



Ocean deoxygenation: Everyone's problem

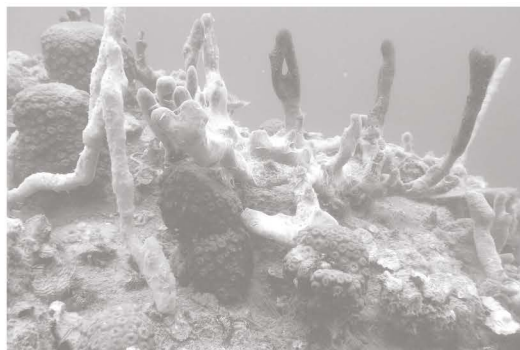
Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter



3.3 Ocean deoxygenation links to harmful algal blooms

Grant C. Pitcher and Gil S. Jacinto



IUCN GLOBAL MARINE AND POLAR PROGRAMME



3.3 Ocean deoxygenation links to harmful algal blooms

Grant C. Pitcher^{1,2} and Gil S. Jacinto³

¹Fisheries Management Branch, Department of Agriculture, Forestry and Fisheries, Cape Town, South Africa. Email: grantp@daff.gov.za

²Department of Biological Sciences, University of Cape Town, Cape Town, South Africa.

³Marine Science Institute, University of the Philippines Diliman, 1101 Quezon City, Philippines.

Summary

- The development of hypoxic or anoxic waters is regularly listed as one of the consequences of harmful algal blooms (HABs).
- Events of low oxygen associated with HABs are characterized by high initial oxygen concentrations, exceptional rates of respiration following bloom senescence, and short timescales.
- Coastal environments subject to high biomass HABs and associated events of low oxygen are typified by elevated inorganic nutrients as a consequence of either natural or cultural eutrophication.
- Eastern boundary upwelling systems are highly productive, nutrient-rich environments, prone to high-biomass HABs, and provide some of the earliest accounts of events of anoxia linked to red tides.
- The expansion of HABs is more readily apparent in Asia than in any other part of the world's ocean and it is here that relationships between the increasing prevalence of HABs and aquaculture operations are increasingly reported.
- Several model predictions show the likelihood for increased nutrient pollution and, correspondingly, for continued regional and global expansion of coastal hypoxia and anoxia linked to HABs.

3.3.1 Introduction

Harmful Algal Blooms (HABs) are usually described as proliferations of algae that can cause massive fish kills, can contaminate seafood with toxins, and alter ecosystems in ways that humans perceive as harmful (GEOHAB, 2001). A broad classification of HAB species distinguishes the toxin producers which can contaminate seafood or kill fish, and the high-biomass producers which can cause indiscriminate mortalities of marine life through various means. The development of hypoxic or anoxic waters is regularly listed as one such means and typically follows bloom degradation which fuels microbial respiration and the consumption of oxygen. These blooms are usually ascribed to flagellated species of phytoplankton, notably dinoflagellates, capable of regulating their depth and accumulating near the surface in high densities. In such cases the ocean may become discoloured leading to phenomena referred to as red tides.

Although red tides are often deemed the cause of hypoxia or anoxia with consequent mortalities of marine life, these events are poorly described in the scientific literature. Low oxygen concentrations in the ocean result from an imbalance between air-sea-fluxes, the transport of oxygen by physical means, and the biological production and consumption of oxygen. Events of oxygen deficiency linked to red tides are characterized by the exceptional biomass generated by these blooms, by the inherently high cellular respiration rates of dinoflagellates and by the often abrupt mortality of blooms and consequent elevated consumption of oxygen through aerobic respiration of organic matter by microbes. Events of low oxygen associated with red tides are therefore typically episodic in character and their local and transient properties have contributed to our poor understanding of these events and inadequate assessment of their impacts (Pitcher & Probyn, 2016). Specifically the causes and timing of bloom death leading to the rapid shift from net autotrophy to net heterotrophy are poorly established. In contrast to the efforts to determine the conditions, i.e. mechanisms and strategies that control phytoplankton cell growth and bloom development, considerably less effort has focused explicitly on phytoplankton death. Until recently phytoplankton were considered somewhat immortal unless eaten by predators, but it is now known that phytoplankton die spontaneously under various adverse environmental conditions and various forms of autocatalytic cellular self-destruction have been identified

(Bidle, 2014). Until such mechanisms controlling abrupt termination of blooms in natural systems are better understood events of anoxia and subsequent mortality of marine life will remain unpredictable.

The hydrodynamic properties of coastal systems conducive to bloom development and the formation of red tides are typically inseparable from those physical conditions required for the development of hypoxia or anoxia. While stratification is usually a key requirement in the development of low oxygen in bottom waters, as it provides a barrier to the diffusion of oxygen from surface waters toward the lower regions of the water column, it also promotes the succession of phytoplankton communities to the flagellate taxa so often the cause of red tides (Figueiras et al., 2006). Similarly, areas of the coastal environment that are subject to retentive circulation and are therefore more susceptible to low oxygen, owing to reduced advective exchange, are also subject to a higher incidence of red tides as bloom dispersal by lateral advection is minimized. Once formed, the dynamics of oxygen depletion in red tides may be driven by: (1) the high cellular respiration rates of dinoflagellates which may lead to severe night-time depletion of oxygen, and / or (2) the microbial consumption of oxygen following bloom senescence.

Coastal environments subject to high biomass HABs and associated events of low oxygen are generally typified by an elevated supply of inorganic nutrients as a consequence of either natural or cultural eutrophication. Examples of HABs and consequent anoxia in systems subjected to each of these forms of eutrophication are presented in the following sections. HABs and anoxia in eastern boundary upwelling systems which are considered naturally eutrophic are examined in subsection 3.3.2. This subsection specifically details bloom development, mechanisms of oxygen depletion and the impact on resources in the southern Benguela as a case study. An increasing majority of coastal environments subject to cultural eutrophication, particularly those common to the coasts of USA, Europe and Asia, are characterized by high biomass HABs (Glibert et al., 2018a). Subsection 3.3.3 examines HAB proliferation and oxygen depletion in Asia in response to cultural eutrophication. Unique to Asia is the large scale of aquaculture that characterizes the region and is considered an important source of nutrient pollution, key to HAB development (GEOHAB, 2010). Subsection 3.3.4 takes a look at future trends

in HABs and anoxia and subsection 3.3.5 concludes in outlining the way forward.

3.3.2 HABs, red tides and anoxia in Eastern Boundary Upwelling Systems

Eastern Boundary Upwelling Systems are highly productive, nutrient-rich environments, prone to high-biomass HABs, and provide some of the earliest accounts of events of anoxia linked to red tides. Within these systems episodic events of anoxia are well known in the Humboldt Current system encompassing much of the west coast of South America where they have been linked to red tides since the 1800s. On the Peruvian coast red tides are known locally as “aguajes”, and have for a long time been considered the principal cause of anoxic events and the production of hydrogen sulphide leading to fish mortalities (Rojas de Mendiola, 1979). In the port of Callao, the blackening effects of hydrogen sulphide on the paintwork of ships led it to be known colloquially as “The Callao Painter” (Figure 3.3.1). The dinoflagellate *Gymnodinium splendens* (known now as *Akashiwo sanguinea*) was considered for many years the most common cause of these events (Rojas

de Mendiola, 1979), however, *Prorocentrum micans*, *Prorocentrum gracile*, *Tripos fusus* (formerly *Ceratium fusus*) and *Tripos furca* (formerly *Ceratium furca*) are now also listed as bloom-forming dinoflagellates in this region (Trainer et al., 2010; Figure 3.3.2).

By way of example, in April 2004 a particularly destructive bloom of *A. sanguinea* occurred in Paracas Bay off the central coast of Peru (Kahru et al., 2005). In late March waters of the bay were a brownish-red colour and concentrations of 3.2×10^6 cells L^{-1} were recorded prior to mass fish mortalities. Severely hypoxic conditions were reported following bloom senescence on 12 April at which time fish mortalities were greatest. The local share in the Peruvian anchovy landings decreased from 8.4% in 2003 to 1.7% in 2004. The port was closed for 22 days to reduce effluent discharge into the bay resulting in an estimated loss in revenue of US\$27.5x10⁶. The local aquaculture sector also reported losses estimated at US\$1x10⁶ (Kahru et al., 2004).

Of the other major EBUS, the California Current system, encompassing much of the Pacific coast of North America, and the Canary Current system, including the



Figure 3.3.1 Water discolorations in the Humboldt Current area known as ‘aguajes’ have been reported to cause anoxia with the subsequent production of hydrogen sulphide since the late 19th century. The blackening effects of hydrogen sulphide on the paintwork of ships led it to be known colloquially as ‘The Callao Painter’. © Wilder Vargas / Shutterstock.com.

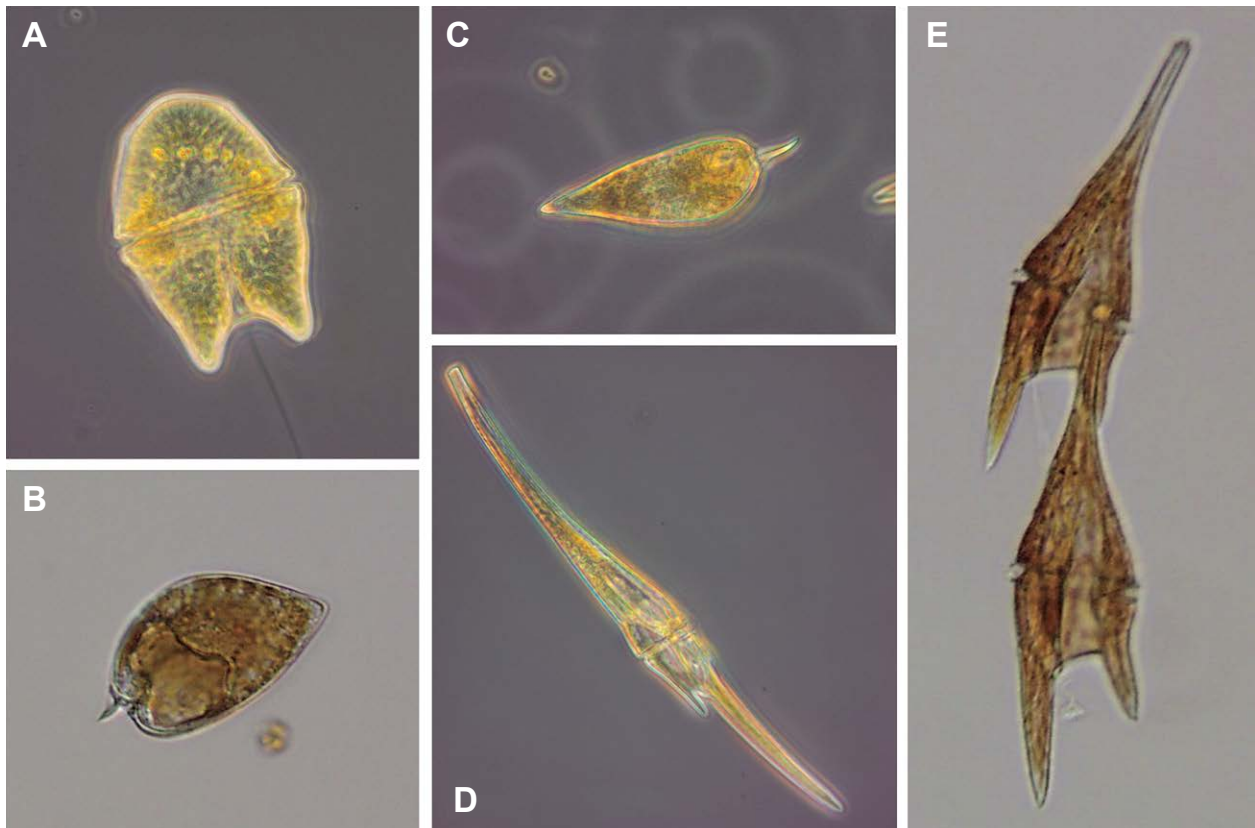


Figure 3.3.2 Aguajes were originally attributed to blooms of the dinoflagellate (A) *Akashiwo sanguinea* (formerly *Gymnodinium splendens*; Rojas de Mendiola, 1979), however, between 1980 and 1995 the dinoflagellates (B) *Prorocentrum micans*, (C) *Prorocentrum gracile*, (D) *Tripos fusus* (formerly *Ceratium fusus*) and (E) *Tripos furca* (formerly *Ceratium furca*) were also reported as the cause of these blooms (Sánchez & Delgado, 1996) © G.C. Pitcher and L.M. Mansfield.

Iberian Peninsula and the north-west African coast, are subject to far fewer events of red tide related anoxia (Trainer et al., 2010). However, the Benguela Current system off the west coast of southern Africa is similar to the Humboldt Current in that events of anoxia linked to red tides are common with reports dating back to the 1800s. Our present knowledge and understanding of these events following scientific investigation over the past 20 years is presented below as a case study of HABs and anoxia in the southern Benguela detailing bloom development, mechanisms of oxygen depletion and the impact on resources.

3.3.2.1 HABs and anoxia in the southern Benguela: A case study

The southern Benguela upwelling system located off the coast of southern Africa has a long history of marine mortalities attributed to red tides and subsequent anoxia (Pitcher & Calder, 2000; Trainer et al., 2010). Here blooms are most often observed in the embayments of St Helena Bay, Saldanha Bay, Table Bay, False Bay and Walker Bay (Figure 3.3.3). Blooms are usually attributed to one or another species of dinoflagellate,

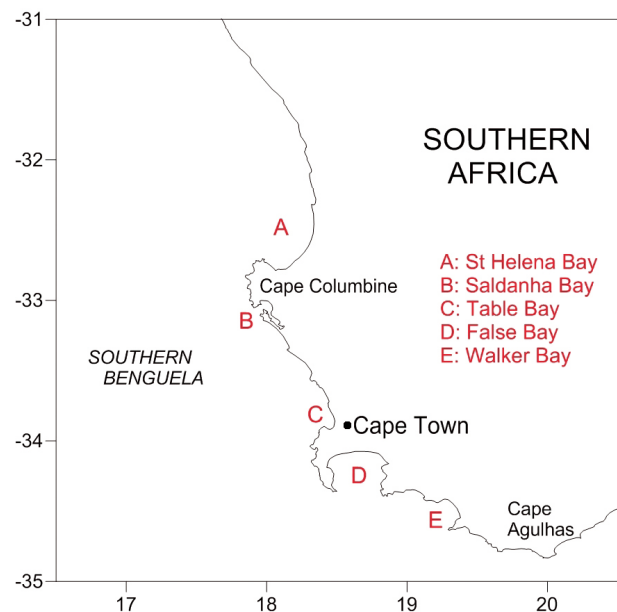


Figure 3.3.3 HAB hotspots in the southern Benguela associated with coastline features ranging from headlands, capes, peninsulas and bays. These mesoscale features interrupt typical upwelling circulation patterns and are more vulnerable to HABs owing to their influence on wind stress and water stratification, and through their retentive circulation that minimizes dispersal by lateral advection. These physical features along with the exceptional productivity of high biomass HABs increase the susceptibility of these areas to oxygen depletion.



Figure 3.3.4 Example red tides in the southern Benguela of (A) the dinoflagellate *Alexandrium catenella* off Elands Bay on 11 April 2012 (© John Foord), (B) a green flagellate of the genus *Tetraselmis* in Saldanha Bay on 15 January 2003 (© Grant Pitcher), (C) *Noctiluca scintillans* on the shoreline of Dassen Island off the west coast of South Africa on 6 October 2006 (© Tony van Dalsen), (D) *Gonyaulax polygramma* in False Bay off the Steenbras River mouth on 25 February 2007 (© Brent Johnson), (E) *Alexandrium minutum* in Cape Town harbour on 26 November 2003 (© Andre du Randt), and (F) the photosynthetic ciliate *Mesodinium rubrum* off Yzerfontein on 10 October 2016 (© Meredith Thornton).

although the photosynthetic ciliate *Mesodinium rubrum*, the raphidophyte *Heterosigma akashiwo*, various coccolithophorids and other flagellates have also been the cause of large blooms and spectacular discoloration of the ocean (Figure 3.3.4, Pitcher et al., 2010).

Some of the earliest accounts of low oxygen events in the southern Benguela that have been attributed to red tides date back to the 1800s (Gilchrist, 1914). In 1869 an incident in Stompneus Bay, a small recess in the south-western corner of St Helena Bay, was described in which fish known locally as geelbek (*Atractoscion aequidens*) were picked up in dark red water, having



Figure 3.3.5 West coast rock lobster (*Jasus lalandii*) © Sabena Jane Blackbird / Alamy stock photo.

been found swimming head above water, apparently in a “stupefied” condition. Another incident in 1907 is described in which Saldanha Bay became filled with red water, known locally as “flower water”, and fish in the bay were seen to be floating belly upwards in a “disabled” condition and were cast ashore in large numbers, apparently on account of the presence of large quantities of decaying matter. The severity of these mortalities led Gilchrist (1914) to list red tides as one of the factors causing fluctuations in fish stocks in the Benguela.

One of the first events to be investigated and documented in the scientific literature was that of a bloom of *Gonyaulax polygramma* in False Bay in March and April 1962 (Grindley & Taylor, 1964). Under westerly winds, the bloom accumulated in the north-eastern corner of False Bay reaching concentrations of approximately 10×10^6 cells L^{-1} ; the sea was reported to have become slimy with rotting plankton and produced an unbearable stench. At this time, dead and dying fish and invertebrates, estimated at over 100 tons, were washed up on the beaches, apparently due to the depletion of oxygen by decaying plankton. Many other accounts of dinoflagellate blooms and events of anoxia in the southern Benguela have followed. However, in April 1978, extensive mortalities in St Helena Bay were for the first time attributed to oxygen depletion following the decay of a bloom of the ciliate *Mesodinium rubrum* (Horstman, 1981). Bloom decay and oxygen depletion followed a dramatic change in colour of the bloom, from the spectacular maroon colour so characteristic of *M. rubrum* blooms, to a rusty-orange discoloration of the ocean.

More recent events of anoxia following dinoflagellate blooms during the 1990s in St Helena Bay have been

associated with some of the largest mortalities recorded within the region. In March 1994 a bloom dominated by the dinoflagellates *Tripos furca* (formerly *Ceratium furca*) and *Prorocentrum micans* (Figure 3.3.2) led ultimately to conditions of anoxia and the production of hydrogen sulphide impacting 30 km of shoreline and causing a mortality of approximately 60 tons of the west coast rock lobster *Jasus lalandii* (Figure 3.3.5) and 1500 tons of fish, primarily the mullet *Liza richardsoni* (Matthews & Pitcher, 1996). This was the first recorded incidence of hydrogen sulphide poisoning in the southern Benguela causing a black discoloration of the sea. In April 1997 the largest ever stranding of 2000 tons of rock lobster followed the decay of a red tide dominated by *T. furca* (Cockcroft et al., 1999). Unprecedented in terms of the magnitude of the loss, which was valued at US\$50x10⁶, the ecological fallout severely impacted the fishing community in the region. The most recent mortality in St Helena Bay occurred in February and March 2015 with the removal of a total of 415 tons of the rock lobster, 21 tons of molluscs, mostly the white mussel *Donax serra*, and 7 tons of various fish species from the beaches. For the first time these mortalities were attributed to blooms of the dinoflagellate *Prorocentrum triestinum* (Ndlovu et al., 2017).

Owing to the severe impacts of red tides on resources in St Helena Bay considerable scientific effort has been directed towards establishing the conditions and processes important to bloom development. Within the inner-shelf environment of upwelling systems, blooms often manifest within embayments where the properties of stratification and retention, which generally favour HABs, tend to be more pronounced (Pitcher et al., 2010). It is for this reason that St Helena Bay, a cape-associated bay, has a particularly high incidence of red tides.

The important role of wind driven circulation in bloom development and transport in St Helena Bay is demonstrated in the conceptual model of Pitcher and Nelson (2006) (Figure 3.3.6 A, B). St Helena Bay is located downstream of Cape Columbine and upwelling-favourable winds result in an upwelling plume off Columbine that tends to isolate the nearshore area in the lee of the cape from the offshore domain, thereby inducing retention on the coastal side of the plume. A positive coupling between upwelling and retention is provided by this structure, with stronger upwelling-favourable winds enhancing retention within the nearshore area, despite the intensification of offshore

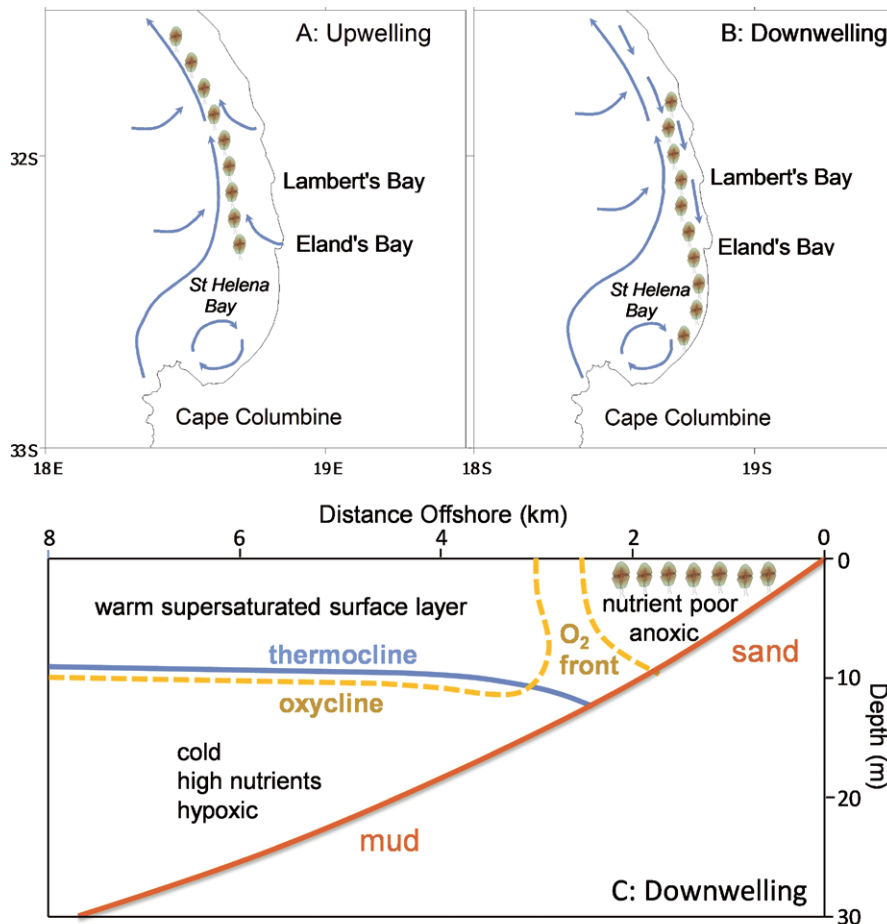


Figure 3.3.6 Conceptualization of harmful bloom events in the greater St Helena Bay region during periods of (A) upwelling and (B) downwelling. Intensified stratification in the lee of Cape Columbine particularly during late summer and autumn favours the seasonal succession and transition to dinoflagellate blooms. Under upwelling conditions dinoflagellates tend to accumulate offshore in a region of convergence, created by a narrow belt of upwelling and the core equatorward flow. Wind relaxation leads to downwelling conditions and the shoreward accumulation of dinoflagellate blooms. Simultaneous development of an inshore counter-current results in the poleward progression of these blooms into the bay. It is at this time that the nearshore regions of the bay are most susceptible to events of anoxia (C). Under conditions of sustained downwelling subthermocline nutrients are inaccessible to these inshore blooms leading to their decay. The exceptional phytodetrital production associated with these blooms and the reduced volume of water within the confines of the shallow nearshore environment result in the depletion of oxygen through the entire water column.

flow associated with upwelling. Intensified stratification in the lee of the Cape particularly during late summer and autumn favours the seasonal succession and transition to dinoflagellate blooms. Under upwelling conditions dinoflagellates tend to accumulate offshore in a region of convergence, created by a narrow belt of upwelling and the core equatorward flow (Figure 3.3.6A). Wind relaxation or reversal is typically associated with the shoreward accumulation of dinoflagellate blooms, and the development of an inshore counter-current results in the general poleward progression of these blooms into the bay (Figure 3.3.6B). It is at this time that the nearshore regions of the bay are most susceptible to events of anoxia.

St Helena Bay is in fact subject to two categories of oxygen deficient waters characterized by different

time scales and mechanisms of depletion (Figure 3.3.6C) (Pitcher & Probyn, 2011; Pitcher et al., 2014). Seasonally recurrent hypoxia is evident in bottom waters as stratification strengthens during the course of the upwelling season, thereby isolating the bottom waters from surface waters, and respiration is fuelled by high bay production and the deposition of increasing amounts of organic matter from the upper water column. Consequently oxygen concentrations in these bottom waters show a seasonal minimum in autumn at which time there is also an expansion in the size of the bottom pool of hypoxic waters. The seasonal expansion of this deep water pool of low oxygen water and inshore incursions of this water, as dictated by the upwelling-downwelling cycle, strongly impact the habitable nearshore zone. Although these hypoxic waters are known to compress the habitat of west coast rock

lobster causing shoreward migrations, which can cause significant stress and overcrowding, these events are not considered the cause of faunal mortalities.

Mass mortalities are rather caused by episodic anoxia following the nearshore accumulation and decay of red tides (Figure 3.3.6C) (Pitcher & Probyn, 2011). These events tend to strip oxygen from the entire water column of shallow nearshore environments and also coincide with corrosive low-pH conditions (Pitcher & Probyn, 2012), and in some cases the production of hydrogen sulphide (H₂S) (Matthews & Pitcher, 1996), which are equally harmful to marine life. Understanding the often rapid transition within these blooms from net autotrophy to net heterotrophy is important in predicting events of anoxia. The development of anoxia overnight has been shown to be achievable owing to the exceptional rates of oxygen utilization at night due to the magnitude of these blooms and the inherently high cellular respiration rates of dinoflagellates (Pitcher & Probyn, 2016). Nutrient stressors are also considered important in driving bloom-to-post-bloom transitions important in determining the biogeochemical fate of the bloom and the onset of anoxia (Pitcher & Probyn, 2016). Concurrent measurements of nutrients and nutrient uptake within blooms in the southern Benguela have shown that nutrient concentrations are unlikely to meet the demands of red tides. The inaccessibility of nutrients particularly during periods of extended downwelling, when subthermocline nutrients are unavailable, is therefore very likely to trigger cell death and bloom mortality further fuelling the microbial foodweb and consumption of oxygen (Figure 3.3.6C) (Pitcher & Probyn, 2011). Such events are regularly responsible for large mortalities of marine life within the St Helena Bay region (Figure 3.3.7), and have severely impacted marine resources in the region (Cockcroft, 2001; Cockcroft et al., 2008).

Oxygen deficient waters in St Helena Bay have specifically impacted the west coast rock lobster which normally dominates faunal mortalities. The west coast rock lobster fishery commenced in the early 1800s and traditionally has been of particular importance to communities on the South African west coast which relied heavily on the seasonal employment it provided (Cockcroft, 2001). Historically fishing has been conducted mainly by traps, deployed from larger vessels in deep water, or by hoopnets in shallow water, operated from dinghies. Lobster mortalities typically occur over a segment of some 80 km of the St Helena

Bay shoreline straddling two fishing zones and have often demonstrated a north-south progression linked to the poleward transport of red tides. A dramatic increase in the number and severity of lobster mortalities attributed to events of anoxia was reported during the 1990s (Cockcroft, 2001). The large mortality in 1994 resulted in a massive 65% decrease in catches in the 1994-95 fishing season. Further mortalities in the late 1990s, including the largest mortality on record in 1997, continued to impact catches. In the fishing seasons of 1998-99 and 1999-2000 catches reached record lows corresponding to 1.3% of the average annual catches made in the 1980s. Lobster mortalities were generally dominated by small females and the recovery of populations following these events was slow particularly in areas where anoxia had severely impacted sessile benthic communities (Cockcroft, 2001). Ultimately the high number of anoxic events during the 1990s is considered to have been an important driver in a major shift of the resource from the traditional fishing grounds on the west coast to more southern fishing grounds. This shift in the resource has led to a decline in the contribution of west coast rock lobster to total lobster landings on the South African coast from about 60% to <10% with major implications for the fishery and fishing community (Cockcroft et al., 2008). The lobster fishery on the west coast has now been reduced to an almost exclusively nearshore hoopnet fishery, and the loss of jobs in lobster processing facilities, coupled with a reduction in the allocation of long-term fishing rights to ensure resource sustainability has resulted in substantial economic hardship for west coast communities.

3.3.3 HABs, red tides and anoxia in Asia

The expansion of HABs is more readily apparent in Asia than in any other part of the world's ocean and it is here that relationships between the increasing prevalence of HABs and aquaculture operations are increasingly reported (GEOHAB, 2010).

3.3.3.1 Japan

Red tides and oxygen deficient waters have for many years posed a significant environmental problem in the coastal waters of Japan owing to increased nutrient loads. The Seto Inland Sea, the largest enclosed coastal sea in Japan, and a major fishing ground and region of intensive aquaculture, was subject to increasing red tides in the 1960s and 1970s in response to eutrophication (Imai et al., 2006). Interestingly, the increase in red

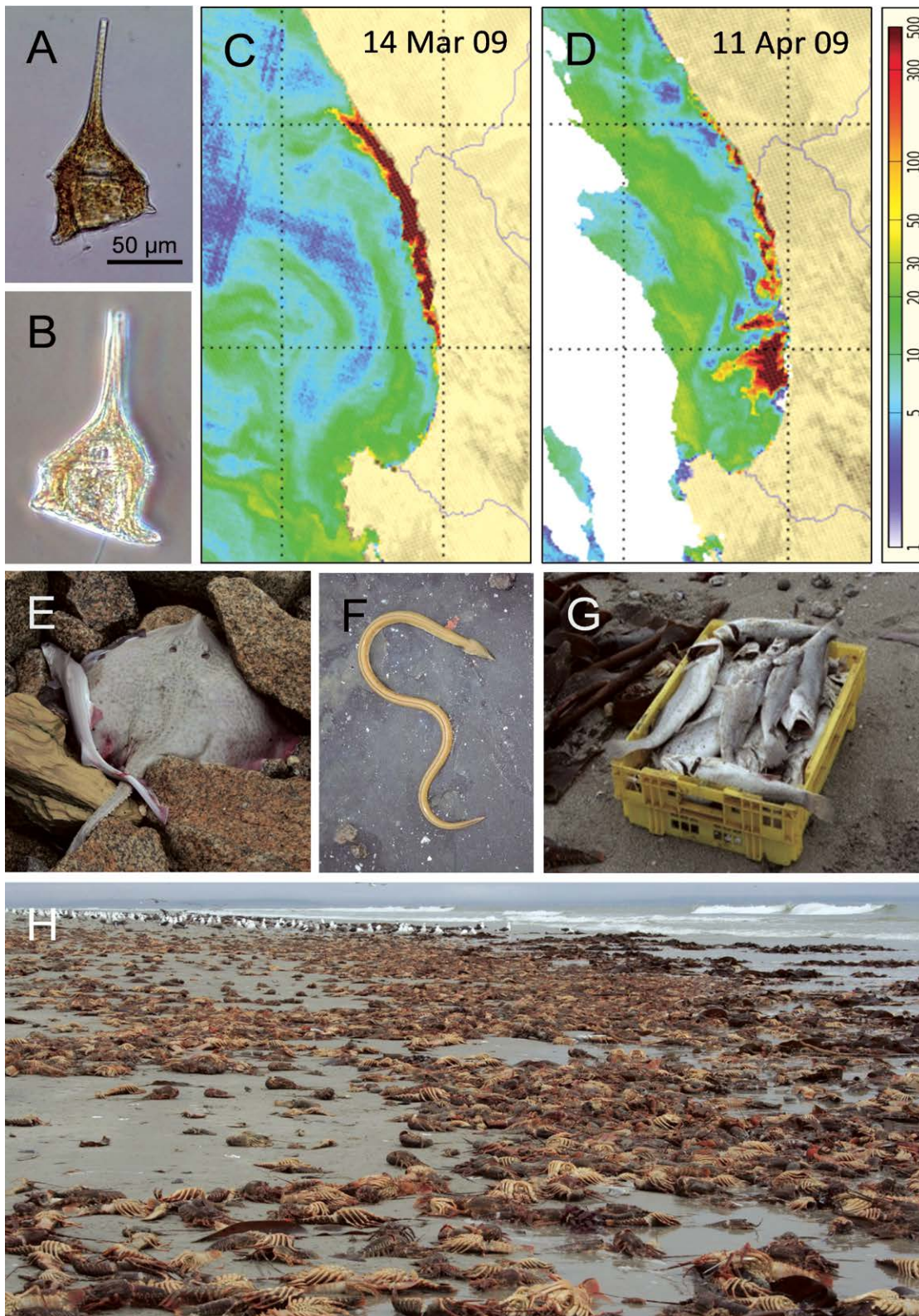


Figure 3.3.7 Light micrographs of the dinoflagellate *Tripes balechii* (formerly *Ceratium balechii*) (A, B) responsible for a red tide in St Helena Bay in 2009. The red tide is effectively tracked by ocean colour data from the MERIS sensor as is evident in images from the 14 March (C) and 11 April 2009 (D) showing bloom development and transport into the bay (Pitcher et al., 2014). Initial build-up of the bloom was observed in February in the northern reaches of the bay. By March blooms were shown to extend in a narrow band over a distance of >100 km. Diminished upwelling and the development of nearshore counter currents in late summer and early autumn resulted in the southward progression of these blooms and their entrainment into the southern reaches of the bay. Here large fish and lobster mortalities resulted from bloom decay and consequent anoxia in early May (E-H; Pitcher & Probyn, 2011). © A, B, E, F, G, H. G.C. Pitcher; C & D from Pitcher et al. (2014).

tide events in the Seto Inland Sea paralleled a rapid rise in the culture of yellowtail (*Seriola quinqueradiata*) (GEOHAB, 2010). Red tide forming species included the dinoflagellates *Gonyaulax polygramma*, *Noctiluca scintillans* and *Scrippsiella trochoidea*, all of which have been associated with indiscriminate fish and invertebrate kills due to oxygen depletion.

While nutrient controls enforced in the Seto Inland Sea in the 1970s led to a reduction in HABs, other bays in western Japan have suffered increased red tides in the 1980s and 1990s, coincident with declining oxygen concentrations and reduced fish and shellfish catches. In 1994 a bloom of *G. polygramma* in and around Uwajima Bay caused mass mortalities of cultured and natural fish and shellfish stocks valued at US\$7x10⁶. The death of fish and shellfish were attributed to anoxic waters and high sulphide concentrations that developed through the whole water column of Uwajima Bay and Hoketsu Bay following decomposition of the bloom (Koizumi et al., 1996). Similarly, the scale of autumn phytoplankton blooms in Ariake Bay has increased markedly and since 1998 red tides have been observed to extend across the entire inner bay (Tsutsumi, 2006). These blooms have markedly impacted nori production with harvests dipping by 35% in some years. Hypoxia in response to the increased prevalence of red tides was first observed in the bottom waters of Isahaya Bay at the head of Ariake Bay in the late 1990s and its spread within the region has coincided with a dramatic decline in the pen shell fishery (*Atrina pectinata*) (Nakata et al., 2010; Tsutsumi, 2006).

3.3.3.2 Korea

Coastal eutrophication caused by industrialization, urbanization and intensive aquaculture, with the consequent development of massive algal blooms has caused severe deoxygenation in Korean coastal regions, particularly on the southern coast (Lee et al., 2018). Here red tides concentrate in embayments such as Jinhae and Gamak Bays leading to enhanced biological consumption of oxygen with negative impacts on benthic ecosystems and aquaculture production. As an example, hypoxia has been known to occur every summer in Jinhae Bay following catastrophic events of mass mortality on oyster farms due to severe hypoxia in 1978 (Lee et al., 2018). Similarly, HABs and the consequent degradation of water quality in Gamak Bay has caused oyster production to decline from 9600 tons in 1991 to 4000 tons in 2008 (Lee & Kim, 2008). These blooms have been attributed

to three phytoplankton species, namely a dinoflagellate belonging to the genus *Prorocentrum*, the raphidophyte *Heterosigma akashiwo* and the diatom *Skeletonema costatum*. Blooms of these species have been shown to be preceded by higher than average precipitation (Lee & Kim, 2008). In some cases artificial structures in the form of dykes have also contributed to hypoxia through the effects of reduced flushing (Lee & Kim, 2008). As an example Shihwa Bay, isolated by means of a dyke as part of a government land reclamation project has subsequently experienced chronic environmental problems relating to red tides and bottom water anoxia leading to massive fish kills (Cho, 2005).

3.3.3.3 China

The number of HABs has increased in all waters of China in the past few decades (Yu et al., 2018). In areas such as the Bohai in north China large volumes of terrestrial pollutants in the form of industrial wastes and domestic sewage drain into the sea from nine rivers adding to bay contamination by intensive shrimp farming. In 1989 the south-west coast of the Bohai was subjected to one of the largest ever red tides in north China dominated by a species of the dinoflagellate *Gymnodinium* (Xu et al., 1993). The bloom seriously impacted 1.5x10⁵ hectares of shrimp ponds with a loss of 1x10⁴ tons of shrimp valued at US\$40x10⁶. Shrimp death was attributed to depleted oxygen concentrations following bloom senescence and a subsequent increase in disease.

One of the most spectacular examples of HAB development in response to eutrophication has been the development of massive blooms of the dinoflagellate *Prorocentrum donghaiense* in the Changjiang Estuary and adjacent East China Sea impacting areas up to 1x10⁴ km² (Gilbert et al., 2018b). Here a 10-fold increase in anthropogenic nutrients exported from the Changjiang stimulated development of these large noxious blooms with corresponding development of hypoxic zones of similar magnitude (Zhu et al., 2011).

Similarly, Tolo Harbour, an enclosed embayment in the north-eastern region of Hong Kong is also subject to severe nutrient pollution linked to increases in the human population. Between 1976 and 1986 the population within the harbour watershed grew 6-fold during which time the number of red tide events increased 8-fold (Lam & Ho, 1989). In 1988 the harbour was subject to a three-month red tide event attributed to the dinoflagellate *Gonyaulax polygramma* (Lam &

Yip, 1990). This was the first reported incidence of a *G. polygramma* dominated bloom in the region with peak concentrations of 23×10^6 cells L^{-1} . Bloom termination coincided with the onset of summer stratification and resulted in anoxia throughout the bay leading to large fish kills and incidents of shellfish mortality. Blooms of *Tripos furca* (formerly *Ceratium furca*) have also been reported to be a common feature of Tolo Harbour with fish kills following night-time depletion of oxygen and bloom die-off (Wong et al., 2010).

3.3.3.4 Philippines

Aquaculture facilities in the Philippines, particularly finfish operations have also been increasingly subject to events of low oxygen attributed to large dinoflagellate blooms. In the northern Philippines, Bolinao Bay in the Lingayen Gulf has been the site of intensive culture of the milk fish *Chanos chanos* since the 1970s. In January and February 2002 fish kills valued at US\$ 9×10^6 followed blooms of the dinoflagellate *Prorocentrum minimum* (Azanza et al., 2005). At the time of bloom senescence oxygen concentrations declined to $1.4 \text{ ml } L^{-1}$ and fish were observed gasping for breath. The intensive nature of fish farming in the region, with a total of 800 fish pens covering an area of 165 ha in 1999, was considered the primary cause of bay enrichment and bloom development (San Diego-McGlone et al., 2008). The presence of fish cages also increases frictional drag thereby reducing currents and flushing rates which further contributes to declining oxygen concentrations.

Fish kills in 2002 were also observed in the southern Philippines in Iligan Bay in March, and were attributed to blooms of the dinoflagellate *Cochlodinium polykrikoides* (Vicente et al., 2002). The presence of dead pelagic and demersal fish coincided with peak dinoflagellate concentrations at which time oxygen concentrations showed dramatic declines particularly with the onset of darkness and night-time respiration. Monitoring within a bloom patch showed afternoon oxygen concentrations in excess of $5 \text{ ml } L^{-1}$ declining to $<0.35 \text{ ml } L^{-1}$ in the early hours of the morning.

Further kills of farmed milk fish occurred in 2010 in the Caquiputan Channel in Anda with an estimated loss of US\$ 1.1×10^6 . This mortality was attributed to oxygen concentrations falling below $0.35 \text{ ml } L^{-1}$ following the decomposition of a massive bloom of the non-toxic diatom, *Skeletonema costatum*, and a toxic

dinoflagellate of the genus *Alexandrium* (Escobar et al., 2013). More recently, in May 2018, a major milkfish kill with an estimated value of US\$ 5×10^5 was reported in Obando, Bulacan, an estuary that empties into Manila Bay (Figure 3.3.8). The Bureau of Fisheries and Aquatic Resources attribute this event to very low oxygen levels and high water temperatures ($34 \text{ }^\circ\text{C}$) evidently preceded by a dinoflagellate bloom.

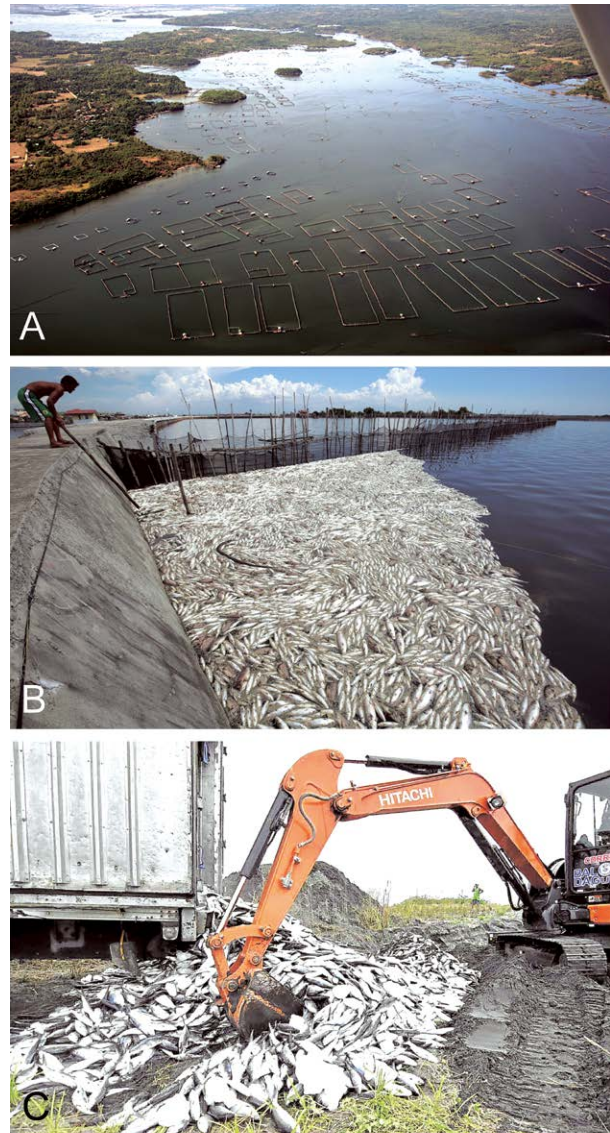


Figure 3.3.8 In Asia an increase in HABS has been observed in response to expanding aquaculture operations. A) As an example a major bloom of *Prorocentrum minimum* is pictured on a fish farm in Pangasinan province in the Philippines in 2013 © Gil Jacinto. B) In May 2018 extensive fish mortalities occurred in response to events of low oxygen following such blooms as depicted by a major mortality of the milkfish *Chanos chanos* in Obando, Bulacan, an estuary leading to Manila Bay as reported by the Bureau of Fisheries and Aquatic Resources, © Michael Varcas of the Philippine Star) and C) in Anda, Pangasinan. © Ray Zambrano of Philippine Daily Inquirer.

3.3.3.5 Malaysia

Malaysia has also experienced considerable growth of the aquaculture sector and finfish farming in particular is considered to pose a significant risk to the environment (Er et al., 2018). Algal blooms associated with massive fish kills have been reported from both the east and west coasts of the Peninsula with aquaculture operations incurring large losses (Teen et al., 2012). In Penang fish kills during 2005-2006 resulted in losses of US\$5x10⁶. These mortalities followed the decomposition of plankton blooms, possibly *Noctiluca scintillans*, and subsequent development of hypoxic and anoxic conditions (Teen et al., 2012). Similarly, Semerak Lagoon, the location of around 1000 fish cages suffered fish mortalities in 2016 following an exceptional bloom of a species of *Skeletonema*. Again low oxygen concentrations of around 2 ml L⁻¹ following bloom decomposition are believed to have been the cause of the mortality (Er et al., 2018).

3.3.3.6 Arabian Sea

Blooms, both red and green, of the dinoflagellate *Noctiluca scintillans* have been associated with events of low oxygen on both the east and west coasts of India (Baliarsingh et al., 2016). Blooms are, however, more frequent in the Arabian Sea where they occur on the south-west coast of India during the monsoon and post-monsoon periods. Here blooms of the red *N. scintillans* have been linked to hypoxic conditions and large mortalities of fish off Cochin in 1998 (Naqvi et al., 1998) while low oxygen conditions following a bloom of the green *N. scintillans* off Mangalore in 2011 were shown to disrupt fishing activities in that fish were observed to avoid low oxygen waters (Sulochanan et al., 2014). In 2008 the south-eastern Arabian Sea was also subjected to large blooms of the dinoflagellate *Gonyaulax polygramma* in the shelf waters off Mangalore (Padmakumar et al., 2018). These blooms were attributed to the large runoff from the Netravathi-Gurpur estuarine system in the post monsoon season and resulted in anoxic conditions with elevated sulphide and ammonia concentrations.

The first ever bloom-associated mass fish mortality in the Arabian Sea was attributed to a bloom of *Prorocentrum minimum* in 1987 in Gwadar Bay, a shallow, semi-enclosed bay on the western shores of Pakistan (Rabbani et al., 1990). Concentrations of *Prorocentrum minimum* of 45x10⁶ cells L⁻¹ were recorded in reddish-brown

waters and oxygen concentrations in post bloom waters dropped to <2 ml L⁻¹. The Arabian Gulf too has been subjected to an increase in HABs attributed to the deterioration of water quality owing to land reclamation and urbanization, and insufficient treatment of sewage and waste water discharge from industries (Rajan & Al Abdessalaam, 2008). Blooms of *P. minimum* and *Prorocentrum micans* have been prominent and in 2003 reached concentrations of 18x10⁷ cells L⁻¹ prior to events of oxygen depletion and the production of hydrogen sulphide, with subsequent fish mortalities.

Since 2000 the northern Arabian Sea has experienced a shift in phytoplankton composition with diatom blooms being replaced by the green *Noctiluca scintillans* which is now one of the dominant HAB-forming species (Figure 3.3.9) (Gomes et al., 2014). In the Sea of Oman a significant correlation has been found between fish kills and the incidence of HABs, with a seasonal trend in fish kills following a decline in oxygen, primarily driven by the decomposition of a series of blooms usually dominated by *N. scintillans* (Harrison et al., 2017).

3.3.4 Future trends in HABs and anoxia

Whereas HABs and resulting events of anoxia have for centuries, consistently characterized some coastal environments, other areas, particularly those subject to cultural eutrophication (as described in subsection 3.3.3), have demonstrated a notable increase in these events in recent decades. Recognition of the expansion of HABs was gained during the 1980s and 1990s and it is now accepted that most of the factors contributing to this expansion are the result of human activities (Anderson et al., 2012; Glibert et al., 2018a). Increases in nutrient loading, overfishing, aquaculture practices, ballast water discharge, and global climate change may all be important contributors. Human-assisted transport and dispersal of harmful species has been achieved by ballast water discharge and the translocation of shellfish. Fishing and the harvesting of shellfish have altered food chains, in some cases leading to a reduction in the control of HAB species through removal of primary grazers. There is emerging evidence that climate change is causing shifts in the composition of coastal phytoplankton communities and there is an expectation that future change will cause shifts in the spatial and temporal ranges of HABs (Wells & Karlson, 2018). Projected increases in stratification to which dinoflagellates are well adapted, as a result of warmer waters, increased precipitation and runoff, and altered

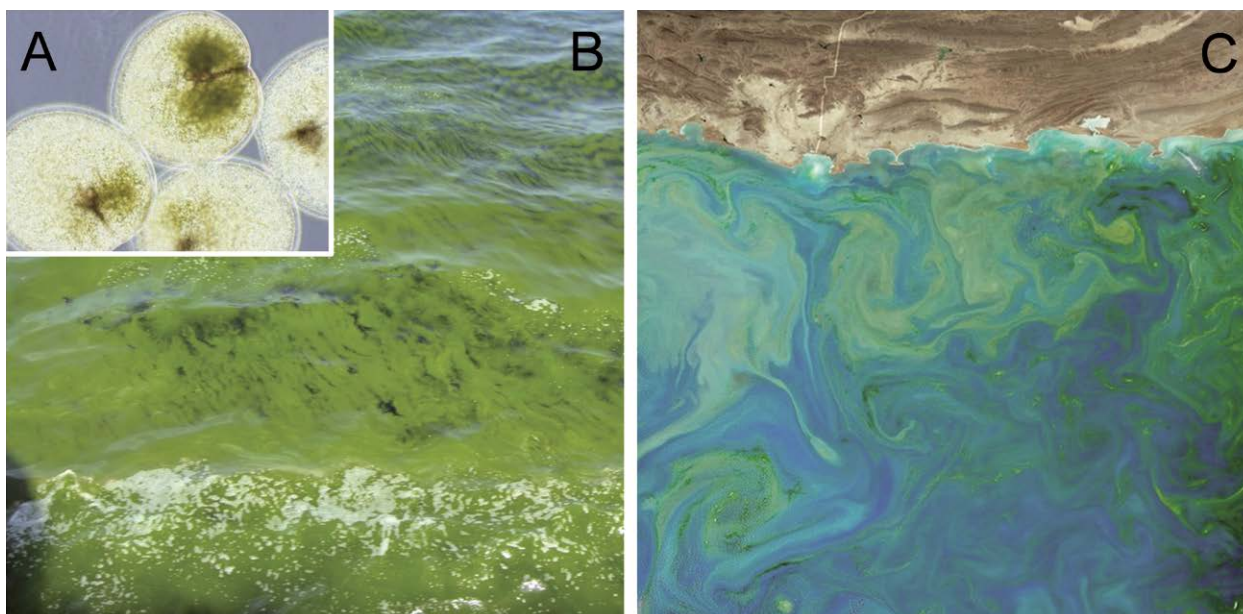


Figure 3.3.9 A) Green *Noctiluca scintillans* was first discovered in south-east Asia by Sweeney (1976). © Joaquim Goes. Compared to the better known red *Noctiluca scintillans* which is a heterotrophic dinoflagellate most common in temperate coastal waters, the green form is characterized by an endosymbiotic population of free swimming cells of *Pedinomonas noctilucae*. In the early 1990s the first large blooms of this dinoflagellate were recorded in the Gulf of Thailand and in Manila Bay of the Philippines, while their sudden appearance in the western Arabian Sea and in the coastal waters of Pakistan was observed in 2000 (Harrison et al., 2017). B) Blooms of green *Noctiluca* are now a regular feature along the coast of Oman. © Joaquim Goes, C) also observed by satellites from space. © Norman Kuring, NASA.

winds, serve as the foundation for much of the intuitive linkage between climate change and an increase in HABs. Furthermore, the direct effects of temperature, altered light fields, changing CO₂ levels, and ocean acidification, on phytoplankton physiology and metabolism are also likely to influence the prevalence of HABs. However, the fundamental driver of the global increase in HABs in recent decades, particularly in high biomass HABs, is the elevated anthropogenic nutrient input to which many coastal environments are subject (Glibert & Burford, 2017; Heisler et al., 2008).

Human activities, such as the use of synthetic fertilizers, energy production, and expansion of industrialized agriculture and aquaculture have had tremendous impacts on the global cycling of nutrients and carbon on land, in fresh waters, and in coastal waters, and an important consequence of such activities in aquatic systems is eutrophication with a resulting increase in HABs (Glibert et al., 2018b). The sources of nutrients that may stimulate blooms include sewage, atmospheric and groundwater inputs, and agricultural and aquaculture runoff and discharge (Anderson et al., 2002; Glibert & Burford, 2017). Global use of N fertilizer has increased nine-fold, and that of P has increased three-fold in the past four decades (Sutton et al., 2013), while agricultural crops take up only 50% of applied N fertilizers (Peoples et al., 1995). Animal production is

also increasing and animal waste is a major source of nutrient pollution. Moreover, aquaculture continues to grow with consequent inputs of nutrients from the culture of both shellfish and finfish. These nutrient sources have led to widespread coastal eutrophication throughout Europe, the USA and Asia (Glibert et al., 2018a) and the corresponding increase in HABs is one of the likely causes for faster declines in oxygen concentrations in the coastal ocean than in the open ocean (Gilbert et al., 2010).

The simplistic perception that more nutrients fuel more biomass through a direct dose-response relationship may still hold for high biomass blooms. However, it is now recognized that the relationship between nutrient pollution and species specific HABs is more complex, in that the composition and relative proportional availability of nutrient pools, and the range of physiological responses by different phytoplankton are all important in determining the linkage between eutrophication and HABs (Anderson et al., 2012). As an example, alterations in the composition of nutrient loads have been correlated with shifts to flagellate-dominated assemblages; more specifically the supply of N in excess of P is considered to promote dinoflagellate dominated HABs. It is therefore important to consider nutrient stoichiometry in addition to total nutrient load in determining any likely increase or decrease in HABs in

response to eutrophication (Glibert & Burford, 2017). It is also important to consider the receiving environment in that nutrient input into a retentive zone is likely to pose significantly greater risk than input into a system with less retentive properties (Glibert et al., 2018c).

The ability to predict how HABs may change with changes in nutrients, at scales from local to regional to global, is critical to the future management and control of HABs and requires a suite of modelling approaches (Glibert & Burford, 2017). A core need for modelling HABs in eutrophic systems is a good estimate of the nutrient load entering the receiving waters. Coupling nutrient discharge to the response of a single species or a group of species requires modelling of the hydrological properties of the receiving waters to determine the retention of the nutrient, and knowledge of the rates and pathways of nutrient consumption and recycling. Understanding the physiological responses of HABs to excess nutrient availability specifically needs to be advanced. Ultimately improved model formulations are needed that will link land-use models with ocean models that incorporate the dynamic physiological behaviour of blooms (Glibert et al., 2018b).

These models will provide management actions to help limit declining oxygen concentrations in response to increasing HABs through a better understanding of the required reduction of nutrients entering the ocean. Nevertheless, present model predictions show the likelihood for increased nutrient pollution and, correspondingly, for continued regional and global expansion of HABs. Scenario analyses for 2050 indicate that this risk will spread to developing countries in South America and Africa, and will continue to increase in the current high risk areas of eastern Asia (Glibert et al., 2018c). For this reason a first-order focus on reducing nutrient loads is critical in order to achieve a long-term reduction in HABs. Traditionally phosphorus reductions have been prescribed for freshwater systems and nitrogen reductions for coastal waters. However, because most systems are hydrologically interconnected dual nutrient reductions are likely to be required to achieve a positive controlling influence on HAB events and their cascading effects of hypoxia and anoxia (Paerl et al., 2018).

3.3.4 Conclusions

Despite the obvious and in many cases dramatic impacts of oxygen depleted waters that may follow the

decay of high biomass HABs there is a considerable need to advance our knowledge and understanding of these events. It is important that we better quantify the frequency and extent of these events, that we provide improved assessments of their impacts and are able to better document future trends. We should continue to improve our understanding, prediction, management and mitigation of HABs globally as guided by the science and implementation plan of *GlobalHAB (Global Harmful Algal Blooms)* – an international programme sponsored by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO. As a listed objective of *GlobalHAB* we must continue to determine the extent to which increased eutrophication influences the occurrence of HABs and their harmful effects. However, in addition to the focus on the role of nutrient input and limitation in bloom development future studies should seek to establish the nature of phytoplankton mortality within HABs and the consequent role of microbial activity in carbon transformation and oxygen consumption. Measurements should be made to quantify microzooplankton grazing, virus-mediated cell lysis and programmed cell death as plankton mortality processes in order to contribute to the prediction of anoxia linked to HABs.

Moving forward, *GlobalHAB* should also seek to interact with the IOC-UNESCO expert group, the *Global Ocean Oxygen Network (GO₂NE)*, formed to address concerns relating to declining oxygen concentrations in the ocean. This international network of ocean oxygen scientists was established in response to the need for a joint global analysis of ocean deoxygenation and its impacts and will specifically benefit investigation of ocean deoxygenation in response to eutrophication and climate change. Formal collaboration between *GlobalHAB* and *GO₂NE* will explicitly serve investigation of the likely global increase in episodic oxygen depletion associated with increasing HABs in the coastal environment.

3.3.5 References

- Anderson, D.M., Glibert, P.M., & Burkholder, J.M. (2002). Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries*, 25, 704-726. <https://doi.org/10.1007/BF02804901>
- Anderson, D.M., Cembella, A.D., & Hallegraeff, G.M. (2012). Progress in understanding harmful algal blooms: paradigm shifts and new technologies. *Annual Review of Marine Science*, 4, 143-176. <https://doi.org/10.1146/annurev-marine-120308-081121>

- Azanza, R.V., Fukuyo, Y., Yap, L.G., & Takayama, H. (2005). *Prorocentrum minimum* bloom and its possible link to a massive fish kill in Bolinao, Pangasinan, Northern Philippines. *Harmful Algae*, 4, 519-524. <https://doi.org/10.1016/j.hal.2004.08.006>
- Baliarsingh, S.K., Lotliker, A.A., Trainer, V.L., Wells, M.L., Parida, C., Sahu, B.K., ... Kumar, T.S. (2016). Environmental dynamics of red *Noctiluca scintillans* bloom in tropical coastal waters. *Marine Pollution Bulletin*, 111, 277-286. <https://doi.org/10.1016/j.marpolbul.2016.06.103>
- Bidle, K.D. (2014). The molecular ecophysiology of programmed cell death in marine phytoplankton. *Annual Review of Marine Science*, 7, 341-375. <https://doi.org/10.1146/annurev-marine-010213-135014>
- Cho, D.O. (2005). Lessons learned from Lake Shihwa project. *Coastal Management*, 33, 315-334. <https://doi.org/10.1080/08920750590952036>
- Cockcroft, A.C. (2001). *Jasus lalandii* 'walkouts' or mass strandings in South Africa during the 1990s: an overview. *Marine and Freshwater Research*, 52, 1085-1093. <https://doi.org/10.1071/MF01100>
- Cockcroft, A.C., Schoeman, D.S., Pitcher, G.C., Bailey, G.W., & Van Zyl, D.L. (1999). A mass stranding, or "walk out" of west coast rock lobster, *Jasus lalandii* in Elands Bay, South Africa: causes, results, and implications. In J.C. Von Vaupel Klein, & F.R. Schram (Eds.) *The Biodiversity Crisis and Crustacea. Crustacean Issues*, 12, 673-688.
- Cockcroft, A.C., van Zyl, D., & Hutchings, L. (2008). Large-scale changes in the spatial distribution of South African West Coast rock lobsters: an overview. *African Journal of Marine Science*, 30, 149-159. <https://doi.org/10.2989/AJMS.2008.30.1.15.465>
- Er, H.H., Lee, L.K., Lim, Z.F., Teng, S.T., Leaw, C.P., & Lim, P.T. (2018). Responses of phytoplankton community to eutrophication in Semerak Lagoon (Malaysia). *Environmental Science and Pollution Research*, 25, 22944-22962. <https://doi.org/10.1007/s11356-018-2389-0>
- Escobar, M.T.L., Sotto, L.P.A., Jacinto, G.S., Benico, G.A., San Diego-McGlone M.L., & Azanza, R.V. (2013). Eutrophic conditions during the 2010 fish kill in Bolinao and Anda, Pangasinan, Philippines. *Journal of Environmental Science and Management, Special Issue 1-2013*, 29-35.
- Figueiras, F.G., Pitcher, G.C., & Estrada, M. (2006). Harmful algal bloom dynamics in relation to physical processes. In E. Granéli, & J.T. Turner (Eds.), *Ecology of Harmful Algae*. Springer-Verlag, Berlin Heidelberg. *Ecological Studies*, 189, 127-138. https://doi.org/10.1007/978-3-540-32210-8_10
- GEOHAB. (2001). *Global Ecology and Oceanography of Harmful Algal Blooms, Science Plan*. P. Glibert, & G. Pitcher (Eds.), SCOR and IOC, Baltimore and Paris, 86 pp.
- GEOHAB. (2010). *Global Ecology and Oceanography of Harmful Algal Blooms, Harmful Algal Blooms in Asia*. K. Furuya, P.M. Glibert, M. Zhou, & R. Raine, (Eds.), IOC and SCOR, Paris and Newark, Delaware, 68 pp.
- Gilbert, D., Rabalais, N.N., Diaz, R.J., & Zhang, J. (2010). Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences*, 7, 2283-2296. <https://doi.org/10.5194/bg-7-2283-2010>
- Gilchrist, J.D.F. (1914). An enquiry into fluctuations in fish supply on the South African coast. *Marine Biological Report, Cape Town*, 2, 8-35.
- Glibert, P.M., & Burford, M.A. (2017). Globally changing nutrient loads and harmful algal blooms: recent advances, new paradigms, and continuing challenges. *Oceanography*, 30, 58-69. <https://doi.org/10.5670/oceanog.2017.110>
- Glibert, P.M., Berdalet, E., Burford, M.A., Pitcher, G.C., & Zhou, M. (2018a). Harmful algal blooms and the importance of understanding their ecology and oceanography. In P.M. Glibert, E. Berdalet, M.A. Burford, G.C. Pitcher, & M. Zhou (Eds.), *Global Ecology and Oceanography of Harmful Algal Blooms*. Springer International Publishing, *Ecological Studies*, 232, 9-25. https://doi.org/10.1007/978-3-319-70069-4_2
- Glibert, P.M., Al-Azri, A., Allen, J.I., Bouwman, A.F., Beusen, A.W.H., Burford, M.A., ... Zhou, M. (2018b). Key questions and recent research advances on harmful algal blooms in relation to nutrients and eutrophication. In P.M. Glibert, E. Berdalet, M.A. Burford, G.C. Pitcher, & M. Zhou (Eds.), *Global Ecology and Oceanography of Harmful Algal Blooms*. Springer International Publishing, *Ecological Studies*, 232, 229-259. https://doi.org/10.1007/978-3-319-70069-4_12
- Glibert, P.M., Beusen, A.H.W., Harrison, J.A., Dürr, H.H., Bouwman, A.F., & Laruelle, G.G. (2018c). Changing land-, sea-, and aircscapes: sources of nutrient pollution affecting habitat suitability for harmful algae. In P.M. Glibert, E. Berdalet, M.A. Burford, G.C. Pitcher, & M. Zhou (Eds.), *Global Ecology and Oceanography of Harmful Algal Blooms*. Springer International Publishing, *Ecological Studies*, 232, 53-76. https://doi.org/10.1007/978-3-319-70069-4_4
- Gomes, H. do R., Goes, J.I., Matondkar, S.G.P., Buskey, E.J., Basu, S., Parab, S., & Thoppil, P. (2014). Massive outbreaks of *Noctiluca scintillans* blooms in the Arabian Sea due to spread of hypoxia. *Nature Communications*, 5, 4862. <https://doi.org/10.1038/ncomms5862>
- Grindley, J.R., & Taylor, F.J.R. (1964). Red water and marine fauna mortality near Cape Town. *Transactions of the Royal Society of South Africa*, 37, 111-130. <https://doi.org/10.1080/00359196409519061>
- Harrison, P.J., Piontkovski, S., & Al-Hashmi, K. (2017). Understanding how physical-biological coupling influences harmful algal blooms, low oxygen and fish kills in the Sea of Oman and the Western Arabian Sea. *Marine Pollution Bulletin*, 114, 25-34. <https://doi.org/10.1016/j.marpolbul.2016.11.008>
- Heisler, J., Glibert, P.M., Burkholder, J.M., Anderson, D.M., Cochlan, W., Dennison, W.C., ... Suddleson, M. (2008). Eutrophication and harmful algal blooms: A scientific consensus. *Harmful Algae*, 8, 3-13. <https://doi.org/10.1016/j.hal.2008.08.006>
- Horstman, D.A. (1981). Reported red-water outbreaks and their effects on fauna on the west and south coasts of South Africa, 1959-1980. *Fisheries Bulletin South Africa*, 15, 71-88.
- Imai, I., Yamaguchi, M., & Hori, Y. (2006). Eutrophication and occurrences of harmful algal blooms in the Seto Inland Sea, Japan. *Plankton and Benthos Research*, 1, 71-84. <https://doi.org/10.3800/pbr.1.71>
- Kahru, M., Mitchell, B.G., & Diaz, A. (2005). Using MODIS medium-resolution bands to monitor harmful algal blooms. *Proceedings*

- of SPIE – The International Society for Optical Engineering, 5885. <https://doi.org/10.1117/12.615625>
- Kahru, M., Mitchell, B.G., Diaz, A., & Miura, M. (2004). MODIS detects a devastating algal bloom in Paracas Bay, Peru. *Eos*, 45, 465-472. <https://doi.org/10.1029/2004EO450002>
- Koizumi, Y., Kohno, J., Matsuyama, N., Uchida, T., & Honjo, T. (1996). Environmental features and the mass mortality of fish and shellfish during the *Gonyaulax polygramma* red tide occurred in and around Uwajima bay, Japan, in 1994. *Nippon Suisan Gakkaishi*, 62, 217-224. <https://doi.org/10.2331/suisan.62.217>
- Lam, C.W.Y., & Ho, K.C. (1989). Red tides in Tolo Harbour, Hong Kong. In T. Okaichi, D.M. Anderson, & T. Nemoto (Eds.), *Red Tides: Biology, Environmental Science and Toxicology*, Elsevier, New York, pp.49-52.
- Lam, C.W.Y., & Yip, S.S.Y. (1990). A three month red tide event in Hong Kong. In E. Granéli, B. Sundström, L. Edler, & D.M. Anderson (Eds.), *Toxic Marine Phytoplankton*, Elsevier, New York, pp. 481-486.
- Lee, M-O., & Kim, J-K. (2008). Characteristics of algal blooms in the southern coastal waters of Korea. *Marine Environmental Research*, 65, 128-147. <https://doi.org/10.1016/j.marenvres.2007.09.006>
- Lee, J., Park, K-T., Lim, J-H., Yoon, J-E., & Kim, I-N. (2018). Hypoxia in Korean coastal waters: a case study of the natural Jinhae Bay and artificial Shihwa Bay. *Frontiers in Marine Science*, 5, 70. <https://doi.org/10.3389/fmars.2018.00070>
- Matthews, S.G., & Pitcher, G.C. (1996). Worst recorded marine mortality on the South African coast. In T. Yasumoto, Y. Oshima, & Y. Fukuyo (Eds.), *Harmful and Toxic Algal Blooms*, Intergovernmental Oceanographic Commission of UNESCO, pp. 89-92.
- Nakata H., Mishina, H., Takahashi, T., & Hirano, K. (2010). A newly emerging environmental issue: development of hypoxia in the bottom water of Ariake Bay. In A. Ishimatsu, & H.-J. Lie (Eds.), *Coastal Environmental and Ecosystem Issues of the East China Sea*, TERRAPUB and Nagasaki University, pp. 1-12.
- Naqvi, S.W.A., George, M.D., Narvekar, P.V., Jayakumar, D.A., Shailaja, M.S., Sardesai, S., ... Binhu, M.S. (1998). Severe fish mortality associated with 'red tide' observed in the sea off Cochin. *Current Science*, 75, 543-544.
- Ndhlovu, A., Dhar, N., Garg, N., Xuma, T., Pitcher, G.C., Sym, S.D., & Durand, P.M. (2017). A red tide forming dinoflagellate *Prorocentrum triestinum*: identification, phylogeny and impacts on St Helena Bay, South Africa. *Phycologia*, 56, 649-665. <https://doi.org/10.2216/16-114.1>
- Paerl, H.W., Otten, T.G., & Kudela, R. (2018). Mitigating the expansion of harmful algal blooms across the freshwater-to-marine continuum. *Environmental Science and Technology*, 52, 5519-5529. <https://doi.org/10.1021/acs.est.7b05950>
- Padmakumar, K.B., Thomas, L.C., Salini, T.C., Vijayan, A., & Sudhakar, M. (2018). Subsurface bloom of dinoflagellate *Gonyaulax polygramma* Stein in the shelf waters off Mangalore south-eastern Arabian Sea. *Indian Journal of Geo Marine Sciences*, 47, 1658-1664.
- Peoples, M.B., Freney, J.R., & Mosier, A.R. (1995). Minimizing gaseous losses of nitrogen. In P.E. Bacon (Ed.), *Nitrogen Fertilization and the Environment*, Marcel Dekker, New York, pp. 565-602.
- Pitcher, G.C., & Calder, D. (2000). Harmful algal blooms of the southern Benguela Current: a review and appraisal of monitoring from 1989 to 1997. *South African Journal of Marine Science*, 22, 255-271. <https://doi.org/10.2989/025776100784125681>
- Pitcher, G.C., & Nelson, G. (2006). Characteristics of the surface boundary layer important to the development of red tide on the southern Namaqua shelf of the Benguela upwelling system. *Limnology and Oceanography*, 51, 2660-2674. <https://doi.org/10.4319/lo.2006.51.6.2660>
- Pitcher, G.C., Figueiras, F.G., Hickey, B.M., & Moita, M.T. (2010). The physical oceanography of upwelling systems and the development of harmful algal blooms. *Progress in Oceanography*, 85, 5-32. <https://doi.org/10.1016/j.pocean.2010.02.002>
- Pitcher, G.C., & Probyn, T.A. (2011). Anoxia in southern Benguela during the autumn of 2009 and its linkage to a bloom of the dinoflagellate *Ceratium balechii*. *Harmful Algae*, 11, 23-32. <https://doi.org/10.1016/j.hal.2011.07.001>
- Pitcher, G.C., & Probyn, T.A. (2012). Red tides and anoxia: an example from the southern Benguela current system. In P. Pagou, & G. Hallegraeff (Eds.), *14th International Conference on Harmful Algae*. International Society for the Study of Harmful Algae and Intergovernmental Oceanography Commission, United Nations Educational, Scientific and Cultural Organization, Paris, pp. 175-177.
- Pitcher, G.C., Probyn, T.A., du Randt, A., Lucas, A.J., Bernard, S., Evers-King, H., ... Hutchings, L. (2014). Dynamics of oxygen depletion in the nearshore of a coastal embayment of the southern Benguela upwelling system. *Journal of Geophysical Research*, 119, 2183-2200. <https://doi.org/10.1002/2013JC009443>
- Pitcher, G.C., & Probyn, T. A. (2016). Suffocating phytoplankton, suffocating waters – red tides and anoxia. *Frontiers in Marine Science*, 3, 186. <https://doi.org/10.3389/fmars.2016.00186>
- Rabbani, M.M., Rehman, A.U., & Harms, C.E. (1990). Mass mortality of fishes caused by dinoflagellate bloom in Gwadar Bay, southwestern Pakistan. In E. Granéli, B. Sundström, L. Edler, & D.M. Anderson (Eds.), *Toxic Marine Phytoplankton*, Elsevier, New York, pp. 209-214.
- Rajan, A., & Al Abdessalaam, T.Z. (2008). Harmful algal blooms and eutrophication: nutrient sources, composition and consequences in the Arabian Gulf bordering Abu Dhabi Emirate. In O. Moestrup, G. Doucette, H. Enevoldsen, A. Godhe, G. Hallegraeff, B. Luckas, ... A. Zingone (Eds.), *12th International Conference on Harmful Algae*. International Society for the Study of Harmful Algae and Intergovernmental Oceanographic Commission of UNESCO, Copenhagen, pp. 226-229.
- Rojas de Mendiola, B. (1979). Red tide along the Peruvian coast. In D.L. Taylor, & H.H. Seliger (Eds.), *Toxic Dinoflagellate Blooms*. Elsevier, Amsterdam, pp. 183-190.
- San Diego-McGlone, M.L., Azanza, R.V., Villanoy, C.L., & Jacinto, G.S. (2008). Eutrophic waters, algal bloom and fish kill in fish farming areas in Bolinao, Pangasinan, Philippines. *Marine Pollution Bulletin*, 57, 295-301. <https://doi.org/10.1016/j.marpolbul.2008.03.028>
- Sánchez, S., & Delgado, E. (1996). Mareas rojas en el área del Callao (12°S) 1980–1995. *Informes Progresivos del Instituto del Mar del Perú*, 44, 19-37

- Sulochanan, B., Dineshababu, A.P., Saravanan, R., Subramanya Bhat, G., & Lavanya, S. (2014). Occurrence of *Noctiluca scintillans* bloom off Mangalore in the Arabian Sea. *Indian Journal of Fisheries*, 61, 42-48.
- Sutton, M.A., Bleeker, A., Howard, C.M., Bekunda, M., Grizzetti, B., de Vries, W., ... Zhang F.S. (2013). Our Nutrient World: the challenge to produce more food and energy with less pollution. Global Overview of Nutrient Management. Centre for Ecology and Hydrology, Edinburgh on behalf of the Global Partnership on Nutrient Management and the International Nitrogen Initiative, United Kingdom.
- Sweeney, B.M. (1976). *Pedinomonas noctilucae* (Prasinophyceae), the flagellate symbiotic in *Noctiluca* (Dinophyceae) in Southeast Asia. *Journal of Phycology*, 12, 464-460. <https://doi.org/10.1111/j.1529-8817.1976.tb02874.x>
- Teen, L. P., Gires, U., & Pin, L.C. (2012). Harmful algal blooms in Malaysian waters. *Sains Malaysiana*, 41, 1509-1515.
- Tsutsumi, H. (2006). Critical events in Ariake Bay ecosystem: clam population collapse, red tides, and hypoxic bottom water. *Plankton and Benthos Research*, 1, 3-25. <https://doi.org/10.3800/pbr.1.3>
- Trainer, V.L., Pitcher, G.C., Reguera, B., & Smayda, T.J. (2010). The distribution and impacts of harmful algal bloom species in eastern boundary upwelling systems. *Progress in Oceanography*, 85, 33-52. <https://doi.org/10.1016/j.pocean.2010.02.003>
- Vicente, H.J., Gaid, R.D., Dejarme, H.E., Roa, E.C., & Azanza, R.V. (2002). Harmful algal bloom in Iligan Bay, Southern Philippines. *Science Diliman*, 14, 59-65.
- Wells, M.L., & Karlson, B. (2018). Harmful algal blooms in a changing ocean. In P.M. Glibert, E. Berdalet, M.A. Burford, G.C. Pitcher, & M. Zhou (Eds.), *Global Ecology and Oceanography of Harmful Algal Blooms*. Springer International Publishing, *Ecological Studies*, 232, 77-92. https://doi.org/10.1007/978-3-319-70069-4_5
- Wong, Y.K., Ng, K.Y., Tong, T.L., & Ho, K.C. (2010). A *Ceratium furca* bloom in inner Tolo Harbour, Hong Kong, In K.-C. Ho, M.J. Zhou, & Y.Z. Qi (Eds.), *13th International Conference on Harmful Algae*. International Society for the Study of Harmful Algae and Environmental Publication House Hong Kong, pp. 13-16.
- Xu, J., Zhu, M., & Liu, B. (1993). The formation and environmental characteristics of the largest red tide in north China. In T.J. Smayda, & Y. Shimizu (Eds.), *Toxic Phytoplankton Blooms in the Sea*. Elsevier Science Publishers B.V., pp. 359-362.
- Yu, R.C., Lü, S.H., & Liang, Y.B. (2018). Harmful Algal Blooms in the coastal waters of China. In P.M. Glibert, E. Berdalet, M.A. Burford, G.C. Pitcher, & M. Zhou (Eds.), *Global Ecology and Oceanography of Harmful Algal Blooms*. Springer International Publishing, *Ecological Studies*, 232, 309-316. https://doi.org/10.1007/978-3-319-70069-4_15
- Zhu, Z.Y., Zhang, J., Wu, Y., Zhang, Y.Y., Lin, J., & Liu, S.M. (2011). Hypoxia of the Changjiang (Yangtze River) estuary: oxygen depletion and organic matter decomposition. *Marine Chemistry*, 125, 108-116. <https://doi.org/10.1016/j.marchem.2011.03.005>

