# Chapter 2
# Harmful Algal Blooms and the Importance of Understanding Their Ecology and Oceanography

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## 2.1 Introduction

Over the decades of the 1980s and 1990s, as the expansion in harmful algal blooms (HABs) was gaining recognition (e.g., Anderson 1989; Hallegraeff 1993; GEOHAB 1998; Smayda 2002), no longer was it sufficient to study bloom events in isolation; many countries were facing a bewildering array of impacts caused by species not previously known or recognized in those regions. The complexity of the HAB problem, its causative factors, and the impacts HABs have on the environment were becoming well characterized. The benefits of collaborative, cooperative, and comparative studies on HABs were recognized to advance the understanding of this phenomenon and to provide scientific guidance to managers. The aim of this chapter is to introduce several aspects of this complex phenomenon, and why an understanding of ecology and oceanography of HAB species and their associated events is so important. This chapter also briefly introduces the effects of global changes in nutrients and climate that are developed more fully in subsequent chapters [see Chap. 4, Glibert et al. (2018b), and Chap. 5, Wells and Karlson

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(2018)], as well as a number of concepts relating to the adaptive strategies of HABs which help to explain why they are so successful in environments subject to many anthropogenic changes.

## 2.2 What Are Harmful Algal Blooms?

The majority of algae in marine and freshwaters are not only beneficial but also necessary to the functioning of aquatic ecosystems; they form the base of the food web, and it is this microscopic life on which all aquatic life ultimately depends for food (Glibert et al. 2005). Algae produce oxygen and also play an important role in regulating atmospheric $CO_2$ by sequestering it during production and transporting it to deeper waters. Yet, a comparatively small subset of the total known microscopic algal species can cause problems. This can occur when they accumulate in sufficient numbers, when they produce toxins, or when they directly or indirectly interfere with other organisms or alter the physical habitat indirectly, negatively impacting the growth of others. These are known as the harmful algae, and their associated proliferation events are referred to as HABs. HABs may be caused by the explosive growth of a single species that rapidly dominates the water column but may also be the result of highly toxic cells that do not accumulate in high numbers. Therefore, in some cases, toxic conditions can also occur when the water is clear with very low cell concentrations. The effects of HABs, detailed in the next section, are as varied as the organisms themselves.

The causative organisms, the harmful algae, were formerly called “red tides” because many were composed of dinoflagellates that in high densities coloured the water red, but blooms may also be green, yellow, or brown, depending on the type of algae present and their pigmentation (Fig. 2.1; Glibert et al. 2005). Many marine HABs are, indeed, dinoflagellates, but other classes of algae, including cyanobacteria, raphidophytes, and diatoms, have members that may form HABs under some conditions. Some HABs organisms are not algae at all, that is, they do not depend on photosynthesis for their nutrition; they obtain their nutrition exclusively through grazing and particle ingestion, while many of them have the ability to use varied sources of nutrition, mixing photosynthesis and inorganic nutrient uptake together with grazing, depending on the environmental conditions [see Chap. 7, Flynn et al. (2018)]. Other harmful algae that also are not technically “algae” are the cyanobacterial HABs, CyanoHABs, some of which have the ability to “fix” their own nitrogen (N) from the atmosphere. The term “HAB” also applies to blooms of some nontoxic micro- or macroalgae (seaweeds), which can grow out of control and cause major ecological impacts such as the displacement of indigenous species, habitat alteration, or oxygen depletion. All of these harmful causative organisms are included under the HAB species umbrella label, and thus the term “HAB” is operational and not technical, but this distinction is irrelevant in terms of human health and ecological and economic impacts. Moreover, with few exceptions, there are no formal definitions of the absolute abundance of a HAB species that determine whether it is a “bloom.”

**Fig. 2.1** Many HABs are produced by the accumulation of vividly coloured cells in surface water. The blooms shown here are from the Philippines (panel **a**, photo: http://taqplayer.info/philippine-red-tide); Florida, USA (panel **b**, photo: http://www.politicnote.com/army-corps-of-engineers-battles-guacamole-thick-florida-algae/); Qingdao, China (panel **c**, photo: www.sailjuice.com); Long Island, NY, USA (panel **d**, photo by C. Gobler); Sydney Harbour, Australia (panel **e**, photo: https://bioweb.uwlax.edu/bio203/f2013/bradford_andr/habitat.htm); and a freshwater lagoon in Uganda (panel **f**, photo by P. Glibert). These high biomass blooms can cause hypoxia, can contribute to toxicity of fish and shellfish, and can cause other environmental problems

## 2.3 How Are HABs Harmful?

HABs can be harmful in several fundamental ways. Many HABs produce toxins, some of which are among the most potent toxins known. These toxins have various vectors by which harmful effects are transferred through the food chain or to human consumers, and there is a wide range of potency (Table 2.1). The range of toxins produced by the common marine HABs includes brevetoxins, the cause of neurotoxic shellfish poisoning (NSP); saxitoxins, the cause of paralytic shellfish poisoning (PSP); okadaic acid (OA), the cause of diarrhetic shellfish poisoning (DSP); domoic acid (DA), the cause of amnesic shellfish poisoning (ASP); azaspiracid, the cause of azaspiracid shellfish poisoning (AZP); and ciguatoxins (CTX), the cause of ciguatera fish poisoning (Landsberg 2002; Glibert et al. 2005). There are no known antidotes for poisonings caused by HAB toxins. Although human poisoning events are few in the developed world due to careful monitoring of seafood products, it has been estimated that direct human poisonings in many parts of Asia from toxic algae number in the thousands annually (Yan and Zhou 2004). In Florida, USA, when *Karenia brevis* blooms occur, increases in hospitalizations have been reported due to gastrointestinal and respiratory irritation that especially affects those that are immune-compromised (Kirkpatrick et al. 2006). CyanoHABs also have a range of human effects, depending on the toxin involved. Some effects are as mild as skin rashes or irritations, while other effects include cancer, particularly liver cancer, caused by long-term exposure to toxins such as microcystins in drinking water (c.f., Backer and McGillicuddy 2006; Bláha et al. 2009, and references therein).

Toxins may kill shellfish or fish directly or may have little effect on them but may cause illness or death of people or other consumers in the food web when fish or shellfish that have accumulated the algal toxins are eaten (Landsberg 2002). Not all fish exposed to algal toxins die; some experience extreme illness. As an example, acute effects of brevetoxin (from *K. brevis*) on fish have been reported to include altered swimming behaviour (swimming in a spiral, twisting behaviour,

**Table 2.1** Major syndromes, vectors, and human health symptoms associated with common HABs

| Illness | Major vector | Symptoms |
|---|---|---|
| *Amnesic* shellfish poisoning (ASP) | Domoic acid from *Pseudo-nitzschia* sp. in shellfish | Short-term memory loss, vomiting, cramps |
| *Diarrhetic* shellfish poisoning (DSP) | Okadaic acid from *Dinophysis* sp. in shellfish | Diarrhoea, vomiting, cramping |
| *Neurotoxic* shellfish poisoning (NSP) | Brevetoxin from *Karenia* sp. in shellfish, aerosolized toxins | Nausea, diarrhoea, respiratory distress, eye irritation |
| *Paralytic* shellfish poisoning (PSP) | Saxitoxin from *Alexandrium* sp. and other species in shellfish | Numbness around the lips and mouth, respiratory paralysis, death |
| Cyanotoxin poisoning | Microcystins and other toxins from cyanobacteria in water | Skin irritation, respiratory irritation, tumour promotion, liver cancer, liver failure |

loss of equilibrium), defecation and regurgitation, paralysis of the pectoral fin, curvature of the caudal fin, and convulsions (Landsberg 2002). Deaths of birds and mammals, such as dolphins, manatees, sea lions, and whales, have also been related to HABs and their toxins and are of immense public and economic concern when they do occur. One of the most well-documented effects of toxin transfer through the food web is that of California sea lions that have been shown to become intoxicated with DA resulting from *Pseudo-nitzschia* blooms, which accumulate in the northern anchovy, a common prey item for the sea lions. Seizures, complications of pregnancy, and death are among the commonly observed effects in these animals (Silvagni et al. 2005). A recent massive whale mortality event in Chile in 2015, including at least 340 primarily sei whales, has been linked to PSP toxicity from feeding near shore (Häussermann et al. 2017).

While the most familiar impact of HABs is their intoxication of shellfish, leading to contaminated seafood, some HAB toxins have also been shown to have adverse effects on very early life stages of consumers, leading to increased mortalities at the larval stage. For example, experiments conducted on embryos and larvae of freshly spawned oysters, *Crassostrea virginica* and *C. ariakensis*, exposed to the toxic dinoflagellate *Karlodinium veneficum* showed increased mortality relative to similar embryos and larvae exposed to a control diet (Glibert et al. 2007; Stoecker et al. 2008). These experiments also demonstrated important behavioural changes in pediveliger larvae when exposed to *K. veneficum* in their diet, leading them to stop swimming and to sink. Even if such effects did not immediately result in mortality, any change in behaviour may influence larval dispersal, reduce feeding and growth, and likely increase the susceptibility of larvae to predation. Related results have been documented for the HAB dinoflagellate *Prorocentrum minimum*. Larvae had poorer survival and lower settling success with only *P. minimum* in the diet, but survival improved when the proportion of *P. minimum* in their diet was reduced (Luckenbach et al. 1993; Wikfors and Smolowitz 1995). In Australia, the related HAB species, *P. rhathymum*, has been associated with mortalities of spat of the Japanese or Pacific oyster, *C. gigas* (Pearce et al. 2005).

The other fundamental way in which HABs are harmful is through high biomass accumulation that may lead to environmental damage, including hypoxia, anoxia, and shading of submerged vegetation, each of which, in turn, can lead to a multitude of negative environmental consequences. These are the blooms that cause visible water discoloration (Fig. 2.1). Such high biomass blooms can cause hypoxia and anoxia, and the global occurrences of such "dead zones" are expanding (Diaz and Rosenberg 2008).

Many types of harmful effects occur from HABs that are not directly toxic. Some HABs have physical structures, such as spines, that can lodge in fish gills and can cause irritation and eventual suffocation. Some HABs have more subtle effects on the ecosystem or effects that are more difficult to quantify in the wild. Blooms that are known to disrupt ecosystem function but which may or may not necessarily be toxic are considered ecosystem disruptive algal blooms (EDABs; Sunda et al. 2006). Blooms of picoplankton, such as the pelagophyte *Aureococcus anophagefferens* (brown tide) and the CyanoHAB *Synechococcus* sp., which can be sustained for long periods of time once established, can have multiple negative ecosystem effects that, in turn, may help to sustain these blooms. The positive feedbacks of reduced grazing and/or bottom shading contribute to the availability of nutrients for these blooms (Sunda et al. 2006). In Laguna Madre, Texas, which experienced a nearly decade-long bloom of the EDAB species *Aureoumbra lagunensis*, the density of protozoan grazers was found to be greatly reduced during blooms, and it was suggested that a thick polysaccharide layer around the cells may make it difficult for the protozoa to feed (Buskey and Stockwell 1993; Buskey et al. 2001). Allelopathic chemicals may also play an important role in maintaining EDAB species (Sunda et al. 2006; Granéli et al. 2008).

In addition to ecological and human health impacts of HABs, the economic impacts can also be very large. The overall economic impact of HABs is difficult to determine, but the costs range from the direct expenses of public health and medical care for those affected to losses in commercial and recreational fishing and in tourism-related activities from water quality deterioration. Single HAB fish kill events in Korea and shellfish kill events in China have been estimated to have cost from $1 to $100 million and $300 million, respectively, in lost fish or shellfish in aquaculture settings, while in Japan such events have been estimated to have resulted in losses of fish worth more than $300 million (GEOHAB 2010; Trainer and Yoshida 2014). Loss of revenue from shellfish harvesting area closures also takes enormous economic toll on communities affected. For example, in 2003, it was estimated that more than $6 million in revenue from sport fishing and tourism due to fish kills were lost in Texas due to a bloom of a small flagellate (*Prymnesium parvum*) in inland rivers and reservoirs. Yet another economic cost in some regions is the effect of HABs on seawater reverse osmosis (SWRO) desalination plants (e.g., Villacorte et al. 2015). In this case, the main concern is biofouling of the RO membranes, which can cause plants to shut down, resulting in a loss of an important utility service in regions where this is a major source of freshwater. In addition, where recurrent HABs are documented, another economic cost of HABs is that of sustained environmental monitoring to protect human health or industries such as aquaculture. Monitoring is one of the most effective ways to prevent human exposure to HAB-related toxins.

## 2.4 Where Do HABs Occur?

HABs are found in all parts of the world, in all types of waters. While marine HABs are emphasized herein, the trends in freshwater HABs are equally concerning. Several examples demonstrate the global expansion of HABs. In the Gulf of Maine, occurrences of the PSP-causative dinoflagellate *Alexandrium fundyense* and PSP toxicity were rare prior to about 1970 but have been frequent in the past three decades. In fact, PSP occurrences have increased globally in this same time frame (e.g., Anderson 1989; Hallegraeff 1993). PSP toxicity has increased in proportion to the growth of the human population in Puget Sound, Washington

State (Trainer et al. 2003). The bloom-forming dinoflagellate *P. minimum* is also now documented to cover most coasts throughout the world and has been documented to have expanded in concert with escalating eutrophication (Heil et al. 2005; Glibert et al. 2008, 2012). Based on analyses of frustules preserved in cores, blooms of the diatom *Pseudo-nitzschia* spp. in the Gulf of Mexico were also rare prior to the 1950s, but have increased significantly in abundance and frequency since then, concomitant with increases in nutrient loading (Parsons et al. 2002). In Europe and Asia, there are also more blooms with more toxic effects than in previous decades (Granéli et al. 1999). *Cochlodinium* (*Margalefidinium*) *polykrikoides* is among the many species of dinoflagellates which are increasingly adversely affecting fisheries, tourism, and economies around the world (e.g., Yuki and Yoshimatsu 1989; Guzman et al. 1990; Kim et al. 1999, 2004; Lee 2008; Tomas and Smayda 2008; Mulholland et al. 2009; Howard et al. 2012; Al-Azri et al. 2014). While previously most commonly observed in tropical systems (Steidinger and Tangen 1997), *C. polykrikoides* is now increasingly observed in temperate systems (e.g., Kudela et al. 2008; Mulholland et al. 2009). As such, *C. polykrikoides* appears to be similar to many other harmful dinoflagellates undergoing global expansion (e.g., Heil et al. 2005; Glibert et al. 2005, 2008; Harrison et al. 2011).

One of the areas where HAB expansion has been particularly pronounced has been in the coastal waters of Asia, as shown, for example, in increasing observations of “red tides” in Chinese coastal waters [GEOHAB 2010; see also Chap. 14, Furuya et al. (2018), and Chap. 15, Yu et al. (2018)]. Microalgae are not the only HABs increasing. In 2008, a bloom of the macroalgal species *Ulva prolifera* (*Enteromorpha prolifera* or sea lettuce) occurred at the venue of the Olympic Games sailing competition, almost blanketing the water with filamentous scum [Hu et al. 2010; Huo et al. 2013; see also Chap. 16, Liu and Zhou (2018)]. Blooms of this magnitude in this region had not previously been observed. One of the features of this species and its blooms is that it tends to float, making detection from remote sensing (satellite imaging) feasible. It is from such approaches that the scale of these blooms and their change over time can be estimated (Hu et al. 2010). A 10-year record of images of the region shows that prior to 2007, the area covered by these green tides was $<21$ km$^2$. In 2008 the scale of the bloom was $>1900$ km$^2$, and in 2009 it was 1600 km$^2$ (Hu et al. 2010).

Similarly, in the past several decades, a massive expansion of dinoflagellate blooms has occurred in the Arabian Sea and Sea of Oman (formerly Gulf of Oman) (Parab et al. 2006; Al-Azri et al. 2007; Gomes et al. 2008; Harrison et al. 2011). These blooms were not observed during the Joint Global Ocean Flux Study (JGOFS) cruises of the 1990s (Gomes et al. 2008) but have expanded considerably, consistent with climate changes and atmospheric warming (Goes et al. 2005) and nutrient loading (Harrison et al. 2011; Goes and Gomes 2016). These recent blooms have been dominated by the heterotrophic dinoflagellate *Noctiluca scintillans* [Parab et al. 2006; Al-Azri et al. 2007; Gomes et al. 2008; Harrison et al. 2011; see also Chap. 17, Goes et al. (2018)]. These examples represent just a sampling of the bloom events that are occurring more often and in more places.

## 2.5 Why Are HABs Expanding?

Although some of the factors contributing to regional and global expansion are natural, such as biological species dispersal, many others are considered to be a result of human activities. Increases in nutrient loading, changes in agriculture and aquaculture practices, overfishing, ballast water discharge, and global climate change may all be important in the global increase in HABs.

By far, the greatest change in the past several decades has been the rate and composition of nutrient loading [see also Chaps. 4, 12, Glibert et al. (2018a, b)]. Population growth and development (with associated large sewage discharges) and the production of food, both crop (with the associated expanding synthetic fertilizer use) and animal production systems (with their associated waste), have resulted in increased runoff from land to both fresh and marine waters. The production and consumption of energy also result in increased atmospheric inputs from $NO_x$ emissions, which can then lead to increased N deposition. These nutrient sources have led to widespread coastal eutrophication throughout Europe, the USA, and Asia.

Another significant alteration in nutrient loading to the coastal zone in some regions comes from the increase in aquaculture activities [see also Chap. 4, Glibert et al. (2018b)]. These industries have altered ecosystems through input of feed and faeces, only a small percentage of which is incorporated in food biomass (Bouwman et al. 2011, 2013a, b). China's expansion of aquaculture has been especially great, and the release of nutrients from aquaculture in some provinces of China exceeds 20% of that from riverine export (Bouwman et al. 2013a). Global models of the impacts of finfish, shellfish, and aquatic plant aquaculture (Bouwman et al. 2011, 2013b) have estimated the alteration of nutrient cycling and particularly in the case of finfish, where external feeding is required, have demonstrated the magnitude of increased nutrient loads. Even mollusc production, which does not depend on exogenous nutrients to be supported, when intensive, can become point sources of nutrients as particulate nutrients are assimilated and excreted in faeces and pseudofaeces.

Fish and shellfish harvesting has also altered ecosystems, leading to changes in food chains/food webs. The exploitation of natural fish stocks has, in some cases, led to a decrease in the control of HAB species by removal of the primary grazers through trophic cascade effects. As an example, altered food webs and trophic interactions, through overfishing and the invasion of the predatory ctenophore *Mnemiopsis leidyi*, have been suggested as possible factors leading to increased HABs in the Black Sea (Lancelot et al. 2002).

Climate controls many of the fundamental parameters regulating algal growth, including water temperature, nutrients, and light, and thus can be expected to result in changes in the species composition, trophic structure, and function of marine ecosystems [Wells et al. 2015; see also Chap. 5, Wells and Karlson (2018)]. Warmer temperatures may contribute to increased growth rates and to range expansion of particular species. The available data, along with modelling approaches, suggest shifts in HAB species and the timing of their outbreaks related to increases in mean water temperature (e.g., Tester et al. 2010; Moore et al. 2008, 2015; Glibert et al. 2014). Temperatures also affect the community of organisms within which the HAB may live, including bacteria, viruses, competing phytoplankton taxa, and grazers (Wells et al. 2015 and references therein). Toxicity of many HABs also increases with warming, but this is not the case in all HABs (Davis et al. 2009; Fu et al. 2012, and references therein). The combination of temperature, together with elevated $pCO_2$ and altered nutrient ratios, appears to be especially potent in terms of toxicity of some HABs. For some species, higher toxicity associated with warming may be associated with slower growth rates (e.g., Ogata et al. 1989; Lewis et al. 1993), but high growth rates are not necessary for HABs to thrive [see Chap. 7, Flynn et al. (2018)].

Higher temperatures are promotive of increased water column stability and increased thermal stratification. This can favour cyanobacterial species that are buoyant because they can float to the surface (e.g., Walsby 1975; Visser et al. 2016, and references therein). Moreover, at higher temperatures water can become less viscous, buoyant cyanobacteria can float faster, and conversely sinking diatoms will sink faster (e.g., O'Neil et al. 2012 and references therein).

Long-term changes in, or intensification of, climate forces such as monsoons or interannual oscillations, such as those related to the El Niño-Southern Oscillation (ENSO), or longer-term cycles, such as North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO), can also alter conditions for HABs. In the northern Iberian Peninsula, the abundance of the harmful dinoflagellate *Gymnodinium catenatum* was high during the mid-1980s when there was a transition from downwelling-favourable conditions to upwelling-favourable conditions following a shift in the North Atlantic Oscillation (NAO) index (Alvarez-Salgado et al. 2003). In late 2013, and continuing through much of 2016, anomalously warm water developed in the northeastern Pacific Ocean (e.g., Bond et al. 2015; Freeland and Whitney 2015), a feature associated with the unusually strong El Niño event and the Pacific Decadal Oscillation (PDO), and an exceptionally large bloom of *Pseudo-nitzschia* developed along the USA west coast, lasting months and causing extensive ecological and economic harm (McCabe et al. 2016).

## 2.6 Why the Need for Advancing Knowledge of HAB Ecology and Oceanography?

Factors leading to the establishment of a bloom usually include environmental, chemical, as well as physical dynamics and may also include changes in trophodynamic interactions. In addition, various physiological adaptive strategies may lead to disproportionate success of a particular species. For example, blooms may result from excystment of resting cells during a restricted set of suitable conditions, transport of cells from a source region where blooms are already established, and enhanced growth due to unusual climatic or hydrographic conditions.

Once a bloom is initiated, physical processes controlling bloom transport are of paramount importance. Coastal currents driven by wind, buoyancy, or other factors can transport blooms hundreds or even thousands of kilometres along the coast, often from one management area to another. Understanding the physical dynamics underlying these transport pathways is essential to effective management and mitigation of HAB effects. A population's range and biomass are affected by physical controls such as long-distance transport, accumulation of biomass in response to water flows and swimming behaviour, and the maintenance of suitable environmental conditions (including temperature and salinity, stratification, irradiance, and nutrient supply). Thus, physical forcing, nutrient supply, and the behaviour of organisms all interact to determine the timing, location, and ultimate biomass achieved by a bloom, as well as its impacts.

Physical processes that are likely to influence the population dynamics of HAB species are operative over a broad range of spatial and temporal scales. The retentive nature of some semi-enclosed coastal systems, such as estuaries and fjords, can produce long residence times leading to prolonged suitable periods for cells to thrive [Cembella et al. 2005; see also Chap. 4, Glibert et al. (2018b)]. A linkage has been demonstrated, for example, between tidally generated fronts and the sites of massive blooms of the toxic dinoflagellate *Gyrodinium aureolum* (*Karenia mikimotoi*) in the North Sea (Holligan 1979). The typical pattern is that of a high surface concentration of cells at the frontal convergence, contiguous with a subsurface chlorophyll maximum which follows the sloping interface between the two water masses beneath the stratified side of the front. The signature of the chlorophyll maximum, sometimes visible as a "red tide," may be 1–30 km wide. Chlorophyll concentrations are generally lower and much more uniform on the well-mixed side of the front. The timing and duration of upwelling is another physical feature that plays an important role in many blooms, as in the case of the Benguela upwelling system, where HABs accumulate subsurface as stratification increases during the upwelling season and move onshore as upwelling relaxes (Kudela et al. 2005).

The importance of small-scale physical processes in HAB development is observed in the layering of the physical, chemical, and biological environment in stratified coastal systems. Off the French coast, for example, a thin layer of dinoflagellates, including the HAB species *Dinophysis* cf. *acuminata*, has been observed in the region of the thermocline (Gentien et al. 2005). The same pattern is found for *Dinophysis norvegica* in the Baltic Sea, where a 1–2-m-thick layer with up to 80,000 cells $L^{-1}$ is usually situated between 20 and 25 m depth, where light is $<1\%$ (Gisselson et al. 2002).

Studies of species responses at the ecosystem level are essential if we are to understand the population dynamics of HABs. The specific growth rate of a species is determined by many metabolic processes, including photosynthesis and nutrient uptake and assimilation, all of which are under both environmental and genetic control. The net population growth of a species is controlled by external environmental factors, including nutrients, physical transport, grazing, and other community interactions.

HAB species do not typically appear to have higher intrinsic growth rates than many other phytoplanktons. Some HABs may actually have lower growth rates than non-HAB species, such as diatoms, but succeed when loss processes are also reduced. In fact, some HABs are actually slower growing than their non-HAB counterparts. They succeed due to the negative impact they can have on competitors or their grazers. Interactions between HAB species and other algae may be an important survival strategy for some HABs. For example, it has long been argued that production of allelopathic exudates allows some harmful species to outcompete co-occurring phytoplankton (e.g., Smayda 1998; Granéli and Johansson 2003). Some species may even use cyst formation as a survival strategy from strong allelochemicals produced by another HAB species (Fistarol et al. 2004). It may well be that some of the HAB species that form thin, subsurface, or surface layers of cells at extraordinary densities do so because this allows them to change the ambient water chemistry and light penetration in a manner that deters grazing, inhibits co-occurring algal species, or facilitates sexuality and gamete encounter rate.

Reductions in grazer abundance can also play a key role in bloom development. This might result from physical factors or behavioural strategies, which lead to spatial separation of harmful algal species and grazers. Local reductions in grazer abundances may be in direct response to HABs (e.g., avoidance or mortality induced by the HABs, Granéli and Johansson 2003) or in response to the effects of past HAB events on grazer populations. The response of zooplankton and other grazers to toxic algae is often species-specific in terms of behavioural responses and toxin susceptibility. Moreover, prey quality can vary, characterized in terms of lipid and protein content and also in terms of elemental stoichiometry. The net effect of the stoichiometric regulation of consumers together with different nutrient requirements of phytoplankton is that not only are grazers affected by food quality, but they, in turn, affect food quality by altering the composition of nutrients available to them. This process of stoichiometric interaction is seen at all levels of the food web, leading to a complex interaction of stoichiometry and trophic cascades and potential for shifts in dominant bloom species as not only is the rate of assimilation efficiency altered, but so too is the rate of regeneration, in turn disproportionately promoting those species that can use the altered nutrient forms (Mitra and Flynn 2005). It is also apparent that prey quality has strong effects on the success of mixotrophs as well (e.g., Lundgren et al. 2016; Lin et al. 2017).

A survival and growth strategy that is important to many HAB species is a complex life cycle, or a life cycle involving resting or benthic stages, such as spores or cysts [see also Chap. 8, Azanza et al. (2018)]. These life cycle stages provide a recurrent seed source or inoculum for planktonic populations, and this characteristic may be a critical factor in determining not only the geographic distribution of species but possibly their eventual abundance as well.

Moving higher in the food web, zooplankton impaired by ingesting harmful algae may be more susceptible to predation and thus may become an important vector for transferring toxins in the pelagic food web. Alternatively, zooplankton faecal pellets may be important sources of toxin to benthic communities. Herbivorous fish can accumulate and transfer toxins and even cause mass mortalities of the marine birds that consume them. During food web transfers, toxins may be bioaccumulated, excreted, degraded, or structurally modified. In order to understand the effects of HAB species on the marine food web, both the direct and the indirect, more subtle pathways by which toxins are transferred and transformed and the differential susceptibility of marine organisms to these toxins must be characterized. In some cases HABs may harm, but not kill, other members of the food web, leaving them stressed and therefore more susceptible to other sources of mortality, such as infection by pathogens (Burkholder and Glasgow 1997; Glibert et al. 2002).

The above represent some well-established examples of the effects of various processes on the distribution of harmful algae. Much has been accomplished in understanding HAB ecology and oceanography, but there are however many examples where the physical and/or biological processes common to particular ecosystems are poorly characterized and understood, and therefore their influence on HAB population dynamics and their harmful properties remain uncertain.

## 2.7 Conclusions and the Role of GEOHAB

In summary, the HAB problem is significant and growing worldwide and poses a major threat to public health, to ecosystem health, as well as to fisheries and economic development. The HAB problem and its impacts are diverse as are the causes and underlying mechanisms controlling the blooms. Winds, tides, currents, fronts, and other environmental features can create discrete patches or streaks of cells at all scales. A full understanding of the many biological, chemical, and physical processes that underlie HABs will continue to be a challenge, given the many different species and hydrographic systems involved.

HABs are a serious and growing problem in the global coastal ocean—one that requires the interplay of all oceanographic disciplines, as well as others such as public health and resource management. Through recognition of the diversity of these interactions, much progress has been made towards understanding the causes and impacts of these events. Nevertheless, there is much work to be done to translate such knowledge in effective management activities that will reduce the severity of such outbreaks or their impacts on ecosystem and human health in future years. The GlobalHAB Programme, the next generation of GEOHAB [see Chap. 22, Berdalet et al. (2018)], will be important in advancing the science and management of HABs on a global scale.

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