The distribution and impacts of harmful algal bloom species in eastern boundary upwelling systems

V.L. Trainer\textsuperscript{a,*}, G.C. Pitcher\textsuperscript{b,c}, B. Reguera\textsuperscript{d}, T.J. Smayda\textsuperscript{e}

\textsuperscript{a}NOAA, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA
\textsuperscript{b}Marine and Coastal Management, Department of Environmental Affairs, Private Bag X2, Rogge Bay, 8012 Cape Town, South Africa
\textsuperscript{c}University of Cape Town, Private Bag, Rondebosch, 7700 Cape Town, South Africa
\textsuperscript{d}Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Cabo Estay, Cunio, 36200 Vigo, Spain
\textsuperscript{e}Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881, USA

\textbf{A R T I C L E   I N F O}

Article history:
Available online 6 February 2010

\textbf{A B S T R A C T}

Comparison of harmful algal bloom (HAB) species in eastern boundary upwelling systems, specifically species composition, bloom densities, toxin concentrations and impacts are likely to contribute to understanding these phenomena. We identify and describe HABs in the California, Canary, Benguela and Humboldt Current systems, including those that cause the poisoning syndromes in humans called paralytic shellfish poisoning (PSP), diarrhetic shellfish poisoning (DSP), and amnesic shellfish poisoning (ASP), as well as yessotoxins, ichthyotoxins, and high-biomass blooms resulting in hypoxia and anoxia. Such comparisons will allow identification of parameters, some unique to upwelling systems and others not, that contribute to the development of these harmful blooms.

\section{1. Introduction}

Four major coastal currents are associated with upwelling on the eastern sides of ocean basins: the California Current, the Canary Current, the Benguela Current and the Humboldt Current. These highly productive upwelling regimes account for a large portion of global fisheries production. Harmful algal blooms (HABs) are prolific in these eastern boundary upwelling systems, and are attributed to those algal species that produce toxins and to “red tide” species that form dense blooms, do not usually produce toxins, but may cause harm through events such as hypoxia and anoxia. Knowledge of the species composition of HABs in eastern boundary upwelling systems is incomplete, but available data do not indicate a HAB flora unique to upwelling systems (Smayda, 2000; Smayda, in this issue).

The negative effects of the somewhat diverse group of microscopic plankton that comprise HAB species in upwelling systems increasingly threaten the economic viability of fisheries and aquaculture, the health and diversity of the ecosystem, and the recreational activities supported within these systems. Here, we discuss what is known about HABs and their impacts in the four major eastern boundary upwelling systems. We detail by location the organisms observed, the frequency and density of blooms, the presence of toxins and their impacts on marine life and human health, and the negative effects of high-biomass blooms, specifically their linkage to hypoxia and anoxia.

\begin{itemize}
  \item \textbf{California Current} – Encompassing the Pacific west coast of North America from approximately the Gulf of Alaska in the north to the Baja California Peninsula in the south (Fig. 1).
  \item \textbf{Canary Current} – Extending from the northwestern tip of the Iberian Peninsula to south of Senegal (Fig. 2). The Iberian upwelling region is separated from the north African system by a break in the coastline forced by the Strait of Gibraltar. Observations of HABs are biased toward the Iberian Peninsula owing somewhat to the excellent monitoring programmes associated with the large shellfish aquaculture industry in this region.
  \item \textbf{Benguela Current} – Extending from the southern point of the African continent and bounded to the north by the Angola–Benguela front off Angola (Fig. 3). The principal upwelling cell in the vicinity of Luderitz effectively divides the system into northern and southern components. HABs in the southern Benguela are better documented than those in the northern Benguela, although this does not necessarily reflect their impact on these components of the system.
  \item \textbf{Humboldt Current} – Extending from central Chile, through northern Chile, the entire coast of Peru and to parts of Ecuador (Fig. 4). Reports of HABs are most common in the particularly productive northern Humboldt off central Peru where red tides have been linked to fish and bird mortalities since the early 1800s.
\end{itemize}
2. The upwelling HAB species

The species known to be responsible for HABs in upwelling regions are listed in Fig. 5. This list comprises 27 dinoflagellate species, the diatom genus *Pseudo-nitzschia* and the raphidophyte *Heterosigma akashiwo*. An indication is provided not only of the presence of each of these species within each of the upwelling systems, but also of the likely level of biomass to be achieved by each species. Those HAB species found in upwelling systems tend mostly to be cosmopolitan in their distribution throughout each system, but not necessarily across systems.

The frequency of blooms and the specific impacts of bloom species, including the poisoning syndromes in humans known as paralytic shellfish poisoning (PSP), diarhetic shellfish poisoning (DSP), and amnesic shellfish poisoning (ASP), as well as the harm caused by yessotoxins, ichthyotoxins and high-biomass blooms resulting in hypoxia or anoxia, vary among upwelling systems. The imbalance of impacts and harmful effects of HABs in each of the world’s major eastern boundary upwelling systems is summarized below, described by region.

2.1. Paralytic shellfish poisoning toxins

The paralytic shellfish toxins, produced by marine dinoflagellates from the genera *Alexandrium*, *Gymnodinium* and *Pyrodinium*, are perhaps the most geographically widespread marine biotoxins worldwide (Fig. 5). These toxins include the potent parent compound saxitoxin and related structures, and cause PSP in humans that have consumed shellfish that have fed upon toxigenic algae. Levels of shellfish toxicity are dependent on the isoform of saxitoxin and the cell toxin quota of the algae upon which they feed, the number and ratio of toxic algae to accompanying species in surrounding waters, the rate of uptake of algae by shellfish, and the capability of shellfish to transform, retain or depurate toxins.

Clinical symptoms of PSP in mild cases include a tingling sensation or numbness around the lips, which occurs usually within 30 min of consumption of shellfish following absorption of the PSP toxins through the buccal mucous membranes. These symptoms spread to the face and neck, and prickly sensations in the fingertips and toes may also be experienced, as are headaches, dizziness, nausea, vomiting and diarrhea. Sometimes, temporary
blindness is also experienced. Most symptoms occur within hours but may last for days, and are almost identical in all cases of PSP. In more severe cases of poisoning, paralysis progresses to the arms and the legs, followed by giddiness and incoherent speech. Ataxia and motor incoordination occur and respiratory difficulties appear first as tightness around the throat. Pronounced respiratory problems and death through paralysis can occur within 2–24 h of shellfish ingestion (Mons et al., 1998).

2.1.1. California Current system

The Pacific coast of North America has a long history of PSP, with the earliest confirmed fatalities recorded in 1793 on the central British Columbia coast (Quayle, 1969). Other early cases of PSP were reported by Europeans settling on the coast of California (Meyer et al., 1928; Sommer et al., 1937). It was, however, not until 1965 that fatalities or illness due to PSP were directly linked to toxins produced by the dinoflagellate *Alexandrium catenella* (Prakash and Taylor, 1966). Within the California Current system, *Alexandrium* species and PSP toxins are now known to be prevalent. In Washington State, shellfish closures due to PSP toxins have occurred every year since monitoring began in the 1940s, differing only in the extent and duration of closures (Trainer et al., 2003). Toxins are typically present in shellfish from May through to October, and levels of toxins in shellfish are usually highest in July and August (Horner et al., 1997). However, despite their regular occurrence, there has been no large-scale effort to study *Alexandrium* blooms in the California Current system.

*A. catenella* is the predominant PSP-toxin producing species in the California Current system and is present along the entire outer open coast (Taylor and Trainer, 2002). Blooms are considered to originate in shallow, nearshore localities and to spread regionally (Taylor et al., 1994); these blooms are generally subsurface, often occurring near the nutricline (Taylor and Trainer, 2002). Observations indicate that blooms are advected into estuaries and embayments from adjacent coastal waters (Horner et al., 1997). However, because there are few datasets from offshore phytoplankton sampling, including maps of sedimentary cysts, it is currently not known whether *Alexandrium* blooms originate from multiple sites or single seedbeds (Price et al., 1991). Although blooms may initiate from benthic cysts, there is no simple correlation of bloom distribution and cyst density in sediments (Cox et al., 2008).

In the southern part of the California Current system, off the western coast of Mexico, both *Gymnodinium catenatum* and *A. catenella* are known to produce PSP toxins. Interestingly, the distribution of these two species does not appear to overlap: *G. catenatum* is found to the north of Acapulco, whereas *A. catenella* occurs along the western coast of Baja California, where it is often found as a component of the phytoplankton but rarely in high numbers (Hernández-Becerril et al., 2007). During the period of record from 1970 to 2004, there were approximately 600 human illnesses or deaths due to PSP in Mexico (Hernández-Becerril et al., 2007). However, the majority of these cases were attributed to the dinoflagellate *Pyrodinium bahamense* var. *compressum*, which occurs to the south of the California Current system.

2.1.2. Canary Current system

*Gymnodinium catenatum* and *Alexandrium minutum* are the two main causes of PSP in the Canary Current system. The first reports of human illness, including several fatalities, were from the Óbidos
Lagoon in Portugal (Correia, 1946; Pinto and Silva, 1956), at which time PSP was attributed to a bloom of *Prorocentrum micans* (Pinto and Silva, 1956). It is likely that these PSP events were caused by *A. minutum*, reported as *Gonyaulax excavata* to form dense blooms in this lagoon in the 1950s and early 1960s (Silva, 1985). *Alexandrium minutum*, reported as *Gonyaulax tamarensis*, was also later linked to PSP on the Galician coast (Blanco et al., 1985). In 1976, a major PSP outbreak affecting 176 consumers in different European countries was traced to mussels from the Galician Rías (Lüthy, 1979). This event was attributed to *G. catenatum*, providing the first report of this species in Europe (Estrada et al., 1984). Reports of PSP caused by *G. catenatum* in Portugal in 1986 followed (Sampayo, 1989). In Morocco, shellfish intoxications were reported in 1971, 1975 and 1982, but it was not until 1994 that a severe outbreak of PSP was linked to a bloom of *G. catenatum* extending along the Atlantic coast from Larache (34°N) to Essaouira (30°30′N) (Tahri-Joutei, 1998, 2007). Hallegraeff and Fraga (1998) suggested that *G. catenatum* could be a recent introduction to the Iberian coast, but cyst records later revealed the presence of cysts of *G. catenatum* off Lisbon dating back to the beginning of the 20th century (Amorim and Dale, 2006). Following the major outbreak of 1976, blooms of *G. catenatum* returned to Galicia only in 1985 (Fraga et al., 1988), occurring annually until 1995. For the following 10 years, blooms of *G. catenatum* were again absent until the appearance of a severe bloom in the autumn of 2005 (Vale et al., 2008).

Information on PSP outbreaks and harmful algae south of Morocco is scarce. However, the cause of a large mortality of the highly endangered Mediterranean monk seal *Monachus monachus* in a reserve off Cape Blanc, Mauritania, in 1997 was linked to PSP (Hernández et al., 1998). The presence of PSP toxins in different organs of the over 100 dead seals, comprising 2/3 of the population, are considered to have originated from blooms of either *A. minutum* or *G. catenatum*.

*Alexandrium minutum* and *G. catenatum* bloom under distinct oceanographic conditions and their toxin profiles are quite different. *Alexandrium minutum* is rarely found in the open rías, but thrives in small embayments, sheltered from the dynamic exchange of water between the rías and the adjacent shelf. Dense blooms of up to $10^7$ cells l$^{-1}$ typically occur in spring and summer, are spatially restricted and associated with stratified conditions induced by freshwater runoff (Blanco et al., 1985; Bravo et al., 2009). Baiona Bay, a sheltered brackish embayment with little influence in the overall dynamics of Ría de Vigo, provides a model example of the environment favouring *A. minutum* blooms within an upwelling system (Bravo et al., 2009). The toxin profile of *A. minutum* is...
tum is dominated by the carbamoyl derivatives of saxitoxin, GTX1-4, and in culture A. minutum has a low to moderate toxin quota of 1–24 fmol cell⁻¹ (Franco et al., 1994). Toxin concentrations in shellfish of around 400 μg STX-equiv. 100 g⁻¹ have been associated with concentrations of A. minutum of 10⁷ cells l⁻¹ (Blanco et al., 1985). Differences of an order of magnitude in the cell toxin quota of different strains of A. minutum explain large differences in shellfish toxin concentrations, which ultimately impact on human health following blooms of A. minutum in Galicia, Portugal and Morocco.

In contrast, G. catenatum is a late-summer, mid-shelf species, which is occasionally found in stratified waters in the lee of the Cape Carvoeiro upwelling plume (Moita et al., 1998, 2003). Its population dynamics, particularly the vegetative phase of growth, is tightly coupled to the upwelling regime (Fraga et al., 1988; Moita et al., 1998). Its toxin profile is dominated by the less toxic sulfo-carbamoyl derivatives of saxitoxin (Anderson et al., 1989; Taleb et al., 2003), and a cell toxin quota of 40–70 pg cell⁻¹ has been measured in cultures (Flynn et al., 1996). Blooms of G. catenatum generally occur on the Portuguese coast earlier than in the Galician Rias, where bloom maxima are associated with the advection of warmer shelf waters that are forced into the rias with the transition to downwelling conditions at the end of the upwelling season (Fraga et al., 1990; Figueiras et al., 1996). Blooms of G. catenatum blooms from the Portuguese to the Galician Rias, where bloom maxima are associated with the advection of warmer shelf waters that are forced into the rias with the transition to downwelling conditions at the end of the upwelling season (Fraga et al., 1990; Figueiras et al., 1996). In practice, the northward progression of G. catenatum blooms from the Portuguese to the Galician coast provides early warning of PSP (Pazos et al., 2006; Vale et al., 2008), leading to prolonged harvesting closures lasting until the following spring.

Different hypotheses have been proposed to explain the abrupt increase of G. catenatum in the Galician Rias in autumn; these include in situ germination of cysts (Figueiras and Pazos, 1991), across-shelf transport of established shelf populations (Crespo et al., 2006), and alongshore transport from Portuguese waters by an inner-shelf buoyant plume (Sordo et al., 2001). Surveys of G. catenatum cysts on the Portuguese shelf (Amorim et al., 2004) and life-cycle studies during blooms in the Ría de Vigo (Figueiroa et al., 2008) fail to support the in situ germination hypothesis. Blooms of G. catenatum in the Canary Current system seem to respond to broad mesoscale processes, with annual trends of occurrence and absence common to the reported range of G. catenatum from Cape Finisterre to Morocco. Observations from the Portuguese (Moita et al., 1998) and the Andalusian (Mamán et al., 2000) monitoring programme in south western Spain suggest sites of multiple origin delimited by capes Finisterre, Roca and San Vicente. Blooms of G. catenatum are very rarely recorded between Cape Gibraltar and the Portuguese border in the Guadiana Estuary, but are endemic to the Alborán eddy in the Southwest Mediterranean Sea (Mamán et al., 2000; Tahri-Joutei, 2007) (Fig. 6). Gymnodinium catenatum typically impacts aquaculture production and public health in the Canary Current system, at moderate concentrations of 10¹⁳–10¹⁵ cells l⁻¹. A visible brown patch of G. catenatum of 2 × 10⁶ cells l⁻¹ was observed on a single occasion in the Ría de Vigo in September 1986. During that year, relatively early mid-September onshore advection was followed by exceptionally calm

Fig. 4. Key geographical features and locations discussed in the text within the Humboldt Current system.
conditions, which are considered to have further promoted in situ growth of the blooms (Fraga et al., 1990).

2.1.3. Benguela Current system

In the southern Benguela, blooms of *A. catenella* are common and PSP toxins regularly threaten the safety of shellfish in this region, which is subjected to recurring cases of PSP (Pitcher and Calder, 2000). Although some of the earlier accounts of possible PSP in the Benguela date back to the 1880s, confirmed cases were only described in 1948 (Sapeika, 1948). Within the region, *A. catenella* has been reported as a low to moderately toxic species with a high proportion of the less toxic sulfocarbamoyl toxins.

Fig. 5. Harmful algal species in upwelling systems including the California, Canary, Humboldt and Benguela Current systems, coded as circles (labeled in lower panel as I–IV). The occurrence of algal species within these upwelling systems is indicated as high-biomass (red circles), moderate-biomass (yellow circles) or low-biomass (green circles) blooms. Filled circles indicate that a species is present but its density is currently not known. Open circles denote species that are currently not known to be present. The relative contribution of each species to the overall biomass does not necessarily equate to the degree of harm caused by this species in a particular upwelling system.
(Pitcher et al., 2001; Ruiz Sebastian et al., 2005). Although the distribution of A. catenella is not clearly defined within the region, it is considered to be restricted to the West Coast, extending only as far south as Cape Point. The highest abundance of cysts of A. catenella is found in the sediments of the southern Namaqua shelf, within the greater St. Helena Bay region (Joyce and Pitcher, 2006), which corresponds also to the coastal region with the highest incidence of PSP-contaminated shellfish (Pitcher et al., 2001). Phytoplankton monitoring has indicated that A. catenella appears almost every year on the Namaqua coast, typically during the latter part of the upwelling season. There, A. catenella is regularly recorded at cell concentrations of several million cells l−1 and toxin concentrations in shellfish often exceed several thousand µg STX-equiv. 100 g−1, as determined by the standard AOAC mouse bioassay (Horstman, 1981; Pitcher et al., 2001). Consequently, these blooms not only render shellfish toxic to consumers but are also seemingly responsible for large shellfish and fish mortalities (Pitcher, 2000; Pitcher and Calder, 2000).

Other potential PSP-causing species within the region include A. minutum, which was first detected in November 2003 following visual discolouration of the waters of Cape Town Harbour (Pitcher et al., 2007). The composition of neurotoxins associated with this species was limited to gonyautoxins, and the composition of accumulated PSP toxins in shellfish collected at the time of the harbour bloom implicated A. minutum as the likely origin. The potential threat of this species to human health is, however, considered to be limited as this species has not been recorded outside of the environs of the harbour. Ruiz Sebastian et al. (2005) reported the presence of Alexandrium tamia-yananikki on the western Agulhas Bank, but this species appears unlikely to render shellfish toxic owing to very low cellular toxin concentrations and the absence of reported blooms. In the northern Benguela, Pieterse and van der Post (1967) identified Alexandrium tamarense as a regular bloom-forming species in Walvis Bay, but never reported mussel poisoning from the region. Recently, Rangel and Silva (2006) reported dense blooms of G. catenatum (1.5 × 10⁵ cell l⁻¹), Gambierdiscus toxicus and Pyrodinium bahamense var. compressum off Luanda on the Angolan coast. However, these blooms may be considered to fall outside of the northern boundary of the upwelling system.

2.1.4. Humboldt Current system

Although there is no recorded history of PSP in the Peruvian system, monitoring imposed for the purpose of export to the European Union has detected moderate levels of saxitoxins in the scallop Argopecten purpuratus of up to 220 µg STX-equiv. 100 g−1 (Antinori et al., 2003). The source of these PSP toxins in scallops has not been identified. Analyses of net hauls rich in the chain-forming Alexandrium affine have tested negative for toxins (Vera et al., 1999). Alexandrium peruvianum, previously reported as Gonyaulax peru-vianum, and known to cause red tide off Callao (Rojas de Mendiola, 1979), has not been tested for toxicity.

2.2. Diarrhetic shellfish poisoning and other lipophilic toxins

Polyether toxins in shellfish included in the traditional ‘DSP complex’ (Yasumoto et al., 1985) can be divided into three groups of toxins with different chemical structures and biological effects: okadaic acid (OA) and its derivatives the dinophysistoxins (DTXs); the pectenotoxins (PTXs); and the yessotoxins (YTXs). Both OA and the DTXs are acid polyethers that inhibit protein phosphatase, and are the only toxins of the DSP complex with diarrheagenic effects in mammals. The PTXs are polyether-lactones, some of which are hepatotoxic to mice by intraperitoneal injection. The YTXs are disulfathated polyethers that are cardiotoxic to mice, but have to date not been associated with human poisonings. Neither the yessotoxins, nor PTX2 and its shellfish-mediated derivative PTX2-secoacid, are toxic to mice when administered orally (Aune, 2001; Aune et al., 2002; Miles et al., 2004), and their potential threat to human health is currently under debate (Anon., 2004a). The three groups of toxins can now be analyzed with independent analytical methods, which have led the European Union to regulate them separately (Anon., 2004b).

The history of misidentifications of the causative toxins and the agents of diarrhetic/lipophilic toxin outbreaks over the past three decades may be attributed to the following: both OA and the PTXs are produced by Dinophysis; OA is also produced by benthic dinoflagellates of the genus Prorocentrum, but P. micans, a species that frequently co-occurs with Dinophysis acuminata, is not a toxin-producer; the producers of YTXs (Lingulodinium polyedrum, Protoceratium reticulatum, Gonyaulax spinifera) and of azaspiracids (AZAs) often co-occur in assemblages of lipophilic toxin-producers; all lipophilic toxins, including OA, the PTXs, YTXs and AZAs, are co-extracted and give a single response in conventional mouse bioassays; and the acute symptoms of DSP are easily confused with gastroenteritis of bacterial origin (Reguera and Pizarro, 2008). Furthermore, only recently was the tiny Heterocapsa-like dinoflagellate Axadinum spinosum identified as the source of AZA (Tillmann et al., 2009), following years of incorrectly assuming
that the heterotrophic dinoflagellate *Protoperidinium crassipes* was the source of the toxin.

European Union directives specify regulatory toxin levels of 160 µg OA + DTXs + PTXs equiv., 1 mg YTX equiv. and 160 µg AZA equiv. kg⁻¹ of shellfish meat (Anon., 2004b). These limits have been adopted by regulatory authorities in South Africa, but not by those in the US and Mexico as shellfish are not currently tested routinely for DSP toxins in these countries. Symptoms of DSP include diarrhea, nausea, vomiting and abdominal pain. The onset of symptoms, which are never acutely lethal, ranges from 30 min to a few hours after ingestion of the toxic shellfish, with complete recovery within three days. Hospitalization is rarely needed. 

The presence of DSP toxins and/or pectenotoxins has been confirmed by chromatographic analysis in single-cell isolates of at least 12 mixotrophic or heterotrophic species of *Dinophysis*. For mixotrophic species of *Dinophysis*, the source of the toxins has been shown to be the dinoflagellate (*Kamiyama and Suzuki, 2009; Hackett et al., 2009*). However, for heterotrophic species, such as *Dinophysis rotundata*, it is likely that their prey are the source of the toxins (*González-Gil et al., in press*). Most *Dinophysis* species are rare, occurring at concentrations of 1–10⁶ cells l⁻¹, but the species *D. acuminata, Dinophysis acuta, Dinophysis caudata, Dinophysis fortii, Dinophysis norvegica, D. rotundata* and *Dinophysis sacculus* are able to reach concentrations >10⁹ cells l⁻¹ in coastal waters and are responsible for chronic DSP events (*Reguera and Pizarro, 2008*). Occasionally, reports of DSP toxins in shellfish have been associated with concentrations of *Dinophysis* as low as a few hundred cells l⁻¹ (*Yasumoto et al., 1985*).

2.2.1. California Current system

Several species of *Dinophysis*, known to cause DSP, are found in the California Current system. However, toxin levels in shellfish from the US West Coast are not routinely monitored and no cases of DSP have been recorded. DSP toxins have nevertheless been measured in several species of shellfish collected off the coast of Washington State (Robertson, personal communication). Furthermore, *D. fortii, D. acuta, D. acuminata* and *D. norvegica* are known to be common components of the phytoplankton, although rarely abundant (*Sutherland, 2008*). Maximum abundances of *Dinophysis* are observed in summer and early autumn, and are usually associated with warm surface water temperatures, stable salinity and low nutrients. *Dinophysis fortii* appears to be the predominant producer of okadaic acid in Monterey Bay, California, but to date toxin levels have not exceeded the US Food and Drug Administration action level of 160 µg kg⁻¹ shellfish. In 2008, the first closure of shellfish harvesting in the US due to DSP toxins occurred along the coastline of the State of Texas, as a result of toxins reaching 450 µg kg⁻¹ in oyster meat (K. Wiles, pers. comm.). Although Texas is not in the California Current system, it is noteworthy to mention this event as it suggests that DSP toxins may be more widespread in the US than previously thought.

Yessotoxin production has been confirmed in *L. polyedrum* strains from the southern part of the California Current system (*Armstrong and Kudela, 2006*). Formerly known as *Gonyaulax polyedra, L. polyedrum* is a widely distributed species in warm-temperate and subtropical coastal waters (*Steidinger and Tangen, 1997*), and is frequently associated with red tide events south of 37°N, particularly along the southern California Bight and Baja Peninsula. Although *L. polyedrum* in the California Current system has been found to produce yessotoxin, as well as the analogue homoyessotoxin (*Draisci et al., 1999; Stobo et al., 2002*), it has rarely been reported to have any direct negative impacts and is not known to have rendered shellfish toxic. Large blooms of *L. polyedrum* have been positively correlated with river runoff (*Hayward et al., 1995*) and anthropogenic nutrient loading (*Kudela and Cochlan, 2000*). Blooms usually occur in late spring or early summer, and are typically dispersed by physical mixing and advection.

2.2.2. Canary Current system

In 1981, over 5000 consumers of mussels from the Galician Rías suffered from gastroenteritis, traced to blooms of *Dinophys* (*Campos et al., 1982*), whereas in Portugal, DSP has been reported over the past two decades (*Vale et al., 2008*). DSP in the Canary Current system is mainly attributed to *D. acuminata, D. acuta* and *D. caudata*, which tend to follow this order in a north to south gradient in abundance from Cape Finisterre off Northwest Iberia to Southwest Morocco.

The mixotrophic species *D. acuminata* and *D. acuta* are the cause of the most severe HAB-related impacts on shellfish harvests in Western Iberia. These species are present throughout most of the year and lead to prolonged shellfish harvest closures at concentrations ranging between 10⁶ and 10⁷ cells l⁻¹. In Galicia and Northern Portugal, *D. acuminata* is a coastal species occurring within a wide range of salinity and temperature, and increases in numbers with the onset of thermaline stratification in late spring. Once the population is established, it exhibits considerable variability linked to pulses of upwelling and downwelling, during the course of the upwelling season from March to October. *Dinophysis acuta* is more seasonal, occurring within narrower ranges of temperature and salinity, and thrives in thermally stratified waters with deeper pycnoclines, in late summer (*Reguera et al., 1993, 1995; Palma et al., 1998*). Both species can form thin layers (*Moita et al., 2006; Velo Suárez et al., 2008*), and during exceptionally hot and dry summers, *D. acuta* replaces *D. acuminata* in Galician waters (*Escalera et al., 2006*) (Fig. 7). During the autumn transition to downwelling, both species appear to be transported northward, by the same alongshore transport mechanism described for *G. catenatum* (*Sordo et al., 2001*). The relative role of transport vs. active growth in bloom development has been evaluated by estimation of *in situ* rates of division (*Velo-Suárez et al., 2009; Escalera et al., submitted for publication*). In essence, elevated numbers of *D. acuminata* and *D. acuta*, can be associated with two scenarios: *in situ* growth, favoured during periods of stratification between moderate pulses of upwelling, leading to co-existence with diatoms, or accumulation during downwelling events, both during the upwelling season and particularly during the autumn transition (*Fig. 8*). Consequently, DSP and its impact on shellfish exploitation is most apparent during downwelling, which favours the displacement of diatoms from the water column and selects for large dinoflagellates, including species of *Dinophysis*. *Dinophysis acuta* blooms can be especially noxious when they are present late in the year, because mussels take longer to deparate under winter conditions (*Escalera et al., 2006*). Putative cysts of *Dinophysis*, comprising <0.1% of the population during exceptional blooms, have not been observed in sediment samples. This observation and the apparent flexibility of the life cycles of these species (*Reguera and González-Gil, 2001*) suggest a holoplanktonic existence, without reliance on cysts as a seeding mechanism (*Escalera and Reguera, 2008*).

In the Gulf of Cádiz in southwest Spain, DSP occurs as early as February and is initially associated with a *Dinophysis ovum*-like form (*Raio et al., 2008*) of the *D. acuminata* complex and later with *D. acuta* (*Jaén et al., 2003*). DSP attributed to blooms of *D. acuminata* and *D. caudata* poses a major threat to Moroccan shellfish resources (*Tahrir-Jouti, 2007*). In the Canary Current system, OA dominates the toxin profile of *D. acuminata*, whereas a more complex profile of OA, DTX2, PTX2 and PTX2SA is associated with
Fig. 7. A seasonal time-series of (a) daily Ekman transport and (b) temperature and cell concentrations of *Dinophysis acuta* in Ría de Pontevedra. The dashed line separates two scenarios under which blooms of *D. acuta* are found: stratified conditions present during the upwelling season, with cell maxima in the region of the pycnocline (left); and a homogeneous water column present at the end of the upwelling season in which cell maxima are found near the surface (right). Modified from Reguera et al. (1995).

Fig. 8. Time-series depicting interannual variability in the (a) Winter NAO index and (b) the cell maxima of *Dinophysis acuminata* and *D. acuta* (integrated hose-samples, 0–15 m) at a fixed station in Ría de Pontevedra. The negative NAO index in 1996 coincided with an almost *Dinophysis*-free year. High positive NAO indices, that correspond to very hot summers and marked thermal stratification coincided with high densities of *D. acuta*. Modified from Escalera et al. (2006).
blooms of *D. acuta* (Fernández et al., 2006; Pizarro et al., 2009; Taleb et al., 2006; Vale et al., 2008).

Blooms of *L. polyedrum* responsible for water discolourations and bioluminescence in summer were apparently common to the north of Lisbon and in the Galician Rías during the first half of the 20th century (Sobrino-Buhigas, 1918; Pinto, 1949; Margalef, 1956). Blooms of this species, and the presence of YTXs in shellfish below regulatory levels, are now reported in southwestern Iberia, where *L. polyedrum* accumulates in warm stratified waters composed by adjacent upwelling in late summer and early autumn (Amorim et al., 2004; Vale et al., 2008). Interestingly, *L. polyedrum* is at present a rare species in the Galician Rías Baixas, although resting cysts of this species are abundant in the sediments (Blanco, 1989). Blooms of *L. polyedrum* of up to 2 x 10^6 cells l^{-1} are common in the Galician embayment of Ría de Ares, found at the northern limit of the Canary Current system, and have been linked to moderate levels of YTXs in mussels (Arévalo et al., 2006). Analyses of YTX were detected below regulatory limits in mussels and cockles harvested from Aveiro Lagoon during 2005 and 2006, but this toxicity has been associated with the presence of *Proto- ceratium* spp. and *G. spinifera* (Vale et al., 2008). Water discolourations caused by blooms of *L. polyedrum* are well known on the Atlantic coast of Morocco (Tahir-Joutei, 2007). The Azaspiracids, AZA1 and AZA2, have been detected below regulatory levels by LC–MS analysis in all commercial shellfish species in northwestern Iberia (Vale et al., 2008), and have been found to co-occur with YTXs in mussels from Morocco (Taleb et al., 2006). However, their specific presence, and that of the YTXs, is usually undetected by the mouse bioassay for lipophilic toxins and the causative agents have not been identified.

### 2.2.3. Benguela Current system

DSP toxins were identified in shellfish for the first time on the South African coast in 1991, and attributed to *D. acuminata* (Pitcher et al., 1993). Subsequent monitoring revealed that DSP is commonplace on the coast of South Africa, extending eastward beyond the boundary of the upwelling system. Although several *Dinophysis* species known to cause DSP have been recognized as a component of the plankton of the region, it is accepted that DSP is usually attributable to *D. acuminata* or *D. fortii*. These species often form lesser components of blooms dominated by other dinoflagellates, but nevertheless can attain high cell concentrations of the order of 10^6 cells l^{-1} (Pitcher and Calder, 2000). Marked interannual variation in cell densities is evident from time-series data, with *Dinophysis* spp. concentrations peaking in autumn (Fig. 9; Pitcher and Calder, 2000). Their intermittent presence at coastal monitoring sites at this time of the year is determined by cycles of upwelling, with higher prevalence during periods of relaxation and the warming of inshore waters (Fawcett et al., 2007).

Okadaic acid has been identified as the primary toxic of *Dinophysis* species in the southern Benguela, although low amounts of PTX2 have been observed in field samples, consistent with the presence of *D. acuminata* and *D. fortii* (Fawcett et al., 2007). Cell toxin quota data indicate that these species are only moderately toxic in the southern Benguela, but time-series data of OA concentrations in shellfish on the West Coast during summer and autumn frequently exceed the harvestable limit (Pitcher and Calder, 2000).

Blooms of *P. reticulatum* are also well known in the southern Benguela (Horstman, 1981), and have recently been shown to produce YTX, resulting in extended shellfish harvest closures in South Africa (Fawcett et al., 2007; Krock et al., 2008). A cell toxin quota of 75 fg YTX cell^{-1} was determined for a local isolate of *P. reticulatum*. Both this isolate and field samples containing *P. reticulatum* were also found to include low levels of arabinofuranosyl-YTX, which has also been reported from Japanese, European and New Zealand isolates (Krock et al., 2008). Interestingly, blooms of this species have on occasions been associated with extensive mortalities of the white mussel *Donax serra* on the West Coast (Grindley and Nel, 1968, 1970; Horstman, 1981).

Motile stages of *L. polyedrum* have not been identified from the plankton of the Benguela. However, cysts have been found in the sediments and in sediment traps deployed on the southern Nam- aqua shelf (Joyce et al., 2005; Pitcher and Joyce 2009), indicating the recent presence of this YTX-producer in the plankton.

### 2.2.4. Humboldt Current system

Several potentially toxic species of *Dinophysis*, including *D. acuminata*, *D. acuta*, *D. caudata* and *D. ovum*, have been reported in the Peruvian region (Ochoa et al., 1999). However, DSP and other lipophilic toxins were unknown in Peru and northern Chile, until PTXs were identified as the only components of the toxin profile of *D. acuminata* and in the scallop *A. purpuratus*. These events led to harvesting closures in northern Chile from 27° to 29°S (Blanco et al., 2006). Reports of toxic species and toxins in shellfish are likely to increase as more rigorous monitoring is undertaken for the purpose of exporting shellfish.

### 2.3. Domoic acid and amnesic shellfish poisoning

Domoic acid (DA) was first isolated from the diatom genus *Pseu- do-nitzschia* after a shellfish poisoning event in 1987 on Prince Edward Island, Canada (Bates, 1998). Different species of *Pseudo- nitzschia* have subsequently been shown to produce varying concentrations of DA, and as analytical methods for toxins gain pim- colar sensitivity, most *Pseudo-nitzschia* isolates are being shown to produce DA. Based on laboratory studies, primarily on cultures of *Pseudo-nitzschia multiseries*, two predominant triggers for the production of DA in *Pseudo-nitzschia* have been suggested: the degree of cellular stress based on Si and P availability (Pan et al., 1996a,b; Bates et al., 1991); and the effects of micronutrient (Fe, Cu) conditions (Maldonado et al., 2002; Rue and Bruland, 2001). However, recent field-based studies have suggested that DA production in at least some geographic regions is not linked to micronutrient stress, but that micronutrient limitation, especially Fe stress, can enhance DA production (Trainer et al., 2009a).

Anecdotal information has indicated that the Japanese once prized seaweed extracts containing DA as a useful tonic. The red alga *Chondria armata*, which contains DA, was used for centuries for the treatment of roundworm disease and also as an insecticide (Higa and Kuniyoshi, 2000). More recently, trials have been undertaken to test the anthelmintic properties of DA and single 20-mg doses of unknown purity were administered to adults and children without harmful effect (Iverson and Tuelove, 1994). However, DA is toxic to both the central and peripheral nervous systems of humans, and is an emetic causing gagging and vomiting as well as amnesia, seizures, coma and sometimes death. Because of its im- pact on memory, among other ill-effects, DA intoxication was named amnesic shellfish poisoning (Todd, 1993; Watters, 1995).

#### 2.3.1. California Current system

*Pseudo-nitzschia* spp. are common members of the coastal phytoplankton community of the California Current system, having been first recorded in the 1930s (Gran and Thompson, 1930). The species associated with DA are present in most water samples from the region, albeit in low numbers (e.g. Walz et al., 1994). Within this system, the most toxic *Pseudo-nitzschia* species along the Washington State coast are *Pseudo-nitzschia pseudeodelicatissima*, *Pseudo-nitzschia cuspidata* and *Pseudo-nitzschia australis* (Trainer et al., 2009b), whereas the most problematic species in California appear to be *P. australis* and *P. multiseries* (Trainer et al., 2000). In Mexico, *P. australis*, *Pseudo-nitzschia delicatissima*, *Pseudo-nitzschia fraudulenta*, *P. multiseries*, *P. pseudeodelicatissima*, *Pseudo-nitzschia*
pungens and *Pseudo-nitzschia subfraudulenta* are considered poten-
tially toxic (Hernandez-Becerril, 1998). Bloom conditions in Cali-
ifornia are generally associated with weak upwelling, fresher
water, transitional periods between anomalously warm and cool
waters, and generally low macronutrient concentrations (Kudela
et al., 2004). However, in the Juan de Fuca eddy region at the bor-
der of the US and Canada, DA production is not linked to macronu-
trient limitation, but may be associated with trace metal limitation
(Wells et al., 2005; Trainer et al., 2009a).

Amnesic shellfish poisoning was first reported on the Pacific
coast of North America in September 1991, when pelicans *Pelec-
nanus occidentalis* and cormorants *Phalacrocorax penicillatus* died in
Monterey Bay, California. The source was traced to DA in anchovy
*Engraulis mordax* that the birds had eaten, which in turn had been
feeding upon the DA-producer, *P. australis* (Fritz et al., 1992; Work
et al., 1993). By October 1991, DA was found in the edible parts of
razor clams *Siliqua patula* on the Oregon-Washington State coasts
and in the viscera of Dungeness crabs *Cancer magister* harvested
offshore (Wekell et al., 1994).

A number of physically retentive sites along the US West Coast
are likely locations of toxic *Pseudo-nitzschia* bloom initiation. These
include Point Conception off the coast of California, Heceta Bank off
the central coast of Oregon State, and the Juan de Fuca eddy at the
border of Washington State and Vancouver Island, Canada (Trainer
et al., 2001; see Fig. 1a). Toxigenic blooms of *Pseudo-nitzschia* initi-
ate in the generally cool, upwelled waters of the eddy region
(Figs. 10 and 11) and then are transported to beaches during down-
welling periods, causing coastwide closures to the harvesting of ra-
zor clams, a species that can retain DA from a single toxic bloom of
*Pseudo-nitzschia* for over a year (Adams et al., 2000; Trainer et al.,

![Graph](image)

**Fig. 9.** (a) The seasonal occurrence of *Dinophysis acuminata* depicted as a composite of weekly means, and (b) the interannual variability of *D. acuminata* depicted as the mean daily concentration, derived from the collection of daily phytoplankton samples from Gordons Bay from 1992 to 2006 (unpublished data).
Between the concentrations of particular outbreaks. Studies on bloom dynamics and the relationship between preceding or co-occurring with species of late stage in the upwelling cycle, following large centric diatoms, At the event scale, Toxic event very difficult. Ultimately, Pseudo-nitzschia flocculates may reach the sediment, which raises the potential for contamination of the benthic fauna. Populations of viable cells from deep water may at the same time inoculate surface waters, allowing rapid population development under favourable conditions (Fryxell et al., 1997; Horner et al., 1997; Trainer et al., 2000).

2.3.2. Canary Current system

Like many other colonial diatoms, Pseudo-nitzschia spp. have a tendency to flocculate (Buck and Chavez, 1994) and settle through the water column. Pseudo-nitzschia spp. have consequently been shown to be associated with thin layers of cells within the water column (e.g. Rines et al., 2002), which makes detection prior to a toxic event very difficult. Ultimately, Pseudo-nitzschia flocculates may reach the sediment, which raises the potential for contamination of the benthic fauna. Populations of viable cells from deep water may at the same time inoculate surface waters, allowing rapid population development under favourable conditions (Fryxell et al., 1997; Horner et al., 1997; Trainer et al., 2000).

Domoic acid was first detected in Galician mussels in the autumn of 1994 following exposure to Pseudo-nitzschia blooms (Miguez et al., 1996). Screening by HPLC-FD analysis of cultures of P. cuspidata, P. fraudulenta, P. australis, P. delicatissima (Míguez et al., 1996). Screening by HPLC-FD analysis of cultures of P. cuspidata, P. fraudulenta, P. australis, P. delicatissima (Míguez et al., 1996). Other species present in the area that remain to be tested are P. multiseries, Pseudo-nitzschia subpacific and P. pseudodelicatissima (Palma, 2003).

Species of Pseudo-nitzschia are common members of the late spring-summer diatom assemblages in the Galician Rías (Figueiras and Ríos, 1993), but can also be present and lead to harvesting closures in early spring or autumn (Moróño et al., 2000; Palma, 2003). At the event scale, Pseudo-nitzschia species appear at an intermediate stage in the upwelling cycle, following large centric diatoms, but preceding or co-occurring with species of Dinophysys and DSP outbreaks. Studies on bloom dynamics and the relationship between the concentrations of particular Pseudo-nitzschia species and the toxin content in shellfish have been hindered by the difficulty of accurate identification of these species by conventional light microscopy techniques used in monitoring programmes. Large differences have been found in the kinetics of uptake and depuration by different commercial shellfish species. Domoic acid does not appear to pose a serious threat to mussel production, because toxins are found only during the late stages of blooms and tend therefore to be very short-term events. However, scallops such as Pecten maximus have a high affinity for DA, and toxin levels in some scallop beds in Galicia permanently exceed regulatory levels (Arévalo et al., 1998). The problem of DA retention in the pectinids P. maximus and Pecten jacobaeus in Atlantic waters off Europe led to implementation of specific regulations for scallops by the European Union (Salgado et al., 2003). A reported concentration of 266 μg DA g⁻¹ in Portuguese scallops (Vale et al., 2008) is an order of magnitude above the regulatory level of 20 μg DA g⁻¹ shellfish. Moderate levels of DA have been found in the sardine Sardinia pilchardus in western Iberia (Vale and Sampayo, 2001), but to date there have been no reports of bird or other mortalities such as those reported from the California Current system.

Pseudo-nitzschia blooms have been found to form thin layers of up to 30 μg chlorophyll a l⁻¹ in the Galician Rías. The formation, shoaling and downward displacement of these layers, which are established at the depth of maximum vertical shear, result from a close coupling of the biology of the species and the physical environment during the upwelling–downwelling cycle. Thin layers of Pseudo-nitzschia pose a problem in terms of their detection within monitoring programmes. Shellfish closures for DA coincide with the downward displacement of mature and aggregated Pseudo-nitzschia populations dominated by P. australis and P. cf pseudodelicatissima, with the latter species embedded in mucilaginous colonies of Chaetoceros socialis. The tendency for benthic shellfish resources to exceed regulatory levels of DA prior to the contamination of mussels suspended from rafts may reflect the subsurface distribution of Pseudo-nitzschia in thin layers (Velo Suárez et al., 2008, in press). A forecast model is presently being developed to predict the onset of Pseudo-nitzschia blooms in Portuguese coastal waters.

Figure 10. Advanced very high resolution radiometer (AVHRR) sea surface temperature (SST) imagery originated from the NOAA CoastWatch West Coast regional node in La Jolla, California. The Juan de Fuca eddy region (shown as a cool gyre) is a site of persistent upwelling through the summer. Blooms of toxic Pseudo-nitzschia are known to initiate in this zone (Trainer et al., 2009b). The duration of upwelling and the timing of fall storms are factors that influence the levels of domoic acid that reach coastal sites. From Trainer et al. (2002).
waters in response to wind-forcing during the upwelling season (Palma et al., 2008).

2.3.3. Benguela Current system

Whereas several *Pseudo-nitzschia* spp. responsible for ASP are known to occur in the Benguela system, for example *P. australis* (Marangoni et al., 2001), shellfish toxicity has yet to be recorded in this region (Pitcher and Calder, 2000). However, DA has recently been measured in seawater samples containing *Pseudo-nitzschia* cells, although the toxigenic species were not identified (Fig. 12; Fawcett et al., 2007). This provided the first conclusive evidence for the presence of ASP toxins in the Benguela system. During this study, particulate DA concentrations derived from filtered plankton samples were found to range from 0.1 to 3 μg L⁻¹ and closely tracked the total cell concentrations of *Pseudo-nitzschia* spp. These values are similar to those reported by Trainer et al. (2000) in the California Current system.

2.3.4. Humboldt Current system

*Pseudo-nitzschia* spp. in the Peruvian system are poorly characterized. *P. delicatissima* has been identified within the region (Hasle, 1965), and has been reported to dominate diatom assemblages (Tarazona et al., 2003), forming “balls of needles” as a possible anti-grazing strategy (Gomez et al., 2007). In northern Chile off Bahía Inglesa at 27°S, DA has been reported above regulatory levels in the scallop *A. purpuratus* following exposure to blooms of *P. australis* (Suárez-Isla et al., 2002). Recently, four species common to this area, *P. australis*, *Pseudo-nitzschia calliantha*, *P. pseudo-delicatissima* and *P. subfraudulenta*, were tested and DA production was confirmed in both *P. australis* and *P. calliantha* (Álvarez et al., 2009).

2.4. Ichthyotoxins

Ichthyotoxic blooms of the raphidophycean flagellate, *Heterosigma akashiwo*, are common to all eastern boundary upwelling systems. The dinoflagellates *Cochlodinium polykrikoides*, *Karlodinium micrum* and *Karenia cristata* are also known to cause marine mortalities, but are not common to all upwelling regions. The toxicity of *H. akashiwo* is not completely understood, but has been tentatively linked to either the production of reactive oxygen species (Yang et al., 1995) or a brevetoxin-like neurotoxin (Khan et al., 1997). The fish-killing effects of *Cochlodinium* species have also been attributed to the production of reactive oxygen species, although recent work by Kim et al. (2009) suggests that other toxins may be involved. The toxins of some *Karenia* species have been isolated and well-described, for example, the suite of lipophilic toxins called brevetoxins that become harmful to fish through ingestion or aerosolization. In contrast, the toxins associated with blooms of *K. cristata* on the South African coast have yet to be characterized. Several toxic compounds, collectively known as the karlotoxins, have been characterized from isolates of *Karlodinium micrum* collected along the east coast of the US (Deeds et al., 2006). These toxins have hemolytic, ichthyotoxic and cytotoxic properties (Deeds and Place, 2006) and have caused the death of both wild and cultured fish (Bachvaroff et al., 2008).

2.4.1. California Current system

*Heterosigma akashiwo* is present within the California Current system (Horner et al., 1997). However, because offshore aquaculture is currently not practiced and wild fish are generally not affected, fish kills have not been observed. In the inland waterways of Puget Sound on the US West Coast, fish kills caused by *H. akashiwo* have resulted in millions of dollars of damage to the culture of finfish (Rensel, 1995). In the northern Mexican Pacific in the Gulf of California and along the coast of Colima, blooms of the dinoflagellate *C. polykrikoides* have occurred, with fish kills common in Sinaloa in the Gulf of California (Hernández-Becerril et al., 2007).

2.4.2. Canary Current system

*Heterosigma akashiwo* is often present in the Ria de Vigo and may dominate during autumn downwelling (Crespo et al., 2006). Blooms of this species occasionally precede blooms of *G. catenatum* (Fraga et al., 1984), but fish aquaculture is not a major activity in Northwest Iberia, and blooms of *H. akashiwo* have never been associated with negative impacts within the region. Similarly, dense blooms of *Karenia*, probably *Karenia mikimotoi*, are known to be
the cause of conspicuous green discolorations of the water, with reported blooms in 1989 of up to 200 μg chl a l⁻¹ (Jiménez et al., 1992), have not been associated with any harmful impacts.

Blooms of *H. akashiwo* do pose a threat to the growing finfish aquaculture initiatives in southern Portugal. A fish kill event in 1992 in the artificial coastal lagoon at Quinta do Lago was considered to have been caused either by *H. akashiwo* or anoxic conditions. Other fish kills attributed to *H. akashiwo* have been observed at fish farm sites in the Algarve (T. Moita, pers. comm.).

### 2.4.3. Benguela Current system

The Benguela is the only upwelling system that is currently plagued by problems associated with *Karenia* species. The species, initially reported as *Gymnodinium* sp. by Horstman et al. (1991), and later described as *Karenia cristata* (Botes et al., 2003), was responsible for large mortalities of abalone and other marine life in the 1980s. Apparently restricted to the western Agulhas Bank, this species shares several characteristics with *Karenia brevis*, common off the coast of Florida, and the recently described species from New Zealand waters, *Karenia brevisulcata*, in that it also produces an aerosol-born toxin responsible for respiratory and skin disorders (Pitcher and Matthews, 1996).

The fish-killing dinoflagellate, *Karlodinium micrum*, was originally described as *Gymnodinium galatheanum* by Braarud (1957) from samples collected in 1950, off the Danish expedition ship, the *Galathea*, during a fish kill off Walvis Bay, Namibia. Well known as the cause of fish mortalities in the region of Walvis Bay (Pieterse and van der Post, 1967), the distribution of this species does not appear to extend into the southern Benguela upwelling system.

Blooms of *H. akashiwo* have been observed in the northern and southern Benguela, but only on a single occasion, in Saldanha Bay in March 2004, have fish mortalities been associated with this species. At that time, high concentrations of this raphidophyte caused a yellow–brown discoloration of the water, and although the mortalities were not particularly extensive, large shoals of disoriented fish were observed in shallow water. Off the South African coast, blooms of *H. akashiwo* are often reported in association with freshwater runoff (Pitcher and Calder, 2000).

### 2.4.4. Humboldt Current system

Fish kills from the Peruvian upwelling system are not well documented although blooms of *H. akashiwo* (reported as *Olisthodiscus luteus*) have been recorded by Antinori et al. (2003). Further south, along the coast of Chile, *H. akashiwo* is known to bloom, with major blooms in 1988 and 2000, impacting negatively on salmon farms in the region (Clément and Lembeye, 1993). However, these blooms tend to occur outside of the upwelling system.

### 2.5. High-biomass, anoxia causing blooms

Not all harm caused by algal blooms is due to the production of a toxin. Many algal species can form blooms that discolor the water and in some cases harmful impacts are attributed to the high biomass that these blooms are able to achieve. Low-oxygen events that suffocate and kill fish and benthic organisms are often linked to oxygen consumption by the high respiratory demand of the settling and sedimentary organic matter following bloom decay, and are perhaps the most common negative effect of high-biomass blooms.

#### 2.5.1. California Current system

In the California Current system, near-bottom waters on the mid- to outer-continental shelf are usually hypoxic late in the upwelling season (Landry et al., 1989), but hypoxia on the inner-shelf, where many sensitive habitats are located, is historically less common. The proximity to low-oxygen water, longer retention times, as well as the high concentration of phytoplankton which eventually sink to the seabed, cause the continental shelf regions off the Washington and Oregon State coasts to be areas of chronic hypoxia (Grantham et al., 2004). Hypoxia on the inner-shelf, along with associated fish kills, has been observed recently both off Oregon and Washington, with some indication of possible increasing severity over time (Chan et al., 2008). Hypoxia is particularly intense on the southern Washington shelf and on Heceta Bank off Oregon, although a dominant phytoplankton species associated consistently with these events has not been identified.
2.5.2. Canary Current system

Discolourations caused by blooms of Noctiluca scintillans, Ceratium furca, Gonyaulax polygramma and the ciliate Myrionecta rubra (Fraga et al., 1984) may appear in small embayments of restricted circulation within the Rias in late summer, but impact only visually on the environment. Anoxia has not been reported for the Northwest Iberian upwelling system, where waters are well ventilated owing to rapid water exchange on the shelf and short renewal times within the Rias (Álvarez-Salgado et al., 2008). However, anoxia and subsequent mortalities have been reported from different locations on the Moroccan coast from Rabat to Laâyoune (34°5–28°N) and have been attributed to blooms of P. micans (Tahri-Joutei, 2007).

2.5.3. Benguela Current system

Harmful impacts attributed to high-biomass blooms, which ultimately lead to low-oxygen events and in some cases the production of hydrogen sulfide, have for many years led to massive mortalities of marine life in both the northern and southern Benguela. The severity of these mortalities led early biologists such as Gilchrist (1914) to list red tides as one of the factors causing fluctuations in fish stocks in the Benguela.

The northern Benguela is particularly prone to hydrogen sulfide poisoning, and in several cases red tides have been implicated (Copenhagen, 1953). Many graphic accounts of these events are provided in newspaper reports dating back to the late 1800s referring to the production of pungent sulfuric gases resulting in the corrosion and discolouration of ships and buildings, and to massive fish mortalities. These events are the net result of the accumulation of large amounts of phytoplankton-derived organic matter on the continental shelf, which leads to the existence of extensive areas of seabed hypoxia, or even total anoxia, beneath which poisonous hydrogen sulfide and methane gas are generated within the accumulated sludge (Emeis et al., 2002). Eruptions of hydrogen sulfide gas along the Namibian coast were originally considered to be local phenomena with only limited ecosystem-scale consequences. However, remote-sensing has now revealed that these events are much more extensive and longer-lasting than previously suspected and may as a result have major effects on the ecology and coastal fisheries of this region (Fig. 13; Weeks et al., 2002, 2004).

Mortalities associated with oxygen depletion in the southern Benguela appear more localized and are typically directly linked to the inshore decay of dinoflagellate blooms of any one of a number of species (Pitcher and Weeks, 2006). In the summer of 1997, the largest ever recorded stranding of rock lobster Jasus lalandii resulted from the decay of a massive bloom of G. furca at Elands Bay on the west coast of South Africa. Strandings of rock lobster as a consequence of low oxygen are common in the vicinity of Elands Bay, one of the richer lobster grounds. However, this particular stranding of some 2000 tonnes of lobster was at that time unprecedented in terms of its magnitude and resulted in losses estimated at $50 million US (Pitcher and Cockcroft, 1998).

Hydrogen sulfide poisoning is less common in the southern Benguela. However, in March 1994, massive mortalities in St Helena Bay on the West Coast were attributed to the first recorded case of hydrogen sulfide poisoning in the southern Benguela (Matthews and Pitcher, 1996). This followed the decay of a phytoplankton bloom dominated by the dinoflagellates C. furca and P. micans. Oxygen concentrations were maintained at < 0.5 ml l⁻¹ in the bottom waters and hydrogen sulfide was recorded in excess of 50 μmol l⁻¹. The mullet Liza richardsoni made up the bulk of the fish mortality of approximately 1500 tonnes.

These anoxia-induced mortalities are typically confined to the west coast of southern Africa, and seldom extend south of the Cape Peninsula. The only exceptions have been two reported cases of anoxia in False Bay, both of which have been attributed to the dinoflagellate Gonyaulax polygramma. In 1962, the decay of a bloom of G. polygramma was responsible for the sea “becoming slimy with rotting plankton and the water produced an unbearable stench” (Grindley and Taylor, 1964). At that time, dead and dying fish as well as invertebrates, estimated at over 100 tonnes were washed up on the beaches of False Bay, apparently due to the depletion of oxygen. No further cases of anoxia were reported in False Bay until the summer of 2007, when G. polygramma was again responsible for high-biomass blooms in both False Bay and Walker Bay (Pitcher et al., 2008) and mortalities of marine organisms were again reported in the north-eastern corner of False Bay.

2.5.4. Humboldt Current system

Water discolourations, known locally as ‘aguajes’, leading to anoxia and the production of hydrogen sulfide have been reported in Peru since the late 19th century. There, the blackening effects of hydrogen sulfide on the paintwork of ships led it to be known col-
loquially as ‘The Callao Painter’. In the 1970s, most of these events were attributed to blooms of *Akashiwo sanguinea*, reported at that time as *Gymnodinium splendens* (Rojas de Mendiola, 1979), whereas a list of species, including *P. micans*, *Proorocentrum gracile*, *A. sanguinea*, *Ceratium fusus* and *C. furca* are reported as the cause of these events between 1980 and 1995 (Sánchez and Delgado, 1996).

Waters off Peru below depths of 20 m are characterized by dissolved oxygen concentrations of <1 ml l$^{-1}$ (Rosenberg et al., 1983). In the northern upwelling zone, oxygen concentrations usually exceed 0.6 ml l$^{-1}$, but to the south oxygen concentrations are most often between 0.3 and 0.6 ml l$^{-1}$. Differences in oxygen deficiency may be explained by complex and non-linear interactions between coastal upwelling, wind mixing and red tide formation (Gutierrez et al., 2008). When winds relax, fronts and thermal stratification migrate toward the coast, favouring the development of red tides that may end in massive phytodetrital sedimentation and decay which can produce local anoxia, thereby decoupling the remotely driven oxygen, temperature and density relations in the water column.

These regions of oxygen deficiency are inhabited by sulfur bacteria, mainly the genus *Thioploca*, which may cover the bottom surface and provide a large portion of the total benthic biomass (Tarazona et al., 2003). These bacteria obtain energy by oxidizing hydrogen sulfide from below the sediment surface with nitrate from the water column.

Both intensity and frequency of oxygenation episodes and anoxia control development of the benthic ecosystems of the Peruvian shelf sediments. Permanent anoxia is unfavourable for both macro-biota and *Thioploca* populations, but nematodes attain highest biomass under these conditions. In Ecuador, high-biomass blooms of diatoms as well as the dinoflagellate *Gyrodinium striatum*, which may attain concentrations of up to $9.4 \times 10^7$ cells l$^{-1}$ or $\sim$500 µg chl a l$^{-1}$, have been found to cause mortalities on prawn farms (Jiménez, 1993).

### 3. Summary

This paper is the first in a series of review articles describing HABs in eastern boundary upwelling systems, the nutrient-rich regions along the world’s coastlines that host the majority of global fish and shellfish production. As summarized here, these algae are a diverse group of marine plankton that exert harm through the effects of anoxia, hypoxia, and fish kills, as well as through the effects of toxins accumulating through the food chain, culminating in the illness or death of humans and marine life. These HABs not only affect seafood availability to local consumers and to export markets, but also result in unsightly or noxious blooms on beaches, which impact activities such as tourism. As global boundaries for seafood markets become more fluid, each region is likely to realize increased socio-economic damage due to HABs. Seafood trade between the eastern boundary upwelling systems is at present severely compromised owing to HABs and a lack of equivalency in seafood monitoring programmes between the regions. For this reason, seafood exports from the Humboldt and Benguela regions to countries of the European Union are largely restricted.

Knowledge of HAB species and their impacts in upwelling systems is incomplete and disparate between the upwelling regions. Whereas the Peruvian coastline is the classic upwelling system for the study of *El Niño* and its impacts on fisheries (e.g. Barber and Chavez, 1983), relatively little is known about HABs in this system as few records of these species or their effects have been documented. Cues from studies of HABs in one upwelling system may ultimately assist with the monitoring and research of HABs in less well-known systems. For example, the considerable understanding of *Dinophysis* blooms developed in the Iberian system, owing largely to their considerable impact on the aquaculture industry in this region, may help to refine research programmes in the California Current system, where the distribution and bloom dynamics of these species are poorly investigated.

The economic impacts of HABs in each upwelling region vary owing to the presence of different species, to the variable toxicity of these species between regions, the foodweb structure through which toxins can be vectored, as well as on the commercial viability of fish and shellfish species that can harbour the toxins. The impacts of domoic acid provide an example of variability between upwelling systems; the impacts of this toxin are realized almost annually in the California Current system through direct toxicity of shellfish and through the effects on the health of marine life, including sea lions, sea otters and birds (Bates and Trainer, 2006); whereas in the Benguela upwelling system, domoic acid appears to have no impact on marine life and has not yet been measured in shellfish, even though it has been detected in seawater. Likewise, DSP toxins pose regular problems to the safe consumption of shellfish in the Canary Current and Benguela systems, but they currently are believed to have little impact on seafood safety in the California Current system. Possible reasons for these apparent disparities among upwelling systems could range from: different physical mechanisms of cell delivery to impacted coastlines; variable toxicity of species owing to differences in the nutrient environment within each system; and differences in foodweb structure equating to more or less retention of toxins by species that vector toxins to humans and other organisms. These differences and similarities in physical, chemical and ecosystem characteristics of upwelling systems, and their application and relevance to HABs, are described in the chapters that follow.

The toxins from certain HABs are common to almost all systems. For example, the PSP toxins are accumulated by shellfish rendering them unsafe for human consumption in each of the four eastern boundary upwelling systems; however, the phytoplankton species and therefore the toxin profiles differ. The dominant PSP producers currently are *A. catenella* in the California Current and Benguela systems, *G. catenatum* and *A. minutum* in the Canary Current system, and an unknown species, likely from the genus *Alexandrium*, in the Humboldt Current system. Conversely, species from the same genus, i.e. *Dinophysis* spp., appear to have very different toxigenic potential in different eastern boundary upwelling systems. Comparative investigations may assist in establishing the reasons for these similarities and differences.

Some HAB species appear to be inimicable to a particular upwelling system. For example, *K. cristata* appears to be unique to the Benguela upwelling system. Although toxins produced by *K. cristata* have not yet been identified, this species has been responsible for widespread mortalities of inter- and subtidal animals. The uniqueness of this species to the Benguela upwelling system highlights the fact that although many of the physical, chemical and biological characteristics are shared by upwelling systems, exceptional qualities within each system may favour one or another species. By studying these similarities and differences in upwelling systems, the complex combination of environmental parameters that select for HABs may be established. Finally, by carefully understanding the distribution of HABs through such comparative efforts, and subsequently documenting the changes in dominant harmful species or their distribution, HABs may be instrumental in monitoring the effects of climate variation or other global ecosystem effects.

### Acknowledgments

We thank T. Moita, K. Lefebvre and B. Bill for their helpful reviews of this manuscript and N. Adams and S. Day for assistance.
with the figures. This is a contribution from the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) Comparative Research Programme on Harmful Algal Blooms in Upwelling Systems. GEOHAB is an initiative of SCOR (Scientific Committee on Ocean Research) and IOC (Intergovernmental Oceanographic Commission of UNESCO). The contribution by V.L.T. was funded by the National Oceanic and Atmospheric Administration’s (NOAA) West Coast Center for Oceans and Human Health.

References


Amorim, A., Dale, B., 2006. Historical cyst record as evidence for the recent


