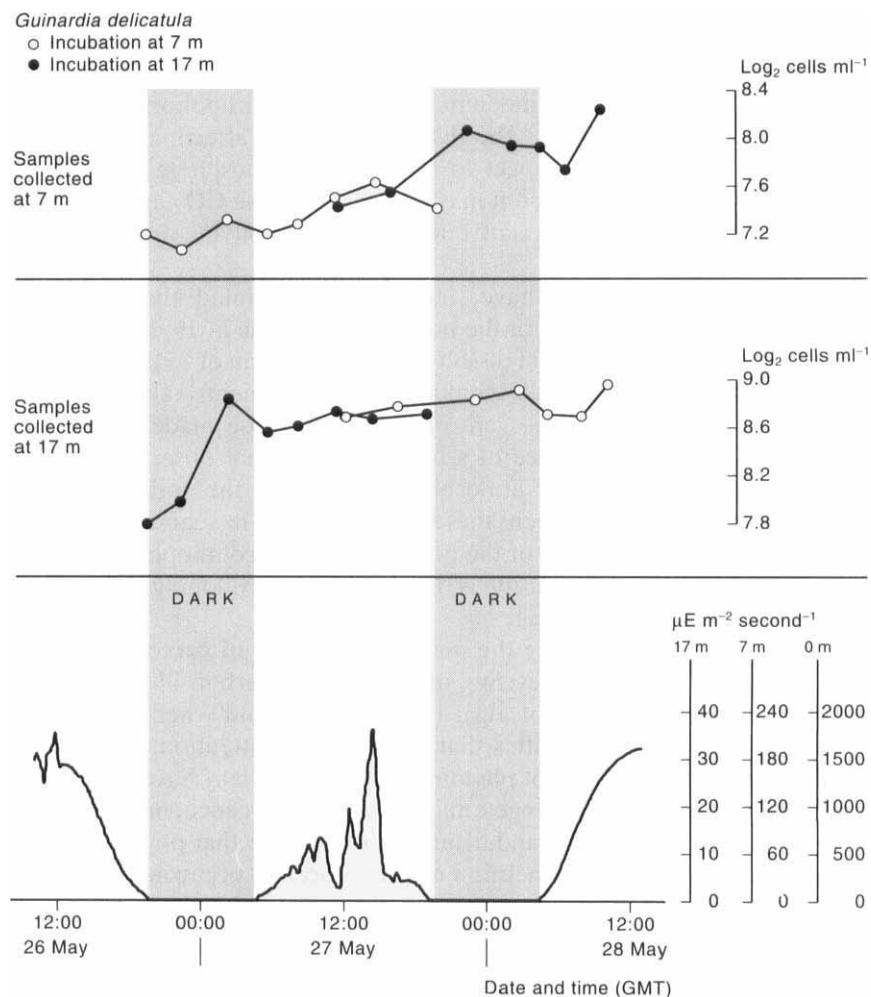


Figure 17 Changes in cell number of the diatom, *Guinardia delicatula*, when naturally occurring phytoplankton populations from 7 and 17 m at a station in the Irish Sea were enclosed in sterile plastic bags and returned to either 7 or 17 m for incubation. Sampling was carried out with the incubation bags remaining at depth. *G. delicatula* was the dominant species at 17 m and was common at 7 m. At 17 m, the *G. delicatula* population underwent a synchronized doubling during the dark period. Although an increase in cell numbers was also recorded at 7 m, it did not amount to a doubling of the population. After 24 h, new samples were taken from the water column. At both depths, the numbers of *G. delicatula* in the incubation bags after 24 h were similar to those in the water column suggesting that the changes recorded in the bags reflected those occurring in nature. The sample taken from the water column at 7 m after 24 h was enclosed in a plastic

with the pycnocline are essentially unialgal as was the case for the *Chrysochromulina polylepis* bloom recorded in the open Kattegat in 1988 (Kaas *et al.*, 1991).

There has been considerable scientific discussion as to whether these subsurface chlorophyll peaks represent accumulations of senescent and moribund phytoplankton sinking out of the water column (Bienfang *et al.*, 1983; le Fèvre, 1986) or represent active populations. However, the presence of actively photosynthesizing phytoplankton and/or high concentrations of grazers in association with these pycnocline peaks has been demonstrated on a number of occasions (Holligan *et al.*, 1984; Kiørboe *et al.*, 1990a; Richardson and Christoffersen, 1991; Nielsen *et al.*, 1993a). Active photosynthesis is, of course, not necessarily proof of *in situ* growth of phytoplankton along the pycnocline. Although fewer studies have examined growth than photosynthesis in subsurface chlorophyll peaks, there is also evidence that some species grow better at depth within the water column.

Heath (unpublished data) took samples from a subsurface phytoplankton peak at 17 m dominated by *Guinardia delicatula*. After placing them in sterile plastic incubation bags, he returned one sample to the sampling depth and one to 7 m. He also took samples from 7 m where *G. delicatula* was also present but at lower concentrations and treated them in the same manner as those taken from 17 m. All incubation bags were fitted with plastic tubes which extended up to the ship's deck, thus allowing sampling from the incubation bags without removal of the incubation bags from the incubation depths. The results (Figure 17) showed better growth in terms of increase in cell numbers in the 17 m samples both for those samples taken from 17 m and those taken from 7 m.

While this growth may not, strictly speaking, be "rapid" because of the limited *in situ* photon flux densities recorded at the pycnocline, there appears to be the potential for many of the phytoplankton biomass accumulations observed at the pycnocline to be the result of *in situ* growth. Thus, we may consider them as phytoplankton "blooms". Quantification of the extent of these pycnocline "blooms" and their importance in terms of the overall carbon fixation by phytoplankton is difficult as this pycnocline layer is often very narrow and difficult to sample. However, Richardson and Christoffersen (1991) estimated that pycnocline blooms

bag and transferred to 17 m. Similarly, the 17 m sample was incubated at 7 m. During the second incubation period, there was again a greater increase in *G. delicatula* cell numbers at 17 m (i.e. sample taken from 7 m) than at 7 m (sample taken from 17 m). These results indicate faster *in situ* growth for *G. delicatula* at 17 m than at 7 m. Light measurements at the various depths and at the surface were made using a cosine collector. (M. R. Heath, unpublished data.)

in the Kattegat were responsible for approximately 33% of the primary production occurring in this region. On a cruise in the North Sea in May 1992, Richardson *et al.* (unpublished data), recorded chlorophyll concentrations in association with the pycnocline of $>10 \mu\text{g l}^{-1}$. At a number of stations, these workers estimated that the photosynthesis occurring within the pycnocline peak accounted for approximately 75% of total water column primary production (Figure 18).

As indicated above, these subsurface "blooms" can be dominated by single species. It is not only harmful species that can come to dominate in these subsurface blooms. However, it is interesting to note that there are a number of harmful phytoplankton that often appear in association with the pycnocline. Examples of such phytoplankton include *Alexandrium* sp. (Anderson and Stolzenbach, 1985; Carreto *et al.*, 1986; Yentsch *et al.*, 1986), *Gyrodinium aureolum* (Holligan, 1979; Lindahl, 1983, 1986; Richardson and Kullenberg, 1987; Dahl and Tangen, 1993) and *Chrysochromulina polylepis* (Dahl *et al.*, 1989; Kaas *et al.*, 1991). In some cases (see, e.g., Lindahl, 1986; Richardson and Kullenberg, 1987; Dahl and Tangen, 1993) it appears that these pycnocline blooms may provide the "seed" population that gives rise to the exceptional or harmful coastal blooms. A mechanism for this seeding appears to be that the subsurface phytoplankton population becomes mixed into surface waters in frontal zones where stratified and mixed waters meet (Holligan, 1979). Given the proper combination of wind and current conditions, these populations can then be transported inshore (Dahl and Tangen, 1993). Thus, an important point to note with respect to the exceptional blooms that attract so much attention in surface waters at coastal sites is that these blooms are not always initiated at the geographic location where they are observed (see Section 5.1).

It is not known why phytoplankton sometimes appear to "bloom" under the low light conditions associated with the pycnocline. However, Richardson *et al.* (1983) argued, on the basis of a literature survey of data relating to the light requirements for growth of various marine phytoplankton species, that dinoflagellates, in general, have a relatively low light compensation point for growth (mean $6.6 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and that, on average, growth saturation for this class occurs at about $47 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ in laboratory studies (Figure 19). Thus, the phytoplankton class most often associated with harmful and toxic blooms (see Table 1) may have a light requirement that is best met when these phytoplankton are in an environment with a relatively low light climate and with limited extremes in the photon flux densities occurring during the day. Such a light climate can often be found near the pycnocline in temperate waters. Thus, although conventional wisdom argues that surface waters with high light intensities should be the most conducive to

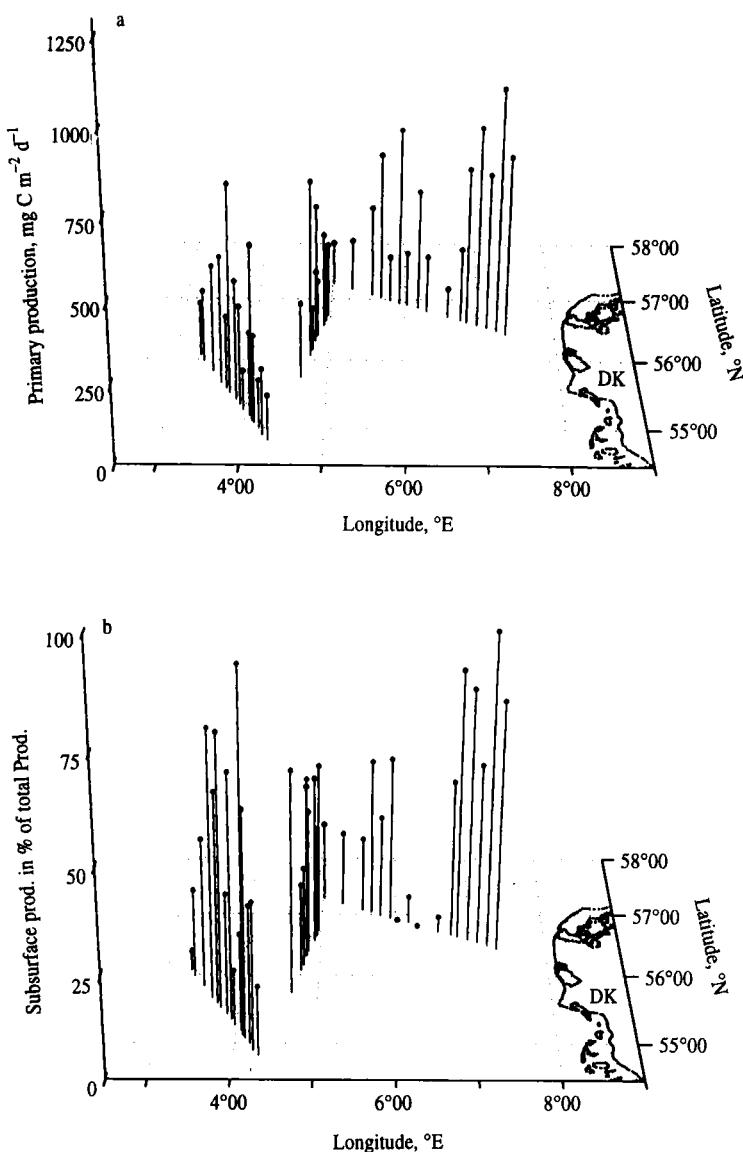


Figure 18 Water column primary production (a) and the percentage of total water column production estimated to occur in the subsurface chlorophyll peak (b) at various stations in the North Sea in May 1992 (K. Richardson *et al.*, unpublished data.)

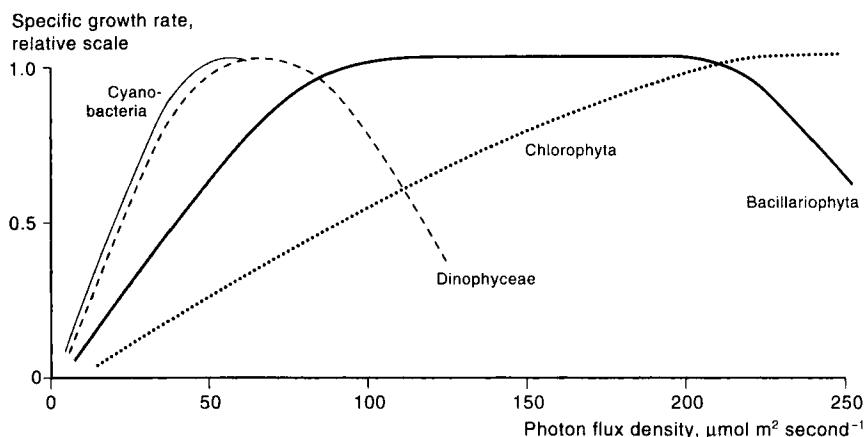


Figure 19 Relative specific growth rates plotted as a function of photon flux density in four major taxonomic groups of marine phytoplankton. (After Raven and Richardson, 1986.)

phytoplankton growth, many dinoflagellates (harmful and non-harmful alike) may actually "prefer" the conditions found further down in the water column.

In laboratory studies, it has been shown (Rasmussen and Richardson, 1989) that the toxic dinoflagellate *Alexandrium tamarensis* (formerly *Gonyaulax tamarensis*) actively accumulates at the pycnocline in an artificial water column when it is introduced in the water column below the pycnocline. When introduced above or in the absence of a pycnocline, the algae accumulated at the surface of the water column where photon flux densities were highest. By adding dye to the surface waters to reduce the incident photon flux density at the pycnocline, these workers showed that the accumulation at the pycnocline was not caused by an inability of the organisms to cross the density gradient. When the dye was present, the dinoflagellates penetrated the pycnocline and concentrated in the high-light surface waters (Figure 20). Thus, it would appear that this organism actively concentrates at a pycnocline if certain conditions concerning light availability are met.

There could be some advantage to such a strategy in nature for an obligate autotroph in a stratified water column as nutrients will normally be available from waters below the pycnocline. Thus, accumulation at a pycnocline where a minimal light requirement is met will optimize the chances of being in the part of the water column where there is the greatest chance of having access to adequate nutrient and light supplies. It is not known how widespread the response observed in *A. tamarensis* is within the phytoplankton flora but there is the suggestion of a similar response

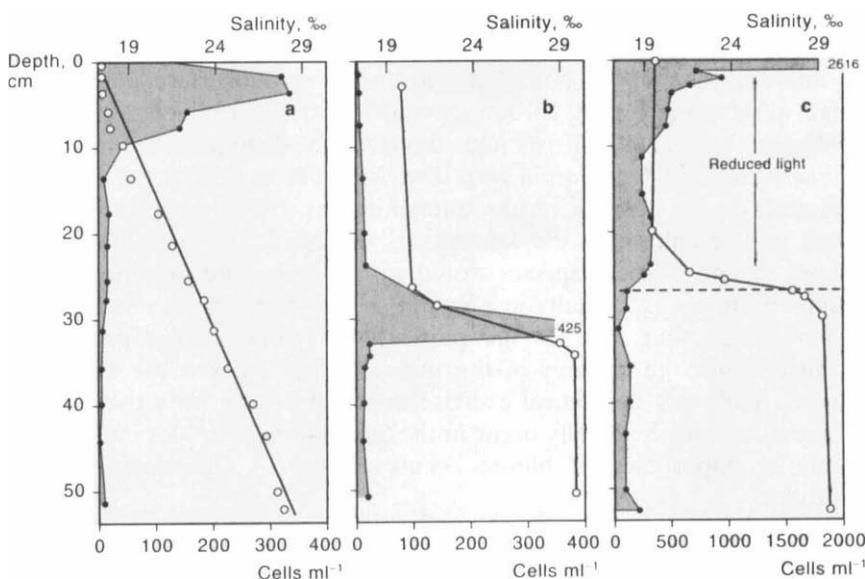


Figure 20 Salinity and *Alexandrium tamarensense* depth distribution profiles in: (a) an artificial water column with gradually increasing salinity from 19‰ near the surface to 29‰ at the bottom. (b) Heterogeneous water column with a salinity difference across the halocline of 10‰. (c) The same water column as in (b) but with the addition of food colour above the pycnocline. Areas shown above the stippled line represent the region where food colour reduced the incident light. ●, Concentration of cells; ○, salinity. (After Rasmussen and Richardson, 1989.)

by the dinoflagellate *Gyrodinium aureolum* (Nielsen *et al.*, 1993a), an organism which has been associated with numerous fish kills (Tangen, 1977; Jones *et al.*, 1982; Dahl and Tangen, 1993).

4.3. Tropical and Subtropical Regions

Cushing's (1959) model of phytoplankton bloom development in open tropical waters suggests the occurrence of only low biomass and very little seasonal fluctuation in these biomasses. However, many of the considerations relating to phytoplankton bloom development at the pycnocline in temperate regions are probably also applicable to tropical regions where it is common that the largest phytoplankton concentrations observed in the water column are located at depth and in association with a pycnocline or nutricline (Jochem and Zeitzschel, 1993; Michaels *et al.*, 1994).

While numerous studies in open tropical waters have indicated the presence of subsurface phytoplankton peaks, little effort has been devoted to quantification of the potential role that these subsurface populations might play in the overall carbon dynamics in tropical regions. However, Goldman *et al.* (1992) isolated three large diatoms (*Stephanopyxis palmeriana*, *Pseudoguinardia recta* and *Navicula* sp.) from the Sargasso Sea and, on the basis of results concerning the growth characteristics of these phytoplankton in the laboratory, suggested that a single 21 day bloom of one of these species would supply the entire new production estimated to occur annually in a region such as the Sargasso Sea. For *S. palmeriana*, about 50% of the particulate organic carbon production occurred after the cultures of the organism had entered the stationary phase. While this theoretical exercise does not demonstrate that blooms of these organisms actually occur in the Sargasso Sea, it does indicate the potential importance of bloom events on carbon dynamics at these latitudes.

Recent studies suggest also that bloom formation in surface waters of the tropical oceans may be much more predictable than previously thought. Longhurst (1993) used coastal zone colour scanner (CZCS) satellite images to examine the timing of tropical surface water blooms occurring in the tropical oceans. He identifies different patterns for the tropical Pacific, Atlantic and Indian Oceans and relates these patterns to the different hydrographic regimes that dominate in the three regions. Generally, offshore tropical waters have not been considered as sites for exceptional/harmful phytoplankton blooms. However, the recent demonstration by Hawser and Codd (1992) of toxicity associated with a bloom of *Trichodesmium thiebautii* in tropical waters suggests that these regions also experience blooms that would be considered as exceptional or harmful if they occurred in an area where they attracted human attention.

4.4. Arctic and Antarctic Regions

The Arctic and Antarctic regions, also, have not really been considered as sites for the occurrence of exceptional/harmful phytoplankton blooms. Again, however, the lack of reports of such blooms probably reflects the fact that their occurrence would be unlikely to interfere with any human activities. Support for this assertion comes from the fact that the dominant phytoplankton in the spring bloom in regions of both the Arctic and Antarctic is often reported to be *Phaeocystis* sp. (Wassmann *et al.*, 1990; Smith, 1993)—a genus considered to be an exceptional/harmful bloom former in temperate waters. While there are differences in the timing and

characteristics of the spring bloom between regions (see, e.g., Wassmann *et al.*, 1991), the general pattern of a single bloom has been observed in open waters in a number of Arctic (e.g. the Greenland Sea: Smith, 1993; arctic Canada: Hsiao, 1988; Barents Sea: Wassmann *et al.*, 1990) and antarctic regions (i.e. western Ross Sea: Nelson and Smith, 1986; Bransfield Strait: Smetacek *et al.*, 1990). Nevertheless, it is increasingly apparent that such single peaked vernal blooms do not occur at all polar localities and that the open polar waters may not be responsible for as much primary production as previously assumed (Smetacek *et al.*, 1990; Codispoti *et al.*, 1991).

It is now accepted that phytoplankton blooms occur sporadically in association with hydrographic events or features throughout much of the year in many polar regions. In particular, there is now increased awareness concerning the role of the ice-edge and the occurrence of blooms. Niebauer (1991) has estimated that approximately 7% of the world's oceans are subject to the advance and retreat of sea ice. The melting of sea ice can stimulate phytoplankton blooms by promoting stability in the nearby water column through the delivery of a layer of relatively fresh water to the region. Thus, blooms can occur locally in the open waters bordering the ice-edge (Conover and Huntley, 1991; Niebauer, 1991).

Even more dramatic than the blooms occurring in association with melting ice, is the occurrence of phytoplankton blooms associated with ice formation (Smetacek *et al.*, 1992). Sakshaug (1989) termed such blooms "superblooms" as the concentrations of chlorophyll recorded in them can exceed $100 \mu\text{g l}^{-1}$. Such blooms have been recorded in the Weddell Sea on a number of occasions (Figure 21). If blooms of such magnitude were occurring in coastal regions of the more densely populated temperate lands, they would almost certainly be considered as being exceptional.

Smetacek *et al.* (1992) examined a "superbloom" of centric diatoms (*Thalassiosira antarctica*, *Porosira pseudodenticulata* and *Stellarima microtrias*) associated with ice platelets underlying pack ice. The maximum chlorophyll concentration recorded in this bloom was $220 \mu\text{g l}^{-1}$ and the diatom cells appeared not to be attached to the ice platelets. The bloom covered an area of approximately $20\,000 \text{ km}^2$. These workers argue that drifting platelet ice offers an ideal habitat for localized algal blooms and that phytoplankton blooms occurring in association with platelet ice under pack ice provide a potentially important food source for grazers (krill) during periods when the rest of the Weddell Sea is at its most barren.

The relationship between ice algae and the open water phytoplankton blooms described by Cushing's (1959) theoretical model is not clear. However, there is at least some evidence that ice algae may "seed" the water column with phytoplankton prior to the spring bloom (Michel *et al.*, 1993). Thus, the importance of algal blooms occurring in association with

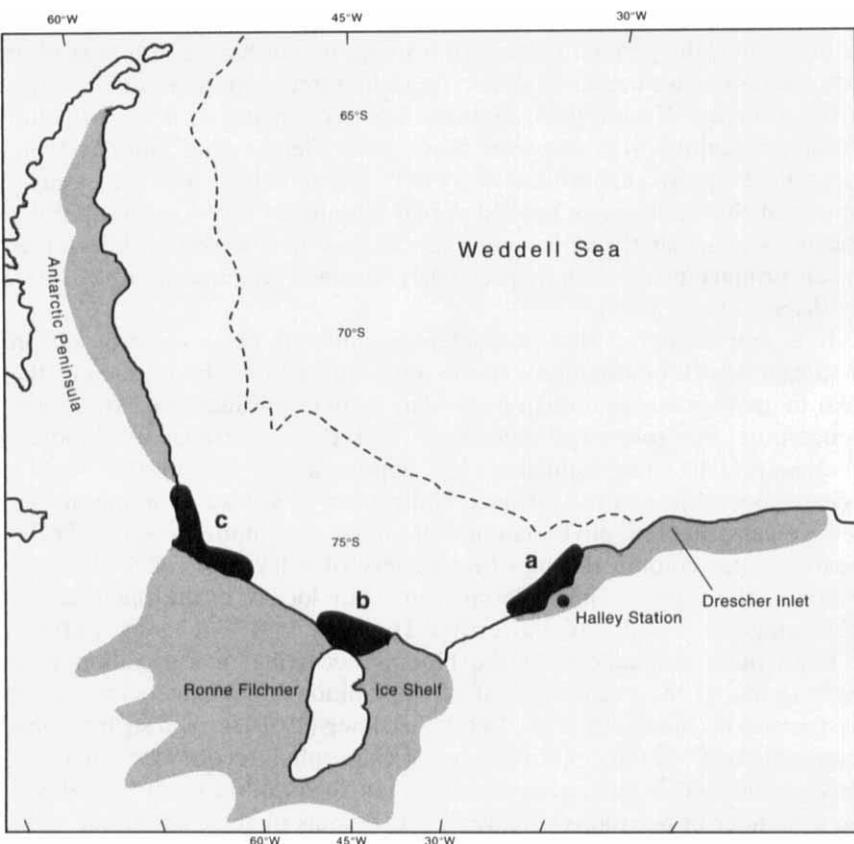


Figure 21 Map of the Weddell Sea. Shaded areas indicate localities of superblooms observed in: (a) October/November 1986 by Smetacek *et al.* (1992); (b) February/March 1983 by Sakshaug (1989); and (c) February/March 1968 by El-Sayed (1971). Dotted areas indicate floating ice shelves, the likely production sites of platelet ice. The stippled line represents the 1000 m isobath. (After Smetacek *et al.*, 1992.)

the edges of the ice pack may be much more important to total productivity and the structure of polar ecosystems than previously realized.

The data relating to the distribution of algal blooms in time and space discussed above suggest that phytoplankton blooms can and do occur whenever and wherever adequate light and nutrient conditions for the bloom species are coincident. In addition to occurring in surface waters, the examples cited above indicate that appropriate conditions for some phytoplankton blooms can also be found, at least at times, at such unlikely sites as under ice cover and in association with hydrographic features deep

in the water column. Exceptional or harmful phytoplankton blooms have most often been recorded in relatively densely populated coastal areas. However, there is at least circumstantial evidence that such blooms are occurring—but go unnoticed—in more remote areas such as the open waters of the tropics and in polar regions.

5. BLOOM DYNAMICS WITH SPECIAL REFERENCE TO EXCEPTIONAL/HARMFUL SPECIES

5.1. Bloom Initiation

In the post-mortem following many exceptional or harmful bloom events, unusual wind/weather/hydrographic conditions are identified as having preceded or accompanied the bloom in question (Cosper *et al.*, 1989; Maestrini and Granéli, 1991; Rhodes *et al.*, 1993). Often, it is not possible to identify a direct (cause and effect) link between the unusual event and the bloom. However, regions exhibiting specific hydrographic conditions (such as coastal upwellings and river discharge areas) are often identified as regions susceptible to phytoplankton blooms (Fraga, 1993). The association of harmful bloom species and specific hydrographic phenomena such as pycnoclines and coastal upwelling features has led to the suggestion that some of the predicted hydrographic changes which would be associated with climate change (global warming) may increase the occurrence of the toxic dinoflagellate, *Gymnodinium catenatum*, along the Galician coast (Fraga and Bakun, 1993).

In some cases, it appears that the wind, weather, tidal or other hydrographic conditions have been related to initiation of nearshore blooms by delivery of the organism into the bloom region (Balch, 1981; Lindahl, 1986, 1993; Richardson and Kullenberg, 1987; Dahl and Tangen, 1993; Delmas *et al.*, 1993; Keafer and Anderson, 1993; Taylor *et al.*, 1994). In some situations, large concentrations of phytoplankton may be transported inshore so that one can say that the bloom, itself, is advected to the coastal site. In other cases, it may be more appropriate to speak of a “seed” population being transported to the coastal site. In addition to transport of phytoplankton blooms from offshore to inshore regions, long-shore transport of blooms from one coastal region to another has also been recorded (Franks and Anderson, 1992).

Coastal blooms of *Gyrodinium aureolum* (see Section 3.3.7) may often result from advection of an offshore population to the coast (Lindahl, 1986, 1993; Richardson and Kullenberg, 1987; Dahl and Tangen, 1993).

This species is known to be associated with shelf sea fronts where it first occurs in dense concentrations at the pycnocline (see Section 4) and later blooms in surface waters associated with the front. It is the blooms associated with surface waters at or near the front that can be advected under the proper wind conditions towards shore. That some coastal blooms of this organism have an offshore origin can often be seen in the salinity characteristics of the associated water (Figure 22).

A number of other potentially harmful dinoflagellates are also known to form pycnocline and surface blooms in association with offshore frontal regions. For a number of these species, there are specific coastal bloom incidents for which the source population can be traced to an offshore bloom. Rasmussen and Richardson (1989) suggested that some dinoflagellates may be adapted to particularly exploit subsurface (pycnocline) conditions (see Section 4). Dinoflagellates represent the phytoplankton group most often associated with harmful and toxic blooms (see Table 1). Thus, this mechanism of bloom initiation in coastal waters whereby blooms or seed populations of phytoplankton are advected onshore from offshore sources may be even more important for the initiation of exceptional/harmful blooms in coastal waters than commonly realized.

There may also be a link between pycnocline populations (blooms) of phytoplankton in offshore stratified waters and coastal blooms of harmful phytoplankton belonging to taxonomic groups other than the Dinophyceae. The observation of dense pycnocline concentrations of *Chrysochromulina polylepis* in the Kattegat and Skagerrak combined with the sudden appearance of the organism in Gulmar Fjord along the Swedish west coast during the 1988 *C. polylepis* bloom in this region has caused some workers (Kaas *et al.*, 1991) to speculate as to whether the coastal bloom may have been initiated by upwelling and advection of a pycnocline population into the coastal region. In any event, it seems clear that the *C. polylepis* bloom in coastal waters was transported along the Scandinavian coast by the Norwegian Coastal Current (Figure 23). Hydrographic influence on the location of this bloom is also evident from the fact that the bloom suddenly appeared in surface waters of the open Skagerrak in mid-May. This was presumably caused by westerly winds in this period which caused a reduction in the outflow of water from the Skagerrak in the Norwegian Coastal Current. Thus, waters in the Norwegian Coastal Current were redirected from the coast forming a gyre in the open Skagerrak.

A number of toxic phytoplankton species (for example, *Alexandrium* spp.; *Pyrodinium* and *Chattonella*) form resting cysts that settle out of the water column. These cysts can be resuspended in the water column and/or transported from one region to another through hydrographic processes. Thus, it is not only blooms or seed populations comprised of active

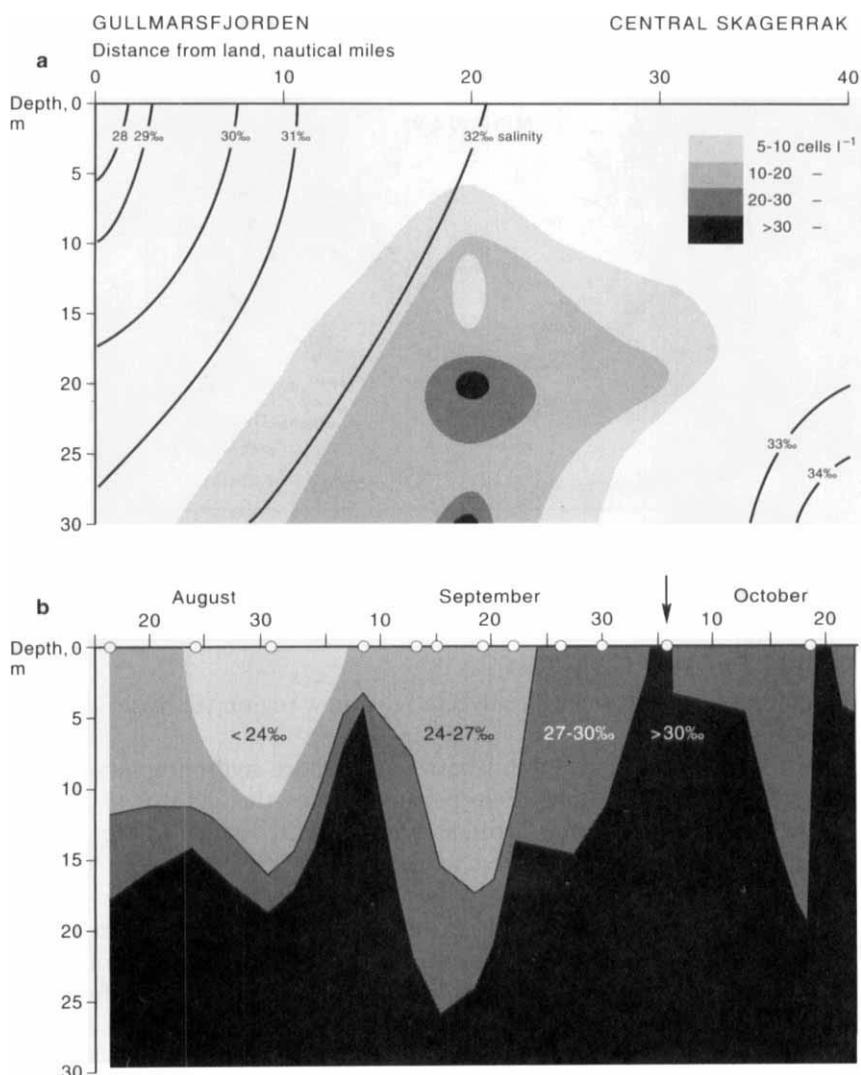


Figure 22 (a) Vertical and horizontal distribution of *Gyrodinium aureolum* (cells l^{-1}) and salinity (‰) along a transect running westward from Gullmarfjorden (Swedish west coast) on 28 and 29 August 1983. (b) Salinity in Gullmarfjorden in 1983. Dots on time axis indicate sampling dates. The arrow shows when *G. aureolum* was found. (After Lindahl, 1986.)

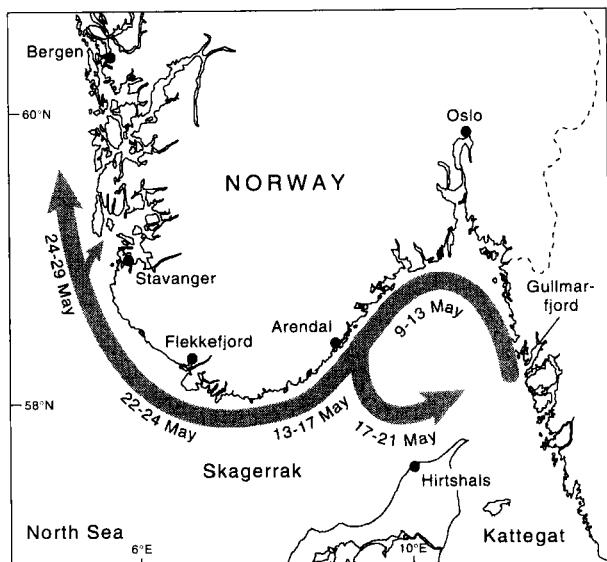


Figure 23 Dates of appearance of *Chrysochromulina polylepis* along the Swedish and Norwegian coasts in 1988. The organism was first observed in Gullmar Fjord on 9 May. (After Dahl, 1989.)

phytoplankton cells that can be advected to a new region via hydrographic processes.

Quantifying the relationship(s) between offshore hydrographic events and the initiation of coastal blooms is hampered by the fact that the focus of studies on harmful blooms is often geographically limited to the bloom site itself, and temporally limited to the period after the onset of the bloom. These limitations obviously do not allow for a description of the mechanisms by which offshore and inshore bloom events may be related. In order to examine these mechanisms more closely, long-term studies are needed in which the advection of phytoplankton (both harmful and non-harmful) from specific hydrographic features is examined in relation to local wind and weather conditions. Identification of the forcing conditions required to transport offshore phytoplankton blooms inshore is necessary in order to be able to predict which offshore events can be of potential coastal significance.

5.2. Bloom Composition

The real enigma with respect to phytoplankton blooms relates not to the fact that they occur but rather to the factors that control which species

will bloom at a given time and place. During recent years there has been an increased appreciation of the fact that individual phytoplankton species have different requirements and responses to the physical environment. These differences have, perhaps, been best studied with respect to requirements for light and different strategies for light adaptation in phytoplankton (Richardson *et al.*, 1983) and both "high light" and "shade" species have been identified. In addition, there is some indication of a pattern with respect to the responses to light availability of the most common taxonomic groups of marine phytoplankton (see Figure 19).

There is also a general appreciation of the fact that different species have different requirements for macronutrients (see discussion and references in Section 3). Kiørboe (1993) points out that size of phytoplankton cells is vitally important to the uptake of nutrients (diffusion-limited nutrient uptake is proportional to $1/\text{cell radius}^2$). Thus, on the basis of size alone, differences in nutrient requirements for different phytoplankton species can be predicted. Superimposed on the limitations/opportunities that size places on the cell with respect to the nutrient environment, are the various taxonomic requirements (diatoms have, e.g., an obligate silicon requirement) and individual or taxonomic requirements for various micronutrients. Our overall understanding of the various phytoplankton species' requirements and tolerances with respect to micronutrients is at a very primitive stage. However, it is clear that there are differences between species in terms of, for example, vitamin (Guillard *et al.*, 1991; Granéli *et al.*, 1993; Honjo, 1993) and trace metal (Sunda, 1989; Price and Morél, 1991; Honjo, 1993) requirements.

At present, it is sometimes possible in the aftermath of a harmful phytoplankton bloom to argue or show that the environmental conditions at the time of the bloom development were especially well suited to the individual requirements of the bloom organism (Maestrini and Granéli, 1991). However, it will not be possible to develop accurate predictive models for the occurrence of harmful phytoplankton blooms until a much better understanding of all of the different requirements that individual species or groups of species have with respect to their environment and the interaction of these requirements with one another. In theory, it should, ultimately, be possible to identify a "fingerprint" for each species or group of species which describes the total set of requirements and tolerances for each species and group of species. Matching the environmental conditions at any given time with the various "fingerprints" in our phytoplankton catalogue would form the basis of a predictive model concerning blooms of individual species but much work is still required to describe the more subtle requirements of individual species.

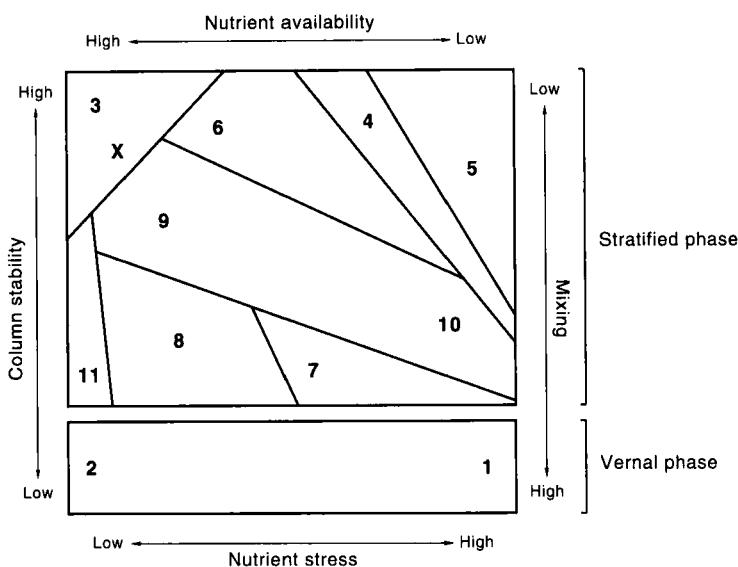


Figure 24 Matrix showing the most likely phytoplankton assemblages as a function of nutrient availability and turbulence during the vernal (spring) bloom and the summer stratified period in a lake system. Assemblages are as follows: 1, *Asterionella*, *Melosira italica*; 2, *Asterionella*, *Stephanodiscus astraea*; 3, *Eudorina*, *Volvox*; 4, *Sphaerocystis*; 5, *Chrysophytes*; 6, *Anabaena*, *Aphanizomenon*; 7, *Tabellaria*, *Fragilaria*, *Staurastrum*; 8, *Melosira granulata*, *Fragilaria*, *Closterium*; 9, *Microcystis*; 10, *Ceratium*; 11, *Pediastrum*, *Coelastrum*; 12, *Oscillatoria agardhii*. (After Reynolds, 1980.)

5.3. Bloom Species Succession

Given the diversity of the marine phytoplankton flora (see Table 1), the description of "fingerprints" describing the various macro- and micronutritional and light requirements for each species is a formidable task indeed. In the short term, valuable information may be gained by elucidating the environmental conditions that lead to the development of different assemblages of phytoplankton species. The seasonal succession of phytoplankton assemblages has been rather better studied in limnological than in marine systems (e.g. Reynolds, 1980, 1984), probably because the easy accessibility of many lake systems has allowed accumulation of more detailed and longer time series of data relating to phytoplankton speciation than has been possible for most marine systems. Already in 1980, Reynolds was able to present a probability matrix identifying the various phytoplankton assemblages and relating their occurrence to nutrient and mixing conditions in the spring bloom period and when the water column

was permanently stratified in (temperate) limnological systems (Figure 24).

While our understanding of phytoplankton assemblage succession is not as advanced for marine systems as is the case for fresh waters, some general patterns are now obvious. Figure 9 shows the distribution of different sizes of phytoplankton in surface waters of the Kattegat in different time periods extending over the periods of the establishment and breakdown of strong summer stratification in these waters. The largest cells are associated with the spring bloom period. While small cells dominate during the period of summer stratification, there are also events during this period when larger cells briefly reappear.

The seasonal succession of large (mostly diatom) cells during the spring bloom followed by smaller cells has been identified and related to hydrographic features (i.e. nutrient and light availability induced by different hydrographic features) by a number of workers (Cushing, 1989; Kiørboe, 1993; Légendre and Rassoulzadegan, 1995). Kiørboe (1993) has also presented evidence that the occurrence of large cells during the period of summer stratification may be related to hydrographic events which, for short periods, create mixing and nutrient conditions that mimic those found at the time of the spring bloom. Thus, a general pattern of phytoplankton succession, at least for seasonally stratified waters, has emerged but not yet at the species level.

For some particularly well-studied marine systems, it is also possible to describe succession in terms of dominating phytoplankton assemblages. One such system is Narragansett Bay, where the relatively long database on species distributions (see Table 4) makes generalizations concerning species succession patterns possible. Smayda and Villareal (1989) have examined the 1985 "brown tide" bloom of *Aureococcus anophagefferens* from the long-term data available. They argue that a characteristic feature of phytoplankton succession in this region is the existence of an "open" phytoplankton niche during the summer in which flagellates or other (mostly) non-diatomaceous phytoplankton often form blooms. They point out that there is poor predictive capability with respect to which species will come to dominate within this open niche and that "predictability is also compromised by significant inter-annual variations in key determinants of niche availability and occupancy, such as factor interactions and hysteresis effects from winter-spring diatom bloom dynamics". With respect to the *Aureococcus* bloom, they point out that a number of other species bloomed concurrently with this species. In all, they conclude that there was a succession of bloom events in Narragansett Bay during the summer of 1985 that involved 15 different species (Figure 25). For two of these species (*Minutocellus polymorphus* and *Fibrocapsa japonica*), they argue that the bloom events were just as "novel" as in the case of

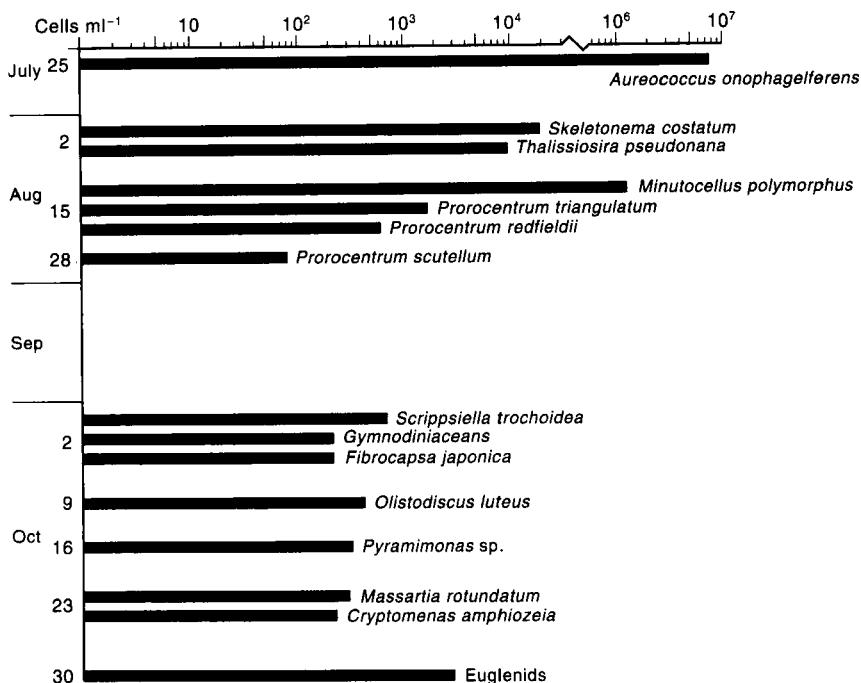


Figure 25 Timing and magnitude of maximal abundance of the major bloom species occurring at a station in Narragansett Bay during late summer and autumn 1985 (during a "brown tide" event—see text. (After Smayda and Villareal, 1989b.)

Aureococcus anophagefferens. In order to understand the dynamics of a harmful algal bloom such as the "brown tide" which occurred in Narragansett Bay, it is essential to understand the interactions between the different species and the factors which lead to their occurrence.

Often, reports of harmful algal blooms focus only on the organism in question and not on the other phytoplankton species present during the bloom. Thus, valuable information concerning the assemblages of phytoplankton which occur together and the conditions which lead to their occurrence may be lost. In times of limited economic resources for scientific research, studies involving the routine collection of taxonomic data concerning phytoplankton speciation often come under severe pressure. It is important to remember, however, that such data are crucial to a better understanding of phytoplankton assemblage succession and, ultimately, to the development of predictive models relating to the occurrence of "harmful" phytoplankton species.

5.4. Bloom Maintenance

In order to be maintained, the growth rate of the phytoplankton in a bloom must exceed the loss rate of phytoplankton in the population. Loss can occur by grazing or through cell lysis sinking or advection away from the bloom site. Various exceptional/harmful bloom-forming species have evolved mechanisms for reducing these loss terms and this may, at least in part, explain why these organisms form blooms.

It has already been pointed out that grazing impact can be important in the development of harmful algal blooms because some phytoplankton species appear to be unpalatable to herbivores (see Section 3). The limited grazing pressure on the unpalatable (often toxic) phytoplankters may be important in allowing large biomasses of these phytoplankton to develop.

Another mechanism by which grazing pressure may affect the development of phytoplankton blooms is by acting as a selection factor in phytoplankton species succession (Smayda and Villareal, 1989b; Olsson *et al.*, 1992). This can be demonstrated by taking the example from Narragansett Bay discussed above where Smayda and Villareal (1989) argued that grazing structure influences the species which occur in the "open" phytoplankton niche during summer months. In particular, they argued that copepod predation determines whether *Skeletonema*, dinoflagellates or other phytoplankton groups will dominate. Thus, factors affecting the abundance of copepods will also impact algal speciation. As harmful algae are not equally distributed among the various phytoplankton groups (see Table 1), grazing structure, by affecting the relative abundance of various phytoplankton groups, will potentially also affect the probability of harmful blooms occurring. Detracting grazers and, thus, reducing grazing pressure is an obvious mechanism by which bloom loss factors may be reduced.

A more subtle strategy (Crawford and Purdie, 1992) for reducing loss factors which may be playing a role in the maintenance of some blooms may be a reduction in loss through advection. This reduction in the loss term may be brought about by vertical migration of the phytoplankton in the water column. It has been suggested (Garcon *et al.*, 1986) that *Alexandrium tamarense* blooms occurring in a tidally flushed embayment near Woods Hole were only able to bloom there because the phytoplankton were essentially confined to regions of the water column below the outflowing surface waters. Their argument is based on the observation that the growth rate of this organism is similar to the flushing rate of the embayment. Thus, if the phytoplankton were equally distributed in the water column, the loss rate through advection would be similar to the increase rate (through growth) of the bloom and increases in biomass should not be observed.

Yet another mechanism by which the maintenance of a particular phytoplankton species may be encouraged is by reduction of the competition for limiting resources experienced by the blooming organism. If nutrients are, for example, limiting, then inhibition of other phytoplankters that will be competing for the same nutrients will serve to optimize the growth conditions for the bloom organism and, thus, maximize the production rate or length of production period of the bloom-forming phytoplankter. Several exceptional/harmful bloom-forming species have been shown to have inhibitory or repressing effects on other phytoplankton species (i.e. *Gymnodinium aureolum*: Arzul *et al.*, 1993; *Heterosigma akashiwo*: Honjo, 1993). Thus, this mechanism of optimizing the production conditions for the bloom organism may be important in the maintenance of some phytoplankton blooms where single species are dominant.

5.5. Bloom Termination and Fate of Bloom Products

As discussed above, a phytoplankton bloom will decline when the loss factors together exceed the increase factors (i.e. growth and/or advective accumulation of the phytoplankton bloom species). Usually, the immediate cause of bloom decline is a decrease in the growth rate of the bloom-forming phytoplankton species brought about by light and/or nutrient limitation of the bloom species—in other words, a change in the environmental conditions which matched the environmental “fingerprint” of the bloom species (see Section 4.2). Often, when physiological stress of the bloom-forming organism has begun and the bloom begins to decline, the process is hastened by bacterial, fungal or viral infestation of the phytoplankton cells (van Donk, 1989; Bruning *et al.*, 1992; Nagasaki *et al.*, 1994).

Generally speaking, the phytoplankton cells from declining phytoplankton blooms can meet two fates (assuming that they are not grazed): they can either sink out of the water column or lyse and release their contents to the surrounding water column. Flagellate blooms appear often to be degraded in the water column (Boekel *et al.*, 1992) while diatom blooms more often sink out of the water column (Smetacek, 1985; Cushing, 1992; Waite *et al.*, 1992a). Different diatoms have different sinking rates and it has been proposed (Waite *et al.*, 1992b) that sinking rate, in addition to being influenced by cell volume, may be affected by physiological state (as expressed by respiration rates).

Often, a sudden collapse or sinking of a diatom bloom is recorded (see, e.g., Cushing, 1992). Recent developments in the application of coagulation theory to phytoplankton cells occurring under bloom conditions

suggests that aggregation may be an important mechanism in terms of the sudden disappearance of diatom blooms (Jackson, 1990; Jackson and Lochmann, 1992). Essentially, it is argued that phytoplankton cells have an inherent natural "stickiness" that will allow them, under some conditions, to stick together (aggregate) upon contact with one another. The rate of the aggregation will be a function of the size, concentration and "stickiness" of the phytoplankton cells as well as the turbulent shear rate that makes the phytoplankton collide with one another. Kiørboe *et al.* (1990b) demonstrated that, under laboratory conditions, different phytoplankton species exhibit different degrees of "stickiness". In addition, age (physiological state) can influence "stickiness" within an individual species.

Jackson's (1990) model implies that a given phytoplankton population will, initially, grow exponentially. Ultimately, it will approach an equilibrium concentration ("critical concentration") where growth and coagulation (leading to sedimentation) will balance. Thus, according to this model, it ought to be possible to predict the maximum concentration that a given algal bloom will attain under various turbulent conditions. Kiørboe *et al.* (1994) compared the maximum concentrations of various algal species recorded during a spring bloom in a Danish fjord with the calculated "critical concentrations" for these species under the given conditions and found good agreement between the predicted and observed maxima in cell numbers for these species (Figure 26). Thus, they argue that aggregate formation controls the vertical flux (sedimentation) of phytoplankton blooms and sets an upper limit for the concentration of the phytoplankton cells.

Much work remains to elucidate the influence of, for example, bacterial and viral invasions on the "stickiness" of individual species before it will be possible to model the sedimentation of specific blooms. However, the application of coagulation theory to phytoplankton populations appears to provide the opportunity to describe the dynamics surrounding phytoplankton bloom culmination and sedimentation in much greater detail than previously possible.

6. SUMMARY AND CONCLUSIONS

Phytoplankton blooms are natural phenomena that play an important role in relation to carbon and energy flow as well as geochemical cycling in marine ecosystems. Phytoplankton growth will occur wherever and whenever adequate light and nutrient (both macro- and micronutrient) conditions occur. Blooms (accumulations of phytoplankton biomass) will

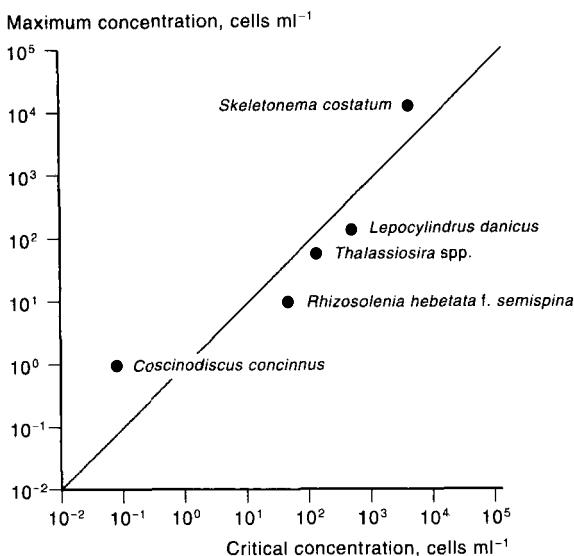


Figure 26 Maximum cell concentration of five diatom species during a study of the dynamics of the spring bloom in a Danish fjord plotted as a function of "critical concentrations" (Jackson, 1990; and see text). The line is $x = y$. (After Kiørboe *et al.*, 1994.)

result when the combined effect of population loss factors (grazing, advection and lysis or sedimentation) is less than the biomass accumulation due to growth of the phytoplankton and via advective processes. Until recently, it was assumed that adequate conditions for bloom development would only be found in surface waters where photon flux densities are greatest. It is now clear, however, that phytoplankton blooms also can and do occur under ice cover and at the base of the euphotic zone in regions where surface waters are nutrient depleted.

It is estimated (see Table 1) that the world's phytoplankton flora consists of approximately 4000 different species. Of these, about 200 species (i.e. approximately 6%) have been identified as causing "harmful" or "exceptional" (i.e. noticeable particularly to the general public through their effects) phytoplankton blooms. About 2% of the world's phytoplankton flora have been implicated as toxin producers. The toxins produced vary in their chemical structures and their effects but their public health implications are important as some are neurotoxins that can cause death at low concentrations and others are, apparently, carcinogenic. Much scientific attention is directed specifically towards elucidating the dynamics of harmful blooms—especially those in which toxic phytoplankton species

are implicated. However, there are no phylogenetic, physiological or structural features that are common to "harmful" phytoplankton and there is no obvious scientific basis to treat "harmful" bloom species as a distinct subset of the total phytoplankton flora.

A number of workers have suggested that there has been an increase in harmful phytoplankton blooms due to anthropogenic activities in recent decades. Owing to the subjectivity in identifying harmful blooms and the lack of relevant long-term comprehensive data sets, it is, for most areas, difficult to address quantitatively the question of whether or not a real increase in such blooms has occurred.

Harmful and toxic species are a small subset of the total phytoplankton flora and we do not know what the naturally occurring interannual variability is with respect to the relative frequency of occurrence of different phytoplankton species. Thus, it is often difficult—even when changes in the relative occurrence of harmful species can be identified—to ascertain what role anthropogenic influences may have had in producing the change. It is clear that harmful phytoplankton blooms occurred in prehistoric times so anthropogenic influence is certainly not a prerequisite for the occurrence of such blooms. Nevertheless, a number of mechanisms by which anthropogenic activities can, theoretically, affect (directly or indirectly) the occurrence of harmful blooms are discussed in this review. These include eutrophication, the use of pesticides which may influence herbivore abundance, and the distribution and transport of harmful species from one geographic region to another via ballast water or in connection with aquaculture activities.

The most interesting question with respect to phytoplankton blooms is not why they occur but, rather, what mechanisms control the species which occur at a given time and place. There is increasing appreciation of the fact that the marine environment provides many different niches that can be exploited by different phytoplankton species and that each species has its own specific combination of requirements to the external environment (light, macro- and micronutrients). Thus, it ought to, at least in theory, be possible to identify a "fingerprint" for each species that describes these external requirements. Matching the environmental conditions at any given time to the "fingerprints" of phytoplankton species potentially occurring in an area would provide a basis for predictive models concerning the potential development of harmful blooms. In practice, however, a total description of the environmental requirements of individual phytoplankton species lies in the far distant future. Nevertheless, understanding the factors that control phytoplankton species succession is crucial to the understanding of why and where harmful phytoplankton blooms occur and research into these factors ought to be an urgent priority.

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