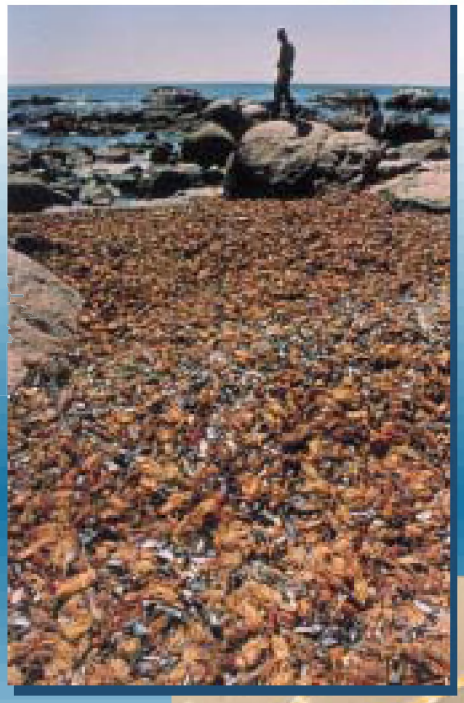
GEOHAB

Global Ecology and Oceanography of Harmful Algal Blooms



GEOHAB CORE RESEARCH PROJECT: HABs IN UPWELLING SYSTEMS

SCOR

SCIENTIFIC COMMITTEE ON OCEANIC RESEARCH

INTERGOVERNMENTAL OCEANOGRAPHIC COMMISSION
UNESCO

GEOHAB

GLOBAL ECOLOGY AND OCEANOGRAPHY OF HARMFUL ALGAL BLOOMS

GEOHAB CORE RESEARCH PROJECT: HABS IN UPWELLING SYSTEMS

AN INTERNATIONAL PROGRAMME SPONSORED BY THE
SCIENTIFIC COMMITTEE ON OCEANIC RESEARCH (SCOR) AND THE
INTERGOVERNMENTAL OCEANOGRAPHIC COMMISSION (IOC) OF UNESCO

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BASED ON CONTRIBUTIONS BY PARTICIPANTS OF THE GEOHAB OPEN SCIENCE MEETING ON HABS IN UPWELLING SYSTEMS AND THE GEOHAB SCIENTIFIC STEERING COMMITTEE

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EXECUTIVE SUMMARY

The Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) programme was initiated in 1999 by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO to develop a research program on the ecological and oceanographic mechanisms underlying the population dynamics of harmful algal blooms (HABs). The end goal of this research is to allow the development of observation systems and models that will enable prediction of HABs, thereby reducing their impacts on the health of humans and marine organisms, as well as their economic and social impacts on society.

The GEOHAB *Implementation Plan* (GEOHAB, 2003) specifies the formation of Core Research Projects (CRPs) related to four ecosystem types—upwelling systems, fjords and coastal embayments, eutrophic systems, and stratified systems. These CRPs are to be initiated through small, focused open science meetings. The first of these open science meetings focused on HABs in upwelling systems and resulted in this plan. The meeting served to identify interested participants and research regions and to bring together the international community to design core research. Meeting participants discussed a wide variety of research topics related to HABs in upwelling systems, which the meeting planning committee distilled into 8 key questions:

A. Are there definable adaptive strategies that characterize HAB species in upwelling systems?

B. What seeding strategies persist within upwelling regions and are they consistent among regions?

C. How do small-scale physical processes affect HAB growth and dispersion in upwelling systems?

D. How do nutrient supply type and ratios determine HAB population dynamics in upwelling systems?

E. What is the role of genetic predisposition versus environmental conditions in toxin production in different upwelling systems within a given genus or species?

F. How does coastal morphology and bathymetry affect HAB dynamics in upwelling systems?

G. What is the relative importance of cross-shelf and along-shore advection in different upwelling systems for HABs?

H. Are climate indicators predictive of HAB events in upwelling systems?

Our understanding of and ability to predict HABs in upwelling systems over the next 5-10 years will reflect the extent to which the GEOHAB CRP can answer these questions.

LIST OF ACRONYMS

ASP	amnesic shellfish poisoning
AVHRR	Advanced Very High Resolution Radiometer
CalCOFI	California Cooperative Oceanic Fisheries Investigations
CCS	California Current System
CLIVAR	Climate Variability and Prediction project
CRP	Core Research Project
DA	domoic acid
DAP	domoic acid poisoning
DIN	dissolved inorganic nitrogen
DSP	diarrhetic shellfish poisoning
EBC	eastern boundary current
ENSO	El Niño-Southern Oscillation
GEOHAB	Global Ecology and Oceanography of Harmful Algal Blooms programme
GLOBEC	Global Ocean Ecosystem Dynamics project
HAB	harmful algal bloom
HNLC	high-nutrient, low chlorophyll
ICES	International Council for Exploration of the Seas
IMAGES	International Marine Aspects of Global Change project
IMBER	Integrated Marine Biogeochemistry and Ecosystem Research project
IOC	Intergovernmental Oceanographic Commission
IPO	International Programme Office
NAO	North Atlantic Oscillation
ORHAB	Olympic Region Harmful Algal Bloom project
PDO	Pacific Decadal Oscillation
PICES	Pacific Marine Sciences Organization
PSP	paralytic shellfish poisoning
RFLP	restriction fragment length polymorphism
SCOR	Scientific Committee on Oceanic Research
SSC	scientific steering committee
SST	sea surface temperature
UNESCO	United Nations Environmental, Scientific, and Cultural Organization

I - INTRODUCTION

The GEOHAB *Science Plan* (2001) and *Implementation Plan* (2003) provide the background and justification for the GEOHAB programme. The purpose of this document is to follow-on from the *Implementation Plan* to describe in greater detail the research that will be conducted for the GEOHAB Core Research Project (CRP) – HABs in Upwelling Systems. This document also serves as an invitation to individuals who could not participate in the Upwelling Open Science Meeting, including scientists from regions on which the plan focuses as well as other regions, to join in the activity.

This plan was developed by a committee co-chaired by Grant Pitcher (South Africa) and Teresa Moita (Portugal). Other members of the committee included Francisco Figueiras (Spain), Raphael Kudela (USA), Trevor Probyn (South Africa), and Vera Trainer (USA). This committee used as its primary source of information for this document an Open Science Meeting that was held in Lisbon, Portugal on 17-20 November 2003 (see program in Appendix I). The planning committee thanks the individuals who participated in the Open Science Meeting (see Appendix II) and helped develop the ideas contained herein. The committee also thanks the organizations that contributed financially to the meeting, specifically the U.S. National Science Foundation (through grants to SCOR), the Intergovernmental Oceanographic Commission, the Luso-American Foundation, and the Instituto Nacional de Investigação Agrária e das Pescas (INIAP-IPIMAR).

This plan will provide a guide for the Core Research Project – HABs in Upwelling Systems over time. It will serve as a nucleus for continued planning and will be augmented as research is funded, results are obtained, and new questions are formulated. The initial phase of this project is planned to last for five years, after which its progress and direction will be evaluated.

II - THE GEOHAB APPROACH TO THE STUDY OF HARMFUL ALGAE IN UPWELLING SYSTEMS

GEOHAB Core Research Projects will address the goals of the GEOHAB *Science Plan* (2001). The CRP – HABs in Upwelling Systems will identify key HAB species in these systems and determine the ecological and oceanographic processes that influence their population and community dynamics. The physical, chemical and biological processes that define or characterise upwelling systems will be identified and the response of HAB species to these processes will be quantified. The prediction of HABs will be improved by integrating biological, chemical and physical studies supported by enhanced observation and modelling systems. Models of HABs in upwelling systems will support fundamental research and prototype early warning and predictive capabilities. The applicability of regional prediction models for other upwelling systems may also be tested and the use of observation technologies will provide a useful comparison of predictions with observations.

In accordance with the GEOHAB strategy the approach of the CRP will be *comparative* from the cellular to the ecosystem level. Research that is *interdisciplinary*, focusing on the important interactions between biological, chemical, and physical processes will be fostered. Research will also be *multifaceted* as the problems relating to HABs in upwelling systems are complex and interactions and processes occur on a broad range of scales. Finally, research will be *international* in scope to encompass the global issues of HAB events and benefit from the skill and experience gained by HAB investigators world-wide.

The CRP – HABs in Upwelling Systems is built on the premise that understanding the ecology and oceanography of HABs in upwelling systems will benefit from a comparative approach, which is the method of choice when controlled experimentation is not practical. To the extent that experimental control in the study of marine ecosystems is problematic, comparison presents a potentially powerful alternative for drawing scientific inference. The comparative method assembles the separate realizations needed for scientific inference by the process of recognition of informative patterns of naturally occurring temporal and spatial variations in existing conditions and phenomena. Comparisons with respect to HABs will incorporate the grouping of species from upwelling systems. Assessment of the extent to which these HAB species respond in a similar way within these systems will allow the oceanographic processes that influence HAB population dynamics and community interactions to be established. Equally important will be identification of upwelling systems that have dissimilar HAB species or groupings. In addition, understanding the response of harmful algae to perturbations within upwelling systems will assist in prediction; identification of divergences from predicted responses will also be informative.

III - AN OVERVIEW OF HABS IN DESIGNATED UPWELLING SYSTEMS

A. General Description of Upwelling Systems

Upwelling systems can be defined according to their physical, chemical and biological characteristics. Along the west coasts of the Americas, the continental shelves of northwest and southwest Africa, and the western edge of the Iberian Peninsula, the winds blow alongshore toward the equator during part of each year. The Ekman transport in the surface boundary layer is directed offshore, and the existence of the coastal boundary imposes a divergence in the surface layer, resulting in upwelling into the surface layer near the coast. The measured cross-shelf transport in the surface boundary layer is in quantitative agreement with that predicted from the wind stress. The boundary along the coast between the upwelled water and the warmer adjacent ocean surface water is usually a front with an associated equatorward jet (Smith, 1995). The biological counterpart to the surface boundary layer is, roughly speaking, the euphotic zone into which nutrients upwell, leading to high productivity.

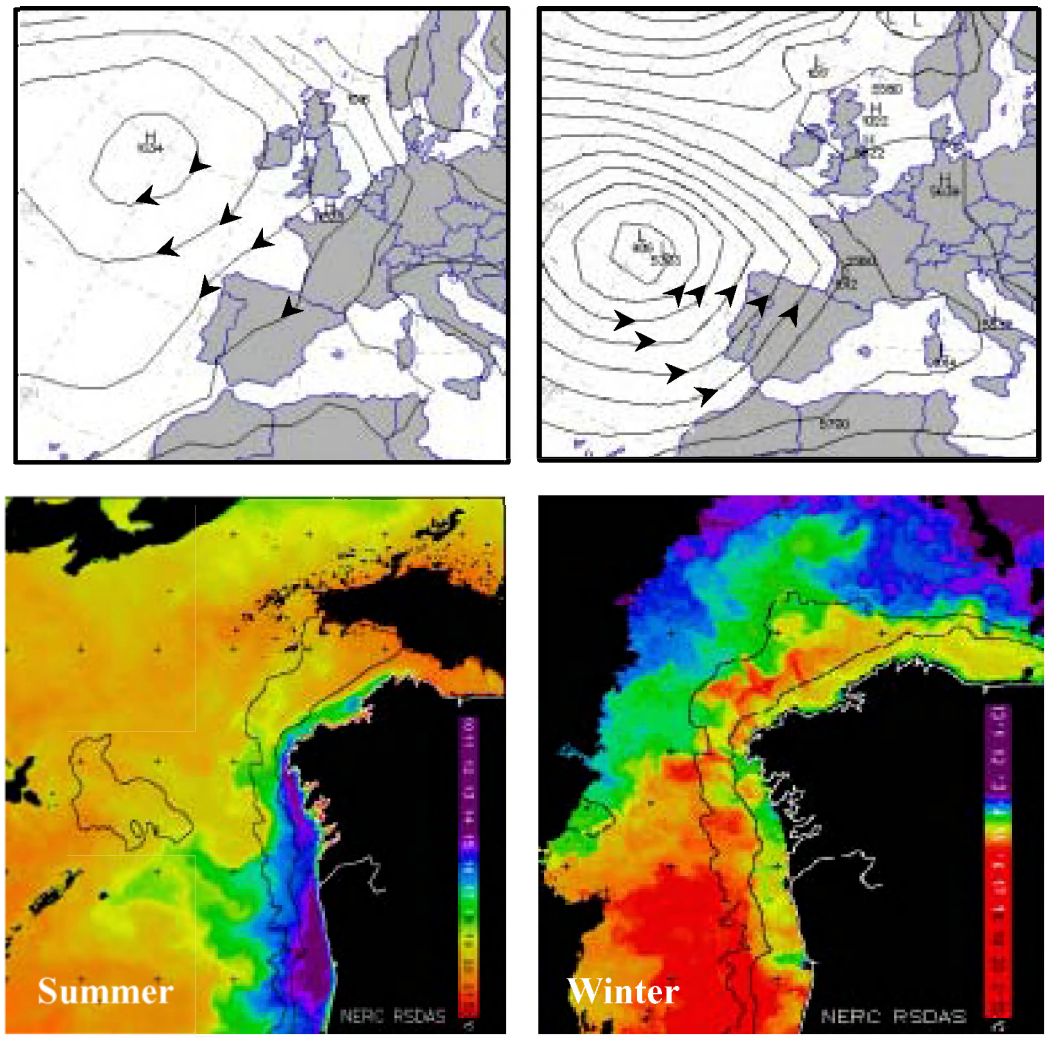

Figure 1: Typical meteorological and oceanographic situations found in the NW Iberian margin during summer and winter. Northerly winds cause upwelling and filament development in summer. During winter southwesterly winds reinforce the surface poleward current. AVHRR images courtesy of the Remote Sensing Data Analysis Service, Plymouth Marine Laboratory.

Consequently, upwelling circulation overrides both the nutrient limitation of stratified waters and the light limitation of well-mixed waters (Hood et al., 1992).

Because wind is the main driving force in upwelling systems, these systems vary considerably at a variety of temporal scales related to atmospheric oscillations. On an annual basis, variability results from the displacement of atmospheric high-low pressures dipoles which influence alongshore winds, favouring either upwelling or downwelling (Figure 1) (Bakun and Nelson, 1991). Transition periods occur in spring and autumn. However, variations in the wind regime due to changes in the position and/or strength of the high-low pressure systems cause short-term variability in upwelling-downwelling cycles within each season (Hickey, 1998; Shillington, 1998). Water column responses to these upwelling-downwelling cycles during the upwelling season are 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. 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), also affect these coastal upwelling systems through modifications of seasonal upwelling-downwelling strength (Shannon et al., 1986; Blanton et al., 1987; Simpson, 1992; Alvarez-Salgado et al., 2003).

Seasonal along-shelf wind forcing in these coastal upwelling systems produces a general shelf circulation pattern that, under upwelling conditions, consists of a surface along-shore equatorward current countered by a poleward undercurrent. The Ekman transport induced at mid-latitudes causes an associated cross-shelf circulation with an offshore stream at the surface and compensating onshore flow at deeper layers. The opposite situation arises during downwelling, when a surface poleward current establishes over the shelf and forces the onshore flow of surface waters. In some upwelling areas, where surface poleward currents in winter are very well defined, for example, the Iberian and northern California-Oregon systems, it is considered that they result from the surfacing of the poleward undercurrent during late fall-early winter.

Within this general context, physical features along the coastline, such as capes and embayments; particular topographic features of the slope and continental shelf such as canyons; and steep variations in the isobaths, the presence of buoyant freshwater plumes, and the dynamics of oceanic margins, generate instabilities in the flow that alter this general circulation pattern at several spatial scales. For example, upwelling filaments, which are usually associated with coastal promontories during upwelling, generally flow equatorward and meander, forming eddies. In general, topography and coastline orientation interact with wind forcing by modifying the along-shore and cross-shelf flows at different levels, resulting in the amplification and/or reduction of upwelling-downwelling. Coastal buoyant plumes arising from continental runoff can prevent the surface expression of upwelling or prevent onshore transport during downwelling (Hickey, 1998; Ribeiro et al., 2005).

The seasonal succession of microplankton in upwelling systems 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 fall. However, this typical pattern shows considerable temporal and spatial heterogeneity caused by wind-forcing cycles and different hydrographic structures, with current and countercurrent systems and associated fronts contributing to conditions of upwelling versus relaxation of upwelling that favour different algal species.

Phytoplankton assemblages often present a band-like distribution around an upwelling centre, corresponding to physico-chemical conditions. In a typical strong upwelling situation, there may be

a phytoplankton-poor inshore region, followed in an offshore direction by a band of diatom dominance and by zones with an increasing contribution of other groups, such as dinoflagellates, better adapted to stratified conditions (Margalef, 1978). This assemblage structure and species distribution will expand and contract in response to pulses of upwelling and relaxation. Consequently, phytoplankton succession in upwelling systems can be partially re-set in a fairly unique way. The physical forcing of upwelling leads to intermittent interruptions of succession, returning to earlier stages. The phase to which the succession is re-set will depend on the combination of wind-forcing intensity, degree of water column stratification and the previous phase of succession (Estrada and Blasco, 1979). Latitudinal variation in successional patterns is largely driven by seasonal variability in temperature and stratification, but may also result from salinity stratification related to differences in continental runoff. HABs are largely influenced by all these physical, chemical and biological processes governing upwelling ecosystems.

B. Identification of Upwelling Systems for Comparison

1) Harmful Algae in the California Current System

Physical and Chemical Environment

The California Current System (CCS) encompasses the Pacific west coast of North America, from approximately the Gulf of Alaska in the north to the Baja California Peninsula in the south (Figure 2). It flows equatorward, carrying colder, fresher subarctic water year-round offshore of the U.S. west coast from the shelf break to a distance of 1000 km from the coast (Hickey, 1989; 1998). The current is strongest at the sea surface, and generally extends over the upper 500 m of the water column. South of Point Conception a portion of the California Current turns south-eastward and then shoreward and poleward. The California Current has a seasonal maximum volume in summer.

The California Undercurrent is relatively narrow (~10-40 km) and flows poleward over the continental slope from Baja California to at least Vancouver Island at depths of approximately 100-400 m. It is the most continuous poleward current along the west coast and thus provides a possible route for transport of phytoplankton cysts, larvae and zooplankton. It also provides the source water for coastal upwelling and hence nutrient renewal. The undercurrent can be continuous over distances of at least 400 km along the slope (Collins et al., 1996; Pierce et al., 2001). The Davidson Current is a surface current that flows poleward in fall and winter from Point Conception (~35°N) to at least Vancouver Island (50°N) and may represent the surfacing of the California Undercurrent during late fall (Huyer and Smith, 1974). This poleward flow is generally broader (~100 km wide) and sometimes stronger than the corresponding subsurface poleward flow in other seasons, and extends seaward of the slope.

The seasonal cycle over the mid- and outer shelves of the CCS is similar to that described for other eastern boundary currents. Mid-water column currents over the continental shelf are generally equatorward from early spring to summer and poleward for the remainder of the year. The duration of seasonal equatorward flow usually increases with distance offshore and with proximity to the sea surface. A poleward undercurrent is commonly observed on continental shelves during the summer and early fall. A strong tendency for poleward flow exists over the inner shelves throughout the water column in all but the spring season.

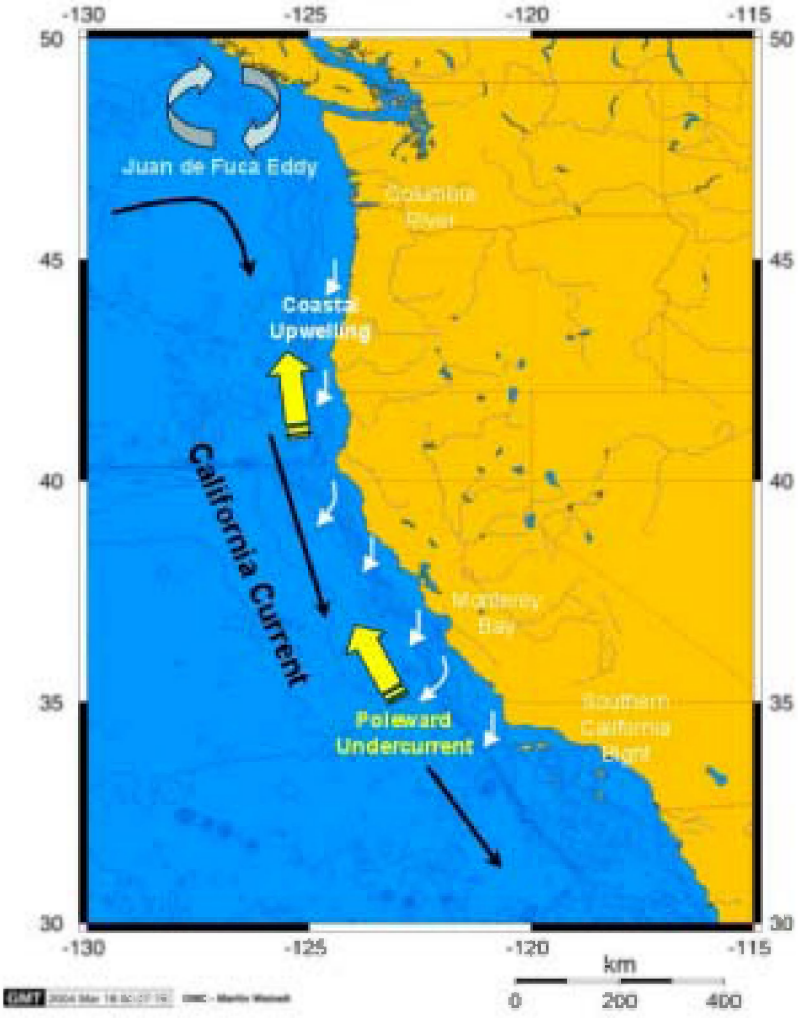

Figure 2: The California Current System, depicting typical flow patterns for spring (adapted from Strub and James, 2000).

The transition of currents and water properties over the continental shelf and slope between winter and spring is a sudden and dramatic event in the CCS (Huyer et al., 1979). Along much of the coast, during the transition, sea level drops at least 10 cm, currents reverse from poleward to equatorward within a period of several days and isopycnals slope upward toward the coast (Strub et al., 1987). A similar rapid transition between summer and fall is not observed.

In spring and summer, upwelling along the coast in the CCS brings colder, saltier and nutrient-rich water to the surface adjacent to the coast. In general, the strength and duration of upwelling seen at the sea surface is at a maximum off northern California, where alongshore upwelling-favourable wind stress at the coast is greatest (Huyer, 1983). Maximum upwelling occurs in spring or summer at most latitudes. Stratification in the CCS is remarkably similar at most locations and is largely controlled by the large-scale advection and upwelling of water masses described above. Nutrient input to the ocean from coastal rivers is negligible, even for the Columbia River, which accounts for the majority of the continental drainage in this region. Both seasonal and event-scale patterns of all macronutrients on the continental shelf are dominated by seasonal and event-scale patterns in the upwelling processes (Hickey, 1989; Landry et al., 1989).

Seasonal conditions are frequently reversed for shorter periods at all locations in the coastal zone of the CCS. Fluctuations in currents, water properties and sea level over the shelf at most locations are dominated by wind forcing, with scales of 3 to 10 days. During periods of fair weather, the stress of southward winds at the sea surface accelerates the coastal currents, producing offshore and alongshore directed currents in the surface Ekman layer (~5-30 m thick), alongshore (and, initially, onshore) currents in the central water column and onshore and alongshore currents in the bottom boundary layer (~5-15 m thick). Plumes of fresher water originating in coastal estuaries tend to spread offshore and to the south. Upwelling reaches the sea surface within a few kilometres of the coast. During periods of rough weather, the patterns reverse and freshwater plumes move back onshore.

At the event scale, as at the seasonal scale, wind-driven upwelling of nutrients from deeper layers fuels coastal productivity, resulting in both a strong seasonal cycle and several-day fluctuations that

mimic changes in the wind direction and, hence, upwelling. During an upwelling event, phytoplankton respond to the infusion of nutrients near the coast and the resulting phytoplankton blooms are moved offshore, continuing to grow while depleting the nutrient supply. When winds reverse, as occurs during storms, blooms move back toward the shore where they can contact the coast and enter coastal estuaries.

Currents seaward of the continental shelf all along the U.S. west coast are dominated by fluctuations with periods much longer than those on the shelf. Satellite images from spring and summer show filaments, jets and eddies emanating from near coastal promontories to regions well seaward of the coast from Cape Blanco south to Point Conception (Kelly, 1985; Kosro and Huyer, 1986); in these regions the circulation is highly three-dimensional and much of the transport is across, rather than along, the continental margin. Filaments are the result of separation from the shelf of coastal jets formed over the shelf during upwelling events (Strub et al., 1991). Shipboard surveys demonstrate that filaments extend from the surface to depths of more than 200 m and they separate fresher, warmer, chlorophyll-depleted water from colder, saltier, chlorophyll-rich, recently upwelled water (Strub et al., 1991). Few filaments are observed north of about 43°N where the coastline is straighter; upwelling is more two-dimensional and transport is primarily along the shelf in those regions.

Although many of the processes on the West Coast act over very large scales, significant mesoscale features also occur along this coast and may be of particular importance to ecosystem variability and, in particular, to HABs. Hickey and Banas (2003) suggest that in regions where large coastal promontories occur, such as off southern Oregon and northern and central California, plankton can be swept offshore and southward by the meandering jets and/or eddies that form where coastal jets detach from the shelf. These organisms rarely return to the coast. In other regions, such as over banks (e.g., Heceta Bank) or within embayments between capes (e.g., Gulf of Farallones) retention and onshore transport of planktonic organisms may be observed. Maps of ocean pigment clearly show that chlorophyll is greater and located farther offshore in the vicinity of these features (Strub and James, 2002). Under weak southward wind conditions or during northward winds associated with storms, plankton in the retention areas can return to the coast or enter coastal estuaries.

Year-to-year variability in the CCS is significant in both physical and biological parameters. Surface transport in the California and Alaskan Current Systems varies out of phase on ENSO time scales: when the Alaska gyre strengthens, as during an ENSO event, the CCS weakens (Strub and James, 2002). As with seasonal changes, the majority of the changes in transport occur along the ocean boundaries in both systems. On interannual scales, some changes in the North Pacific Current also occurs, but these changes follow those along the boundary. Much of this variability is related to the ENSO phenomenon, occurring at periods of 3 to 7 years.

The Northeast Pacific Ocean also has lower frequency fluctuations, with periods of 22 and about 52 years, associated with the Pacific Decadal Oscillation (PDO) (Chavez et al., 2003). The PDO has oceanic and atmospheric patterns similar to those of ENSO, but with much longer duration. The PDO is a pattern of low sea surface temperatures in the central North Pacific Ocean and high sea surface temperatures along the eastern Pacific boundary. The major pattern reverses at 25- to 30-year intervals. The ecosystem seems to respond to the PDO; for example, salmon production in the northern Gulf of Alaska is positively correlated with the PDO, and salmon production in Washington State/Oregon is negatively correlated with the PDO (Mantua et al., 1997). Although most evident from the effect on fisheries, the PDO has also been linked to regime shifts affecting the CCS at all levels, from physics, through phytoplankton productivity and community structure, culminating in the

observed changes in commercial fish stocks (Chavez et al., 2003).

Phytoplankton Dynamics

The spatial and temporal distribution of phytoplankton in the CCS is largely controlled by the regional oceanographic conditions described above. Although several regional programs have examined phytoplankton spatial and temporal succession, there has been no detailed study of the entire CCS. The sampling at the Scripps Institution of Oceanography Pier in Southern California, which occurred daily/weekly for approximately 20 years, is the longest and most comprehensive phytoplankton data set available (Allen, 1936; 1941; Tont, 1987). Bolin and Abbott (1963) analyzed weekly samples collected from six stations over a seven-year period (1954-1960) in Monterey Bay; this was later extended by the Monterey Bay Aquarium Research Institute (Pennington and Chavez, 2000), with an ongoing sampling program starting in 1989. Smaller programs, consisting of one to several cruises, have contributed to our understanding of species assemblages and associations in and around the CCS.

Spring and summer upwelling tends to dominate the CCS, occurring nearshore (0-100 km) from Washington State to Baja California, and resulting in lowered sea level, low sea surface temperatures, high salinities and enhanced nutrients. Although there is a large latitudinal gradient, upwelling typically occurs in the CCS from approximately February to September. During the remainder of the year, the CCS is dominated by either poleward flows, or the intrusion of "oceanic" waters from offshore. In waters such as the CCS that are supplied with high nutrient concentrations, phytoplankton biomass tends to be dominated by large netplankton, and in particular diatoms (e.g., Probyn, 1985; Eppley, 1986; Wilkerson et al., 2000). During vigorous upwelling, large diatom genera such as *Chaetoceros* and *Nitzschia* are typically dominant (Allen, 1939, 1941; Venrick, 1998; Pennington and Chavez, 2000), and the larger plankton size classes dominate both biomass and productivity (e.g., Wilkerson et al., 2000).

During non-upwelling periods, the phytoplankton assemblages are typically more varied, and composed of a mix of smaller diatoms, flagellates, and picoplankton characteristic of both offshore and southern waters (e.g., Pennington and Chavez, 2000). This period is characterized by an annual minimum in both biomass and productivity, associated with the absence of a larger size class of phytoplankton (e.g., Wilkerson et al., 2000). Although this view is undoubtedly influenced by the predominance of netplankton sampling until relatively recently, several more recent studies (e.g., Buck et al., 1992; Chavez, 1995; 1996; Kudela et al., 1997) confirm the dominance of diatoms during upwelling, and the importance of smaller size classes (e.g., *Synechococcus* and red fluorescing picoplankton) during the winter months.

Local and interannual oceanographic conditions also strongly influence the distribution of phytoplankton. Although there is generally an annual peak in productivity occurring in the late spring to early summer following the spring transition and a trend toward greater biomass and increased complexity nearshore, tending toward more oceanic conditions offshore, shifts in phytoplankton species dominance occur over alongshore distances of less than 100 km and time periods of days (e.g., Abbott et al., 1990; Venrick, 1998). Abbott et al. (1990) found that species composition along a drifter track changed over time scales of 2 to 3 days, similar to results from deckboard grow-out experiments (e.g., Kudela et al., 1997). Interannual (e.g., ENSO) and decadal changes are also apparent, with changes in biomass, species composition and productivity (e.g., Chavez, 1996; Hayward, 1997; Pennington and Chavez, 2000; Chavez et al., 2002).

Despite the expected complexity at both short and long space and time scales, it is useful to examine the annual successional patterns of phytoplankton relative to the dominant physical forcing in Monterey Bay (Figure 3). Sea surface temperature (SST) is well correlated with local winds, and shows, as expected, cooler temperatures in the spring and summer and warmer temperatures in the winter. Deeper waters (100 m) reach a minimum temperature in June, slightly later than SST and more in phase with the upwelling indices, indicative of the upwelling source water, which is typically 50-100 m deep at this latitude. Salinity is generally higher during spring (upwelling), and lower during oceanic periods and winter, and associated with riverine input. During November-January, the shallow water column (<50 m) is unstratified and moderately warm and fresh relative to other times of the year. Nutrient concentrations generally mirror SST, with increasing values during upwelling and decreases due to both source concentrations and biological depletion during the winter months. Seasonal cycles of chlorophyll and primary production are well correlated with each other and with the subsurface fields of nitrate and temperature. Consistent with the general description for the CCS, they display a broad maximum centred on May and June. The centric diatoms are well correlated with the broad seasonal maximum in chlorophyll and primary production, indicative of the dominance of centric diatoms in biological productivity. The other taxonomic groups – pennate diatoms, dinoflagellates and *Synechococcus* – show maximum concentrations in the late summer and fall during the oceanic period. Overall, the upwelling signal occurs in spring and early summer at this latitude, and is evident in winds, currents, temperature, nitrate, chlorophyll, primary production and centric diatoms. During late summer and early fall (the oceanic period) there are increases in temperature, a shoaling and intensification of the poleward undercurrent, decreases in nitrate concentration, chlorophyll and primary production, and a shift in species assemblages. A deeper mixed layer and minima in biological and chemical properties characterize the winter.

Harmful Algal Blooms

Two major toxin syndromes caused by HABs are found along the North American west coast. These are paralytic shellfish poisoning (PSP) caused by members of the dinoflagellate genus *Alexandrium* and amnesic shellfish poisoning (ASP), also known as domoic acid poisoning (DAP), caused by members of the diatom genus *Pseudo-nitzschia*. A third major toxin syndrome, yessotoxin poisoning, may be present (associated with the dinoflagellates *Protoceratium reticulatum* in the north and *Lingulodinium polyedrum* in the south), but has not been evaluated at this time. The CCS also has members of the dinoflagellate genera *Dinophysis*, responsible for diarrhetic shellfish poisoning (DSP) and *Prorocentrum lima*, responsible for okadaic acid poisoning, but these latter toxin syndromes are considered of secondary importance compared to PSP and DAP, and typically are not well monitored or studied. Other problem species include the diatom genus *Chaetoceros* that kill fish primarily at aquaculture sites, but are not known to be harmful to humans; the dinoflagellates *Noctiluca scintillans* and *Ceratium* species and the ciliated protozoan *Mesodinium rubrum*, which cause obvious water discolorations; and the raphidophyte *Heterosigma akashiwo*, which is primarily found in coastal embayments and aquaculture sites, but may be spreading.

The Pacific coast of North America has a long history of HAB problems, with the earliest confirmed fatalities from PSP recorded in 1793 in an area on the central British Columbia coast now called Poison Cove (Quayle, 1969). To the south in California, the early Native Americans did not eat shellfish when bioluminescence was present in the water, even placing sentries to watch for it during very hot weather (Meyer et al., 1928). PSP cases were not uncommon in the latter half of the nineteenth century, with reports of mass intoxications in Native Americans and individual cases in white settlers (Meyer et al., 1928; Sommer et al., 1937). Additional cases of PSP, including deaths, occurred in California in the early twentieth century and by 1927, health officials recognized its serious potential.

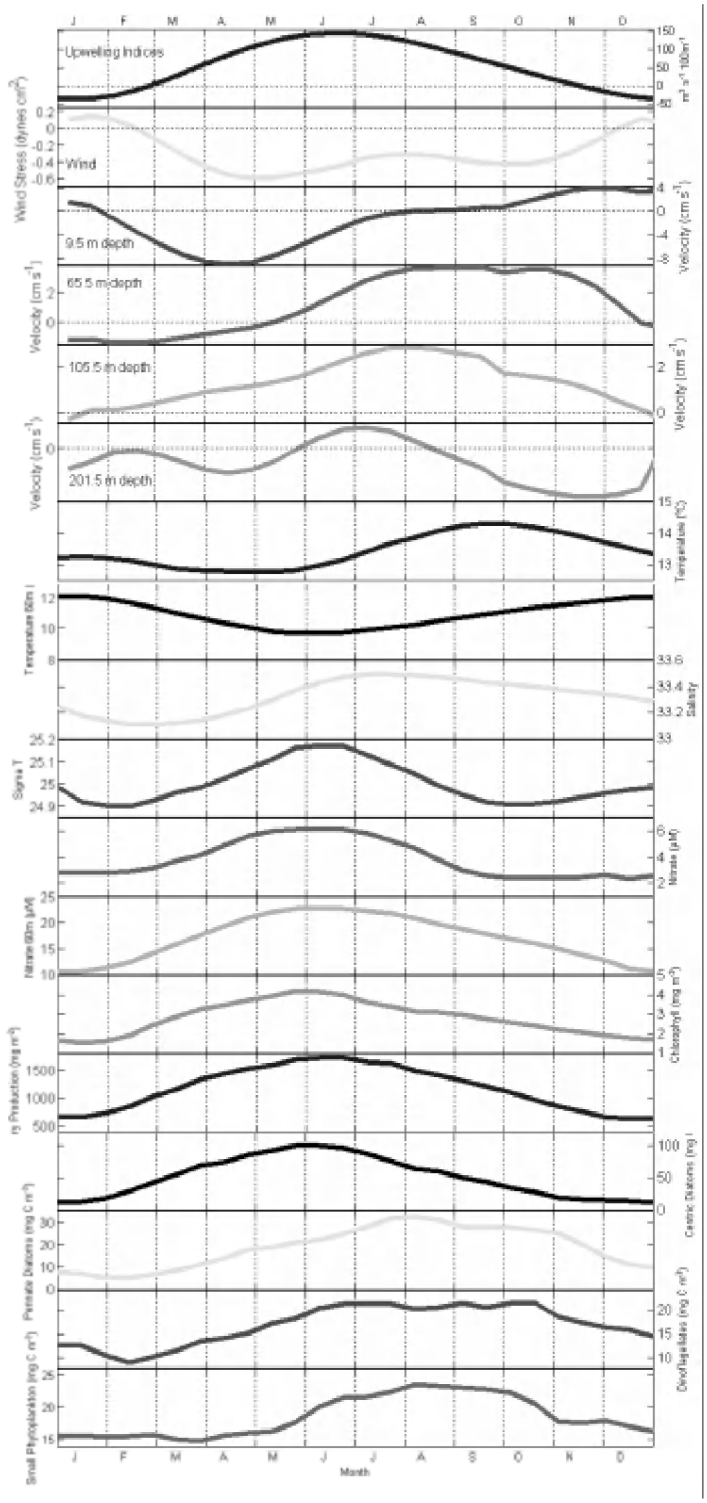

Figure 3: Seasonal cycles of physical, chemical and biological properties from the Monterey Bay Aquarium Research Institute time series (central California, 1989-1998) are plotted. The upper panels represent physical and chemical trends, the lower panels represent the corresponding biological response. From the top, panels show the upwelling index at 36° N, 122° W; alongshore winds; alongshore currents, sea surface temperature, sea surface salinity, nitrate concentrations (μM) at the surface and 60 meters depth, surface chlorophyll, depth integrated primary productivity and major phytoplankton taxa (centric diatoms, pennate diatoms, dinoflagellates, and picoplankton) (from Chavez et al., 2000).

Within the larger context of the CCS, *Alexandrium* species and PSP are prevalent throughout the west coast. In British Columbia, toxicity has occurred every year since monitoring began in the 1940s, differing only in the extent and duration of closures, and virtually everywhere on the coast has been toxic at some time, with some areas toxic every year. But, there has been no large-scale effort to study *Alexandrium* outbreaks. Blooms are initiated from benthic cysts, but there is no simple correlation of bloom distribution and cyst density in sediments. Blooms seem to originate in shallow, nearshore localities and spread regionally (Taylor et al., 1994); these blooms are generally subsurface, often occurring near the nutricline (Taylor and Trainer, 2002). There is no apparent link with pollutants (Taylor and Horner, 1994) nor with aquaculture (Taylor et al., 1994). While blooms of toxic *A. tamarense* and *A. catenella* occur during spring, summer, and fall, toxicity in shellfish is highest in late autumn and early winter (Chiang, 1985; 1988). There are at least three, and possibly more than five species of *Alexandrium* implicated in PSP in British Columbia. *A. catenella* is predominant along the entire outer open coast; *A. tamarense* is dominant in more estuarine waters, especially on the east side of the Strait of Georgia; and *A. acatenella* also occurs in this strait. *A. hiranoi* and *A. ostenfeldii* have also been identified, but are not known to produce spirolides (Taylor and Trainer, 2002).

As in British Columbia, there has been no large-scale effort to study PSP or *Alexandrium* for Washington

State, and even less is known about PSP in Oregon. Although there is some information on toxins in shellfish, relatively little is known about the distribution and biology of *Alexandrium*. A project that monitored phytoplankton biweekly for three years at five sites in Puget Sound and five on the open coast found that *Alexandrium* was present from April to December and occurred more frequently in Puget Sound (except not in Hood Canal) than on the open coast (Horner and Postel, unpubl. obs.). The causative species for PSP in Oregon is *Alexandrium catenella*, but detailed distribution and abundance studies have not been done.

In California, PSP was first recorded in 1903. There have been 510 illnesses and 32 deaths since records were first kept (Langlois, 2001). *Alexandrium catenella* is the causative species for PSP in California as it is all along the Pacific coast of North America. Toxic events occur most years along the coast, primarily in the summer and fall. Most PSP events occur between June and September, with July being the peak month. However, toxicity peaks are seen in March, late July, and September. These peaks appear to correlate with the relaxation of upwelling that results in the transport of toxic cells to the coast (Langlois, 2001).

California imposes an annual quarantine for sport-harvested mussels along the entire coast each year from 1 May through 31 October (Price et al., 1991) and implements this with special quarantines for other species when needed. However, blooms can occur after 31 October and before 1 May. Saxitoxins have been found in all of the coastal counties and in some years appear to have higher PSP levels than other years (G. Langlois, pers. comm.). For example, in the 28 years between 1962 and 1989, toxic events occurred in 22 years and two or more events were reported for 10 of the years (Price et al., 1991). A 24-month survey of *A. catenella* in Monterey Bay that began in June 2000 found cell concentrations $>10^3$ l^{-1} on nine occasions, with the average event duration being about 1.5 weeks; only one event (April 2001) occurred outside the state-mandated shellfish quarantine period. Highest PSP toxins apparently occur in Marin County (near San Francisco) with levels of toxins declining to both the north and south.

DAP was first reported on the Pacific coast of North America in September 1991 when pelicans (*Pelecanus occidentalis*) and cormorants (*Phalacrocorax penicillatus*) died in Monterey Bay, California. The source was traced to domoic acid in their food, anchovies (*Engraulis mordax*), that were feeding on phytoplankton dominated by *Pseudo-nitzschia australis* (Fritz et al., 1992; Work et al., 1993). By November 1991, domoic acid was found in the edible parts of razor clams (*Siliqua patula*) on the Oregon-Washington State coasts and in the viscera of Dungeness crabs (*Cancer magister*) harvested offshore. Although domoic acid poisoning was first discovered in eastern Canada in 1987, most of the domoic acid events since that time have been on the Pacific coast, but there have been no confirmed human cases of ASP in this region.

Domoic acid has been known off British Columbia since 1991 and although *Pseudo-nitzschia* species are present and often abundant in all British Columbia waters, the biggest blooms seem to occur over the outer continental shelf (Forbes and Denman, 1991). In Washington State, species of *Pseudo-nitzschia* are common and sometimes abundant in Puget Sound and on open coast beaches, occurring in all months. Even though high cell numbers of several potentially toxic species occur in Puget Sound, only low concentrations of domoic acid have been reported there (Horner et al., 1997; Trainer et al., 1998). A five-year monitoring project, the Olympic Region HAB (ORHAB) project, is in progress on the coast to study coastal blooms of *Pseudo-nitzschia*. Data collected from ships of opportunity in recent years show that the Juan de Fuca Eddy, a retentive feature discussed above, usually contains much higher concentrations of particulate domoic acid (DA) than elsewhere on the Washington coast. High levels of particulate DA are usually associated with high cell numbers of

Pseudo-nitzschia, usually *P. pseudodelicatissima*. Measurements made during cruises and beach sampling of seawater and shellfish in 1997 and 1998 are all consistent with the possibility that during some years, DA-containing *Pseudo-nitzschia* cells from the eddy move southward during prolonged upwelling events and then onshore during the first major storm of the fall season, causing high levels of DA in razor clams on coastal beaches. Blooms of *Pseudo-nitzschia*, resulting in elevated levels of DA in razor clams, occur in both spring and late summer/fall. In both Washington State and Oregon, *Pseudo-nitzschia* species reported include *P. australis, P. fraudulenta, P. heimii, P. multiseries, P. pungens,* and *P. pseudodelicatissima* (Fryxell et al., 1997).

Since the 1991 seabird kill in Monterey Bay that led to the identification of domoic acid on the U.S. west coast, *Pseudo-nitzschia* has become the focus of toxic algal research in California. With the ability to distinguish the toxic forms among a host of similar-appearing species, formerly misplaced under the umbrella of "*Nitzschia*" or "*Nitzschia seriata*" (Garrison et al., 1992; Fryxell et al., 1997), it has become possible to study temporal and spatial patterns of the toxic species. As with the remainder of the west coast, it is now clear that multiple species are present and that they frequently co-occur. Villac (1996) found 14 species in Monterey Bay alone and local clones of two species produced toxin in culture. During the 1991 bloom, up to seven species co-occurred in the water at one site (Walz et al., 1994) and nine species were found in the digestive systems of anchovies (Altwein et al., 1995). Different toxin-producing species may dominate at different locations, as found during a 1998 bloom spanning much of the west coast, where *P. multiseries* dominated in northern California (San Francisco region), while *P. australis* dominated in the south (Los Angeles region), and *P. australis* (Oregon) and *P. pseudodelicatissima* (Washington State) dominated further north (Figure 4). During the 1991 event, however, *P. australis* was found from southern California north to the mouth of the Columbia River and was the only source of toxin identified (Villac et al., 1993).

As in other areas of the North American west coast, *Pseudo-nitzschia* species are common members of the coastal phytoplankton community and have been at least since the 1930s, but could not be differentiated using light microscopy (Garrison et al., 1992; Fryxell et al., 1997). It is now known that *Pseudo-nitzschia* species associated with toxin production are frequently present, albeit in low numbers, in most water samples (e.g., Walz et al., 1994). Bloom conditions are generally associated with weak upwelling, fresher water, transitional periods between anomalously warm and cool waters, and generally low macronutrients (Kudela et al., in press). There is no consistent evidence for macronutrient or iron concentrations to be directly attributable to toxic events. When tested directly, *Pseudo-nitzschia* was generally nitrogen limited, with little or no iron stress (Kudela et al., in press), although it is possible that DA production and a lack of iron stress are correlated, if DA is a chelator (Rue and Bruland, 2001).

Like many other colonial diatoms, *Pseudo-nitzschia* has a tendency to flocculate and settle through the water column, ultimately reaching the sediments. For toxic species, this raises the potential for contamination of the sub-euphotic zone pelagic and benthic faunas. The descent rate for *P. australis* has been measured in Monterey Bay with sediment traps placed at 450-500 m depths receiving between 10^6-10^7 cells $m^{-2}d^{-1}$ (Buck et al., 1992). During the 2000 bloom in Monterey Bay, divers observed large numbers of *Pseudo-nitzschia* aggregates in the water and collected flocculent layers of *Pseudo-nitzschia* with high toxicity on the sediment surface in water depths of 10-20 m (R. Kvitek and M. Silver, unpubl. obs.). Several authors have argued that populations of viable cells from deep water are the source of innocula to surface water, thereby allowing rapid population development in favourable conditions (Fryxell et al., 1997; Horner et al., 1997; Trainer et al., 2000). *Pseudo-nitzschia* is likely often associated with thin layers (e.g., Rines et al., 2002), which

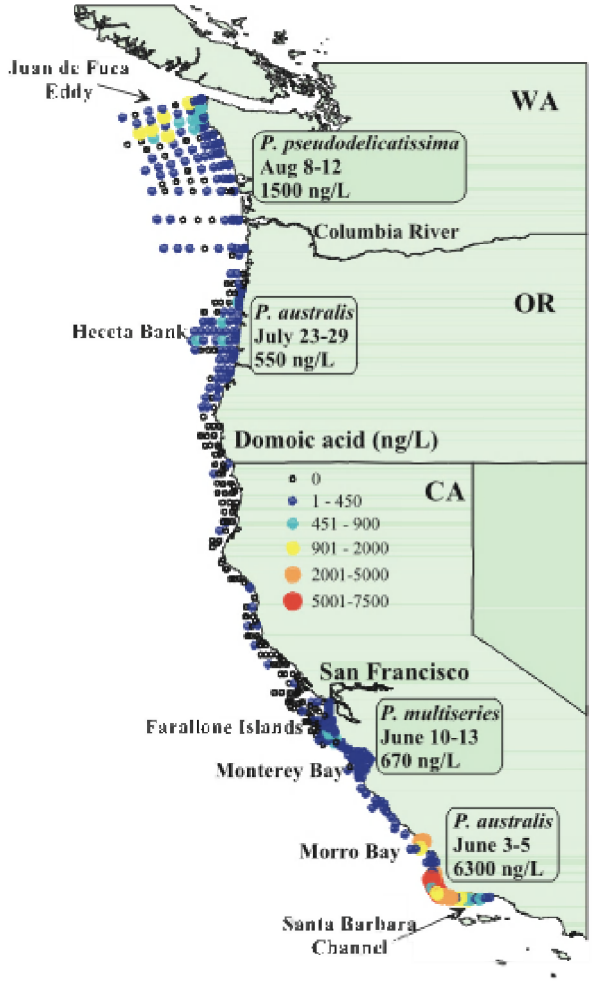

Figure 4: Dominance of different toxin-producing *Pseudo-nitzschia* species in the CCS in 1998 (from Trainer et al., 2001).

may make detection difficult prior to a major toxic event.

Species of the dinoflagellate genus *Dinophysis* linked to DSP, including *D. fortii*, *D. acuta*, *D. acuminata*, and *D. norvegica*, are all common but never abundant in the CCS. These species appear to be present during most months, but are typically not dominant during diatom-dominated upwelling periods. *Prorocentrum lima*, a known okadaic acid and prorocentrolide producer, is common in sandy benthic sediments in British Columbia, but has not been tested for toxin production (F.J.R. Taylor, unpubl. obs.). *Protoceratium reticulatum* (also known as *Gonyaulax grindleyi*) is common and sometimes abundant as far south as Oregon. It produces yessotoxins that have contaminated shellfish in New Zealand, but it is not known if the local forms produce these toxins.

Lingulodinium polyedrum (also known as *Gonyaulax polyedra*) is a widely distributed species found in warm temperate and subtropical waters of coastal areas (Steidinger and Tangen, 1997), and is frequently associated with red tide events south of 37°N (Monterey), with extensive red tides along much of the Southern California Bight and Baja Peninsula. Although *L. polyedrum* has been determined to produce yessotoxin, as well as the analog, homoyessotoxin (Draisci et al., 1999; Stobo et al., 2002), *L. polyedrum* on the North American west coast has rarely been reported to have direct toxic effects on other marine organisms, although a toxin similar to PSP was isolated from this species in California (Schradie and Bliss, 1962) and elsewhere (Bruno et al., 1990), presumably a yessotoxin derivative. Large blooms of *L. polyedrum* have been positively correlated with river runoff (Hayward et al., 1995) and anthropogenic nutrient loading (Kudela and Cochlan, 2000; B. Dale, pers. comm.). Blooms usually occur in late spring or early summer, and are typically dispersed by physical mixing and advection.

Species that kill fish primarily at aquaculture facilities include the diatom species *Chaetoceros concavicornis* and *C. convolutus,* the raphidophyte flagellate *Heterosigma akashiwo,* and the dinoflagellate *Cochlodinium* cf *polykrikoides.* The diatoms are most abundant in summer and fall in the Strait of Georgia (Haigh and Taylor, 1990) and coastal inlets (Taylor et al., 1994). Since 1999, fish kills on the west coast of Vancouver Island have been linked to blooms of the naked dinoflagellate *Cochlodinium* sp., possibly *C. polykrikoides.* The cause of death is unknown although oxygen radical production leading to gill damage is suspected.

Heterosigma akashiwo has been associated with mortalities of both free-ranging and penned fish, producing losses to stocks of commercial, research and endangered species (Harrell, 1990; Taylor,

1990, 1993; Honjo, 1992; Hershberger et al., 1997; Connell et al., 2001). *H. akashiwo* has been the main killer of farmed salmon since 1986 in British Columbia. The first confirmed *Heterosigma* bloom associated with finfish mortalities was at a tribal aquaculture facility near Lummi Island, Washington State, in 1976 (Gaines and Taylor, 1986). Episodic, unpredictable and often destructive blooms of *Heterosigma* have occurred in the Main Basin of Puget Sound since the late 1980s. Causes of *Heterosigma* blooms are unclear and are apparently diverse (e.g., Taylor and Horner, 1994; Horner et al., 1996). Further, blooms are now apparently occurring in more areas on the west coast, for example, San Pedro and San Francisco bays, California (Herndon and Cochlan, 2003; L. Connell, pers comm.), although this could be an artefact of increased surveillance.

2) Harmful Algae in the Iberian Upwelling System

Physical and Chemical Environment

The Canary Current-Iberian upwelling system extends from the northern Iberian Peninsula at 43°N to the south of Senegal at approximately 10°N (Figure 5). The Atlantic Iberian margin forms part of the eastern boundary system of the North Atlantic Ocean and is driven by large-scale climatology and thermohaline forcing from the ocean interior. At the regional level, the oceanography is dominated by mesoscale features, embedded in larger scale circulation. These structures are tens to hundreds of kilometers in size and represent the variability of the ocean relating to the weather, and the local response of the ocean to coastline geometry and bottom topography.

The Iberian upwelling region is separated from the north African system by a break in the coastline forced by the Strait of Gibraltar (Figure 5). This break interrupts the continuity of the flow along the coast, and allows for water exchange between the Mediterranean Sea and the Atlantic Ocean. Consequently, HABs are common in the Alboran Sea on the Mediterranean side of the Strait of Gibraltar, owing probably to inflowing Atlantic waters. The coastal margin is, however, continuous below the depth of 300m.

Upwelling is seasonal along the western Iberian coast, owing to the latitudinal shift of the trade wind system (Wooster et al., 1976), which determines not only the surface circulation along the Iberian margin, but also drives phytoplankton succession and, consequently, HABs. The surface circulation is characterized by the presence of a perennially weak current, the Portugal Current, that flows southwards (Krauss, 1986), and shows a complex pattern at the oceanic margin with distinctive seasonal variability driven by the coastal wind regime (Huthnance et al., 2002). Dominant northeasterly winds, favourable to upwelling during spring and summer (Wooster et al., 1976; Bakun and Nelson, 1991), cause southward flow of the surface waters of the the Portugal Coastal Current, which is compensated by a northward undercurrent, the Portugal Coastal Under Current, on the slope (Meincke et al., 1975; Fiúza, 1983; Barton, 1989). For the rest of the year, the predominance of southwesterly winds promote the surfacing of the slope undercurrent (Ambar and Fiúza, 1994) engendering a northward flow of slope and shelf waters, at least from 39°N off Lisbon (Wooster et al., 1976; Frouin et al., 1990; Haynes and Barton, 1990), which causes coastal downwelling (Castro et al., 1997; Pelíz and Fiúza, 1999).

Transitions between seasonal upwelling- and downwelling-favourable periods show remarkable differences (Figure 6a). Whereas the spring transition to upwelling can occur anytime from February to April, the autumn transition to downwelling is confined to a shorter period of about one month, from the end of September to the end of October (Figueiras et al., 2002; Alvarez-Salgado et al.,

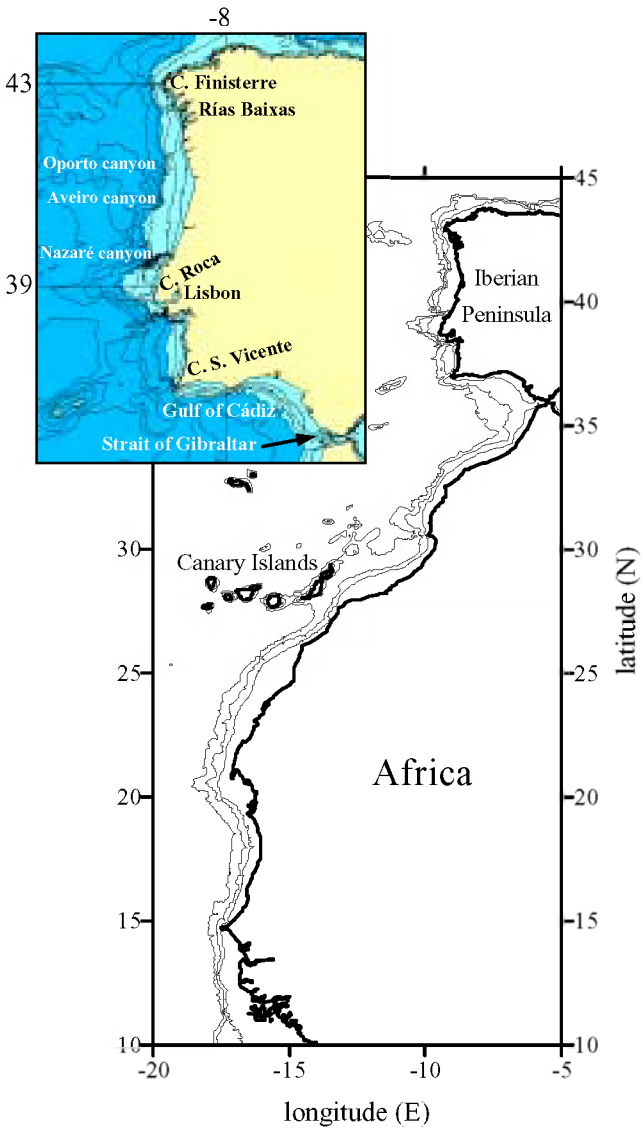

Figure 5: Map of the Canary Current/Iberian system including a detailed insert of the Western Iberian margin.

2003). Although the intensity and extension of the upwelling and downwelling seasons vary according to a decadal cycle largely linked to NAO (Figure 7), the major part of the variability of the wind regime is, nevertheless, associated with shorter time periods (Figure 6b), of usually less than one month (Alvarez-Salgado et al., 2003). Coastal upwelling intensifies at typical periods of four to ten days, the same periodicity that characterizes the variability in meteorological forcing (Fiúza, 1983; Vitorino, 1989), decaying during calm periods and receding with inversions in the wind field. As a result, the upwelling season is better described as a succession of upwelling-relaxation events, during which a short-lived near-shore poleward counter-current develops following the relaxation of upwelling (Sordo et al., 2001; Peliz et al., 2002) and coexists with the southward flow derived from upwelling. Consequently, the main circulation pattern on the western Iberian margin is dominated by along-shore flow that causes offshore transport at the surface layers and onshore compensation at depth during summer, while in winter onshore transport prevails through much of the water column with offshore compensation restricted to the near-bottom layer.

This general circulation pattern is significantly modified by changes in coastline configuration and orientation, and by the upper slope and shelf bathymetry at several locations on the coast. At the northern edge of the Iberian coast, the Rías Baixas (see Figure 5) constitutes an unusual ecosystem in which the 3-dimensional variability of the continental shelf circulation is transformed into two dimensions. The topography of the Rías and their almost perpendicular orientation to the coastline, causes the intensification of physical, chemical and biological signals by enhancing cross-shelf transport (Alvarez-Salgado et al., 2000; Figueiras et al., 2002). Offshore transport is enormously favoured in the Rías during upwelling, while they act as very efficient retention zones during downwelling. The dynamics of the system is also influenced by differences in the extension of the continental shelf along the Western Iberian margin (see Figure 5).

The northwestern shelf, that is the shelf to the north of Cape Roca, is much wider (30-60 km) and flatter than the southwestern shelf, which causes differences in stratification characteristics (Moita, 2001). The continental shelf in the Gulf of Cádiz is also wide, of the order of 50 km, and extends mainly to the east. Another important feature of the Iberian upwelling area is the abrupt change in coastline orientation off Cape Finisterre and in the region of Cape Roca, forming the Lisbon-Setúbal large embayment.

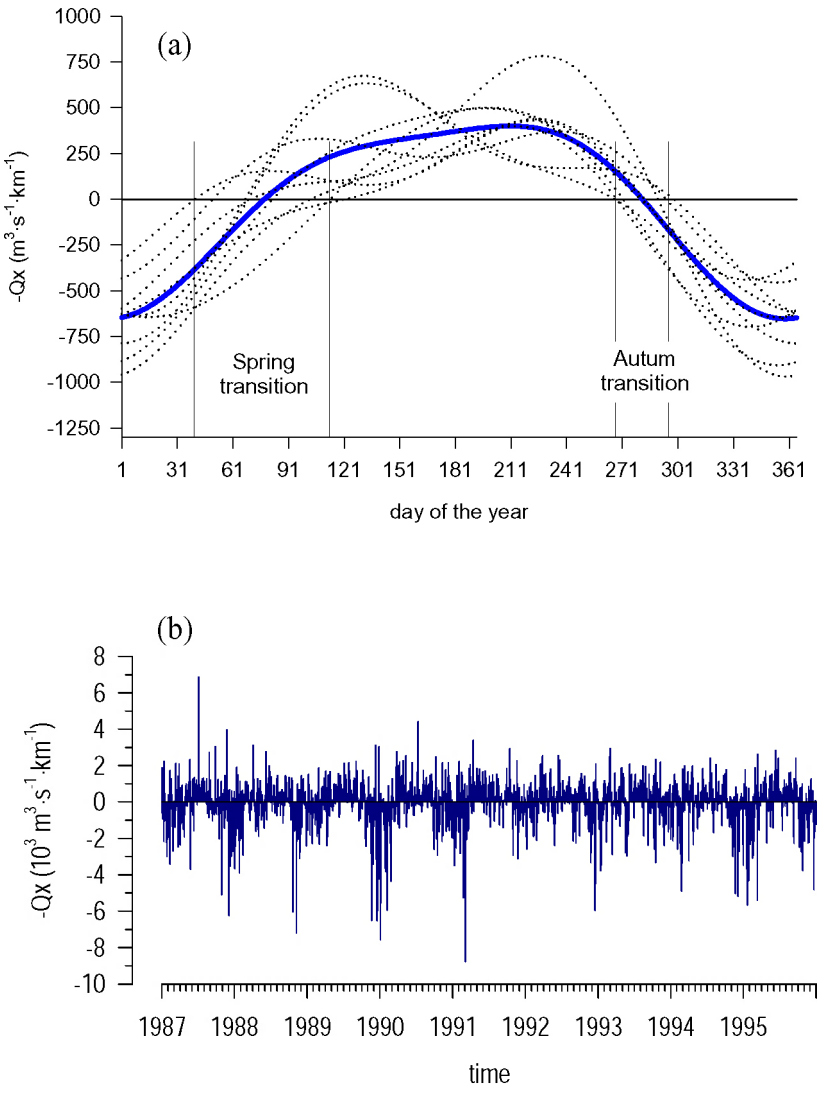

Figure 6: An upwelling index off Cape Finisterre for the period 1987-1995. (a) Seasonal cycle (solid line - average seasonal cycle; dotted line - average for each year (b) Daily-time series of upwelling index (from Kluwer Academic Publishers' journal *Hydrobiologia*, Volume 484, 2002. This figure appears as Figure 2 on page 123 of the article entitled "Coastal upwelling, primary production and mussel growth in the Rías Baixas of Galicia" by Figueiras, F.G., U. Labarta and M. J. Fernández Reiriz. Used with kind permission of Springer Science and Business Media and the authors).

The Iberian margin is particularly complex in the Cape S. Vicente region where the western and southern coasts of Iberia intersect at right angles. Cape S. Vincente represents the southern limit of the Iberian system, which is separated from the northwest African system by the Gulf of Cádiz and the entrance to the Mediterranean. The Cape thus represents a point of discontinuity in the Iberian coastal upwelling system where the equatorward jet associated with upwelling looses the constraint of the coast and may follow any of three possible pathways. Upwelled water may turn eastward along the southern shelf break thereby following coastal bathymetry; it may flow directly southward resulting in the development of a cold filament; or it may meander eastward of Cape S. Vincente (Sousa and Bricaud, 1992; Relvas and Barton, 2002). Satellite-derived images of SST during the upwelling season reveal the alongshore development of a warm coastal countercurrent along the southern Iberian coast, which may at times round Cape S. Vicente and progress northward (Figure 8). This inshore countercurrent is seen to interact with the equatorward jet, by separating the cold upwelled water from the coast. In other instances it is seen to flow westward and offshore, thereby separating cold water features in the south from those in the north. The change in coastline orientation at Cape S. Vincente determines that upwelling on the southern coast of Iberia is dependent on westerly winds (Fiúza, 1993). Thus, although circulation patterns of the west coast are typical of an eastern boundary current upwelling system, these patterns are somewhat modified on the south coast (Relvas and Barton, 2002).

Other persistent characteristics of the western Iberian margin are the filaments of cooler water delimited by strong gradients of temperature which detach from the southward current during upwelling and dissipate at the beginning of the downwelling season (Fiúza, 1983; Sousa and Bricaud, 1992; Haynes et al., 1993). These filaments, which often end in eddy-like structures as the season progresses,

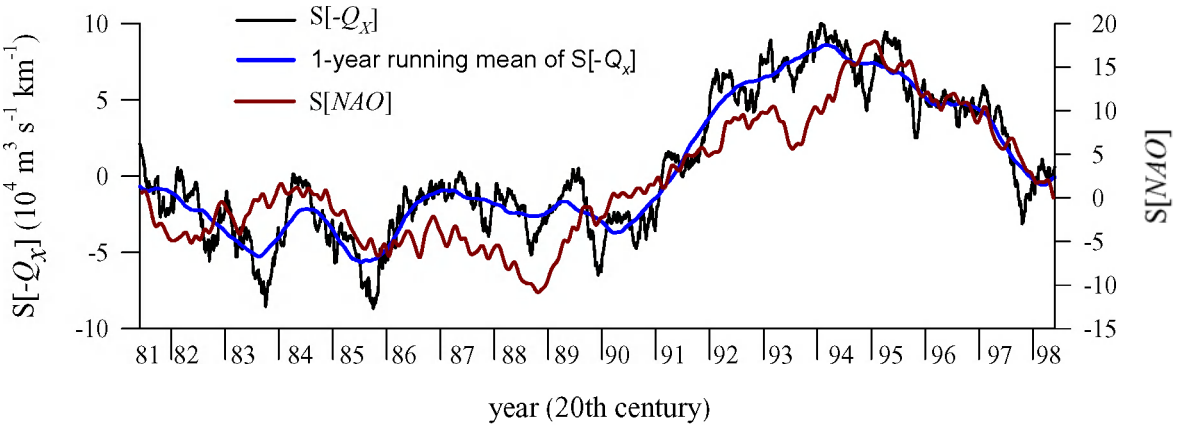

Figure 7: Deseasonalised cumulative sums of offshore Ekman transport values S[- Q_X] and the NAO index S[NAO] for the period 1981-1998. Reprinted from *Progress in Oceanography*, Volume 56, Alvarez-Salgado, X.A., F.G. Figueiras, F.F. Pérez, S. Groom, E. Nogueira, A. Borges, L. Chou, C.G. Castro, G. Moncoiffe, A.F. Ríos, A.E.J. Miller, M. Frankignoulle, G. Savidge and R. Wollast; The Portugal Coastal Counter Current off NW Spain: new insights on its biogeochemical variability; pages 281-321, Copyright (2003), with permission from Elsevier.

form not only off capes, like Cape Finisterre in the north and Capes Roca and S. Vicente in the south, but also south of the Rías Baixas (Joint et al., 2001). Here they originate probably as the result of topographic forcing of wind stress, with the Rías Baixas funnelling the wind to the southwest. Cross-shelf transport is also favoured by the presence of several submarine canyons, the Nazaré Canyon being the most important (van Weering et al., 2002), and also by coastline protrusions. In climatological terms, during the upwelling season, cross-shelf flow can reach 50% of along-shore flow, at least off the southern part of Iberia (Sánchez and Relvas, 2003). By contrast, buoyant plumes derived from continental runoff can prevent cross-shelf transport, particularly onshore surface flow at the northernmost locations during winter (Ribeiro et al., 2005). Freshwater runoff is also of particular importance to the north of Lisbon where it increases water column stratification along the northwestern continental shelf.

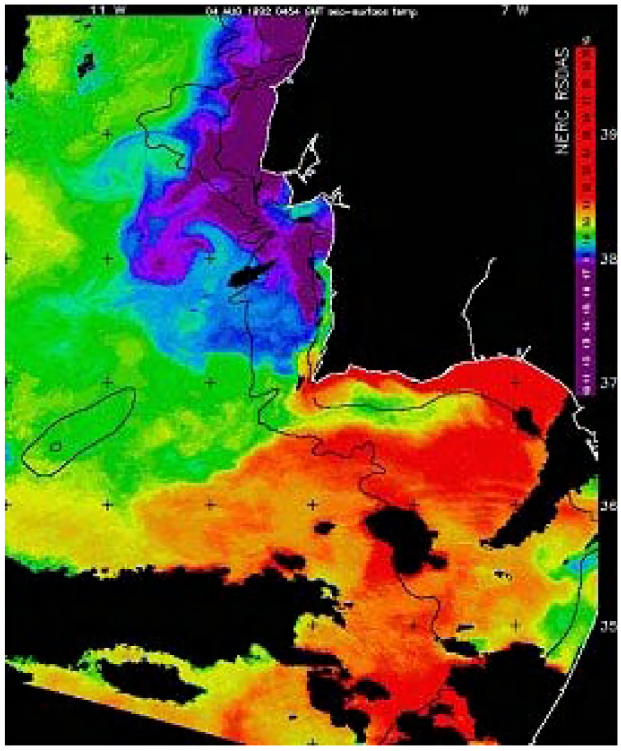

Figure 8: SST image showing the warm inshore counterflow off southern Iberia and it interaction with upwelled waters. Courtesy of the Remote Sensing Data Analysis Service, Plymouth Marine Laboratory.

Phytoplankton Dynamics

The main patterns of phytoplankton biomass are related to water column stratification, nutrient availability and the intensity and persistence of upwelling conditions. Maximum values of chlorophyll usually occur in spring and summer (Nogueira et al., 1997; Moita, 2001), although high chlorophyll values may also be recorded in autumn, particularly in zones with elevated retention characteristics; for example, high chlorophyll concentrations are found in the Rías Baixas, at the time of the seasonal transition from upwelling to downwelling (Nogueira et al., 1997;

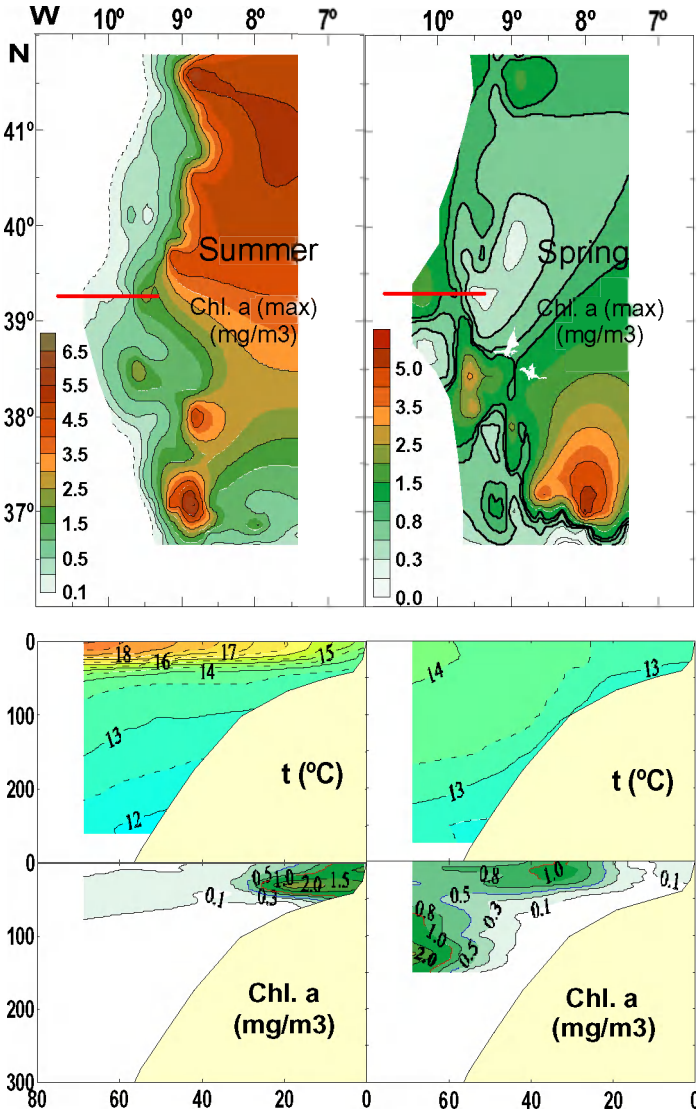

Figure 9: Horizontal distribution of maximum concentration of chlorophyl and vertical distributions of temperature and chlorophyll off the western coast of Portugal during summer and spring (from Moita, 2001). Used with permission from author.

Figueiras et al., 2002). In summer, a recurrent band of high chlorophyll concentration is found near the coast and associated with upwelled waters and strong cross-shelf gradients that separate upwelled and oceanic waters (Figure 9). Maximum values of chlorophyll near the coast occur in surface waters, while offshore these maxima extend subsurface and coincide with the nutricline (Moita, 2001; Tilstone et al., 2003). Pulses of weak-to-moderate upwelling disrupt stratification and bring nutrients into the photic zone allowing phytoplankton growth on the inshore side of a well-developed thermal front, while stratified oceanic waters offshore of the front remain poor in phytoplankton owing to nutrient depletion (Moita, 2001). During strong upwelling events and weak thermal stratification, features typical of early spring, phytoplankton blooms are advected from the coast and occur offshore of a poorly developed upwelling front (Figure 9). Under these conditions, chlorophyll maxima are often found in an area of convergence or retention formed by poleward-flowing slope water which serves as a barrier to the offshore flow of surface upwelled waters (Moita, 2001; Santos et al., 2004).

Upwelling modifies the phytoplankton assemblage composition, which follows a mixing-stratification gradient (Figure 10). Chain-forming diatoms of medium and large size, such as *Lauderia anulata*, *Detonula pumila*, *Chaetoceros* spp., *Pseudo-nitzschia* spp. and *Thalassiosira* spp. (e.g. *T. rotula, T.* cf *subtilis*), dominate spring and summer upwelling events in coastal waters (Figueiras and Ríos, 1993; Moita, 2001). The offshore extent of the assemblage depends on the intensity of upwelling. Outside the areas of upwelling, in stratified and 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). 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 Ríos, 1993; Moita, 2001), are partially responsible for the elevated concentrations of dissolved organic matter and regenerated nutrients present in the

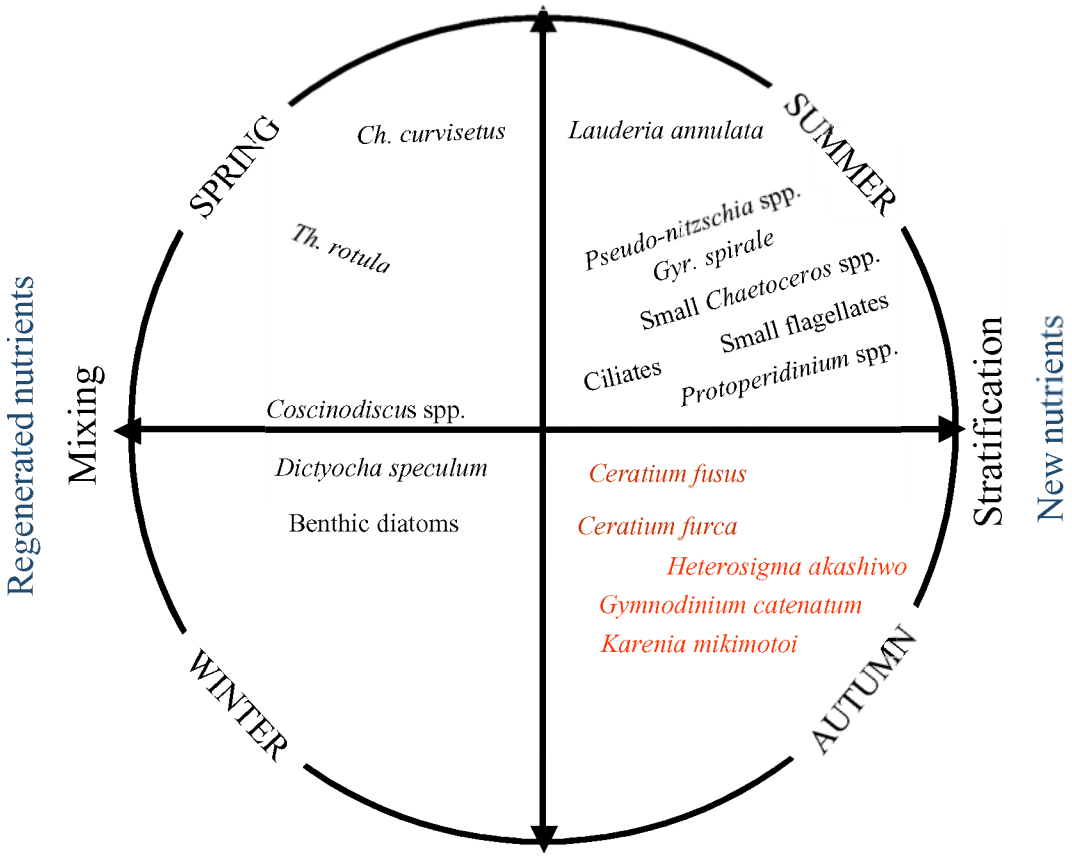

Figure 10: Annual cycle of phytoplankton abundance in the Rias Baixas of Galicia according to a mixing-stratification (new vs regenerated nutrients) gradient (redrawn from Figure 6, page 127 of Figueiras, F.G., U. Labarta and M.J. Fernández Reiriz. 2002. Coastal upwelling, primary production and mussel growth in the Rías Baixas of Galicia, *Hydrobiologia*, Volume 484. Used with kind permission of Springer Science and Business Media and the authors).

photic layer at the end of summer (Alvarez-Salgado et al., 1997; 1999). Some of these species, for example, *Noctiluca scintillans* and *Mesodinium rubrum,* are responsible for recurrent discoloration of the water (Cabeçadas et al., 1983). In August 1982, the autotrophic dinoflagellate *Scripsiella trochoidea* formed blooms extending over 100 km on the northwestern shelf of Portugal. Blooms of efficient swimmers, several of them chain-forming dinoflagellates, such as *Gymnodinium catenatum* and *Alexandrium affine*, characterize the autumn upwelling-downwelling transition, when they concentrate in zones of convergence (Moita et al., 1998). Especially remarkable are the blooms of these species in the Rías Baixas, in which retention is enhanced (Fraga et al., 1988; Figueiras et al., 1996).

Differences in stratification and in the intensity and pattern of upwelling imposed by the configuration and orientation of the coastline are reflected in the relative abundance of diatoms versus dinoflagellates and in their distribution. For example, the intensification of upwelling associated with the Capes Roca and S. Vicente give rise to small-scale spatial variability in the distribution of phytoplankton assemblages, with diatoms dominating upwelling plumes and dinoflagellates accumulating in the lee of these plumes (Moita et al., 2003). Also, particularly notable are the effects of upwelling and downwelling in the Rías Baixas where rapid changes between phytoplankton communities dominated by diatoms and dinoflagellates are regularly observed during summer and autumn (Figueiras et al., 1994).

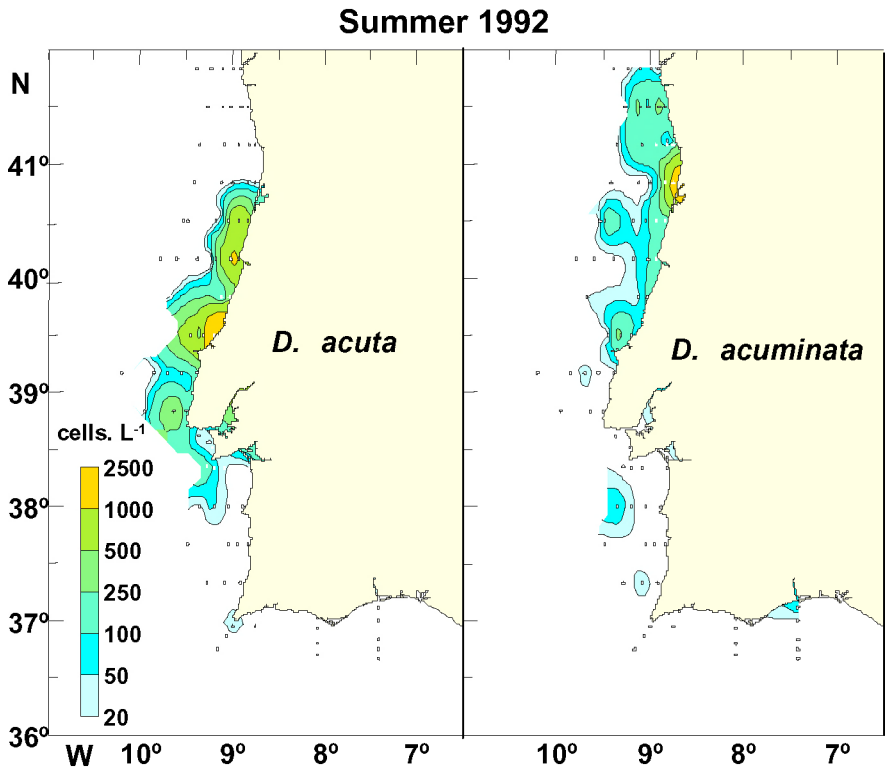

Figure 11: Distribution of *D. acuta* and *D. acuminata* during the summer of 1992 on the Western Iberian coast of Portugal (from Palma et al., 1998).

Harmful Algal Blooms

Harmful species in the Iberian upwelling system correspond to seasonal cycles modified by along-shore and cross-shelf gradients of stratification and upwelling intensity. Thus, *Pseudo-nitzschia* species are common members of the phytoplankton assemblage during the upwelling season (Figure 10; Palma et al., submitted). Hence, blooms of *Pseudo-nitzschia* species that produce ASP toxins are mainly associated with pulses of upwelling, although they can also be recorded in spring (Palma, 2003) and as early as February in the Galician Rías (Moroño et al., 2000) when winter conditions still prevail. A phytoplankton time series from Cascais Bay indicates an increase in *Pseudo-nitzschia* species 5 or 6 days following an upwelling event (Palma et al., submitted). Similar results were observed on the Galician coast (Cuadrado et al., in press). Short-lived blooms of *Pseudo-nitzschia* species, preceding dinoflagellate blooms, can also occur during the autumn transition following intermittent upwelling events. Of all the Iberian *Pseudo-nitzschia* species that have been isolated, cultured, and tested for the presence of toxicity, only *P. australis* has been proven to produce domoic acid. However, several species present in the region, for example, *P. multiseries*, *P. subpacifica* and *P. pseudodelicatissima*, remain to be cultured and tested.

The mixotrophic species *Dinophysis acuminata* and *D. acuta* are most abundant at the end of spring and during summer or in well-stratified water columns in upwelling shadows, where they are able to benefit from regeneration processes and food availability (Ríos et al., 1995). Despite their preference for stratified waters, these species bloom inshore of the upwelling front during summer and may at times be the only dinoflagellate representatives within chain-forming diatom assemblages (Moita, 2001). *Dinophysis* species have the greatest economic impact on shellfish harvests owing to their persistence in the Iberian system for much of the year, albeit in very moderate numbers (10^2 – 10^3 cells l^{-1}). *D. acuminata* and *D. acuta* often coexist but maximum concentrations do not coincide in

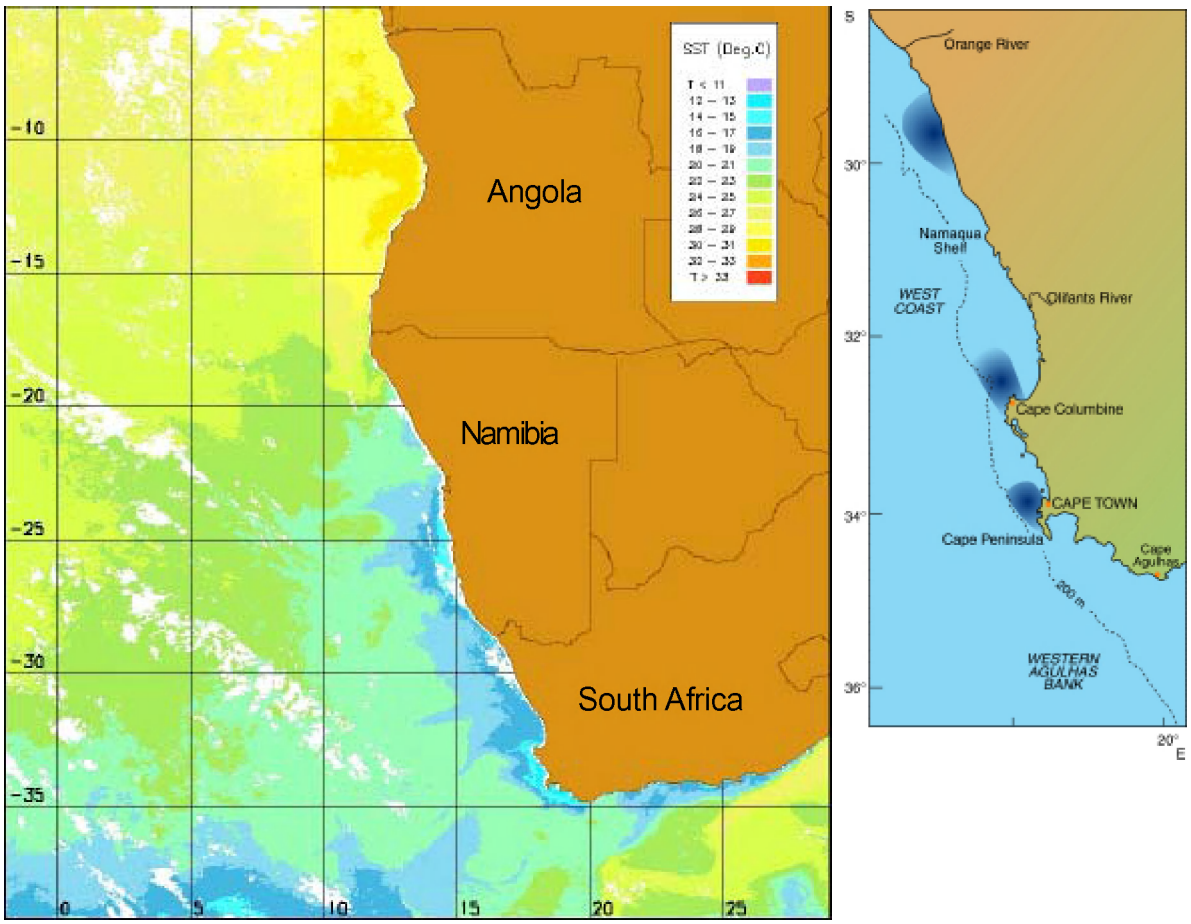

Figure 12: (a) A composite AVHRR (8-14 April 1999) image of SST off southern Africa and (b) an insert of the southern Benguela depicting the Namaqua, Cape Columbine and Cape Peninsula upwellings cells.

space or in time. *D. acuminata* maxima are typically found in the north (Figure 11) and associated with lower temperatures and salinities, whereas *D. acuta* concentrations are typically higher in the south (Reguera et al., 1993; Palma et al., 1998). Consequently, when both species bloom along the western coast of Iberia, the highest concentrations of *D. acuminata* typically occur to the north of *D. acuta*. As summer progresses blooms of *D. acuta* can be displaced northward, reaching the Galician Rias. *D. acuta* on the Iberian coast therefore shows a marked seasonal presence occurring first on the Portuguese coast with autumn peaks to the north associated with the autumn upwelling-downwelling transition (Reguera et al., 1995; Sordo et al., 2001). In Galician waters it has also been suggested that extremely dry and hot summers combined with moderate upwelling favour thermocline development within the Rías at a depth providing optimum conditions for unusual blooms of *D. acuta* during August (Reguera et al., 1995). The presence of increased numbers of *Dinophysis* species and DSP outbreaks has therefore been associated with two different scenarios: *in situ* growth favoured by periods of stratification between moderate pulses of upwelling, and downwelling events that favour the accumulation of *Dinophysis* (Reguera et al., 1995, 2003; Sordo et al., 2001).

The autotrophic dinoflagellates *Gymnodinium catenatum*, *Karenia mikimotoi* and *Lingulodinium polyedrum* are efficient swimmers and are frequently found in late summer-early autumn, at the time of the seasonal transition from upwelling to downwelling, when convergences are well developed along the western Iberian coast (Fraga et al., 1988; Figueiras et al., 1996; Moita et al., 1998; Pazos et al., 2003; Amorim et al., in press). Their enhanced swimming capabilities (Fraga et al., 1989; Hallegraeff and Fraga, 1998) provide these species with an advantage in areas of convergence. Between 1985 and 1995, major toxic events on the Iberian coast were ascribed to blooms of the

chain-forming dinoflagellate and cyst producer *G. catenatum*, a species that seems to have spread along the Iberian coast over the years. However, the most recent blooms have been restricted to the Alboran Sea eddy in the Mediterranean Sea (Morales et al., 2003). In recent years, *L .polyedrum* has bloomed in the southern Iberian Atlantic area, in warm stratified waters compressed by adjacent upwelling (Amorim et al., in press), and in the northern Rías of Galicia, where major blooms were recorded in 2003 (Arévalo et al., in press).

3) Harmful Algae in the Benguela Upwelling System

Physical and Chemical Environment

The Benguela system is characterised by upwelling circulation along the entire west coast of southern Africa (Figure 12), and is unique in that it is bound at both the equatorward and poleward ends by warm water regimes, notably the Angola-Benguela front in the north and the Agulhas retroflection area in the south (Shannon and Nelson, 1996). Cape Agulhas is considered the appropriate southern boundary as upwelling typically extends that far during summer and for this reason the Western Agulhas Bank is considered an integral part of the productive west coast. Nevertheless, there are some important biogeographic differences between the west coast and Western Agulhas Bank which are reflected in the composition of HABs (Pitcher and Calder, 2000).

The winds responsible for upwelling in the Benguela are controlled by anticyclonic motion around the South Atlantic high pressure system, by the seasonal low pressure field over the sub-continent, and by eastward-moving cyclones that cross the southern part of the continent (Nelson and Hutchings, 1983). The principal semi-permanent upwelling cell in the vicinity of Luderitz in southern Namibia effectively divides the system into northern and southern components, with the southern Benguela experiencing greater seasonality. Here, upwelling-favourable winds reach a maximum during spring and summer with modulation of upwelling at periods of 3 to 6 days in response to wind relaxation or reversal associated with the passage of cyclones south of the continent (Nelson and Hutchings, 1983). Associated with the approach of cyclonic systems is the appearance of cells of low pressure which form near Luderitz and travel around the subcontinent as trapped waves. The cyclonic rotation of air about these cells suppresses upwelling locally as they travel along the coast and the relaxation of the wind at the centre causes suitable conditions for the generation of inertial motions and shelf waves. In winter, the northward shift of the South Atlantic high pressure system has a stronger influence in the south, resulting in a greater frequency of westerly winds, which do not produce upwelling. There are also distinct interannual variations in the synoptic-scale wind field, of which the most significant is related to ENSO. During El Niño, upwelling winds in the southern Benguela tend to weaken, while during La Niña long-shore upwelling-favourable winds tend to strengthen (Preston-Whyte and Tyson, 1988).

The Benguela current is topographically steered. Shelf waters are very responsive to the wind in the classical Ekman sense, resulting in equatorward flow at the surface and in shelf-edge baroclinic jets. Net subsurface flow on the Benguela shelf and over the continental slope is poleward, as is the case in most eastern boundary upwelling regions. Particularly important to coastal blooms is the presence of an inshore surface counter-current responsible for southward flow when barotropic reversals take place in long-shore flow. There exists over much of the Benguela a well-developed long-shore thermal system of fronts demarcating the seaward extent of upwelled water. The oceanic front, shelf-break front and upwelling front are often referred to without distinction. Although this may be appropriate where the three fronts are coincident, there are areas where two or three fronts can be resolved (Shannon and Nelson, 1996). Upwelling filaments are characteristic of the oceanic

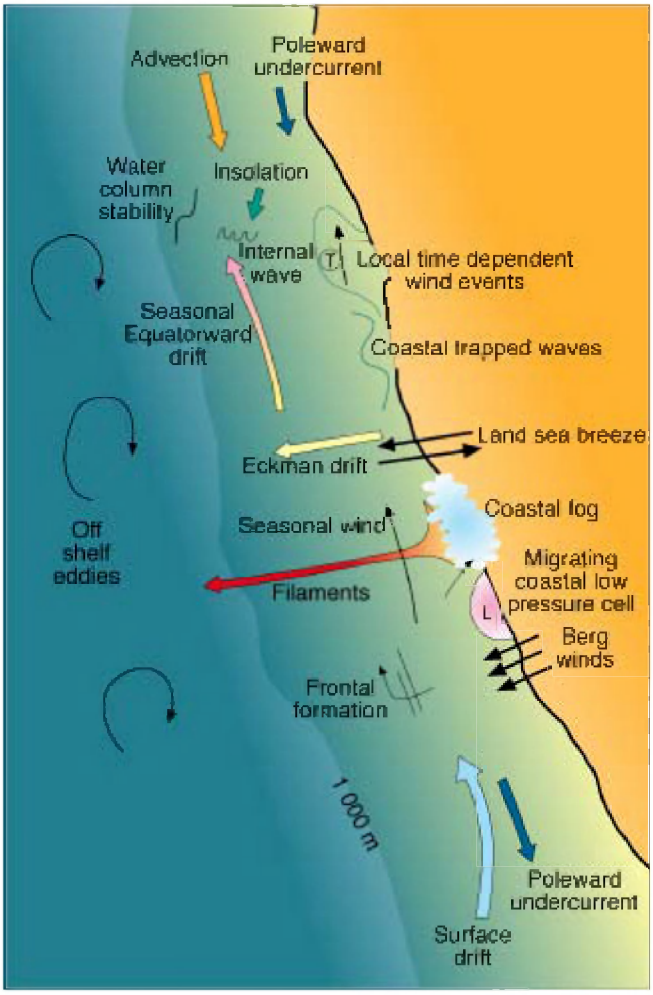

Figure 13: A schematic representation of the complex array of physical influences in the Benguela eastern boundary system. Wind is a dominant factor at all spatial scales, having a direct influence on large-scale currents, local upwelling and frontal dynamics, and the dynamics of the surface mixed layer. Consequently, HABs are closely linked to the prevailing winds of the Benguela (from Figure 26, p. 202, in Shannon and Nelson, 1996). Used with permission from authors and from Springer-Verlag GmbH & Co.

front, are orientated perpendicular to the coast and have a life-span of a few days to several weeks.

Continental shelf bathymetry and upwelling winds provide the large-scale upwelling mechanism in the southern Benguela, whereas local topography and meteorology create an alternating pattern of active and passive upwelling circulations along the coast. Consequently, clearly defined tongues of cool water extend offshore from upwelling centres. Long-shore variability is therefore often as dramatic as the expected offshore changes and is most apparent in comparing sites of active upwelling to those downstream, on the leeward side, of upwelling centres.

Phytoplankton Dynamics

Phytoplankton biomass is highest during summer and autumn but superimposed on this seasonal variation are shorter cycles related to wind reversals (Pitcher et al., 1992). Consequently, nearshore waters of the Benguela have been classified into three types that follow sequentially after water has upwelled (Barlow, 1982). Type 1 water corresponds to newly upwelled water with a temperature of <10°C, a chlorophyll a concentration of <1 mg m^{-3} and high concentrations of inorganic nutrients. Type 2 water corresponds to maturing upwelled water and is characterised by temperatures >10 °C, chlorophyll a concentrations of 1-20 mg m^{-3} and nitrate concentrations of 2-15 mmol m^{-3}. Type 3 water of between 12 and 16 °C corresponds to aged upwelled water and contains low concentrations of nitrate of <2 mmol m^{-3} and chlorophyll a concentrations typically range between 5 and 30 mg m^{-3}. The high productivity of the southern Benguela has in the past generally been ascribed to diatoms (Shannon and Pillar, 1986). However, Mitchell-Innes et al. (2000) claim that highest productivity is observed in shelf waters on the west coast in late summer and can be attributed largely to dinoflagellate populations. A number of production estimates have been made within these high-biomass dinoflagellate blooms. Brown et al. (1979) estimated a productivity of 405 mg C m^{-3} h^{-1} within a *Gymnodinium* bloom on the south coast, Walker and Pitcher (1991) measured a productivity of 520 mg C m^{-3} h^{-1} in a *Ceratium furca* bloom in St Helena Bay and Mitchell-Innes et al. (2000) also reported productivity estimates of >500 mg C m^{-3} h^{-1} for blooms of *C. furca* on the Namaqua shelf.

Species successions within the Benguela are associated with the spatial and temporal transitions from turbulent to stratified water columns, in which there is a shift in the control of production

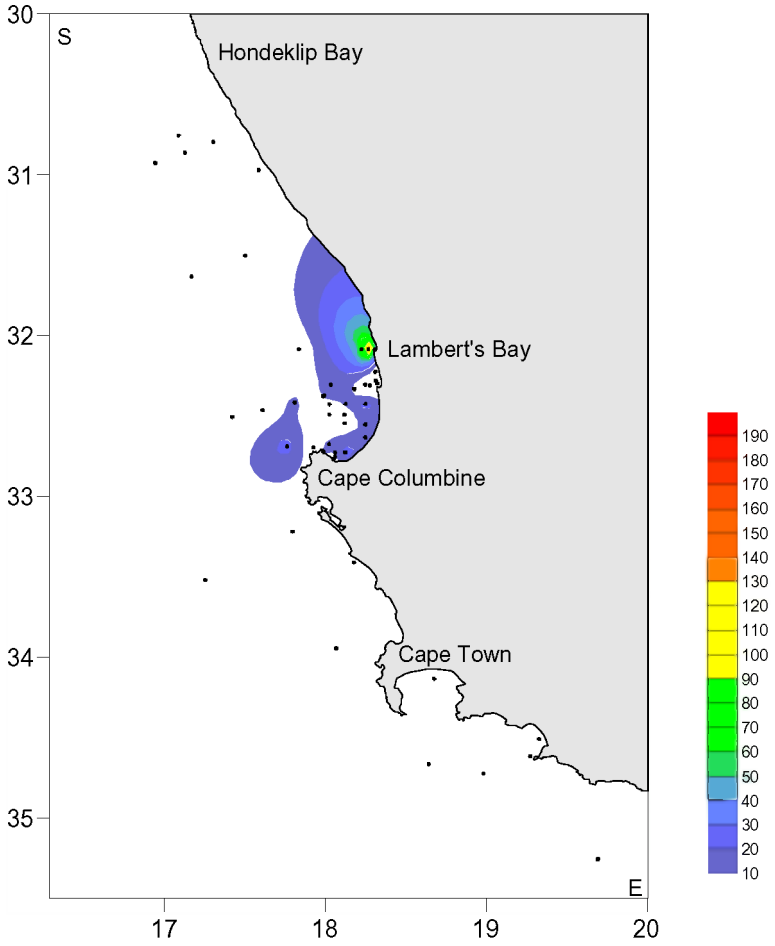

Figure 14: Distribution of cysts of *Alexandrium catenella* (cysts ml^{-1} wet sediment) in the southern Benguela (from L. Joyce, unpublished data).

dynamics from a dependence on new nitrogen to regenerated nitrogen (Hutchings et al., 1995). The rampant growth of diatoms typically follows upwelling. As stratification strengthens and persists, dinoflagellate blooms may follow and typically precede small-sized flagellate blooms after new nutrients become limited. Large blooms of coccolithophorids may characterise these late stages of succession (Weeks et al., 2004). 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.

Harmful Algal Blooms

HABs in the Benguela are typically attributed to one or another dinoflagellate species and most harmful impacts are associated with either their high biomass or the toxigenicity of some species. Harmful impacts attributed to high biomass dinoflagellate blooms, which ultimately led to low oxygen events and in some cases the production of hydrogen sulphide, have for many years lead to spectacular mortalities of marine organisms in the Benguela. Referred to as red tides, Gilchrist (1914) listed these blooms as one of the factors causing fluctuations in fish stocks in the Benguela. Monitoring has indicated that the distribution of these blooms is clearly associated with the upwelling system, with few red tides reported east of Cape Agulhas (Pitcher and Calder, 2000).

HABs are closely linked to the prevailing winds of the Benguela, as wind is a dominant factor at all spatial scales, having a direct influence on large-scale currents, local upwelling and frontal dynamics, and the dynamics of the surface mixed layer (Figure 13). The focus of research on HABs has been in the southern Benguela, where three upwelling centres may be distinguished, all of which coincide with a narrowing of the shelf: the Cape Peninsula, Cape Columbine and Namaqua upwelling centres (Shannon, 1985). These upwelling cells are normally located near regions of cyclonic wind-stress curl and are associated with changes in the orientation of the coastline. The region between the Cape Columbine and Namaqua cells is known as the Namaqua shelf. Here, the shelf is broad, favouring stratification that appears to be conducive to the development of harmful blooms and their negative impacts. Under conditions of upwelling the surface drift is mainly northerly and dinoflagellate blooms are associated with the frontal system demarcating the inshore band of upwelling. Wind reversals cause this frontal system and associated dinoflagellate bloom to move shoreward, and the development of an inshore counter current may result in the southward progression of blooms along the Namaqua coast (Pitcher et al., 1998).

Monitoring data have also demonstrated the seasonality of blooms, with the highest incidence of blooms occurring in late summer, corresponding to increased stratification, which depends in a predictable way on the wind and increased solar irradiance. The seasonal incidence of blooms does, however, vary spatially. In the Namaqua region the incidence of blooms increases steadily through the upwelling season, reaching a peak in February and March. At this time blooms are absent further south, 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 HABs south of Cape Columbine is in April and May.

The Benguela is characterized by a variety of toxic dinoflagellates that vary spatially in their distribution. The northern Benguela is characterised by the fish-killing dinoflagellate *Gymnodinium galatheanum*, a species described by Braarud (1957) from samples collected off Namibia by Steeman Neilson in 1950 during a fish kill. The distribution of this species does not, however, appear to extend into the southern Benguela. Another fish-killing dinoflagellate is the newly described species *Karenia cristata* (Botes et al., 2003). Initially responsible for large abalone mortalities in the 1980s, this species appears to be restricted to the Western Agulhas Bank. This species shares several characteristics with *Karenia brevis* and the recently described species from New Zealand waters, *Karenia brevisulcata*, in that it also produces an aerosol toxin responsible for respiratory and skin disorders.

In the southern Benguela, blooms of *Alexandrium catenella* responsible for PSP are common and have historically been the primary concern of marine scientists and managers. Although some of the earlier possible accounts of PSP in the Benguela date back to the 1880s, confirmed cases of PSP were only described in 1948 (Sapeika, 1948). The full northern extent of *Alexandrium catenella* is not clearly defined, but it is known to extend into southern Namibia. *A. catenella* has not been recorded east of Cape Point, but an undescribed *Alexandrium* species has recently been isolated from the Western Agulhas Bank (Ruiz Sebastian et al., in press). The latter, however, does not appear to form substantial blooms and the cell toxin quota is low; thus, it is unlikely to render shellfish toxic. The distribution of these species is confirmed by the incidence of PSP-contaminated shellfish, with no recordings of PSP east of Cape Point, while the highest incidence of contaminated shellfish is found as expected in the Namaqua region downstream of the Cape Columbine upwelling cell. Concentrations of *A. catenella* cysts in the sediments similarly correspond to this distribution (Figure 14). Monitoring on the Namaqua coast has indicated that *A. catenella* appears almost every year, typically during the latter part of the upwelling season. *A. catenella* in the Benguela can be found at exceedingly high cell concentrations of many million cells l^{-1} and these blooms not only render shellfish toxic to consumers, but are also seemingly responsible for fish and shellfish mortalities (Pitcher and Calder, 2000).

The other very common form of shellfish poisoning in the Benguela is DSP, usually attributable to *Dinophysis acuminata* or *Dinophysis fortii*. *Dinophysis* species often form relatively minor components of blooms dominated by other dinoflagellates, but can nevertheless attain high cell concentrations of the order of one million cells l^{-1} (Pitcher et al., in prep). Despite considerable interannual variation in cell densities, time-series data have revealed the intermittent presence of *Dinophysis* spp. throughout the upwelling season, with concentrations peaking in the late summer and autumn (Pitcher and Calder, 2000), at which time their distribution is often widespread (Figure 15). For both *D. acuminata* and *D. fortii*, cell toxin quota data indicate that these species are only moderately toxic in the Benguela, with okadaic acid identified as the primary toxin. Time-series data from the Namaqua coast of okadaic acid concentrations in mussels reveals that toxin concentrations

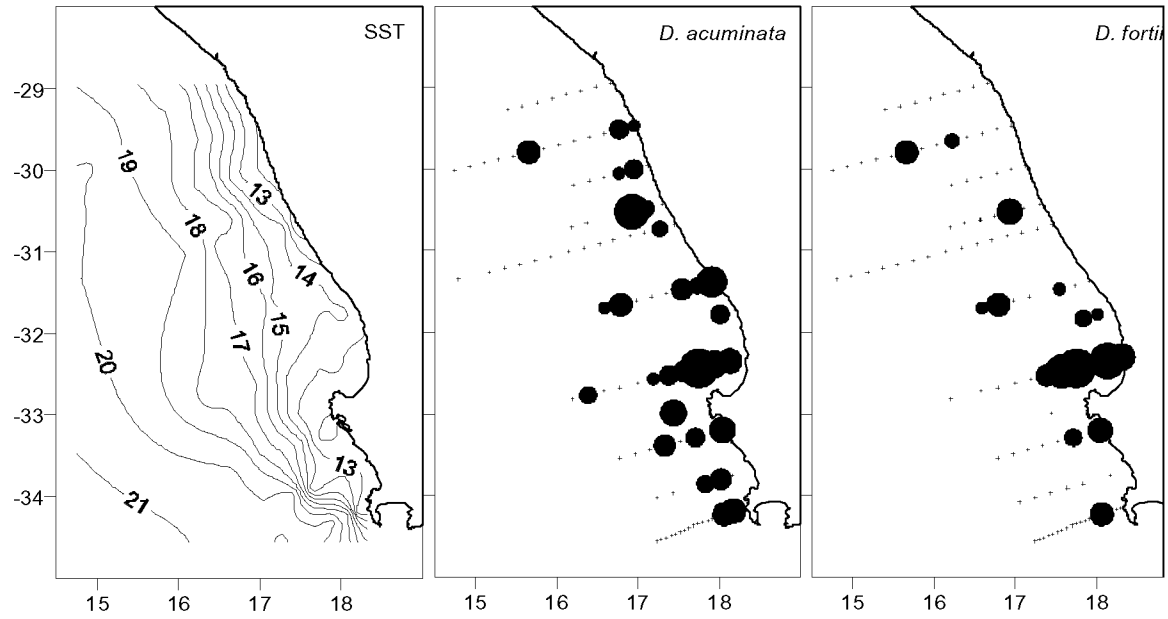

Figure 15: Surface distributions of SST, *Dinophysis acuminata* and *Dinophysis fortii* in the southern Benguela in March 2001 (scale range: 0 - 4675 cells l^{-1}; from Pitcher et al., in prep).

during summer and autumn frequently exceed the harvestable limit, indicating the severity of the problem posed by DSP in the Benguela (Pitcher et al., in prep).

Other algal species reported to form red tides or to be toxic are listed by Pitcher and Calder (2000). Common in the Benguela, but only of potential harm are various species of *Pseudo-nitzschia*. *Pseudo-nitzschia australis*, for example, has been identified as a very common bloom-forming species in the Benguela, but to date no trace of domoic acid has been found in cultures of this species and no form of shellfish poisoning has been associated with these blooms (Marangoni et al., 2001). Similarly, *Protoceratium reticulatum* (formerly *Gonyaulax grindleyi*) is known to bloom in the southern Benguela (Horstman, 1980), but no attempts have been made to determine the presence of yessotoxins. *Lingulodinium polyedrum* (formerly *Gonyaulax polyedra*) has also been recorded within the region (Kruger, 1980), but no harmful effects have been attributed to this dinoflagellate.

IV - KEY QUESTIONS TO BE ADDRESSED IN UNDERSTANDING THE ECOLOGY AND OCEANOGRAPHY OF HABS IN UPWELLING SYSTEMS

Based on the current knowledge and understanding of HABs in the three target upwelling systems, eight key questions were developed for this Core Research Project. These questions are intended to provide research foci that will help GEOHAB achieve its goals and as foci for regional and international research collaboration.

A. Are there definable adaptive strategies that characterize HAB species in upwelling systems?

Background

Harmful algal species exhibit a wide variety of life-cycle strategies, trophic types, physiology, morphology and harmful effects. Flagellate species account for 90% of the HAB species, and among the flagellates, the dinoflagellates stand out as a particularly noxious group (Smayda, 1997). Although it is uncertain as to whether a distinctive physiological profile distinguishes these harmful flagellates from non-harmful taxa, HAB flagellates are considered to exhibit greater biophysical vulnerability to turbulence, greater bloom dependence on watermass stratification, greater nutritional diversity involving mixotrophic tendencies, greater potential use of allelochemical mechanisms and unique behavioural consequences associated with their motility (Smayda, 1997).

Table 1: Predominant dinoflagellate bloom taxa along an onshore-offshore gradient of decreasing nutrients, reduced mixing and deepening euphotic zone (from Smayda and Reynolds, 2001). Permission granted from Oxford University Press for use of this figure from the Smayda and Reynolds article in *Journal of Plankton Research*, Volume 23(5), 2001.

- **Type I (= Gymnodinioids)**

Gymnodinium* spp., *Gymnodinium instriatum*, *Katodinium rotundatum

- **Type II (= Peridinians / Prorocentroids)**

Heterocapsa triquetra*, *Scripsiella trochoidea*, *Prorocentrum micans*, *Prorocentrum minimum

- **Type III (= Ceratians)**

Ceratium tripos*, *Ceratium fusus*, *Ceratium lineatum

- **Type IV (= Frontal Zone Taxa)**

Gymnodinium mikimotoi*, *Alexandrium tamarense

- **Type V (= Upwelling Relaxation Taxa)**

Gymnodinium catenatum*, *Lingulodinium (Gonyaulax) polyedra

- **Type VI (= Coastal Current Entrained Taxa)**

Gymnodinium breve*, *Ceratium* spp., *Pyrodinium bahamense* var. *compressum

- **Type VII (=Dinophysoids)**

Dinophysis acuta*, *Dinophysis acuminata

- **Type VIII (= Tropical Oceanic Flora)**

***Amphisolenia*, *Histioneis*, *Ornithocerus*, *Ceratium* spp.**

- **Type IX (= Tropical Shade Flora)**

Pyrocystis noctiluca*, *Pyrocystis pyriformis

Upwelling regions are considered by Smayda (2000) to be the most complex habitats in which dinoflagellates are selected, but in general the flora are not considered unique as many species also bloom in nutrient-enriched non-upwelling systems. Nevertheless, certain dinoflagellate life-forms, for example, ceratian, prorocentroid and gymnodinian, may be selected over others in being better adapted to upwelling habitats. The rarity of other phytoflagellate groups in developing blooms in upwelling systems is notable, and blooms of the microbial loop predator *Noctiluca scintillans* and the endosymbiotic *Mesodinium rubrum* are ubiquitous in upwelling regions.

Upwelling habitats are mosaics of multiple and shifting sub-habitats, whose physical and chemical properties exhibit sharp spatial and temporal heterogeneities, a variability that leads to many niche types and disruptions. Within upwelling systems species need to cope with strong physical forcing and the biophysical consequences of varying turbulence, and entrainment within advective currents and frontal zones. Diatoms and dinoflagellates represent extremes in terms of their adaptive strategies and are consequently spatially and temporally segregated. For dinoflagellates the problem is to survive turbulent water masses, without biophysical impairment, to access mixing zones and strata of high nutrient availability and to achieve population growth over a time period adequate for the completion of their life cycles.

Smayda and Reynolds (2001) have identified nine distinct and diverse habitat types in which dinoflagellates may bloom (Table 1 and Figure 16). Associated with each habitat are dinoflagellate life-form types which ordinate on a habitat template along onshore-offshore gradients of decreasing nutrient, reduced mixing and deepening of the euphotic zone. Several of these habitat types are associated with upwelling systems incorporating near-shore, coastal and shelf environments, and fronts, coastal currents and upwelling events.

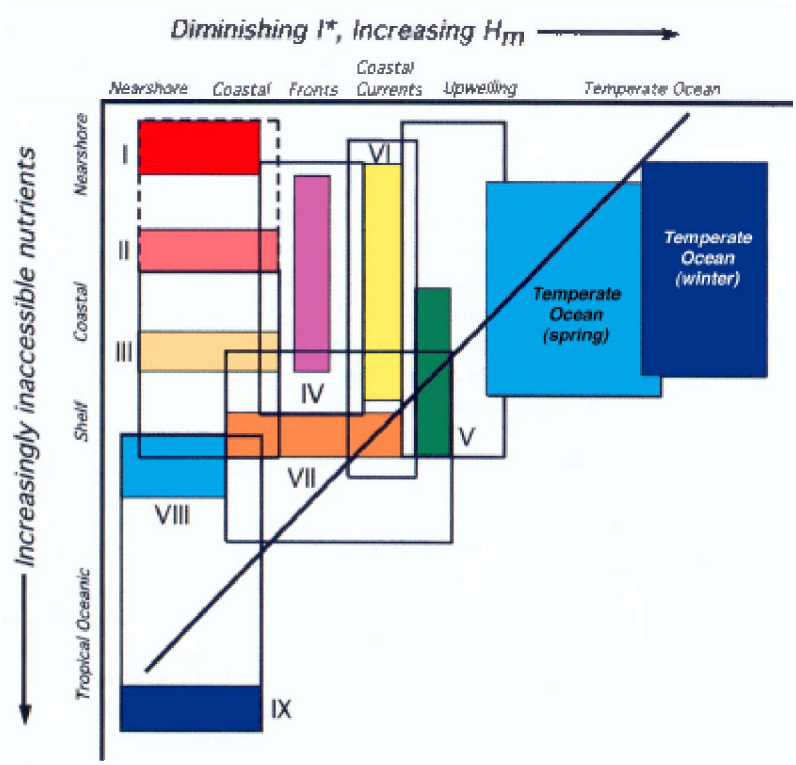

Figure 16: Schematic matrix of pelagic marine habitats along an onshore-offshore gradient separating deep-mixed and well-stratified, but nutrient-deficient systems (from Smayda and Reynolds, 2001). Permission granted from Oxford University Press for use of this figure from the Smayda and Reynolds article in *Journal of Plankton Research*, Volume 23(5), 2001.

A major unresolved issue is whether there are adaptive features characteristic of the species common to upwelling systems and how these may differ from those features characteristic of species in non-upwelling systems.

Justification for Comparative Approach

Comparison of HAB species in different upwelling systems will allow assessment of the cellular properties and environmental mechanisms that select for species or assemblages common to upwelling systems. These comparisons will allow identification of the characteristics of upwelling species that determine their potential for growth and persistence in upwelling systems. Comparison will also allow confirmation of groups of co-occurring taxa or assemblages within upwelling systems, incorporating functional groups in which HAB species are found, and determination of their temporal succession within upwelling systems.

Detailed Questions

- Can specific photoadaptive strategies, nutritional modes, allelochemical or allelopathic strategies, or behavioural or life-history strategies be linked to particular HAB species common to upwelling systems?

- To what extent are HAB dynamics in upwelling systems influenced by "top-down" processes (i.e., predation and viral attack)?

- Can the formulation of functional groups provide the potential for prediction owing to the distinctive ecophysiological properties of various life-forms significant to their bloom dynamics, habitat selection and successions?

Research Approach

A detailed comparison is required of the HAB species in upwelling systems by characterising them using morphology, molecular genetics, biochemical composition and other cellular properties. The functional role of cell properties, including morphological, physiological, behavioural and life-history characteristics common to HAB species in upwelling systems will require identification and comparison. This comparison will require quantification, parameterisation and prioritisation of ecophysiological processes at the cellular level that will assist in identification of any key adaptive strategies common to species in upwelling systems. Ultimately, this approach will provide an ecologically based classification of the different species found in upwelling systems based on their adaptive strategies.

B. What seeding strategies persist within upwelling regions and are they consistent among regions?

Background

Upwelling systems are inherently advective, and as such provide a unique selective pressure on phytoplankton population maintenance. To counter advective washout, phytoplankton may require species-specific seeding strategies to facilitate bloom initiation and persistence. Cells or assemblages are expected to use such strategies when environmental conditions are less than favourable, typically

during the winter months, but these processes are potentially important at all times of the year. Two extreme types of seeding strategies are distinguishable: one in which seeding is achieved by fugitive vegetative cells in the surface layer and the other by deep-living refuge resting cells. Important to these strategies is the incorporation by some species of a spore or cyst stage in their life cycle. Characterisation of environmental influences on life history events is therefore necessary and synchronization of cyst germination in response to specific environmental cues indicative of favourable growth conditions may play an important role in seeding success (Anderson, 1998).

Alexandrium species are well known, for example, to form cysts that reside in sediments. The location of these seed beds is relatively well characterized in some upwelling zones, but poorly characterised in others. In the Benguela system, persistent seed beds of *A. catenella* have been observed in the nearshore environment (Figure 14). In contrast, little is known about the location or presence of seed beds of *A. catenella* in the CCS. In the Iberian upwelling system the cyst-forming *Gymnodinium catenatum* is responsible for recurrent blooms and Figueiras and Pazos (1991) have considered cyst germination to play an important role in the development of local blooms in the Rías Baixas, although Bravo and Anderson (1994) have indicated that bottom temperatures of >15 °C are necessary for the germination of *G. catenatum* cysts, and these temperatures are observed only during downwelling. Cyst mapping along the Iberian shelf (Blanco, 1995a; Bravo and Ramilo, 1999; Moita and Amorim, 2002) has indicated a low density of cysts suggesting that cysts may germinate continuously, supplying a constant inoculum to the water column. These cells could be concentrated in retention or accumulation areas, such as those found downstream of major capes or inside the Rías during downwelling, thereby providing the source inoculum for blooms (Blanco, 1995b; Moita and Amorim, 2002). This situation contrasts with *Lingulodinium polyedrum,* the cysts of which appear to accumulate in large numbers in the sediments of the Iberian shelf, thereby providing seedbeds that may play an important role in bloom initiation.

The seeding strategies of other HAB species are less well known. In nearshore areas, *Pseudo-nitzschia* species are known to be a major component of marine snow that sinks to form flocculent deposits in the benthos, and viable cells are often found at depths significantly below the euphotic zone. However, it is not known whether these flocculent layers are the main mechanism that *Pseudo-nitzschia* cells use for overwintering. There have been some indications that *Pseudo-nitzschia* may form a resting stage, but this has not been clearly demonstrated. Similarly, it has been suggested for the CCS that *Pseudo-nitzschia* may be associated with mesoscale retentive features, such as the Juan de Fuca Eddy, which could serve as an alternative seed source for coastal populations. Smayda (2002) has argued that frontal systems provide a physical setting suitable to act as a pelagic seed source.

Because the seeding strategies for HAB organisms are poorly understood and the sites of seed beds are not described for upwelling systems, little is known about the inter- and intraspecific differences in seeding strategies among upwelling regions, or the role of seeding in maintenance of HAB populations. Establishment of the sites of HAB initiation and characterisation of environmental influences on the life history stages of HAB species in upwelling systems therefore remains a priority.

Justification for Comparative Approach

Comparative studies among upwelling systems will assist in assessing whether the differences in a given species' success or dominance are attributable to differences in seeding or initiation strategies. Comparative studies are needed to test the robustness of our understanding of seeding strategies

across upwelling systems. Comparisons will help identify the sensitivity of seeding strategies to different biological, chemical and physical factors. One of the characteristics of many overwintering stages is the existence of a mandatory dormancy period, the length of which is known to be affected by internal and abiotic factors. From the literature it is clear that dormancy periods of overwintering stages may vary among species and even within a single species among geographically different populations. Comparative studies incorporating standardized methods in different upwelling systems will help us understand how HAB dynamics are dependent on seed population characteristics, both across species and within species from geographically different populations.

Detailed Questions

- To what extent are refuge resting stages versus fugitive vegetative populations used as seeding strategies?

- Do geographically different populations of a given harmful species utilize the same seeding strategies across upwelling regions?

- What environmental influences (light, temperature, nutrients, etc.) or intrinsic cellular signals (biological clock) are responsible for controlling life-history events and are they similar across upwelling systems?

- To what extent are bloom dynamics influenced by the physical introduction or resuspension of seed populations versus biological initiation of cell growth or germination?

Research Approach

Studies during non-bloom periods or winter are particularly useful in providing information about HAB seeding strategies as this is an ideal time to search for slowly metabolizing vegetative cells in the water column, for resting cells in bottom flocculent layers and for cysts in the sediments.

The process of encystment during HABs may be characterized by following blooms using a drogue or some other tracer. Floating sediment traps are ideal for this type of study. Upwelling systems generally have well characterized mid-shelf mud belts where encysting organisms are likely to be found. Benthic studies are needed in these areas to determine the extent of cyst populations and circulation models may be utilized to identify potential areas of accumulation. A comparative study of sediment types in which the cysts of HAB species are found will provide insight into regions where seed beds might be located. To better evaluate the importance of seed beds to bloom initiation new molecular techniques aimed at identifying life cycle stages and the physiological status or viability of cysts and overwintering stages should be developed.

For overwintering to be successful, the seed population needs to be entrained back into the surface boundary layer. It is important to establish whether physical mechanisms are required for this entrainment or whether cysts are able to germinate in the sediments and actively swim into surface waters. To better understand the cue for HAB initiation from known cyst beds, inverted traps may be used to assess physical entrainment versus cell germination. A comparison of the timing of initiation with known physical and chemical parameters will assist in determination of the environmental cues important in excystment and similar processes. If no environmental cues can be identified, it is possible that excystment is a response to an endogenous signal (biological clock). Although laboratory

studies are unlikely to reproduce all of the potential environmental conditions associated with excystment, this approach can complement field research by addressing specific cues or processes.

One approach to answering these questions is to fully characterize a well-known system, and to apply this knowledge to other systems to ultimately establish similarities and differences among systems.

C. How do small-scale physical processes affect HAB growth and dispersion in upwelling systems?

Background

The importance of small-scale physical processes in effecting phytoplankton selection is observed in the vertical dimension (i.e., the dynamics of the surface boundary layer). Owing to this factor, stratification following upwelling has been identified as a habitat feature operative in regulating spatial and temporal differences in phytoplankton assemblages and clustering taxa with shared features. Diatom- and dinoflagellate-dominated communities tend, therefore, to be spatially and temporally segregated and predictable in terms of the degree of stratification.

These observations are consistent with the conceptual model of Margalef (1978) in which functional groups of phytoplankton, sharing various life-form properties, are variously adapted to a turbulent environment, defined in terms of nutrient availability and turbulence. The model combines the interactive effects of habitat mixing and nutrient conditions on the selection of phylogenetic morphotypes. In this context, the typical phytoplankton succession, from fast-growing diatoms to motile dinoflagellates, is driven by changes leading from a well-mixed, nutrient-rich water column to a nutrient-poor stratified environment. Later redesign of the Margalef model included "red tide" development as a parallel trajectory to the typical succession, in an environment in which a relatively high nutrient concentration is associated with relatively low turbulence. Smayda and Reynolds (2001) have further distinguished the habitat preferences of dinoflagellate bloom species along a continuum of progressively decreasing nutrient levels, increasing inertia of water masses against mixing, and deepening of the stratified layer.

Turbulent mixing determines much high-frequency environmental fluctuation and in so doing can control nutrient, irradiance, and phytoplankton patchiness, and is also known to affect plankton growth rates. Interactions of water motion and phytoplankton communities are important in life form and species-specific selection of phytoplankton. Large-scale turbulence can affect a range of biological processes, mostly related to the bulk distribution of cells, whereas small-scale turbulence influences primarily physiological processes at the level of individual phytoplankton cells. Turbulence, stability and stratification are often used interchangeably in relating phytoplankton dynamics to water mass mixing characteristics, but small-scale turbulence is a biophysical parameter operating primarily at the cellular level, while stratification is a habitat parameter operating at the level of the population (Smayda, 1997).

Although the causes of shifts in phytoplankton community structure favouring flagellate taxa and their blooms have yet to be resolved (Smayda and Reynolds, 2001), stratification has been recognized as a precondition for the development of some major types of harmful algae. Dinoflagellates are, for example, considered particularly susceptible to turbulence, being well adapted to lower energy, stratified conditions (Cullen and MacIntyre, 1998; Estrada and Berdalet, 1998). Dinoflagellate blooms

are therefore thought to be negatively influenced by turbulence through physical damage, physiological impairment and behavioural modification. Many HAB species are motile, and under certain environmental conditions their swimming behaviour may result in the formation of high-density aggregations (e.g., Franks, 1992; Cullen and MacIntyre, 1998; Kamykowski et al., 1998). Diel vertical movement by motile cells in a stratified environment undoubtedly has functional significance, maximizing encounter frequencies for sexual reproduction, minimizing grazing losses, and allowing cells to optimize nutrient acquisition at depth and light-dependent photosynthetic reactions near the surface.

Justification for Comparative Approach

The surface boundary layer is the conduit between atmospheric forcing, both wind stress and surface heat flux, and the oceanic response, incorporating the response of the phytoplankton community to changes in the upper water column structure. Lentz (1992) has found the surface boundary layer in coastal upwelling regions to be characterised by a mixed layer of between 0 and 20m, with most variability at diurnal and subtidal periods. Near-surface current profiles are similar, in that offshore flow associated with equatorward winds is relatively uniform within the surface mixed layer, with a transition region of large shear below the surface mixed layer. Cross-shelf transport is also in good agreement with the Eckman transport computed from wind stress.

Temporal and spatial patterns in wind forcing within upwelling systems are therefore the primary determinant of upper water column structure. Varying responses in terms of the succession of species within and between upwelling systems will allow inferences of the properties of the upper water column regulating species succession and the development of HABs.

Detailed Questions

- How do surface boundary layer conditions and mixed-layer depth influence the growth rate of HAB species?

- To what extent is the growth rate of HAB species determined by turbulence through its influence on the transport of nutrients, the mixing of phytoplankton through gradients of light, and by direct impairment of growth?

- How are the behavioural responses of phytoplankton, particularly swimming, influenced by surface boundary layer conditions?

Research Approach

Features of the surface boundary layer of upwelling systems, particularly those that support morphological, physiological and life-history features common to HAB species in upwelling systems, need to be identified and quantified. In addition, functional groups (or groups of co-occurring taxa) incorporating HAB species need to be defined and related to these features of the surface boundary layer. Controlled laboratory and mesocosm studies of the response of different HAB species to small-scale physical processes are required to confirm field observations, and these must accurately reflect surface boundary layer conditions in upwelling systems.

D. How do nutrient supply type and ratios determine HAB population dynamics in upwelling systems?

Background

Nutrient supply rates – either by physical or biological means – are often the primary determinant of biomass increase through control over cellular and population growth rates of phytoplankton assemblages. The critical issue with regard to population and community increase is the injection of new nutrients (Dugdale and Goering, 1967) to the photic zone from deep water reservoirs or from terrestrial and atmospheric input. Coastal upwelling ecosystems represent the extreme case of natural new nutrient input and thus can be expected to be characterized by intense blooms of both harmful and benign species.

The nutrient most often implicated in the limitation of growth in the sea is N, though clearly Si may serve a limiting role for diatoms. In a number of instances changes in the ratio of Si to N have been implicated in the establishment of dinoflagellate blooms. Smayda (1990) offers compelling evidence from a number of regions that the global increase in novel phytoplankton blooms may be related to a declining ratio of Si to N as a result of eutrophication, thereby favouring species that do not require Si. Iron has received much attention as an important limiting micronutrient particularly in oceanic high nutrient, low chlorophyll regions. Although terrigenous input may offset deficiencies in certain coastal marine environments, recent evidence indicates Fe limitation in parts of the Peruvian and Californian upwelling regions where riverine, aeolian and/or sediment supplies are reduced (Hutchins and Bruland, 1998: Hutchins et al., 1998, Eldridge et al,. 2004). The stimulation of diatom growth, including *Pseudo-nitzschia* spp., by Fe addition and the relative abundance of dinoflagellates in Fe-limited waters, suggests Fe availability may play a role in the development of HABs (Hutchins et al., 1998).

Dinoflagellate blooms off the Iberian Peninsula and in the Southern Benguela are generally associated with downwelling conditions following a relaxation in upwelling conditions that allows for the onshore and/or poleward transport of existing populations (Fraga et al., 1988; Pitcher and Boyd, 1996; Moita and da Silva, 2000; Sordo et al., 2000; Probyn et al., 2000). Similarly, toxic events resulting from *Alexandrium catenella* blooms off California occur during relaxation of upwelling and onshore advection (Langlois, 2001). In contrast, blooms of *Lingulodinium polyedrum* off California appear to be associated with high levels of nutrient input to near-surface waters via upwelling (Eppley and Harrison, 1975), although blooms can also occur outside the upwelling season, presumably fueled by high-nutrient freshwater runoff (Hayward et al., 1995; Kudela and Cochlan, 2000). *L. polyedrum* has been termed a good indicator of increased nutrient supply (Lewis and Hallet, 1997), although measured uptake affinities for NO_3 and reduced N indicate a strong competitive capability under N-depleted conditions (Kudela and Cochlan, 2000). Although blooms of *Pseudo-nitzschia* species are generally associated with coastal upwelling zones (Lange et al., 1994; Trainer et al., 2000, 2001), time-series data suggest that major toxic blooms occur during periods of weak upwelling (Kudela et al., in press). Although mooted as a possible driving mechanism, freshwater nutrient input is not clearly established as an important contributor to *Pseudo-nitzschia* blooms (Kudela et al., in press).

Given the variable association of HABs with different phases of the upwelling cycle and potentially, terrestrial input, it may be expected that different HAB life forms are characterized by distinct nutrient acquisition strategies. There have been remarkably few studies that address the nutrient

utilization characteristics, importantly N, of natural populations of bloom-forming species typical of upwelling regions. From the limited data available it appears that reduced N can be of major significance to dinoflagellate blooms. Such an observation at first appears counter-intuitive for an upwelling environment but is in accord with the general belief of a succession from new nutrient-fueled diatoms to regeneration-based flagellate assemblages following upwelling. Based on direct measurements with ^{15}N-labeled substrates, Kudela and Cochlan (2000) have shown that *Lingulodinium polyedrum*-dominated assemblages can meet all their N requirements through utilization of NH_4 and urea. This is contrary to earlier studies that had indicated an important role for NO_3 in the nutrition of this species (MacIsaac, 1978). Similar studies on a *Karenia mikimotoi* bloom in the English Channel demonstrated that NO_3 was relatively unimportant, with NH_4 regenerated through the microbial loop contributing 90% of the N requirements (Le Corre et al., 1993). Uptake kinetics determined for a natural bloom of *Alexandrium catenella* indicates a preference for NH_4 over a broad range of concentrations (Collos et al., 2004). Studies in the southern Benguela (Probyn, unpublished data) show that a dense bloom of *Gyrodinium zeta,* was maintained almost exclusively by NH_4 and urea, with NO_3 contributing <5% of the N requirements. It has also been inferred, by means of a box model approach (Rios et al., 1995), that regenerated NH_4 provided 91% of the total N taken up by a phytoplankton community in which *Dinophysis acuta, Gymnodinium catenatum, Ceratium fusus* and *C. furca* comprised 85% of the autotrophic biomass.

HABs are now generally recognized as occurring over a wide range of habitats from oligotrophic to hypernutrified. The occurrence of dinoflagellate HABs in nutrient-depleted waters is inconsistent with the general pattern of this group having a low affinity for nutrient uptake by comparison with diatoms (Smayda, 1997; 2000). However, some evidence does exist for highly efficient DIN uptake systems in certain species, for example, *Karenia mikimotoi* (Yamaguchi, 1994 cited in Gentien, 1998), *Karenia brevis* (Steidinger et al., 1998) and *Lingulodinium polyedrum* (Kudela and Cochlan, 2000). Other species may exploit alternative nutrient acquisition strategies such as vertical migration and mixotrophy. Strong swimmers such as *Gymnodinium catenatum* can retrieve nutrients from depth to supplement the depleted surface layer (Figueiras and Fraga, 1990; Fraga et al., 1992). A vertical migration strategy would be most advantageous in situations with a nutrient-depleted surface layer bounded by a shallow, steep thermocline (Eppley and Harrison, 1975). Such behaviours involve geotaxis, phototaxis and/or diel rhythms and imply an ability to take up nutrients (NO_3) at low levels of irradiance and in the dark (Cullen and Horrigan, 1981; Heaney and Eppley, 1981; Dortch and Maske, 1982). Species with a poor capability for NO_3 uptake in the dark may exploit deep zones of enhanced NH_4 production. Other species may use particulate or dissolved organic nutrients during periods of DIN depletion or as their primary nutrient acquisition strategy. Phytoplankton, including dinoflagellates, have long been known to sequester urea and amino acids directly from their environment. Some species possess cell-surface amino acid oxidases that catalyze the release of NH_4 that can then be utilized to supplement growth demands (Palenik and Morel, 1990). However, it is generally thought that ambient amino acid and other simple monomer concentrations are too low to constitute an important resource (Carlsson and Graneli, 1998). A number of dinoflagellate species have ecto-enzymatic activities that can provide an alternative supply of amino acids from proteins and polypeptides (Stoecker and Gufstafson, 2003). Evidence exists that *Alexandrium catenella* may be able to utilize N bound in high molecular weight humic material directly for growth (Carlsson and Graneli, 1998). Dissolved organic material processed through bacteria and heterotrophic flagellates/ ciliates would also provide an additional source of nutrients.

In addition to the osmotrophic assimilation of organic nutrients many dinoflagellate species are capable of some form of phagotrophy. In a number of photosynthetic species, feeding occurs primarily

under conditions of inorganic nutrient limitation rather than as a means of maintaining C nutrition during periods of low irradiance (e.g., Stoecker et al., 1997; Smalley et al., 2003). Furthermore, the induction of feeding appears to be a response to the relative availability of ambient nutrients and cellular nutrient ratios rather than absolute concentrations. For instance, feeding in field populations of *Gyrodinium galatheanum* was negatively correlated with ambient dissolved inorganic P:N ratios (Li et al., 2000). Phagotrophy by *Ceratium furca* in culture was only initiated once certain cellular threshold C:N:P ratios were achieved and increased markedly as these ratios deviated further from that found under optimal growth conditions (Smalley et al., 2003). Although the feeding response to nutrients is complex, it is clear that phagotrophy provides a potentially important alternative mechanism by which certain HAB-forming dinoflagellates could supplement their nutrient demands during periods of deprivation (Stoecker et al., 1997).

Coastal regions are appreciably influenced by terrigenous sources of nutrients delivered through surface or ground water inflows, or by atmospheric deposition (Paerl et al., 1990; Paerl, 1997). Terrestrial nutrient inputs are becoming of increasing concern as cultural eutrophication of coastal waters accelerates. In fact, the apparent global expansion of HABs has been ascribed by some to increased anthropogenic eutrophication of coastal waters (Smayda, 1989, 1990; Paerl, 1997; Riegman, 1998; Anderson et al., 2002). Although large parts of the coastline of the four major eastern boundary currents systems are arid to semi-arid with little freshwater input, significant riverine input of dissolved and particulate nutrients occurs at sub-regional scales, such as the high Si and Fe Columbia River plume (Hickey and Banas, 2003). Aeolian deposition is likely to be minimal during the upwelling season when prevailing winds blow roughly parallel to the coast (Hutchins et al., 1998). However, land-sea winds such as the berg winds in the Benguela could play a major role in sand and dust transport on the event time scale (Shannon and Anderson, 1982). The relative role of terrigenous new nutrients as opposed to upwelled nutrients to HABs in coastal upwelling ecosystems is largely unknown and should be studied in future research.

In addition to their effects on growth rates, nutrients have been shown to have a profound effect on the expression of harmful effects through control of toxin content. These effects occur in response to absolute concentration and nutrient ratios, as well as nutrient speciation. For instance, deficiencies in inorganic P and increased availability of inorganic N have been shown to enhance PSP toxin content in *Alexandrium* species (Boyer et al., 1985; 1987; Anderson et al., 1990; Matsuda et al., 1996; Bechamin et al., 1999; Guisande et al., 2002). Similarly, P and Si depletion has been shown to be necessary for domoic acid production in *Pseudo-nitzschia multiseries* (Pan et al., 1996a, 1996b; Bates, 1998). Nutrient speciation effects are of particular interest with regard to the availability of oxidized and reduced N. It has been demonstrated, for example, that NH_4 utilization leads to a greater enhancement of toxin content than NO_3 utilization in *Alexandrium* species (Levasseur et al., 1995; John and Flynn, 2000; Hamasaki et al., 2001) and in *Gymnodinium catenatum* (Flynn et al., 1996).

Justification for Comparative Approach

Central water and upwelled water signatures, as well as upwelling rates, differ both seasonally and spatially within and between upwelling systems. This variation in both absolute concentrations and nutrient ratios provides a range of potential production conditions that could lead to HAB events. A comparison of the realization of this production potential would provide valuable understanding of the driving mechanisms responsible for such blooms.

There is a commonality in the occurrence of certain HAB taxa in the three regions; for example, species of *Pseudo-nitzschia, Alexandrium, Dinophysis* and *Ceratium.* Comparative studies of similar taxa will provide insight to the importance of genetic as opposed to life-form attributes in relation to nutrient variability.

There is a quantitative difference among upwelling systems in the magnitude of freshwater input to the coastal zone. Such inputs provide an additional source of new nutrients, particularly in areas suffering from intense cultural eutrophication. Although of probable minor importance by comparison with upwelling inputs, terrigenous nutrient supply may be of significance under exceptional circumstances.

Detailed questions

- To what extent does the availability of nutrients (N, P, Si and Fe) dictate the sequence of HAB events?

- What role does nutrient regeneration play in the maintenance of HABs? If certain HAB species possess grazing deterrents, then nutrients regenerated from other sources provide scope for population increase.

- How important is the assimilation of dissolved or particulate organic nutrients to specific HAB events or phases?

- Are alternative sources of new nutrients, from terrestrial or atmospheric input, important in any of the upwelling systems?

- How do nutrient ratios and nutrient speciation (e.g., NH_4 vs NO_3) affect toxin synthesis and content of the different HAB species?

Research Approach

The approach should focus on the nutritional physiology of target species as related to the natural variation in nutrient signals. Regular field measurements of nutrient concentrations over time can provide valuable insight to nutrient dynamics, provided that trans-boundary fluxes are quantified. However, such an approach has serious limitations in situations where nutrients are rapidly turning over in the water column (e.g., NH_4 and PO_4) and can grossly underestimate the importance of the underlying processes. To this end, direct measurements of regeneration and assimilation rates need to be performed using isotope tracer methodology.

^{15}N flux measurements should provide the focus of process-orientated field research as they provide a convenient tracer of a number of different substrates and because N is often the limiting factor. A range of both inorganic and organic N resources can be employed to address specific questions related to the significance of different nutrient sources in fueling HABs. Clearly, the concept of NO_3 uptake representing new production and reduced N regenerated production will not strictly apply in coastal systems receiving substantial terrestrial N sources. Tight coupling between the benthos and the water column in shallow systems will also complicate interpretation. Notwithstanding these limitations, ^{15}N tracer methodology provides a powerful tool for studying phytoplankton physiology

and associated food web functioning that may be of critical importance in determining the fate of blooms.

Ideally, process studies should include time-series measurements within a single water body. This may involve tracking by means of drogues or satellite-identified features. Where such capability is not available, time-series measurements at a fixed station position can provide useful information. However, such an approach is likely to be compromised to the extent that advective forces dominate. Nutrient availability also needs to be viewed in the context of other potentially limiting or controlling factors. The interaction between nutrients and irradiance or temperature, for example, should be considered in both field and laboratory studies. The overall goal of both field and laboratory measurements is to provide meaningful input to biogeochemical models that can be employed in a predictive manner when coupled with the primary hydrodynamic forcing typical of upwelling ecosystems. Existing three-dimensional biogeochemical models may be used and may include HAB species as additional state variables.

E. What is the role of genetic predisposition versus environmental conditions in toxin production in different upwelling systems within a given genus or species?

Background

It is well known that toxic HAB species exhibit variability in toxin production, both at the species and genus level, within a given upwelling system. For example, the well-characterized domoic acid events along the U.S. west coast in 1998 were attributed to three species of *Pseudo-nitzschia,* all of which exhibited variable levels of toxicity under similar oceanographic conditions. For example, domoic acid has been associated with *P. pseudodelicatissima* in the Juan de Fuca Eddy region off Washington State, but this species is not known to produce toxin in Monterey Bay. Toxicity within a given species has similarly been found to vary between upwelling regions. *P. australis* is a common bloom-forming species in all three upwelling systems (CCS, Canary Current, Benguela), but is apparently not toxic in the Benguela upwelling system, while it is persistently toxic in the CCS, and is more variable in the Canary Current system.

Multiple environmental factors (e.g., nutrient concentrations and ratios) have been shown to trigger the production of domoic acid by the genus *Pseudo-nitzschia* (Bates, 1998) and it is possible that the entire range of observed spatial and cell-specific variability in toxin production is a response to subtle environmental cues. However, variability in genotypes is a common feature of phytoplankton. These genotypic differences are responsible for markedly different phenotypic expression in response to environmental cues within the same putative species. Therefore, the variability in toxin production is likely caused by a combination of genotype and environmental conditions. A primary goal of the GEOHAB programme is to develop a predictive capability for HAB dynamics; it is clearly necessary to elucidate the role of genotypic versus environmental variability in toxigenicity, since predictive relationships require a priori knowledge of whether a given phytoplankton assemblage is predisposed to toxin production.

Although species of *Pseudo-nitzschia* are an obvious example of this phenomenon, other HAB species may exhibit similar properties. For example, *Lingulodinium polyedrum* is known to produce yessotoxins in the Canary Current, but there are to date no known toxigenic events associated with *L. polyedrum* in the CCS or Benguela. However, it is not clear whether this is because *L. polyedrum* in

the CCS and Benguela have different genotypes, or because yessotoxin has not been detected in these regions.

Justification for Comparative Approach

Pseudo-nitzschia occurs in all three upwelling systems, but exhibits markedly different toxigenicities. A comparative study of this diatom in these three distinct systems will provide an ideal opportunity for examining why *Pseudo-nitzschia* is typically toxic and blooms in large numbers in the CCS, is at lower concentrations and toxicity in the Iberian system, and is often abundant but never toxic in the Benguela system. Similarly, *L. polyedrum* occurs in all three regions, but has no reported toxicity in the CCS or Benguela.

Comparative studies are necessary to identify processes common in all upwelling systems that can help us to differentiate between the ecological factors and genetic predisposition that contribute to cellular toxicity. Comparative studies will also help to define what conditions are similar enough to promote toxigenic blooms of different species within the same genus in seemingly similar systems. Finally, comparative studies will also help us identify the gaps in our understanding of these HAB processes, both molecular and ecological. Overall, our knowledge of HAB organisms will be enhanced when we compare and contrast the responses of these organisms in similar yet, in some respects, different upwelling regions.

Detailed Questions

- What is the inter- and intra-specific variability in toxin production in HAB organisms in upwelling systems?
- Are *Pseudo-nitzschia australis* isolated from Benguela genetically incapable of producing domoic acid?
- Are morphologically identified species (e.g., *L. polyedrum* from California vs. Iberia) genetically similar, or are they subpopulations within the species?
- What are the common or unique environmental triggers for toxin production in upwelling systems?

Research Approach

To address these questions, a combination of comparative field and laboratory approaches is required. A first step would be to assemble a collection of isolates from the three regions for each HAB species of interest for evaluation of physiological and genetic variability under controlled conditions. Since environmental factors leading to domoic acid production are not well defined, the characterization of genes or gene products required for domoic acid production would be useful. Samples of *Pseudo-nitzschia* from different upwelling zones could then be probed for molecular or biochemical features important for toxin production under certain environmental conditions.

Because the pathways for toxin synthesis are not known, it is currently impossible to detect the genes and/or enzymes involved in toxin production. Ideally, molecular techniques for toxic algae would focus on the detection of genes that are "turned on" during toxin production, not merely on cell or toxin detection alone. New molecular techniques, such as subtractive hybridization, permit the

identification of genes that are differentially expressed in organisms grown under different conditions, for example, those that induce toxin production and those that do not induce toxin synthesis. Similar methods, such as restriction fragment length polymorphism (RFLP) or micro-satellite analysis, can be used to differentiate genetically distinct sub-populations within a species.

These molecular and physiological approaches should be carried out within the framework of a field-sampling programme to correlate toxin production with environmental factors. As hypotheses or techniques are developed in the laboratory, these can then be tested in the field to evaluate the predictability and role of environmental cues.

Several specific research areas should be encouraged to address these questions. First, representative isolates from each of the three upwelling regimes need to be cultured, with subsequent archival by national or international culture collections. Second, molecular characterization (e.g., sequence analysis for application of RNA/DNA molecular probes) needs to be performed for HAB species in each region. Third, differences in absolute toxicity of a given species in separate upwelling regions should be exploited to allow characterization of genes important in toxin synthesis.

F. How does coastal morphology and bathymetry affect HAB dynamics in upwelling systems?

Background

The dynamics of coastal upwelling systems are largely determined by the continental shelf and upper slope bathymetry, and by coastline morphology. Bathymetric differences along an upwelling coast determine the offshore distance of upwelling plumes and fronts, may create retention and/or initiation areas, and produce changes in stratification conditions that favour the development of particular HAB species. Conditions of stratification may, for example, be enhanced where the shelf is broad and flat, and for this reason species of *Dinophysis* are favoured on the flat northwestern Iberian coast during the upwelling season (Palma et al., 1998). Other bathymetric features, such as the presence of canyons and promontories, may also have an important influence on HAB dynamics. Canyons may channel nutrient-enriched upwelling water towards the coast. Promontories are usually associated with the development of upwelling plumes and may have contrasting effects on the dynamics of HABs. Off northern California, large coastal promontories are linked with a reduction in domoic acid levels owing to the offshore transport of toxigenic *Pseudo-nitzschia* populations. In the Iberian and Benguela systems shoreward flow on the leeward side of upwelling plumes seem to be areas where HAB species, such as *Gymnodinium catenatum* and *Alexandrium catenella* can develop and accumulate in close proximity to upwelling centres without being advected away (Moita et al., 2003).

The existence of discontinuities along a coastline such as coastal embayments, pronounced capes, or Rías in northwestern Iberia, are known in some cases to be sheltered from wind forcing, giving rise to upwelling shadows where phytoplankton species can be accumulated through different retention mechanisms (Jones et al., 1988; Graham and Largier, 1997). Many of these areas may favour bloom initiation since they allow species to reach threshold cell concentrations for bloom development and may function as sedimentary basins accumulating benthic cysts and spores of HAB species that will later function as bloom innocula.

Justification for Comparative Approach

Comparative studies on the relative importance of coastal morphology and bathymetry for the initiation, development and demise of HABs within and among upwelling systems, will assist in testing the robustness of our understanding of these features in the retention and dispersion of HABs. Within the Benguela, Californian and Iberian upwelling systems physically different regimes can be considered to occur as a continuum providing both a range of stratification-mixing conditions and retention-dispersion mechanisms which may vary both spatially and temporally. This presentation of different physical regimes makes upwelling systems amenable to comparative studies that will allow a better understanding as to why any particular HAB species is favoured in any particular area within an upwelling system.

Detailed Questions

- How are particular species of HABs influenced by variations in the turbulent mixing of surface boundary layers due to wind field heterogeneities associated with coastal morphology?

- How do changes in wind forcing and surface circulation, induced by the coastal morphology, influence the dynamics of HABs?

- Do the retention areas associated with coastal discontinuities or bathymetry favour sexual reproduction by increasing the probability of gamete encounter, thereby leading to enhanced cyst production?

- How does coastal morphology influence the formation of cyst seed beds (e.g., *Alexandrium catenella* in Benguela versus *Gymnodinium catenatum* in Iberia)?

- How do retention-dispersion mechanisms associated with coastal morphology and bathymetry relate to differences observed in the toxicity of *Pseudo-nitzschia*?

Research Approach

Comparative research within and among upwelling systems should be undertaken to establish the influence of various areas of retention, accumulation and dispersion on the initiation, development and demise of particular HABs. These studies will assist in separating local versus basin-scale influences and responses.

Repeated synoptic high-resolution surveys should focus on areas of retention, accumulation and dispersion, and should be complemented by various forms of satellite data. Surface circulation should be monitored using ground-based coastal radar (CODAR) and cyst beds should also be mapped. Regional ocean and meteorological models should be developed to study the ocean response to meteorological forcing at local scales, and field studies must be used to configure and test numerical physical and biophysical models to determine conditions conducive to bloom formation and/or toxin production. The use of freely available research models, or so-called community models, should be encouraged.

G. What is the relative importance of cross-shelf and along-shore advection in different upwelling systems for HABs?

Background

Along-shore and cross-shelf currents are among the most prominent physical features of coastal upwelling systems. These currents are responsible for the transport and exchange of various physical, chemical and biological properties and, are therefore fundamental to the dynamics of HABs. The importance of these currents in the transport, accumulation and dispersion of HAB populations in various stages of development has been recognised in several upwelling systems (e.g., Fraga et al., 1988; Figueiras et al., 1994; Pitcher and Boyd, 1996; Trainer et al., 2002). HABs may be initiated at various sites on the shelf and subsequently transported into coastal environments following relaxation of upwelling. Along-shore advection of HABs may also take place through the development of an inshore poleward current that coincides with downwelling. For example, along-shore and cross-shelf advection are considered key mechanisms for the initiation of autumn blooms of *Gymnodinium catenatum*, *Dinophysis acuta* and *Karenia mikimotoi*, in coastal waters of Iberia. Similarly, coastal blooms in late summer in the southern Benguela also appear to be the result of advection in response to atmospheric forcing rather than to *in situ* development (Pitcher et al., 1998). Coastal-shelf interactions are also considered decisive for initiation, maintenance and dissipation of other HAB species, such as *Dinophysis acuminata* and various species of *Pseudo-nitzschia* that seem to develop *in situ* in the Iberian upwelling system. Onshore transport of surface waters during downwelling events has also been related to the appearance of high levels of domoic acid and high numbers of *P. pseudodelicatissima* on the central coast of the California-Oregon upwelling system. In the southern Iberian system *Lingulodinium polyedrum* develops on the warmer side of upwelling plumes that are compressed shoreward by offshore mesoscale circulation, or in warm along-shore counter-currents that flow between upwelling plumes and the coast (Amorim et al., in press). It has also been suggested that these currents could be implicated in the decay of HABs (e.g., Pazos et al., 1995). Strong upwelling events may disperse HAB populations into open oceanic waters through enhanced offshore transport, whereas intense and persistent downwelling could force coastal populations into deep waters leaving them in unfavourable conditions for growth.

Sedimentary resting stages are also likely to be affected by along-shore and cross-shelf flows. Along-shore transport of cysts and spores may be important in the Californian and Iberian systems, where a winter poleward current over the shelf establishes by the surfacing of the poleward undercurrent (e.g., Blanco, 1995b). The offshore flow, which in these cases is confined to the bottom layer, may resuspend resting stages from the shelf sediments. Near-bed onshore transport during upwelling may provide the necessary innocula for HAB initiation.

Justification for Comparative Approach

Differences in the wind regime and the presence of specific topographic features induce modifications in along-shore and cross-shelf flows at several temporal and spatial scales characteristic for each upwelling system. Thus, cross-shelf transport can be relatively more significant in areas with embayments and promontories, where accumulation and dispersion may be favoured, while along-shore transport may be more important in places with straight coastlines. To assess the relative importance of along-shore and cross-shelf transport on the initiation, development and decay of HABs, as well as on the dynamics of resting stages, research within and among upwelling systems with varying wind regimes, coastal morphology and shelf bathymetry is needed. The various upwelling

systems offer a broad range of physical characteristics and HABs in which the relative significance of along-shore and cross-shelf transport can be determined.

Detailed Questions

- How important is the interaction between along-shore advection and cross-shelf transport in introducing HABs to particular coastal areas?

- How do the along-shore currents over the shelf influence the distribution of resting stages in the sediment?

- Is the on-shore transport of resting stages during upwelling an important mechanism for HAB initiation?

Research Approach

Multidisciplinary research is essential to understanding the responses of HABs to changes in the intensity and direction of along-shore and cross-shelf currents induced by variations in atmospheric forcing. In addition to characterisation of the physical field, it is necessary to focus attention not only on HAB development and decay, but also on stages prior to bloom generation when plankton assemblages have yet to evolve into HABs. Research should comprise coastal, shelf and oceanic waters with the aim of embracing all significant physical-biological coupled processes. The simultaneous use of satellite imagery during field studies can assist in the design of biological sampling and in the interpretation of data. Mapping of cyst beds and sampling within the nepheloid layer above the sediments is required to derive information on the role of along-shore and cross-shelf currents on the dynamics of resting stages.

Previous research conducted in upwelling systems has demonstrated the existence of specific regions were HABs are prevalent and are strongly influenced by oceanographic processes. Research should target these regions to elucidate the relative importance of cross-shelf transport and along-shore advection to the species that characterise these regions. High resolution field observations, primarily focused on phytoplankton assemblages and their variability in relation to the environment, should provide information on the importance of cross-shelf transport in HAB initiation, development, accumulation and decay. These observations, when combined with large- and mesoscale surveys directed to clarify the role of advection in spreading HABs along the coast, will contribute to a better understanding of HAB dynamics in upwelling systems.

H. Are climate indicators predictive of HAB events in upwelling systems?

Background

Earth's climate has warmed by approximately 0.66°C over the past 100 years, showing an acceleration in warming since the mid-1970s (Walther et al., 2002). Significant evidence exists to demonstrate that variations in upwelling intensities and locations have occurred in concert with this warming trend. A very direct connection exists between upwelling, its interannual variability, and equatorial forcing (the source of many climate change-related signals). An analysis of data from a number of the major coastal upwelling ecosystems indicates that equatorward alongshore wind stress during the upwelling season has increased over the last few decades (Bakun, 1990). In fact, changes in upwelling

intensity provide one of the more substantiated lines of evidence for warming climatic trends (Bakun, 1994). Locally driven upwelling is a necessary, but insufficient, condition for nutrient transport to the surface layer. Rather, basin-scale variations in nutricline and thermocline depth interact with locally driven vertical transport processes in determining nutrient variability on time scales of climate variations (Barber, 1992). Marine organisms similarly respond to climate change and variations in upwelling intensity (Ware and Thomson, 1991; Jacobson et al., 2001) and marked, decadal-scale regime shifts are evident, notably associated with strong El Niño episodes (Bakun, 1994). Of particular relevance to variations in upwelling and marine populations is the "optimal environmental window" hypothesis (Cury and Roy, 1989). In this scheme, the reproductive success of small pelagic fish is highest at intermediate wind intensity and decreases at the both higher and lower wind intensities. The key issues are the variation in nutrient supply and turbulence with upwelling intensity, factors which also have a profound influence on HABs. The degree to which HABs vary with climate variations is virtually unknown, although there is evidence for correlation of certain HABs on the coast of Chile with the ENSO cycle. ENSO and NAO are two large-scale oscillations of climate that are often treated as examples of the possible expression of global warming. The apparent association of HABs with ENSO events suggests that future warming trends may lead to an increase in HABs (Hales et al., 1998). In support, micropaleontological evidence from the Scandinavian region indicates prehistoric and historic blooms of *Gymnodinium catenatum* ostensibly associated with periods of warming (Dale and Nordberg, 1993).

Because eastern boundary current upwelling systems represent a natural source of nutrients, linkages between HABs and upwelling, manifest through interannual variability, contribute to our understanding of the interaction between HABs and another important component of global change, anthropogenic eutrophication (Vitousek, 1994). The coastal ocean is a small part of the global ocean yet is responsible for a disproportionately large contribution to oceanic biological production. It is also characterized by high biodiversity and close interaction with human populations. Increased ocean temperatures are most evident in shallow waters. Levitus (2000) has shown that the mean ocean temperature between 0 and 300 m has increased by 0.31°C since the mid-20th Century. The accelerated rise in mean sea level and increase in storm surge in response to global warming is also clearly a coastal phenomenon. An overarching question of international significance is whether the effects of climate change on these economically vital coastal systems can be predicted in a reliable manner.

GEOHAB will approach this question from a HAB perspective, particularly related to the role of HABs as indicators of climate change in upwelling ecosystems and the linkages between the nature, frequency and intensity of HABs and global climate signals.

Climate change is a necessary and natural focus of many international science projects. Therefore, there are opportunities for cooperative activities between GEOHAB and other projects, such as the Global Ocean Ecosystem Dynamics (GLOBEC) project, the Climate Variability and Prediction (CLIVAR) project, and the Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) project. Many issues of importance to the International Council for the Exploration of the Seas (ICES) and the North Pacific Marine Sciences Organization (PICES) also relate to HABs and global change. Cooperation among related projects provides opportunities for greater scientific and financial leverage among projects, as well as potential cross-project integration.

Justification for Comparative Approach

There is a need to compare annual variability among upwelling systems as well as different latitudes within any single system. Ideally, to establish a linkage between HABs and climatic effects, all four eastern boundary current systems should be studied: the Canary (northwestern Africa and Iberian systems), California, Humboldt, and Benguela. However, a minimum of three can serve this purpose. Separation of the systems between the hemispheres allows comparisons to be made on the effects of the seasonal timing of arrival of climatic signals on HABs. For example, the ENSO signal arrives in summer in one hemisphere, but in winter in the other hemisphere. Of fundamental importance is whether established effects of NAO and ENSO events on HABs can now provide insight into the effects of future directional climate changes.

HABs are local phenomena and as with other organisms, populations or ecological communities are likely to respond to regional changes more than approximated global averages (Walther et al., 2002). Comparisons between regions give insight to the separation of local versus basin or climate scales. Remote sensing and modelling can help extrapolate local signals to regional scales. A major challenge is to identify to what extent global responses can be distinguished from local within-system and inter-regional responses. To this end, the geo-morphological diversity that characterises the different regions is regarded as an essential component for the identification and definition of common processes and structures, and the separation of local from basin or climate-related responses.

Detailed Questions

- Can we relate climate change to the temporal evolution of biogeography?
- How does climate variability affect the distribution of species and their potential ability to cause HABs?
- Can the sedimentary record of HAB species in upwelling systems provide information on the effects of climate on these phenomena?
- What is the linkage between short timescale variability associated with the incidence of HABs and climate change or interannual variability?
- How will terrestrial and/or atmospheric expressions of climatically induced changes affect coastal HABs in upwelling systems?

Research Approach

The past record, coupled with recent and current observations provides a coherent basis for predicting future global trends. GEOHAB will need to address the biogeography of modern and recent past HAB organisms as a basis for interpreting past records and understanding how biogeography has changed in response to climate-related signals. Numerical models will provide the important linkage between the paleo-record and modern observations achieved through field programmes, monitoring and satellite data.

Tools and approaches relevant to studying climate impacts on HABs in upwelling systems include data mining, statistical linkages between biogeographic data, satellite data and climate-related metrics

(e.g., ENSO and NAO), and numerical models to examine relationships, hindcasts and forecasts. It is important to make use of other long-term records that may be indicators of climate change to provide insight to the relationship of this change to HABs. Comparisons among systems with regard to these relationships will provide understanding of local- versus basin-scale responses. Well-constrained systems such as the Santa Barbara Basin sediments provide a long-term record from which to start.

In brief, research necessary to examine linkages between HABs and climate change includes environmental micro-palaeontology, biogeography, satellite data and time-series analysis, coupled with numerical models.

V - FRAMEWORK ACTIVITIES

According to the GEOHAB *Implementation Plan*, Framework Activities are those activities that are not research, but will facilitate the implementation of GEOHAB. They serve to enhance the value of research by ensuring consistency, collaboration, and communication among researchers.

A. Scientific Networking and Coordination of Resources

GEOHAB CRPs will be coordinated by the GEOHAB SSC through the establishment of separate sub-committees for each CRP composed of SSC members and leaders of CRP activities. The sub-committees will primarily work by correspondence, but may also meet on an opportunistic basis and when identified resources allow for meetings to address major planning and co-ordination issues. The subcommittee for each CRP will work with the GEOHAB SSC and International Programme Office (IPO) to encourage scientific networking and co-ordinate research activities and resources.

An important aspect of international activities like GEOHAB is the sharing of scarce resources among participating nations. Such sharing makes possible research activities of a scale and breadth that are not otherwise feasible, and thereby enable the comparison of ecosystems of a similar type in different parts of the world. The CRP – HABs in Upwelling Systems will promote the application of national resources, in terms of scientific expertise, sampling platforms and equipment to the key research questions identified in this document. GEOHAB has already initiated the sharing of expertise and development of an international research community on the topic of HABs in upwelling systems by supporting the OSM. GEOHAB will continue to promote sharing of expertise by creating a CRP Subcommittee to help implement this research plan. Presently, international GEOHAB activities are sponsored by funding from IOC and from SCOR (through grants from the U.S. National Science Foundation and National Oceanic and Atmospheric Administration). Development of the CRP – HABs in Upwelling Systems will depend on increased funding from other national and international organizations.

GEOHAB will identify, and draw the attention of responsible bodies to, opportunities for co-ordination of resources that will add value to ongoing and planned research. Individuals involved in studying each key question will be responsible for developing plans relating to the sharing of expertise and equipment and how they will contribute to the continued coordination of the CRP.

GEOHAB and the CRP Subcommittee will encourage the publication of results from the CRP – HABs in Upwelling Systems in relevant peer-reviewed scientific journals, with appropriate reference to the relation of the research to GEOHAB. In addition to this publication in the primary scientific literature, GEOHAB will seek to disseminate both the programme status and research results more broadly to the worldwide community of managers and scientists interested in HABs. *Harmful Algae News* is distributed regularly by the IOC and is available as a forum to communicate news of GEOHAB activities and research results. It is the responsibility of each CRP sub-committee to announce events, calls for proposal contributions, availability of core research working documents and results, and summaries of these, in *Harmful Algae News* and at the GEOHAB Web site (see http://ioc.unesco.org/hab/GEOHAB.htm). The GEOHAB IPO will assist in this dissemination.

The CRP Subcommittee will promote the involvement of individuals from the three identified

upwelling regions, and from other major upwelling systems. The Subcommittee will also assist the scientific teams working on the different questions to work together. Successful conduct of research on this topic will require the pooling, coordination, and joint use of several different types of measurement platforms:

1. Ships may be used to (a) conduct transects or grids of upwelling regions through upwelling-relaxation cycles, (b) track blooms of interest by means of drogues to investigate various aspects of bloom population dynamics, and (c) collect sediment cores in appropriate locations underlying sites of regular HABs and/or retentive features of ocean physics.

2. In situ observing systems will be needed to establish appropriate time-series data sets. A variety of systems are already installed in, or planned for, upwelling systems in support of the GOOS.

3. Satellites will be needed to detect bloom events, allow adaptive sampling and extrapolate ship-based and in situ measurements to regional scales.

B. Data Management and Data Sharing

The collective value of data is greater than its dispersed value and comparative research requires effective data sharing among scientists working in different regions; therefore, data management and exchange are important components of GEOHAB CRPs. The development of an appropriate GEOHAB data management plan is a fundamental and critical activity upon which the ultimate success of GEOHAB will depend, and GEOHAB is working with other international marine research projects to develop basic guidelines for data management and sharing (see www.jhu.edu/scor/DataMgmt.htm). Each CRP will need to develop its own specific plans, conforming with the principles adopted by GEOHAB.

GEOHAB will use a decentralized data management and distribution system with a centralized metadata index. The components, centralized under the supervision of the GEOHAB IPO, will include a comprehensive inventory of databases relevant to GEOHAB, as well as meta-data, with links to their locations and contact persons. Each CRP will create an inventory of data and data products. The GEOHAB Data Manager will assist the CRP by tracking planned, ongoing, and completed research, and by providing links to research information. All investigators should be prepared to share their data and data products with other investigators in their research projects as soon as possible, and with the general scientific community within two years from the time those data are processed, and should recognize the "proprietorship" (rights to first publication or authorship) of data acquired from other investigators. Each GEOHAB CRP should address the long-term archival of observational data and data products to ensure a lasting contribution to marine science. Specifically, data from the CRP – HABs in Upwelling Systems will be contributed to the World Data Centre for Marine Environmental Data (WDC-MARE) at the end of the project, with the assistance of the GEOHAB IPO data manager.

C. Protocol and Quality Control

Specification of protocols within elements of the CRP – HABs in Upwelling Systems will ensure that data generated are reliable and compatible, thereby facilitating synthesis and modelling. Each key question will require measurement of somewhat different parameters, although for each question, a set of parameters should be measured in each region. Likewise, the CRP – HABs in Upwelling Systems will include a set of core parameters that will be measured in each location. This information

will make it possible to draw inferences across systems, construct models of HABs in upwelling systems, and contribute information that will be useful for other CRPs. The GEOHAB SSC will work with CRP subcommittees to identify GEOHAB and CRP core parameters, as well as the standard measurement protocols and any appropriate standard reference materials.

Recommendations on methods and measurements will be disseminated through the IPO and through the GEOHAB Web site. The methods adopted to ensure quality control and the protocols used for data collection will be fully documented in information files (meta-data) accompanying data sets.

Where possible, well-defined, internationally agreed descriptions of methods will be adopted. Where required, the GEOHAB SSC will initiate Framework Activities that lead to the development of appropriate protocols and methods to ensure data collection in a uniform manner for comparative studies. GEOHAB investigators retain the primary responsibility for quality control and assurance.

D. Capacity Building

GEOHAB encourages a "training through research" approach that offers opportunities for student participation in cruises and instruction in marine research disciplines relevant to HABs. Exchange of post–doctoral fellows and senior scientists are equally important for the CRPs. Training activities that would benefit GEOHAB research will be organized by the GEOHAB SSC and proposals for specific training activities can be submitted to the SSC for endorsement as GEOHAB activities.

E. Co-ordination of Modelling Activities

Several models of different upwelling systems have been developed and applied. GEOHAB will therefore identify relevant existing modelling activities through a Task Team that has the responsibility to organise model inter-comparison exercises, including comparison of predictive models for HABs. It may, however, also be necessary to initiate a new generation of modelling activities to address key questions appropriately. The CRP – HABs in Upwelling Systems should interact closely with the GEOHAB Modeling Subcommittee, to ensure that the results of the CRP are included in GEOHAB models and that the CRP collects data needed to parameterize GEOHAB models and create appropriate equations for the models. In addition the CRP Subcommittee will consult with other groups using and developing models of upwelling systems, such as the GLOBEC Small Pelagics and Climate Change (SPACC) project.

F. Interaction With Other International Programmes and Projects

GEOHAB exists in the context of several other large international programmes and projects that study aspects of global change that could be relevant to the CRP – HABs in Upwelling Systems, particularly in relation to the key questions related to seeding strategies, nutrient supply, and climate indicators:

- Seeding Strategies—Some HAB species, specifically those that form cysts, are seeded from one HAB event to another. Cysts typically fall to the seafloor and stay there until they are resuspended or excysted. The cysts of some species can exist in this dormant state for many years. Sampling of cysts in sediments provides opportunities to study bloom initiation, and possibly to correlate blooms with other ocean conditions through known paleoceanographic indicators. IMAGES (International Marine Aspects of Global Change Study) is a sub-project of the Past Global Changes (PAGES) project, which has been initiated to respond to the challenge of understanding

the mechanisms and consequences of climatic changes using oceanic sedimentary records. IMAGES collects large-diameter cores in many coastal areas of the world, specifically to examine paleoceanographic conditions of the past 0 to 40,000 years. The CRP – HABs in Upwelling Systems will seek opportunities to work with IMAGES to analyze previously collected samples and to gather new samples in upwelling systems and to relate cyst information with other paleoceanographic variables. Especially important will be cores collected in anoxic basins with high sedimentation rates, where climate and upwelling signals can be correlated with HAB events.

- Nutrient Supply—The Land-Ocean Interactions in the Coastal Zone (LOICZ) project has compiled information about the supply of macro-nutrients from the land to the ocean, information that could be useful to the CRP – HABs in Upwelling Systems in studying the relationship between nutrient supply (amount, timing, and sequence), type (inorganic versus organic), and ratios, and HABs. The new Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) project will conduct observations and process studies related to the effects of nutrient inputs to coastal areas and subsequent phytoplankton blooms. Some of IMBER's activities might provide useful input to the CRP – HABs in Upwelling Systems and other CRPs.

- Climate Indicators—A program of the World Climate Research Programme called the Climate Variability and Prediction (CLIVAR) project is studying how climate oscillations, such as ENSO and NAO, operate and are expressed in the ocean and atmosphere. GEOHAB will request to make a presentation to the CLIVAR SSG to begin to explore common research interests and possible co-operative activities, particularly in relation to the CRP – HABs in Upwelling Systems. GEOHAB will also seek advice from CLIVAR on individuals who might be involved in continued planning and implementation of this CRP.

- The Global Ocean Observing System (GOOS) could provide important information for the CRP – HABs in Upwelling Systems, insofar as GOOS provides long-term continuous monitoring in upwelling areas. GEOHAB has linkage with GOOS through the participation of one GEOHAB SSC member on the GOOS Coastal Ocean Observations Panel, and through IOC, which sponsors both programs.

- The Global Ocean Ecosystem Dynamics (GLOBEC) project pays special attention to physical processes and zooplankton in the support of marine fisheries. Activities of this project will be important in determining the trophic positioning of HABs and the "top-down" versus "bottom-up" control of HABs.

VI - NEXT STEPS

This document will form the basis for a Core Research Project of GEOHAB, with each of the 8 key questions being addressed by one or more teams of scientists funded through national funding mechanisms.

The highest priority research activities include:

- An ecologically based classification of the different species found in upwelling systems based on their adaptation to the multiple sub-habitats characteristic of upwelling ecosystems. Included in this classification of HAB species in upwelling systems will be the functional role of morphological, physiological, behavioural and life-history characteristics, at the cellular level.

- Identification of the seed strategies employed by HAB species within upwelling systems. Establishment of the sites of HAB initiation and characterisation of environmental influences on the life history stages of HAB species in upwelling systems is a priority in developing a predictive capability.

- Determination of the influence of small-scale physical processes on the growth and dispersion of HAB species. Turbulent mixing determines much high-frequency environmental fluctuation and in so doing can control nutrient, irradiance, and phytoplankton patchiness, and is also known to affect plankton growth rates. Varying responses in terms of the succession of species within and between upwelling systems will allow inferences of the properties of the upper water column regulating species succession and the development of HABs.

- An investigation of the nutritional physiology of target species as related to the natural variation in nutrient signals. Although time-series field measurements of nutrient concentrations can provide valuable insight to nutrient dynamics, provided that trans-boundary fluxes are quantified, direct measurements of regeneration and assimilation rates also need to be performed using isotope tracer methodology. These measurements will serve to provide meaningful input to biogeochemical models that can be employed in a predictive manner when coupled with the primary hydrodynamic forcing typical of upwelling ecosystems.

- An assessment of genetic predisposition versus environmental conditions in the toxin production of target species in different upwelling systems. Variability in toxin production is likely caused by a combination of genotype and environmental conditions and elucidation of these respective roles in toxigenicity is critical in developing a predictive capability. Differences in the absolute toxicity of a given species in separate upwelling regions may be exploited to allow characterization of genes important in toxin synthesis.

- Determination of the importance of coastal morphology and bathymetry on the dynamics of HABs in upwelling systems. These influences are responsible for creating alternating patterns of active and passive upwelling circulations along the coast which may serve in creating sites favouring bloom initiation, retention, dispersion, etc. Characterisation of these sites will assist in understanding their role in the dynamics of HABs.

- Field-based observations incorporating measurements of cross-shelf and along-shore advection and their role in the initiation, transport, accumulation and dispersion of HABs. These observations should be made with reference to both vegetative and resting stages of HAB species.

- Identification of climate indicators as predictors of HAB events in upwelling systems. Significant evidence exists that variations in upwelling intensities and locations, and also ecosystems, have occurred in concert with warming of Earth's climate. Research is required to relate the effects of climate change, and associated variation in the predominant physical and chemical forcing mechanisms, on HAB species and communities that typify coastal upwelling environments.

Several steps need to be taken following publication of this plan, to ensure that the research is funded and coordinated appropriately:

1. The plan must be disseminated to the interested research community and to the national agencies that fund HAB research. National GEOHAB committees should help in this effort. This step will be most effective if carried out by national scientists, but SCOR and IOC will also help distribute the plan to their member nations.

2. National and international teams of scientists must propose research related to the 8 key questions, and affiliate their research to international GEOHAB, to ensure that the overall CRP – HABs in Upwelling Systems is coordinated.

The GEOHAB SSC will help provide international coordination for the CRP – HABs in Upwelling Systems, through the following actions:

1. Establishment of a GEOHAB CRP Subcommittee. This subcommittee will be responsible to work with scientists involved in the CRP – HABs in Upwelling Systems to ensure that they coordinate their research, using the same measurement protocols, sharing data, and contributing to model development. One or two members of the CRP Subcommittee will be members of the international GEOHAB SSC, to ensure a strong linkage between the subcommittee and the SSC. The work of the subcommittee will be conducted primarily by email.

2. Assistance from the GEOHAB Modelling Subcommittee. The GEOHAB Modelling Subcommittee will assist CRP scientists in locating and adapting appropriate physical-biological models that can be applied in upwelling systems to HAB research questions.

3. Work with the CRP Subcommittee to identify priority targeted research and measurement protocols.

4. Work with the Global Ocean Observing System (GOOS) to ensure that GOOS observations are available and useful to the CRP scientists.

5. Provide access to *Harmful Algal News* and the GEOHAB Web site to promote communication among Upwelling CRP scientists.

6. Provide assistance from the GEOHAB IPO (when established) in tracking research planned, funded, ongoing, and completed, including maintaining metadata records of data holdings by individual scientists and scientific teams.

7. Communicate with national and international funding agencies about the need for funding for general and targeted research.

Finally, several priority Targeted Research activities need to be undertaken to enable scientific advances on our understanding of HABs in upwelling systems. The *GEOHAB Implementation Plan* defines Targeted Research as research that "addresses specific objectives outlined in the *GEOHAB Science Plan*". Targeted Research may be solicited by the SSC as the need arises from Core Research Projects. Targeted Research includes, but is not limited to:

- *Studies on autecological, physiological, and genetic processes related to harmful algae*

- *Studies on sub-grid formulations of physical, chemical, and biological interactions affecting harmful algal blooms*

- *Development and comparison of specific models and observational systems*

Targeted research differs from Core Research in scope and scale. Whereas Core Research must be comparative, integrative, and multi-faceted, Targeted Research activities may be more tightly focused and directed to a research issue or element. It is expected that such studies will facilitate the wider and larger-scale studies. For example, investigations on specific methods for model comparisons and intercalibration are targeted activities, valuable in their own right, yet are also essential to conduct comprehensive field studies and modelling in Core Research Projects.

Targeted Research activities particularly needed for the CRP – HABs in Upwelling Systems include:

- Develop new measures of ecophysiological processes at the cellular level that HAB species use to adapt to conditions related to upwelling-relaxation cycles. These methods should be designed for application in the field.

- Develop genetic probes for toxin production.

- Develop biochemical indicators of non-cyst forming HABs in sediments.

- Conduct laboratory/mesocosm studies of the behaviour and toxin production of HAB species in simulated upwelling and relaxation conditions (including a variety of physical and nutrient conditions).

- Conduct laboratory research on triggers of encystment and excystment.

- Develop methods to trace encystment/excystment events.

- Develop HAB models that include encystment/excystment.

- Develop molecular techniques to identify HAB life-cycle stages and the status/viability of cysts and overwintering stages.

- Improve methods for satellite detection of HABs.

- Establish a collection of isolates of HAB species from the target upwelling regions.
- Document the biogeography of target species in upwelling systems over time.
- Create a database of HAB events over time in relation to climate cycles.

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APPENDICES

Appendix I – Open Science Meeting Program

GEOHAB Open Science Meeting on HABS in Upwelling Systems
17-20 November 2003
Lisbon, Portugal
PROGRAMME

Monday, 17 November

9:30-10:00	Welcome
	Teresa Moita, Instituto Nacional de Investigação Agrária e das Pescas - IPIMAR, Lisbon, Portugal
	Carlos Costa Monteiro, Director of Instituto Nacional de Investigação Agrária e das Pescas - IPIMAR, Lisbon, Portugal
	Ed Urban, Scientific Committee on Oceanic Research (SCOR)
	Henrik Enevoldsen, Intergovernmental Oceanographic Commission (IOC)
10:00-10:20	GEOHAB Core Research Project: HABs in Upwelling Systems – *Grant Pitcher*, Marine and Coastal Management, Cape Town, South Africa
SESSION 1:	**Overview of HABs in Californian, Iberian and Benguela upwelling systems**
Chair:	**Pedro Monteiro**
10:20-11:00	Overview of the ecology of HABs in upwelling systems on the U.S. West Coast – *Vera Trainer*, U.S. National Oceanic and Atmospheric Administration, Seattle, Washington, USA
11:00-11:30	COFFEE
11:30-12:10	Ecology and oceanography of HABs in the Portuguese Iberian upwelling waters – *Teresa Moita*
12:10-13:30	LUNCH
13:30-14:10	Ecology and oceanography of HABs in southern Benguela – *Grant Pitcher*

14:10-14:30 Conclusion of Session 1: Discussion

SESSION 2: Identification of the HAB species in given upwelling systems

Chair: Allan Cembella

14:30-14:50 Molecular approaches to the ecology of algal blooms – *Carlos Pedros Alio*, Institut de Ciències del Mar, Barcelona, Spain

14:50-15:10 HABs in upwelling systems: A view from the dinoflagellate cyst record – *Barrie Dale*, University of Oslo, Oslo, Norway

15:10-15:30 Phylogenetic analysis of toxic *Alexandrium* (Dinophyceae) isolates from South Africa: Implications for the global phylogeography of the *A. tamarense* species complex – *Carlos Ruiz Sebastian*, University of Cape Town, South Africa

15:30-15:50 Distribution of *Dinophysis* spp. in Western Iberian Shelf waters during an unusual spring poleward current event – *Beatriz Reguera,* Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Spain

15:50-16:10 Conclusion of Session 2: Discussion

16:10-16:30 COFFEE

SESSION 3: Posters

16:30-18:00 Posters

18:00 PORTO ICEBREAKER at IPIMAR

Tuesday, 18 November

SESSION 4: Identification of the physical, chemical and biological processes that define or characterise upwelling systems and quantification of the response of HAB species to these processes

Chair: Marta Estrada

9:00-9:20 Some aspects of the upwelling dynamics along the western coast of Portugal – *João Vitorino*, Instituto Hidrográfico, Lisboa, Portugal

9:20-9:40 Coastal retention and nearshore algal blooms in upwelling systems – *John Largier*, Scripps Institution of Oceanography, La Jolla, USA

9:40-10:00	Physical oceanography and HABs in the California Current System – *Barbara Hickey*, University of Washington, Seattle, Washington, USA
10:00-10:20	Downwelling and HABs in the NW of the Iberian Peninsula: The Rias Baixas of Galicia – *Francisco Figueiras*, Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científica (CSIC), Vigo, Spain
10:20-10:50	COFFEE
11:10-11:30	Discussion of physical influences on HABs
11:30-11:50	Carbon and nutrient cycles in the NW Iberian upwelling system: Seasonal- and event-scale variability – *Xose Anton Alvarez Salgado*, Instituto de Investigacións Mariñas Consejo Superior de Investigaciones Científica (CSIC), Vigo, Spain
11:50-12:10	Nitrogen utilization by a novel dinoflagellate bloom off the west coast of South Africa – *Trevor Probyn*, Marine and Coastal Management, Cape Town, South Africa
12:10-13:40	LUNCH
13:40-14:00	From the laboratory to the field: Can we apply knowledge of *Pseudo-nitzschia* physiology in the real world? – *Raphael Kudela*, University of California Santa Cruz, USA
14:00-14:20	Discussion of chemical and biological influences on HABs
SESSION 5:	**Development of observation systems and models of HABs in upwelling systems to support fundamental research and predictive capabilities**
Chair:	**Paulo Relvas**
14:20-14:40	The coastal monitoring applications of a bio-optical reflectance model to derive algal size and biomass – *Stuart Bernard*, University of Cape Town, South Africa
14:40-15:00	Satellite remote sensing in eastern boundary currents: Multiple programmatic roles – *Andy Thomas*, University of Maine, Orono, Maine, USA
15:00-15:20	Remote sensing and monitoring of harmful algal blooms in different upwelling conditions: Gulf of Mexico and Washington, USA – *Richard P. Stumpf,* NOAA National Ocean Service, Silver Spring, Maryland, USA
15:20-15:40	Discussion of remote sensing in HAB research

15:40-16:10 COFFEE

16:10-16:30 Hydrodynamic models as a basis to understand HAB bloom accumulation and advection in upwelling systems – *Pedro Monteiro*, Coast Programme, CSIR, Stellenbosch, South Africa

16:30-16:50 Integrated modeling of physical and biological processes in the Iberian upwelling system – *Ramiro Neves*, Instituto Superior Técnico, Lisbon, Portugal

16:50-17:10 Discussion of modeling in HAB research

17:10 Adjourn for the Day

Wednesday 19 November

9:00

SESSION 6: Identification of interested participants and designated regions for comparative research

SESSION 7: Review of current national and regional projects/programmes in order to identify elements of research that could contribute to the core research

SESSION 8: Identification of gaps in national and regional research projects/programmes

18:00 Adjourn for the day

Thursday, 20 November

9:00

SESSION 9: Formulation and design of a plan to guide core research in upwelling systems

SESSION 10: Identification of framework activities to support the research plan

17:30 Adjourn for the day

17:30 BUS TOUR OF LISBON AND DINNER

Friday 21 November

SESSION 11: CLOSED SESSION - The Core Research Project Planning Committee will meet to finalize a report of the Open Science Meeting comprising an implementation plan to guide core research

Appendix II – Meeting Participants

GEOHAB Open Science Meeting on HABs in Upwelling Systems

J. Icarus Allen	United Kingdom
Ana Amorim	Portugal
Stewart Bernard	South Africa
Maria De Fatima Borges	Portugal
Vanda Brotas	Portugal
Allan Cembella	Germany
Barrie Dale	Norway
María Dolores Doval	Spain
Kerstin Ebert	Germany
Henrik Enevoldsen	IOC
Marta Estrada	Spain
Francisco G. Figueiras	Spain
Inga Hense	Finland
Barbara Hickey	USA
Carlos Jimenez	Spain
Anél Kemp	South Africa
Raphael Kudela	USA
John L. Largier	USA
Sofia Loureiro	Portugal
Claudio Marangoni	South Africa
Rosa Martinez	Spain
Jose Carlos Mendes	Portugal
Maria Teresa Moita	Portugal
Maria Isabel Monteiro	Portugal
Pedro M. Scheel Monteiro	South Africa
Jesus Morales	Spain
Ramiro Neves	Portugal
Paulo B. Oliveira	Portugal
Yolanda Pazos	Spain
Carles Pedrós-Alió	Spain
Alvaro Peliz	Portugal
Aires José Pinto Dos Santos	Portugal
Grant C. Pitcher	South Africa
Trevor A Probyn	South Africa
Beatriz Reguera	Spain
Paulo Relvas	Portugal
Xosé Antón Álvarez Salgado	Spain
Ricardo Sánchez Leal	Portugal
Miguel P. Santos	Portugal
Carlos Ruiz Sebastian	South Africa
Sophie Seeyave	France
Richard P. Stumpf	USA
Andrew Thomas	USA
Ricardo Torres	United Kingdom
Jesus M. Torres Palenzuela	Spain
Vera L. Trainer	USA
Ed Urban	SCOR
Vitor Vasconcelos	Portugal
Joao Vitorino	Portugal