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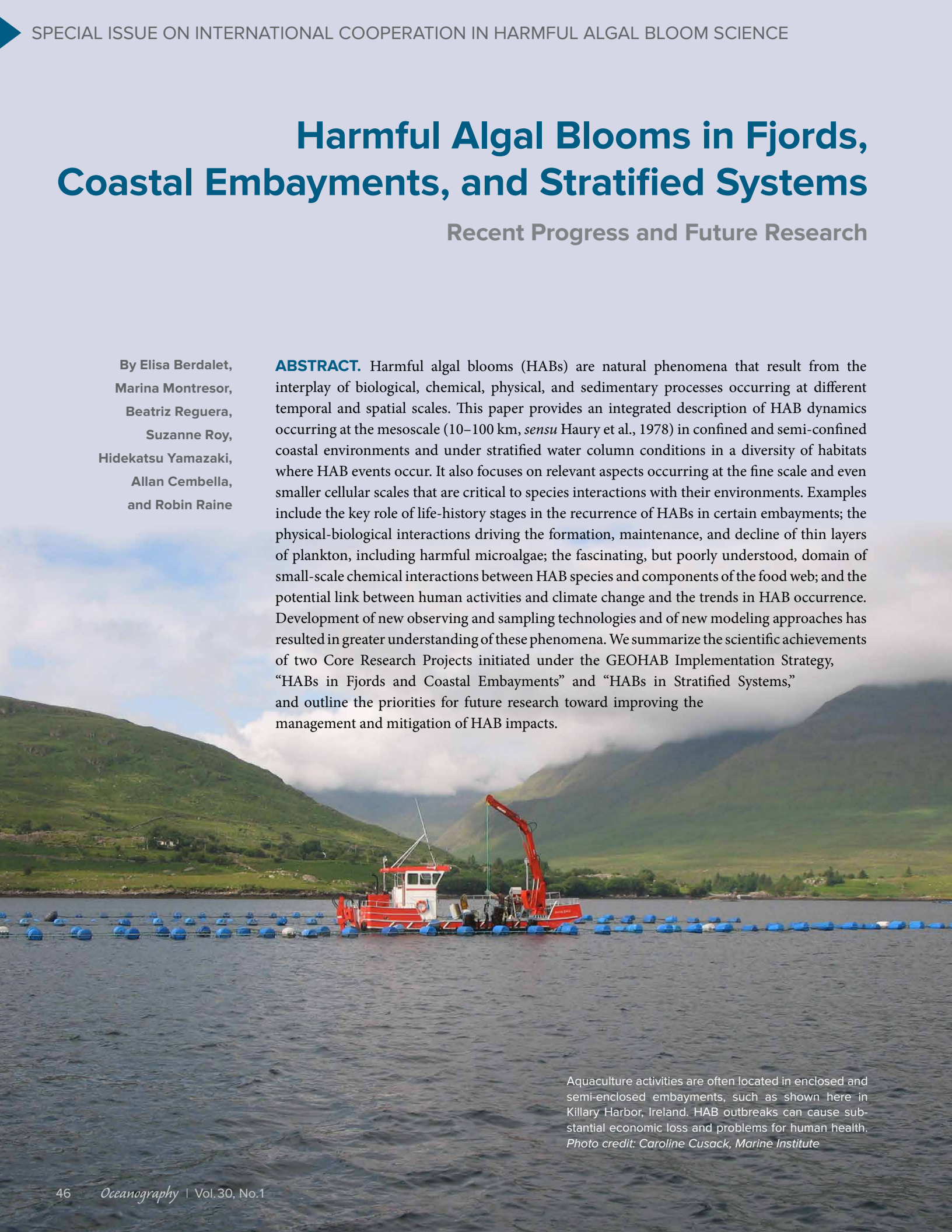
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Harmful Algal Blooms in Fjords, Coastal Embayments, and Stratified Systems

Recent Progress and Future Research

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ABSTRACT. Harmful algal blooms (HABs) are natural phenomena that result from the interplay of biological, chemical, physical, and sedimentary processes occurring at different temporal and spatial scales. This paper provides an integrated description of HAB dynamics occurring at the mesoscale (10–100 km, *sensu* Haury et al., 1978) in confined and semi-confined coastal environments and under stratified water column conditions in a diversity of habitats where HAB events occur. It also focuses on relevant aspects occurring at the fine scale and even smaller cellular scales that are critical to species interactions with their environments. Examples include the key role of life-history stages in the recurrence of HABs in certain embayments; the physical-biological interactions driving the formation, maintenance, and decline of thin layers of plankton, including harmful microalgae; the fascinating, but poorly understood, domain of small-scale chemical interactions between HAB species and components of the food web; and the potential link between human activities and climate change and the trends in HAB occurrence. Development of new observing and sampling technologies and of new modeling approaches has resulted in greater understanding of these phenomena. We summarize the scientific achievements of two Core Research Projects initiated under the GEOHAB Implementation Strategy, “HABs in Fjords and Coastal Embayments” and “HABs in Stratified Systems,” and outline the priorities for future research toward improving the management and mitigation of HAB impacts.



Aquaculture activities are often located in enclosed and semi-enclosed embayments, such as shown here in Killary Harbor, Ireland. HAB outbreaks can cause substantial economic loss and problems for human health. Photo credit: Caroline Cusack, Marine Institute

“Complex hydrodynamic processes (estuarine circulation, wind mixing, tidal dynamics, salinity, and thermal stratification) and pelagic-benthic coupling can play a major role in the dynamics of HABs in [confined or semi-confined coastal] systems.”

INTRODUCTION

A major goal of the research conducted worldwide over the past two decades within the framework of the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) program has been to achieve a deeper understanding of HAB dynamics and biogeography. This objective was addressed by linking the strategies implemented within various Core Research Projects (CRPs). Among the CRPs, the projects on “Harmful Algal Blooms in Fjords and Coastal Embayments” (F&CE-HAB) and “Harmful Algal Blooms in Stratified Systems” (Strat-HAB) provided an ideal template for data integration and created novel syntheses based on observations in comparative systems that were stratified and hydrographically constrained.

The F&CE-HAB CRP (Cembella et al., 2005; GEOHAB 2010, 2013) focused on coastal systems that are partially surrounded by land and thus affected by land-sea interactions (runoff, sediment dynamics) operating at spatial scales much smaller than those in open coastal or upwelling systems. Complex hydrodynamic processes (estuarine circulation, wind mixing, tidal dynamics, salinity, and thermal stratification) and pelagic-benthic coupling can play a major role in the dynamics of HABs in these systems. Fjords and coastal bays often act as “seed beds” for benthic cysts or relic populations of HAB species when there is limited water exchange with open coastal waters. Such coastal habitats are

often heavily occupied by human populations whose activities not only foster HABs but are then negatively affected by their consequences.

The Strat-HAB CRP (Gentien et al., 2005; GEOHAB, 2008) was a cross-cutting theme focused on understanding small-scale hydrographic features that are encountered in virtually all aquatic systems, including upwelling areas, fjords, and coastal regions and bays, whether or not they are affected by eutrophication. A particular emphasis was on thin layers (TLs), where many harmful phytoplankton organisms can thrive, and on rheological properties. In addition, technological and modeling challenges to resolve biological and physical interactions at fine and small scales were tackled (GEOHAB 2011, 2013; Berdalet et al., 2014).

Based on the state of knowledge of their themes, the two CRPs addressed specific key questions (GEOHAB, 2008, 2010) identified by the participants at Open Science Meetings held prior to the launch of each CRP. Details presented in the GEOHAB CRP reports, including mid-term and final program reviews, are openly available (<http://www.geohab.info>). Processes occurring at submeso-scale as well as fine and small physical scales (Figure 1) are common features of both CRPs. For this reason, the achievements of both CRPs are presented together in this article, along with some future research priorities to be addressed by the new GlobalHAB program ([\[www.globalhab.info\]\(http://www.globalhab.info\); Berdalet et al., 2017, in this issue\). This paper is also a tribute to our colleague and friend Patrick Gentien, who passed away in 2010. Patrick inspired and fostered research on the fine- and small-scale processes involved in HAB dynamics.](http://</p></div><div data-bbox=)

LIFE-HISTORY STRATEGIES OF HARMFUL SPECIES IN CONFINED AND SEMI-CONFINED ENVIRONMENTS

Although HAB species thriving in fjords and coastal embayments are not generally specific to these environments, an exception could be the harmful brown tides of the pelagophytes *Aureococcus anophagefferens* and *Aureoumbra lagunensis*. Blooms of these species reported from enclosed systems are characterized as thriving in high organic nutrient concentrations (Gobler and Sunda, 2012). The fish-killing *Aureococcus* can attain high biomass levels when inorganic nutrient concentrations are low because it can utilize organic forms of carbon, nitrogen, and phosphorus, and produce allelochemicals (biologically active compounds that elicit specific responses in target organisms) that harm its potential predators.

In confined and semi-confined areas, recurrent or chronic infestations of HAB species can develop as a consequence of the life-history strategy to produce benthic resting stages. During the past decade, there has been a major effort to understand the life histories of the main

HAB species that rely on resting stages. As a result of major technological advances, we now have better insights into different life forms, not always clearly associated with different morphologies, and their functionality (e.g., Brosnahan et al., 2015; see section below). Complex life cycles involving vegetative cells, a sexual phase, and temporal and resting cysts have been described for many dinoflagellates (Figures 1 and 2; Kremp, 2013; Bravo and Figueroa, 2014). Although resting stage formation has not been reported in species of the potentially toxigenic diatom *Pseudo-nitzschia* (Montesor et al., 2013), sexual events required for the formation of large-sized cells occur during blooms (Figure 3). In this genus, laboratory studies indicate that sex is a cell density-dependent mechanism (as reviewed by Montesor et al., 2016).

The different life forms provide alternative adaptive strategies in response to nutrient availability, dispersion avoidance, and protection against grazers and parasites (Fistarol et al., 2004; Alves

de Souza et al., 2015). They allow the organisms to occupy different ecological niches in the water column (holoplanktonic species), and also in the benthos (meroplanktonic species). Benthic resting cysts can be a safety mechanism for a planktonic cell population driven to virtual extinction at the end of the blooming period (Estrada et al., 2010). In addition, cyst beds are known to play key roles in the recurrence of the blooms in certain cases. For instance, in open coastal waters and at a wide spatial scale, cyst distribution patterns of the dinoflagellate *Alexandrium fundyense*, which is the source of paralytic shellfish poisoning (PSP), have been linked to inter-annual variability in the intensity and extension of the blooms of this species (McGillicuddy et al., 2011). Anderson et al. (2014) developed a model for empirical forecast of the geographic extent of a forthcoming bloom based on cyst abundances. However, this link varies among species and habitats, and interpretation is complicated by many natural factors,

such as resuspension, encystment, and germination rates and oxygen levels in the sediment (reviewed in Azanza et al., in press). Díaz et al. (2014a) observed a very rapid depletion of cysts from the sediments (<3 months), suggesting that resting cyst deposits play a minor role in the recurrence of blooms of PSP-causing *Alexandrium catenella* along the southern Chilean coast.

Furthermore, the intensity of some *Alexandrium* spp. blooms in inshore bays apparently does not depend on cyst distribution or abundance (Cosgrove et al., 2014; Ralston et al., 2014). These blooms are determined by a combination of retention of vegetative cells behind bathymetric barriers (shallow sills), daily vertical migration, and temperature that controls cell division rates (Crespo et al., 2011). In the case of the tropical and subtropical dinoflagellate *Pyrodinium bahamense*, the most common cause of PSP in the Philippines and in Southeast Asia, blooms are inoculated by cyst germination in small tropical bays but not in open coastal waters. Vegetative cells and cyst densities of *P. bahamense* seem to be governed primarily by the monsoons that may disperse them (Azanza, 2013). In shallow systems, *P. bahamense* often undergoes several cycles of transformation between pellicle cysts and vegetative cells during a single bloom period (Onda et al., 2014). A major challenge is to characterize the transition between the particular life-history phases in natural habitats (e.g., Ní Rathaille and Raine, 2011). This requires a sound understanding of the biological and environmental factors that control the life-history phases and their transitions. For instance, in the case of cysts, physical and sedimentary processes, such as resuspension from the bottom layer by bottom currents or sediment dredging, may play a greater role than previously suspected. The initiation of *A. fundyense* blooms along the eastern US coast seems to be linked to the resuspension of cysts from benthic nepheloid layers (reviewed in Azanza et al., in press).

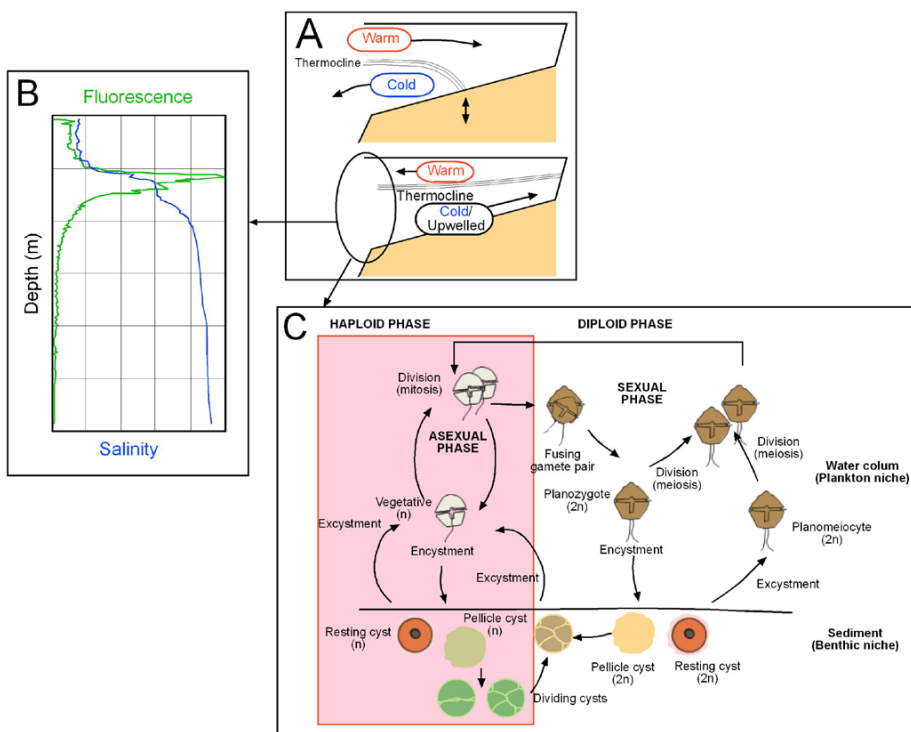


FIGURE 1. Submesoscale to small-scale processes relevant to understanding of HAB dynamics in confined and semiconfined environments. (A) Physical forcings important to the confinement or dispersion of the cells. Redrawn from Reguera et al. (2012). (B) Thin layer formation. (C) Life history of a dinoflagellate. Redrawn from Bravo and Figueroa (2014). The diatom life cycle is shown in Figure 3.

Life-history strategies can also display intraspecific genetic diversity, as recently revealed using molecular tools. This diversity could reflect unique life-cycle properties that are responding to environmental variability or ecological pressures, and/or different germination timing of the cyst pool in the sediments. For example, genetically distinct populations within the species *A. fundyense* coexist in the same coastal ponds but bloom at different times (e.g., Richlen et al., 2012). Analysis of rRNA transcripts allowed reconstruction of the demographic history of two genetically different *A. minutum* populations, where an ancestral divergence was followed by a secondary contact of the two populations, resulting in gene flow (Le Gac et al., 2016). Moreover, functional differences between the two groups were identified, linked to calcium and potassium fluxes across membranes, the calcium transduction signal, and saxitoxin production. These studies are examples of how population genetics coupled with genomic approaches can shed light on the mechanisms that lead to population differentiation and structure in space and time (reviewed in Rengefors et al., 2017).

PHYSICAL FACTORS IN HAB DYNAMICS WITHIN ENCLOSED AND SEMI-CONFINED BASINS

Many HAB events are caused by the bulk transport of cells from nearshore waters into semi-confined basins. Wind-driven water exchange occurs in many northwestern European bays because they are axially aligned to the prevailing southwestern wind direction (Raine et al., 2010). In combination with water column stratification, potentially harmful phytoplankton populations are advected into the bays either with the influx of cool bottom water, as has been observed with *Karenia mikimotoi* (a fish-killing dinoflagellate at high cell densities), or with the subsequent influx of warm surface water, a situation more typical of blooms of lipophilic, toxin-producing *Dinophysis* species that cause diarrhetic shellfish poisoning (DSP; Raine, 2014).

Once inside confined and semi-confined environments, cells can be retained or dispersed by different physical factors. For instance, in the microtidal estuary of Alfacs Bay (northwest Mediterranean Sea), an active aquaculture site threatened by HAB events (Fernández-Tejedor et al., 2008), phytoplankton accumulation occurs preferentially in the northeastern part of the estuary throughout the year (Artigas et al., 2014). Cell retention is determined by the interplay between freshwater input from land (irrigation of the surrounding rice fields and submarine groundwater discharge) and wind-induced turbulence that controls the strength of the estuarine circulation and vertical stratification. Weak stratification facilitates cell retention, whereas flushing rates are higher during increased stratification and stronger estuarine flow periods. These mechanisms apply to harmful species as well as other planktonic organisms. Other retentive,

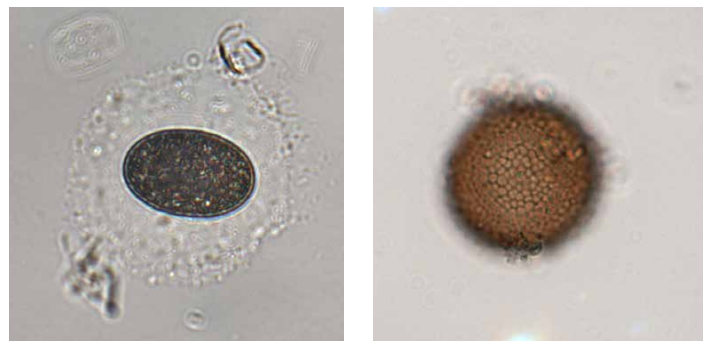


FIGURE 2. Resting cysts of two dinoflagellates, *Alexandrium mediterraneum* (left) and *Gymnodinium nolleri* (right). Photo credits: M. Montresor, SNZ

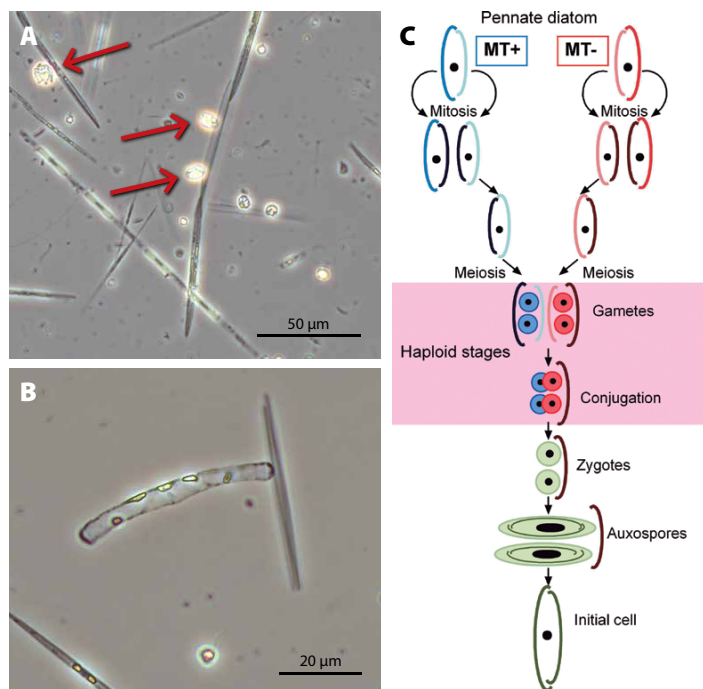


FIGURE 3. (A) Early-stage *Pseudo-nitzschia* auxospores (arrows; i.e., the diploid stage produced by gamete conjugation) in a natural phytoplankton sample. (B) One auxospore still connected to the frustule of the gametangium. (C) Schematic drawing of the life cycle of a *Pseudo-nitzschia*. The sexual phase can be induced when cells of opposite mating types contact one another. It includes gametogenesis, syngamy, and formation of a specialized zygote, the auxospore, where the large initial cell is produced. (A) and (B) photo credits: M. Montresor. (C) Redrawn from Montresor et al. (2016)

often stratified environments that can act as plankton “incubators” (including HAB species) are the “upwelling shadows” developed adjacent to the landward side of promontories and within bays, where surface wind forcing is relatively weak and retentive oceanic circulation develops (e.g., Ryan et al., 2010).

In addition to hydrodynamics, bay morphology in association with freshwater inputs of nutrients and humic acids (see section below on nutrients) modulates phytoplankton biomass, productivity, and community structure in semi-confined systems (Raine et al., 2010). The aquaculture sites in Alfacs and Fangar Bays of the Ebro Delta in the northwest Mediterranean provide a case

study related to morphology. Llebot et al. (2011) characterized the seasonal patterns of phytoplankton community variability in both bays and their coupling with environmental forcing based upon a 13-year time series. Plankton dynamics in the two bays was subjected to the typical climatology of the Mediterranean Sea and local meteorological forcing. Alfacs Bay receives lower nutrient inputs than Fangar Bay. However, Alfacs Bay is about 10 times larger and thus has a longer residence time than Fangar Bay, which has higher flushing rates. The resulting circulation patterns, turbulence intensity, and stratification in each bay determine the typically higher phytoplankton biomass levels in Alfacs Bay compared to Fangar Bay.

NUTRIENT SUPPLY FROM LAND, HUMAN ACTIVITIES, AND HABs IN COASTAL EMBAYMENTS

Land-sea interactions directly affect coastal ecosystems, which are often under disruptive pressure from human activities that varies with the degree and type of land and water uses. Increased nutrient supply has been linked with high phytoplankton biomass and eutrophic conditions in many bays (e.g., GEOHAB, 2010). This is illustrated, for instance, by the positive correlation between nitrogen loads and the relative abundance of *Pseudo-nitzschia pungens* in the 100-year record of diatoms from sediment cores in a Danish fjord (Lundholm et al., 2010). However, establishing a definitive causal link between an increase in HABs and a change in either nitrogen or phosphorus as the limiting nutrient is not usually possible (Davidson et al., 2012).

Traditionally, research on nutrient concentrations and fluxes has mainly focused on the inorganic nutrient forms (i.e., nitrate, phosphate, and silicate). However, recent studies show the importance of organic nutrient sources, including urea (coming from agricultural fertilizers) and humic acids (e.g., GEOHAB, 2010). For instance, HAB associations with high organic nutrients include the

brown tides caused by the pelagophyte *Aureococcus anophagefferens* in estuaries and bays of the eastern United States and South Africa (Gobler and Sunda, 2012), and the local blooms of the *Alexandrium catenella/tamarense* species complex in Thau lagoon, southern France (Collos et al., 2014). Nutrients can reach coastal embayments through both direct runoff and submarine groundwater discharges. In Alfacs Bay, this process could deliver a nutrient supply from the surrounding rice fields in periods when direct runoff from irrigation channels is artificially restricted (Rodellas et al., 2017).

Nutrient availability can play an important role in determining the nature and degree of harmful effects. For example, the toxicity of *Pseudo-nitzschia* blooms was heightened during the late phases of blooms under certain nutrient-limited conditions (e.g., phosphorus limitation; Timmerman et al., 2014). Furthermore, uncoupling between cell division and toxin production rates resulted in maximal cell-toxin quota during the stationary growth phase of *Dinophysis* populations (Pizarro et al., 2009). Still, the link between nutrient availability and toxicity shows unclear trends and requires further intensive research.

Fish farms and other aquaculture activities that represent important food sources for the increasing human population, especially in developing countries, are often located in enclosed and semi-enclosed embayments. HAB outbreaks can dramatically affect these activities, causing substantial economic losses and problems for human health. Considerable research has addressed the implementation of effective monitoring programs for HAB species and their toxins. However, limited information is available on the potential effects of aquaculture activities on the geographic distribution, frequency, and intensity of HABs (e.g., Bouwman et al., 2013). Increased inorganic and organic nutrient loading, application of pharmaceuticals and pesticides to the local environment, and

introduction of cyst-forming alien species are among the features linked to aquaculture that can alter the marine environment and favor HAB blooms, especially in confined environments. Determining the possible links between marine aquaculture and HAB occurrence, and finding efficient methods to protect farmed seafood products from HABs impacts, is one of the objectives included in the new program on HAB research, GlobalHAB (<http://www.globalhab.info>).

Ship ballast water discharge near or within harbors and in other coastal environments also contributes to harmful microalgal transfer worldwide (Roy et al., 2012). Efforts have been invested in the last decade to prevent such invasive species introductions (e.g., see International Convention for the Control and Management of Ships' Ballast Water and Sediments; IMO, 2017). However, predicted increases in global shipping highlight the need to continue efforts to decrease the risk of aquatic species invasions, including those of HAB taxa, into new habitats.

INTERPLAY BETWEEN PHYSICAL AND BIOLOGICAL PROCESSES IN THE DYNAMICS OF THIN LAYERS AND AT SMALL SCALES

Thin layers are discontinuities in the vertical structure of the wind-mixed surface layer of a stratified water column that exhibit physical, chemical, and biological signatures distinct from the surrounding water. Lasker (1978) was the first to propose that TLs play a major trophic role in aquatic ecosystems because they favor an abundance of planktonic organisms and thus satisfy the growth requirements of fish larvae. Plankton TLs can persist for days or longer (McManus et al., 2003), with horizontal length scales on the order of kilometers and vertical extents from several meters to millimeters.

The understanding of HAB dynamics changed when advances in sampling and observational methods revealed that TL structures are important to HAB ecology (Figures 1B and 4; Gentien et al., 2005).

Some harmful microalgae can concentrate into TLs; examples include the dinoflagellates *Karenia mikimotoi* (also known as *Gyrodinium aureolum*), *Akashiwo sanguinea* (high biomass bloom-forming species, also known as *Gymnodinium sanguineum*), and *Dinophysis* spp., as well as diatoms in the genus *Pseudo-nitzschia* (revised in Gentien et al., 2005; Berdalet et al., 2014).

TL dynamics involves interactions between fine-scale physical, chemical, and biological processes, as illustrated in the conceptual model presented in Figure 5. Biological processes that promote the accumulation of phytoplankton in TLs include enhanced growth rate, active aggregation by swimming and/or buoyancy control, and grazer avoidance within the layer.

For instance, swimming seems to have played a major role in the accumulation of *Akashiwo sanguinea* in a TL observed in Monterey Bay (Steinbuck et al., 2009). High cell densities of this dinoflagellate were located in the thermocline of a 20.5 m water column between a strongly turbulent surface mixed layer and a weakly turbulent stratified interior. Swimming balanced the diffusion by turbulent mixing on both sides of the layer, while sinking or growth processes were not major drivers. The study combined high-resolution sampling, an Eulerian advection-diffusion model, and a Lagrangian particle-tracking model. A combination of vertical migration and phototaxis may also create a TL, as shown by a numerical model that produces realistic mixing and turbulent conditions (Yamazaki et al., 2014). In the systems described, TL formation would occur at wind speeds below 5 m s^{-1} .

Although TL formation can be facilitated by vertical migration (due to phototaxis, nutrient availability, or other triggers such as reproduction, sexual and asexual encystment rhythms, and waterborne chemical cues), this behavior seems to be species- and location-specific. The vertical distribution of the same species likely varies according to physiological

conditions and the vertical structure of the water column, including depth and gradient definition of the pycnocline. Several niches could also exist across the pycnocline in which different phytoplankton may be found (i.e., resulting in “a thin layer within a thin layer”; Raine, 2014, and references there in). In coastal waters around Ireland, fine-scale sampling led to the observation of mixed populations of *D. acuminata* and *D. ovum* in a high-density layer ($40,000 \text{ cells L}^{-1}$) of thickness ca. 30 cm within a 3 m thick subsurface layer of *D. acuta*, at a density of ca. $10^4 \text{ cells L}^{-1}$.

Gradients in turbulence and vertical shear are important physical controls in the formation and persistence of TLs (Dekshenieks et al., 2001; Ryan et al., 2008; Durham et al., 2009). Vertical shear tends to tilt and stretch an existing phytoplankton patch, as one part moves horizontally relative to a deeper part of the water column. Furthermore, gyrotactic trapping (Durham et al., 2009) couples biological processes (active swimming of cells) and hydrodynamic shear in the

generation of TLs. Regions of enhanced shear could disrupt vertical migrations of plankton cells and promote sharp-peaked cell accumulations. Besides, pycnoclines may act as retention areas for non-swimming phytoplankton, such as *Pseudo-nitzschia* and other diatoms. The respective TLs of these *Pseudo-nitzschia* blooms have been observed in association with steep density gradients in the Northeast Pacific Ocean and in Monterey Bay (Rines et al., 2002) and in pycnoclines established after upwelling pulses in the Galician Rias (Velo-Suárez et al., 2008).

Eddies can also facilitate formation and persistence of TLs by minimizing lateral dispersion of plankton populations. In this way, the Juan de Fuca Eddy acted as an incubator for *Pseudo-nitzschia* populations that were then transported to the Washington coast (Trainer et al., 2002). The high abundances of these diatoms caused a quick rise to above regulatory levels in the content of the neurotoxin domoic acid in shellfish from the area. Persistent eddies in the Bay of Biscay have been involved in the local accumulation

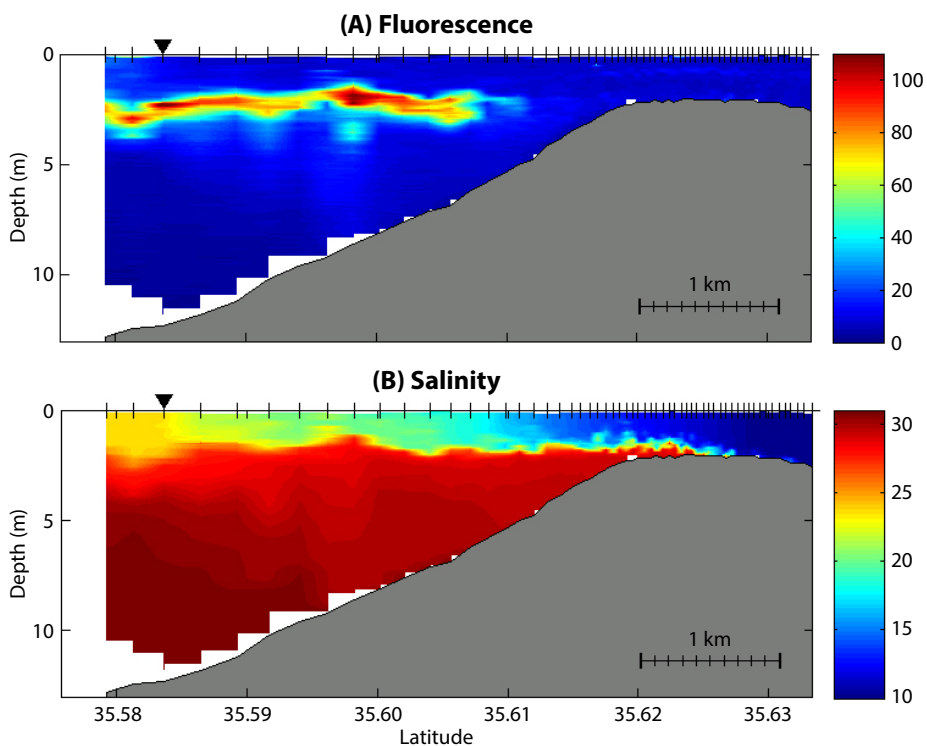


FIGURE 4. Representative profiles of salinity and fluorescence in a stratified system with a well-developed thin layer. (A) Fluorescence and (B) salinity observed on May 19, 2011, in Tokyo Bay. From Masunaga and Yamazaki (2014)

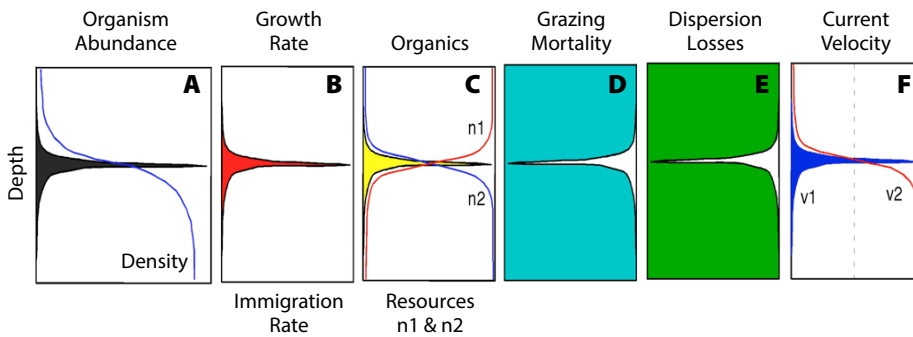


FIGURE 5. General conceptual model of mechanisms controlling thin layers. Credit: P.L. Donaghay

of *Dinophysis acuminata* and *K. mikimotoi* in the pycnocline (Patrick Gentien, data unpublished before his death; Xie et al., 2007). These structures protect the integrity of the HAB species patch until the eddy disperses at the coast and the HAB organisms within it are released and thereby cause harm.

Local reduction in horizontal and vertical dispersal can facilitate the formation of small (7 km in diameter and about 3 m thickness at 20 m depth) but high-density patches of *Dinophysis acuta* cells (10^4 – 10^5 cells L^{-1}) in open waters off southern Ireland (Farrell et al., 2012).

In some cases, TLs seem to be quite dynamic structures that can be formed and eroded rapidly. After moderate upwelling pulses in the Galician Rias, a *Pseudo-nitzschia* TL was formed by shear, which favored passive aggregation of cells in the pycnocline. The TL was eroded during the next downwelling period and formed again in the subsequent upwelling pulse (Díaz et al., 2014b). Likewise, a downwelling event eroded a TL of a senescent diatom community where *P. australis* was dominant (Velo-Suárez et al., 2008). Yamazaki et al. (2010) characterized the layered structures of small-scale biophysical signals within a 24-hour period at a station in Lake Biwa (Japan). Using an LED fluorescence probe mounted on TurboMAP-L, the study showed the dynamic formation and dissipation of chlorophyll TLs in the water column, within the surface mixed layer. While the study was being conducted, the turbulent kinetic energy dissipation rate (ϵ) reached almost 10^{-6} W kg^{-1} during

the night. Physical dispersion is, doubtless, a key factor contributing to the collapse of TLs, but the natural life processes of plankton must be involved as well. For instance, processes inducing cell encystment could cause the decay of dinoflagellate populations within the TLs. These processes are still speculative. More studies are required to improve understanding of the formation, maintenance, and decay of harmful phytoplankton TLs.

BIOLOGICAL AND CHEMICAL INTERACTIONS AT SMALL SCALES

Chemical cues mediate interactions between marine micro- and metazoan grazers and their prey, and allelochemical (and/or toxic) substances produced by various HAB taxa could constitute defenses against predators and competitors and regulate other species interactions (reviewed by Ianora et al., 2011). Such “top-down” interactions could modulate the equilibrium among species and hence affect both species-specific population dynamics and community structure. Known responses of toxic dinoflagellates exposed to metazoan predators (i.e., copepods) or their waterborne chemical cues include initiation of life-history transitions, colony size changes, and alterations in swimming behavior to escape predation. The induction and increase of PSP toxin (saxitoxin analogs) production by *A. minutum* and *A. tamarense/fundyense* exposed to copepods and/or to their chemical signals (Wohlrab et al., 2010; Selander et al., 2015), and the recent

identification of the chemical structures of one class of these waterborne cues known as copepodamides (Selander et al., 2015), supports a defensive function for these phycotoxins.

Chemically mediated species interactions within the plankton are complex, but we do know how they can be regulated at the gene level. For instance, *Alexandrium* populations comprise multiple genotypes that display phenotypic variation for traits such as the ability to lyse co-occurring competitors and potential grazers. In laboratory experiments, exposure of two *A. fundyense* strains to the presence of *Polykrikos kofoidii* (a dinoflagellate grazer) induced differential transcriptomic changes in gene expression (Wohlrab et al., 2016). The affected genes are involved in endocytotic processes, cell cycle control, and outer membrane properties, and the observed trends suggest different competitive capacities at the strain level.

Allelochemistry and chemically mediated species interactions may play an important role in the dynamics of HABs within spatially constrained fjords and embayments, notably at small scales, particularly within TLs occurring at sharp density discontinuities (e.g., pycnocline interfaces). Trophic interactions between different components of plankton food webs are likely to be particularly active in TLs. For example, zooplankton feeding could be higher in high phytoplankton density TLs compared to most parts of the water column where there are lower food concentrations. Given the high cell density of particular species within a TL, sexual recombination rates would be facilitated due to an increased gamete encounter rate (Wyatt and Jenkinson, 1997; Persson et al., 2013), and interactions between harmful microalgae and bacteria, parasites, or viruses may also exhibit particular dynamics. Unfortunately, these interactions have been mainly described in the laboratory over the last 20 years (e.g., Kjørboe, 2010) and are only rarely documented in the field (Allredge et al., 2002; Timmerman

et al., 2014). There is a need to incentivize progress and utilization of technologies to directly observe plankton behavior in situ within and around the edges of TLs in stratified systems. Semi-confined systems, given the relative physical constraints on advection and dispersion of blooms, offer suitable conditions for this challenging investigation in the future.

Other understudied processes operating at micro- and nanoscales may also play roles in HAB dynamics. During recent decades, studies have been devoted to investigating the direct impact of small-scale turbulence on harmful phytoplankton cells. Observed effects include facilitation of nutrient uptake, and in certain dinoflagellates, physiological responses include inhibition of cell division, decrease of cell toxin concentration, increase in dimethylsulfoniopropionate (DMSP) content, or alteration of swimming patterns (e.g., Berdalet et al., 2011, and references therein). Reduced turbulence (within a TL or not) may promote some life-cycle transitions (pellecyst formation; e.g., Smith and Persson, 2005; Gentien et al., 2007) that are otherwise inhibited under high-agitation conditions.

Important research efforts have been designed to understand how viscosity and other rheological properties influence, and are influenced by, several aspects of plankton dynamics, including HABs (e.g., Jenkinson and Sun, 2010). Dense phytoplankton patches are often associated with increased viscosity as well as elasticity of the seawater or freshwater medium. Based on the knowledge gained, including the few available measurements of rheological properties of some algal cultures and phytoplankton blooms, models have been proposed to describe how organic exopolymeric substances (EPS) could change pycnocline thickness. The studies emphasize the need for new measurements under natural oceanic concentrations as well as future experimental and in situ investigations into the modulation of pycnocline dynamics by phytoplankton

blooms. Microalgae may have mechanisms to make the water more viscous by generating loose or sticky EPS, to engineer ambient fluidics to protect themselves from predators, and to favor nutrient diffusion (Jenkinson et al., 2015). Furthermore, EPS production can constitute another harmful effect of some high-biomass blooms. A surfactant-like protein in the organic matter released by a dense, senescent-phase bloom of *Akashiwo sanguinea* occurring along the west coast of the United States (Jessup et al., 2009) coated birds that encountered the bloom-generated foam. This caused loss of the insulating capacity of the birds' feathers and led to mortality by hypothermia.

ADVANCES IN TECHNOLOGY AND MODELING

Major advances in knowledge of the life history of HAB species dwelling in confined and semi-confined environments and stratified systems have been achieved in recent years thanks to sophisticated moored instruments. For example, the original Flowcytobot, capable of fixed-depth, high-resolution imaging of different life-cycle stages during blooms of *Alexandrium* and *Dinophysis* has now been developed into a yo-yo system that records the whole water column in shallow embayments (Campbell et al., 2010; Brosnahan et al., 2015).

Advances in sampling and observation methods have been fundamental to understanding TL structure and dynamics. Traditional bottle sampling at fixed depths is inefficient and often completely misses TLs (Escalera et al., 2012). Satellite remote-sensing detection of subsurface structures is restricted to waters with specific properties. In the last 15 years, technologies have progressed to allow fine-scale vertical resolution monitoring of essential phytoplankton properties (chlorophyll fluorescence, absorption, or bioluminescence) and direct sampling of cells and certain key physical parameters (GEOHAB, 2008, 2013, and references therein). Examples of such technologies include the fine-scale sampler (FSS; Lunven et al., 2005; Figure 6) capable of taking 15 samples, 20 cm apart, over a vertical distance of 3 m, and the high-resolution Ifremer Particle Size Analyzer Profiler (IPSAP; Lunven et al., 2005; Figure 6) that combines particle size analysis with microphotographic video. Tow-body systems such as the SCANFISH (undulating CTD) and Acrobat (SeaSciences), and autonomous underwater vehicles (AUVs) like the Monterey Bay Aquarium Research Institute *Dorado*, have been used to quantify the horizontal extent of thin phytoplankton layers on scales of 1 km to 100 km. New modeling tools have been fundamental to understanding of



FIGURE 6. (left) Fine Scale Sampler (Ifremer). (right) Patrick Gentien sets up the Ifremer Particle Size Analyzer Profiler during the HABIT 2005 cruise on board R/V *Mytilus* (CSIC, Spain). Photo credit: B. Reguera

TL dynamics (GEOHAB, 2011, 2013). Among the instruments that allow estimates of the turbulent kinetic energy dissipation rate and shear within TLs, there are free-fall microstructure turbulence profilers (Figure 7), the free-gliding, quasi-horizontal profiler TurboMAP-G (Foloni-Neto et al., 2014; see GEOHAB, 2013, cover photo), and various ship-board autonomous profilers.

The IPSAP profiler combined with the FSS have proven to be useful tools for studying TL characteristics. In 2007, these instruments were deployed off the south coast of Ireland to sample a high-density, 3 m thick, subsurface layer of *Dinophysis acuta* with density peaks of 8,000 cells L⁻¹. At one location, repeated IPSAP casts, followed by the FSS, identified a high cell density TL of *D. acuminata* <40 cm thick in the middle of the layer of *D. acuta* (Raine, 2014). Such an observation of interleaving of fine layers would not be possible with conventional technologies. Furthermore, both species were present in densities >10⁵ cells L⁻¹, while as few as 200 cells L⁻¹ can make shellfish unfit for human consumption, provided

sufficient exposure time. The result supports the idea that *D. acuta* and *D. acuminata* have distinctly different ecological niches. Furthermore, using the FSS and IPSAP, Velo-Suárez et al. (2008) showed very heterogeneous vertical distribution of *D. acuminata* at fine scale (decimeter resolution) in the Ría de Pontevedra (northwest Spain).

Characterizing the temporal development of TLs is a major challenge. In a unique study, Ryan et al. (2010) estimated that phytoplankton cell density in a TL dominated by *A. sanguinea* in Monterey Bay, California, doubled during a four-day period. The process was concurrent with increased stratification and internal tide-driven nutrient supply. The investigation acquired nearly 7,000 profiles with an AUV in a set of sections repeated almost continuously for a week.

Few studies have documented the role of nutrients in HAB formation and sustenance in TLs. Fine-scale chemical gradients and chemically distinct TLs may exist in stratified coastal environments (Lunven et al., 2005; Ryan et al., 2010). Formation of such TLs may provide advantages in all kinds of nutritional conditions. There may be concurrent favorable light and nutrient conditions if TLs are located in the upper part of the nutricline. Such high-prey density layers can be favorable for mixotrophic species (e.g., *Dinophysis* spp.; Velo-Suárez et al., 2008), and breakdown products from senescent cells could accumulate in the density gradient (pycnocline). These factors favor nutrient recycling and phytoplankton productivity.

CLIMATE CHANGE AND HABs IN CONFINED AND SEMI-CONFINED ENVIRONMENTS

Recent studies have examined how climate change might influence HABs in the global ocean. The response of planktonic communities to changes in the physical environment (e.g., higher temperature, increased stratification, heavy precipitation) is expected to be the result of many factors, including complex

interactions (Hallegraeff, 2010). This complexity, associated with limited knowledge of physiological acclimation and adaptive responses of unicellular microalgae and genetic strain diversity, calls for further studies.

Fjords provide a good testing ground for climate change and HAB studies. Higher temperatures will coincide with the additive effect of increased snowmelt and stratification. In particular, recent attention to HAB biodiversity and biogeography has begun to focus on frontier locations within and adjacent to fjords in the Arctic and sub-Arctic, where the effects of climate change are anticipated to be most rapid and dramatic and may yield evidence of regime shifts in these habitats. Application of metagenomic and metatranscriptomic approaches by parallel amplicon sequencing of 28S rRNA in comparative Arctic fjords reveals differential patterns of molecular diversity in plankton size fractions and identifies links between the occurrence of particular HAB taxa and their toxins (Elferink et al., 2016).

There is evidence that climate-related regime shifts may have led to changes in HAB biogeography in the fjord regions of the Chilean coast. In 2016, blooms of *Pseudochattonella* caused mortalities of 20% of the total Chilean salmon production: about 30 million fish were killed in a few days (Clement et al., 2016). These events were followed by exceptional blooms of *Alexandrium catenella* (in terms of their northward expansion), which devastated shellfish production and led to social upheaval (Hernández et al., 2016). These phenomena were clearly associated with climate anomalies and were linked to one of the strongest El Niño signals in the southeastern Pacific Ocean in recent decades.

Wells et al. (2015) present a broad overview of the knowledge and gaps in knowledge about the environmental conditions that favor initiation and maintenance of HABs in order to forecast changes in near-future scenarios. These authors highlight the lack of uniform



FIGURE 7. This free-fall microstructure turbulence profiler on board R/V *Ramón Margalef* (IEO, Spain) was used to investigate the role of mixing in phytoplankton community structure in the Galician Rias (northwest Iberian Peninsula). Photo credit: B. Mouriño-Carballido, University of Vigo, Spain

experimental protocols, which limits the quantitative cross-investigation comparisons essential to improving our knowledge. GlobalHAB program objectives include advancing understanding of global patterns in HAB responses to climate change, in terms of magnitude, frequency, and distributional shifts, through comprehensive region-specific studies that integrate biological processes with downscaled climate projections (<http://www.globalhab.info>; Berdalet et al., 2017, in this issue).


CONCLUSIONS AND NEXT STEPS

The GEOHAB program provided a solid foundation for coordinated research on HABs worldwide. The objectives identified in the two CRPs presented in this paper were complementary and allowed synergies to advance the understanding of HAB dynamics. Here, we summarized improved knowledge of processes at sub-mesoscale and fine and small scales that also apply to upwelling (Pitcher et al., 2017) and eutrophic (Glibert and Burfort, 2017) systems also described in this special issue of *Oceanography*.

At the end of GEOHAB, we identified some priorities to be addressed by the new GlobalHAB program, including developing better predictive tools and strategies to prevent and mitigate HAB impacts. Addressing these priorities will require financial support and international collaboration. Some of these priorities include the following:

1. Identify and quantify the various life-history stages (gametes, zygotes) of HAB taxa in the field. Estimate the in situ dynamics of the transitions among life-history stages (induction of resting forms, deposition and emergence fluxes, germination rates) while identifying the factors affecting the viability and abundance of the different life forms. New moored and profiling instruments, with capacity to observe cells in situ, offer optimistic estimates of progress in the near future. However, their high cost hampers generalized deployment in

HAB-threatened environments.

2. Improve knowledge of submesoscale processes (<10 km) of importance to HABs in coastal environments, integrating biology, chemical ecology, biogeochemistry, physical oceanography, and sedimentary studies.
3. Investigate the influence of coastal aquaculture (shellfish and fish farming) on the development of HABs; this will contribute to the sustainable use of renewable resources.
4. Investigate the role of toxins and other allelochemical substances in structuring food webs, in cell defense, and in nutrient acquisition. Further research on the modulation of toxin production by nutrients or the presence of predators, which is especially challenging to study in the field, is required. Due to their dimensions and hydrodynamic features, fjords and coastal embayments and associated TL structures offer suitable scenarios for in situ research.
5. Improve knowledge of physical-biological processes at small scales, including rheological properties related to cell aggregations.
6. Investigate the ongoing trends of HAB events in the context of global change that is expected to induce more pronounced impacts in coastal environments, particularly at polar latitudes. 

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