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Harmful Algal Blooms in Eastern Boundary Upwelling Systems

A GEOHAB CORE RESEARCH PROJECT

By Grant C. Pitcher, A. Bernales Jiménez, Raphaël M. Kudela, and Beatriz Reguera

Satellite image of a massive bloom of phytoplankton off the coast of Oregon and Washington on July 26, 2014. Image courtesy NASA Earth Observatory.

ABSTRACT. This paper highlights advances in knowledge about the ecology and oceanography of harmful algal blooms (HABs) as guided by the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) Core Research Project “HABs in Upwelling Systems.” The diverse group of plankton that comprise HAB species in upwelling systems remains dynamic in terms of the organisms observed, the frequency and density of blooms, and the presence or absence of toxins. Topics covered include emerging HAB problems and the forever-changing threat that HABs pose to the economic viability of fisheries and aquaculture, the health and diversity of upwelling systems, and the recreational activities supported within these systems. We provide an update of our knowledge of the seeding and nutrient strategies of HAB species in upwelling systems, as well as further evidence of the strong influence of physical processes in HAB development and transport on a spectrum of scales. We also assess our progress toward achieving the GEOHAB goal of improved prediction of HABs through evaluation of a variety of predictive models. Finally, we seek to identify the response of HABs to global change through the increasing availability of long-term data sets.

INTRODUCTION

The international science program Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) was established with the goal of improving prediction of harmful algal blooms (HABs; GEOHAB, 2001). Program implementation was intended to be comparative through the establishment of Core Research Projects (CRPs) in which international collaborative research would be undertaken in ecosystems sharing common features (GEOHAB, 2003). Following an Open Science Meeting in 2004, a science plan for the CRP “HABs in Upwelling Systems” was developed (GEOHAB, 2005). A special issue of *Progress in Oceanography* was dedicated in 2010 to describing the progress made in the understanding of HABs in upwelling systems as guided by this science plan (Pitcher and Pillar, 2010). With the conclusion of GEOHAB, this paper highlights further advances in our knowledge of HABs, their impacts, and the processes important to their development in upwelling systems. We specifically assess achievements in terms of improved prediction of HABs accomplished through improved observation and modeling systems and also seek to identify the responses of HABs to global change.

EMERGING HAB PROBLEMS

Trainer et al. (2010) described the distribution and impacts of harmful algal bloom species in eastern boundary upwelling systems of the California, Canary, Benguela, and Humboldt Currents, including those that can cause the poisoning syndromes in humans called paralytic shellfish poisoning (PSP), diarrhetic shellfish poisoning (DSP), and amnesic shellfish poisoning (ASP), as well as yessotoxins, ichthyotoxins, and high-biomass blooms resulting in hypoxia and anoxia. The distribution and impact of the diverse group of plankton that comprise HAB species in upwelling systems nevertheless remains dynamic in terms of the organisms observed, the frequency and density of blooms, and the presence or absence of toxins. Consequently, the threat posed to the economic viability of fisheries and aquaculture, the health and diversity of upwelling systems, and the recreational activities supported within these systems are forever changing.

Problems relating to the neurotoxin domoic acid, which is responsible for ASP, appear, for example, to be more severe particularly in the California Current System where evidence of trophic transfer and contamination is more widespread.

In the spring of 2015, a coast-wide bloom of the toxigenic diatom *Pseudo-nitzschia* resulted in the largest ever recorded outbreak of domoic acid poisoning along the North American west coast (McCabe et al., 2016; Figure 1). Elevated toxins were measured in numerous stranded marine mammals and resulted in geographically extensive and prolonged closures of razor clam, rock crab, and Dungeness crab fisheries. This was the first *Pseudo-nitzschia* bloom to simultaneously impact both shellfish and fish harvest industries, as well as marine mammal health, along the entire US and Canadian west coasts. The impact of this toxic diatom bloom propagated up the food chain to include many species of marine mammals. Between March and November, domoic acid was detected in whales, dolphins, porpoises, seals, and sea lions ranging from southern California to northern Washington. The outbreak was initiated by anomalously warm ocean conditions, with *Pseudo-nitzschia australis* existing north of its typical range in warm, nutrient-poor water that spanned the Northeast Pacific in early 2015. The seasonal transition to upwelling subsequently provided the nutrients necessary for development of a large-scale bloom, and a series of spring storms delivered the bloom to the coast. McKibben et al. (2017) later provided evidence of climatic regulation of these events through assessment of domoic acid in shellfish in the northern California Current System over the past 20 years.

In the Canary Current System, domoic acid outbreaks are attributed primarily to *P. australis*, which commonly causes annual mussel harvesting closures. In 2015, the first case of ASP in Europe followed the consumption of mussels by a Galician family who collected the mussels from an area closed to harvesting (Pazos et al., 2016). Domoic acid specifically has impacted scallop production,

as these bivalves show a great capacity for the uptake and retention of this toxin (Trainer et al., 2010). To mitigate harvesting closures, the European Union introduced specific regulations that permitted testing for the presence of toxins following removal of the hepatopancreas and gonads of scallops. To date, there are no records of bird or mammal mortalities attributed to ASP in the Canary Current System, but domoic acid has been detected in small pelagic fish. Although domoic acid poisoning has been considered less of a problem in eastern boundary systems of the Southern

Hemisphere, recent studies demonstrate the prevalence of *Pseudo-nitzschia* spp. in both the Humboldt (Tenorio et al., 2016) and Benguela (Louw et al., 2016; Hubbart et al., 2012) Current Systems. Despite clear evidence of the production of domoic acid by some of these species, the absence of any recorded impact of this toxin in these systems is somewhat contrary to observations in the California and Canary Current Systems.

In the Benguela Current, blooms of *Lingulodinium polyedrum*, known to produce yessotoxins, were until recently unknown despite being common in

the California, Canary, and Humboldt Current Systems (Trainer et al., 2010). However, in the summer of 2013–2014, *L. polyedrum* was responsible for the most extensive bloom ever recorded on the South African coast, impacting nearly 1,000 km of coastline (van der Lingen et al., 2016). Although cysts of *L. polyedrum* were known to be present in the sediments of the Benguela, *L. polyedrum* had not been previously recorded as a component of the plankton. This bloom followed extensive blooms of *Gonyaulax polygramma* in the same region in 2011, which coincided with



FIGURE 1. An unprecedented bloom of *Pseudo-nitzschia* in 2015 was the first to negatively impact both shellfish and fish harvest industries, as well as marine mammal health, along the entire US and Canadian west coasts. Shaded areas with shellfish symbols on land denote shellfish closures. Fish symbols indicate northern anchovy closures at designated landing sites. Shaded or hatched areas offshore (Dungeness crab and rock crab) correspond to the closures listed on the left. Stranded marine mammals with detectable domoic acid (DA) (orange) and California sea lions diagnosed with DA poisoning (red) are pictured with the number of individuals indicated. DA poisoning is defined as the presentation of at least two of the following: neurologic signs (seizures, head weaving, ataxia), detectable DA, histopathologic lesions, and/or blood chemistry changes. From McCabe et al. (2016)

nearshore aggregations and beaching of the sardine *Sardinops sagax* (van der Lingen et al., 2016). Sardines within the bloom area were shown to be in poor physical condition, suggesting that these blooms could pose a significant risk to sardines and the associated fishery in this region (Figure 2).

In the summer of 2016–2017, blooms co-dominated by *L. polyedrum* and *G. spinifera*, both yessotoxin producers, for the first time significantly impacted farms of the abalone *Haliotis midae* on the southwest coast of South Africa, causing large mortalities and major stock losses (personal observation of author Pitcher). These events followed a mass mortality of the red abalone *Haliotis rufescens* on the Californian coast in 2014, also attributed for the first time to yessotoxin poisoning (De Wit et al., 2014). This abalone mortality was part of the largest invertebrate die-off ever recorded in the region, with crabs and sea urchins also affected. Mortalities in shallow waters were as high as 48%, resulting in a statewide reduction of the yearly harvest limit for abalone. Yessotoxin as the cause of the mortality was implied by means of forensic genomics (De Wit et al., 2014).

Dinophysis spp., as producers of the lipophilic shellfish toxins okadaic acid, the dinophysistoxins, and the pectenotoxins are the primary cause of shellfish harvesting closures in western Europe, including along the Iberian coast. In 2012, an exceptional bloom of *Dinophysis acuminata*, in terms of both early initiation and record cell densities, was observed in the Galician Rias¹ (Díaz et al., 2013). Although short-term variability in *Dinophysis* spp. in response to environmental conditions in the Galician Rias had been the subject of several investigations, less was known at that time of the causes of interannual variability. Subsequent analysis of a 28-year

time series was therefore undertaken to identify the meteorological and environmental conditions responsible for the exceptional bloom of *D. acuminata* in 2012. Early initiation of blooms was shown to coincide with anomalous winter upwelling, the persistence of scattered *D. acuminata* populations inside the rias during winter, and the likely availability of prey. As is typical, peak cell densities were evident following thermal stratification after periods of moderate upwelling.

Upwelling systems generally have a long history of PSP, with *Alexandrium catenella* the dominant PSP toxin producer in the Benguela and California

Current Systems and *Gymnodinium catenatum* and *Alexandrium minutum* the common cause of PSP in the Canary Current System. *A. minutum*, which tends to be limited to small embayments or harbors, was considered to be confined to the Canary Current System prior to its identification in 2003 in the Benguela (Trainer et al., 2010). However, Baylón et al. (2015) subsequently provided the first record of *A. minutum* on the Peruvian coast following its identification as the species responsible for blooms in Callao Bay during the austral summers of March 2006 and February 2009. Reports such as these contribute

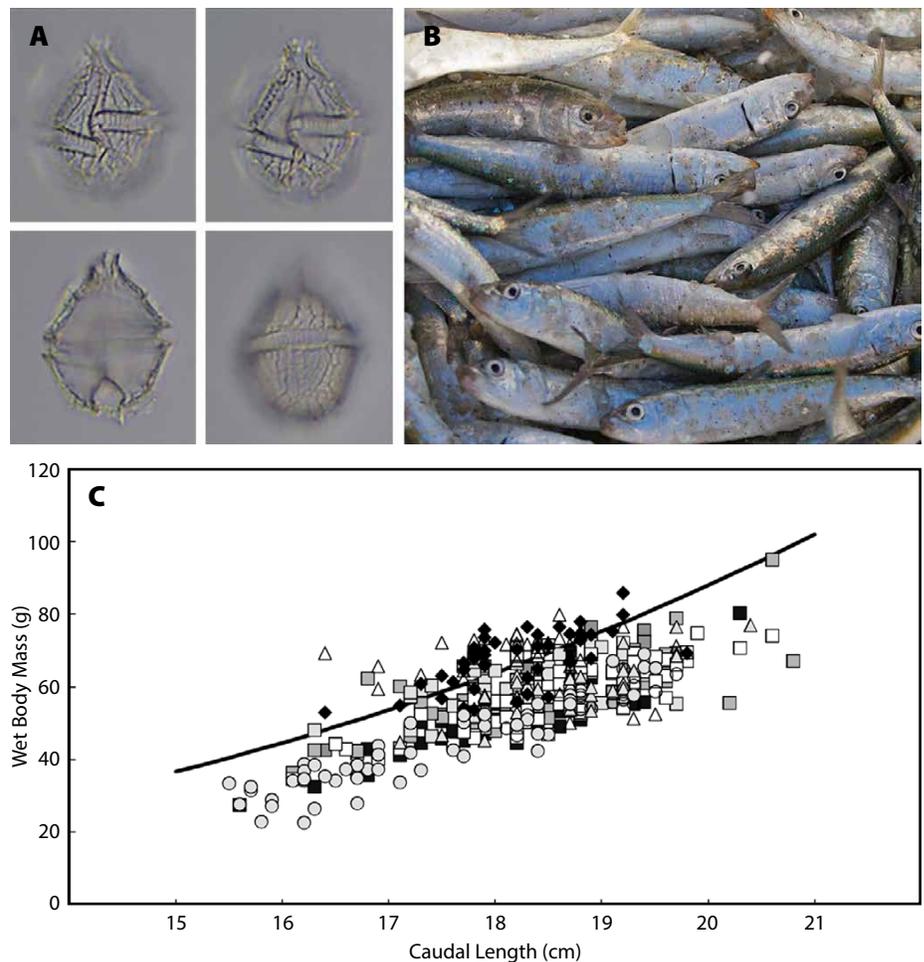


FIGURE 2. In 2011, the South African coast was subject to a massive bloom of *Gonyaulax polygramma* (A) with a spatial extent that coincided with near-shore aggregations and wash-ups in some localities of sardine *Sardinops sagax* (B). Sardines in the bloom areas were also in poor condition compared to those elsewhere as is evident from the scatter plot of their wet body mass against caudal length (different symbols represent fish from different localities either washed up on beaches or concentrated in the nearshore) in relation to the long-term length-mass regression (solid line, C). The retention of these dinoflagellates on sardine gill rakers is considered to have “irritated” the fish in some way such that they ceased feeding and lost condition. Given the substantial economic and ecological importance of sardines in the Benguela Current ecosystem, these observations are a serious concern. Adapted from Van der Lingen et al. (2016); Photo credits: G. Pitcher and R. Tarr

¹ Rias are long, narrow coastal inlets that are formed by the flooding of river valleys. They differ from fjords in that they have no sill and gradually decrease in depth and width with distance from the coast. Within upwelling systems, rias are unique to the Iberian Peninsula.

to the continued geographic expansion of records of HAB species in upwelling systems provided primarily through the expansion of observation and monitoring programs.

Similarly, records of toxins and toxin-producing species are expanding as a function of improved methods of toxin analysis. Toxicity tests using the mouse bioassay have in many instances been replaced by chemical quantification of various lipophilic toxins using liquid chromatography–mass spectrometry (LC–MS), which has revealed complex toxin profiles in the lipophilic shellfish extracts. While many lipophilic toxins, including okadaic acid, the dinophysistoxins, the pectenotoxins, and/or yessotoxins are still problematic, azaspiracids (AZA), the toxins that cause azaspiracid poisoning (AZP) in humans, have emerged as a new issue in shellfish off the coasts of Galicia, Portugal, and Southwest Spain, and an AZA-producer, *Amphidoma languida*, has been identified off the coast of Southwest Spain (Tillmann et al., 2017).

Concerns relating to high biomass HABs referred to as red tides, and their association with events of episodic

anoxia within upwelling systems, continue to grow. Mass mortalities attributed to these events typically occur following the nearshore accumulation and decay of red tides (e.g., Kahru et al., 2008; Pitcher and Probyn, 2011). Consequent oxygen depletion may also coincide with corrosive low-pH conditions, and in some cases, the production of H₂S, that are equally harmful to marine life. Specifically in the southern Benguela, events of episodic anoxia have had major impacts on living marine resources. During the late 1980s and 1990s, the contribution of the West Coast rock lobster resource to total lobster landings on the South African coast declined from about 60% to <10%. This decline was linked to an increase in the number and severity of lobster mortalities attributed to increasing anoxia events associated with an increase in the frequency of red tides (Pitcher et al., 2014). Such anoxia events continue to regularly impact the St Helena Bay region of the southern Benguela, with a major lobster mortality as recently as 2015 attributed for the first time to blooms of the dinoflagellate *Prorocentrum triestinum* (Figure 3).

In the California Current, red tides

produced by the dinoflagellate *Akashiwo sanguinea* have emerged as a new type of HAB. While the organism itself is not known to produce toxins, and has not been associated with anoxic events in California, it has been linked to massive bird mortalities (Jessup et al., 2009) caused by the production of a surfactant foam. This foam interferes with the natural waterproofing properties of bird feathers, likely causing impacted birds to succumb to hypothermia. First identified in Monterey Bay in 2007, a second, larger event in 2009 resulted in the mortality of hundreds of birds (Phillips et al., 2011). Similar to the 2015 domoic acid event, these blooms were associated with climate anomalies leading to unusually warm and calm conditions, and may have been initiated by pelagic seed banks of cells (White et al., 2014).

The diversity of HAB species and their impacts in upwelling systems serve to demonstrate the challenges of achieving the GEOHAB goal of improved prediction. The required explicit representation of the biology of HAB species for model development ensures that the requirement for species-specific information continues to be a priority (Pitcher,



FIGURE 3. In the southern Benguela, episodic events of low oxygen following the decay of red tides have had major impacts on living marine resources within the region. In February and March 2015, St Helena Bay was once again subject to large marine mortalities, with a total of 415 tons of rock lobster (*Jasus lalandii*), 21 tons of molluscs (mostly the white mussel *Donax serra*), and seven tons of various fish species removed from the beaches (D. van Zyl, Department of Agriculture, Forestry and Fisheries, *pers. comm.*, 2016). The causative dinoflagellate was identified as *Prorocentrum triestinum*. The events of 2015 provide the first records in the southern Benguela of mortalities of marine life linked to anoxia following the decay of *P. triestinum* blooms. Photo credits: J. Foord, S. Sym, and G. Pitcher

2012). However, this biological complexity needs to be matched with appropriate complexity in the representation of environmental and ecological parameters that characterize sub-habitats to further predictive capabilities. We provide an update of the understanding of HABs through assessment of their seeding and nutrient strategies and of the physical processes so important in controlling their development and movement.

SEEDING AND NUTRITION OF HABs

The origins of phytoplankton populations and the life-history stages of the cells that inoculate blooms in upwelling systems are generally poorly established. Blooms most often appear as a consequence of active cellular growth, the physical accumulation of populations from far-field sources, local advection, or a combination of these factors (Smayda and Trainer, 2010). Phytoplankton population maintenance in upwelling systems is challenged by the need to counter cell dispersal. During active upwelling when diatoms typically bloom, dinoflagellates are usually found offshore, at fronts, or in outer shelf currents. These populations may serve as refuge seed banks and may inoculate nearshore blooms when upwelling relaxes (Smayda, 2002). A variation of this seeding mechanism has been demonstrated for toxic *Pseudo-nitzschia* in southern California (Seegers et al., 2015) and for *D. acuminata* in the Rías Baixas on the Iberian coast (Velo-Suárez et al., 2014) in that the delivery of subsurface or bottom-dwelling offshore populations to nearshore surface waters occurs during active upwelling.

HABs that incorporate life-cycle transitions in their seeding strategies are considered particularly amenable to prediction. Specifically, bloom simulation through quantification of the benthic-pelagic coupling of life-cycle stages that include a benthic cyst is likely to be predictive. Progress in the parameterization of life-cycle transitions and their incorporation into species-specific numerical

models has, however, been limited in upwelling systems. Furthermore, most dinoflagellates in upwelling systems are holoplanktonic in that they lack a sexual resting cyst and rely on vegetative cells to survive inhospitable conditions and to seed blooms (Smayda and Trainer, 2010). This domination of holoplanktonic dinoflagellates suggests that a cyst stage may in fact provide little benefit for growth in upwelling systems.

Cyst-forming or meroplanktonic dinoflagellates are a minority in upwelling systems and are dominated by heterotrophic dinoflagellates (Pitcher and Joyce, 2009). However, within this minority, cyst-forming toxic species *Alexandrium catenella*, *Gymnodinium catenatum*, *Lingulodinium polyedrum*, and *Protoceratium reticulatum* are prominent. Therefore, further consideration should be given to the predictive value of a better understanding of the life-cycle stages of these species. Of interest is the role played by seeding in the long-term irregularity of some dinoflagellate blooms. As an example, observations of benthic resting cysts of *L. polyedrum* in the southern Benguela were made for many years prior to 2014 without evidence of pelagic blooms, while in the Galician Rias, *L. polyedrum*, known to form red tides during the first half of the twentieth century, is now rare despite the abundance of cysts in the sediment (Trainer et al., 2010). These observations suggest that bloom behavior cannot be inferred from the capacity of a species to produce resting cysts, or from the presence of cysts in sediments (Pitcher and Joyce, 2009). Varying dormancy periods further complicate the role of dinoflagellate cysts. In the southern Benguela, the presence of a short dormancy period in *A. catenella* suggests a rapid cycling between benthic and planktonic stages rather than an overwintering strategy (Joyce and Pitcher, 2006). It may be that phytoplankton species in upwelling systems are able to opportunistically exploit multiple seeding options conferred by their life cycle rather than depending on

a single seeding mode in which case prediction is more difficult.

Following successful seeding, the important role nutrients play in the ordination of phytoplankton is widely acknowledged (Margalef, 1978; Wyatt, 2014), and the clear link between nutrient availability and supply, and the physical forcing of upwelling systems, points to the need to understand the nutrient eco-physiology of HAB species in attempting to predict blooms. Predictable changes in the uptake of new and regenerated nitrogen, as depicted by changes in the *f*-ratio associated with the upwelling-downwelling cycle, are accompanied by predictable changes in the phytoplankton community, indicative of changing nutritional strategies. Recognition of these changes has led to attempts, based on measurements of nitrogen uptake rates, to ascertain the role nutrients play in determining not only community succession but also the selection of HAB species (Seeyave et al., 2009). Although selective and contrasting species-specific nutrient strategies have been observed, trends are inconsistent and typically attributed to interspecific differences or differences in nutrient history.

There has been a general perception that anthropogenic nutrient input in upwelling systems is small compared to nutrients supplied by upwelling and is therefore unlikely to influence HAB development. However, recent studies on the California coast show a significant input of nitrogen from wastewater effluent, riverine runoff, submarine groundwater discharge, and atmospheric deposition (Reifel et al., 2013; Howard et al., 2014; Lecher et al., 2015). Compared to the input from upwelling, these nutrient sources are smaller by at least an order of magnitude at system or regional scales. However, at scales relevant to HAB development in the nearshore, natural and anthropogenic nutrient contributions are in some cases equivalent, particularly for some seasonal time periods, and may stimulate bloom development.

THE STRONG INFLUENCE OF PHYSICAL FORCING

Physical forcing on a range of scales strongly influences HABs in upwelling systems. The importance of small-scale

physical processes in affecting phytoplankton selection has been recognized in the cycles of water column mixing and stratification that are effective in regulating spatial and temporal differences in

phytoplankton assemblages. These selection processes are consistent with the Margalef (1978) conceptual model in which functional groups of phytoplankton are variously adapted to an environment defined in terms of turbulence and nutrient availability. Further progress in addressing the role of small-scale physical processes in HAB development has been achieved through technological advances in high-resolution observations of the small-scale complexity of physically driven niche diversification and species-specific behavior.

Investigations have been undertaken to further understanding of the biological, chemical, and physical mechanisms involved in the formation, maintenance, and dissipation of subsurface thin layers, which are often associated with water column stratification. For example, Velo-Suárez et al. (2010) demonstrated the role differences in shear profiles play in the formation of thin layers of *Pseudo-nitzschia* in Ría de Pontevedra on the Galician coast. Maximum values of shear during upwelling events when the vertical variation in horizontal inflow velocity is enhanced, coupled with maximum buoyancy frequency, tend to shape subsurface populations into thin layers. The vertical distribution of the thin layers is in turn controlled by the upwelling-downwelling cycle, with erosion of the layers during downwelling and strengthening of the layers during upwelling. Tidal forcing further modulates the distribution of *Pseudo-nitzschia*, with cell maxima appearing during low tides and maximum water column stratification (Figure 4; Díaz et al., 2014).

Rigorous investigation of vertical structure with reference to HABs has also taken place in Monterey Bay where autonomous underwater vehicle (AUV) surveys were instrumental in examining the scales and processes of phytoplankton thin-layer development (Ryan et al., 2010). These studies also included investigation of the role played by species-specific phytoplankton properties in creating disparate patterns in the vertical distribution

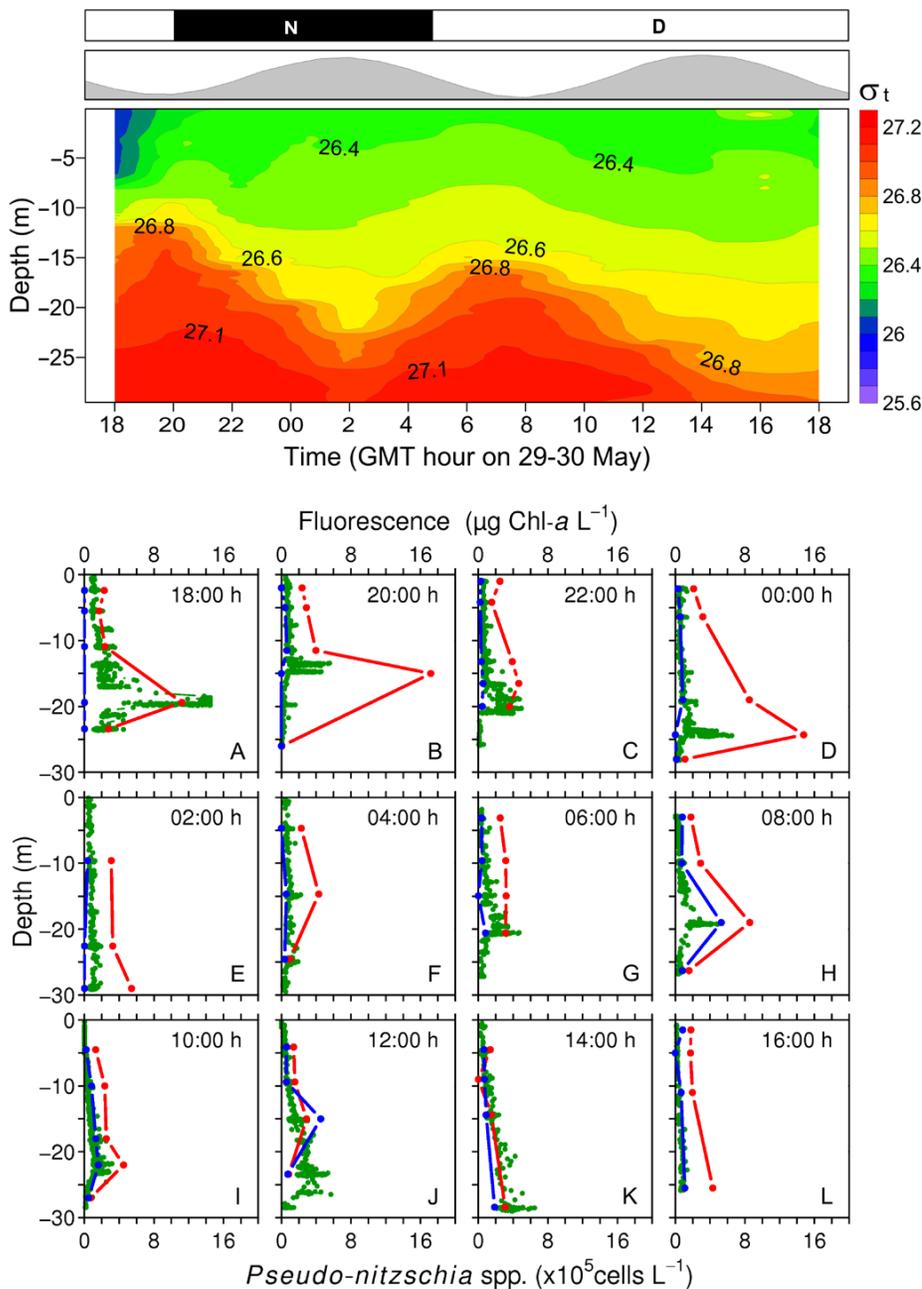


FIGURE 4. High-resolution measurements were undertaken in the Ría de Pontevedra to study physical-biological interactions in the distribution of cells of the *Pseudo-nitzschia seriata* and the *Pseudo-nitzschia delicatissima* groups. Intra-tidal density (σ_t) distribution is depicted for a 24-hour experiment on May 29–30, 2007, along with the vertical distributions of the *Pseudo-nitzschia seriata* (red) and *P. delicatissima* (blue) groups, and chlorophyll *a* (Chl-*a*) fluorescence (green). The state of the tide and light and dark periods are indicated on the horizontal bar above. A thin layer of chlorophyll dominated by the *P. seriata* group was initially observed with maximum cell densities at 15 m depth at low tide (20h00). With the rising tide, the thin layer deepened and was eroded. A thin layer dominated by the *P. delicatissima* group was re-established at the next low tide (08h00) in association with a new chlorophyll maximum at 17 m depth. The rising tide was again associated with the erosion of this layer. These observations demonstrated tidal modulation of the distribution of *Pseudo-nitzschia* with cell maxima appearing at low tides and maximum water column stratification. From Díaz et al. (2014)

of individual taxa (Rines et al., 2010). As an example, the swarming behavior of *Akashiwo sanguinea* was shown to result in the formation of intense thin layers near the pycnocline at night followed by migration to near-surface waters at dawn (Figure 5). Migration is clearly responsive to nutrient distribution, with nighttime observations showing thin layers aligned with a nitrate isopleth that significantly diverges from the isotherms owing to nutrient uptake during downward migration (Ryan et al., 2010). Internal tidal pumping from Monterey canyon onto the shelf is thought to support the growth of these vertically migrating phytoplankton by enhancing nutrient availability at the thermocline during periods of stratification. Laboratory studies have likewise demonstrated vertical migration by *A. sanguinea* and also *Prorocentrum micans* in their acquisition of both nitrate and iron (Peacock and Kudela, 2014). HABs are often associated with nutrient depletion in surface waters, and the assimilation of micro- and macronutrients at depth by strong-swimming dinoflagellates could provide an important ecological advantage in environments where light and nutrients are vertically separated.

Although typically considered more operative in the vertical, Shanks et al. (2016) recently demonstrated the role small-scale physical processes play in the alongshore variation of exposure of intertidal organisms to toxic *Pseudo-nitzschia* species as determined by surf zone hydrodynamics. The ingress of *Pseudo-nitzschia* into surf zones and consequent contamination of shellfish was shown to vary dramatically between reflective and dissipative surf zones. Both *Pseudo-nitzschia* and particulate domoic acid concentrations were shown to be markedly higher at dissipative beaches where rip currents facilitated greater exchange of surf zone water with offshore water.

At a larger scale, the importance of cross-shelf and alongshore currents in the transport, accumulation, and dispersion of HAB populations is well

recognized in upwelling systems (Pitcher et al., 2010). Fluctuations in wind direction and consequent changes in cross-shelf currents are known to cause rapid changes in the phytoplankton at the event scale. Observations of shoreward accumulation of dinoflagellate-dominated blooms when upwelling winds relax are common. As an example, Veloso-Suárez et al. (2014) demonstrated rapid increases of *D. acuminata* in a Galician Ria in response to wind relaxation and downwelling (Figure 6). Their conceptual model of the mechanisms by which *D. acuminata* blooms develop in a ria incorporates not only the physical transport of blooms but also their mixotrophic nutrition and behavior. The biological processes include nutritional status as determined by availability of its prey *Mesodinium rubrum*, the possible role of parasitism, and an overwintering stage.

Appreciation of the role alongshore currents play in dictating the distribution of HABs in upwelling systems is increasing. Poleward countercurrents on the inner shelf during the latter stages of the

upwelling season are particularly important in the transport of HABs. Escalera et al. (2010) demonstrated the role the Portugal Coastal Countercurrent plays in the poleward transport of *Dinophysis acuta* and the occurrence of DSP in the Galician Rias in autumn. The decline of *Dinophysis acuta* off the Portuguese coast at the end of the upwelling season is associated with its appearance off the Galician coast, and is attributed to transport by the inner shelf counter current. Maximum cell concentrations in the Galician Rias when estimates of cell division are almost zero clearly indicate the role of advection, in the form of inshore poleward flow combined with cross-shelf transport, in explaining cell increases in the rias at the end of the upwelling season.

Adams et al. (2000) first described the complexity of bloom transport pathways for toxic *Pseudo-nitzschia* from sites of development to razor clam beaches in the Pacific Northwest. Seasonal changes in the prevailing currents have been shown to be critical in determining the source of toxic blooms. In summer and

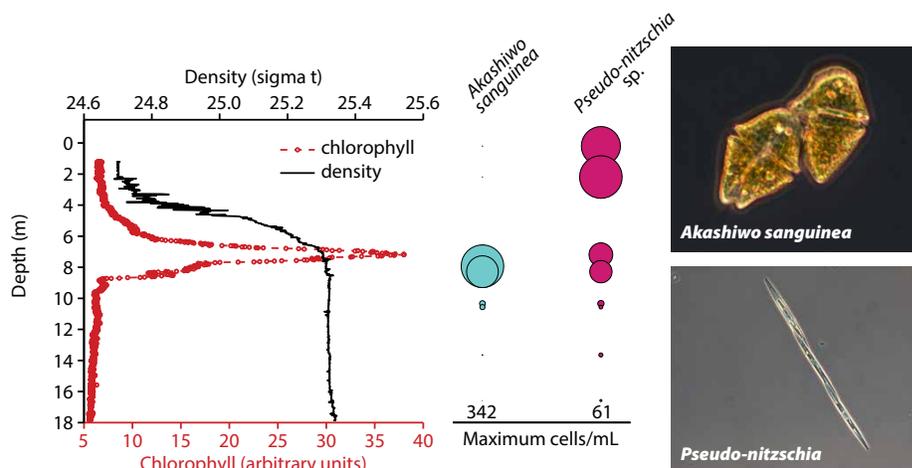


FIGURE 5. During the summer of 2005, experiments were undertaken in Monterey Bay to understand the properties of densely concentrated thin layers of plankton and the processes governing their dynamics. The vertical distributions of selected layer-forming and nonlayer-forming phytoplankton taxa in relation to density and chlorophyll as depicted at 23:14 h on August 26, 2005, allow elucidation of the role that species-specific properties of phytoplankton play in thin layer dynamics. For each taxon, circle size is proportional to cell concentration normalized by the maximum observed concentration in this profile. Numbers under circles indicate the maximum observed cell concentrations (cells mL^{-1}) for each taxon. *Pseudo-nitzschia* was present in the upper water column, but was not reflected in the chlorophyll profile. The most striking taxon in the upper water column was the large, motile dinoflagellate *Akashiwo sanguinea*, which is capable of strong migration. It formed dense, patchy slicks during the day, migrated downward to form intense, high-chlorophyll layers at the pycnocline at night, and returned to the surface at dawn. This vertical migration was driven by elevated nutrient concentrations at the base of the pycnocline. Modified from Rines et al. (2010)

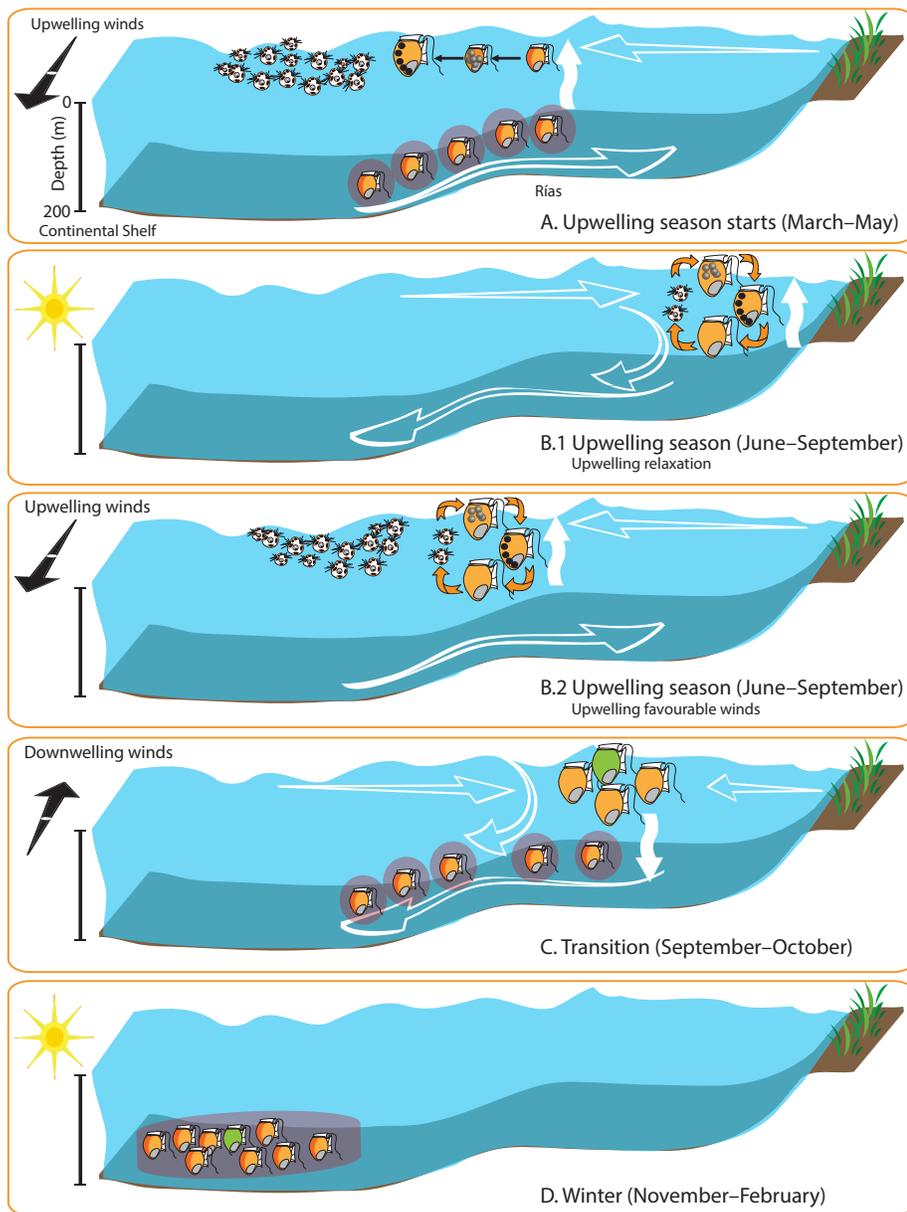


FIGURE 6. A simplified conceptual model describing seasonal trends of *D. acuminata* in the Rias Baixas in Spain. Black and hollow white arrows show wind and current directions, respectively. Filled white lines indicate active *D. acuminata* swimming. Changes in *Dinophysis* populations not observed in the field (hypothetical steps) are shadowed with circles or boxes. The introduction of *D. acuminata* seed populations from shelf bottom waters into the rias is typically associated with strong pulses of upwelling (A). Cells concentrate in the upper 0–10 m following upward swimming, and surface populations may be transported out of the rias during periods of upwelling (A). The encounter of *D. acuminata* cells with their prey *Mesodinium rubrum* is important as heterotrophic feeding provides essential nutritional needs and enhances growth rates (B.1). A change in cell appearance follows feeding, with a progression from small, non-vacuolated cells, to large, highly vacuolated, and to starch-containing cells. In situ cell division and the physical accumulation of cells during periods of downwelling lead to high-density patches of *D. acuminata* and *M. rubrum* (B.1). The distribution of both *D. acuminata* and *M. rubrum* is strongly influenced by the upwelling-downwelling cycle, and they may become spatially separated (B.2). Little is known about the termination of *D. acuminata* blooms, but observations of cells near the seabed suggest the possible transition of vegetative cells to an “over-wintering” stage that behaves like a “functional cyst” with low nutritional requirements (C). Cells in bottom waters may be transported from the rias onto the continental shelf during downwelling (D). From Velo-Suárez et al. (2014)

autumn when upwelling-favorable winds and equatorward flow dominate, the Juan de Fuca Eddy serves as the source of *Pseudo-nitzschia*. At this time, brief transitions to downwelling-favorable winds are required to move *Pseudo-nitzschia* blooms shoreward onto coastal beaches. However, in early spring when poleward flow is prevalent, toxic *Pseudo-nitzschia* from Heceta Bank provide the source of toxin in razor clams (Hickey et al. 2013). Transport pathways are further complicated by the buoyant Columbia River plume, which serves primarily as a barrier at some locations during summer and autumn and as a conduit during winter and spring. Knowledge of these transport mechanisms demonstrates the potential use of circulation models in conjunction with real-time observations in the prediction of blooms.

Mesoscale features that interrupt typical upwelling circulation patterns are well known for controlling the spatial distribution of HABs within upwelling systems (Pitcher et al., 2010). Biophysical interactions in coastal upwelling environments acquire a strong, spatially explicit component as a consequence of coastline configuration and orientation and bottom topography. The resulting coastline features, ranging from headlands, capes, peninsulas, rias, bays, and estuaries, are often more vulnerable to HABs owing to their influence on wind stress and water stratification, and through their retentive circulation that minimizes dispersal by lateral advection (Pitcher et al., 2010). HAB hotspots on the US West Coast, identified through satellite-derived measurements of fluorescence line height are, by way of example, attributed to such coastline features and the elevated biomass with which they are associated (Frolov et al., 2013). In assessing the spectrum of coastline configurations found in upwelling systems, Pitcher et al. (2010) concluded that open bays with cyclonic retention, such as Monterey Bay, Paracas Bay, Lisbon Bay, False Bay, and St Helena Bay, are most susceptible to high biomass HABs. These environments are thought

to offer the required balance between mixing and stratification, and between advective dispersion and retention, allowing adequate exchange with the adjacent coastal environment, thereby facilitating introduction of coastal seed populations and adequate delivery of nutrients.

HAB PREDICTION AND RESPONSE TO CLIMATE CHANGE

Many HAB species are recognized as regular components of the seasonal succession of phytoplankton, yet few can be predicted with a great deal of certainty. The development of models is fundamental to HAB prediction in upwelling systems, but the models tend to lag our theoretical understanding. To date, most HAB models have employed either conceptual or empirical approaches, and the development of new models has been restricted by lack of data. Employing the interactive effects of habitat mixing and nutrient conditions, the Margalef (1978) mandala offered one of the first models for the prediction of red tides in upwelling systems. In its simplest form, this model has been used to temporally and spatially segregate diatom- and dinoflagellate-dominated communities in upwelling systems based on their predictable responses to varying regimes of turbulence and nutrients (e.g., Pitcher and Nelson, 2006). This ecological classification of diatoms and dinoflagellates has led to the development of several empirical or statistical models.

Statistical models have been used with some success in predicting *Pseudo-nitzschia* abundance in the California and Iberian upwelling systems based on an ecological relationship between *Pseudo-nitzschia* species and potentially causative environmental variables. Anderson et al. (2009) used time-series data to define the ranges of environmental conditions associated with *Pseudo-nitzschia* blooms in the Santa Barbara Channel. Applying these environmental conditions, statistical models incorporating satellite ocean color and sea surface temperature observations were able to correctly predict 98% of toxic blooms but with a high rate

of false positive identification. Similarly, Lane et al. (2009) developed predictive logistic models of toxigenic *Pseudo-nitzschia* blooms for Monterey Bay. Chlorophyll *a* (Chl-*a*) and silicic acid were used as predictors, but significant refinement to the models was achieved by period-specific inclusions of temperature, an upwelling index, river discharge, or nitrate data. Palma et al. (2010) also achieved some success in the prediction of *Pseudo-nitzschia* blooms in Lisbon Bay using statistical models in the application of regression analysis to the relationship of *Pseudo-nitzschia* blooms to sea surface temperature and an upwelling index. Models developed for three oceanographic seasons allowed forecasting of the presence of *Pseudo-nitzschia* in spring and summer, revealing a lag of four to six days between upwelling events and the appearance of *Pseudo-nitzschia* blooms.

Hydrodynamic circulation models are being used with increasing success for identifying and constraining the physical processes governing bloom dynamics in upwelling systems. These models can be used to track bloom trajectories, and they are useful for predicting the timing and spatial impact of blooms. Off the Iberian Peninsula, Lagrangian particle tracking of HABs using numerical models of ocean circulation compared favorably with observations at coastal monitoring stations (Mateus et al., 2013; Pinto et al., 2016). The use of regional models in conjunction with information from remote sensing and in situ monitoring networks has been central to the development of HAB forecast systems on the Iberian coast as part of the Applied Simulations and Integrated Modelling for the Understanding of Harmful Algal Blooms (ASIMUTH) project. The Portuguese Coast Operational Model System (PCOM) and the Regional Ocean Modeling System (ROMS) have been used in the development of forecast systems for the Iberian coast (Pinto et al., 2016; Silva et al., 2016) and the Galician Rias (Ruiz-Villarreal et al., 2016), respectively. These models provide forecasts of

oceanographic variables important to HABs and are also coupled to Lagrangian particle-tracking models, which simulate alongshore transport of HABs and their movement between the shelf and the rias.

Prediction of *Pseudo-nitzschia* blooms in the California Current System has also been achieved through numerical simulations employing ROMS. Anderson et al. (2011) used a combination of satellite observations, statistical models, and hydrodynamic models to spatially map and predict *Pseudo-nitzschia* blooms and domoic acid events in Santa Barbara Channel. For the Pacific Northwest coast, Giddings et al. (2014) used a realistic numerical simulation of the region and particle tracking experiments to investigate possible *Pseudo-nitzschia* transport pathways from the Juan de Fuca Eddy and from Heceta Bank, two known hotspots of bloom formation. These simulations confirmed the existence of northern and southern transport pathways and also revealed the influence of the Columbia River plume on these pathways. Hindcasts were, consequently, able to capture most of the observed harmful *Pseudo-nitzschia* beach events, although many false positives were again recorded. Predictability was improved by incorporation of phytoplankton biomass data from a coupled biogeochemical model that was shown to significantly reduce the number of false positives.

The likely impact of climate change, and more specifically global warming, on the incidence of HABs also provides a significant predictive challenge. Upwelling systems and the HABs common to these systems are likely to be sensitive to climate change because of their strong dependence on environmental drivers. With increasing availability of long-term data sets, changing trends in HABs related to climate are emerging.

Díaz et al. (2016) describe the seasonal and interannual variability of *Dinophysis acuta* in the Galician Rías Baixas in relation to climate based on descriptive analysis of a 30-year time series of this lipophilic, toxin-producing dinoflagellate. In

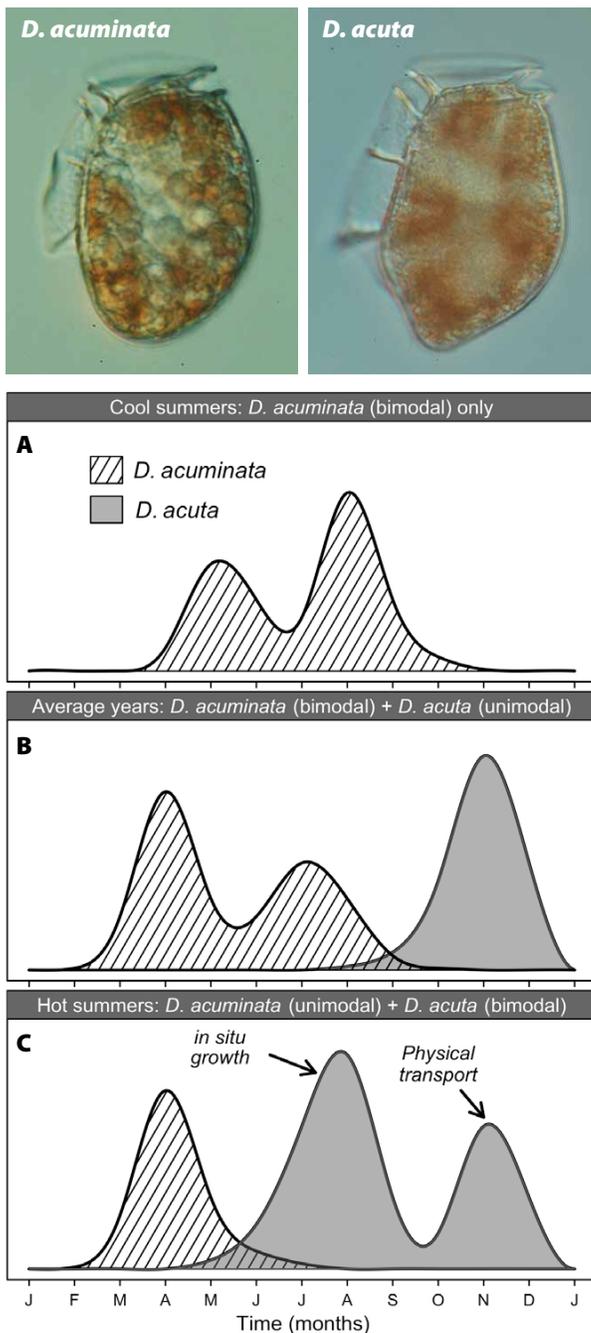


FIGURE 7. A conceptual model of the seasonal distribution of the lipophilic toxin producers *Dinophysis acuminata* and *Dinophysis acuta* in the Galician Rías Baixas under three different climatic scenarios. Based on a 30-year time series, the first pattern (A) is characterized by the occurrence of only *D. acuminata*, with a clear bimodal distribution, with maxima, in late spring and in late summer-early autumn. This pattern is observed during years with cool summers. In the second pattern (B), short-lived blooms of *D. acuta*, associated with alongshore transport, follow *D. acuminata* during the autumn transition. This second pattern is observed during years with normal hot summers and is dependent on the presence of good growth conditions off the Portuguese coast. In the third pattern (C), *D. acuta* replaces *D. acuminata* in late summer. In these cases, *D. acuta* shows a bimodal distribution, with a first maximum in late summer due to in situ growth, and another maximum in the autumn transition that is linked to physical transport. This pattern occurs in years when very hot summers combine with moderate upwelling conditions, resulting in increased stratification and deepening of the thermocline. Adapted from Díaz et al. (2016); Photo credits: L. Escalera

addition, the study tests a statistical model using climate indicators as predictors of these blooms. Three seasonal patterns in the occurrence of *D. acuta* and *D. acuminata* were identified under different climatic scenarios (Figure 7). In most years, *D. acuta* was generally absent from the plankton, but in some years, it occurred either during autumn or during summer and autumn. Exceptional blooms that occurred in the late 1980s were characterized by the latter pattern, associated with hotter than average summers and moderate upwelling. Prediction of these patterns was achieved through application of a generalized additive model that incorporated an inoculum of *D. acuta*, a cumulative upwelling index, monthly average sea surface temperature, and tidal cycle and range.

Several studies on the Iberian coast have addressed long-term trends in the occurrence of HABs in response to reduced upwelling. Álvarez-Salgado et al. (2008) applied statistical approaches to long-term data sets from the Rías Baixas on the Iberian coast to demonstrate a correlation between wind patterns on the shelf, which control the flushing of these large coastal inlets, and closures of mussel cultivation areas. These relationships were established on the ecological basis of a dynamic segregation of diatoms and dinoflagellates determined by the residual circulation of the Rías Baixas. Over the past 40 years, dinoflagellates, including lipophilic toxin producers, have been favored by a decrease in the extent and intensity of the upwelling season and a consequent increase in the renewal time of the rias (Álvarez-Salgado et al., 2008). In the smaller Ría de Ares-Betanzos (Rías Altas), Álvarez-Salgado et al. (2011) show similar correlations between mussel harvesting closures due to lipophilic toxins and both coastal winds and precipitation. Closures during summer were predicted by the average continental runoff during the preceding spring, while closures during autumn were predicted by average offshore Ekman transport during the preceding summer. A rainy spring was thus found to lead to extensive closures in summer, and a windy summer to high closures in autumn. These observations of harvesting closures forced by meteorological conditions allow the prediction of shellfish toxicity based on the prediction of climate factors such as wind and precipitation.

Pérez et al. (2010) also addressed the impacts of weakened upwelling off the Iberian coast and observed contrasting ecosystem responses on the inner and outer shelf, coincident with increasing sea surface temperatures. The expected decrease in Chl-*a* on the outer shelf was confirmed by remote-sensing observations, but in the rias, Chl-*a* increased. Here, weaker upwelling was shown to reduce flushing, which favored stratification and the local recycling of nutrients. The resulting increases in nitrite, ammonium, and phosphate led to increases in dinoflagellate and *Pseudo-nitzschia* concentrations, although the total abundance of diatoms decreased.

More regular *Pseudo-nitzschia* blooms of a greater magnitude have also been reported for the California Current System (Sekula-Wood et al., 2011; Barron et al., 2013). Examination of a 15-year time series (1993–2008) of sediment trap samples from the Santa Barbara Basin by Sekula-Wood et al. (2011) revealed a shift to increasing *Pseudo-nitzschia* abundance and domoic acid toxicity in 2000 that was attributed to increasing blooms of *P. australis*. The shift was related to

climate variability and a change in phase of the North Pacific Gyre Oscillation that affected the upwelling of waters into Santa Barbara Basin. These observations were further supported through examination of a sediment core sample from Santa Barbara Basin spanning 1748 to 2007, which also provided evidence of regional cooling in 1999 accompanied by a change to *Pseudo-nitzschia* species (Barron et al., 2013).

McKibben et al. (2017) provide further evidence of climatic regulation of domoic acid in shellfish over the past 20 years in the northern California Current. They show the timing of elevated domoic acid to be strongly related to warm phases of the Pacific Decadal Oscillation and to Oceanic Niño Index events. Ocean conditions in the Northeast Pacific associated with warm phases of these indices, including changes in prevailing currents and advection of anomalously warm water onto the continental shelf, are thought to contribute to increases in this toxin. In warm-phase years, the spring biological transitions date, indicative of the seasonal transition of the northern California Current to southward flow, occurs later; alongshore currents tend to be weaker in association with warm Pacific Decadal Oscillation values; estuarine and offshore water temperatures are elevated; the copepod species richness anomaly is positive and there is a shift in copepod composition to species of a predominantly offshore or southern origin; and domoic acid levels in Oregon coast razor clams exceed closure values (McKibben et al., 2017). If global warming causes these warm ocean regimes to become more persistent, as is hypothesized, domoic acid events on the US West Coast may increase in persistence and frequency (McKibben et al., 2017).

Predictions of HAB responses to climate change have been realized by the development of a heuristic model of toxic blooms of *Alexandrium* in Puget Sound using long-term trends of PSP toxins in shellfish tissues (Moore et al., 2009). A temporal window of opportunity for

blooms, identified through examination of various time series of environmental conditions leading to toxic events, has been used to evaluate past and future bloom scenarios. Climate change projections based on global climate models and regional climate models for the Pacific Northwest predict a wider window of opportunity for *Alexandrium* blooms by the end of the twenty-first century (Moore et al., 2011). Blooms are predicted to begin two months earlier and persist for one month longer than present-day blooms, and these changes may be detectable within the next 30 years. Moore et al. (2015) further developed these projections using a mechanistic modeling approach to evaluate the effects of different climate pathways on the proliferative phase of *Alexandrium* in Puget Sound. Growth responses to temperature and salinity derived experimentally, combined with simulations of regional climate and hydrology, have shown bloom favorable conditions to increase by 30 days a year by 2050.

In addition to changes in the timing, location, and scale of HABs, climate-related changes are also likely to influence toxin production. For example, Tatters et al. (2013) demonstrated important influences on growth, carbon fixation rates, and total cellular toxicity of an *Alexandrium catenella* culture isolated from the California coast and subjected to combinations of temperature, $p\text{CO}_2$, and phosphate concentrations. Increased $p\text{CO}_2$ generally led to enhanced toxicity, suggesting that acidification of the California Current System may exacerbate the threat posed by this toxic dinoflagellate, especially when combined with nutrient limitation. Increases in cellular toxicity of the diatom *Pseudo-nitzschia fraudulenta* in the coastal California upwelling system have similarly been demonstrated in response to increasing anthropogenic acidification and episodic silicate limitation (Tatters et al., 2012).

Better knowledge of the linkages between HABs and climate will emerge only through the establishment and

maintenance of long-term phytoplankton monitoring programs supported by environmental monitoring. Our present-day understanding and ability to predict how climate may select for HABs is limited by the scarcity of long-term records, which are required for assessment of past climate variability on HABs and for the development and assessment of predictive models.

CONCLUSION

Our knowledge of the ecology and oceanography of HABs in upwelling systems has been significantly advanced through system-based studies and the comparative approach, as endorsed by GEOHAB. Despite limitations on meaningful comparisons because of a lack of data, GEOHAB facilitated valuable communication between scientists and provided much needed direction to HAB research in upwelling systems. Further, the development of common research objectives and approaches contributed significantly to improving the availability of comparable data and provided for a greater focus on the ultimate GEOHAB goal of improved prediction. Continued comparison of HAB phenomena in the California, Canary, Benguela, and Humboldt Current Systems will undoubtedly continue to contribute to our understanding, prediction, management, and mitigation of HABs in the major eastern boundary upwelling systems, as proposed in the science and implementation plan of GlobalHAB, the successor to GEOHAB.

GEOHAB specifically facilitated cooperation among biologists investigating HABs and physical oceanographers, statisticians, and modelers, and thus contributed to improving prediction. Physical models provided a very useful first step in the prediction of HABs in upwelling systems owing to the strong influence of physical forcing in dictating the development and movement of blooms through advection. Advanced subgrid-scale parameterizations for mixing are now included in models of coastal upwelling systems, allowing good representation

of several of their properties and characteristic features (GEOHAB, 2011). The required model representation of meso-scale activity as dictated by weather and various coastline configurations and topographical structures is now possible, and equations describing the transport and fate of HABs can be coupled to hydrodynamic models. Advances in the development of coastal observation systems now allow for the assimilation of data in the numerical simulation of ecosystem dynamics. Close coordination of observation and modeling efforts will contribute to future advances in the prediction of HABs.

Greater focus on development of biological models and their coupling to physical models is nevertheless also required to further advance prediction of HAB outbreaks. Explicit representation of the biology of HAB species is an essential element to model development of their bloom dynamics. Although the factors controlling the growth of a species can often be identified, top-down processes, such as grazing, also have a considerable bearing on population numbers. Therefore, there is a need for HAB species to be treated as components of communities in which there are complex interactions between the environment and the activities of a wide range of species. Further insight into this biological complexity needs to be matched with appropriate complexity and accuracy in the representation of the environment. ☒

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