REVIEW

OCEAN CLIMATE CHANGE, PHYTOPLANKTON COMMUNITY RESPONSES, AND HARMFUL ALGAL BLOOMS: A FORMIDABLE PREDICTIVE CHALLENGE[1]

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Prediction of the impact of global climate change on marine HABs is fraught with difficulties. However, we can learn important lessons from the fossil record of dinoflagellate cysts; long-term monitoring programs, such as the Continuous Plankton Recorder surveys; and short-term phytoplankton community responses to El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) episodes. Increasing temperature, enhanced surface stratification, alteration of ocean currents, intensification or weakening of local nutrient upwelling, stimulation of photosynthesis by elevated CO_2, reduced calcification through ocean acidification ("the other CO_2 problem"), and heavy precipitation and storm events causing changes in land runoff and micronutrient availability may all produce contradictory species- or even strain-specific responses. Complex factor interactions exist, and simulated ecophysiological laboratory experiments rarely allow for sufficient acclimation and rarely take into account physiological plasticity and genetic strain diversity. We can expect: (i) range expansion of warm-water species at the expense of cold-water species, which are driven poleward; (ii) species-specific changes in the abundance and seasonal window of growth of HAB taxa; (iii) earlier timing of peak production of some phytoplankton; and (iv) secondary effects for marine food webs, notably when individual zooplankton and fish grazers are differentially impacted ("match-mismatch") by climate change. Some species of harmful algae (e.g., toxic dinoflagellates benefitting from land runoff and/or water column stratification, tropical benthic dinoflagellates responding to increased water temperatures and coral reef disturbance) may become more successful, while others may diminish in areas currently impacted. Our limited understanding of marine ecosystem responses to multifactorial physicochemical climate drivers as well as our poor knowledge of the potential of marine microalgae to adapt genetically and phenotypically to the unprecedented pace of current climate change are emphasized. The greatest problems for human society will be caused by being unprepared for significant range expansions or the increase of algal biotoxin problems in currently poorly monitored areas, thus calling for increased vigilance in seafood-biotoxin and HAB monitoring programs. Changes in phytoplankton communities provide a sensitive early warning for climate-driven perturbations to marine ecosystems.

Key index words: adaptation; algal blooms; climate change; continuous plankton recorder; ENSO; NAO; ocean acidification; range expansion

Abbreviations: DMS, dimethylsulfoxide; ENSO, El Niño-Southern Oscillation; GOOS, Global Ocean Observation Systems; IMOS, Integrated Marine Observing System; IPCC, Intergovernmental Panel on Climate Change; NAO, North Atlantic Oscillation episodes; OOI, Ocean Observatories Initiative

HABs in a strict sense are completely natural phenomena that have occurred throughout recorded history. Even nontoxic algal blooms can have devastating impacts, for instance, when they lead to kills of fish and invertebrates by generating anoxic conditions in sheltered bays. Other algal species, even though nontoxic to humans, can produce exudates or reactive oxygen species that can damage the gill tissues of fish (raphidophytes *Chattonella* and *Heterosigma*, and dinoflagellates *Cochlodinium, Karenia,* and *Karlodinium*). Whereas wild fish stocks can swim away from problem areas, caged fish in intensive aquaculture operations are trapped and thus can suffer catastrophic mortalities. Of greatest concern to human society are algal species that produce potent neurotoxins that can find their way through shellfish and fish to human consumers where they produce a variety of gastrointestinal and neurological illnesses. One of the first recorded fatal cases of food poisoning after eating contaminated shellfish happened in 1793, when English surveyor Captain George Vancouver and his crew landed in British Columbia (Canada) in an area now known as Poison Cove. He noted that, for local Indian tribes,

it was taboo to eat shellfish when the seawater became bioluminescent due to algal blooms by the local dinoflagellate *Alexandrium catenella,* which we now know to be a producer of paralytic shellfish poisons (PSP) (Dale and Yentsch 1978).

The increase in shellfish farming worldwide is leading to more reports of paralytic, diarrhetic (first documented in 1976 in Japan), neurotoxic (reported from the Gulf of Mexico as early as 1840), amnesic (first identified in 1987 in Canada), or azaspiracid shellfish poising (first identified in 1998 in Ireland). The English explorer Captain James Cook already suffered from the tropical illness of ciguatera fish poisoning when he visited New Caledonia in 1774. Worldwide, close to 2,000 cases of food poisoning from consumption of contaminated fish or shellfish are reported each year. Some 15% of these cases will prove fatal. If not controlled, the economic damage through the slump in local consumption and export of seafood products can be considerable. Whales and porpoises can also become victims when they take up toxins through the food chain via contaminated zooplankton or fish. In the USA, poisoning of manatees in Florida via seagrasses and their faunal epiphytes, and, in California, of pelicans and sea lions via contaminated anchovies have also been reported. In the past three decades, HABs seem to have become more frequent, more intense, and more widespread (Hallegraeff 1993, Van Dolah 2000). There is no doubt that the growing interest in using coastal waters for aquaculture is leading to a greater awareness of toxic algal species. People responsible for deciding quotas for pollutant loadings of coastal waters, or for managing agriculture and deforestation, should be made aware that one probable outcome of allowing polluting chemicals to seep into the environment will be an increase in HABs or a change in community structure affecting a change in food web. In countries that pride themselves on having disease- and pollution-free aquaculture, every effort should be made to quarantine sensitive aquaculture areas against the unintentional introduction of nonindigenous harmful algal species. Nor can any aquaculture industry afford not to monitor for an increasing number of harmful algal species in water samples and for an increasing number of algal toxins in seafood products using increasingly sophisticated analytical techniques. Last but not least, global climate change is now adding a new level of uncertainty to many seafood safety and HAB monitoring programs. Whereas in the past two decades unexpected new algal bloom phenomena have often been attributed to eutrophication (Smayda 1990) or ballast water introduction (Hallegraeff 1993, Lilly et al. 2002), increasingly novel algal bloom episodes are now circumstantially linked to climate change.

The Intergovernmental Panel on Climate Change (IPCC 2008) is planning to include HAB risk forecasts under a range of climate change scenarios. A number of scattered publications have started to address the topic of HABs and climate change, but they usually have focused on single environmental factors (e.g., CO_2, temperature increase, stratification), single biological properties (photosynthesis, Beardall and Stojkovic 2006; calcification, Rost and Riebesell 2004; nutrient uptake, Falkowski and Oliver 2007), or addressed selected species categories of regional interest only (Peperzak 2005, Moore et al. 2008b). Complex factor interactions are rarely considered in climate simulation scenarios, and eco-physiological experiments rarely cover the full range of genetic diversity and physiological plasticity of microalgal taxa. Prediction of the impact of global climate change on algal blooms is fraught with uncertainties. It is unfortunate that so few long-term records exist of algal blooms at any single locality, where ideally we need at least 30 consecutive years. However, we can learn important lessons from the dinoflagellate cyst fossil record (Dale 2001), from the few long-term data sets available, such as the Continuous Plankton Recorder surveys (Hays et al. 2005) and short-term phytoplankton community responses to ENSO and NAO episodes. Whereas the Continuous Plankton Recorder surveys were initially designed to primarily sample zooplankton, these instruments also collect phytoplankton down to even coccolithophorids (Hays et al. 1995). Started in 1931 in the North Atlantic, gradually these surveys have expanded to the North Pacific (since 1997) and, more recently, also the Western Atlantic, Australia, and the Southern Ocean (Richardson et al. 2006). The present review seeks to provide a broad overview of the complexity of climate variability and factor interactions, examine marine phytoplankton responses with a focus on the HAB species niche, and identify major research gaps.

The global climate system. The term ''climate'' is used here to include both anthropogenic climate change as well as the large-scale decadal oceanographic patterns such as the ENSO, Pacific Decadal Oscillation (PDO), and NAO. This use is in contrast to ''weather,'' which occurs over short timescales of days to weeks (cf. Moore et al. 2008b). The earth's climate system comprises the atmosphere (air, water vapor, constituent gases, clouds, particles), hydrosphere (oceans, lakes, rivers, groundwater), and cryosphere (continental ice sheets, mountain glaciers, sea ice, surface snow cover). The oceans are a core component of the global climate system because they store 93% (=39,100 gigatonnes, Gt) of the world's carbon, but more and more, we are now becoming aware of the quantitative contribution to climate by marine phytoplankton, accounting for 50% of global primary productivity (Longhurst et al. 1995). All the microalgal cells in the world oceans could be packed in a plank, 386,000 km long, 7 cm thick, and 30 cm wide, that is, stretching from the earth to the moon (Andersen 2005). This increased recognition of phytoplankton as a climate driver is

well demonstrated by the commercial interests in ocean fertilization to combat anthropogenic climate change (Glibert et al. 2008). Annually, the oceans absorb 1.8 Gt of carbon through photosynthesis and 2 Gt via abiotic absorption. The oceans thus have acted as a sink for 30% of all anthropogenic carbon emissions since the onset of the Industrial Revolution. The oceans are particularly effective in absorbing heat and have taken up >90% of the increase in heat content of the earth since 1961. Climate change in the past has occurred naturally due to internal fluctuations in the atmosphere, hydrosphere, and cryosphere, but it has also been influenced by volcanic eruptions, variations in the sun's output, the earth's orbital variation, and change in the solid earth (e.g., continental drift).

Climate on our planet has been constantly changing, over scales of both millions of years (glacial to interglacial periods) and short-term oscillations of tens of years (ENSO, NAO). The earth's climate in the distant past has at times been subject to much higher ultraviolet-B (UVB) levels and CO_2 concentrations than we are seeing at present. The first photosynthetic cyanobacteria evolved 3.5 billion years ago at CO_2 levels 1,000× those of the present, followed by green algae 1,000 million years ago (mya; 500× present) and dinoflagellates 330–400 mya (8× present), whereas more recently evolved diatoms and haptophytes operated under comparatively low CO_2 environments (2–3× present) (Beardall and Raven 2004; Fig. 1).

During the past 800,000 years, atmospheric CO_2 has fluctuated between 180 ppm in glacial and 300 ppm in interglacial periods, but in the past 200 years, this has increased from 280 ppm to >380 ppm at present, with values of 750–1,000 ppm predicted by 2100. In the past 1,000 years, our planet has gone through episodes warmer than present, such as the medieval warm period AD 550–1300, and colder than now, such as the little ice age AD 1300–1900. Global temperatures in the past 20–30 years (Fig. 1, bottom) have increased significantly with a further rise of 2°C–4(6)°C predicted over the next 100 years. Undoubtedly, climate change of the magnitude that we will be experiencing in the next 100 years has happened before, albeit in the past proceeding at a much slower pace and starting from a cooler baseline than present (IPCC 2008). Past episodes of climate change over long periods of geological and evolutionary history allowed organisms to adapt to their changing environment. Because of their short generation times and longevity, many phytoplankton are expected to respond to current climate change with only a very small time lag. They are expected to spread quickly with moving water masses into climatic conditions that match the temperature, salinity, land runoff, and turbulence requirements of the species. However, our knowledge of the potential of marine microalgae to adapt is very limited. Collins and Bell (2004) grew
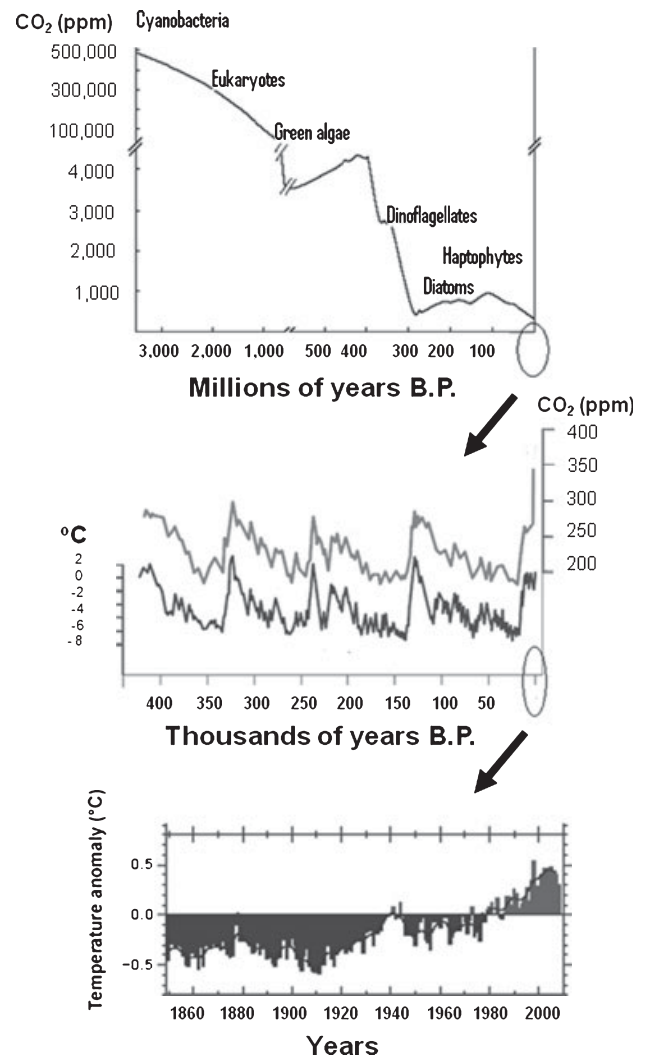

Fig. 1. Climate change is a matter of scale and time and can be viewed in terms of thousands of millions of years [evolution of life on our planet (top), after Beardall and Raven 2004], hundreds of thousands of years [glacial-interglacial periods, from Vostok Ice Core data (middle), Lorius et al. 1990], or the past hundred years [from Hadley Centre for Climate Prediction and Research, (bottom)]. From a geological perspective, there is nothing remarkable about the magnitude of climate change we are experiencing now, except that it appears to proceed at a faster pace and starts from a warmer baseline.

the freshwater microscopic alga *Chlamydomonas* over 1,000 generations at almost 3× present atmospheric CO_2 concentration. The cells acclimated to the change but did not show any genetic mutations that could be described as adaptation.

Defining the niche of HABs. Most HABs are more or less monospecific events, and the autecology of the causative organisms thus becomes crucial in understanding the factors that trigger these phenomena. Defining the niche of key HAB species is crucial when trying to predict winners or losers from climate change. An implicit assumption in ecological studies is that there exists a critical

relationship between form and function in organisms, and that life-form therefore is a better predictor of fitness than phylogenetic affinities. Overall, morphotaxonomy has worked well with HAB species, but it is increasingly obvious that ecophysiological experiments based on single culture strains can be highly misleading (Burkholder and Glibert 2006). The development in the past three decades of the discipline of HAB ecology is evidenced by the increased frequency and size of international meetings since the first HAB meeting in 1974 and the creation in 2002 of the dedicated journal *Harmful Algae*. A first major review of harmful algal ecology was produced as a result of a Bermuda NATO-ASI workshop in 1996 (Anderson et al. 1998), followed by an update by Graneli and Turner (2006). The brief summary below (see also Table 1) is largely based on these two sources.

The commonality of the PSP-producing dinoflagellates *Alexandrium, Pyrodinium,* and *Gymnodinium catenatum* lies in the absence of a rapid growth strategy and reliance on benthic resting cysts in lifecycle transitions (Hallegraeff 1998). *Alexandrium* does not usually produce dense biomass blooms that persist throughout the year. Instead, seasonal bloom events appear to be restricted in time by cyst production (Anderson 1997). The persistence of these cysts through long-term unfavorable conditions allows these dinoflagellates to colonize a wide spectrum of habitats and hydrographic regimes. The tropical dinoflagellate *Pyrodinium* prefers high salinities (30‰–35‰) and high temperatures (25°C–28°C) (Azanza and Taylor 2001). A soil extract requirement in culture may explain this species' association with rainfall events and land runoff from mangrove areas. Benthic cyst stages of *G. catenatum* (short dormancy period of 2 weeks) do not play a role in seasonal bloom dynamics, and their major function is to sustain this species through long periods when water column conditions are unfavorable for bloom formation (Hallegraeff et al. 1995). The success of the haptophyte *Phaeocystis* in marine systems has been attributed to its ability to form large gelatinous colonies during its life cycle. These colonies occupy the same niche in turbulent, tidally or seasonally mixed water columns as colony-forming spring diatom blooms (Smayda and Reynolds 2001). The fish killers *Heterosigma, Chattonella, Prymnesium, Chrysochromulina,* and *Karenia mikimotoi* have in common the production of high biomass blooms together with the production of allelopathic chemicals (including reactive oxygen species) that play a role in predator avoidance (Hallegraeff 1998). Raphidophyte blooms of *Heterosigma* are sensitive to temperature for cyst germination, but chemical conditioning of the water by land runoff and other growth promoters (e.g., from aquaculture wastes) determines the outcome of competition with diatoms. Similarly, the raphidophyte *Chattonella* includes a benthic cyst stage in its

life history, but the growth of the germling cells as affected by nutrient conditions and the presence of diatom competitors holds the key to its bloom development. The capacity of *Chattonella* to undergo vertical migration in stratified water columns with a shallow nutricline (i.e., nutrients available only at depth under dim light) provides a competitive advantage (Imai et al. 1998). While harmful marine blooms of *Chrysochromulina* appear to be exceptional events (in Scandinavia in 1988 and 1991), fish-killing *Prymnesium* bloom events in inshore (low salinity), eutrophic waters are recurrent in many parts of the world. The expression of toxicity by *Chrysochromulina* and *Prymnesium* is variable and can be enhanced by phosphate limitation (Graneli and Turner 2006). The fish-killing dinoflagellate *Karenia brevis* is a K-strategist, adapted to low nutrient, oligotrophic environments. Blooms in the Gulf of Mexico are initiated offshore before being transported into nearshore waters where they cause fish kills, discolored water, human respiratory irritation, and occasionally neurotoxic shellfish poisoning (NSP) in human shellfish consumers. Taxonomically related dinoflagellate species of the eurythermal and euryhaline *K. mikimotoi* species complex are associated with marine fauna kills but not human intoxications. Poorly characterized lipophilic exotoxins and mucus production play an allelopathic role against other algae and also act as agents that repress zooplankton grazing (Gentien 1998). This species is especially successful in frontal regions and in stratified water columns where it accumulates in the pycnocline (often also a nutricline), thriving on regenerated ammonia and benefitting from polyamine growth factors from decaying diatoms. Recent success in culturing the dinoflagellate *Dinophysis* has confirmed its mixotrophic feeding behavior on cryptomonad and/or *Mesodinium* prey (Park et al. 2006) and pointed out that the incidence of occasionally high biomass is the result of active growth and not passive cell accumulation. The unusual, large phagotrophic dinoflagellate *Noctiluca* depends upon high prey biomass (mostly diatoms) and optimal water temperatures during the prebloom stage, with starved cells coming to the surface and aggregating at fronts during calm weather conditions and wind mixing terminating the blooms. Diatom blooms of the cosmopolitan genus *Pseudo-nitzschia* are common in coastal waters all over the world. Blooms generally occur during colder seasons, and seed populations can derive from both inshore or offshore waters (Bates et al. 1998). The community dynamics of epiphytic/benthic tropical *Gambierdiscus* ciguatera dinoflagellates and their associated macroalgal canopy are dictated to a large extent by the degree of water movement, with other physical and chemical factors such as temperature, salinity, gases, and inorganic and organic nutrients only playing a role with diminishing hydrodynamics (Bagnis et al. 1985).

TABLE 1. Summary of physicochemical and biological niche-defining factors for key HAB species.

Key HAB species and their impact	Temperature	Salinity	Inorganic nutrients	Micronutrients (land runoff)	Organic nutrition (mixotrophy)	Allelopathy; grazer avoidance	Life history	Sensitive to turbulence
Alexandrium (PSP)	Cyst germination; bloom window			Fe, Cu			+	Notably chain formers
Gymnodinium catenatum (PSP)	Bloom window			Se			+	+
Pyrodinium bahamense (PSP)	Tropical			Se; mangrove runoff			+	+
Chattonella (fish kills)	Cyst germination			Mn, Fe, Cu	Responds to aquaculture wastes			+
Heterosigma (fish kills)	Cyst germination	Freshwater on top of water column		Mn, Fe, Cu	Responds to aquaculture wastes	+		+
Cyanobacteria	Bloom window		Phosphate					
Microcystis (microcystins)	Freshwater summer blooms		Phosphate			+		+
Nodularia spumigena (nodularin)		Brackish water	Phosphate	Fe for N fixation				
Trichodesmium ("red-tide")	Tropical							+
Karenia brevis (NSP, fish kills)	Demise of bloom	River flow		Fe, Mn	Vitamins, amino acids	+		+
Karenia mikimotoi (fish kills)					Polyamines	+		Pycnoclines fronts
Noctiluca ("red-tide")	Bloom window		Indirect; high prey biomass		Phagotrophy			
Pseudo-nitzschia (ASP)		?Responds to rainfall	Nitrate					
Pfiesteria[a] *Cryptoperidiniopsis*[a]			Change in nutrient regime		Cryptomonad prey		+	
Karlodinium (fish kills)					Cryptomonad prey			
Phaeocystis (gelatinous blooms)			Change in nutrient regime	Fe?		+		
Chrysochromulina (rarely fish kills)				Se, Fe, Cu, Vit B$_{12}$	+	+		
Prymnesium (fish kills)						+		
Dinophysis (DSP)					+	+		
Gambierdiscus (CFP)	Tropical					Macroalgal substrate		+

Taxa identified as responsive to temperature, land runoff, nutrients and mixed-layer depth, and physical turbulence appear most vulnerable to climate change. "?" indicates limited evidence. PSP, paralytic shellfish poisoning; NSP, neurotoxic shellfish poisoning; ASP, amnesic shellfish poisoning; DSP, diarrhetic shellfish poisoning; CFP, ciguatera food poisoning.
[a]Disputed HAB species.

Most HAB species have been demonstrated to have either some capability of mixotrophy/organic nutrient uptake or a requirement for micronutrients (Graneli and Turner 2006). Temperature plays a crucial role in the bloom dynamics of the cyst-forming PSP dinoflagellates and raphidophytes, as well as for species such as *G. catenatum, Noctiluca,* and many cyanobacteria, which have well-defined seasonal temperature windows. However, once cells of these species enter the water column, other factors such as nutrients, turbulence, and grazing determine the outcome of competition. HAB species show a perplexing diversity of biomass and toxicity patterns (Cembella 2003), ranging from species such as *Dinophysis* and *Chrysochromulina,* which can cause toxicity problems even at very low cell concentrations, to species such as *Phaeocystis* and *Noctiluca,* which are basically nontoxic but whose nuisance value derives from their high biomass production. Persistent near-monospecific algal blooms of, for example, *Aureococcus, Chrysochromulina, Prymnesium,* and *Nodularia* have recently been referred to as ecosystem disruptive algal blooms (EDABs), in which toxic or unpalatable algal species disrupt grazing and thus diminish nutrient supply via recycling (Sunda et al. 2006). Could climate perturbations perhaps create a niche for such HAB species?

From progress in the past three decades, it has become abundantly clear that the niche of HAB species is much wider than originally envisaged. HAB species are not restricted to dinoflagellates but also include diatoms, haptophytes, raphidophytes, and cyanobacteria. Furthermore, they cover the complete range from r-strategists (e.g., *Pseudo-nitzschia, Chattonella*), whose success is due to their high growth rates (r) and efficient use of nutrients, to K-strategists (e.g., *G. catenatum*), which can achieve high biomass levels by being energy (light) efficient, for example, by vertical migration (Margalef 1978, Smayda and Reynolds 2001). Taxa identified in Table 1 as responsive to temperature, land runoff, nutrients and mixed-layer depth, and physical turbulence appear most vulnerable to climate change. When and where climate-driven perturbations open a new "niche," any number of ecologically similar organisms have the opportunity to emerge from the background to become a HAB phenomenon.

Algal bloom range expansions and climate change. For many HAB species, significant bloom episodes can serve as stepping stones toward range expansions via natural current systems, sometimes facilitated by local climate events or ship ballast water dispersal. The dinoflagellate *Pyrodinium bahamense* is presently confined to tropical, mangrove-fringed coastal waters of the Atlantic and Indo-West Pacific. A survey of cyst fossils (named *Polysphaeridium zoharyii*) going back to the warmer Eocene 50 mya indicates a much wider range of distribution in the past. For example, in the Australasian region at present, the alga is not found farther south than Papua New

Guinea, but some 120,000 years ago, the alga ranged as far south as Bulahdelah (32°S) just north of Sydney (McMinn 1988, 1989). There is concern that, with increased warming of the oceans, this species may return to Australian waters (Fig. 2). In the tropical Atlantic, in areas such as Bahia Fosforescente in Puerto Rico and Oyster Bay in Jamaica, the bioluminescent blooms of *Pyrodinium* are a major tourist attraction, but *Pyrodinium* blooms gained a more sinister reputation in 1972 in Papua New Guinea after red-brown water discolorations coincided with the fatal food poisoning of three children in a seaside village, diagnosed as PSP. Since then, the incidence of toxic blooms has spread to Brunei and Sabah (1976), the central (1983) and northern Philippines (1987), and Indonesia (North Mollucas). *Pyrodinium* is a serious public health and economic problem for tropical countries, all of which depend heavily on seafood for protein. In the Philippines alone, *Pyrodinium* has now been responsible for >2,000 human illnesses and 100 deaths resulting from the consumption of contaminated shellfish as well as sardines and anchovies (Hallegraeff and Maclean 1989). There exists circumstantial but debated evidence of a coincidence between *Pyrodinium* blooms and the ENSO (Maclean 1989, Azanza and Taylor 2001). In the Pacific Basin, trade winds and strong equatorial currents normally flow westward, and cold upwelling occurs off Peru. In contrast, during an ENSO event, trade winds are weak, and anomalously warm equatorial water flows eastward, and stratification is enhanced. Erickson
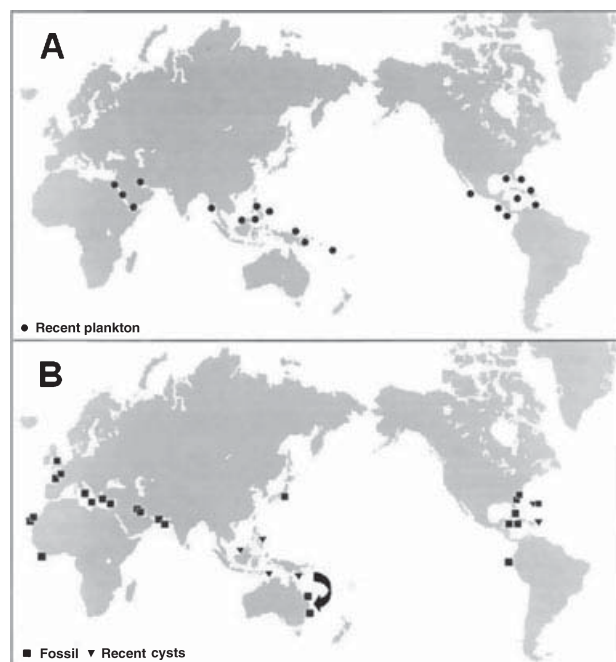

Fig. 2. Global distribution of *Pyrodinium bahamense* in recent plankton (A) and much wider distribution in the fossil cyst record (B) (after Hallegraeff 1993).

and Nishitani (1985) similarly reported exceptional PSP episodes by *Alexandrium tamarense/catenella* in the Pacific Northwest during seven out of nine ENSO events between 1941 and 1984 (but see Moore et al. 2008a for an alternative interpretation). An exceptional *Karenia digitata* red-tide event in Hong Kong in 1998 (HK$250 M loss to aquaculture) was associated with El Niño and altered oceanographic conditions (Yin et al. 1999). In the North Atlantic, the NAO reflects a north–south oscillation in atmosphere mass between the Iceland-low and the Azores high-pressure center. A high NAO means increased westerly winds and milder temperatures over northern Europe, and a low NOA causes cooler temperatures due to decreased westerly winds. Belgrano et al. (1999) found significant correlations between NAO, phytoplankton biomass, primary production, and *Dinophysis* concentrations off Sweden.

Until recently, NSP by the dinoflagellate *K. brevis* was considered to be endemic to the Gulf of Mexico and the east coast of Florida, where red tides had been reported as early as 1844. An unusual feature of NSP is the formation of toxic aerosols by wave action, which can lead to respiratory asthma-like symptoms in humans. In 1987, a major Florida bloom was dispersed by the Gulf Stream northward into North Carolina waters, even though it has not persisted there (Tester et al. 1991, 1993). Unexpectedly, in early 1993, >180 human NSPs were reported from New Zealand. Most likely, this mixed bloom of *K. mikimotoi* and related species was again triggered by the unusual weather conditions at the time, including higher than usual rainfall and lower than usual temperature, which coincided with El Niño (Rhodes et al. 1993, Chang et al. 1998).

Ciguatera caused by the benthic dinoflagellate *Gambierdiscus toxicus* is a food-poisoning syndrome caused by ingesting tropical fish and is well known in coral reef areas in the Caribbean, Australia, and especially French Polynesia (Fig. 3). Whereas, in a strict sense, this is a completely natural phenomenon, from being a rare disease two centuries ago,
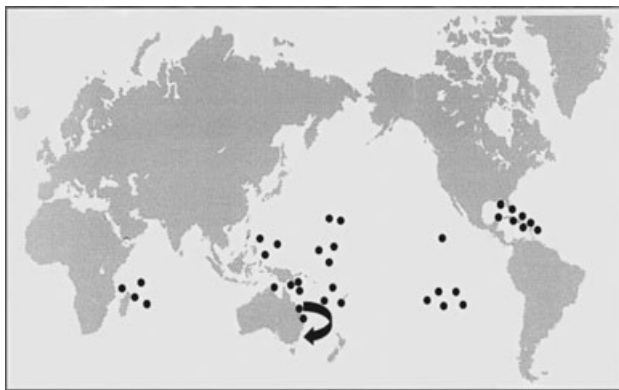
ciguatera has now reached epidemic proportions in French Polynesia. From 1960 to 1984, >24,000 patients were reported from this area, which is more than six times the average for the Pacific as a whole (Bagnis et al. 1985). Evidence is accumulating that reef disturbance by hurricanes, military and tourist developments, as well as coral bleaching (linked to global warming), increased water temperatures (>29°C preferred in culture), and perhaps in future increasing coral damage due to ocean acidification (Hoegh-Guldberg 1999) are increasing the risk of ciguatera by freeing up space for macroalgae for *Gambierdiscus* to colonize upon. During El Niño events, ciguatera increased on Pacific islands where sea surface temperatures increased (Hales et al. 2001). In the Australian region, *G. toxicus* is well known from the tropical Great Barrier Reef and southward to just north of Brisbane (25°S), but in the past 5 years, this species has undergone an apparent range expansion into southeast Australian seagrass beds as far south as Merimbula (37°S), aided by a strengthening of the East Australian Current (S. Brett, M. de Salas, and G. Hallegraeff, unpublished data). A similar expansion of *Gambierdiscus* into the Mediterranean and eastern Atlantic has been reported (Aligizaki et al. 2008), and blooms of the associated benthic dinoflagellate genus *Ostreopsis* are also an increasingly common phenomenon in temperate regions worldwide (Shears and Ross 2009).

In the same Australian region, the red-tide dinoflagellate *Noctiluca scintillans* (known from Sydney as early as 1860) has expanded its range from Sydney into Southern Tasmanian waters since 1994 where it has caused problems for the salmonid fish farm industry (Fig. 4). In the North Sea, an analogous northward shift of warm-water phytoplankton

Fig. 3. Current global distribution of ciguatera food poisoning from fish (after Hallegraeff 1993).
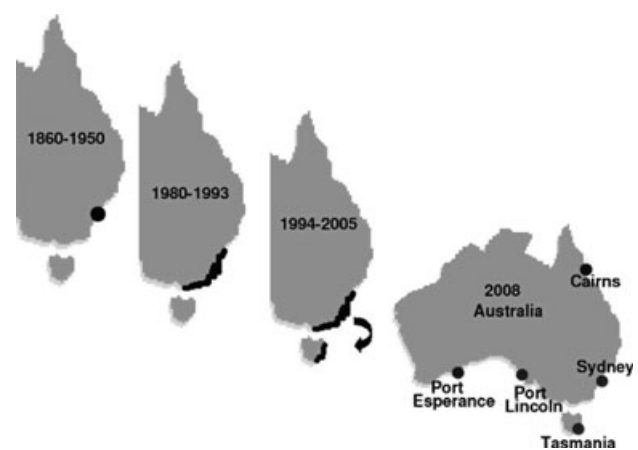

Fig. 4. Apparent range expansion of *Noctiluca scintillans* in the Australian region, comparing distribution records in 1860–1950, 1980–1993 (expansion of blooms in the Sydney region), 1994–2005 (range extension into Tasmania), and 2008 (first reports in Queensland, West Australia, and South Australia). After Hallegraeff et al. (2008).

Prorocentrum spp.   *Ceratium furca*   *Dinophysis* spp.   *Noctiluca scintillans*

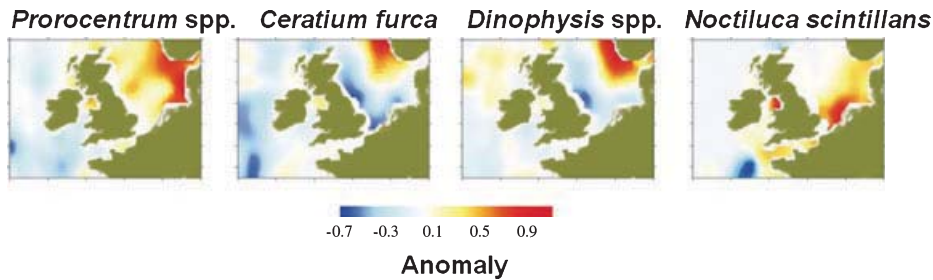-0.7   -0.3   0.1   0.5   0.9
Anomaly

FIG. 5. Decadal anomaly maps (difference between long-term 1960–1989 mean and the 1990–2002 period) for four common HAB species (from left to right): *Prorocentrum*, *Ceratium furca*, *Dinophysis*, and *Noctiluca* in the North Atlantic. Note the increase in *Prorocentrum, C. furca*, and *Dinophysis* along the Norwegian coast, and increase in *Noctiluca* in the southern North Sea, reportedly associated with a contraction of the Subpolar Gyre to the west allowing subtropical water to penetrate farther north (adapted from Edwards et al. 2008, with permission).

has occurred due to regional climate warming (Edwards and Richardson 2004, Richardson and Schoeman 2004). For example, *Ceratium trichoceros*, previously found only south of the British Isles, has expanded its geographic range to the west coast of Scotland and the North Sea, and the subtropical *Ceratium hexacanthum* moved 1,000 km northward in 40 years (Hays et al. 2005). At the same time, *Prorocentrum, Ceratium furca,* and *Dinophysis* increased along the Norwegian coast, and *Noctiluca* increased in the southern North Sea (Fig. 5). It is difficult to untangle the role of climate change and eutrophication in some of these species patterns. Dale (2009) used the dinoflagellate cyst record from the last 100 years to discriminate between the role of local eutrophication events within the Skagerrak (indicated by a shift to heterotrophic dinocysts, reflecting increased diatom prey) and the role of regional variation in the NAO, thought to have increased transport of relatively nutrient-rich North Sea water into the system (indicated by increased *Lingulodinium* benefitting from added nutrients during warm summers and increased stratification). In the same Skagerrak area, Thorsen et al. (1995), working with a much longer sediment core, documented the immigration into the region ~6000 B.P. (before present) of *Gymnodinium nolleri* (initially reported as *G. catenatum*), which achieved bloom proportions from 2000 to 500 B.P. during a warming period, followed by a near extinction during the cooling period that commenced in 300 B.P. (Fig. 6). Reduction between 1997 and 2002 of Arctic ice by 33% allowed greater flow through the trans-Arctic pathway from the Pacific to the Atlantic and was associated with the first appearance in 800,000 years in the Labrador Sea of the diatom *Neodenticula seminae* (Reid et al. 2007). While warm-water species can be expected to expand their distribution, cold-water species will contract their range (compare Beaugrand et al. 2002 for zooplankton). For example, the cold-water dinoflagellate cyst *Bitectatodinium tepikiense* currently is confined to Tasmania (43°S), but in the last interglacial period (120,000 years ago), it was found as far north as Sydney (34°S) (McMinn and Sun
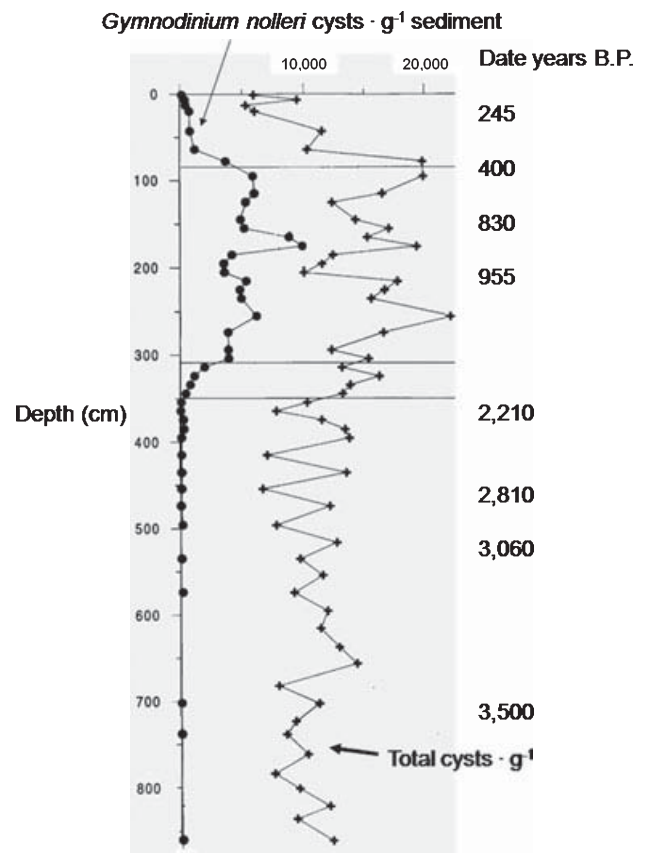

FIG. 6. Quantitative distribution of *Gymnodinium nolleri* cysts and total dinoflagellate cysts (cysts · g^{-1} dry sediment) in an 860 cm long sediment core from the southern Kattegat (after Thorsen et al. 1995).

1994). On top of range extensions driven by gradual climate change, ship ballast water translocations continue to alter species distributions. The two mechanisms interact since ecosystems disturbed by pollution or climate change are more prone to ballast water invasions (Stachowicz et al. 2002). Similarly, melting of Arctic sea ice and opening of new Arctic shipping lanes will encourage range expansions via both natural current dispersal as well as ballast water invasions.

Impact of global warming and sea surface temperature change. Phytoplankton grow over a range of temperatures characteristic of their habitat, and growth rates are usually higher at higher temperature, but considerably lower beyond an optimal temperature (Eppley 1972). Natural populations of phytoplankton often occur at temperatures suboptimal for photosynthesis, and it is believed that this distribution is designed to avoid risking abrupt declines in growth associated with the abrupt incidence of warmer temperatures (Li 1980). Temperature effects on phytoplankton growth and composition are more important in shallow coastal waters, which experience larger temperature fluctuations than oceanic waters. Predicted increasing sea surface temperatures of 2°C–4°C may shift the community composition toward species adapted to warmer temperatures as observed in the temperate North Atlantic (Edwards and Richardson 2004). Several well-studied PSP dinoflagellates, such as *A. catenella* in Puget Sound (Moore et al. 2008b) and *G. catenatum* in Tasmania, Australia (Hallegraeff et al. 1995), bloom in well-defined seasonal temperature windows (>13°C and >10°C, respectively). Climate change scenarios are predicted to generate longer-lasting bloom windows (Fig. 7).

In the North Sea, the NAO has been shown to affect the length of the phytoplankton growing season, which has increased in parallel with the warming of sea surface temperatures (Barton et al. 2003). Seasonal timing of phytoplankton blooms is now occurring there up to 4–6 weeks earlier (Fig. 8). However, where individual zooplankton or fish grazers are differentially impacted by ocean warming, this may have cascading impacts on the structure of marine food webs ("match-mismatch" sensu Cush-
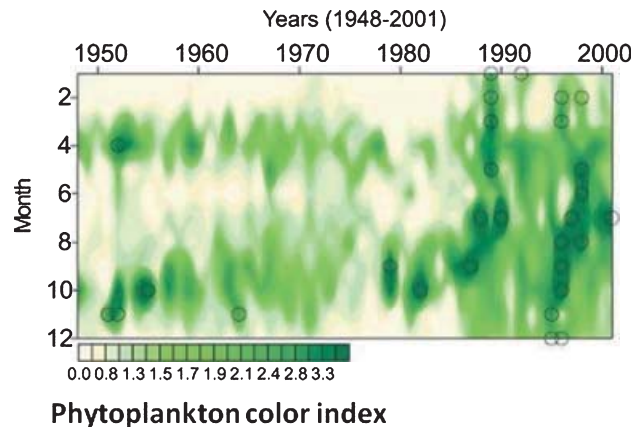

FIG. 8. Long-term monthly values of "phytoplankton color" in the central North Sea from 1948 to 2001. Circles denote >2 SD above the long-term monthly mean and a major regime shift ~1998. Note an apparent shift toward earlier spring and autumn phytoplankton blooms (after Edwards 2004, with permission).

ing 1974). Replacement in the North Sea of the cold-water copepod *Calanus finmarchicus* by the warm-water *Calanus helgolandicus* has been circumstantially associated with the decline of cod (Edwards et al. 2008). Similarly, Attrill et al. (2007) predict an increasing occurrence of jellyfish in the central North Sea over the next 100 years related to the increased Atlantic inflow to the northern North Sea.

Sea-level rise, wind, and mixed-layer depth. Increasing sea surface temperature and water column stratification (shallowing of the mixed layer) can be expected to have a strong impact on phytoplankton because of the resource requirements and temperature ranges that species are adapted to. Wind determines the incidence of upwelling and downwelling, which in turn strongly affect the supply of macronutrients to the surface (recognized as drivers of *G. catenatum* blooms off Spain; Fraga and Bakun 1990). Climate change may thus affect the timing and strength of coastal upwellings. Broad changes in ocean circulation such as those comprising the deep-ocean conveyor belt (Rahmstorf 2002) can also cause displacements to current systems and associated algal bloom phenomena. Wind-driven currents can transport phytoplankton away from a region and affect the size and frequency of formation of mesoscale features such as fronts and eddies. Locally, wind intensity strongly influences depth and intensity of vertical mixing in the surface layer, thereby affecting phytoplankton access to nutrients, light availability for algal photosynthesis, and phytoplankton exposure to potentially harmful UVB radiation. Winds can also influence the supply of iron to the surface ocean through aeolian transport of dust from land to sea, contributing micronutrients such as iron, which has been shown to stimulate *K. brevis* blooms off Florida (Walsh and Steidinger 2001). Extreme climate events such as hurricanes
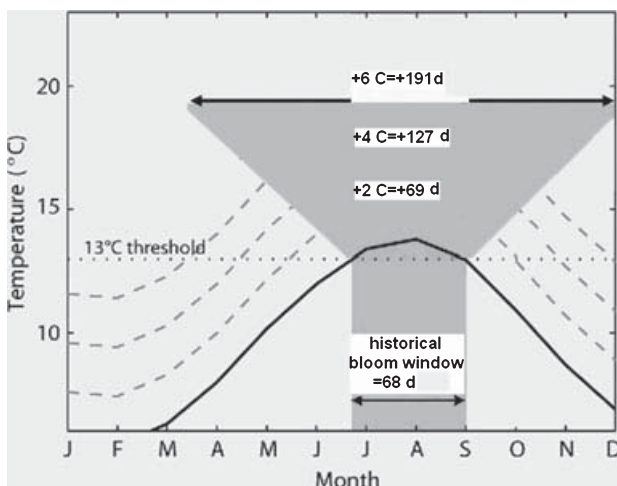

FIG. 7. Scenarios for warmer sea surface temperature conditions in Puget Sound by 2, 4, and 6°C would widen the >13°C window (in gray) of accelerated growth for the PSP dinoflagellate *Alexandrium catenella*. After Moore et al. (2008b). PSP, paralytic shellfish poisoning.

are also known to expand the existing distribution of cyst-producing toxic dinoflagellates (e.g., *A. tamarense* in New England after a 1972 hurricane; Anderson 1997). Sea-level rises of 18 to 59 cm (up to 1 m) predicted by 2100 (IPCC 2008) have the potential to increase the extent of continental shelf areas, providing shallow, stable water columns favoring phytoplankton growth. The proliferation of coccolithophorids in the Cretaceous geological period has been attributed to expanding continental shelf areas (Bown et al. 2004).

Finally, increasing temperature driven by climate change is predicted to lead to enhanced surface stratification, more rapid depletion of surface nutrients, and a decrease in replenishment from deep nutrient-rich waters (Fig. 9A). This in turn will lead to changes in phytoplankton species, with smaller nano- and picoplankton cells with higher surface area:volume ratios (better able to cope with low nutrient levels) favored over larger cells. A decline in silica concentrations is widely expected in a warming world (reported, e.g., from the Mediterranean; Goffart et al. 2002), and this is anticipated to restrict the abundance of diatoms. Mixing depth affects sea surface temperature, the supply of light (from above) and nutrients (from below), and phytoplankton sinking losses within the surface layer. Climate models predict changes in mixed-layer depth in response to global warming for large regions of the global ocean. In the North Pacific, decadal-scale climate and mixed-layer variability, (Hayward 1997) and, in the North Atlantic, longer-term changes in wind intensity and stratification since the 1950s have been associated with considerable changes in phytoplankton community structure (Richardson and Schoeman 2004). In regions with intermediate mixing depth, increased stratification is expected to result in decreased phytoplankton biomass due to reductions in nutrient supply. The observed reductions in open-ocean productivity (''desertification'') during ENSO warming events provide insight on how future climate change can alter marine food webs (Behrenfeld et al. 2006). Conversely, in high-latitude regions with relatively deep mixing and nonlimiting nutrients, decreasing mixing depth is expected to result in higher phytoplankton biomass because of increased light availability (Fig. 9B; Doney 2006).

Impact of heavy precipitation and storm events and flash floods. Episodic storm events affect the timing of freshwater flow, residence time, and magnitude and time of nutrient pulses. Changes in the amount or timing of rainfall and river runoff affect the salinity of estuaries and coastal waters. Salinity is relatively constant throughout the year in most oceanic waters and in coastal areas that receive little freshwater input. Coastal phytoplankton is subject to more variation in salinity than phytoplankton in oceanic waters. While some species grow well over a wide range of salinities, other species grow best only at salinities that are low (estuarine), intermediate (coastal), or high (oceanic species). Freshwater also modifies the stratification of the water column, thereby affecting nutrient resupply from below. While diatoms seem to be negatively affected by the inhibition of mixing associated with river discharge, dinoflagellates often benefit as this usually increases stratification and the availability of humic substances for growth (Graneli and Moreira 1990, Doblin et al. 2005). PSP dinoflagellate blooms of *G. catenatum* (in Tasmania; Hallegraeff et al. 1995) and *A. tamarense* (off Massachusetts; Anderson 1997) tend to be closely associated with land runoff events. In Hiroshima Bay, blooms of the fish-killing raphidophyte

FIG. 9. Predicted phytoplankton response to increased temperature in ocean surface waters: (A) reduced productivity in the thermally stratified water of tropical and midlatitudes caused by reduced nutrient supply; (B) increased productivity at polar and subpolar salt-stratified oceans where reduced mixing keeps plankton closer to the well-lit nutrient-sufficient surface layers. Adapted from Doney (2006).
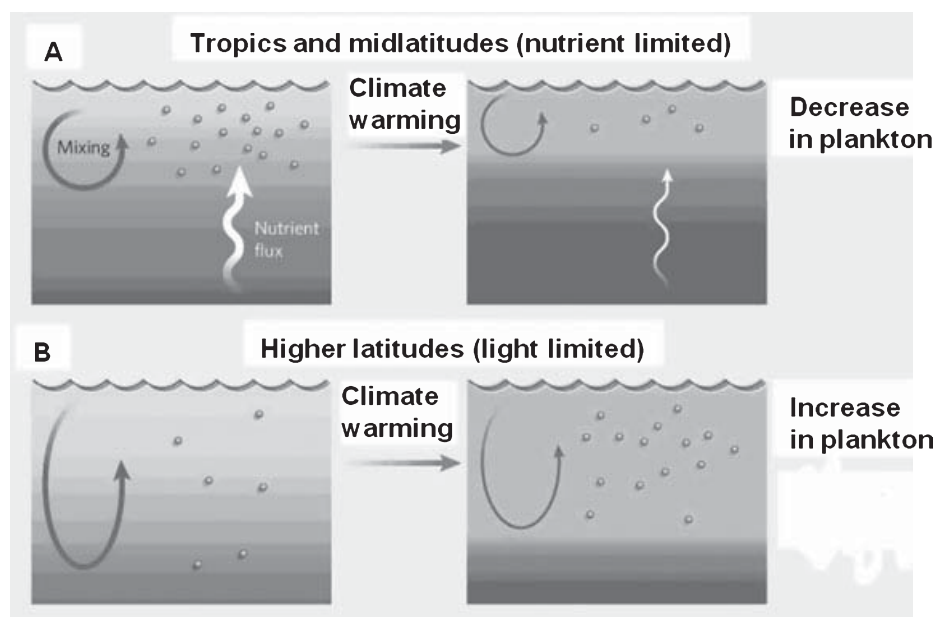
Chattonella marina followed typhoon-induced accretion of nutrient-rich land runoff (Kimura et al. 1973). Climate change is predicted to cause rainfall to occur in more concentrated bursts followed by long dry periods, thus favoring dinoflagellates.

Increased CO_2 and ocean acidification. Increasing atmospheric CO_2 is leading to ocean acidification, which could potentially have an adverse impact on calcifying organisms, the most important of which in terms of biomass and carbon sequestration is the coccolithophorid *Emiliania huxleyi* (Riebesell et al. 2000). Calculations based on CO_2 measurements of the surface oceans indicate that uptake by the oceans of approximately half the CO_2 produced by burning fossil fuels has already led to a reduction of surface pH by 0.1 unit. Under the current scenario of continuing global CO_2 emissions from human activities, average ocean pH is predicted to fall by 0.4 units by the year 2100 (Orr et al. 2005). Such pH is lower than has been experienced for millennia, and, critically, this rate of change is 100 times faster than ever experienced in the known history of our planet (Raven et al. 2005b). Experimental manipulations of pH in *E. huxleyi* cultures have both produced reduced (Riebesell et al. 2000) and enhanced calcification and growth (Iglesias-Rodriguez et al. 2008). Strikingly, depression of calcification under high CO_2 is most expressed under high-light conditions (Feng et al. 2008; Fig. 10), emphasizing the need to carefully consider factor interactions in ecophysiological experiments. Decreasing pH < 8.0 has been observed to negatively affect nitrification in marine bacteria and therefore could potentially reduce nitrate availability for plankton algae. The nitrogen-fixing tropical cyanobacterium *Trichodesmium* may be a beneficiary of ocean acidification, however (Hutchins et al. 2007). Decreasing pH has also been found to increase the availability of toxic trace elements such as copper. As the relative consumption of HCO_3^- and CO_2 differs between phytoplankton species, changes in their availability may affect phytoplankton at the cellular, population, and community levels. Most HAB species tested thus far lack carbon concentrating mechanisms (CCMs), and hence their photosynthetic performance may benefit from increased atmospheric CO_2 (e.g., *E. huxleyi* in Fig. 11). However, photosynthetic performance in diatom species such as *Skeletonema,* for which photosynthesis is already CO_2 saturated, will remain constant (Beardall and Raven 2004). In bioassays in the equatorial Pacific, high CO_2 (750 ppm) favored the haptophyte *Phaeocystis* at the expense of diatoms, whereas at low CO_2 (150 ppm), diatom growth was stimulated (Tortell et al. 2002). Riebesell et al. (2007), working with mesocosms dominated by diatoms and coccolithophorids, observed increases in productivity of 27% and 39% when CO_2 levels were elevated to 700 and 1,050 ppm, respectively. Similarly, Schippers et al. (2004) predict in nutrient-replete systems
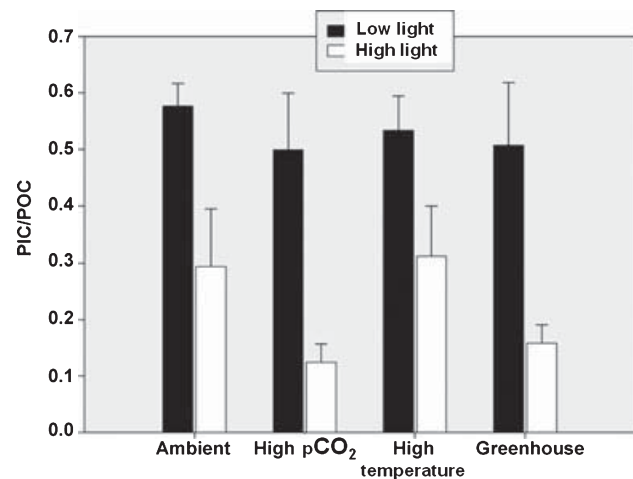

Fig. 10. Calcification of the coccolithophorid *Emiliania huxleyi* (expressed as the particulate inorganic carbon [PIC] to particulate organic carbon ratio [POC]) as a function pCO_2 (ambient 375 ppm or high 750 ppm), temperature (ambient 20°C or high 24°C), and light (low = black bars; high = open bars). Neither pCO_2, light, nor temperature influences PIC:POC under low light, but calcification is most reduced under a combination of high light × high pCO_2 (after Feng et al. 2008).
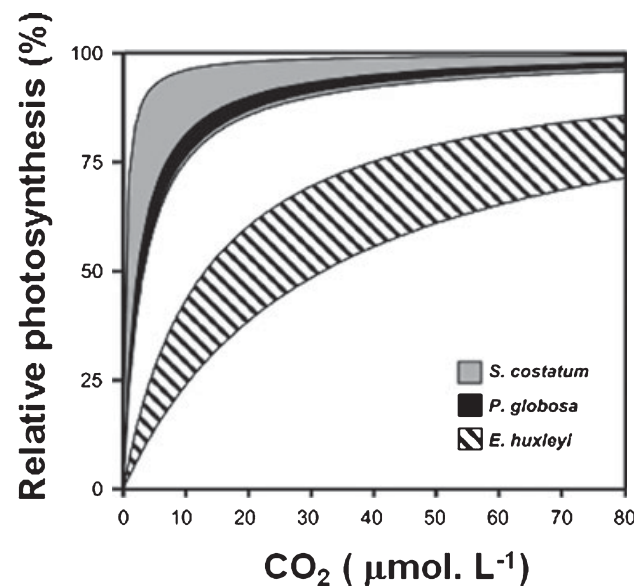

Fig. 11. Photosynthesis of three different phytoplankton species (diatom *Skeletonema costatum*, haptophytes *Phaeocystis globosa* and *Emiliania huxleyi*) with respect to CO_2 sensitivity (adapted from Rost and Riebesell 2004). Microalgal species differ in their responses to CO_2, which implies that a high-CO_2 ocean will induce shifts in phytoplankton species composition.

a 10%–40% increase of marine productivity for species with low bicarbonate affinity, thus potentially aggravating some coastal algal blooms.

UV radiation. Although the implementation of the Montreal Protocol has done much to slow the build-up of chlorofluorocarbons in the stratosphere, elevated UVB levels from the Arctic and Antarctic

ozone holes are expected to persist until at least 2050. UVB can negatively affect several physiological processes and cellular structures of phytoplankton, including photosynthesis, nutrient uptake, cell motility and orientation, algal life span, and DNA (Häder et al. 1991). Whereas shorter wavelengths generally cause greater damage per dose, inhibition of photosynthesis by ambient UVB increases linearly with increasing total dose. In clear oceanic waters, UVB radiation can reach depths of at least 30 m. Although some phytoplankton may acclimate to, compensate for, or repair damage by UVB, this involves metabolic costs, thereby reducing energy available for cell growth and division. Raven et al. (2005a) suggest that UVB intensity affects the size ratio in phytoplankton communities because small cells are more prone to UVB and have comparatively high metabolic costs to screen out damaging UVB. Many surface-dwelling red-tide species of raphidophytes and dinoflagellates possess UVB-screening pigments, which give them a competitive advantage over species lacking such UV protection (Jeffrey et al. 1999). In some species, nutrient limitation of either N or P (from increased water column stratification) can enhance the sensitivity of cells to UVB damage (Shelly et al. 2002).

Feedback mechanisms. One cannot talk about the impact of climate on phytoplankton without also considering the impact of phytoplankton on climate (Fig. 12). Phytoplankton play a key role in several global biogeochemical cycles and thereby exert important feedback effects on climate by influencing the partitioning of climate-relevant gases between the ocean and the atmosphere. Some species (e.g., *Emiliania, Phaeocystis*) are producers of dimethylsulfonium propionate, a precursor of dimethylsulfoxide (DMS), which in the atmosphere is oxidized into sulfate, which forms condensation nuclei for clouds (Charleson et al. 1987). Subsequent work on DMS has clarified that it is not just phytoplankton, however, but also zooplankton and bacterial food-web structure and dynamics that drive oceanic production of atmospheric sulfur. Phytoplankton, therefore, indirectly affect albedo and precipitation and hence coastal runoff, salinity, water column stratification, and nutrient supply.

Through the process of photosynthesis, phytoplankton constitute a major consumer of CO_2. The ability of the oceans to act as a sink for anthropogenic CO_2 largely relies on the conversion of this gas by phytoplankton into particulate
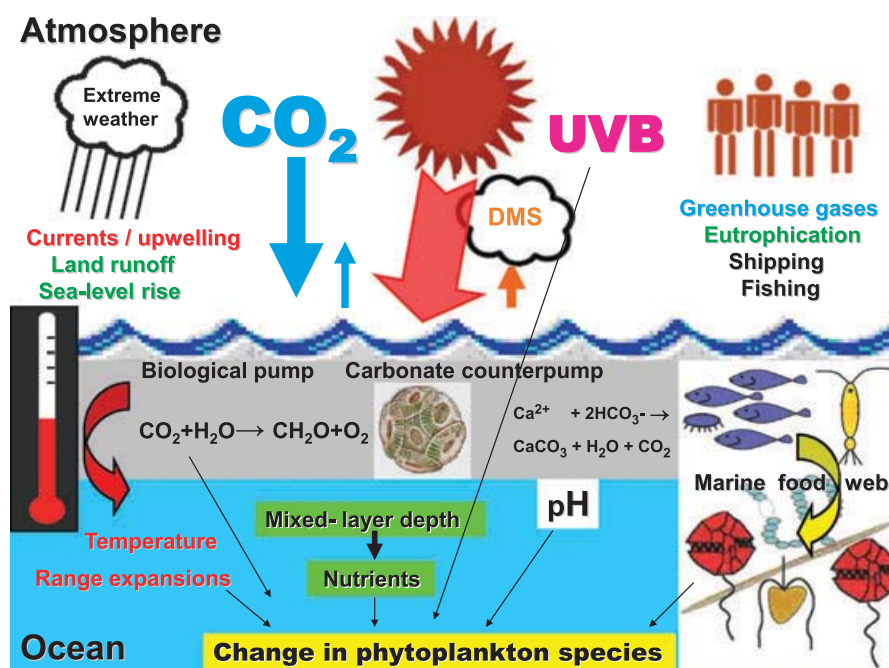

Fig. 12. Summary diagram of known feedback mechanisms between physicochemical climate variables and biological properties of marine phytoplankton systems. Red: Greenhouse warming raises surface temperatures and causes a shoaling of mixed-layer depths but can also have broader impacts on global currents, upwelling, and even the deep-ocean conveyor belt. Blue: Increased atmospheric CO_2 drives the biological pump, can alter phytoplankton species composition, and can alter ocean pH, influencing calcification of coccolithophorids but also nutrient availability. Green: Nutrient impacts from water column stratification, as well as linked to shifts in marine food-web structure, influenced by fishing, eutrophication, and even ship ballast water invasions. Yellow: Marine food-web structure, including top-down as well as bottom-up influences on phytoplankton species composition. Orange: Selected phytoplankton such as coccolithophorids produce dimethylsulfoxide (DMS), acting as cloud condensation nuclei, thereby reducing solar irradiation. Other anthropogenic influences in terms of eutrophication, shipping (ballast water introductions), and fishing are also indicated. Without exception, all perturbations will drive changes in phytoplankton species composition.

organic matter and subsequent partial loss to the deep ocean (so-called biological pump). Any reduction in net ocean CO_2 uptake caused by shifts in ocean circulation or reduced phytoplankton growth in surface waters reducing the export of organic matter to the deep sea via the biological pump could lead to an acceleration in the rate of atmospheric CO_2 increase and global warming. Models have estimated that a 50% decrease in oceanic calcification from ocean acidification thus would reduce atmospheric CO_2 by 10–40 ppm (Heinze 2004, Munhoven 2007), equivalent to 5–20 years of industrial emissions. Conversely, an increase in calcification would increase CO_2 levels by a similar amount (carbonate counterpump). Coupled climate-carbon models are increasingly revealing feedback mechanisms, which were completely unpredicted from first principles. Stratosphere ozone depletion increases the strength of Southern Ocean winds and thereby the ventilation of carbon-rich deep water, with consequences of reduced ocean carbon uptake and enhanced ocean acidification (Lenton et al. 2009).

Woods and Barkmann's (1993) ''plankton multiplier'' is an example of a positive feedback mechanism linking greenhouse warming to the biological pump. Enhanced greenhouse CO_2 induces ocean surface warming, diminishing winter convection and nutrient availability and thereby primary production, thus weakening the biological pump and further enhancing atmospheric CO_2. These authors suggested that a similar mechanism may have underpinned global warming at the end of the ice ages when the Milankovich effect enhanced greenhouse warming. Surface phytoplankton blooms influence the oceanic heat budget, and this is dependent not only on the chl biomass but also on its precise vertical distribution (Frouin and Lacobellis 2002).

Finally, another powerful mechanism for algal bloom formation occurs through ''top-down control'' of the marine food web (Turner and Granéli 2006). Overfishing removes top fish predators, stimulating small fish stocks, which graze away zooplankton, thus relieving phytoplankton grazing pressure. Differential impacts of climate change on individual zooplankton or fish grazers (uncoupling between trophic levels) thus can result in stimulation of HABs. Figure 12 summarizes known feedback mechanisms between physicochemical climate variables and biological properties of marine phytoplankton systems, altogether confronting us with a formidable predictive challenge. Without exception, all physicochemical climate stressors drive changes in phytoplankton species composition, but the precise direction of such changes (i.e., whether they may lead to HABs) remains largely unpredictable in view of our current incomplete knowledge of phytoplankton ecophysiology.

CONCLUSIONS

Climate change confronts marine ecosystems with multifactorial stressors, such as increased temperature, enhanced surface stratification, alteration of ocean currents, intensification or weakening of nutrient upwelling, stimulation of photosynthesis by elevated CO_2, reduced calcification from ocean acidification, and changes in land runoff and micronutrient availability. Complex factor interactions are rarely covered by simulated ecophysiological experiments, and the full genetic diversity and physiological plasticity of phytoplankton taxa are rarely considered. Traditional experimental challenges last days to weeks and impose new growth conditions rather quickly, thus only allowing for limited acclimation (testing short-term physiological plasticity but without genetic changes). Predicted global change will occur gradually over decades, allowing for adaptation of species to perhaps become genetically and phenotypically different from the present population. Laboratory studies should aim to mimic environmental conditions as closely as possible (Rost et al. 2008). A typical example is the problem of the potential impact of increased CO_2 on the coccolithophorid *E. huxleyi*. Initial concerns focused on reduced calcification (Riebesell et al. 2000), but we now recognize that increased CO_2 at the same time stimulates photosynthesis (Iglesias-Rodriguez et al. 2008). Complex factor interactions between increased CO_2, light, and temperature on the calcification versus photosynthesis dynamics of *E. huxleyi* have been demonstrated by Feng et al. (2008), while geographic strain variability of this ''cosmopolitan'' taxon has confounded the extensive literature on this taxon (Langer et al. 2009). At the same time, field observations of *E. huxleyi* are suggesting an apparent range expansion in the past two decades toward both the Arctic (Bering Sea; Merico et al. 2003) and Antarctic (Cubillos et al. 2007), but the environmental drivers underpinning this are by no means clear. Undoubtedly, there will be winners and losers from climate change, and one thing we can be certain about is local changes in species composition, abundance, and timing of algal blooms.

The greatest problems for human society will be caused by being unprepared for significant range extensions of HAB species or the increase of algal biotoxin problems in currently poorly monitored areas. While, for example, ciguatera contamination would be expected and monitored for in tropical coral reef fish, with the apparent range extension of the causative benthic dinoflagellate into warm-temperate seagrass beds of Southern Australia, other coastal fisheries unexpectedly could be at risk. Range expansion of *Noctiluca* from Sydney to Tasmania exposed the salmonid aquaculture industry to a novel HAB problem. Polar expansion of domoic-acid-producing *Pseudo-nitzschia australis* could pose a

novel threat to krill-feeding whales (Lefebvre et al. 2002). Similarly, incidences of increased surface stratification in estuaries or heavy precipitation or extreme storm events are all warning signs that call for increased vigilance of monitoring seafood products for algal biotoxins even in areas not currently considered to be at risk. Changes in phytoplankton communities provide a sensitive early warning for climate-driven perturbations to marine ecosystems.

Only with improved global ocean observation systems (GOOS) can we hope to quantitatively monitor the key variables identified in this review. New, improved, and expanded ocean sensor capabilities (e.g., argo floats, ocean gliders, coastal moorings and coastal radar, multiwavelength and variable fluorometers, optical sensors) are necessary to realize the full potential of in situ ocean-observing networks in support of integrated satellite-derived ''ocean color'' maps and expanded biological and biogeochemical observations (continuous plankton recorder, ecogenomics). Observations from the individual components of such systems must be integrated through data management and communication capabilities that provide open searchable access and routine delivery to all users. Sustained observations, process research, and modeling should determine fluxes and cycling of biogeochemical variables, identify impacts on ecosystems, and resolve feedback from ecosystems on climate. Achieving this will require extensive infrastructure investment and poses a major challenge for the marine science community. It is pleasing to see that a number of national (e.g., the U.S. NSTC Joint Subcommittee on Ocean Science and Technology 2007 Ocean Observatories Initiative [OOI], the Australian Integrated Marine Observing System [IMOS 2009]) and international programs (e.g., the Intergovernmental Oceanographic Commission of UNESCO's GEOHAB) are actively pursuing these ambitious goals, but necessary if we wish to define management options, forecast ocean-related risks to human health and safety, and shed light on the impact of climate variability on marine life and humans in general.

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