The physical oceanography of upwelling systems and the development of harmful algal blooms

G.C. Pitcher[a,b,*], **F.G. Figueiras**[c], **B.M. Hickey**[d], and **M.T. Moita**[e]

[a]Marine and Coastal Management, Private Bag X2, Rogge Bay, 8012 Cape Town, South Africa

[b]University of Cape Town, Private Bag, Rondebosch, 7700 Cape Town, South Africa

[c]Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científícas (CSIC), Eduardo Cabello 6, 36208 Vigo, Spain

[d]University of Washington, School of Oceanography, Box 355351, Seattle, WA 98195-5351, USA

[e]Instituto de Investigacao das Pescas e do Mar (IPIMAR), Av. Brasilia, 1449-006 Lisbon, Portugal

Abstract

The upwelling systems of the eastern boundaries of the world's oceans are susceptible to harmful algal blooms (HABs) because they are highly productive, nutrient-rich environments, prone to high-biomass blooms. This review identifies those aspects of the physical environment important in the development of HABs in upwelling systems through description and comparison of bloom events in the Benguela, California and Iberia systems. HAB development is dictated by the influence of wind stress on the surface boundary layer through a combination of its influence on surface mixed-layer characteristics and shelf circulation patterns. The timing of HABs is controlled by windstress fluctuations and buoyancy inputs at the seasonal, event and interannual scales. Within this temporal framework, various mesoscale features that interrupt typical upwelling circulation patterns, determine the spatial distribution of HABs. The inner shelf in particular provides a mosaic of shifting habitats, some of which favour HABs. Changes in coastline configuration and orientation, and bottom topography are important in determining the distribution of HABs through their influence on water stratification and retention. A spectrum of coastline configurations, including headlands, capes, peninsulas, Rías, bays and estuaries, representing systems of increasing isolation from the open coast and consequent increasing retention times, are assessed in terms of their vulnerability to HABs.

1. Introduction

The eastern boundaries of the world's oceans are notably productive (Hill et al., 1998). Here, the major currents, including the California, Canary, Benguela and Humboldt, are driven by winds that blow alongshore toward the equator for a substantial part of the year (Smith, 1995). These winds force offshore Ekman transport in the surface boundary layer, and the existence of a coastal boundary imposes a divergence in the surface layer, resulting

*Corresponding author. Address: Marine and Coastal Management, Private Bag X2, Rogge Bay, 8012 Cape Town, South Africa. Tel.: +27 21 4307015; fax: +27 21 43428899. gpitcher@deat.gov.za (G.C. Pitcher).

in the upwelling of cold, nutrient-rich water into the euphotic zone. The measured across-shelf transport in the surface boundary layer is in quantitative agreement with that predicted from the wind-stress, an equatorward frontal jet current forms the boundary between the upwelled water and the adjacent ocean, and a compensating poleward undercurrent occurs at depth over the slope. The enrichment of surface waters inshore of the front supports high productivity and a high frequency of harmful algal blooms (HABs) (GEOHAB, 2005). Several comparative research programmes have been initiated within the major upwelling systems because of the benefits that may be derived from comparison of ecosystems of similar functioning. The SCOR-IOC Programme on the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB, 2001) extended this comparative approach to the study of HABs and the oceanographic processes that influence their population dynamics.

Most HABs in upwelling systems have in the past been attributed to one or another dinoflagellate species, but more recently harmful impacts have also been ascribed to other groups of phytoplankton, including the diatoms (Trainer et al., in this issue). The majority of species contributing to HABs constitute regular components of the phytoplankton assemblages of upwelling systems, and their harmful impacts are associated with either their toxic properties or the high biomass such blooms can achieve. Although some toxic species are potentially harmful at low densities, their impacts are more severe at high densities. For this reason, many HABs are associated with elevated biomass, a feature common to the shelf environment of upwelling systems.

Although the causes of shifts in phytoplankton community structure in marine systems have yet to be fully resolved, mixing and stratification have been identified in many regions as habitat features operative in regulating differences in phytoplankton assemblages (Margalef, 1978; Margalef et al., 1979; Smayda and Reynolds, 2001). These differences tend therefore to be associated with temporal and spatial transitions from turbulent to stratified water columns, in which there is often a shift in the control of production dynamics from a dependence on new nitrogen to regenerated nitrogen (Hutchings et al., 1995), and the resulting patterns of succession afford some degree of predictability. The incidence and distribution of HABs within upwelling systems is therefore related to the dynamics of the surface boundary layer in that the upper mixed layer is important in effecting the composition of phytoplankton communities and in that fields of flow determine bloom transport and concentration (Trainer et al., 2002; Pitcher and Nelson, 2006; Crespo et al., 2007). Surface boundary-layer characteristics are in turn modified by the interaction of varying windforcing cycles with changes in coastline configuration and orientation, bottom topography, and buoyant freshwater plumes. These result in complex time- and space-dependent patterns of active and passive upwelling circulations, which favour the presence of different algal groups and dramatically influence shelf productivity (Figueiras et al., 2006).

This review identifies those aspects of the physical environment important in the development and control of HABs in upwelling systems through recognition of common or consistent observations, and demonstrates their influence using examples from the major eastern boundary current systems. Windforcing cycles at the seasonal, event and interannual scales are considered in terms of their influence on the timing of HABs. Within this

temporal framework, the review focuses on various mesoscale features found to interrupt typical upwelling circulation patterns, thereby influencing the spatial distribution of HABs. In particular, the influences of coastline orientation and discontinuities on HABs are considered through their influence on water stratification and retention. Included are the influences of a spectrum of coastline configurations, including headlands, capes, peninsulas, Rías, bays and estuaries, representing systems of increasing isolation from the open coast and consequent increasing retention times.

2. The timing of HABs as determined by atmospheric oscillations

Coastal upwelling regimes are highly time-dependent systems as they are driven primarily by rapid responses to windstress fluctuations with upwelling taking place as a series of 3–10 day events (Hill et al., 1998). Changes to phytoplankton assemblages are dictated by the influence of wind stress on the surface boundary layer through a combination of its influence on surface mixed-layer characteristics and shelf circulation patterns. For this reason, temporal changes in phytoplankton assemblages are influenced in all upwelling systems by atmospheric oscillations at seasonal, event and interannual scales. In addition to wind, buoyancy forcing through the seasonal input of freshwater is also an important contributor to hydrodynamic variability in regions such as the northern California Current system, affecting circulation patterns, stratification and turbidity (Hickey et al., 2005).

2.1. Seasonal

Upwelling is seasonal in that it may be restricted to particular seasons, or where it is perennial, it is usually stronger in one or another season. This variability on an annual basis results primarily from the displacement of atmospheric high-low pressure dipoles, which influence alongshore winds, favouring either upwelling or downwelling, with seasonal transition periods often occurring in spring and autumn (Fig. 1; Bakun and Nelson, 1991). Typically, upwelling-favourable winds reach a maximum during spring and summer. As a result, thermal stratification is weakest in spring but strengthens in late summer and early autumn.

The response of phytoplankton biomass to seasonal upwelling is lagged and is consequently highest during summer and autumn. The seasonal succession of phytoplankton typically follows the general pattern of coastal temperate seas, with diatom dominance in spring, a progressive contribution of heterotrophic components during summer and a major contribution of dinoflagellates in late summer and early autumn (Margalef, 1978; Figueiras and Rios, 1993; Pitcher and Weeks, 2006). Therefore, although the phytoplankton community remains unpredictable at the species level, it shows systematic temporal and spatial trends in the dominance patterns of higher taxonomic levels, leading to some predictability in the occurrences of HABs. Winter is usually characterized by a deeper mixed layer and minima in chemical and biological properties. In areas influenced by the presence of river plumes, stratification and high nutrient levels may be maintained during winter (Landry et al., 1989).

In addition to driving phytoplankton succession through its influence on the dynamics of the upper mixed layer, seasonal winds also drive surface circulation patterns important in the

transport of HABs. Of particular importance are inner shelf, poleward counter-currents, which may coexist with farther offshore, equatorward flow when upwelling winds relax or reverse to downwelling winds (Hickey, 1989; Sordo et al., 2001; Torres and Barton, 2007; Fawcett et al., 2008). These poleward flows tend to strengthen during the latter stages of the upwelling season, and have in some cases been associated with the poleward progression of HABs (Pitcher et al., 1998; Pitcher and Weeks, 2006).

2.1.1. The seasonal succession of phytoplankton on the Galician coast—

Seasonal upwelling along the western Iberian coast is a function of the latitudinal shift of the trade-wind system (Wooster et al., 1976), which also drives a seasonal succession of phytoplankton and consequently HABs. The seasonal transitions between upwelling- and downwelling-favourable periods show notable differences in their timing (Fig. 2a). Whereas the spring transition to upwelling occurs anytime from February to April, the autumn transition to downwelling is confined to a shorter period from the end of September to the end of October (Figueiras et al., 2002; Alvarez-Salgado et al., 2003).

The phytoplankton assemblage composition as modified by this upwelling regime is well documented for the Galician coast, and follows a mixing-stratification gradient (Fig. 2b). Chain-forming diatoms of medium and large size, including the toxic *Pseudo-nitzschia* spp., dominate spring and summer upwelling events in coastal waters (Figueiras and Rios, 1993; Moita, 2001). The offshore extent of the assemblage depends on the intensity of upwelling. Outside the areas of upwelling, in stratified oligotrophic oceanic waters, phytoplankton is dominated by pico- and nanoplanktonic forms, where species of subtropical coccolithophorids such as *Calcidiscus leptoporus* are conspicuous (Cachão and Moita, 2000). This group of phytoplankton is a good indicator of oceanic waters converging over the shelf during upwelling relaxation or downwelling events and of the presence of the winter poleward current (Estrada, 1984; Castro et al., 1997; Figueiras et al., 1998; Moita, 2002; Calvo-Díaz et al., 2004; Crespo and Figueiras, 2007). In summer, during stratified conditions, dinoflagellates in general and in particular species of the genera *Ceratium, Dinophysis, Protoperidinium, Gymnodinium, Gyrodinium* and *Prorocentrum*, and the diatom *Proboscia alata*, are abundant. The many heterotrophic species of this assemblage, including many ciliates (Figueiras and Rios, 1993; Moita, 2001), are partially responsible for the elevated concentrations of dissolved organic matter and regenerated nutrients present in the photic layer at the end of summer (Alvarez-Salgado et al., 1997, 1999). Some of these species, e.g. *Noctiluca scintillans* and *Mesodinium rubrum*, are responsible for recurrent discolouration of the water (Cabeçadas et al., 1983). Blooms of efficient swimmers, including the toxic chain-forming dinoflagellate *Gymnodinium catenatum*, characterize the autumn upwelling–downwelling transition, when they concentrate in zones of convergence (Moita et al., 1998). Especially prominent are the blooms of these species in the Rías Baixas, in which retention is enhanced (Fraga et al., 1988; Figueiras et al., 1996).

2.1.2. The seasonal transport of toxic blooms on the Iberian coast—Seasonal
circulation patterns are likely to influence the seasonal distribution of HABs. The detection of *G. catenatum* blooms in the lee of the upwelling plumes off Capes Roca and Carvoeiro in the summers of 1985 and 1994, prior to their appearance off the western Iberian coast in

autumn, provided the first evidence of the poleward transport of blooms in this region (Moita et al., 2003). These observations were supported in 2005 by recordings of *G. catenatum*, initially detected in August and September on the Lisbon shelf prior to its progressive detection at coastal monitoring sites to the north of Lisbon (Fig. 3; Pazos et al., 2006). In October these blooms were advected into the Galician Rías and shellfish harvesting was banned until mid-February 2006 (Pazos et al., 2006). The presence of poleward surface flow, typical of the latter stages of the upwelling season, was confirmed by data obtained off the Galician Rías from a Lagrangian drifter (NOAA/CoastWatch). The rate of propagation of the bloom, based on the alongshore detection of *G. catenatum* densities >10^3 cells l^{-1}, was calculated to be ~0.06 m s^{-1}, an order of magnitude lower than the surface current velocities of 0.2–0.6 m s^{-1} determined from the Lagrangian drifter.

Similar observations of the possible alongshore transport of blooms of *Dinophysis acuta* were made in 2005 by Escalera et al. (2006). Following the initial detection of *D. acuta* off Aveiro at the end of July, subsequent detection demonstrated poleward progression, and by early November record autumn concentrations of *D. acuta* were observed off the Galician coast. Estimates of the rate of poleward transport, based on the alongshore detection of densities >10^3 cells l^{-1}, was calculated to be ~0.03 m s^{-1}. It may be argued that the poleward appearance of the species reflect poleward changes in the conditions favouring these species rather than their poleward transport.

2.1.3. The seasonal incidence of red tides in the southern Benguela—

Monitoring in the southern Benguela has similarly demonstrated a strong seasonal signal in the incidence of red tides. The highest number of observations of blooms occurs in late summer and autumn, coincident with the seasonal increase of dinoflagellates relative to diatoms, as stratification increases during the course of the upwelling season, as a result of decreasing winds and increased solar irradiance. However, the seasonal incidence of blooms varies spatially (Fig. 4; Pitcher and Calder, 2000). On the West Coast, blooms are usually first observed to the north of Cape Columbine, owing to a broadening of the shelf, increased stratification, and retentive circulation patterns within this region (Pitcher et al., 1998). Here, the number of observations of blooms increases steadily through the upwelling season, reaching a peak in February and March. During summer, few blooms are reported south of Cape Columbine, until they are advected from the north by currents associated with barotropic reversal during the latter part of the upwelling season (Probyn et al., 2000). Consequently, the highest incidence of red tides in the vicinity of Cape Town is in April and May (Pitcher and Calder, 2000).

2.1.4. The seasonal cycle in the northern California Current—

Although the northern California Current is subjected to the same large-scale seasonal wind patterns as the rest of the US West Coast, and hence also undergoes episodic wind-driven upwelling throughout the summer, the magnitude of upwelling winds is reduced in this region by almost an order of magnitude from that in the central California Current. High productivity is nevertheless maintained and is in part attributed to the modulation of upwelled nutrient supply by the presence of freshwater sources. In particular, nitrate supply at the northern end of the California Current is enhanced and its delivery is more persistent than that attributed

to wind-driven upwelling due to the presence of the Strait of Juan de Fuca, whose outflow delivers deep coastally-upwelled nutrients, pulled into the strait as estuarine return flow (MacFadyen et al., 2008). Although delivery of terrigenous nitrate by the Columbia, by far the largest river on the US West coast, is an order of magnitude smaller than that due to the Strait or to coastal upwelling (Hickey and Banas, 2008), its output can be important during periods when downwelling winds persist (Bruland et al., 2008).

The intermittency of wind-driven upwelling as well as the modulation of nutrient supply by freshwater mechanisms may be responsible in part for the lack of a seasonal diatom to dinoflagellate progression in this region (Frame and Lessard, 2009). Furthermore the presence of freshwater inputs such as from the Columbia River ensures that the region is never iron limited in contrast to areas of the central California Current (Kudela and Peterson, 2009). For these reasons toxic blooms of Pseudo-nitzschia, resulting in elevated levels of domoic acid in razor clams, in both Washington State and Oregon can occur from spring through to early autumn (Fryxell et al., 1997).

Freshwater plumes from coastal estuaries and straits in the northern California Current influence coastal upwelling by altering circulation and stratification patterns, turbidity and nutrient pathways (Hickey and Banas, 2003, 2008; Hickey et al., 2005). For example, river plumes have been shown to delay the onset of coastal upwelling along the inner shelf because the freshwater caps the upwelling waters (Hickey et al., 2005, 2008).

Freshwater plumes can also directly influence the alongshore and across-shelf transport of HABs. In the absence of wind and other ambient flows, the rotational tendency is for river plumes to turn to the right in the northern hemisphere. However, in upwelling systems, which generally develop mean flows opposing this tendency, river plumes such as that from the Columbia River, tend to be bi-directional (Hickey et al., 2005, 2008b), transporting blooms to either the north or southwest of the river mouth. The strong alongshore front associated with the seaward edge of the freshwater plume may be able to inhibit shoreward advection of HABs. Interannual variability in the toxicity of razor clams on the central and southern Washington coasts is hypothesized to be controlled in part by the presence of plumes from the Columbia River, which are likely to act as a barrier to the onshore transport of toxic blooms from the Juan de Fuca eddy (Hickey et al., 2005).

2.2. Event scale

Seasonal conditions are frequently reversed for shorter periods owing to variations in the wind regime as a result of changes in the position and or strength of the atmospheric high-low pressure dipoles characteristic of upwelling systems (Hickey, 1998; Shillington, 1998). Fluctuations in currents, water properties and sea level over the shelf are therefore dominated by windforcing, at scales of 3–10 days. The degree of intermittency of winds varies between and within upwelling systems, and is considered to be important in the development and retention of high-biomass blooms (Hickey and Banas, 2008). Water column responses to these upwelling–downwelling cycles during the upwelling season are generally modulated by the degree of thermal stratification, which at temperate latitudes evolves from the weakest stratification in spring to the strongest in late summer–early autumn. The seasonal succession of phytoplankton tends therefore to be interrupted by

upwelling at the event scale, re-setting the system by several days. The phase to which the system is reset depends on the combination of windforcing intensity, degree of water column stratification and the previous stage of succession (Estrada and Blasco, 1979). In regions with significant buoyant fluxes entering from rivers, stratification may be controlled by river input, which peaks in winter and spring but may be present year-round (Hickey et al., 1998, 2005, 2008).

Across-shelf and alongshore currents are among the most prominent physical features of coastal upwelling systems at the event scale and their importance in the transport, accumulation and dispersion of HAB populations in various stages of development has been recognized (e.g. Fraga et al., 1988; Figueiras et al., 1994; Pitcher and Boyd, 1996; Trainer et al., 2002). In general, fluctuations in across-isobath currents near the surface are largely determined by fluctuations in wind direction, with offshore flow during upwelling-favourable winds and onshore flow during downwelling-favourable winds owing to frictional effects in the surface Ekman layer. Alternately, onshore flow may be driven by an onshore pressure gradient in the surface layer that is not in geostrophic balance and cannot be maintained in the absence of wind (Dale et al., 2008). Important in the alongshore delivery of HABs is a short-lived nearshore poleward counter-current that develops following the relaxation of upwelling or during downwelling (Sordo et al., 2001; Peliz et al., 2002; Hickey et al., 2005; MacFadyen et al., 2008) and may coexist with offshore equatorward flow derived during upwelling.

2.2.1. Event scale dynamics of a Gymnodinium catenatum bloom in the Ría de Vigo—Fermin et al. (1996) demonstrated the important role of the upwelling–downwelling cycle in the development of blooms of *G. catenatum* in the interior of the Ría de Vigo, based on a time-series of observations from 24 September to 8 October 1993 (Fig. 5; Fermin et al., 1996). Initial conditions were characterized by weak upwelling and positive estuarine circulation within the Ría. The presence of southwesterly winds on 29 September favoured the reversal of the positive circulation resulting in the introduction of coastal surface waters into the Ría. This reversal poses a selective force on the phytoplankton assemblage. Diatoms are unable to counteract the downwelling conditions and are therefore removed from the water column. The population of *G. catenatum* introduced into the Ría from outer stations was able to concentrate within the Ría owing to its ability to vertically migrate and thereby counteract the downwelling forces and maintain themselves in the water column. Re-establishment of positive estuarine circulation during the latter stages of monitoring, reinforced by increased runoff, tends to disperse the dinoflagellates and again favours the growth of diatoms.

2.2.2. Event-driven changes in toxigenic phytoplankton in the southern Benguela—Contrasting wind patterns during two periods of study, in the autumn of 2005 and 2006, at a nearshore station on the southern Namaqua shelf, resulted in dramatically different phytoplankton assemblages (Fawcett et al., 2007). The contrasting toxigenic phytoplankton during these periods of observation were driven by event scale differences in water column structure and mesoscale circulation (Fig. 6; Fawcett et al., 2007).

Whilst wind patterns during both study periods were dominated by upwelling-favourable winds, there were several sustained periods of wind relaxation and reversal during the 2005 study (Fig. 6a), typical of late summer, while in 2006, upwelling-favourable winds reversed only briefly (Fig. 6b). Near-surface currents were well correlated with these alongshore winds, with the magnitude of local wind reversals dictating the magnitude of the current response (Fig. 6c and d). Net flow in the nearshore region was therefore poleward in 2005, in contrast to net equatorward flow in 2006. In both years, near-surface current reversals lagged wind reversals; by 8 h in 2005 and 7 h in 2006. The intercept of the regression line at the optimum lag period was negative in both years, implying poleward flow in the absence of wind. The impact on water column structure of net poleward flow in 2005 was the establishment of warm, stratified conditions, whereas during the 2006 study, persistent equatorward flow was associated with a cooler, moderately mixed water column (Fawcett et al., 2007).

These contrasting hydrodynamic environments resulted in markedly different phytoplankton assemblages. In 2005, the toxic species *Dinophysis acuminata, Dinophysis fortii* and *Protoceratium reticulatum* formed a small but important component of a high-biomass dinoflagellate bloom dominated by *Prorocentrum triestinum*. Okadaic acid and yessotoxin concentrations as extracted from filtered plankton field samples during the 2005 study corresponded closely with cell concentrations of *Dinophysis* spp. and *P. reticulatum* respectively (Fig. 6e). During the 2006 study, *Pseudo-nitzschia* spp. co-dominated a large diatom bloom along with *Chaetoceros* spp. Total domoic acid concentrations derived from filtered plankton samples collected during the 2006 study closely tracked the total cell concentrations of *Pseudo-nitzschia* spp. (Fig. 6e). Thus, the presence of very different harmful algae could be traced to changes in phytoplankton life-form during the respective periods of study, owing to contrasting wind patterns, surface currents and water column structure, at the event scale.

2.3. Interannual

Interannual fluctuations related to the *El Niño*-Southern Oscillation (ENSO) and longer-term cycles, such as the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO), affect coastal upwelling systems through modification of seasonal upwelling–downwelling strength (Shannon et al., 1986; Blanton et al., 1987; Simpson, 1992; Alvarez-Salgado et al., 2003). The most striking form of interannual variability is the ENSO cycle, which affects the Pacific margin. Although there is little reduction in upwelling-favourable winds during *El Niño* events, the nutricline is depressed and upwelling supplies a reduced level of new nitrogen to the coastal ecosystem. The closest to an Atlantic equivalent of Pacific *El Niños* is probably the Benguela *Niños* of the South Atlantic (Hill et al., 1998). Although their mechanism remains unexplained, they may be tied to the ENSO through atmospheric teleconnections. Unfortunately the effect of these long-term cycles on phytoplankton assemblages and HABs is poorly documented owing to inadequate long-term records.

2.3.1. Long-term trends in the flushing of Rías Baixas and HABs—A decrease in the extent and intensity of the upwelling season on the Iberian coast over the past 40 years

has resulted in an increase in the flushing time of the Rías Baixas, which has in turn caused an increase in the occurrence of HABs in these systems (Alvarez-Salgado et al., 2008).

Over the past 40 years a significant decrease is evident in calculated values of Ekman transport ($-Q_X$), which serves as an index of upwelling, with the annual average $-Q_X$ declining from an upwelling-favourable index in the early 1960s to a slightly downwelling-favourable value in the early 2000s (Fig. 7a). Superimposed on this declining trend are two cycles with periods of 15–20 years, consistent with the NAO (Visbeck et al., 2001). Analysis of this dataset has revealed a decrease in the intensity of upwelling during the upwelling season, an increase in the intensity of downwelling during the downwelling season and a shortening of the upwelling season. As a result, flushing rates of the Rías Baixas, determined from the inverse of the offshore Ekman transport, and the volume and length of the mouth of the Rías indicate an increase in flushing time of 240%.

Associated with the increased flushing time is an increase in the number of days that mussel rafts are closed to harvesting owing to the increased presence of harmful algae (Fig. 7b). Residual circulation patterns are considered to determine the microplankton composition in the Rías Baixas during the upwelling season. Upwelling enhances positive residual circulation and transports dinoflagellates to the shelf, leaving the Rías Baixas dominated by diatoms. Conversely, during downwelling, dinoflagellates are advected to the inner parts of the Rías Baixas, where species of *Dinophysis* are most often responsible for the suspension of mussel harvesting (Alvarez-Salgado et al., 2008).

3. The distribution of HABs as related to coastal morphology and bathymetry

Coastal upwelling in its simplest two-dimensional form, while contributing to the enrichment of surface waters and high productivity, also contributes to the transport or export of production from the shelf and coastal regions (Largier et al., 2006). The presence of topographic variations has, however, a profound influence on coastal circulation, either by disrupting or redirecting along-shore coastal flow, by creating regions of weaker flow, or by enhancing mixing. In regions where isobaths change direction abruptly, coastal currents are forced off the shelf by the rapid change in orientation of the bottom topography. Flow in the vicinity of such features generally produces offshore jets or filaments, as well as eddies in the lee of these features. In addition to topographic forcing, filaments may also be forced by the instability of the frontal jet (Barth, 1989a,b), by offshore eddies (Hill et al., 1998) or by plumes from coastal rivers (Banas et al., 2008). Upwelling systems are therefore fundamentally three-dimensional in nature, with marked alongshore variability, and with onshore–offshore flows rarely in balance for any given section of coastline. This alongshore variability results in areas in which alongshore position is maintained in the presence of general equatorward flow and has important biological consequences.

3.1. Coastline orientation

Upwelling systems are generally characterized by meridional alignment of the coastline, and deviation from this alignment tends to alter the upwelling process. The physical

consequences of abrupt changes in coastal orientation associated with the California Bight (Jones et al., 1988; Hickey, 1992; Harms and Winant, 1998), the Gulf of Cadiz (Relvas and Barton, 2005; Relvas et al., 2007) and Cape Point in the southern Benguela (Nelson and Hutchings, 1983), are well documented; all of which influence the biology within these regions, including the distribution of HABs.

3.1.1. Cape Point – a biogeographic break—Cape Agulhas, the southern point of the African continent, is typically considered the southern boundary of the Benguela upwelling system (Nelson and Hutchings, 1983). However, upwelling between Cape Point and Cape Agulhas is reduced owing to a change in the orientation of the coastline and windfield at Cape Point (Andrews and Hutchings, 1980). A biogeographic break is thus formed, with a cold-temperate region to the west of Cape Point, and a warm-temperate region to the east, referred to as the western Agulhas Bank. The incidence and distribution of harmful blooms on the South African coast is reflected within these boundaries and current systems; in that few blooms occur outside of the upwelling system to the east of Cape Agulhas; in that there are fewer blooms on the western Agulhas Bank compared to the West Coast owing to the reduction in upwelling in this region; and in that the species assemblages that dominate the West Coast and the western Agulhas Bank regions differ (Pitcher and Calder, 2000). The surface circulation on the western Agulhas Bank is generally northwestwards and a convergent current funnels water of the western Agulhas Bank into the permanent northward-flowing baroclinic jet off the Cape Peninsula thereby contributing Agulhas water to the West Coast shelf offshore of the Coastal Transition Zone Front (CTZF) (Nelson and Hutchings, 1983). The retroflection at Cape Point of periodic poleward flow on the West Coast, inshore of the CTZF, maintains the distinction between blooms of the West Coast and those of the western Agulhas Bank.

This spatial distribution and separation of dinoflagellate assemblages of the West Coast and western Agulhas Bank, and their association with the current systems of the southern Benguela, are well documented (Pitcher and Boyd, 1996; Pitcher et al., 1998, 2008). The distinct separation of two dinoflagellate assemblages was depicted by a series of transects of these systems in February and March 1994 (Fig. 8; Pitcher and Boyd, 1996). The species *Prorocentrum rostratum* and *Prorocentrum gracile* dominated the relatively stratified western Agulhas Bank and were widely distributed over the shelf. In the region of enhanced upwelling off the Cape Peninsula, this population was confined to the Benguela jet current, thereby transporting the bloom northward along the shelf edge. The West Coast population of *Prorocentrum balticum, Prorocentrum micans, Ceratium lineatum* and *Ceratium furca* dominated the stratified waters north of St. Helena Bay, and the inshore counter-current off Cape Columbine in February, and extended as far south as the Cape Peninsula in March.

3.1.2. Toxic Pseudo-nitzschia in the Santa Barbara Channel—Upwelling within the Santa Barbara Channel is decoupled from that along most of the west coast of North America owing to the change in the orientation of the coastline at Point Conception (Harms and Winant, 1998). Along the north–south orientated coast of central and northern California, northwesterly winds drive upwelling, but at Point Conception, the mainland turns eastward and upwelling can occur only when winds blow from the west. New nutrients

within the Santa Barbara Channel are therefore derived either from water upwelled by northwesterly winds in the region of Point Conception and advected into the channel, or from upwelling driven by westerly winds within the channel itself, both of which influence the distribution of blooms of toxic *Pseudo-nitzschia*.

Circulation within the Santa Barbara Channel comprises states of upwelling, relaxation and convergence. The relaxation and convergent modes are characterized by recurring anticlockwise turning of the flowfield centered over the Santa Barbara Basin, and at times this circulation closes to form an eddy which spans most of the western channel (Harms and Winant, 1998; Oey et al., 2001; Winant et al., 2003). This recurrent feature maintains a convergent surface circulation capable of concentrating plankton (Nishimoto and Washburn, 2002), including HABs. The formation of this cyclonic eddy, following local upwelling in the Santa Barbara Channel, strongly influences the distribution and toxicity of blooms of *Pseudo-nitzschia* (Fig. 9; Anderson et al., 2006). Blooms of *Pseudo-nitzschia australis* have been shown to be fueled initially by upwelling both within and outside of the channel prior to the transition to convergent flow within the channel. The net result is a toxigenic *Pseudo-nitzschia* bloom, with the most toxic cells in the convergent centre of the eddy. The accumulation of high biomass under suboptimal conditions within the eddy is considered to contribute to the higher toxicity of cells within the eddy. Propagation of the eddy transports the bloom to the west, indicating the possible use of coherent circulation features in predicting the fate of HABs (Anderson et al., 2006).

3.2. Banks, canyons and islands

Coastal features such as banks, canyons and islands can all have important local impacts in influencing spatial variability within upwelling systems (Hill et al., 1998). A rise in the bottom topography is typically effective in creating preferred conditions for upwelling, and canyons that intersect the continental slope may influence local circulation by permitting increased across-slope motion. In some cases offshore islands are located within the coastal transition zone and may result in the generation of cyclonic eddies that may contribute to downstream mesoscale activity. These features all influence the distribution of phytoplankton populations and, in some cases, also favour the development of HABs.

3.2.1. The Juan de Fuca Eddy and Heceta Bank: sites of initiation of toxic Pseudo-nitzschia—On the US West Coast, domoic acid concentrations reflect the three-dimensional nature of upwelling within the California Current system in that they are low in regions where coastal jets occur, and high in regions where the circulation is more retentive, such as the Juan de Fuca eddy, the Heceta Bank, the Farallone Islands, Monterey Bay and the Santa Barbara Channel (Fig. 10; Hickey and Banas, 2003). These features tend to be retentive in that phytoplankton and other particles accumulate to higher densities than on open, straight coastlines (e.g., MacFadyen et al., 2005; Barth et al., 2005a). Here blooms may also draw down nutrients and thereby experience stress, contributing to toxin production (Schnetzer et al., 2007).

In the northern California Current system, the Juan de Fuca eddy, a cold, cyclonic gyre located over the continental shelf near the mouth of the Juan de Fuca Strait, is characterized

by enhanced phytoplankton biomass (Trainer et al., 2002, 2009) and productivity (Marchetti et al., 2004; MacFadyen et al., 2008). The eddy persists throughout the summer and is a result of the interaction between the outflow from the Strait, equatorward wind-driven currents along the continental slope, and the underlying topography, a spur of the Juan de Fuca submarine canyon. The photic zone in this area is therefore characterized by high nutrients supplied primarily by topographically controlled upwelling of California undercurrent water, and by outflow from Juan de Fuca Strait, where nutrient-rich coastal water is advected to the surface by estuarine circulation and tidal mixing (MacFadyen et al., 2008). The eddy increases in spatial extent from early to late summer as California undercurrent water is upwelled onto the shelf.

The Juan de Fuca eddy has been implicated as a site for the initiation of toxic *Pseudo-nitzschia* affecting the Washington coast, particularly during summer and autumn (Trainer et al., 2002, 2009). Owing to the offshore location of the eddy, any impact on shellfish also requires equatorward transport of 20–100 km, followed by onshore transport to coastal beaches. Toxic blooms therefore impact the coastal environment only during periods of downwelling-favourble winds and associated onshore surface currents (Trainer et al., 2002). A circulation model presented by MacFadyen et al. (2005) details the conditions under which offshore toxic *Pseudo-nitzschia* might impact Washington beaches (Fig. 11). These results suggest that it is only through a delicate combination of upwelling and downwelling wind conditions that surface waters from the eddy may impact the Washington coast. Potentially toxic *Pseudo-nitzschia* are expected to exit the eddy to the southeast during upwelling-favourable winds and are then advected onshore during subsequent downwelling periods, at which time toxic *Pseudo-nitzschia* may be ingested by shellfish such as razor clams.

Heceta Bank, off central Oregon, is another region where blooms of toxic *Pseudo-nitzschia* have been observed (Fig. 10; Hickey and Banas, 2003), and are considered a function of retention due to flow-topography interactions over the bank (Barth et al., 2005b). Bloom advection from this region may be responsible for HAB events on the Washington shelf in early spring, when nearshore coastal currents are generally poleward.

Indications of topography-induced flow in this region are apparent from satellite-derived images of SST; and from observations of chlorophyll-rich upwelled water seaward of the continental shelf break south of Heceta Bank (Barth et al., 2000). An offshore excursion of upwelled water occurs as the southward-flowing upwelling jet interacts with the bank to create a finite-amplitude meander in alongshore flow (Barth et al., 2005b; Gan and Allen, 2005). In contrast, northward flow is often observed inshore of the bank, arising from cyclonic motion of the flow as it adjusts to the deepening water column at the southern end of the bank. By creating an east–west perturbation in the coastal upwelling front, the flow-topography interaction introduces an alongshore pressure gradient that can also drive flow to the north during wind relaxation. This combination of northward flow inshore on the bank and the southwestward flowing coastal upwelling jet on the outer bank, can lead to complete recirculation of water around the bank on a time scale of several days (Barth et al., 2005a). Here, high near-surface values of chlorophyll are the result of favourable conditions for phytoplankton growth outweighing advective loss in this region. Associated with the

elevated biomass and *Pseudo-nitzschia* blooms is the periodic appearance of hypoxic bottom waters over the inshore side of Heceta Bank and the subsequent die-offs of fish and invertebrates in this region (Grantham et al., 2004).

3.3. Capes and promontories

Capes and promontories result in embayments of water bordered by land on two sides and clearly modulate the upwelling process by influencing across-shelf structure in alongshore flow thereby creating zones of retention. Equatorward currents that develop in response to equatorward wind stress tend to separate from the coast at capes, and upwelling is intensified within the vicinity of the cape. Water residence time within the cape-associated embayment is increased, evidenced by the presence of warmer water in the bay, a lag between the change of water temperature inside and outside the bay, and increased water column stratification within the bay (Graham and Largier, 1997). These embayments thus act as retention zones for several forms of plankton and typically function to enhance productivity.

Of the earlier models that describe time-variable upwelling, most present an upwelling cycle as a symmetric two-dimensional process, in which the warming of inshore waters following the relaxation of upwelling-favourable winds is described as an across-shelf advection of heat. However, subsequent studies have shown that reversed alongshore flow is usually responsible for observed warming inshore, and in many cases this alongshore flow is clearly related to features in coastline topography (Send et al., 1987; Fawcett et al., 2007). Alongshore pressure gradients, indicated in the surface elevation field, and set up by the interaction of wind-forced shelf flow with alongshore variations in the coastline, are considered to force inshore counter-currents downstream of capes following wind relaxation or reversal (Send et al., 1987; Gan and Allen, 2002a,b). The resulting across-shelf and alongshore gradients in the strength and direction of surface flow patterns, and in particular the development of weak, poleward currents over the inner shelf in response to relaxations of equatorward winds, drive cyclonic circulation. These inshore current reversals have an important influence on the transport and accumulation of coastal blooms (Sordo et al., 2001; Pitcher et al., 2004).

3.3.1. St. Helena Bay—In the southern Benguela, the Cape Columbine headland is associated with a discrete cell of upwelling. The area downstream of the headland, incorporating the greater St. Helena Bay region, demonstrates altered current patterns and mixing regimes as a result of the topographic and bathymetric influences of the headland, which in turn have a marked influence on the distribution of phytoplankton (Pitcher and Nelson, 2006). The shelf broadens to the north of Cape Columbine and is characterized by stratified, warmer water and higher phytoplankton biomass, as identified from remotely sensed SST and ocean colour data respectively (Fig. 12; Pitcher and Weeks, 2006). Here, phytoplankton biomass is highest during the latter half of the upwelling season when the contribution of dinoflagellates to the phytoplankton community is greatest and the region is particularly prone to harmful blooms and their negative impacts (Cockcroft et al., 2000; Pitcher and Calder, 2000).

The processes important to the development of HABs in the greater St. Helena Bay region have been conceptualized (Fig. 12; Pitcher and Nelson, 2006), and are supported by observations of nearshore currents (Fawcett et al., 2008) and the barotropic model of Penven et al. (2000) in the simulation of a coastal jet retention mechanism. During upwelling (Fig. 12c), alongshore currents form a coastal equatorward jet, which is interrupted by Cape Columbine and separated from the coast. The upwelling plume formed off Columbine tends to isolate the nearshore area from the offshore domain, thereby inducing retention on the coastal side of the plume. A positive coupling between upwelling and retention may be provided by such structures, with stronger upwelling-favourable winds enhancing retention within the nearshore area, despite the intensification of offshore flow associated with upwelling. The limited across-shelf exchange of water is depicted in clear and consistent delineation of phytoplankton assemblages representing the offshore and nearshore regions, with a shallowing of the surface mixed layer in the lee of the Cape favouring the development of dinofagellate blooms.

In addition to the intensified upwelling off Cape Columbine, a narrow band of upwelling may extend along the coast to the north of Dwarskersbos (Jury, 1985; Tauton-Clark, 1985). Under upwelling conditions the inshore dinoflagellate population tends therefore to accumulate offshore in a region of convergence, created by the narrow belt of upwelling and the core equatorward flow (Fig. 12d). 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 (Fig. 12d). The presence of this nearshore poleward counter-current was first detected by drift card returns and is most pronounced during late summer and autumn (Duncan and Nell, 1969). The separation of the equatorward jet from the coast by Cape Columbine is considered to result in the development of a negative pressure gradient to the north of the cape (Gan and Allen, 2002a,b). During relaxation, this pressure gradient drives the poleward flow and strengthens cyclonic circulation to the north of Cape Columbine, thereby contributing to the retentive nature of circulation within the region and to the poleward transport of coastal blooms. This conceptual model is supported by the patterns of circulation within the model domain of Penven et al. (2000), whereby equatorward windforcing produces a cyclonic eddy in the lee of Cape Columbine, which contributes to create a dynamic boundary between the coastal and the offshore domains. The high incidence of dinoflagellate blooms and the retentive circulation characteristics of the area further promote the formation and deposition of dinoflagellate cysts. The region may therefore also favour bloom initiation by functioning as a sedimentary basin accumulating benthic cysts that later serve as bloom innocula (Joyce et al., 2005).

3.3.2. Point Arena – Bodega Bay – Point Reyes—The strength of upwelling at headlands, and the presence of nearshore poleward flow and stratification between headlands, drives significant alongshore variability off northern California (Fig. 13; Roughan et al., 2006). A strong and persistent upwelling centre is present in the vicinity of Point Arena, and strong fluctuations in currents and vertical structure are observed to the south of this upwelling centre in response to fluctuations in windforcing. Most notably, poleward flows and warmer waters are observed nearshore during periods in which

equatorward windforcing relaxes (Send et al., 1987; Huyer and Kosro, 1987; Kosro, 1987). The biological importance of these mechanisms is that they provide a way for maintaining alongshore position in the presence of equatorward flows, thereby affecting shelf residence times. Consequently, high-biomass coastal waters are able to persist in this strongly advective and wind-dominated system, owing at least partially to the presence of physically retentive features associated with headlands and embayments.

Satellite imagery, together with HF radar and drifter data, provide good resolution of these upwelling structures and the role of wind-driven transport in the productivity of the region (Fig. 14; Largier et al., 2006). Windstress gradients in the area result in shifting patterns of windstress curl and upwelling, resulting in a marked across-shelf structure in surface currents. During the upwelling season, wind-driven currents over the outer shelf and slope tend to be strong and persistently equatorward, with the presence of an upwelling jet at the shelf break. Here, equatorward surface currents are persistent, even in the absence of equatorward windforcing, and may be assisted on the outer shelf by the main flow of the California Current. Over the inner shelf, nearshore currents are as often poleward as equatorward (Kaplan et al., 2005; Kaplan and Largier, 2006). Weaker winds, increased frictional drag in shallower waters, and the development of significant pressure gradients are considered to drive this poleward flow (Gan and Allen, 2002a,b). Mean flow over the inner shelf is consequently near-zero. West of Bodega Head, equatorward flow over the shelf edge may meander onshore and interact with poleward flow over the inner shelf. Equatorward-flowing offshore waters may thus be entrained onshore and into the poleward nearshore current (Kaplan and Largier, 2006). These circulation patterns result in observations of higher chlorophyll fluorescence under relaxation conditions, and a net poleward transport of chlorophyll over the inner and mid-shelf off Bodega Bay (Fig. 14; Largier et al., 2006; Wilkerson et al., 2006). Bodega Bay itself is relatively small and subject to several co-occurring forces during upwelling conditions, including strong equatorward flow past the mouth of the bay, alongshore pressure gradients due to along-shore variations in windforcing, windstress on the surface of the bay, and the presence of dense upwelled waters at the mouth of the bay (Roughan et al., 2005). These forcing mechanisms interact with coastal topography, bottom stress and tidal forcing to determine both the circulation within the bay and exchange between it and the shelf.

To the south of Bodega Bay, the coastline turns sharply to the west to form the large promontory of Point Reyes, which produces an offshore deflection of the equatorward upwelling jet (Fig. 14). Point Reyes is the northern boundary of the Gulf of Farallones and can act as an upwelling shadow trapping upwelled waters in its lee. The waters that are retained in the lee of the headland are warmed and may return towards the region of upwelling during relaxation periods when the general alongshore flow reverses and a strong poleward current moves around Point Reyes within 20 km of the peninsula (Send et al., 1987; Wing et al., 1998). This poleward flow around the point has been shown to form a retention area of slightly warmer and more productive water on the upstream side of Point Reyes (Vander Woude et al., 2006). The strength of poleward flow past Point Reyes results in a separation eddy on the north side of the point and onshore flow between Point Reyes and Bodega. Surface waters may therefore be retained, allowing surface aging of upwelled

waters and the development of higher biomass in nearshore zones both north and south of the Point Reyes promontory (Largier et al., 2006).

3.3.3. Lisbon and Setúbal Bays—The Lisbon and Setúbal Bays, associated with Capes Roca and Espichel respectively, represent important discontinuities along the central Iberian coast. Here, HABs are common, and of particular importance are the toxin-producing dinoflagellates *G. catenatum* (Moita et al., 2003, 2006) and *Lingulodinium polyedrum* (Amorim et al., 2004). These bays are contiguous and are both influenced by canyons and rivers, which impart a complex three-dimensional character to upwelling in this area. A localised plume of cold, nutrient-rich water rooted off Cape Roca and extending southward during upwelling conditions clearly influences Lisbon Bay, and to a lesser extent Setúbal Bay as it is further removed from the upwelling plume. Nutrient input into Setúbal Bay is also reduced owing to lower river discharge (Cabeçadas et al., 2000).

Strong equatorward flow is present along the plume axis during upwelling, but the presence of relatively warmer waters on the coastal side of the plume suggests return flow and the creation of a retentive zone. Chlorophyll *a* and phytoplankton assemblages consequently exhibit asymmetrical distributions with reference to the upwelling plume. The highest biomass is observed on the inner or coastal side of the plume, where chain-forming dinoflagellates, including *G. catenatum* dominate, whereas diatoms tend to dominate the core and outer side of the plume (Moita et al., 2003).

Blooms of *G. catenatum* in 1985, 1994 (Moita et al., 2003) and 2005 (Moita et al., 2006), were all shown to form on the leeward side of the Cape Roca plume owing to poleward flow in this area, while cysts of *G. catenatum* showed preferential accumulation in the sediments of Setúbal Bay following blooms in 1994 and 1995 (Amorim et al., 2004). In 1990, a bloom of *L. polyedrum* in the stratified waters of Setúbal Bay was associated with an unusual eastward displacement of the Cape Roca plume, driven by offshore circulation patterns (Amorim et al., 2004), whereas a bloom of *L. polyedrum* in 2005 was considered to have formed as a result of poleward advection of warm inshore waters from Cape Sines into Setúbal Bay. The circulation features responsible for these observations, including the cold water plume off Cape Roca, the warm counter-current on the leeward side of the plume and the persistent retention of warm water in Setúbal Bay, are all prominent features of a hydrodynamic model of the region (Fig. 15; Oliveira et al., 2009). Model results indicate that the asymmetric distribution of chlorophyll *a* is driven by both asymmetric advective patterns and spatial variations in the depth of the surface mixed layer. The physical environment downstream of capes not only favours the accumulation of phytoplankton through patterns of retention, but the shallowing of the mixed layer sets the physical conditions specifically favouring the growth of dinoflagellates.

3.4. Open bays

Open bays are defined here as those bordered by land on three sides, while retaining a large open mouth. Few bays of this type are found in upwelling systems, but do include the very prominent bays of Monterey Bay in the California Current system and False Bay in the southern Benguela system, both of which comprise the largest bays within these regions.

The bays remain stratified during the upwelling season and are characterized by cyclonic circulation under upwelling-favourable conditions. Both bays feature upwelling shadows important in the dynamics of HABs.

3.4.1. Monterey Bay—In Monterey Bay, in the Central California Current upwelling system, phytoplankton productivity and abundance are greatly augmented by wind-driven upwelling of nutrient-rich waters. Although flow up the Monterey Canyon delivers nutrient-rich waters onto the shelf (Ryan et al., 2005a), upwelling in which subthermocline water breaks the surface, rarely occurs within Monterey Bay. Most surface-upwelled water originates outside the bay and is advected into it through the interplay of upwelling plumes rooted at the headlands to the north and south of the bay, and a persistent anticyclonic California Current meander offshore of the bay (Rosenfeld et al., 1994; Ramp et al., 2005). The upwelling centres at Point Ano Nuero to the north and Point Sur to the south are clearly driven by the prevailing northwesterly winds, while the anticyclonic California Current meander, a quasi-permanent oceanic feature of the region during the upwelling season, is clearly not generated by local wind stress, but does respond to it.

During strong upwelling-favourable winds, there is equatorward flow from the Point Ano Nuevo upwelling centre across the mouth of the bay, which bifurcates, such that some upwelled water flows offshore and some flows into Monterey Bay (Rosenfeld et al., 1994). At this time, well-defined cyclonic circulation is evident within the bay (Paduan and Cook, 1997; Ramp et al., 2005; Fig. 16). This pattern changes very quickly when the wind stops, resulting in less-defined circulation in the bay. During relaxation events, the surface current and temperature response is dominated by the onshore translation of the offshore California Current meander and by local surface heating in the bay itself.

An important feature of Monterey Bay is the coherent pattern of sea-surface warming in the northern parts of the bay, owing to the slow, cyclonic recirculation of water during periods of upwelling, and to reduced winds in the shadow of the Santra Cruz Mountains. This allows for the development of a shallow surface mixed layer and greater local heating due to solar insolation. This feature, referred to as an upwelling shadow, typically forms and strengthens during periods of active upwelling (Graham and Largier, 1997). The upwelling shadow circulation is not directly wind-driven but rather appears to be driven by the flow of upwelled water past the mouth of the bay. A sharp thermal front forms where the recirculating bay water meets the south-flowing upwelled water, and serves as a barrier to exchange between warm, nearshore water and cold, offshore water. The northern recess of the bay therefore serves as a region of retention, and plankton communities in this upwelling shadow are very different from those in adjacent, recently upwelled waters (Graham et al., 1992; Graham and Largier, 1997).

Dinoflagellate blooms in Monterey Bay are a characteristic feature of phytoplankton populations during autumn, resulting in a high incidence of potentially harmful red tides (Ryan et al., 2005b). An account of red tide in October 2002, dominated by *C. furca* and *Ceratium dens*, provided insight into the physical settings required for bloom development (Fig. 17; Ryan et al., 2005b). The intrusion of chlorophyll-poor California Current water is considered to have led to enhanced stratification of bay waters. Red tide developed initially

in the northern bay upwelling shadow, where the low-chlorophyll intruding waters met remnants of resident high-chlorophyll bay waters. From the northern bay, the bloom spreads under the influence of the anticyclonic California Current meander around the bay and out into the adjacent sea. Airborne and satellite remote-sensing identified the influence of two physical processes on convergent flow patterns and bloom patchiness (Fig. 17). The first was the sharp increase of chlorophyll concentration in the frontal zone where bloom waters converged with the intruding low-chlorophyll waters of the anticyclonic meander. The second was the concentration of phytoplankton in convergence zones formed by internal waves. Both the frontal and internal waveforcing during the height of the red tide acted upon bloom biomass to create highly concentrated patches.

In the autumn of 2004, record levels of dinoflagellates in Monterey Bay, following nearly two decades of monitoring, and observations of blooms dominated by *Cocohlodinium, Akashiwo* and *Ceratium*, served to support many of the observations of 2002 (Ryan et al., 2009). The 2004 bloom appeared first in nearshore waters of the northern recess of Monterey Bay, confirming the importance of the upwelling shadow in regional dinoflagellate ecology. Cyclonic flow within the bay resulted in the spreading of the bloom, although it was contained within the inshore flank of the upwelling filament flowing southward from Point Ano Nuevo. Ultimately, wind and current reversals caused the bay to be flushed with chlorophyll-poor waters while bloom waters were forced out of the bay to the north. Despite the flushing of most of the bay, remnant populations of the bloom remained in the far northern reaches of the upwelling shadow, thereby providing seed material for future blooms.

3.4.2. False Bay—False Bay forms an integral part of the western Agulhas Bank of the southern Benguela and many of the harmful blooms of this region manifest themselves within this bay (Grindley and Taylor, 1964; Horstman et al., 1991; Pitcher and Calder, 2000; Botes et al., 2003), which is recognized as an area of elevated phytoplankton biomass (Pitcher and Weeks, 2006). False Bay is an approximately square body of water, which shoals gradually northward from a depth of about 80 m at its mouth. Although present understanding of the interaction of the currents of the western Agulhas Bank with those within the bay is limited, it is recognized that the structure and functioning of the bay are strongly influenced by mesoscale processes outside the bay system. As in other parts of the Benguela, blooms in False Bay are most common in late summer and autumn, and are thought to reflect strong seasonal stratification patterns. Little or no stratification is evident in False Bay in winter, but a thermocline is established in summer, partially through the influx of cold bottom water, and strong stratification is maintained into autumn when dinoflagellate concentrations tend to peak (Pitcher and Calder, 2000).

Average flow in False Bay is considered to have a simple cyclonic character, with water entering the bay along the western side and leaving along the eastern side (Botes, 1988; Grundlingh et al., 1989). Cyclonic surface currents dominate, specifically under southeasterly or upwelling-favourable winds, at which time blooms may be introduced to the bay. The majority of blooms are first reported on the western and northern sides of the bay and their eastward movement provides supporting evidence of clockwise circulation within the bay (Horstman et al., 1991). The presence of a semi-permanent eddy within the

northeastern recess, formed by Gordon's Bay, results in a unique circulation that is independent of the rest of the bay (Atkins, 1970). Here, water flow is weak and mixing of the water column is reduced. For this reason, blooms in False Bay are especially evident in Gordon's Bay, rendering this region of the bay more vulnerable to the negative impacts of HABs (Grindley and Taylor, 1964; Pitcher et al., 2008).

Concurrent observations of a bloom of *Gonyaulax polygramma* in False Bay and Walker Bay in February 2007 (Fig. 18; Pitcher et al., 2008) provided support to the view that these blooms are local expressions of a widespread bloom, and that these bays serve only as sites of bloom accumulation. On the western side of the Agulhas Bank, the sluggish Benguela drift carries water equatorward, and under upwelling conditions cyclonic circulation introduces blooms into the bay where strongly stratified conditions characteristic of late summer further advance bloom development. Reversal of upwelling-favourable winds, particularly toward the end of the upwelling season, tend also to force reversal of surface currents in False Bay, which favours the leakage of blooms from the bay and their entrainment into the Benguela jet current off the Cape Peninsula (Fig. 20). This northward-flowing current therefore serves as a mechanism of export of the bloom from False Bay along the shelf edge of the West Coast.

3.5. Rías

Rías comprise long, narrow coastal inlets and are formed by the flooding of river valleys. Within upwelling systems, Rías are unique to the Iberian Peninsula. They differ from fjords in that they gradually decrease in depth and width with distance from the coast, and are often described as very large estuaries at the mouths of relatively insignificant rivers.

3.5.1. Rías Baixas—The Rías Baixas constitute a unique set of four embayments, at the northern edge of the Iberian coast, in which the three-dimensional variability of the continental shelf circulation is transformed into two dimensions (Alvarez-Salgado et al., 2000; Figueiras et al., 2002). The topography of the Rías and their almost perpendicular orientation to the coastline cause the amplification of upwelling and downwelling signals through enhanced across-shelf transport. Coastal upwelling and downwelling therefore greatly influence the circulation in the Rías, and the exchange between the Rías and the adjacent shelf, including the exchange of phytoplankton populations (Figueiras et al., 1994; Fermin et al., 1996; Alvarez-Salgado et al., 2000; Tilstone et al., 1994, 2000). Offshore transport is enormously favoured in the rías during upwelling, while they act as very efficient retention zones during downwelling. Upwelling forces a two-layer density-induced positive circulation in the Rías, characterized by the outflow of surface water and a compensating inflow of cold bottom water (Figueiras et al., 2002; Piedracoba et al., 2005; Crespo et al., 2006; Fig. 19a). Downwelling establishes a circulation during which surface coastal waters enter the Rías to develop a downwelling front at the location where coastal waters meet inner waters of higher continental influence (Crespo et al., 2006; Fig. 19b). During this reverse circulation, especially important during the transition to seasonal downwelling in autumn (Figueiras et al., 2002; Crespo et al., 2007), the outflow towards the ocean in the outer circulation cell takes place in the bottom layer, while the inner cell maintains a positive circulation, forced by runoff. The driving force of the two-layered

circulation in the inner cell during winter is the high runoff, which also causes salinity stratification of the water column and the consequent formation of two layers. Under these circumstances the relative strength of downwelling and runoff determines the position of the downwelling front within the Ría. The formation of the two layers in summer is the result of thermal stratification.

Red tides in the Rías Baixas, dominated by dinoflagellates, are well-known phenomena, particularly during the seasonal transition to downwelling (Margalef, 1956). Toxic episodes of Diarrhetic Shellfish Poisoning and Paralytic Shellfish Poisoning resulting from blooms of *D. acuta* and of *G. catenatum* respectively are recurrent in these embayments in late summer and early autumn (Fraga et al., 1988; Figueiras and Pazos, 1991; Reguera et al., 1993, 1995). *Dinophysis acuminata* also causes regular outbreaks of Diarrhetic Shellfish Poisoning, typically in summer in association with periods of stratification between moderate pulses of upwelling (Reguera et al., 1993, 1995), which favours the *in situ* growth of *D. acuminata* (Reguera et al., 2003). Other harmful dinoflagellates include *Karenia mikimotoi and Prorocentrum minimum*, which bloom in late summer and early autumn (Crespo et al., 2007). There are conflicting opinions on the origins of these dinoflagellate blooms. Some maintain that the blooms are generated in coastal waters beyond the boundaries of the Rías and are introduced at times of downwelling, through the reversal of estuarine circulation (Fraga et al., 1988; Sordo et al., 2001), whereas others suggest that the outer part of the Rías are the site of red tide population growth (Figueiras et al., 1994; Fermin et al., 1996). The coincidence of the autumn upwelling–downwelling transition with the onset of an inshore poleward current on the shelf (Frouin et al., 1990; Alvarez-Salgado et al., 2003) has led to the suggestion that initial populations could be advected into the Rías from either offshore waters (Fraga et al., 1988) or from the northwestern coast of Portugal (Sordo et al., 2001).

During upwelling, the phytoplankton composition is characterized by the dominance of diatoms inside the Rías and a higher incidence of dinoflagellates on the shelf (Tilstone et al., 1994). At this time, between the spring and autumn blooms, the absence of summer phytoplankton blooms may be a function of the positive circulation imposed by upwelling that induces the export of material from the rías towards the shelf (Tilstone et al., 2000), where it is transported in a southwesterly direction (Fig. 20). Downwelling typically confines shelf populations to a narrow band near the coast and thereby favours the advection of dinoflagellates to the interior of the Rías (Fig. 20). Their accumulation at the downwelling front (Fraga et al., 1988; Figueiras et al., 1994; Fermin et al., 1996; Crespo et al., 2007) is attributed to the vertical swimming capability of dinoflagellates, which allows them to compensate the downward velocity generated in this convergence (Figueiras et al., 1995). Diatoms, unable to counteract the downward velocity, are removed from the surface waters and exported towards the shelf by the bottom outflow (Figueiras et al., 1994, 1996). A mechanism is therefore provided whereby harmful dinoflagellates, occurring in low numbers on the shelf as habitual components of the spring–summer phytoplankton community, may be accumulated in the interior of the Rías Baixas during downwelling, whereas strong upwelling or runoff tends to disperse these dinoflagellates into shelf waters (Crespo et al., 2007).

3.6. Narrow-mouth bays

Several bay systems are characterized by relatively shallow, expansive bodies of water connected to the coastal upwelling system by means of a narrow mouth. Many, but not all, of these semi-enclosed bodies of water are classified as estuaries, which have a free connection with the open sea, and within which seawater mixes with freshwater. Riverine input and tides are often important in maintaining a dynamic relationship between these two bodies of water. The input of freshwater may also act to stabilize the water column through salinity stratification, and strong benthic–pelagic coupling, owing to the shallow nature of these systems, is often a defining feature. Consequently, they are, in many cases, turbid habitats in which the availability of light is limited, and tend also to be nutrient-rich because of inputs from the land surface (Cloern, 1996).

Within these turbulent advective systems, the pelagic and its biota are often dispersive and transient. In those systems with significant riverine input, the pelagic habitats are time-varying mixtures of seawater and freshwater, situated within spatial gradients of salinity, temperature, nutrients and turbidity along a river-ocean continuum (Cloern and Dufford, 2005). Plankton populations distinct from those beyond the freshwater and ocean interfaces are maintained and controlled by either *in situ* processes or horizontal transports that displace or mix water parcels (Cloern, 1996). Therefore, horizontal transport is an important mechanism of bloom regulation, providing a source of phytoplankton when either coastal or riverine blooms are advected into these ecosystems.

3.6.1. Saldanha Bay—The phytoplankton dynamics of Saldanha Bay, located within the southern Benguela, are driven by changes in the physical state of the bay as determined by inputs of energy at the interfaces with the coastal upwelling system and the atmosphere (Pitcher and Calder, 1998). At the coastal-bay interface, upwelling processes on the shelf determine the advective transport of phytoplankton and the input of nutrients from the coastal upwelling system. These horizontal exchanges are dictated by event-scale fluctuations in wind-stress, which control the exchange of subthermocline water to and from Saldanha Bay through wind-driven coastal upwelling. At the atmosphere-bay interface, local windstress controls vertical shear through vertical mixing and determines the rate of entrainment that provides nutrient input into the euphotic zone.

During the upwelling months, the water becomes highly stratified, because of intermittent upwelling on the shelf and subsequent penetration of cold bottom water into the bay, and sun-warming of the surface water (Monteiro et al., 1998). A nutrient-depleted upper layer is therefore typically found overlying a nutrient-rich lower layer, as the thermocline never upwells to the surface, and there are essentially always two layers to the system during the upwelling season. High light in this upper layer favours the growth of phytoplankton and the necessary flux of nutrients into the upper layer to sustain this growth occurs when the turbulent upper layer entrains nutrient-rich lower-layer water across the thermocline (Pitcher and Calder, 1998). The bottom supply of NO_3 coupled with its vertical turbulent flux therefore drives new production in Saldanha Bay, and the rate of entrainment is directly proportional to the windstress.

There is a strong link between stratification in Saldanha Bay and the exchange between bay and coastal waters, with bay stratification determined by the inflow and outflow of cold upwelled water, which is driven by changing baroclinic pressure gradients between the coastal and bay domains (Monteiro and Largier, 1999). One of the most important aspects of this density-driven coastal-exchange is its impact on the renewal of bay water, because it tends to flush the bay more rapidly than tidally driven exchange. During active upwelling, the bay is strongly stratified due to the bottom inflow of cold upwelled water, and the shallowing of the thermocline results in an outflow of surface water and an advective loss of phytoplankton from the bay. On the other hand, during periods of relaxation, the wedge of cold, bottom water retreats as the bay returns to an isothermal condition, favouring the advective introduction of coastal blooms into the bay. These phases are closely correlated to fluctuations in the equatorward windstress that drive coastal upwelling.

High-biomass dinoflagellate blooms, including those of the toxic species *Alexandrium catenella*, *Dinophysis* spp. and *P. reticulatum*, have all been reported in Saldanha Bay, but are considered to originate on the southern Namaqua shelf to the north of the bay (Probyn et al., 2000). They are advected into the bay when upwelling relaxes, and the density gradient between the bay and the shelf drives surface inflow and bottom-water outflow. The relaxed phase of the upwelling cycle therefore serves as a mechanism by which harmful coastal blooms can be rapidly imported into the bay. These flows are reversed with the resumption of upwelling over the shelf, resulting in the intrusion and entrainment of bottom water and surface outflow (Fig. 21). This implies that the residual volume of bottom water during downwelling is less than the original volume advected into the bay. Entrainment therefore results in a rectified flow of water through the system, with water entering in the bottom layer and flowing out at the surface. Entrainment thus dictates that the bay acts as a net importer of bottom water and net exporter of surface water over a synoptic cycle. The net outflow of surface water from Saldanha Bay consequently limits the opportunities for coastal blooms to be imported into the bay. This system of exchange between Saldanha Bay and the shelf therefore curtails the duration and severity of toxic episodes in the bay relative to the shelf. This is confirmed by observations of fewer dinoflagellate cysts in the sediments of Saldanha Bay compared to the southern Namaqua shelf (Joyce et al., 2005). The presence of fewer cysts in the bay further reduces the likelihood of *in situ* bloom development initiated through excystment.

3.6.2. Willapa Bay—Willapa Bay is the largest in a series of shallow, coastal plain estuaries that span the US Pacific Northwest coast. It is a macrotidal estuary, whose river and ocean end members are both highly variable on seasonal and event time scales. Over the course of a year Willapa Bay therefore cycles over an enormous range of possible hydrographic states. Order of magnitude changes in river input are common, while the dominant mode of ocean end-member variability in water properties is forced by wind-driven upwelling–downwelling transitions (Hickey et al., 2002; Banas et al., 2004).

Under high-flow river input during winter, both density-driven and tide-driven circulations are important contributors to exchange, whereas during spring and summer, when river input is generally low, tidal effects dominate, and horizontal tidal stirring is the primary flushing mechanism in Willapa Bay (Banas and Hickey, 2005). Exchange between the bay and the

coast appears to be cushioned by a high baseline flushing rate, independent of the river-driven circulation, and tidal stirring, in the form of strong lateral exchange flow in the seaward reach of the bay, causes the bulk of this baseline exchange (Banas and Hickey, 2005). Tidal-residual currents are strong enough to stir new coastal water 20 km into Willapa Bay in a few days, although the strength of tidal stirring drops off by a factor of 20 from mouth to head. This gradient means that although half the volume of the bay enters and leaves with every tide, and 30% of this intertidal volume is replaced with new coastal water on every tide, the average water age in the landward reach of the estuary is 3–5 weeks (Banas and Hickey, 2005).

Riverflow and terrestrial nutrient input into Willapa Bay in summer is close to zero and the bay acquires the characteristics of the nearshore coastal ocean (Banas et al., 2007). Accordingly, primary production is fueled by upwelled coastal nutrients or the direct import of coastal phytoplankton blooms (Banas and Hickey, 2005). Coastal upwelling and horizontal transport are therefore the most important physical controls on primary production (Hickey and Banas, 2003). With the relaxation of upwelling-favourable winds, blooms may be advected across the shelf to the coast and subsequently into Willapa Bay (Roegner et al., 2002). The dynamics of coastal-estuary exchange is thus a very basic control on the ecology of Willapa Bay (Banas and Hickey, 2005).

Phytoplankton biomass and production in Willapa Bay have strong spatial gradients in summer, typically high near the mouth and low in the interior (Newton and Horner, 2003). As upwelled coastal water is stirred into Willapa Bay by tides, nutrients are rapidly depleted and over most of the estuary phytoplankton biomass generally declines, even as growth on regenerated nutrients remains high. This indicates a net transfer of phytoplankton from the coast to the estuary. Experiments with a non-conservative tracer in a spatially detailed circulation model suggest that the intertidal benthic grazers of Willapa Bay have the filtration capacity to account for most of the loss of phytoplankton biomass observed (Banas et al., 2007). Willapa Bay in summer is thus considered a sink for upwelling-fueled phytoplankton production, a net importer in which more phytoplankton biomass is consumed and transferred to higher trophic levels than is locally produced. However, despite the high clearance rates by the benthos, the model predicts that most of the coastal phytoplankton that enter the bay are also flushed from the bay as they spend insufficient time over intertidal areas to be grazed (Banas et al., 2007).

Few HABs have been reported within Willapa Bay, but it appears reasonable to assume that their presence would reflect the composition of the phytoplankton of the coastal environment. In the autumn of 2002, a *Pseudo-nitzschia* bloom in Willapa Bay offered the opportunity to investigate its origin and possible importation through the introduction of coastal waters (Cox et al., 2003). Association of the bloom with higher salinity, colder water and elevated nitrate levels, all indicated the intrusion of coastal waters. Similar trends in the incidence of *Pseudo-nitzschia* in Willapa Bay and at two coastal stations, Twin Harbors and Long Beach, further implicated the influx of coastal water into the estuary as the likely mechanism of their introduction into the bay (Cox et al., 2003).

3.6.3. San Francisco Bay—Phytoplankton blooms in San Francisco Bay are supported by terrestrial nutrients and tightly controlled by stratification dynamics, on spring-neap, seasonal and interannual time scales. Although San Francisco Bay has high nutrient concentrations, summer–autumn blooms are rare because wind-induced turbulence and tidal currents overcome buoyancy inputs from surface heating and prevent stratification (Cloern et al., 2005). Continuous mixing between a shallow photic zone and deeper aphotic zone thus restricts phytoplankton growth through light limitation and increased mortality by delivering phytoplankton cells to benthic suspension-feeders. During summer and autumn, San Francisco Bay tends therefore to be a well-mixed, high nutrient, low-chlorophyll system. Blooms do occur in spring when density gradients from runoff induced stratification are strong enough to resist mixing forces, thereby reducing light limitation, and the euphotic-zone depth increases as sediment suspension is dampened during weak neap tides. Owing to these controls, the seasonal succession of phytoplankton in temperate latitudes, corresponding to diatom dominance in spring and the proliferation of dinoflagellates in late summer and autumn, does not occur. Diatoms therefore overwhelmingly dominate the phytoplankton community of San Francisco Bay, contributing to over 80% of the biomass in the bay, and dinoflagellates are uncommon (Cloern and Dufford, 2005).

Despite their infrequency, dinoflagellate blooms have been reported in San Francisco Bay, one of which, a bloom of the dinoflagellate *Akashiwo sanguinea* in September 2004, was ascribed to a climate anomaly (Fig. 22; Cloern et al., 2005). Although the bloom was extremely patchy, chlorophyll *a* concentrations as high as 195 mg m^{-3} were recorded. Blooms of this magnitude had not been observed over the past three decades of sampling in that area. The exceptional nature of this bloom is placed in perspective by the 27-year mean chlorophyll *a* value for August and October of <3 mg m^{-3}.

Akashiwo sanguinea can form dense blooms in the eastern Pacific, from California to Peru, but typically extends only in the seaward regions of San Francisco Bay (Cloern and Dufford, 2005), suggesting that it is an allocthonous species produced in the coastal ocean and transported into the bay, by density-driven currents or tidal dispersion. This species typically occurs in autumn, when equatorward winds diminish or reverse and the central California coastal ocean switches from a diatom-producing upwelling system to a warm, stratified system with onshore or weak offshore transport that favours the growth of dinoflagellates.

The bloom in San Francisco Bay in 2004 was considered a coupled response to a short-term weather anomaly that produced an opportunity for rapid population growth of the dinoflagellate within the bay, preceded by a seasonal-scale coastal anomaly that introduced seed stock of *A. sanguinea* into the bay to exploit this opportunity. The summer of 2004 produced the weakest August-mean upwelling index for the region since record keeping was initiated in 1946. The resulting weakened offshore flow, coupled with surface warming, promoted the growth of dinoflagellates in the adjacent California Current system prior to the development of red tide inside the bay. The anomalous thermal stratification and red tide observed in the bay in September coincided with four consecutive days of record high air temperatures and weak winds coupled with low-energy neap tides. Satellite imagery is consistent with this speculation, revealing high surface temperatures and high phytoplankton biomass in the nearshore coastal ocean during late August, compared to the typical summer

upwelling state of low nearshore surface temperature and offshore transport of cold, chlorophyll-rich water within filaments (Fig. 22). Thermal stratification in the bay broke down, and the red tide dissipated as local winds increased and tidal currents accelerated during the neap-spring transition (Cloern et al., 2005).

4. Summary

HABs in upwelling systems have historically been attributed to flagellate species, in particular the proliferation of dinoflagellates. This allowed studies on the ecology and oceanography of HABs to focus on those conditions favouring the development of these phytoplankton groups. The inclusion of other phytoplankton species, specifically those of the diatom *Pseudo-nitzschia*, as harmful has required a broadening of approach to the study of the ecology and oceanography of HABs in upwelling systems. Phytoplankton assemblages in upwelling regions were originally considered to be diatom-dominated, and the presence of dinoflagellate blooms or red tides were considered unusual phenomena. The concept of dinoflagellate blooms as normal components of the phytoplankton of upwelling systems was considered to be in conflict with the apparent requirement of increased water stability. Blasco (1975) was one of the first to question this thinking and to demonstrate the large contribution of dinoflagellates, often in the form of red tides, to the productivity of upwelling ecosystems, and it is now accepted that dinoflagellates and red tides are frequent and fundamental features of upwelling systems (Pitcher and Weeks, 2006). In most marine ecosystems, nutrient supply is likely to regulate phytoplankton biomass levels, and although high biomass is not necessarily a requirement for a HAB, it is likely to contribute to the potentially harmful properties of a bloom. Upwelling systems are therefore susceptible to HABs, largely owing to the fact that they are highly productive nutrient-enriched environments, prone to high-biomass blooms.

Changes to phytoplankton assemblages are dictated by influences of windstress on the surface boundary layer through a combination of its influence on surface mixed-layer characteristics and shelf circulation patterns. Windstress fluctuations and buoyancy inputs in upwelling systems vary at seasonal, event and interannual scales, and thereby clearly control the timing of blooms, whereas their spatial distribution is controlled largely by inner-shelf dynamics. Continental shelves represent the interface between the populated coastline and the open oceans, and there is now an increasing perception that inner-shelf dynamics may be somewhat independent from outer-shelf dynamics (Relvas et al., 2007). Traditionally, physical processes over the continental shelf of upwelling systems are defined in terms of Ekman dynamics, which predicts across-shelf transport proportional to the wind-stress and associated alongshore currents due to geostrophic adjustment. However, closer inshore where water depth is reduced, surface and bottom boundary layers tend to overlap, reducing across-shelf transport. This has ecological consequences by reducing transport between the inner and outer shelf, so that alongshore dispersion and retention of phytoplankton may prevail over the inner shelf. Many examples of the distinctive behaviour of the inner-shelf circulation have been observed, in particular the recurrent development during the upwelling season of warm, inshore counter-currents of particular relevance to the development and delivery of HABs to the coastal environment.

Upwelling systems are generally characterized by meridional alignment of the coastline, which presents the upwelling cycle as a symmetric two-dimensional process. Phytoplankton within such systems, while deriving nutrients from upwelling, must also contend with the problem of advective dispersion of the developing population. If advection is too strong, the balance between washout and growth may preclude a bloom event. Consequently, coastlines of this nature are distinguished by a low incidence of blooms. Local deviations from this alignment alter the upwelling process, and surface boundary-layer characteristics are modified by the interaction of windforcing cycles with changes in coastline configuration and orientation, bottom topography, and buoyant freshwater plumes. The inner shelf of upwelling systems therefore provides a mosaic of multiple and shifting subhabitats for phytoplankton, where physical and chemical properties exhibit sharp spatial and temporal heterogeneities that lead to frequent ecological niche disruptions, some of which favour the development of HABs (Smayda, 2000).

Within the inner-shelf environment, blooms often manifest within a variety of embayments as a result of local modulation of the coastal upwelling process in response to variable coastal geomorphology. The properties of stratification and retention, which generally favour HABs, tend to be more pronounced the more isolated the bay is from the open coast. However, limiting mechanisms of exchange with the coastal environment tend also to limit the delivery of nutrients and the likelihood of introduction of coastal blooms to these environments.

In upwelling systems open embayments tend to be the most susceptible to bloom development, because they provide sufficiently high nutrients but remain stratified and accessible to the introduction, concentration and retention of coastal blooms. In waters bordered by land on two sides, namely those bays associated with headlands and capes, across-shelf structure in along-shore flow, and in particular poleward flow over the inner shelf during periods of relaxation from upwelling-favourable winds, drive retentive cyclonic circulation patterns and increases stratification (Relvas and Barton, 2005; Fawcett et al., 2007, 2008). The limited across-shelf exchange of water results in the clear delineation of phytoplankton assemblages in the lee of the headland or cape from those offshore of them. This delineation is considered to be driven by both asymmetric advective patterns and spatial variations in the depth of the surface mixed layer. Bays enclosed on a third side, but retaining good exchange by means of a large mouth, tend also to develop cyclonic surface circulation patterns during upwelling conditions and equatorward flow across the mouth of the bay further increases bay residence time and stratification.

Systems with declining ratios of mouth area to contained water volume tend to be less susceptible to HABs. Upwelling of cold, subthermocline water to the surface is less likely within these embayments, although upwelled water may be advected into the region below a typically shallow, but strong, thermocline. Coastal-bay exchange and the possible propagation of coastal blooms into these narrow-mouth systems may be accomplished by both baroclinic, density-driven mechanisms, and by barotropic, density-independent mechanisms, such as lateral stirring by tidal and wind-driven currents. In general, tide- and wind-driven mechanisms dominate in shallow well-mixed systems, and density-driven exchange dominates in deeper, stratified systems. Typical of the deeper bays is the

juxtaposition of cold coastal water with surface-warmed bay water, producing a bay-coastal density gradient that results in vertically sheared exchange flow. In such systems, coastal-bay coupling is primarily baroclinic whereby the influx of a dense, upwelled water mass at depth is balanced by outflow in the surface layer. One of the most important aspects of density-driven coastal-exchange flow is its impact on the renewal of bay water, because subtidal, density-driven exchange flushes the bay more rapidly than tidally driven exchange. Wind-driven vertical entrainment of cold bottom water into the surface layer of the bay further reduces this period, because entrainment results in a rectified flow of water through the system, with water entering in the bottom layer and flowing out at the surface. The bottom supply of nutrients coupled with their vertical turbulent flux drive new production, but the net outflow of surface water limits the opportunities for coastal blooms, including harmful blooms, to be accumulated within or imported into these bays. In shallow, well-mixed bays, exchange with the coastal system is primarily tidal and barotropic. In these systems, tidal mixing typically increases horizontal exchange and thus serves as the likely mechanism of import of coastal phytoplankton blooms. However, once introduced into the bay, there is no mechanism of supply of nutrients to sustain the bloom, although some embayments tend also to be fueled by terrestrial nutrients, which may favour *in situ* development of blooms.

Acknowledgments

References

Alvarez-Salgado XA, Castro CG, Perez FF, Fraga F. Nutrient mineralization patterns in shelf waters of the Western Iberian upwelling. Continental Shelf Research. 1997; 17(10):1247–1270.

Alvarez-Salgado XA, Doval MD, Perez FF. Dissolved organic matter in shelf waters off the Ria de Vigo (NW Iberian upwelling system). Journal of Marine Systems. 1999; 18(4):383–394.

Alvarez-Salgado XA, Figueiras FG, Perez FF, Groom S, Nogueira E, Borges AV, Chou L, Castro CG, Moncoiffe G, Rios AF, Miller AEJ, Frankignoulle M, Savidge G, Wollast R. The Portugal coastal counter current off NW Spain: new insights on its biogeochemical variability. Progress in Oceanography. 2003; 56:281–321.

Alvarez-Salgado XA, Gago J, Miguez BM, Gilcoto M, Perez FF. Surface waters of the NW Iberian margin: upwelling on the shelf versus outwelling of upwelled waters from the Rias Baixas. Estuarine, Coastal and Shelf Science. 2000; 51:821–837.

Alvarez-Salgado XA, Labarta U, Fernandez-Reiriz MJ, Figueiras FG, Roson G, Piedracoba S, Filgueira R, Cabanas JM. Renewal time and the impact of harmful algal blooms on the extensive mussel raft culture of the Iberian coastal upwelling system (SW Europe). Harmful Algae. 2008; 7(6):849–855.

Amorim, A.; Moita, MT.; Oliveira, P. Dinoflagellate blooms related to coastal upwelling plumes off Portugal. In: Steidinger, KA.; Landsberg, JH.; Tomas, CR.; Vargo, GA., editors. Harmful Algae 2002. Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography, and Intergovernmental Oceanographic Commission of UNESCO. 2004. p. 89-91.

Author Manuscript

Author Manuscript

Author Manuscript

Author Manuscript

Anderson CR, Brzezinski MA, Washburn L, Kudela R. Circulation and environmental conditions during a toxigenic *Pseudo-nitzschia australis* bloom in the Santa Barbara Channel, California. Marine Ecology Progress Series. 2006; 327:119–133.

Andrews WRH, Hutchings L. Upwelling in the southern Benguela current. Progress in Oceanography. 1980; 9:1–81.

Atkins GR. Wind and current patterns in False Bay. Transactions of the Royal Society of South Africa. 1970; 39(2):139–148.

Bakun A, Nelson CS. The seasonal cycle of wind–stress curl in subtropical eastern boundary current regions. Journal of Physical Oceanography. 1991; 21:1815–1834.

Banas NS, Hickey BM. Mapping exchange and residence time in a model of Willapa Bay, Washington, a branching, macrotidal estuary. Journal of Geophysical Research. 2005; 110:C11011.10.1029/2005JC002950

Banas NS, Hickey BM, MacCready P, Newton JA. Dynamics of Willapa Bay, Washington: a highly unsteady, partially mixed estuary. Journal of Physical Oceanography. 2004; 34:2413–2427.

Banas NS, Hickey BM, Newton JA, Ruesink JL. Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. Marine Ecological Progress Series. 2007; 341:123–139.

Banas NS, MacCready P, Hickey BM. The Columbia River plume as cross-shelf exporter and along-coast barrier. Continental Shelf Research. 2008; 29(1):292–301.

Barth JA. Stability of a coastal upwelling front. Part I. Model development and a stability theorem. Journal of Geophysical Research. 1989a; 94:10844–10856.

Barth JA. Stability of a coastal upwelling front. Part II. Model results and comparison with observations. Journal of Geophysical Research. 1989b; 94:10857–10883.

Barth JA, Pierce SD, Castelao RM. Time-dependent, wind-driven flow over a shallow midshelf submarine bank. Journal of Geophysical Research. 2005a; 110:C10S05.10.1029/2004JC002761

Barth JA, Pierce SD, Cowles TJ. Mesoscale structure and its seasonal evolution in the northern California Current system. Deep-sea Research Part II. 2005b; 52:5–28.

Barth JA, Pierce SD, Smith RL. A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current system. Deep-sea Research Part II. 2000; 47:783–810.

Blanton JO, Tenore KR, Castillejo F, Atkinson LP, Schwing FB, Lavin A. The relationship of upwelling to mussel production in the rias on the western coast of Spain. Journal of Marine Research. 1987; 45:497–511.

Blasco, D. Red tides in the upwelling regions. In: LoCicero, VR., editor. Proceedings of the First International Conference on Toxic Dinoflagellate Blooms. The Massachusetts Science and Technology Foundation; Massachusetts: 1975. p. 113-119.

Botes WAM. Lagrangian Current Measurements by using Drifting Radio Transmitting Buoys. CSIR Report EMA-T. 1988; 8811:42.

Botes L, Sym SD, Pitcher GC. *Karenia cristata* sp. nov. and *Karenia bicuneiformis* sp nov (Gymnodiniales, Dinophyceae): two new *Karenia* species from the South African coast. Phycologia. 2003; 42(6):563–571.

Bruland KW, Lohan MC, Aguilar-Islas AM, Smith GJ, Sohst B, Baptista A. Factors influencing the chemistry of the near-field Columbia River plume: nitrate, silicic acid, dissolved Fe, and dissolved Mn. Journal of Geophysical Research. 2008; 113:C00302.10.1029/2007JC004702

Cabeçadas G, Cunha ME, Moita MT, Pissarra J, Sampayo MA. Red tide in Cascais Bay, Portugal. Boletim do Instituto Nacional de Investigação das Pescas. 1983; 10:81–123.

Cabeçadas, G.; Brogueira, MJ.; Cabeçadas, L. Southern Portugal: the Tagus and Sado estuaries. In: Sheppard, CRC., editor. Seas at the Millenium: an Environmental Evaluation. Elsevier Science Ltd.; 2000. p. 151-165.

Cachão M, Moita MT. *Coccolithus pelagicus*, a productivity proxy related to moderate fronts off Western Iberia. Marine Micropaleontology. 2000; 39:131–155.

Calvo-Díaz A, Morán XAG, Nogueira E, Bode A, Varela M. Picoplankton community structure along the northern Iberian continental margin in late winter–early spring. Journal Plankton Research. 2004; 26(9):1069–1081.

Castro CG, Álvarez–Salgado XA, Figueiras FG, Pérez FF, Fraga F. Transient hydrographic and chemical conditions affecting microplankton populations in the coastal transition zone of the Iberian upwelling system (NW Spain) in September 1986. Journal of Marine Research. 1997; 55:321–352.

Cloern JE. Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California. Reviews of Geophysics. 1996; 34(2):127–168.

Cloern JE, Dufford R. Phytoplankton community ecology: principles applied in San Francisco Bay. Marine Ecology Progress Series. 2005; 285:11–28.

Cloern JE, Schraga TS, Lopez CB, Knowles N. Climate anomalies generate an exceptional dinoflagellate bloom in San Francisco Bay. Geophysical Research Letters. 2005; 32:L14608.10.1029/2005GL023321

Cockcroft, AC.; Schoeman, DC.; Pitcher, GC.; Bailey, GW.; van Zyl, DL. A mass stranding, or "walkout", of west coast rock lobster, *Jasus lalandii*, in Elands Bay, South Africa: causes, results and implications. In: Von Kaupel Klein, JC.; Schram, FR., editors. The Biodiversity Crisis and Crustacea. Vol. 12. 2000. p. 673-688.

Cox K, Newton J, Bos J, Trainer V, Adams N, Baugh K, Cheney D, Christy A. On the origin of harmful Algal Bloom species in Pacific coast estuaries: perspectives from the Olympic Region Harmful Algal Bloom (ORHAB) Project. Proceedings of the 2003 Georgia Basin/Puget Sound Research Conference. 2003

Crespo BG, Figueiras FG. A spring poleward current and its influence on microplankton assemblages and harmful dinoflagellates on the western Iberian coast. Harmful Algae. 2007; 6:686–699.

Crespo BG, Figueiras FG, Groom S. Role of across-shelf currents in the dynamics of harmful dinoflagellate blooms in the northwestern Iberian upwelling. Limnology and Oceanography. 2007; 52(6):2668–2678.

Crespo BG, Figueiras FG, Porras P, Teixeira IG. Downwelling and dominance of autochthonous dinoflagellates in the NW Iberian margin: the example of the Ria de Vigo. Harmful Algae. 2006; 5:770–781.

Dale AC, Barth JA, Levine MD, Austin JA. Observations of mixed layer restratification by onshore surface transport following wind reversal in a coastal upwelling region. Journal of Geophysical Research. 2008; 113:C01010.10.1029/2007JC004128

Duncan CP, Nell JH. Surface currents off the Cape Coast. Investigational Report Division of Sea Fisheries South Africa. 1969; 76:1–19.

Escalera, L.; Reguera, B.; Moita, T.; Moroño, Á.; Cerejo, M.; Ruiz-Villareal, M.; Cabanas, JM. Follow up of an autumn bloom of *Dinophysis acuta* in NW Iberia: along-shore transport versus in situ growth. 12th International Conference on Harmful Algae, Programme and Abstracts; Copenhagen, Denmark. 2006. p. 169

Estrada M. Phytoplankton distribution and composition off the coast of Galicia (northwest of Spain). Journal Plankton Research. 1984; 6(3):417–434.

Estrada M, Blasco D. Two phases of the phytoplankton community in the Baja California upwelling. Limnology and Oceanography. 1979; 24(6):1065–1080.

Fawcett A, Pitcher GC, Bernard S, Cembella AD, Kudela RM. Contrasting wind patterns and toxigenic phytoplankton in the southern Benguela upwelling system. Marine Ecology Progress Series. 2007; 348:19–31.

Fawcett AL, Pitcher GC, Shillington FA. Nearshore currents on the southern Namaqua shelf of the Benguela upwelling system. Continental Shelf Research. 2008; 28(8):1026–1039.

Fermin EG, Figueiras FG, Arbones B, Villarino ML. Short-time scale development of a *Gymnodinium catenatum* population in the Ria de Vigo (NW Spain). Journal of Phycology. 1996; 32:212–221.

Figueiras, FG.; Alvarez-Salgado, XA.; Castro, CG.; Villarino, ML. Accumulation of *Gymnodinium catenatum* Graham cells in western Iberian shelf waters in response to poleward flowing slope currents. In: Reguera, B.; Blanco, J.; Fernández, ML.; Wyatt, T., editors. Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO. 1998. p. 114-117.

Figueiras, FG.; Gomez, E.; Nogueira, E.; Villarino, ML. Selection of *Gymnodinium catenatum* under downwelling conditions in the Ria de Vigo. In: Yasumoto, T.; Oshima, Y.; Fukuyo, Y., editors.

Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO. 1996. p. 215-218.

Figueiras FG, Jones KJ, Mosquera AM, Alvarez-Salgado XA, Edwards A, MacDougall N. Red tide assemblage formation in an estuarine upwelling ecosystem: Ria de Vigo. Journal of Plankton Research. 1994; 16(7):857–878.

Figueiras FG, Labarta U, Fernández Reiriz MJ. Coastal upwelling, primary production and mussel growth in the Rías Baixas of Galicia. Hydrobiologia. 2002; 484:121–131.

Figueiras FG, Pazos Y. Hydrography and phytoplankton of the Ria de Vigo before and during a red tide of *Gymnodinium catenatum* Graham. Journal of Plankton Research. 1991; 13(3):589–608.

Figueiras, FG.; Pitcher, GC.; Estrada, M. Harmful Algal Bloom dynamics in relation to physical processes. In: Graneli, E.; Turner, JT., editors. Ecology of Harmful Algae, Ecological Studies. Vol. 189. Springer-Verlag; Berlin: 2006. p. 127-138.

Figueiras, FG.; Rios, AF. Phytoplankton succession, red tides and the hydrographic regime in the Rías Bajas of Galicia. In: Smayda, TJ.; Shimizu, Y., editors. Toxic Phytoplankton Blooms in the Sea. Elsevier Science Publishers B.V.; 1993. p. 239-244.

Figueiras, FG.; Wyatt, T.; Alvarez-Salgado, XA.; Jenkinson, IR. Advection, diffusion and patch development in the Rias Baixas. In: Lassus, P.; Arzul, G.; Erard, E.; Gentien, P.; Marcaillou, C., editors. Harmful Marine Algal Blooms. Technique et Documentation-Lavoisier, Intercept Ltd; 1995. p. 579-584.

Fraga S, Anderson DM, Bravo I, Reguera B, Steidinger KA, Yentsch CM. Influence of upwelling relaxation on dinoflagellates and shellfish toxicity in Ria de Vigo, Spain. Estuarine, Coastal and Shelf Science. 1988; 27:349–361.

Frame ER, Lessard EJ. Does the Columbia river plume influence phytoplankton community structure along the Washington and Oregon coasts? Journal of Geophysical Research. 2009; 114:C00B09.10.1029/2008JC004999

Frouin R, Fiuza AFG, Ambar I, Boyd TJ. Observations of a poleward surface current off the coasts of Portugal and Spain during winter. Journal of Geophysical Research. 1990; 95(C1):679–691.

Fryxell GA, Villac MC, Shapiro LP. The occurrence of the toxic diatom genus *Pseudo-nitzschia* (Bacillariophyceae) on the West Coast of the USA, 1920–1996: a review. Phycologia. 1997; 36(6): 419–437.

Gan J, Allen JS. A modeling study of shelf circulation off northern California in the region of the coastal ocean dynamics experiment: response to relaxation of upwelling winds. Journal of Geophysical Research. 2002a; 107(C9):3123.10.1029/2000JC000768

Gan J, Allen JS. A modeling study of shelf circulation off northern California in the region of the coastal ocean dynamics experiment 2. Simulations and comparisons with observations. Journal of Geophysical Research. 2002b; 107(C11):3184.10.1029/2001JC001190

Gan J, Allen JS. Modeling upwelling circulation off the Oregon coast. Journal of Geophysical Research. 2005; 110:C10S07.10.1029/2004JC002692

GEOHAB. Global Ecology and Oceanography of Harmful Algal Blooms. In: Glibert, P.; Pitcher, G., editors. Science Plan. SCOR and IOC; Baltimore and Paris: 2001. p. 86

GEOHAB. Global ecology and oceanography of harmful algal blooms. In: Pitcher, G.; Moita, T.; Trainer, V.; Kudela, R.; Figueiras, P.; Probyn, T., editors. GEOHAB Core Research Project: HABs in Upwelling Systems. IOC and SCOR; Paris and Baltimore: 2005. p. 82

Graham WM, Field JG, Potts DC. Persistent "upwelling shadows" and their influence on zooplankton distributions. Marine Biology. 1992; 114:561–570.

Graham WM, Largier JL. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. Continental Shelf Research. 1997; 17(5):509–532.

Grantham BA, Chan F, Nielsen KJ, Fox DS, Barth JA, Huyer A, Lubchenco J, Menge BA. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature. 2004; 429:749–754. [PubMed: 15201908]

Grindley JR, Taylor FJR. Red water and marine fauna mortality near Cape Town. Transactions of the Royal Society of South Africa. 1964; 37(2):111–130.

Grundlingh ML, Hunter IT, Potgieter E. Bottom currents at the entrance to False Bay. Continental Shelf Research. 1989; 9:1029–1048.

Harms S, Winant CD. Characteristic patterns of the circulation in the Santa Barbara Channel. Journal of Geophysical Research. 1998; 103(C2):3041–3065.

Hickey, BM. Patterns and processes of circulation over the Washington shelf and slope. In: Landry, MR.; Hickey, BM., editors. Coastal Oceanography of Washington and Oregon. Elsevier Press; Amsterdam, The Netherlands: 1989. p. 41-115.

Hickey BM. Circulation over the Santa Monica–San Pedro basin and shelf. Progress in Oceanography. 1992; 30:37–115.

Hickey, BM. Coastal oceanography of western North America from the tip of Baja California to Vancouver Island. In: Brink, KH.; Robinson, AR., editors. The Sea. Vol. 11. John Wiley and Sons Inc.; New York: 1998. p. 345-393.

Hickey BM, Banas NS. Oceanography of the US Pacific northwest coastal ocean and estuaries with application to coastal ecology. Estuaries. 2003; 26(48):1010–1031.

Hickey BM, Banas NS. Why is the northern end of the California Current system so productive? Oceanography. 2008; 21:90–107.

Hickey B, Geier S, Kachel N, MacFadyen A. A bi-directional river plume: the Columbia in summer. Continental Shelf Research. 2005; 25:1631–1656.

Hickey BM, McCabe R, Geier S, Dever E, Kachel N. Three interacting freshwater plumes in the northern California Current system. Journal of Geophysical Research. 200810.1029/2008JC004907

Hickey BM, Pietrafesa LJ, Jay DA, Boicourt WC. The Columbia River plume study: subtidal variability in the velocity and salinity fields. Journal of Geophysical Research. 1998; 103:10339–10368.

Hickey BM, Zhang X, Banas N. Coupling between the California Current system and a coastal plain estuary in low riverflow conditions. Journal of Geophysical Research. 2002; 107(C10): 3166.10.1029/1999JC000160

Hill, AE.; Hickey, BM.; Shillington, FA.; Strub, PT.; Brink, KH.; Barton, ED.; Thomas, AC. Eastern ocean boundaries coastal segment (E). In: Robinson, AR.; Brink, KH., editors. The Global Coastal Ocean, Regional Studies and Syntheses, The Sea. Vol. 11. John Wiley and Sons, Inc.; New York: 1998. p. 29-67.

Horstman DA, McGibbon S, Pitcher GC, Calder D, Hutchings L, Williams P. Red tides in False Bay, 1959–1989, with particular reference to recent blooms of *Gymnodinium* sp. Transactions of the Royal Society of South Africa. 1991; 47:611–628.

Hutchings, L.; Pitcher, GC.; Probyn, TA.; Bailey, GW. The chemical and biological consequences of coastal upwelling. In: Summerhayes, CP.; Emeis, K-C.; Angel, MV.; Smith, RL.; Zeitzschel, B., editors. Upwelling in the Ocean: Modern Processes and Ancient Records. John Wiley and Sons Ltd.; 1995. p. 65-81.

Huyer A, Kosro PM. Mesoscale surveys over the shelf and slope in the upwelling region near Point Arena, California. Journal of Geophysical Research. 1987; 92:1655–1681.

Jones BH, Atkinson LP, Blasco D, Brink KH, Smith SL. The asymmetric distribution of chlorophyll associated with a coastal upwelling center. Continental Shelf Research. 1988; 8(10):1155–1170.

Joyce LB, Pitcher GC, Du Randt A, Monteiro PMS. Dinoflagellate cysts from the surface sediments of Saldanha Bay, South Africa: an indication of the potential risk of harmful algal blooms. Harmful Algae. 2005; 4:309–318.

Jury MR. Mesoscale variations in summer winds over the Cape Columbine – St Helena Bay region, South Africa. South African Journal of Marine Science. 1985; 3:77–88.

Kaplan DM, Largier J. HF radar-derived origin and destination of surface waters off Bodega Bay, California. Deep-sea Research Part II. 2006; 53:2906–2930.

Kaplan DM, Largier J, Botsford LW. HF radar observations of surface circulation off Bodega Bay (northern California, USA). Journal of Geophysical Research. 2005; 110:C10020.10.1029/2005JC002959

Kosro PM. Structure of the coastal current field off northern California during the coastal ocean dynamics experiment. Journal Geophysical Research. 1987; 92(C2):1637–1654.

Kudela RM, Peterson TD. Influence of a buoyant river plume on phytoplankton nutrient dynamics: what controls standing stocks and productivity? Journal of Geophysical Research. 2009; 114:C00B11.10.1029/2008JC004913

Landry, MR.; Postel, JR.; Peterson, WK.; Newman, J. Broad-scale patterns in the distribution of hydrographic variables. In: Landry, MR.; Hickey, BM., editors. Coastal Oceanography of Washington and Oregon. Elsevier Press; Amsterdam, The Netherlands: 1989. p. 1-41.

Largier JL, Lawrence CA, Roughan M, Kaplan DM, Dever EP, Dorman CE, Kudela RM, Bollens SM, Wilkerson FP, Dugdale RC, Botsford LW, Garfield N, Kuebel Cervantes B, Koracin D. WEST: a northern California study of the role of wind-driven transport in the productivity of coastal plankton communities. Deep-sea Research Part II. 2006; 53:2833–2849.

MacFadyen A, Hickey BM, Cochlan WP. Influences of the Juan de Fuca Eddy on circulation, nutrients and phytoplankton production in the northern California Current system. Journal of Geophysical Research. 2008; 113:C08008.10.1029/2007JC004412

MacFadyen A, Hickey BM, Foreman MGG. Transport of surface waters from the Juan De Fuca eddy region to the Washington coast. Continental Shelf Research. 2005; 25:2008–2021.

Marchetti A, Trainer VL, Harrison PJ. Environmental condition and phytoplankton dynamics associated with *Pseudo-nitzschia* abundance and domoic acid in the Juan de Fuca eddy. Marine Ecology Progress Series. 2004; 281:1–12.

Margalef R. Estructura y dinamica de la "purga de mar" en la Ria de Vigo. Investigacion Pesquera. 1956; 5:113–134.

Margalef R. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologia Acta. 1978; 1:493–509.

Margalef, R.; Estrada, M.; Blasco, D. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In: Taylor, DL.; Seliger, HH., editors. Toxic Dinoflagellate Blooms. Elsevier; New York: 1979. p. 89-94.

Moita, MT. PhD Thesis. University of Lisbon; Portugal: 2001. Estrutura, variabilidade e dinâmica do fitoplâncton na costa de Portugal Continental; p. 272

Moita, MT. O fitoplâncton marinho do sistema de afloramento de Portugal. In: Loução, MA., editor. Fragmentos em Ecologia. Faculdade de Ciências da Universidade de Lisboa e Escolar Editora; Lisboa: 2002. p. 27-43.

Moita MT, Oliveira PB, Mendes JC, Palma AS. Distribution of chlorophyll *a* and *Gymnodinium catenatum* associated with coastal upwelling plumes off central Portugal. Acta Oecologica. 2003; 24:S125–S132.

Moita, MT.; Palma, S.; Oliveira, PB.; Vidal, T.; Silva, A.; Vilarinho, MG. The return of *Gymnodinium catenatum* after 10 years: bloom initiation and transport off the Portuguese coast. 12th International Conference on Harmful Algae, Programme and Abstracts; Copenhagen, Denmark. 2006. p. 242

Moita, MT.; Vilarinho, MG.; Palma, AS. On the variability of *Gymnodinium catenatum* Graham blooms in Portuguese waters. In: Reguera, B.; Blanco, J.; Fernández, ML.; Wyatt, T., editors. Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO. 1998. p. 118-121.

Monteiro PMS, Largier JL. Thermal stratification in Saldanha Bay (South Africa) and subtidal, density-driven exchange with the coastal waters of the Benguela upwelling system. Estuarine, Coastal and Shelf Science. 1999; 49:877–890.

Monteiro PMS, Spolander B, Brundrit GB, Nelson G. Shellfish mariculture in the Benguela system: estimates of nitrogen-driven new production in Saldanha Bay using two physical models. Journal of Shellfish Research. 1998; 17(1):3–13.

Nelson G, Hutchings L. The Benguela upwelling area. Progress in Oceanography. 1983; 12:333–356.

Newton JA, Horner RA. Use of phytoplankton species indicators to track the origin of phytoplankton blooms in Willapa Bay, Washington. Estuaries and Coasts. 2003; 26(4):1071–1078.

Nishimoto MM, Washburn L. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. Marine Ecology Progress Series. 2002; 241:183–199.

Oey L-Y, Wang D-P, Hayward T, Winant C, Hendershott M. "Upwelling" and "cyclonic" regimes of the nearsurface circulation in the Santa Barbara Channel. Journal of Geophysical Research. 2001; 106(C5):9213–9222.

Oliveira PB, Nolasco R, Dubert J, Moita T, Peliz A. Surface temperature, chlorophyll and advection patterns during a summer upwelling event off Central Portugal. Continental Shelf Research. 2009; 29:759–774.

Paduan JD, Cook MS. Mapping surface currents in Monterey Bay with CODAR-type HF radar. Oceanography. 1997; 10(2):49–52.

Pazos, Y.; Moroño, A.; Triñanes, J.; Doval, M.; Montero, P.; Vilarinho, MG.; Moita, MT. Early detection and intensive monitoring during an anusual toxic bloom of *Gymnodinium catenatum* advected into the Galician Rías (NW Spain). 12th International Conference on Harmful Algae, Programme and Abstracts; Copenhagen, Denmark. 2006. p. 259

Peliz A, Rosa T, Santos AMP, Pissarra JL. Jets, eddies and counterflows in the Western Iberian upwelling system. Journal of Marine Systems. 2002; 35(1-2):61–77.

Penven P, Roy C, Colin de Verdiere A, Largier J. Simulation of a coastal jet retention process using a barotropic model. Oceanologica Acta. 2000; 23(5):615–634.

Piedracoba S, Álvarez-Salgado XA, Rosón G, Herrera JL. Short-timescale thermohaline variability and residual circulation in the central segment of the coastal upwelling system of the Ría de Vigo (northwest Spain) during four contrasting periods. Journal of Geophysical Research. 2005; 110:C03018.10.1029/2004JC002556

Pitcher GC, Bernard S, Ntuli J. Contrasting bays and red tides in the southern Benguela upwelling system. Oceanography. 2008; 21(3):82–91.

Pitcher, GC.; Boyd, AJ. Across-shelf and alongshore dinoflagellate distributions and the mechanisms of red tide formation within the southern Benguela upwelling system. In: Yasumoto, T.; Oshima, Y.; Fukuyo, Y., editors. Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO. 1996. p. 243-246.

Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA. Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. Marine Ecology Progress Series. 1998; 172:253–264.

Pitcher GC, Calder D. Shellfish mariculture in the Benguela system: Phytoplankton and the availability of food for commercial mussel farms in Saldanha Bay, South Africa. Journal of Shellfish Research. 1998; 17(1):15–24.

Pitcher GC, Calder D. Harmful algal blooms of the southern Benguela current: a review and appraisal of monitoring from 1989–1997. South African Journal of Marine Science. 2000; 22:255–271.

Pitcher, G.; Monteiro, P.; Kemp, A. The potential use of a hydrodynamic model in the prediction of harmful algal blooms in the southern Benguela. In: Steidinger, KA.; Landsberg, JH.; Tomas, CR.; Vargo, GA., editors. Harmful Algae 2002. Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography, and Intergovernmental Oceanographic Commission of UNESCO. 2004. p. 11-13.

Pitcher GC, Nelson G. 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. 2006; 51(6):2660–2674.

Pitcher, GC.; Weeks, SJ. The variability and potential for prediction of harmful algal blooms in the southern Benguela ecosystem. In: Shannon, V.; Hempel, G.; Malanotte-Rizzoli, P.; Moloney, C.; Woods, J., editors. Benguela: Predicting a Large Marine Ecosystem, Large Marine Ecosystems. Vol. 14. Elsevier, B.V.; 2006. p. 125-146.

Probyn TA, Pitcher GC, Monteiro PMS, Boyd AJ, Nelson G. Physical processes contributing to harmful algal blooms in Saldanha Bay, South Africa. South African Journal of Marine Science. 2000; 22:285–297.

Ramp SR, Paduan JD, Shulman I, Kindle J, Bahr FL, Chavez F. Observations of upwelling and relaxation events in the northern Monterey Bay during August 2000. Journal of Geophysical Research. 2005; 110:C07013.10.1029/2004JC002538

Reguera B, Bravo I, Fraga S. Autoecology and some life history stages of *Dinophysis acuta* Ehrenberg. Journal of Plankton Research. 1995; 17:999–1015.

Reguera B, Garcés E, Pazos Y, Bravo I, Ramilo I, Gonzalez-Gil S. Cell cycle patterns and estimates of *in situ* division rates of dinoflagellates of the genus *Dinophysis* estimated by a postmitotic index. Marine Ecology Progress Series. 2003; 249:117–131.

Reguera, B.; Mariño, J.; Campos, MJ.; Bravo, I.; Fraga, S.; Carbonell, A. Trends in the occurrence of *Dinophysis* spp. in Galician waters. In: Smayda, TJ.; Shimizu, Y., editors. Toxic Phytoplankton Blooms in the Sea. Elsevier Science Publishers B.V.; 1993. p. 559-564.

Relvas P, Barton ED. A separated jet and coastal counterflow during upwelling relaxation off Cape Sao Vicente (Iberian Peninsula). Continental Shelf Research. 2005; 25:29–49.

Relvas P, Barton ED, Dubert J, Oliveira PB, Peliz A, da Silva JCB, Santos AMP. Physical oceanography of the western Iberia ecosystem: latest views and challenges. Progress in Oceanography. 2007; 74:149–173.

Roegner GC, Hickey BM, Newton JA, Shanks AL, Armstrong DA. Wind-induced plume and bloom intrusions into Willapa Bay, Washington. Limnology and Oceanography. 2002; 47(4):1033–1042.

Rosenfeld LK, Schwing FB, Garfield N, Tracy DE. Bifurcated flow from an upwelling center: a cold water source for Monterey Bay. Continental Shelf Research. 1994; 14(9):931–964.

Roughan M, Garfield N, Largier J, Dever E, Dorman C, Peterson D, Dorman J. Transport and retention in an upwelling region: the role of across-shelf structure. Deep-sea Research Part II. 2006; 53:2931–2955.

Roughan M, Mace AJ, Largier JL, Morgan SG, Fisher JL, Carter ML. Subsurface recirculation and larval retention in the lee of a small headland: a variation on the upwelling shadow theme. Journal of Geophysical Research. 2005; 110:C10027.10.1029/2005JC002898

Ryan JP, Chavez FP, Bellingham JG. Physical–biological coupling in Monterey Bay, California: topographic influences on phytoplankton ecology. Marine Ecology Progress Series. 2005a; 287:23–32.

Ryan JP, Dierssen HM, Kudela RM, Scholin CA, Johnson KS, Sullivan JM, Fischer AM, Rienecker EV, McEnaney PR, Chavez FP. Coastal ocean physics and red tides: an example from Monterey Bay, California. Oceanography. 2005b; 18(2):246–255.

Ryan JP, Fischer AM, Kudela RM, Gower JFR, King SA, Marin R III, Chavez FP. Influences of upwelling and downwelling winds on red tide bloom dynamics in Monterey Bay, California. Continental Shelf Research. 200910.1016/j.csr.2008.11.006

Schnetzer A, Miller PE, Schaffner RA, Stauffer BA, Jones BH, Weisberg SB, DiGiacoma PM, Berelson WM, Caron DA. Blooms of *Pseudo-nitzschia* and domoic acid in the San Pedro Channel and Los Angeles harbor areas of the southern California Bight, 2003–2004. Harmful Algae. 2007; 6:372–387.

Send U, Beardsley RC, Winant CD. Relaxation from upwelling in the coastal ocean dynamics experiment. Journal of Geophysical Research. 1987; 92(C2):1683–1698.

Shannon LV, Boyd AJ, Brundrit GB, Taunton-Clark J. On the existence of an El Niño-type phenomenon in the Benguela system. Journal of Marine Research. 1986; 44:495–520.

Shillington, FA. The Benguela upwelling system off southwestern Africa. In: Robinson, AR.; Brink, KH., editors. The Global Coastal Ocean, Regional Studies and Syntheses, The Sea. Vol. 11. John Wiley and Sons Inc.; New York: 1998. p. 583-604.

Simpson JJ. Response of the Southern California Current system to the mid-latitude North Pacific coastal warming events of 1982–1983 and 1940–1941. Fisheries Oceanography. 1992; 1:57–77.

Smayda TJ. Ecological features of harmful algal blooms in coastal upwelling ecosystems. South African Journal of Marine Science. 2000; 22:219–253.

Smayda TJ, Reynolds CS. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. Journal of Plankton Research. 2001; 23(5):447–461.

Smith, RL. The physical processes of coastal ocean upwelling systems. In: Summerhayes, CP.; Emeis, K-C.; Angel, MV.; Smith, RL.; Zeitzschel, B., editors. Upwelling in the Ocean: Modern Processes and Ancient Records. John Wiley and Sons Ltd.; 1995. p. 39-64.

Sordo I, Barton ED, Cotos JM, Pazos Y. An inshore poleward current in the NW of the Iberian Peninsula detected from satellite images, and its relation with *G. catenatum* and *D. acuminata* blooms in the Galician Rias. Estuarine, Coastal and Shelf Science. 2001; 53:787–799.

Tauton-Clark, J. The formation, growth and decay of upwelling tongues in response to the mesoscale wind field during summer. In: Shannon, LV., editor. South African Ocean Colour and Upwelling Experiment. Sea Fisheries Research Institute; Cape Town: 1985. p. 47-61.

Tilstone GH, Figueiras FG, Fraga F. Upwelling–downwelling sequences in the generation of red tides in a coastal upwelling system. Marine Ecology Progress Series. 1994; 112:241–253.

Tilstone GH, Miguez BM, Figueiras FG, Fermin EG. Diatom dynamics in a coastal ecosystem affected by upwelling: coupling between species succession, circulation and biochemical processes. Marine Ecology Progress Series. 2000; 205:23–41.

Torres R, Barton ED. Onset of the Iberian upwelling along the Galician coast. Continental Shelf Research. 2007; 27:1759–1778.

Trainer VL, Hickey BM, Horner R. Biological and physical dynamics of domoic acid production off the Washington coast. Limnology and Oceanography. 2002; 47(5):1438–1446.

Trainer VL, Hickey BM, Lessard EJ, Cochlan WP, Trick CG, Wells ML, MacFadyen A, Moore SK. Variability of *Pseudo-nitzschia* and domoic acid in the Juan de Fuca eddy region and its adjacent shelves. Limnology and Oceanography. 2009; 54(1):289–308.

Trainer VL, Pitcher GC, Reguera B, Smayda TJ. The distribution and impacts of harmful algal bloom species in eastern boundary upwelling systems. Progress in Oceanography. in this issue. 10.1016/j.pocean.2010.02.003

Vander Woude AJ, Largier JL, Kudela RM. Nearshore retention of upwelled waters north and south of Point Reyes (northern California) – Patterns of surface temperature and chlorophyll observed in CoOp WEST. Deep-sea Research Part II. 2006; 53:2985–2998.

Visbeck MH, Hurrell JW, Polvani L, Cullen HM. The North Atlantic Oscillation: past, present, and future. Proceedings of the National Academy of Sciences. 2001; 98(23):12876–12877.

Wilkerson FP, Lassiter AM, Dugdale RC, Marchi A, Hogue VE. The phytoplankton bloom response to wind events and upwelled nutrients during the CoOP WEST study. Deep-sea Research Part II. 2006; 53:3023–3048.

Winant CD, Dever EP, Hendershott MC. Characteristic patterns of shelf circulation at the boundary between central and southern California. Journal of Geophysical Research. 2003; 108(C2):3021.10.1029/2001JC001302

Wing SR, Botsford LW, Ralston SV, Largier JL. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnology and Oceanography. 1998; 43(7):1710–1721.

Wooster WS, Bakun A, McLain DR. The seasonal upwelling cycle along the eastern boundary of the north Atlantic. Journal of Marine Research. 1976; 34:131–141.
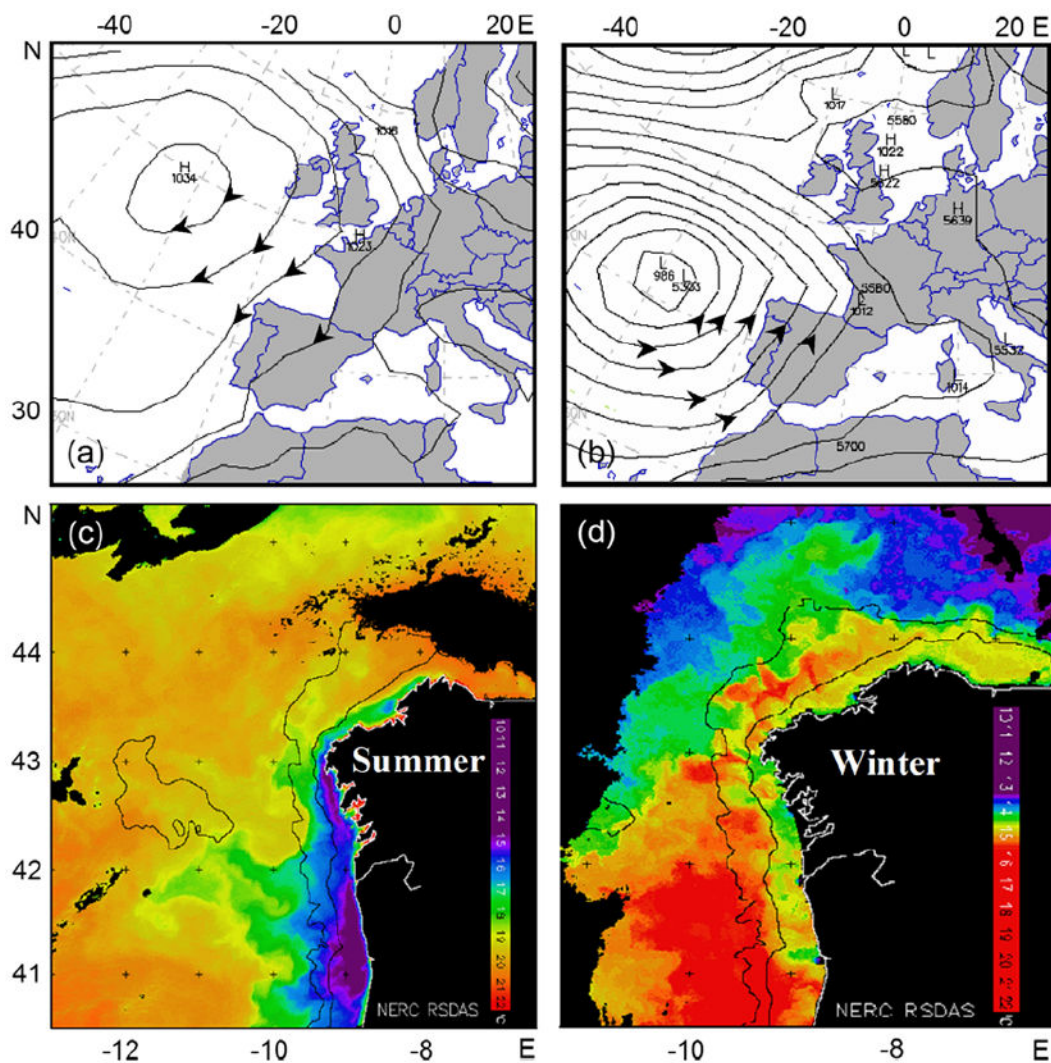
Fig. 1.
(a) and (b) Typical meteorological and (c) and (d) oceanographic conditions off the NW Iberian coast during summer and winter. Equatorward winds cause upwelling and filament development in summer. During winter southwesterly winds reinforce a surface poleward current. AVHRR images courtesy of the Remote Sensing Analysis Service, Plymouth Marine Laboratory.
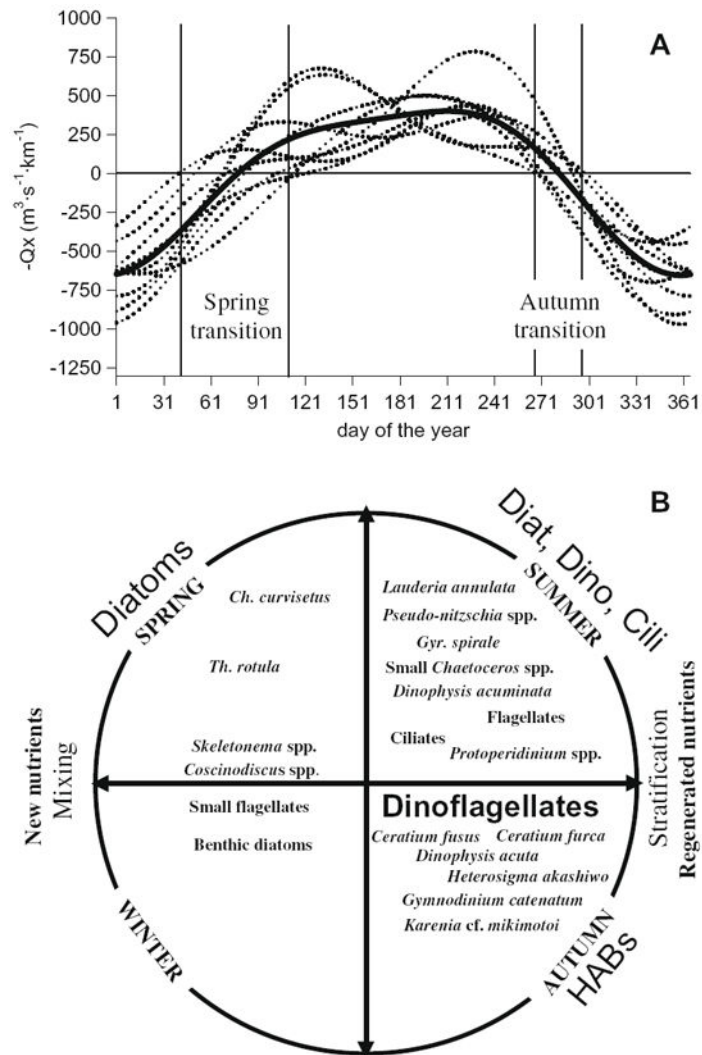
Fig. 2.
An upwelling index off Cape Finisterre for the period 1987–1995: (a) showing a strong seasonal cycle (solid line – average seasonal cycle; dotted line – average for each year) and (b) an annual cycle of phytoplankton abundance in the Rias Baixas as determined by a mixing-stratification (new vs. regenerated nutrients) gradient. Redrawn from Figueiras et al. (2002).
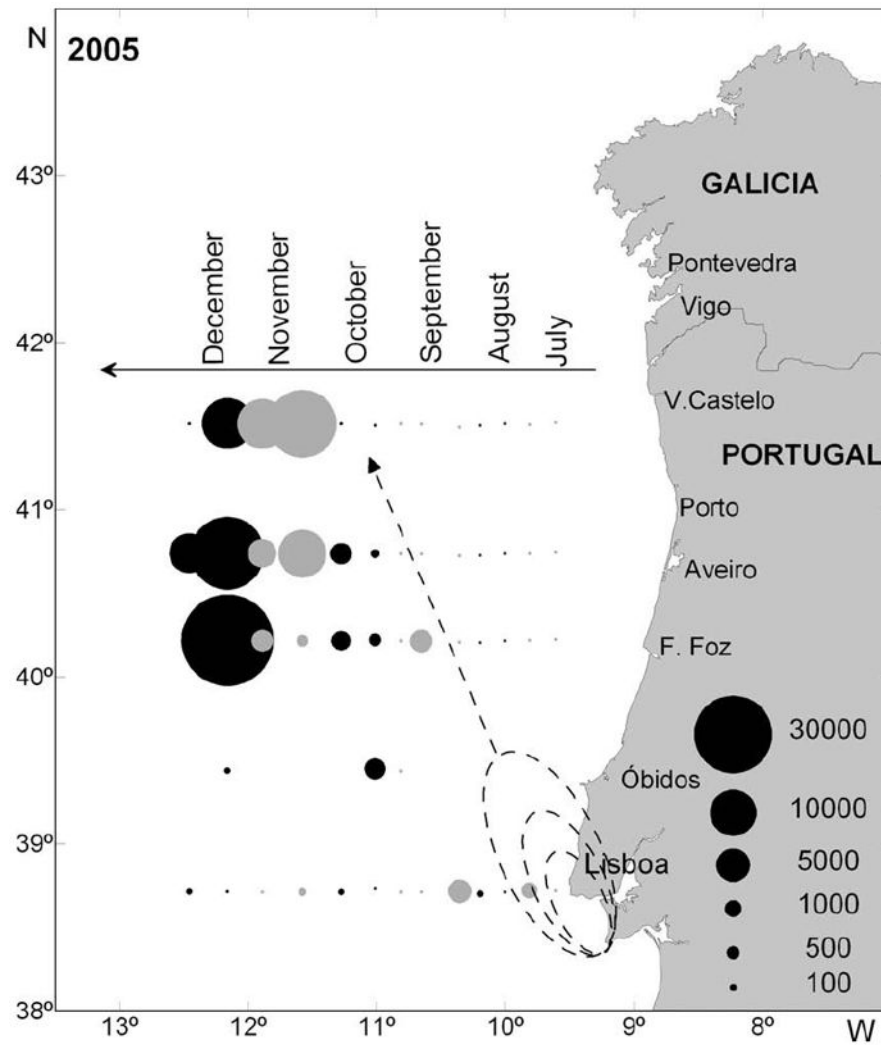
Fig. 3.
Fortnightly distributions of maximum *Gymnodinium catenatum* concentrations (cells l^{-1}) at monitoring stations on the northwest coast of Iberia during the summer and autumn of 2005, showing the poleward development and propagation of the bloom. Redrawn from Pazos et al. (2006).
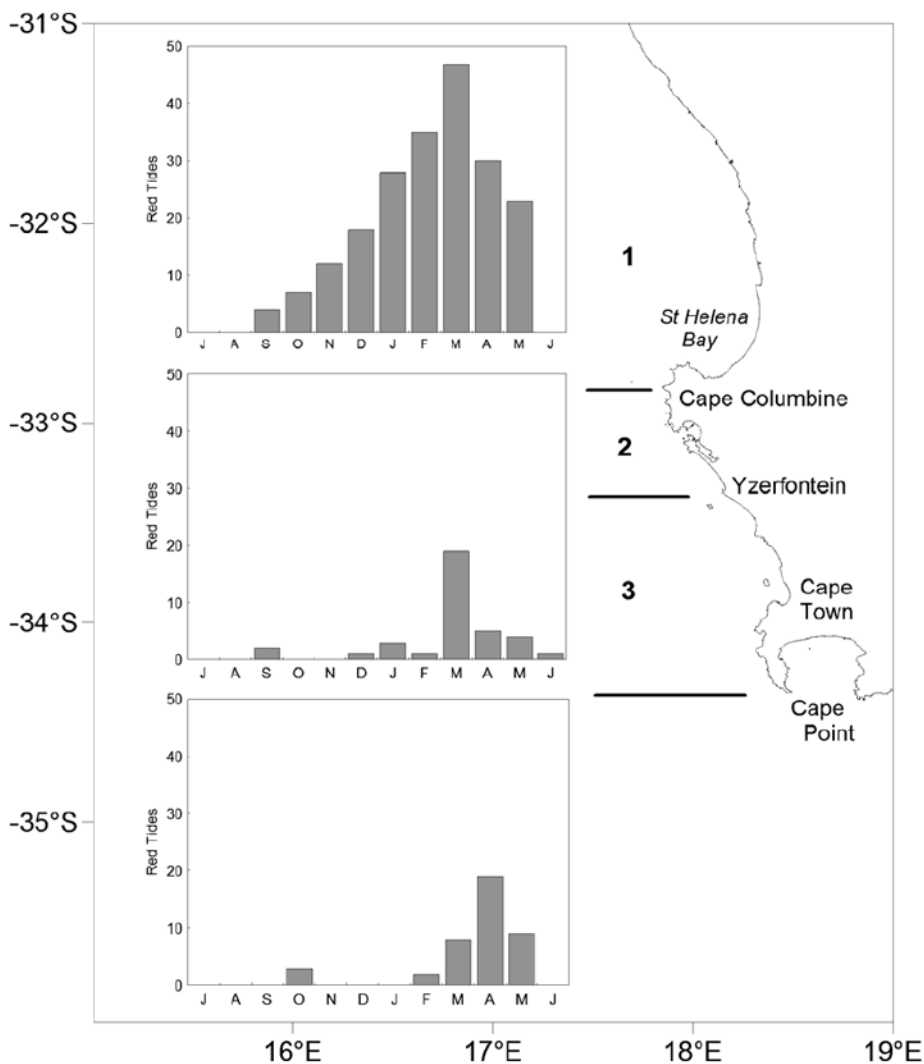
Fig. 4.
Seasonal incidence of dinoflagellate-dominated red tides for three sectors of the west coast of the southern Benguela. Blooms are first observed north of Cape Columbine, in the strongly stratified waters of the St. Helena Bay region. These blooms are later advected southward by poleward currents that manifest during the latter half of the upwelling season. Adapted from Pitcher and Calder (2000).
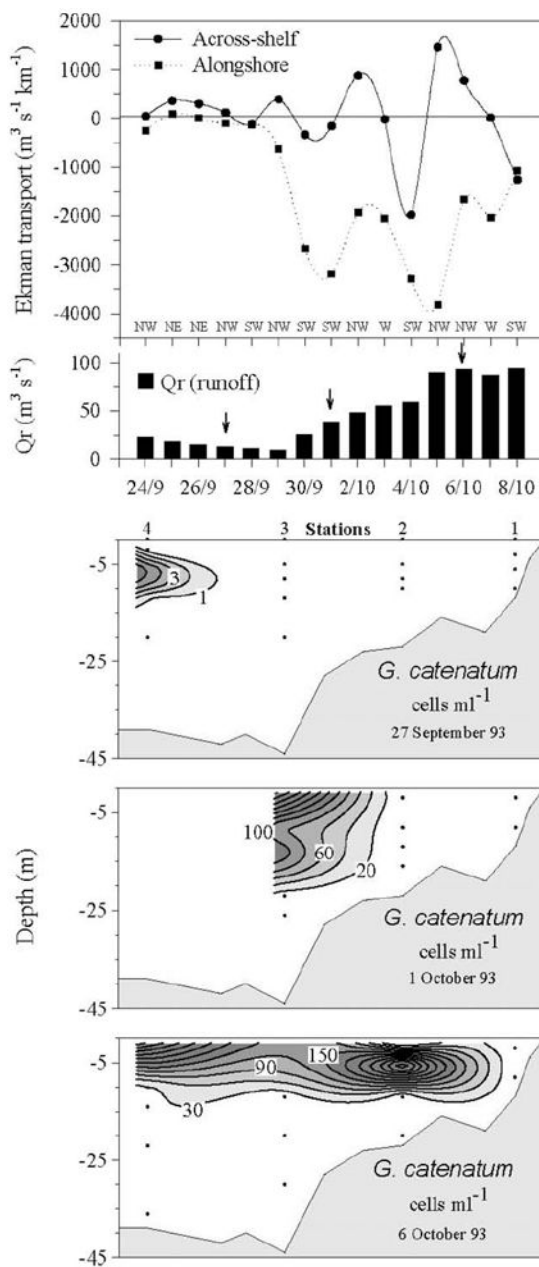
Fig. 5.
Wind depicted as components of Ekman transport, and runoff in the Ria de Vigo from 24 September to 8 October 1993. The distribution of *Gymnodinium catenatum* within the ria is shown as sampled on 27 September, and 1 and 6 October 1993. Adapted from Fermin et al. (1996).
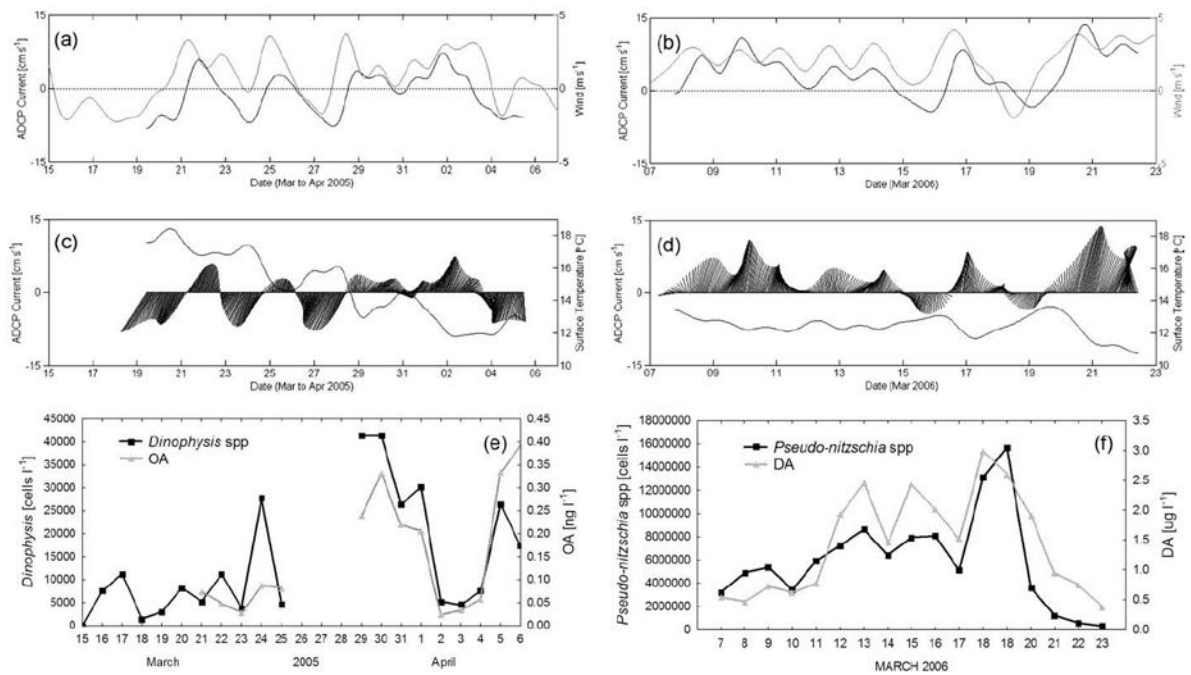
Fig. 6.
A time-series off Lambert's Bay on the southern Namaqua shelf of alongshore currents (black line) and winds (grey line) for (a) 15 March–6 April 2005 and (b) 7–22 March 2006, surface current vectors and surface temperature for (c) 15 March–6 April 2005 and (d) 7–22 March 2006, and (e) *Dinophysis* spp. cell counts and okadaic acid concentrations for 15 March–6 April 2005, and (f) *Pseudo-nitzschia* cell counts and domoic acid concentrations for 7–23 March 2006. From Fawcett et al. (2007).

a $y = 203(\pm30)-7(\pm1)*(x-1960)$
$R = -0.75, n = 35, p < 0.001$

b $y = 365*[1-\exp(-x/37(\pm2))]$
$R^2 = 0.79, n = 42, p < 0.001$
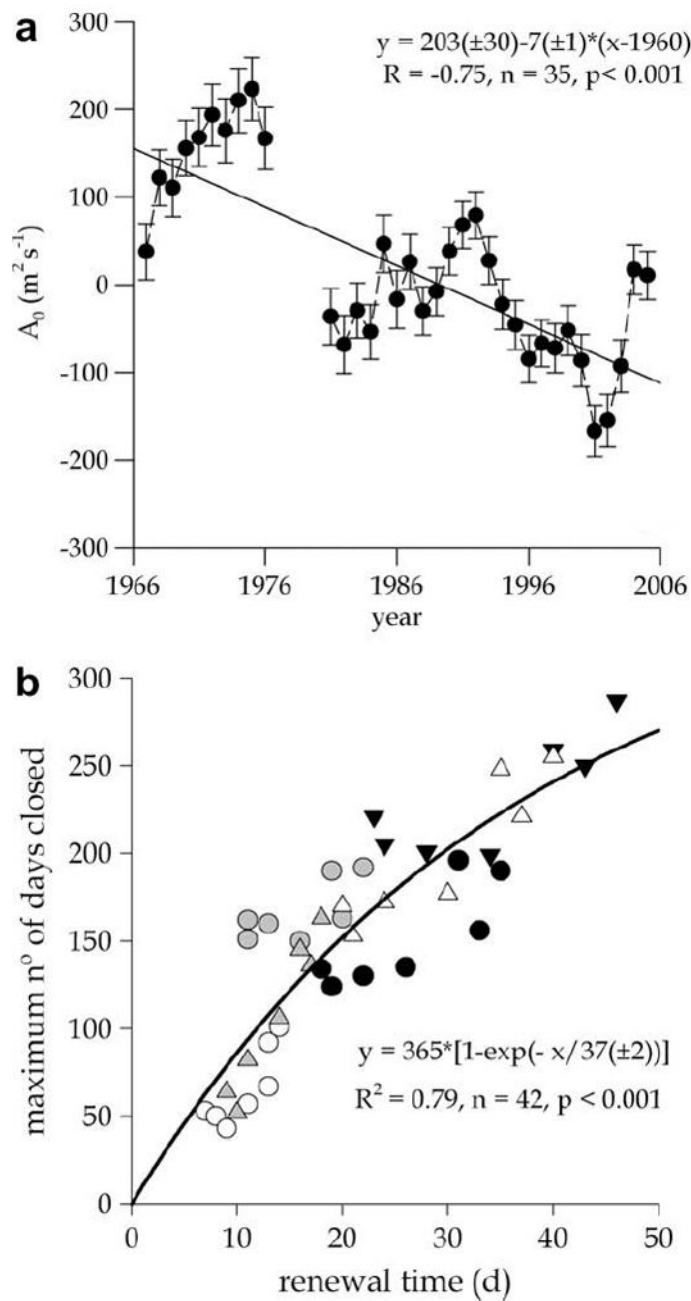
Fig. 7.
(a) A 40-year time-series of offshore Ekman transport, $-Q_X$ (where A_0 is the annual average $-Q_X$) on the Iberian coast and (b) the number of days per year for which a given mussel cultivation area in the Rías Baixas is closed to harvesting in relation to the renewal time for each of the six study areas (as represented by different symbols). Modified from Alvarez-Salgado et al. (2008).
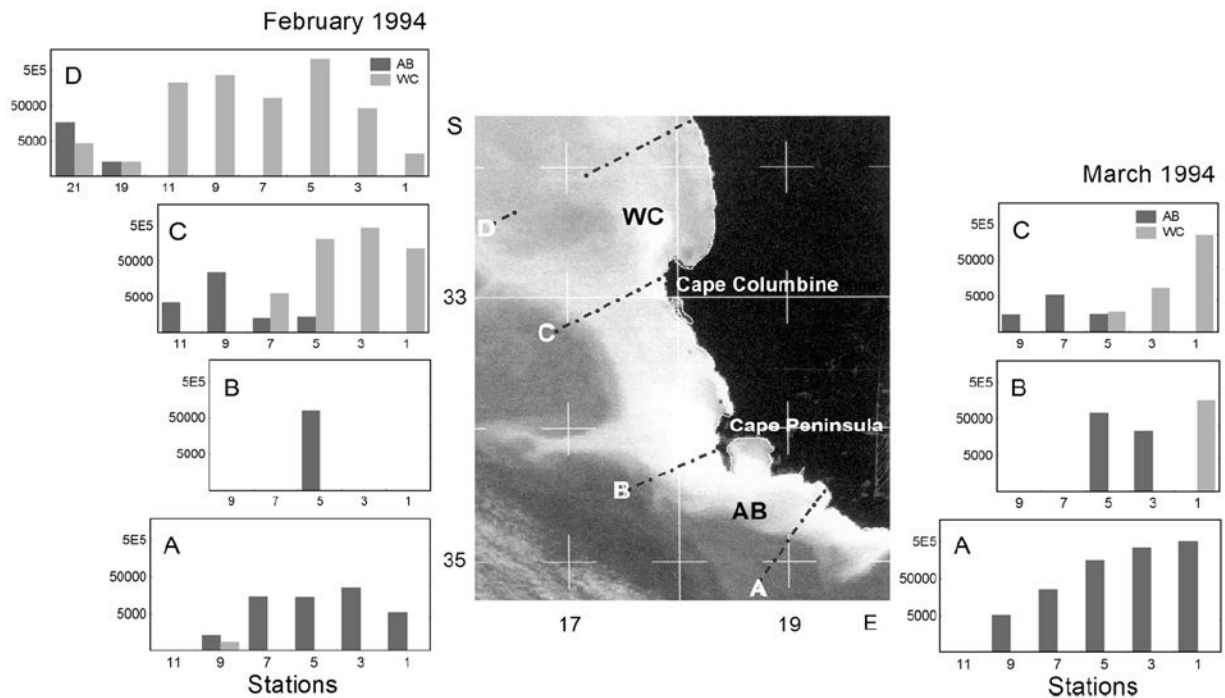
Fig. 8.
Transects of the southern Benguela upwelling system during February and March 1994
depicting surface dinoflagellate distributions in relation to large-scale circulation patterns.
Transect positions and sea surface temperature determined from infrared satellite imagery on
22 February 1994 (central panel), and across-shelf dinoflagellate distributions as determined
from 16 to 20 February 1994 (left panels), and from 15 to 18 March 1994 (right panels),
show two clearly separate populations, namely an Agulhas Bank and a West Coast
population. Adapted from Pitcher and Boyd (1996).
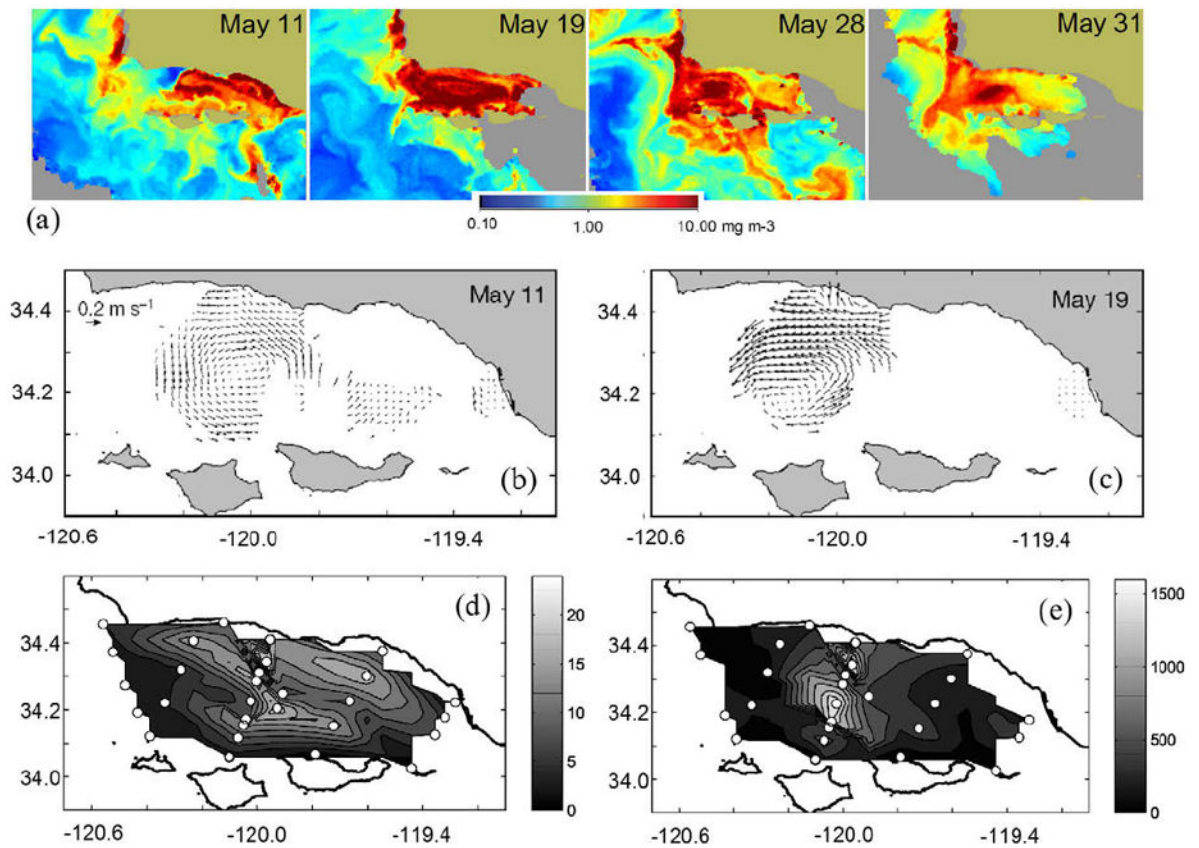
Fig. 9.
Santa Barbara Channel time series of: (a) SeaWiFs images of chlorophyll concentration, 24 h means of surface current vectors from HF radar on (b) 11 May and (c) 19 May, and channel-wide measurements of (d) *Pseudo-nitzschia australis* cell abundance, and (e) particulate domoic acid in May 2003. Adapted from Anderson et al. (2006).
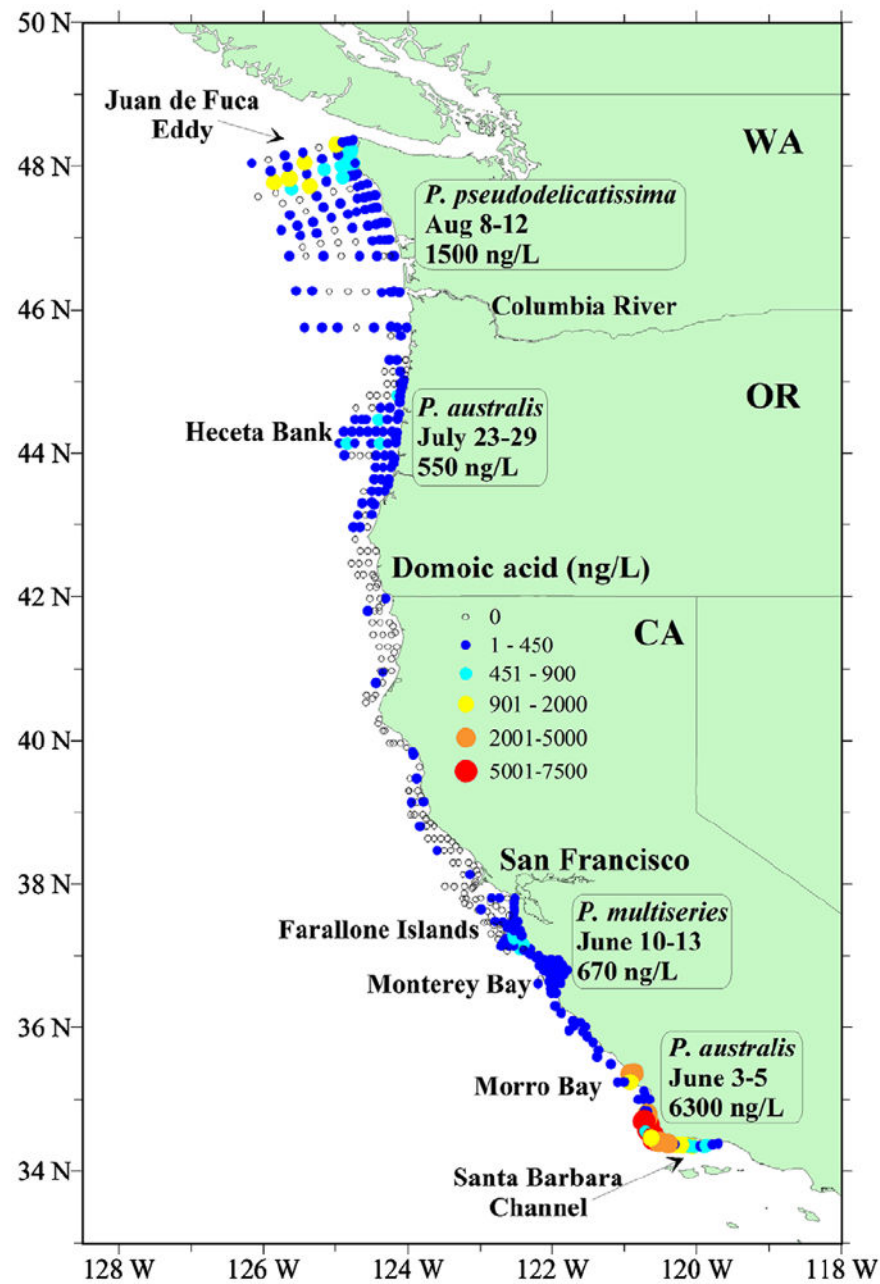
Fig. 10.
Particulate domoic acid in *Pseudo-nitzschia* species on the US Pacific West Coast in 1998.
Maximum concentrations of domoic acid and the identity of the toxic species are indicated
for each area of high toxin. Each of these areas is associated with some form of retentive
circulation patterns. From Hickey and Banas (2003).
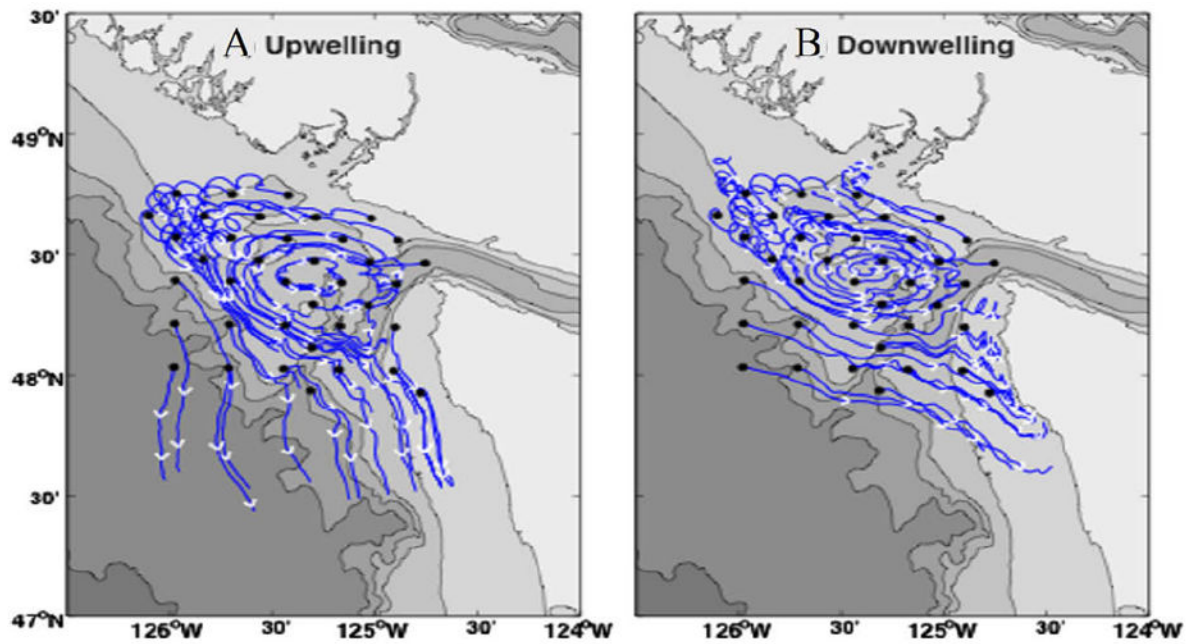
Fig. 11.
Modelled circulation as depicted by surface drifters in the vicinity of the Juan de Fuca eddy, a known source of toxic *Pseudo-nitzschia* blooms. (a) Upwelling winds allow particles to escape the eddy and to subsequently move equatorward along the coast, whereas (b) onshore movement in the surface frictional layer during downwelling-favourable wind conditions moves surface particles, and, potentially, toxic *Pseudo-nitzschia* to the coast. From MacFadyen et al. (2005).
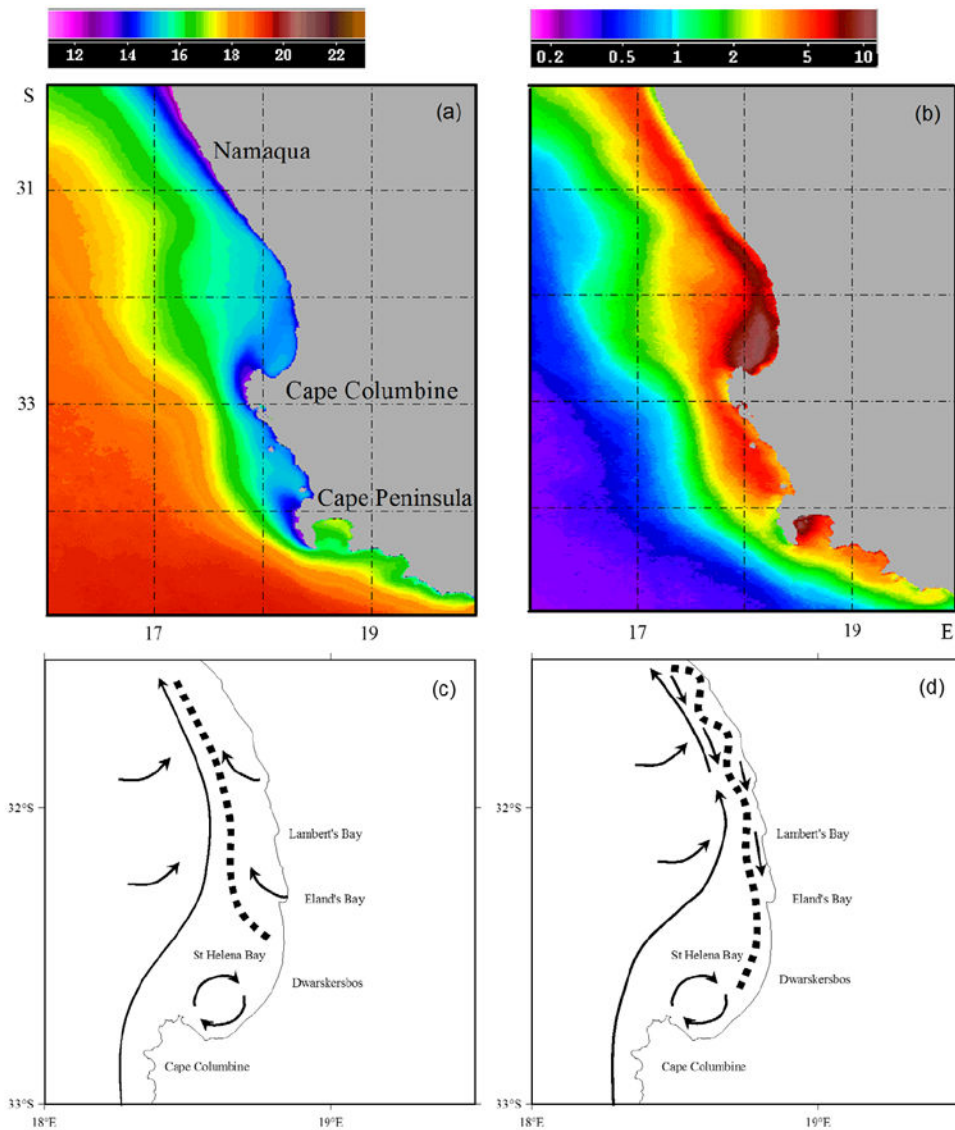
Fig. 12.
A 5-year (July 1998–June 2003) composite of (a) SST, and (b) chlorophyll, derived from daily high resolution (1 km) NOAA AVHRR and SeaWiFS ocean colour data. Upwelling processes are influenced to a large degree by shelf bathymetry and local topography resulting in the Cape Peninsula, Cape Columbine and Namaqua upwelling cells. Harmful bloom events in the greater St. Helena Bay region are conceptualized during periods of (c) upwelling (d) and relaxation or downwelling. The broken line demarcates the area of highest dinoflagellate abundance. From Pitcher and Nelson (2006) and from Pitcher and Weeks (2006).
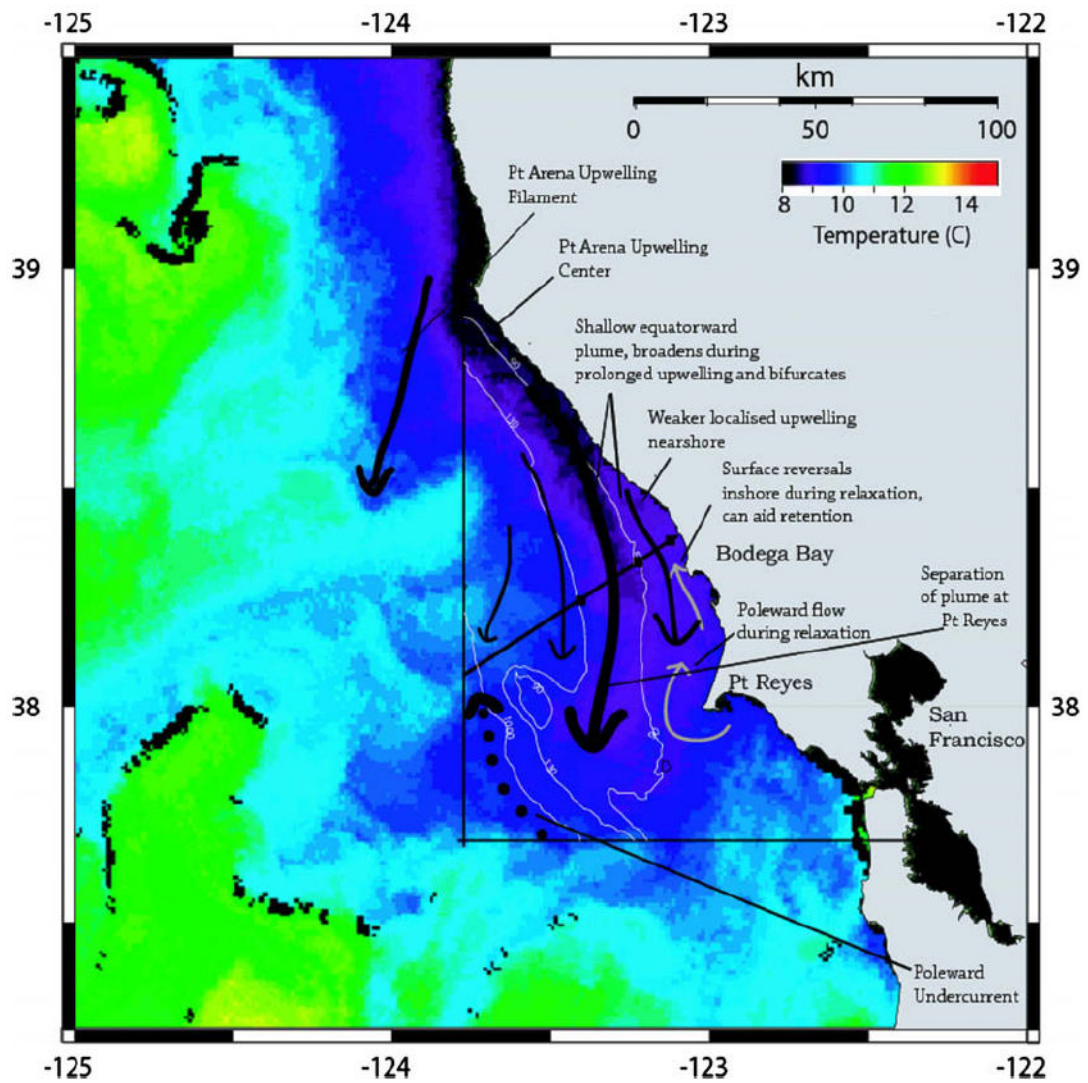
Fig. 13.
Schematic diagram of the velocity field during the upwelling season overlaid on a satellite image of SST from 8 June 2002 from the NOAA-15 AVHRR sensor. The arrows show the zonation across the shelf, the alongshore advection of the plume and the retention over the inner shelf (during relaxation). The thin white lines show the bathymetry within the study site. From Roughan et al. (2006).
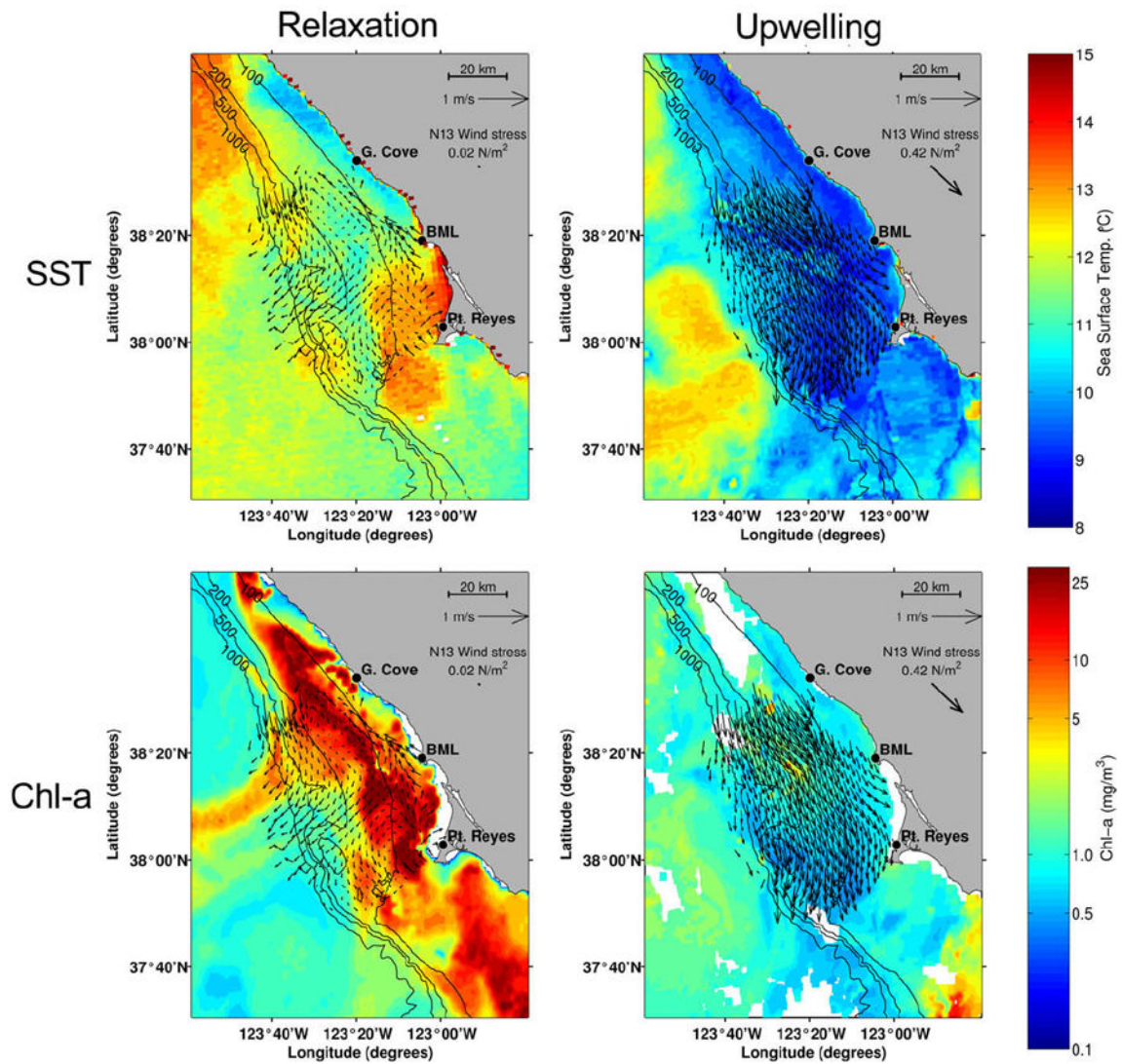
Fig. 14.

Maps of surface current (HF radar) overlaid on satellite-derived SST (upper panels) and chlorophyll (lower panels) patterns in June 2003. Left panels: typical relaxation conditions are represented by HF radar data from 10 June 2003 and satellite data from 2 to 3 days later, showing the transport effect of observed flow on these tracer distributions (SST composite from 12 to 13 June; chlorophyll composite for 11–14 June). Right panels: typical upwelling conditions are represented by HF radar data from 17 June 2003 and satellite data from 2 to 3 days later, showing the transport effect of observed flow on these tracer distributions (SST and chlorophyll composites for 19–20 June). From Largier et al. (2006).
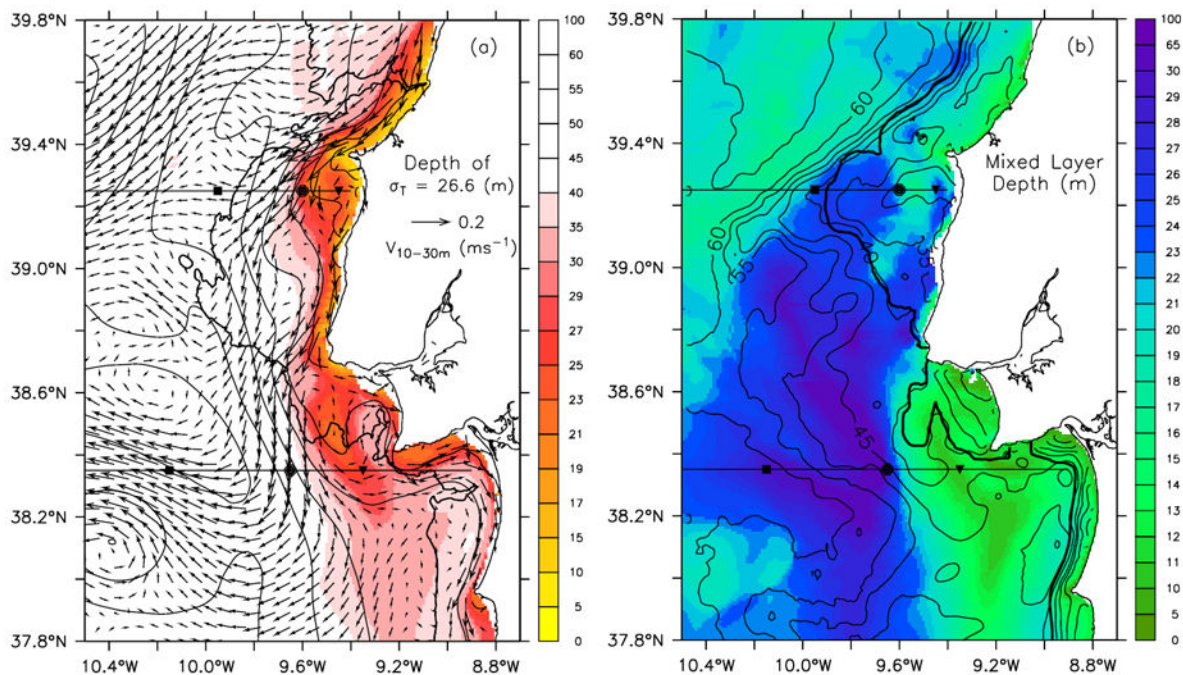
Fig. 15.
Model solutions for (a) the topography of the $\sigma_T = 26.6$ isopycnal and (b) the mixed layer depth, drawn from 8-day (30 June–7 July 2005) averaged fields. Vectors in (a) represent the 8-day average velocity of the 10–30 m layer. Contours in (a) represent the average surface elevation (1 cm interval) and the 200 m isobath (thick contour); and in (b) the euphotic-zone depth (m) and area with average chlorophyll > 1 mg m^{-3} (thick contour). From Oliveira et al. (2009).
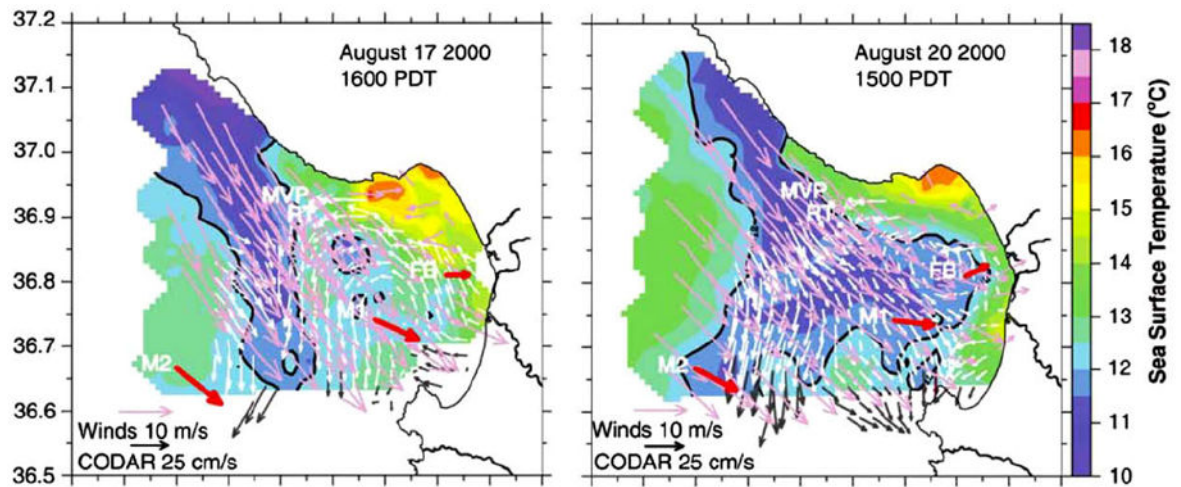
Fig. 16.
Aircraft and mooring data from 17 and 20 August 2000 during an upwelling-favourable windstress event. Aircraft winds at 100 m (magenta vectors) and CODAR surface currents (white vectors) are overlaid on SST. The surface winds from the MBARI M-buoys are included as red vectors for comparison. A distinct upwelling plume extends south–southeastward off Point Ano Nuevo. A coherent southward jet held these cold waters offshore on 17 August but broke down sometime between 17 and 20 August allowing the advection of cold water from the north into the centre of the bay. The SST maps clearly show the warm patch of water in the northernmost corner of the bay as a result of a wind shadow in this region. From Ramp et al. (2005).
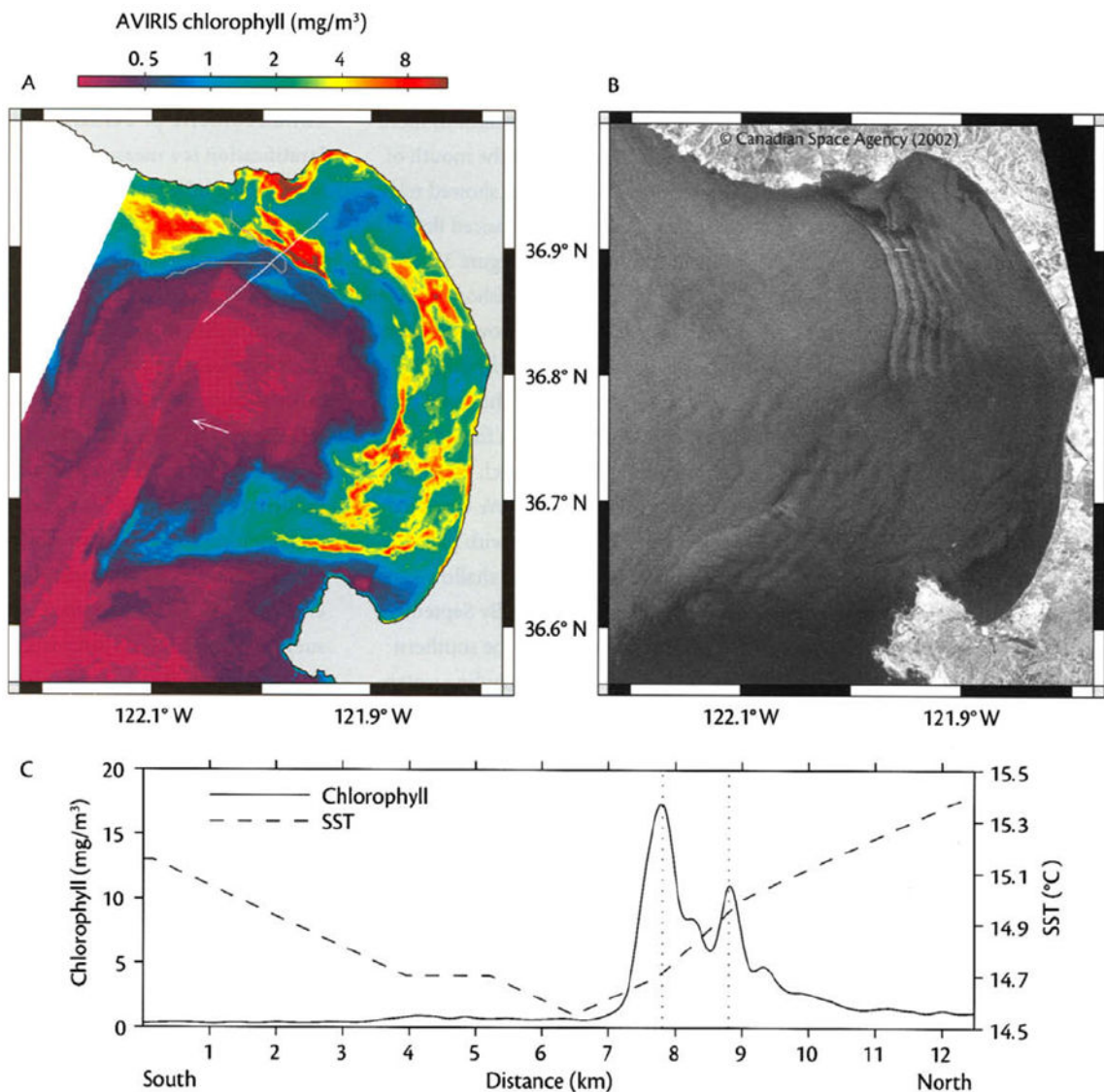
Fig. 17.

High resolution remote sensing combined with *in situ* observations describe the physical processes important in development of a bloom of *Ceratium furca* and *Ceratium dens* in Monterey Bay on 7 October 2002. Clockwise wrapping of red tide was apparent around a low-chlorophyll anticyclonic meander. Bloom patchiness was detailed by (a) the high-resolution view of AVIRIS. The concentration of dinoflagellates in convergence zones was indicated at multiple scales, in association with the confluence of water masses along the bloom periphery, and in wave like aggregations having the scale of internal waves that propagate through the bloom. The internal wave signature of parallel dark-light bands was pronounced in the northern bay as evident in (b) synthetic aperture radar (SAR) imagery. The scale of 1 km was evident across the wave fronts (white scale bar in b) and in a transect of AVIRIS chlorophyll concentrations across a path influenced by the internal wave. The transect location is shown in (a), and chlorophyll concentrations are shown relative to AVHRR SST in (c); the vertical dotted lines in (c) are 1 km apart. From Ryan et al. (2005b).
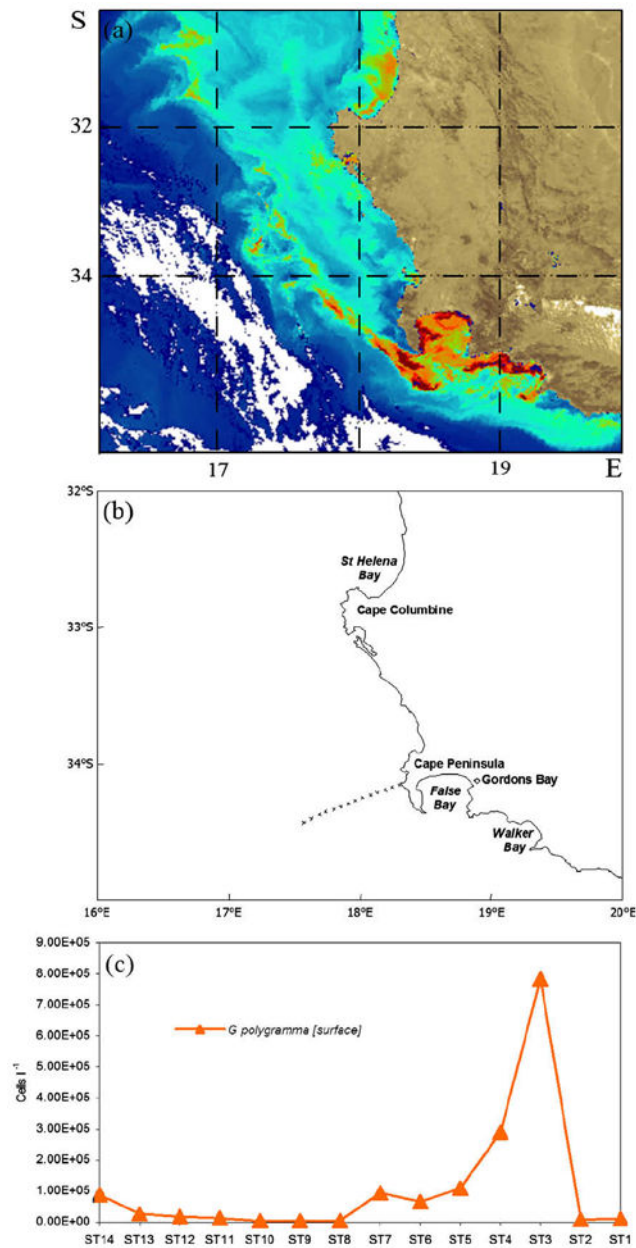
Fig. 18.
A satellite image of (a) chlorophyll *a* from the MERIS sensor showing the presence of a bloom of *Gonyaulax polygramma* in False Bay and Walker Bay on 13 March 2007. Its export from the bay through entrainment into the Benguela jet current off the Cape Peninsula is evident, and confirmed through sampling of (b) a transect off the Cape Peninsula on 26 February 2007, and (c) depiction of surface cell concentrations of *G. polygramma* along the transect. Adapted from Pitcher et al. (2008).
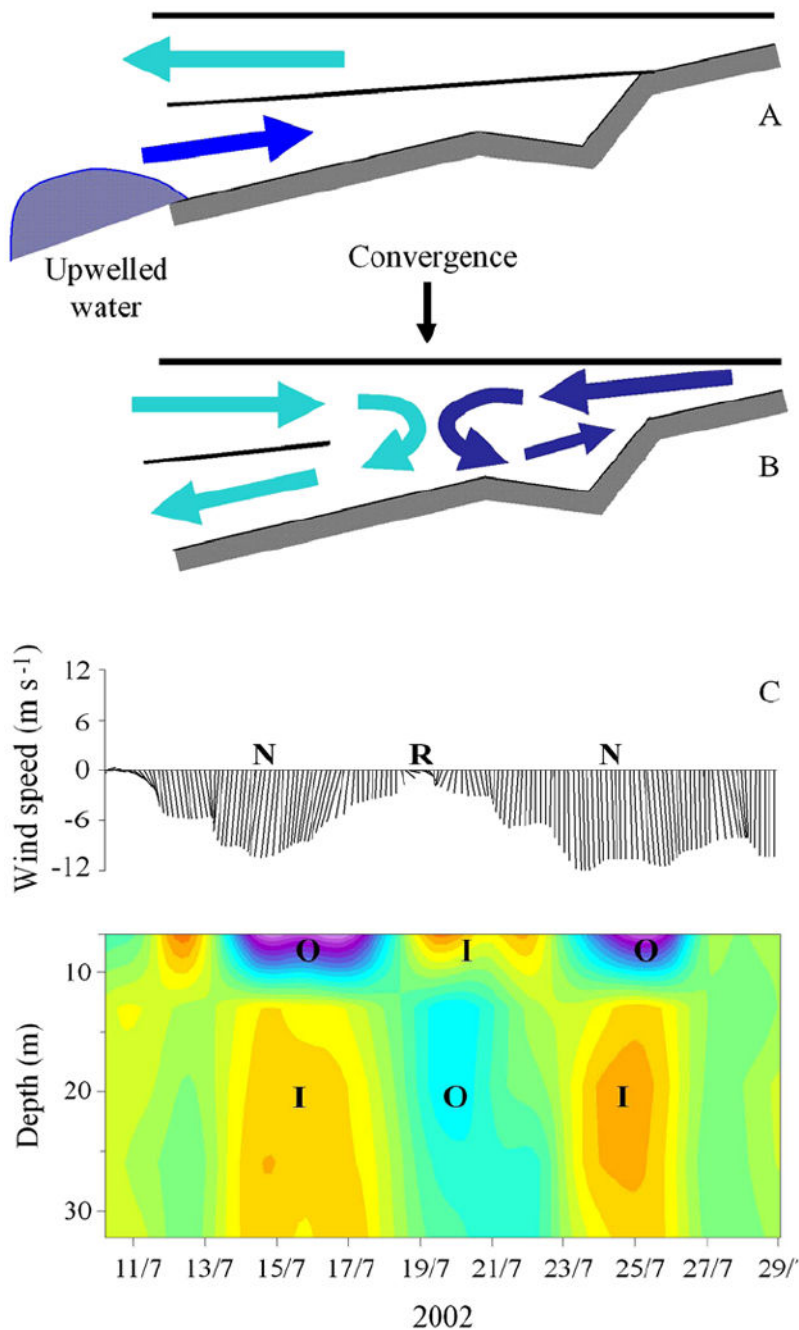
Fig. 19.
A schematic representation of circulation within the Rias Baixas of Galicia during (a) upwelling, and (b) downwelling, and (c) circulation in the Ría de Vigo over a 2-week period in July 2002. N and R represent periods of northerly winds and wind relaxation respectively; and O and I represent water outflow and inflow respectively. Adapted from Crespo et al. (2006) and Piedracoba et al. (2005).
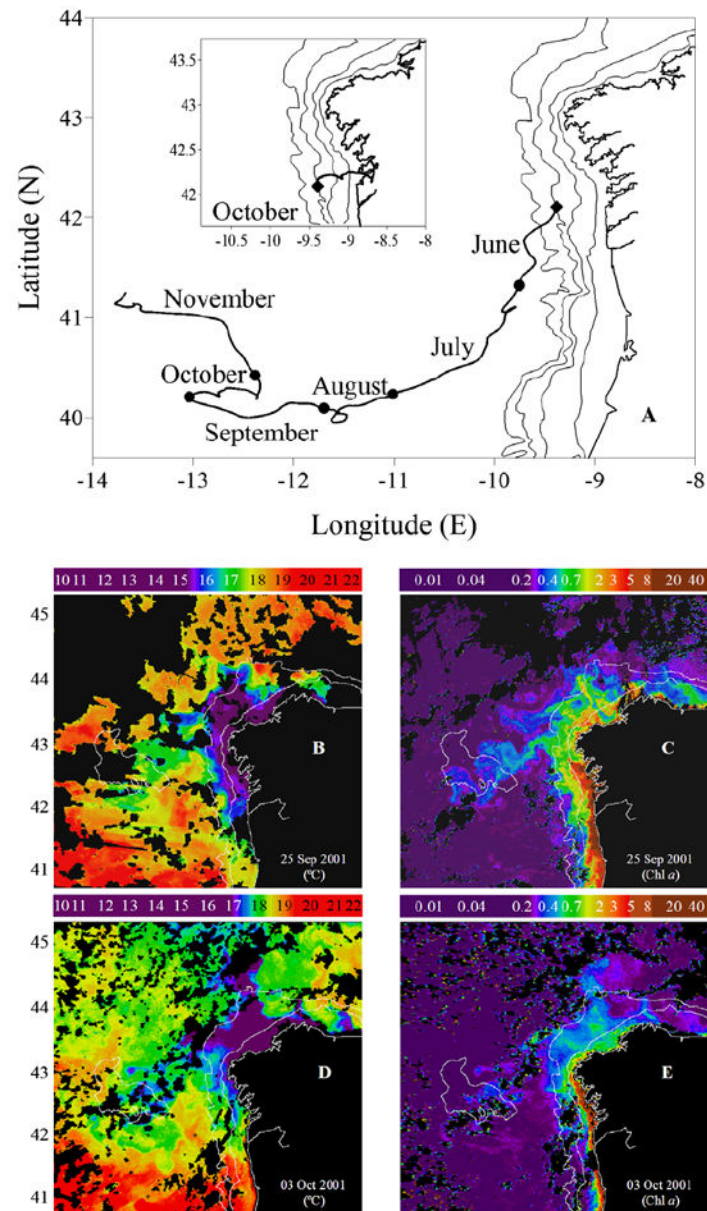
Fig. 20.
Progressive vector diagram of (a) the surface currents recorded on the NW Iberian shelf from June to November 2001. The inset in (a) depicts the currents associated with downwelling in October showing the possible advection of shelf waters into the interior of the Rías. Satellite images correspond to the seasonal upwelling–downwelling transition that took place during the week 25 September–3 October 2001. AVHRR SST images were collected on (b) 25 September 2001 and (d) 3 October 2001 and chlorophyll images derived from SeaWiFS on (c) 25 September 2001 and (e) 3 October 2001. The chlorophyll-rich waters occupying the entire shelf during upwelling (c) were confined to a narrow band (e) following the transition to downwelling. Adapted from Crespo et al. (2007).
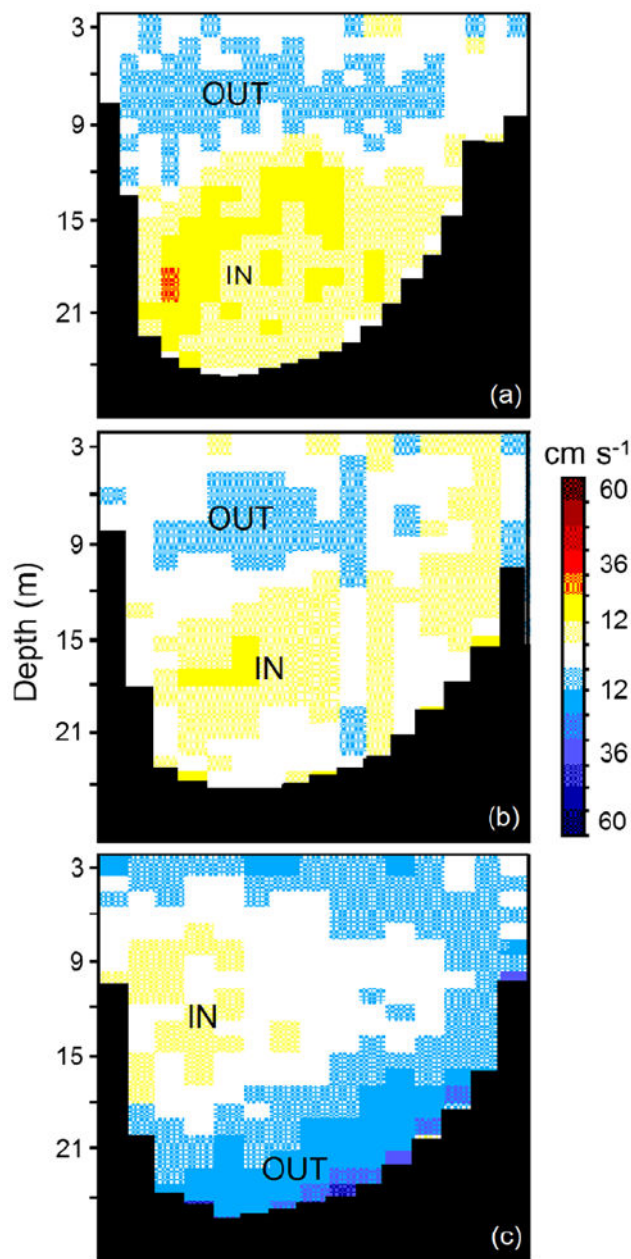
Fig. 21.
ADCP sections across the mouth of Saldanha Bay during an incoming or slack phase of the tidal cycle showing the two-layered flow on (a) 1 March, (b) 2 March and (c) 3 March 1997. Sections show north to south underway ADCP measurements along the same transect. A clear reversal in current direction is evident from 1 to 3 March, indicating the transition between upwelling and relaxation conditions. Modified from Probyn et al. (2000).
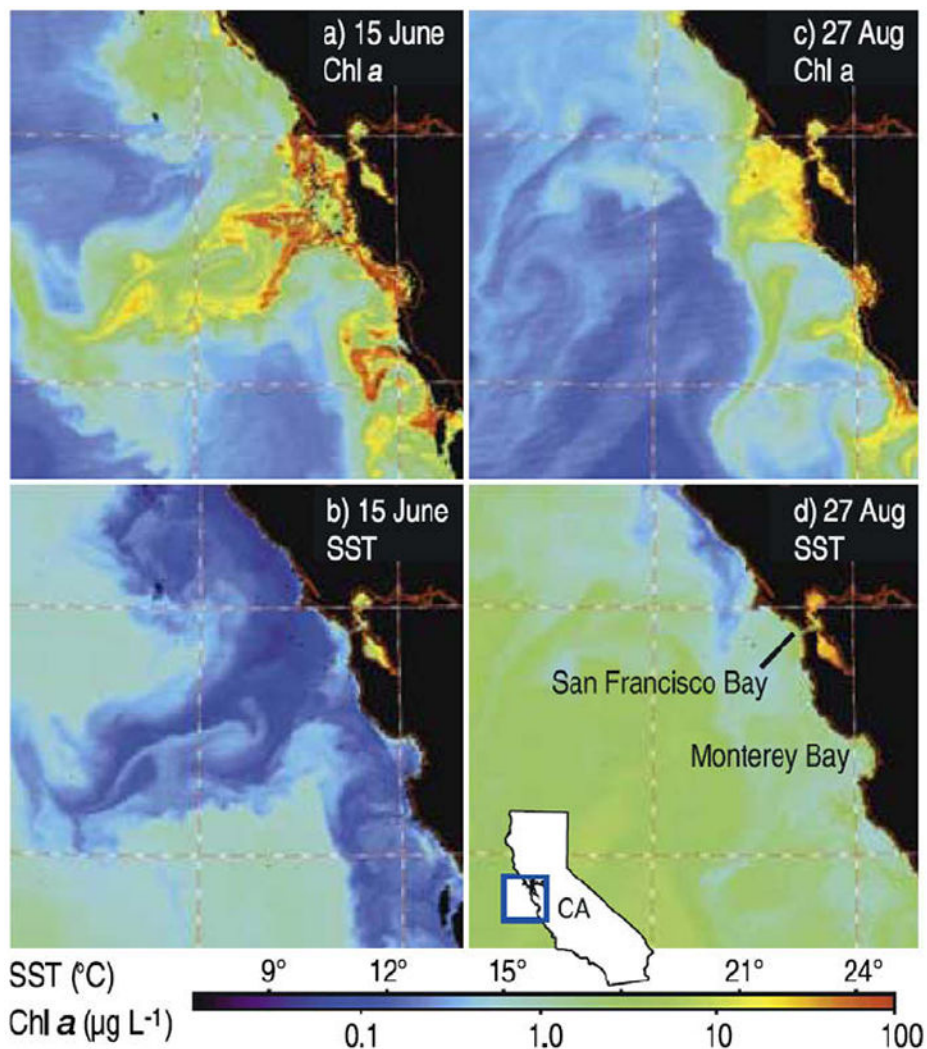
Fig. 22.
MODIS chlorophyll a (top) and surface temperature (bottom) images from 15 June (strong upwelling, left panel) and 27 August 2004 (weak upwelling, right panel). The typical summer upwelling state in June of (a) chlorophyll-rich water within filaments and (b) low nearshore surface temperature, is in contrast to the (c) high phytoplankton biomass caused by a bloom of *Akashiwo sanguinea* in the nearshore coastal zone, in association with (d) high surface temperature during late August. From Cloern et al. (2005).