28 Climate Change and Harmful Algal Blooms

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28.1 Introduction

Some authors have suggested that harmful algal blooms (HABs) are increasing throughout the world due to anthropogenic influences (Hallegraeff 1993). Others have stressed that climate variability may be an equally important contributor to the apparent increases (Sellner et al. 2003). Understanding the possible effects of climate change is therefore a critical requirement in the development of the risk assessments needed for the effective management of HABs. This chapter considers the effects of past, present and future climatic variability on HABs.

The one thing we are certain of regarding climate is that it is changing – and it always has been. The geological and historical records show alternations between periods of relative warming and cooling at all timescales: extremes of glaciated to ice-free conditions on scales of millions of years to shorter-term oscillations on scales of a few to tens of years, such as the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO). The last 1,000 years included periods as warm or warmer than now (at least in some regions) during the Medieval Warm Period (MWP), 550–1300 A.D., and colder than now during the Little Ice Age (LIA) 1300–1900 A.D.

A major scientific effort is currently underway coordinated by the International Panel on Climate Change (IPCC) to assess the extent of human impact on climate, through the burning of fossil fuels, etc. This work has resulted in a much greater appreciation of the complex nature of climate, where temperature is only one of many factors to be considered. This complexity imposes a high degree of uncertainty on the predictive models used. There is a clear and convincing scientific consensus that anthropogenically forced global warming is taking place, but the extent of future warming, especially in the next 100 years, remains uncertain. In considering possible effects on phytoplankton, it is important to realize that at least in some regions, recent global warming has so far involved mainly a warming of winter temperatures. Continued

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Ecology of Harmful Algae

warming could eventually lead to elevated summer temperatures; in the North Sea and northeastern Atlantic, this has already occurred (Edwards and Richardson 2004) with a recognizable impact on plankton.

Water temperature, light, and nutrients, are the main parameters affecting phytoplankton, including HAB species. Each species has a temperature window within which it can survive, and a range within this of low to optimal growth. These are vital factors defining the biogeographic boundaries within which a species can live. Seasonal variations in temperature may be important for determining when optimal growth can occur at any location. The direct effect of global warming – elevated water temperature – therefore may affect both the seasonal composition of the phytoplankton (e.g., increased growth in winter/spring-blooming species as winter temperature increases), including changes in seasonal succession, and the position of biogeographic boundaries (e.g., migration towards higher latitudes for warmer-water species as summer temperatures increase).

However, from physiological experiments it is known that many species show a robust tolerance for moderate shifts in temperature. Most HAB organisms are coastal/estuarine species that may be expected to tolerate at least moderate swings in temperature of several degrees on a daily basis. Their present-day occurrence, in part, is likely to reflect selection pressures from recent climatic oscillations (variations of several degrees average temperatures between the MWP and the LIA within the past 1,000 years). Therefore, temperature as such may not be the dominant factor in phytoplankton response to climate change; other, indirect effects need to be considered. These include:

Stratification increased temperature often causes increased stratification of the upper water column (e.g., favoring flagellates that can swim down to obtain dissolved nutrients from lower levels when surface water nutrients are depleted),

Upwelling climatic variations involve changes in oceanic circulation, including upwelling (e.g., Bakun 1990),

Freshwater run-off from land, and cloud-cover increased temperature often causes increased evaporation and atmospheric precipitation (rain and snow) with a consequent enrichment with nutrients of freshwater run-off from land to aquatic environments; increased cloud cover produced through the same process may reduce available light to the phytoplankton,

Feedback mechanisms blooms of algae take up more heat from the sun leading to a further enhancement of sea temperatures.

28.2 Evidence from the Past

Time-series data are required in order to assess variation in natural phenomena. For HABs, two main sources are important: long-term phytoplankton records, and the microfossil record in bottom sediments. The few available long-term plankton records show important variation in the frequency and intensity of HABs at the decadal time scale (e.g., the recurring blooms of *Karenia brevis* around Florida, Walsh and Steidinger 2001). Since climate also shows decadal variation, at least on a regional scale (e.g., ENSO, and the NAO), records of several to many tens of years are needed to reveal any convincing relationship between climate and HABs.

The ideal basic requirements for phytoplankton records would cover at least 30 consecutive years of consistent monitoring at a site of known HAB problems. The example from Florida cited above has provided the only such data published so far. Several other long-term records cover the required length of time, and presumably will contribute relevant data when published (e.g., from Rhode Island, USA, Sherkin Island, Ireland, the Skagerrak, and Helgoland, Germany). Most data relevant to the topic considered here has come from the Continuous Plankton Recorder (CPR) survey (Warner and Hays 1994; Reid et al. 1998). Although designed mainly to monitor zooplankton, and therefore only providing direct information for a number of larger HAB organisms, the CPR has routinely identified approximately 170 phytoplankton taxa since the 1950s throughout various regions of the North Atlantic.

Long-term plankton records thus provide very few examples linking HABs to climate variation. Most records of HABs cover too short a time period to allow statistically sound comparisons with climate. However, since HAB species are distinguished from other plankton only by their harmful effects to human health and economics, it is worth considering data on the interaction of *any* species of phytoplankton with climate. Also, the list of known causal species is being added to regularly, as more is learned about HABs.

Microfossils produced by some groups of phytoplankton accumulate in bottom sediments and provide an alternative source of integrated time-series data. The main group including HAB species is the dinoflagellates. These produce resting cysts (cysts) protected by fossilizeable cell walls that are strengthened with sporopollenin-like material (comparable to the walls of pollen grains) or calcareous material. The siliceous frustules of diatoms also may fossilize. The main limitation to the cyst record is that only around 10 % of dinoflagellate species are known to form cysts (Dale 1996) although this includes some HAB species. Dinoflagellate cysts, diatoms and other groups of microfossils also provide evidence of other forms of environmental change (e.g., eutrophication and marine pollution), and environmental micropaleontology is now an integral part of environmental sciences (Dale and Dale 2002).

As with plankton records, the greatest challenge is how to differentiate the various environmental signals.

While there certainly is strong evidence that increased phytoplankton biomass and algal blooms are associated with elevated nutrients in some regions of the world (Sellner et al. 2003), assessing larger-scale changes on regional ecosystems is more problematic. For example, while elevated anthropogenic effects in the North Sea have been reported, this has been accompanied by a period of marked climate change over the last few decades. Distinguishing the effects of anthropogenic eutrophication embedded in the climate variability is therefore extremely difficult and needs extensive baseline data. While there have been more studies focusing on the role of eutrophication and HABs, there has been limited work on the role of climate oscillations (Rhodes et al. 1993; Hales et al. 1998; Belgrano et al. 1999; Edwards et al. 2001) and very few on the impact of climate change (Reid et al. 1998; Beaugrand et al. 2002).

28.3 Results from Plankton Records

The relationship between long-term (50 years) phytoplankton changes and the NAO have been discussed in relation to (1) changes in West wind strength and hence water-column stability, (2) changes in sea-surface temperature (SST), and (3) changes in the oceanic inflow into the North Sea (Edwards et al. 2001). According to results from the Continuous Plankton Recorder (CPR) survey, at the regional to oceanic scale, climate variability and regional climatic warming appears to play a dominant role in the long-term changes in phytoplankton assemblages and total biomass (Reid et al. 1998; Edwards et al. 2001).

Regarding HABs and climate, it seems that oceanographic circulation is an important factor, and that changes in circulation patterns often are associated with decadal climate oscillations. The large phytoplankton biomass values and *Dinophysis* blooms recorded off the coast of Sweden in the late 1980s have been associated with inflowing Atlantic water associated with positive NAO values (Belgrano et al. 1999). This period also coincided with one of the most globally known and widely reported bloom events to occur over the last few decades. The *Chrysochromulina* bloom off the Norwegian Skagerrak coast in 1988 not only caused widespread ecological disturbances but was also estimated to have caused an economic loss for the fish farming community of approximately 10 million Euro (Skjodal and Dundas 1991). The bloom in this area was associated with relatively high temperatures and low salinities, resulting in highly stable conditions in the Norwegian Coastal current. This was again associated with the NAO index (Gjøsæter et al. 2000) and coincided with the timing of a regime shift in the planktonic ecosystem of the North Sea (Reid and Edwards 2001).

The NAO has also been implicated as a driver of upwelling-induced blooms along the Spanish coast (Fraga and Bakun 1993). Basin-scale circulation can also act as an effective factor for the transportation of potential HAB taxa. *Alexandrium* populations in the Gulf of Maine, for example, have been associated with transportation via coastal currents (Anderson 1997), and the devastating appearance of the neurotoxic red-tide organism *Karenia brevis* off North Carolina was also associated with current transportation (Tester et al. 1991). Regional climate change therefore, has important consequences for bloom events driven by circulation and meteorology.

While the causative role of changes in SST for long-term phytoplankton dynamics are still rather obscure, there is certainly evidence to suggest that changes in SST can cause a shift from diatoms to flagellates within the phytoplankton community structure. In the context of climate change and HABs this is important, as the majority of HABs are associated with noxious and toxic flagellate species. Recent studies have shown that rising SST has been associated with a shift from diatoms to dinoflagellates in the North Atlantic and North Sea (Edwards et al. 2001) in the southern North Sea (Hickel 1998) and in the Baltic Sea (Wasmund et al. 1998). Therefore, climatic warming may favor flagellate dominance in the phytoplankton community. Rising SST in the North Sea has also been correlated with the earlier appearance of dinoflagellates in the seasonal cycle. Changes in phenology of some dinoflagellate species have resulted in a shift forward of over a month from their typical seasonal peak, whereas the seasonal timing of diatoms has remained relatively static (Edwards and Richardson 2004). It is not yet known, however, why dinoflagellate seasonal timing is correlated with warmer temperatures and whether this is due to a direct physiological response or to an indirect response to SST via enhanced or earlier stratification. It also seems likely that an important environmental impact caused by climate change is an increase in the presence of haline stratification in regions susceptible to such changes, resulting in an increase in dinoflagellate bloom formation (Edwards et al. 2005). For example, in the Grand Banks region there has been an increase in the abundance of dinoflagellate species (notably *Ceratium arcticum*). These changes, since the early 1990s, have been linked to hydro-climatic variations, specifically increased stratification and stability in the region. These indicate a progressive freshening of waters in this region caused by regional climatic warming (Johns et al. 2003).

Recent macroscale research has shown that the increase in regional sea temperatures has triggered a major reorganization in calanoid copepod species composition and biodiversity over the whole North Atlantic Basin (Beaugrand et al. 2002). During the last 40 years there has been a northerly movement of warmer water plankton by 10° latitude in the Northeast Atlantic and a similar retreat of colder water plankton to the north. This geographical movement is much more pronounced than any documented terrestrial study, presumably due to advective processes. Rising SST may also have the potential to shift the biogeographical boundaries of certain phytoplankton species, which may include HAB taxa. However, there have been only limited studies in this area. Warmer-water species of the *Ceratium* genus have certainly been noted further north in the North Atlantic over the last few years (Edwards et al. 2006), and according to Nehring (1998), some thermophilic phytoplankton species have established themselves in the southern North Sea. In experimental studies the physiological response to climatic warming has been studied for a number of HAB taxa (Peperzak 2003). Climate-warming scenarios (expressed as an increase of 4 °C or more), coupled with water-column stratification, led to a doubling of growth rates of potentially harmful dinoflagellates of *Dinophysis* spp. and *Prorocentrum* spp. (Peperzak 2003). Long-term trends in the abundance of *Prorocentrum* spp., as well as the red-tide forming *Noctiluca scintillans,* have been correlated with SST in some regions of the North Sea (Edwards et al. 2006). Biogeographical boundary shifts mediated by climate change in phytoplankton populations, also have the potential in the future to lead to the occurrence of species with southern biogeographical affinities not yet considered to be detrimental in temperate regions.

28.4 Results from the Sedimentary Record of Dinoflagellate Cysts

Dinoflagellates account for many of the different forms of HABs, and their fossil record is a potential source of long-term records of HABs. Unfortunately for science, most toxic species do not produce fossilizeable cysts, and those that do are not always toxic. *Pyrodinium bahamense*, a species responsible for severe PSP in Southeast Asia, produces cysts with a fossil record of at least 20 million years, but seems not to be toxic in parts of its present-day range (e.g., the Caribbean). Reports from the fossil record of this species having caused mass mortality of birds (Emslie et al. 1996) and fish are therefore speculative. *P. bahamense* is a lagoonal species that often heavily dominates cyst assemblages at the present day without causing such dramatic effects. On the other hand, the fossil record is dotted with events such as fish kills, usually thought to have been caused by catastrophic shifts in salinity or oxygen content, for example through isolation of smaller parts of basins. Present day mass mortality of fish and birds is usually associated with species leaving no fossil record (e.g., *Prymnesium parvum* in Lake Koronia in Greece, reported by Moustaka-Gouni et al. 2004).

Long-term records seemingly linking climate change to HAB-producing species of *Alexandrium* have been reported from Atlantic and Pacific Canada (Mudie et al. 2002). When summer SST was up to 5 °C warmer than present during the late glacial–early Holocene, these authors showed a period of sustained high production of “red tide blooms” which strongly implicated global warming in the historical increase in the frequency of HABs. These reports were surprising, since comparable fossil cysts have not been recorded in many studies of sediments from other regions prone to toxic blooms of *Alexandrium*. Follow-up work instead suggests these cysts may be the remains of inner walls of calcareous cysts belonging to a different species with no known connections to HABs (Head et al. 2006).

The distinctive fossilizeable cyst of the HAB species *Gymnodinium catenatum* seems to be a likely candidate for tracing past blooms, but results from the first attempts were surprising. Dale et al. (1993) showed records of very similar cysts from the past few thousands of years in the Kattegat/Skagerrak region of Scandinavia. The species was not recorded from recent plankton there, and the nearest present-day distribution along the coasts of northern Spain and Portugal suggested its need for warmer water. Two periods of unusually high concentrations of these cysts were identified: around 4500 years B.P. during warmer climate, and between 1000 and 500 B.P. during the warmer MWP. This was presumed to pre-date causative human impact, and since the species waned as the cooler LIA set in, and other changes in the cyst assemblage suggested climatic warming, this was identified as the most likely cause of the 'bloom periods' (Dale et al. 1993; Dale and Nordberg 1993; Thorsen and Dale 1998). Subsequent biological studies, however, have shown this to be a non-toxic species separate from, but very similar to *G. catenatum* (Ellegaard and Moestrup 1999). Records of actual *G. catenatum* cysts that are slightly larger, from sediments off the Portuguese coast have been linked to eutrophication rather than climate change (Amorim and Dale 2006).

As yet there are no unequivocal examples of cyst records of HABs, although the literature cited above suggests otherwise. Nevertheless, there are many long-term records of cysts from other species showing assemblage changes corresponding to environmental change, including climatic variation. Such records contain a wealth of information also relevant to considering the HAB species. For example, the Kattegat/Skagerrak work still offers one of the few documented examples of the 'invasion' and subsequent dominance of a warmer-water species due to climatic warming, and the main observations by Mudie et al. (2002), linking climate change to productivity of some dinoflagellates also suggest changes likely to affect HAB species.

In considering the cyst record, it is necessary to distinguish between coastal/shelf records and those from the deep sea. The many long-term deep-sea records attempting to document climate change give poor resolution for the decadal scale changes of interest here, due to low sedimentation rates and uncertainties regarding long-range transport of cysts. The coastal/shelf cyst records covering the past few hundreds of years show a notable amount of variation within the assemblages. There is no reason to suppose that the cyst-forming species alone are affected by environmental change, and the cyst record therefore suggests more change in the phytoplankton than is generally indicated by plankton records. Furthermore, this variation involves distinctive changes previously correlated with known, present-day environmental parameters, such as SST, salinity, nutrients, and water stability (Dale 1996).

While based on few examples so far, first attempts are being made to develop the cysts as indicators, or signals, of different forms of environmental change (Dale and Dale 2002). Again, the main challenge is to separate the various signals within the data. Records from coastal waters so far suggest distinctive cyst signals mainly reflecting influence from the obvious human impact associated with industrialization within the past 150 years, and that any climatic signals are relatively minor by comparison. The timing of these assemblage changes offers support for this interpretation, occurring as they do at clearly different times, sometimes between localities only a few kilometers apart, rather than simultaneously as may be expected from more regional effects of climate.

Records spanning the MWP, roughly 550–1300 A.D., provide some of the most appropriate evidence relevant to predicting possible effects of global warming. The average temperature increase of around 1–2 degrees estimated for the MWP is of the order of changes predicted by climate models for global warming for the next 100 years. Early Holocene temperatures may have been 4–5 degrees warmer than at present, more comparable to the highest estimates within the uncertainties of predicted global warming, but both dating and temperature estimates may well be less reliable for periods of warming prior to the MWP. Although limited to the cyst-forming species, this evidence therefore represents much of what is known regarding phytoplankton response to several degrees of warming.

Records spanning the MWP in Scandinavian waters indicate distinct cyst assemblage changes associated with climatic warming (e.g., Thorsen and Dale 1998; and largely unpublished core data from archeological work in the Oslofjord mentioned by Dale and Dale 2002). The cyst signals involved may be summarized below.

The first signal of climatic warming is a marked increase in the highly cosmopolitan species *Protoceratium reticulatum* (opportunistic development to exploit a changing environment – also seen as a first signal of eutrophication, and with changes to cooler conditions of the LIA). Detailed records often show this as a distinct spike of dominance.

The first stage of climatic warming may be marked by an increase in *Pentapharsodinium dalei*. On first consideration, this seems anomalous, since the species represents the colder element of the assemblage, but is now realized as an indicator of the first phase of warming – affecting largely winter temperatures. Warmer winters give a longer, warmer window of opportunity for the colder water dinoflagellate species blooming in spring (Dale 2001).

Sustained climatic warming leads to increased amounts of the warmer water species blooming in late summer (e.g. some of the *Gonyaulax spinifera* group, and *Lingulodinium polyedrum*). These species may also extend their biogeographic boundaries to higher latitudes, while more-warmer-water species 'invade' by similar expansion from lower latitudes, although this is impossible to prove since even long intervals with no recorded cysts in between the warmer periods cannot be taken as evidence for the complete absence of a species. Thus far, there is a lack of corresponding information from mid-low latitudes.

The cyst records of the past few hundreds of years include the relatively minor oscillations of temperature associated with the NAO. Ironically, some of the cyst records with highest time resolution have proved hardest to relate to climate. Harland et al. (2004) produced one such record from a Swedish fjord on the Skagerrak coast, showing an abrupt major assemblage change from about 1940 to the present, involving a ten-fold increase in the total amounts of cysts, including a substantial increase in *Lingulodinium polyedrum*. This is very similar to the eutrophication signal described elsewhere (Dale 2001), but there was no evidence of eutrophication, despite the obvious influence of Baltic water reported by others to be eutrophic (Elmgren 2001). Instead, Harland et al. (2004) favored a link to the NAO, while admitting that such data may be impossible to interpret fully (the abrupt assemblage change also correlated with a major dredging operation that may have altered the hydrography at the studied site). Comparable records from nearby fjords should suggest if this really is a more regionally expressed climatic signal linked to the NAO.

28.5 Conclusions

The long-term plankton records and the sedimentary records of cysts reported so far can provide only a few examples of direct evidence for the effects of climate change on HABs. This is not surprising, since with only few exceptions long-term monitoring has not been utilized in HAB research, and most of the data cited here were gathered for other scientific purposes. The CPR data is targeted to reveal long-term variability in plankton from the North Atlantic system, and therefore does not include most regions of highest HAB activity, affecting mainly coastal waters, or most of the HAB species which are too small or infrequent in the more oceanic waters covered. The cyst data are mostly from studies of human impact on the more coastal environments, but not specifically aimed at HAB species since many do not fossilize.

Nevertheless, both plankton and cyst records provide complementary information on the effects of climate on other species of phytoplankton, suggesting effects that almost certainly must have influenced at least some past and present HABs. The main effects of interest here are that climatic warming may have increased the occurrence and magnitude of HABs at any particular site through:

(1) Shifts toward relatively more flagellates in some regional ecosystems (many HAB species are flagellates);
(2) Earlier spring blooms of flagellates (increased window of opportunity for these species);
(3) Expansion of the biogeographic ranges of warmer-water species into higher latitudes.

At the same time, it is important to note that such changes may also have the potential to *decrease* the occurrence and magnitude of HABs. None of the effects of climate change discussed here are restricted to just the relatively few HAB species, allowing for the possibility that in at least some cases other species could better exploit the resulting changes in the environment and outcompete the HAB species. There is insufficient evidence to resolve this issue.

Considering the prediction of future HABs, this is one of many examples where scientists are increasingly being asked to predict the effects of global change in environments with few or no records to show the effects of previous change. In this case, the paucity of long-term plankton records has been suggested as one of the main reasons for our limited understanding of HABs and how to predict them despite over 40 years of research (Dale 2005). Without such records, the work discussed here can offer no more than a framework for beginning to assess the possible changes in HABs to be expected from the uncertain predictions of future global warming. Information from the fossil record shows clear links between some bloom species of dinoflagellates and climate, suggesting likely responses to future warming, but as yet no unequivocal records of past HABs. Information from recent and living plankton on HAB – climate links is also still too tenuous to suggest how blooms will respond in the future. It is also difficult to extrapolate from this information, which is largely from the Atlantic, to the rest of the world.

References

Amorim A, Dale B (2006) Historical cyst record as evidence for the recent introduction of the dinoflagellate *Gymnodinium catenatum* in the North Eastern Atlantic. Afr J Mar Sci (in press)

Anderson DM (1997) Bloom dynamics of toxic *Alexandrium* species in the northeastern U.S. Limnol Oceanogr 42:1009–1022

Bakun A (1990) Global climate change and intensification of coastal ocean upwelling. Science 247:198–201

Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002) Reorganisation of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694

Belgrano A, Lindahl M, Hernroth B (1999) North Atlantic oscillation, primary productivity and toxic phytoplankton in the Gullmar Fjord, Sweden (1985–1996). Proc R Soc Lond, ser B 266:425–430

Dale B (1996) Dinoflagellate cyst ecology: modeling and geological applications. In: Jansonius J, McGregor DC (eds) Palynology: principles and applications. The Am Assoc Stratigr Palynol Found, Publishers Press, Salt Lake City, pp 1249–1276

Dale B (2001) The sedimentary record of dinoflagellate cysts: looking back into the future of phytoplankton blooms. Scientia Marina 65:257–272

Dale B (2005) The sedimentary record shows the need for long-term monitoring of phytoplankton. In: Solbé J (ed) Long-term monitoring. Why, what, where, when & how? Sherkin Island Marine Station, Ireland, pp 106–113

Dale B, Dale A (2002) Dinoflagellate cysts and acritarchs. In: Haslett SK (ed) Quaternary environmental micropalaeontology. Arnold Publishers, London, pp 207–240

Dale B, Nordberg K (1993) Possible environmental factors regulating prehistoric and historic "blooms" of the toxic dinoflagellate *Gymnodinium catenatum* in the Kattegat-Skagerrak region of Scandinavia. In: Smayda TJ, Shimizu Y (eds) Toxic phytoplankton blooms in the sea. Elsevier, Amsterdam, pp 53–57

Dale B, Madson A, Nordberg K, Thorsen TA (1993) Evidence for prehistoric and historic "blooms" of the toxic dinoflagellate *Gymnodinium catenatum* in the Kattegat-Skagerrak region of Scandinavia. In: Smayda TJ, Shimizu Y (eds) Toxic phytoplankton blooms in the sea. Elsevier, Amsterdam, pp 47–52

Edwards M, Richardson A (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884

Edwards M, Reid PC, Planque B (2001) Long–term and regional variability of phytoplankton biomass in the north–east Atlantic (1960–1995). ICES J Mar Sci 58:39–49

Edwards M, Licandro P, John AWG, Johns DG (2005) Ecological status report: results from the CPR survey 2003/2004. SAHFOS Tech Rep ISSN 1744-0750, 2:1–6

Edwards M, Johns DG, Leterme SC, Svendsen E, Richardson AJ (2006) Regional climate change and harmful algal blooms in the north-east Atlantic. Limnol Oceanogr 51(2):820–829

Ellegaard M, Moestrup Ø (1999) Fine structure of the flagellar apparatus and morphological details of *Gymnodinium nolleri* sp. Nov. (Dinophyceae), an unarmoured dinoflagellate producing a microreticulate cyst. Phycologia 38:289–300

Elmgren R (2001) Understanding human impact on the Baltic ecosystem: changing views in recent decades. Ambio 30:222–230

Emslie SD, Allmon WD, Rich FJ, Wrenn JH, de France SD (1996) Integrated taphonomy of an avian death assemblage in marine sediments from the Late Pliocene of Florida. Palaeogeogr Palaeoclimatol Palaeoecol 124:107–136

Fraga S, Bakun A (1993) Global climate change and harmful algal blooms: the example of *Gymnodinium catenatum* on the Galician coast. In: Smayda TJ, Shimizu Y (eds) Toxic phytoplankton blooms in the sea. Elsevier, Amsterdam, pp 59–65

Gjøsæter J, Lekve K, Stenseth NC, Leinaas H P, Christie H, Dahl E, Danielssen DS, Edvardson B, Olsgard F, Oug E, Paasche E (2000) A long–term perspective on the *Chrysochromulina* bloom on the Norwegian Skagerrak coast 1988: a catastrophe or an innocent incident? Mar Ecol Prog Ser 207:201–218

Hales S, Weinstein P, Woodward A (1998) Ciguatera (fish poisoning), El Niño, and Pacific sea surface temperatures. Ecosystem Health 5:20–25

Hallegraeff GM (1993) A review of harmful algal blooms and their apparent global increase. Phycologia 32:79–99

Harland R, Nordberg K, Filipsson H (2004) A higher resolution dinoflagellate cyst record from latest Holocene in Koljö Fjord, Sweden. Rev Palaeobot Palynol 128:119–141

Head MJ, Lewis J, de Vernal A (2006) The cyst of the calcareous dinoflagellate *Scrippsiella trifida*: resolving the fossil record of its organic wall with that of *Alexandrium tamarensis*. J Paleontol 80(1):1–8

Hickel W (1998) Temporal variability of micro- and nannoplankton in the German Bight in relation to hydrographic structure and nutrient changes. ICES J Mar Sci 55:600–609

Johns DG, Edwards M, Richardson A, Spicer JI (2003) Increased blooms of a dinoflagellate in the northwest Atlantic. Mar Ecol Prog Ser 265:283–287

Moustaka-Gouni M, Cook CM, Gkelis S, Michaloudi E, Pantlelidakis K, Pyrovetsi M, Lanaras T (2004) The coincidence of a *Prymesium parvum* bloom and the mass kill of birds and fish in Lake Koronia. Harmful Algae News 26:1–2

Mudie PJ, Rochon A, Levac E (2002) Palynological records of red tide-producing species in Canada: past trends and implications for the future. Palaeogeogr Palaeoclimatol Palaeoecol 180:159–186

Nehring S (1998) Establishment of thermophilic phytoplankton species in the North Sea: biological indicators of climate change? ICES J MarSci 55:818–823

Peperzak L (2003) Climate change and harmful algal blooms in the North Sea. Acta Oecologia 24:139–144

Reid PC, Edwards M, Hunt HG, Warner AJ (1998) Phytoplankton change in the North Atlantic. Nature 391:546

Rhodes LL, Haywood AJ, Ballantine WJ, MacKenzie AL (1993) Algal blooms and climate anomalies in north–east New Zealand, August–December 1992. New Zeal J Mar Fresh 27:419–430

Sellner KG, Doucette GJ, Kirkpatrick GJ (2003) Harmful algal blooms: causes, impacts and detection. J Ind Microbiol Biotechnol 30:383–406

Skjoldal HR, Dundas I (1991) The *Chrysochromulina polylepis* bloom in the Skagerrak and the Kattegat in May–June 1988: environmental conditions, possible causes and effects. ICES Coop Res Rep 175:1–59

Tester PA, Stumpf RP, Vukovich FM, Fowler PK, Turner JT (1991) An expatriate red tide bloom: transportation, distribution and persistence. Limnol Oceanogr 36:1053–1061

Thorsen T, Dale B (1998) Climatically influenced distribution of *Gymnodinium catenatum* during the past 2000 years in coastal sediments of southern Norway. Palaeogeogr Palaeoclimatol Palaeoecol 143:159–177

Walsh JJ, Steidinger KA (2001) Sahara dust and Florida red tides: the cyanophyte connection. J Geophys Res 106 (C6):11597–11612

Warner AJ, Hays GC (1994) Sampling by the Continuous Plankton Recorder survey. Prog Oceanogr 34:237–256

Wasmund N, Nausch G, Matthaus W (1998) Phytoplankton spring blooms in the southern Baltic Sea – spatio-temporal development and long-term trends. J Plankton Res 20:1099–1117