

GEOHAB

Global Ecology and Oceanography of Harmful Algal Blooms



**GEOHAB CORE RESEARCH PROJECT:
HABs IN FJORDS AND COASTAL EMBAYMENTS**

**SECOND OPEN SCIENCE MEETING:
PROGRESS IN INTERPRETING LIFE HISTORY AND
GROWTH DYNAMICS OF HARMFUL ALGAL BLOOMS
IN FJORDS AND COASTAL ENVIRONMENTS**



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GEOHAB

GLOBAL ECOLOGY AND OCEANOGRAPHY OF HARMFUL ALGAL BLOOMS

CORE RESEARCH PROJECT: HABs IN FJORDS AND COASTAL EMBAYMENTS

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PROGRESS IN INTERPRETING LIFE HISTORY AND GROWTH DYNAMICS OF HARMFUL ALGAL BLOOMS IN FJORDS AND COASTAL ENVIRONMENTS

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Executive Summary

As part of the activities of the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) programme, Open Science Meetings (OSMs) have been organized to discuss and synthesize research efforts on various aspects of harmful algal blooms (HABs), and to plan future collaborative activities relevant to the research theme.

Within this framework, the steering committee of the GEOHAB Core Research Project on HABs in Fjords and Coastal Embayments has organized two OSMs. The first OSM was held in 2004 in Santiago, Chile; the major goals were to identify the primary research priorities and to initiate an agenda to further our understanding of HAB dynamics in these small-scale coastal systems.

The second OSM was held in May 2012 in Victoria, Canada to highlight the progress accomplished since the first OSM and to focus attention on the importance of a comparative approach in conducting ecosystem studies to improve our understanding of HABs. This second OSM addressed four major themes for which significant advances have been made in recent years, with particular focus on their application to semi-enclosed basins linked to coastal ecosystems: (1) Life history of HAB species; (2) Chemical ecological and toxin interactions; (3) Genetic diversity and (4) Transport and mixing of blooms in small-scale, mesoscale and semi-confined systems.

This Report presents the major outcomes of this OSM, followed by recommendations for future collaborative studies. These recommendations include the maintenance of international activities on the ecology and oceanography of HABs after the end of the GEOHAB programme in December 2013. A future agenda should focus on a few key questions with clearly identifiable deliverables. These questions should include the development of (i) improved methods to determine the rates of cyst formation and germination in the field, and (ii) coupled biological-physical-chemical models more appropriate to small-scale environments and which incorporate the role of allelochemicals and toxins, as well as the pelagic and benthic coupling components. Research devoted to life history stages should be continued, particularly with respect to fish-killing algal species that cause particular damage in coastal environments. The influence of aquaculture activities on the development of HABs is poorly understood and should be of greater concern in future research on HABs. The influence of climate change, which may be exacerbated in coastal environments, also should be a focus of future research. Long-term ecological research should be encouraged in this respect, in order to make better predictions in the future concerning the development of HABs in coastal environments.

List of Acronyms

BBL	benthic boundary layer
BFAR	Bureau of Fisheries and Aquatic Resources of The Philippines
BNL	benthic nepheloid layer
CRP	Core Research Project
ECOHAB	Ecology and Oceanography of Harmful Algal Blooms research programme (USA)
ENSO	El Niño-Southern Oscillation
ESP	environmental sample processor
EST	expressed sequence tag
GEOHAB	Global Ecology and Oceanography of Harmful Algal Blooms programme
GoM	Gulf of Maine
GOMTOX	Dynamics of <i>Alexandrium fundyense</i> distributions in the Gulf of Maine programme (USA)
HAB	harmful algal bloom
IOC	Intergovernmental Oceanographic Commission (United Nations Educational, Scientific and Cultural Organisation)
ISMER	Institut des Sciences de la Mer, Université du Québec à Rimouski
LSU	larger sub-unit of ribosomes
OSM	open science meeting
Pbc	<i>Pyrodinium bahamense</i> var. <i>compressum</i>
PCR	polymerase chain reaction
PET	plankton emergence traps
PhilHABs	Ecology and Oceanography of Harmful Algal Blooms programme in The Philippines
PICES	North Pacific Marine Science Organization
PSP	paralytic shellfish poisoning
PST	paralytic shellfish toxins
rDNA	ribosomal deoxyribonucleic acid
SCOR	Scientific Committee on Oceanic Research (International Council for Science)
SEED	Life Cycle Transformations among HAB Species programme
SEOS	School of Earth and Ocean Sciences (University of Victoria)
VENUS	Victoria Experimental Network Under the Sea programme (Canada)

I. Introduction

The Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) programme was initiated in 1999 by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO to develop a research programme on the ecological and oceanographic mechanisms underlying the population dynamics of harmful algal blooms (HABs). The ultimate goal of this programme is to allow the development of observational systems and models that will enable prediction of HABs, thereby reducing their impacts on the health of humans and marine organisms, as well as their economic and social impacts on societies (see GEOHAB *Science Plan*: GEOHAB, 2001).

The GEOHAB Implementation Plan (GEOHAB, 2003) specified the formation of Core Research Projects (CRPs) related to four ecosystem types—upwelling systems, fjords and coastal embayments, eutrophied systems, and stratified systems. The Core Research Project on HABs in Fjords and Coastal Embayments was described in detail in a previously published document (GEOHAB, 2010). Fjords and coastal embayments share features such as the importance of geographical constraints on water exchange and bloom retention, and the dominance of meso-scale structures.

Classic fjords, usually characterised by a high ratio of length to width, a deep wedge-shaped basin, freshwater input, and a sill located toward the mouth, create retention and/or initiation zones that favour the proliferation of a particular suite of HAB species. Many groups of key species (e.g., *Alexandrium* spp., *Pseudo-nitzschia* spp., and various raphidophytes) are virtually identical (similar community composition) in fjords in the Northern and Southern hemispheres at similar latitudes and are thereby amenable to comparative studies. Such fjordal ecosystems are often only marginally affected by human activities because of low population densities in remote coastal areas, for example, of Norway, British Columbia, Chile, New Zealand, etc.; thus, they are usually not directly subject to eutrophication.

Coastal embayments are a broader category of an ecosystem type; generally, such systems comprise relatively shallow near-shore marine environments, partially surrounded by land, and often affected by terrigenous run-off, but on a smaller spatial scale than open coastal or upwelling systems. As with fjords, the hydrodynamic processes of coastal embayments may be complex, with an accentuated role of tidal flux, storm surges, wind-driven mixing, and salinity and thermal stratification. The physical processes associated with HABs in these systems are most often related to “density adjustment” issues, that is, buoyancy and frontal

dynamics, geostrophic adjustment, establishment of a pycnocline after a storm, and perhaps topographic frontal motion.

The effects of benthic-pelagic coupling are likely to be crucial in understanding HAB dynamics in fjords and coastal embayments. Coastal embayments with limited exchange to the open coast may serve as “seed beds” for benthic cysts or relict populations of HAB species. Such systems are particularly vulnerable to anthropogenic changes in the biological and chemical regime, as well as the introduction of exotic species via ship deballasting and transfer of aquaculture stock. Many fjords and coastal embayments are well characterised in terms of long-term plankton records and toxicity events. Optical data sets on ocean color and relevant plankton patches are becoming increasingly available from these systems as spatial and spectral resolution is improved. Furthermore, basic circulation models (both 2-D and 3-D) are already available for several locations around the world.

During the first Open Science Meeting (OSM) of this CRP, held in 2004 in Chile, several research priorities were identified to further our understanding of HAB dynamics in fjords and coastal embayments. Since then, significant progress has been made in evaluating the processes and mechanisms involved in HAB dynamics, notably with respect to genetic diversity, life history of key harmful species, allelochemical and toxic interactions affecting HAB populations, and the importance of coastal morphology, hydrodynamics and associated physical retention or dispersion of cells within the coastal zone. Examples of this recent progress include predictions of blooms based upon extrapolation from cyst mapping, identification of putative allelochemicals and the role of toxins in chemical defence against predators and competitors. Furthermore, detection of cryptic diversity in many key species has challenged not only our taxonomic and phylogenetic identification capabilities, but has also opened a new perspective on the complex structure of HAB populations. In a few cases, these biological parameters have now been combined with hydrodynamic measurements and models to improve understanding of the role of stratification and circulation to retain or advect blooms within coastal ecosystems.

The Scientific Committee of the CRP on Fjords and Coastal Embayments proposed a second OSM to highlight this progress and the importance of a comparative approach to improve our understanding of HABs. This second OSM focused on four themes: (1) Life history of HAB species; (2) Chemical ecological and toxin interactions; (3) Genetic diversity and (4) Transport and

mixing of blooms in small-scale, mesoscale and semi-confined systems. This Report presents the major outcomes of this OSM followed by recommendations for future studies.

The GEOHAB Scientific Steering Committee of the CRP on Fjords and Coastal Embayments is grateful for the generous financial and logistical support for this meeting from the Intergovernmental Oceanographic

Commission (IOC); Scientific Committee on Oceanic Research (SCOR); the School of Earth and Ocean Sciences (SEOS) of the University of Victoria, B.C., Canada; the Institut des Sciences de la Mer (ISMER) of the Université du Québec à Rimouski, QC, Canada; Victoria Experimental Network Under the Sea (VENUS); Neptune Canada, and the North Pacific Marine Science Organization (PICES).



II. GEOHAB Core Research Projects: The GEOHAB Approach to Study Harmful Algae

The GEOHAB approach to study harmful algae has been described in the previous document from this CRP (GEOHAB, 2010); it is also available on the GEOHAB Web site (www.geohab.info). GEOHAB research is characterized by a comparative approach, from the cellular to the ecosystem level. The GEOHAB programme was developed on the basis of the comparative approach because it is often difficult to establish experimental studies on HABs with tight controls on environmental variables, particularly with respect to

larger field projects as proposed within the integrative CRPs. The promotion of interdisciplinary research, highlighting the important interactions among biological, chemical, and physical processes, is also central to the GEOHAB approach. Most of the progress presented below results from this approach. These various studies are good examples of the success of the GEOHAB approach to better understand the processes and mechanisms underlying harmful algal blooms and their dynamics.

III. Research Priorities for Understanding HAB Dynamics in Fjords and Coastal Embayments

Seven key questions were identified following the first Open Science Meeting of the CRP on Fjords and Coastal Embayments. These are:

1. Are there definable adaptive strategies that characterize HAB species in confined and semi-confined systems?
2. What is the importance of life history transitions and cyst distribution in bloom initiation and maintenance – endogenous seed beds versus exogenous introduction?
3. How do physical dispersion and aggregation processes within a semi-confined basin affect HAB growth and distribution?
4. What is the relative contribution of nutrient flux and supply ratios to HAB dynamics in eutrophic versus non-eutrophic coastal embayments?
5. What is the importance of spatial scale and retention time in the expression and effects of allelochemicals/toxins in semi-confined systems?
6. How do embayment morphology, bathymetry and hydrodynamics affect HAB dynamics?
7. Are the effects of anthropogenic activities (e.g., aquaculture) and global climate change on HAB dynamics magnified in enclosed and semi-enclosed embayments?

IV. Progress since the First Open Science Meeting

Since the first OSM of this CRP, significant progress has been made in evaluating the processes and mechanisms involved in HAB dynamics. Not all of the key questions posed at the previous OSM were reviewed in detail at the subsequent meeting because of partial overlap in the themes with other CRPs and their respective OSMs. For example, nutrients and eutrophication and thin-layer systems within fjords and coastal embayments were not considered for special attention as these issues have been comprehensively addressed at other GEOHAB OSMs. The progress within the CRP on Fjords and Coastal Embayments is described in the following sections through the summaries of oral presentations given by keynote speakers during the second OSM.

A. LIFE HISTORY OF HAB SPECIES

1. Review of Past Programmes on HABs that Have Included Life Cycle Approaches

1.1 Diversity and Complexity of the Life Histories of Harmful Algal Species and the Impact on their Ecology (Outcomes of the SEED Project)

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The SEED project was a collaborative European Union - United States project that aimed to understand the extent to which environmental and physiological factors influence transitions among life cycle stages of harmful microalgal species, thereby contributing to the increase in harmful algal blooms in marine, fresh, and brackish waters. The project focused on the life histories of some of the most relevant HAB taxonomic groups, including examples of freshwater (Raphidophyceae), estuarine (Cyanobacteria) and marine (Dinophyceae and Bacillariophyceae) species, and drew on a wide range of coastal locations (Western Mediterranean, Atlantic Ocean, North Sea, Baltic Sea and Swedish lakes). All of these environments have heavy anthropogenic influences: fisheries, urban development, aquaculture and tourism. All are subject to frequent occurrence of

HABs, with a variety of detrimental impacts, including human intoxications, closure of shellfish farms, and water discoloration causing a negative impact on tourism, all with consequent economic impacts.

The SEED research was multifaceted, as the problems in life history transitions are complex and processes occur over a wide range of scales. SEED combined field studies with laboratory experiments. Field work was centred on areas where on-going monitoring programmes and much baseline information about distribution of species and physical-chemical data already exist.

The project allowed a unique *comparative approach*, from species to the ecosystem level (highlighted in the *Deep-Sea Research II* special issue, volume 57 (3-4), February 2010; see also the SEED project Web site: <http://www.icm.csic.es/bio/projects/seed/>). Our results show that harmful algal events are widely different and that the life cycles of several congeneric species show unexpected complexities. However, some common features among harmful algal events have also been observed, such as the production of benthic resting stages and presence of sexual phases within the life cycle of the concerned species. The results obtained from the SEED project will have an important impact on the understanding of the ecology of bloom events for a range of phylogenetic groups.

Some of the main results obtained during SEED research include:

1. The characterization and quantification of the different stages of the life cycle associated with bloom development for multiple HAB species in laboratory and in field studies, including those of *Alexandrium*, *Kryptoperidinium*, *Gymnodinium*, *Pseudo-nitzschia*, *Peridinium*, *Gonyostomum*, *Scrippsiella/Woloszynskia* complex, *Peridiniella*, *Nodularia*, *Anabaena*, and *Aphanizomenon*. Study areas included the Catalan and Galician coasts (Spain); Sardinia, the Tyrrhenian coast, and Sicily (Italy); Gulf of Finland (Finland); Estonian coast (Estonia); Cork (Ireland) and the British coast (United Kingdom). A main conclusion is that a heteromorphic life stage represents an advantageous survival strategy for a population since it allows the allocation of the species biomass into stages of different size ranges, morphology, and different ecological niches. Based on their life

histories, it is possible to divide phytoplankton species studied into two groups: holoplanktonic (present only as planktonic stages in the water column), and meroplanktonic (with a planktonic stage and documented resting stage that inhabits the benthos). In some cases, the resting stage has been identified, but with no indication of bloom initiation from this benthic resting stage.

2. The magnitude of pelagic-benthic transitions in microalgae (encystment and excystment in the case of dinoflagellates) was found to be determined by their life cycle features (Fig. 1) and the factors that regulate resting stage formation and germination. The documentation of life cycles in our studies has shown that these processes and their regulatory factors may be very different, depending on which species are considered. Through these resting stage processes, microalgae develop their unique ecological strategies, such as the occurrence of life cycle processes aligned with specific environmental conditions. The possible reversibility of the sexual stage (e.g., of the planozygote in dinoflagellates), which does not always transform into a resting cyst, is a new feature in the life cycle of dinoflagellates confirmed during the project (Figuera *et al.*, 2006). Moreover, SEED research revealed that some dinoflagellate species may also produce asexual resting cysts that allow survival from one growing season to the next without requiring sex.
3. The control of encystment and excystment was shown to be determined by intrinsic factors unique to each species, whereas the timing and scale of responses appear to be modulated by environmental factors. SEED work regarding the excystment process addressed three main topics: seasonality, the temperature “windows” for germination, and field-determined cyst formation and deposition. Field and laboratory studies provided evidence for seasonality in the germination and/or bloom initiation of meroplanktonic species. Regarding germination, the dormancy period was also found to be species-specific and modulated by temperature. For the first time, the flux of akinetes (resting stages) was reported for the three major bloom-forming genera of cyanobacteria in the Baltic Sea (Suikkanen *et al.*, 2010). Akinetes are produced through asexual differentiation of a vegetative cell that takes place in rapid response to the onset of physiological stress. This finding is significant with respect to the survival strategies and bloom dynamics of cyanobacteria.
4. Mapping the distribution of benthic resting stages of HAB species (dinoflagellates, raphidophytes, haptophytes, cyanobacteria) in superficial sediments is relevant: it allows the establishment of a baseline for monitoring of spreading events, the introduction of new species, and human-assisted dispersal. Some dinoflagellate blooms seem to be largely controlled by the coupling between benthic and pelagic systems. During calm conditions, fluxes towards the sediment are favoured; organic matter, cysts, and other substances accumulate in the uppermost layer of the bottom sediment, which is continually modified by the addition of newly settled particles and by the subsequent degradation of the accumulated material. Two main processes occur under these conditions: (1) the formation of a layer of accumulated resting cells on the sediment surface; and (2) the settling of organic particles that are important for the cycling of nutrients.
5. Molecular and immunological techniques were explored to identify specific life cycle stages of key HAB species (Erdner *et al.*, 2010; Penna *et al.*, 2010a). The rapid development of molecular methods makes it possible to investigate the genetic diversity, phylogenetic relationships and – in the near future – the molecular bases of the life cycles of microorganisms. The real-time polymerase chain reaction (PCR) assay is one of the most promising methods to monitor the presence of harmful species and for risk assessment analysis. This method has also been developed for the detection of dinoflagellate resting stages in sediment samples. Furthermore, it allows the processing of high numbers of samples, and prior knowledge of cyst morphology is not required. This technique can also be developed for an array of different species for which sequence data are available.
6. A reproductive barrier was identified between different toxic and non-toxic genotypes of *A. tamarense* that can explain the population genetic boundaries between them (Brosnahan *et al.*, 2010). Specifically, a method was developed to detect the parentage of hybrids between Group I (toxic) and Group III (non-toxic) genotypes within the *A. tamarense* complex. Hybrid cysts from these matings germinated but did not survive, demonstrating outbreeding lethality. This also suggests a possible mitigation strategy whereby non-toxic strains could be introduced into a region with toxic species, leading to a reduction in the viable cyst population needed to initiate future blooms.
7. Different types of models were explored as useful tools for investigating the relevance of life cycle features in HAB development. The results of the simulations in *Alexandrium minutum* highlighted the importance of knowing not only the magnitude and variability of growth and life-cycle transition rates, but also those of loss rates (both in the water column and in the sediment) due to physical and biological factors (Estrada *et al.*, 2010). Excystment fluxes can enhance population densities of vegetative cells during times of low or negative net growth rate and during the initial phases of a

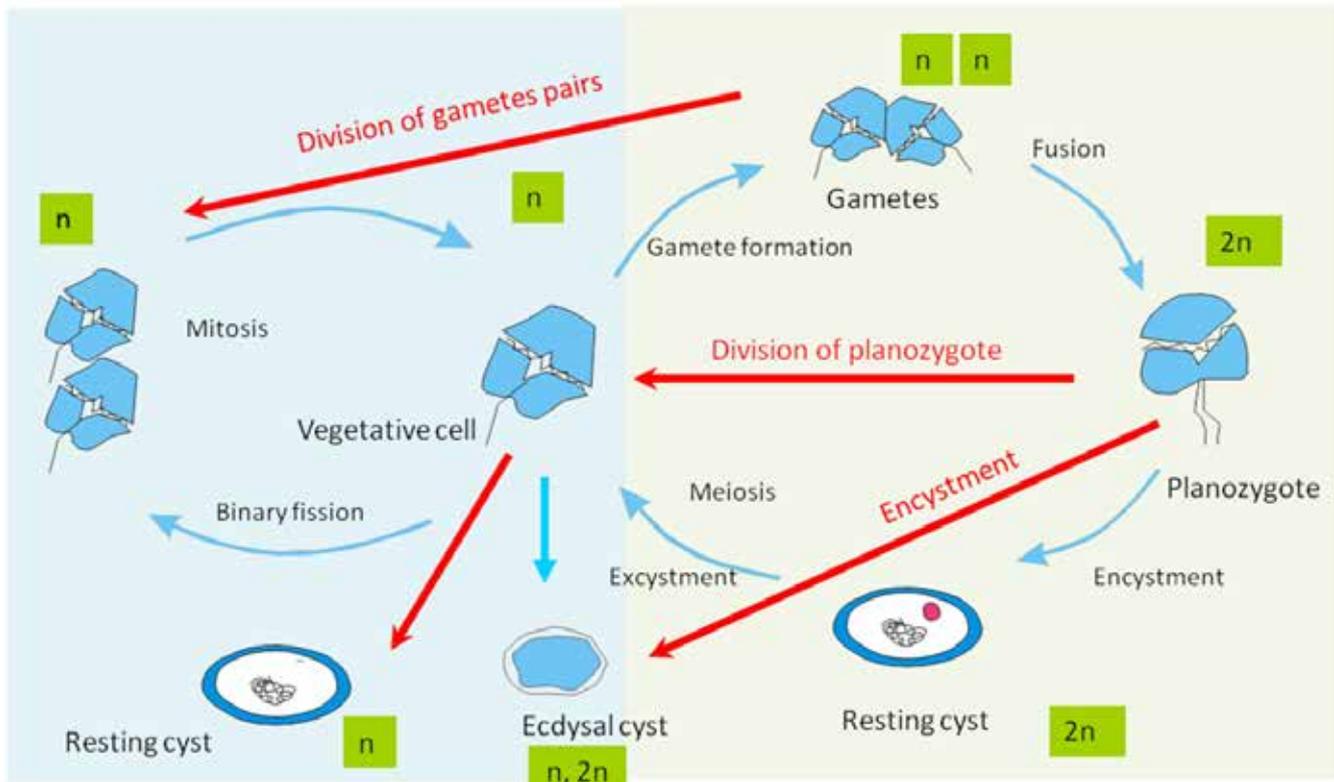


Figure 1. Typical life cycle of dinoflagellates, with new features confirmed during the SEED project (courtesy of R.I. Figueroa, unpublished).

- bloom, but once exponential growth had started, additional excystment had negligible effect on bloom magnitude. However, even if cysts do not determine the magnitude of larger blooms, they do represent a safety mechanism for reintroduction of the species when the vegetative cell population is no longer present in the water column due to unfavourable environmental conditions.
- The relative balance between physical and biological forcing controls the timing of microalgal blooms. By choosing a range of sites, from the Mediterranean Sea (e.g., Basterretxea *et al.*, 2007; van Lenning *et al.*, 2007) to cooler latitudes further north (Gulf of Finland, Estonian coast, Ireland; see Kremp *et al.*, 2008; Touzet *et al.*, 2010b), the predictability of blooms was observed to increase with the degree of physical forcing that controls them. *Alexandrium minutum* has been the target species for most investigations during this project and it is a useful organism for comparative studies when considering latitudinal gradients. This organism exhibits plasticity in its growth characteristics. There are, however, some commonalities across Europe relating to this organism. It is indeed a very robust

species capable of existing in a wide range of environmental conditions.

- Diatom species of the genus *Pseudo-nitzschia* also have complex life cycles, including a sexual phase required for the formation of large-sized cells to circumvent the progressive cell size reduction that occurs during mitotic divisions. A simultaneous and massive sexual event involving two *Pseudo-nitzschia* species has been recorded at the LTER station in the Gulf of Naples (Sarno *et al.*, 2010). The recurrent biennial timing of sexual reproduction has been inferred for *P. multistriata* by following cell size over a decade and has been modelled based on experimental parameters and information from natural populations (D'Alelio *et al.*, 2010).

Finally, topics that remain to be addressed were presented and discussed, such as the tools needed to detect and quantify different life stages (gametes and zygotes) in the natural environment, the contribution of cells germinated from surface sediments to the bloom inoculum, and site-specific differences in sexual cycle strategies.

1.2 *Alexandrium fundyense* Cyst Dynamics in the Gulf of Maine: Results from the ECOHAB-Gulf of Maine and GOMTOX Programmes

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The Gulf of Maine (GoM) is a continental shelf sea that supports productive shellfisheries that are frequently impacted by blooms of the dinoflagellate *Alexandrium fundyense* and outbreaks of paralytic shellfish poisoning (PSP). Near-shore resources are monitored by state agencies, whereas most offshore stocks have little or no routine monitoring. As a result, large areas are permanently closed or underexploited because of the threat from PSP toxins (PSTs) and the lack of scientific understanding and management tools.

PSP is a relatively new phenomenon in the northeastern United States (Anderson, 1997). Toxicity was restricted to far-eastern Maine until 1972, when a massive, visible red tide of *A. fundyense* stretched from Maine to Massachusetts, causing toxicity in southern areas for the first time. In virtually every year since 1972, western Maine has experienced PSP outbreaks, and for the first 20 years of that interval, Massachusetts has as well. That pattern was a direct result of *A. fundyense* cysts being retained in western GoM waters after the 1972 bloom and subsequent events (Anderson and Wall, 1978). Between 1994 and 2004, toxicity was infrequent in Massachusetts and the southern GoM, but, in 2005, another massive bloom occurred (Anderson *et al.*, 2005a), closing shellfish beds from Maine to southern Massachusetts and 40,000 km² of offshore federal waters as well. Economic losses from that event are now estimated to be \$50 million for the Massachusetts shellfish industry alone. Since that year, PSP outbreaks have been extensive, similar to those from the 1970s and 1980s.

For the past decade, the *Alexandrium* blooms in the GoM have been the focus of two major investigations funded by the ECOHAB programme in the United States – the ECOHAB-GoM and GOMTOX programmes. Each was a five-year effort combining extensive laboratory, field, and modelling studies of *Alexandrium* bloom dynamics. Both were multi-institutional, multi-investigator programmes that used series of large-scale field surveys to provide data that were

combined with mooring observations, satellite-tracked drifters, and numerical model simulations to document the complex dynamics of *A. fundyense* blooms within the GoM region. The geographic focus of ECOHAB-GoM extended from the Bay of Fundy to Massachusetts Bay, and about 80 km offshore. For GOMTOX, this area was expanded to include the offshore waters of Georges Bank and Nantucket Shoals, with an emphasis on the mechanisms that deliver toxins to deep-water shellfish.

There are many accomplishments and research findings from these two programmes. A special issue of *Deep-Sea Research II* summarized ECOHAB-GoM results (Anderson *et al.*, 2005a), and a second special issue in the same journal is now in preparation for GOMTOX. Studies cited hereafter as “unpublished data” represent submitted papers for the second special issue, with an expected publication date of 2013. With more than 50 papers either published or in preparation from ECOHAB-GoM and GOMTOX, it is obviously impossible to summarize the accomplishments and findings of these programmes in detail. Selected highlights include the following:

Cyst Seedbeds. A key element of *A. fundyense* bloom dynamics is the existence of two large, benthic accumulations of dormant cysts, termed “seedbeds”. These were revealed in survey cruises that mapped out the concentrations of cysts in bottom sediments from Massachusetts Bay to the Bay of Fundy (Anderson *et al.*, 2005b). Cyst maps are now available for 1997, and 2004 – 2011, each with about 100 stations sampled. In all of these surveys, two large areas of accumulation are evident – one at the mouth of the Bay of Fundy, and the other offshore of Penobscot and Casco bays in central Maine. In between these deposition sites, cysts are found, but at much lower concentrations. Figure 2 shows an example cyst distribution map for 2004.

Conceptual models. Two conceptual models have been developed for the region. In the model of Anderson *et al.* (2005b), cysts germinate from the Bay of Fundy seedbed, causing recurrent blooms that are self-seeding with respect to future outbreaks in that area (Fig. 3). The blooms also contribute to populations in the Eastern Maine Coastal Current, as some cells escape the Bay of Fundy and enter the Eastern Maine Coastal Current, where they bloom. Some cells travel south and west with the Eastern Maine Coastal Current, while others deposit cysts in the mid-coast Maine seedbed. In subsequent years, these latter cysts germinate and, together with advected vegetative cells from the Eastern Maine Coastal Current blooms, cause PSP toxicity in western portions of the GoM and possibly offshore waters as well. The conceptual model of McGillicuddy *et al.* (2005) complements this sequence by emphasizing the patterns of temperature and nutrient availability. Cells germinated from the two cyst beds are advected in the alongshore direction from east to west in

the coastal current. Growth of the vegetative cells is limited primarily by temperature from April through June throughout the GoM, whereas nutrient limitation occurs in July and August in the western GoM. Thus, the observed seasonal shift in the centre of mass of cells from west to east can be explained by changing growth conditions: growth is more rapid in the western GoM early in the season due to warmer temperatures, whereas growth is more rapid in the eastern GoM later in the season due to severe nutrient limitation in the western GoM during that time period.

Development of a numerical model of *Alexandrium* population dynamics. A physical/biological model has been developed to simulate regional hydrography and *A. fundyense* population dynamics (McGillicuddy *et*

al., 2005; Stock *et al.*, 2005; He *et al.*, 2008; Li *et al.*, 2009). Currently, realistic simulations of bloom development are possible using observed cyst distributions, cyst germination rates (Anderson *et al.*, 2005b), vegetative cell growth rates, and continuous real-time river flow and hydrographical data (e.g., He *et al.*, 2008). Hindcasts as well as near-real-time nowcasts and forecasts of *A. fundyense* blooms in the GoM have been run routinely each year since 2005 (McGillicuddy *et al.*, 2011). The model uses a nested hydrographical simulation of the GoM, coupled to a biological sub-model that is based on the annual *Alexandrium* cyst survey map, with the timing and rate of cyst germination and subsequent vegetative cell growth parameterized by laboratory experiments.

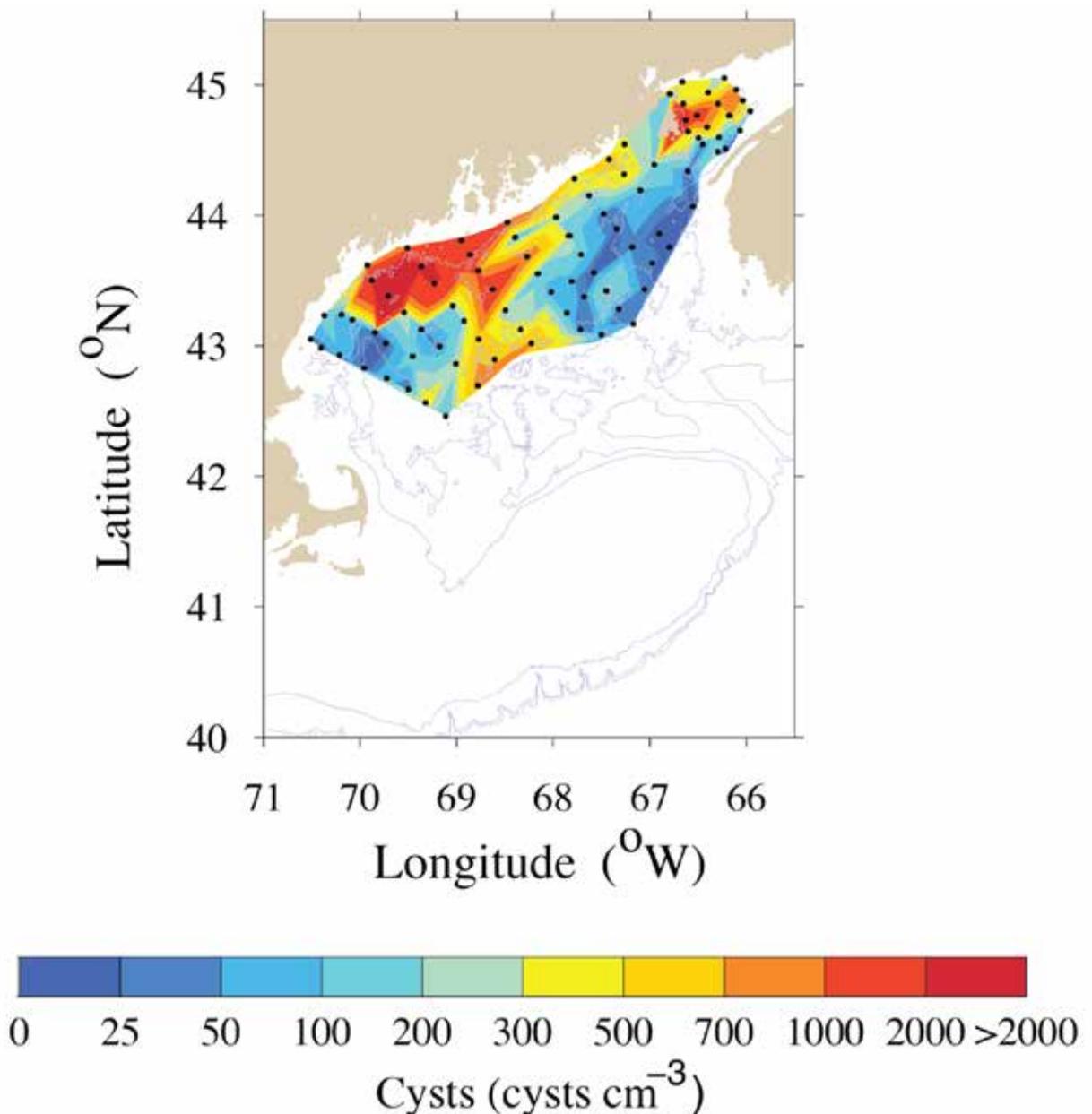


Figure 2. Map showing major *Alexandrium fundyense* cyst accumulation zones in the Gulf of Maine in 2004. Data are for the top 1 cm of sediment. Source: Anderson *et al.*, unpublished data.

Interannual variability in cyst abundance. Large-scale surveys of *A. fundyense* cyst abundance were conducted in the fall (late October-early November) of 1997 and 2004-2011. If all of the cysts in the top centimetre of sediment are summed over a common sampling domain or area, it is possible to compare the cyst abundance across years. Significant inter-annual variability in cyst abundance is evident. The year 1997 had, by far, the lowest cyst abundance, as much as ten-fold lower than the highest levels, which were observed in 2009. Of the three sub-regions (western Maine, eastern Maine, Bay of Fundy), the Bay of Fundy had the least variable cyst abundance, with a factor of approximately five between the lowest and highest levels over the nine years surveyed.

Linkages between cyst abundance and subsequent blooms. Cyst abundance (measured in the fall or winter) appears to be a first-order predictor of regional bloom magnitude the following year in the western GoM (McGillicuddy *et al.*, 2011). Although this hypothesis is supported by correlations between annual cyst abundance and the geographic extent of PSP closures along the GoM coast for the subsequent year (Anderson *et al.*, unpublished data), this need not be the case. With certain meteorological conditions, a regional bloom could occur within the central GoM, with relatively few cells being carried to shore by the downwelling-favourable winds that are needed to cause toxicity in near-shore shellfish. Likewise, other physical and chemical processes could modulate the bloom development, as appears to have happened in 2010 (McGillicuddy *et al.*, 2011).

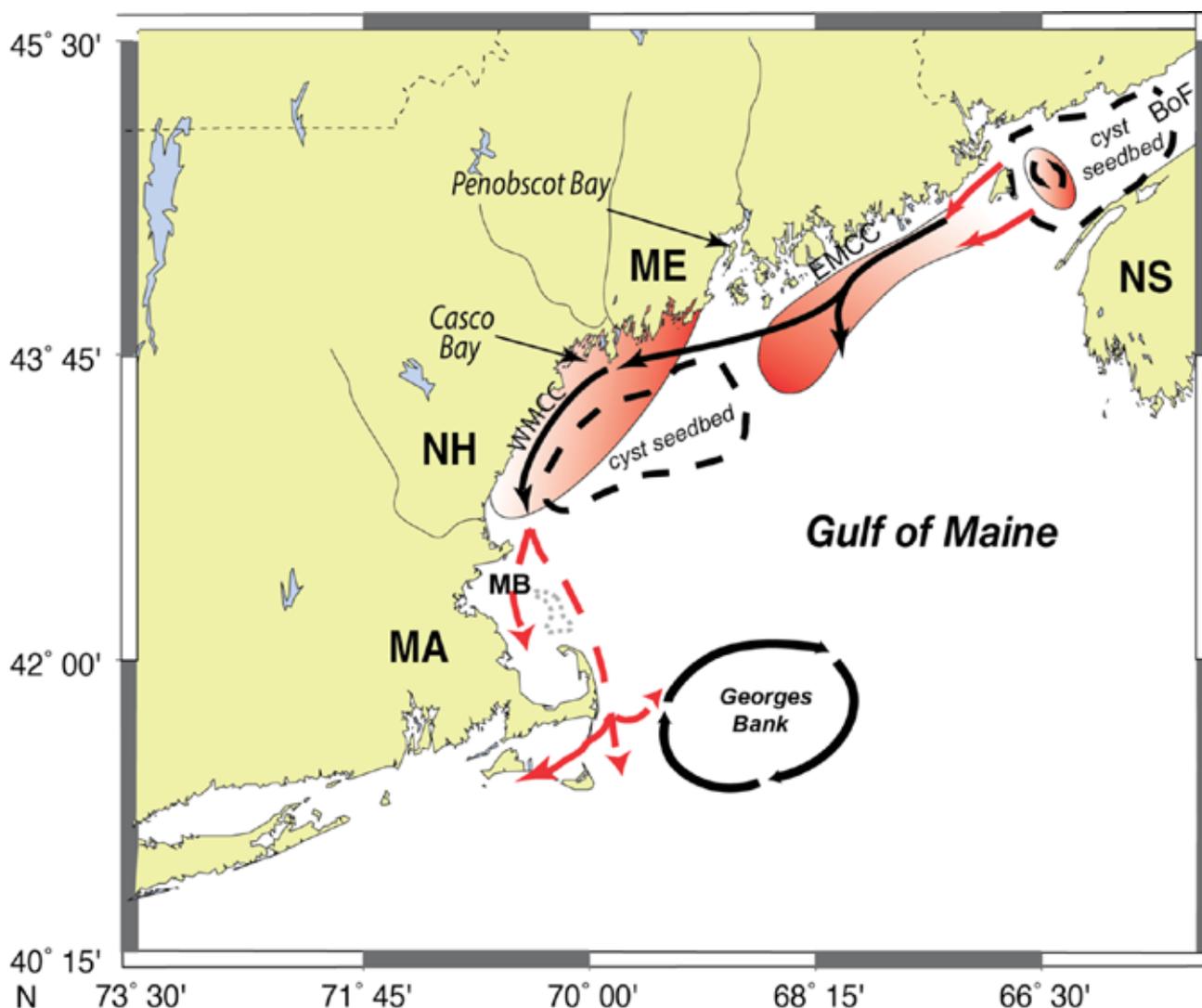


Figure 3. Conceptual model of *A. fundyense* bloom dynamics and PSP toxicity. Solid black lines denote the eastern and western segments of the Maine Coastal Current system (EMCC and WMCC, respectively). Long, solid black lines also depict the circulation around Georges Bank. Short, dashed black lines delimit the cyst seedbeds in the Bay of Fundy (BoF) and mid-coast Maine. The red shaded areas represent portions of the EMCC and WMCC where *A. fundyense* blooms tend to occur, with the highest color intensity denoting areas with higher cell concentrations. Dashed red lines show the transport pathways of these water masses and their associated *Alexandrium* cells. Modified from Anderson *et al.* (2005b).

Linkages between blooms and the abundance of deposited cysts that same year. There is no relationship between surface cyst abundance and the geographic extent of the preceding bloom. Instead, there are correlations between bloom metrics that are more indicative of cell abundance (cumulative toxicity and bloom termination date) and the number of cysts measured later that year (Anderson et al., submitted). This may reflect rapid alongshore transport of blooms (i.e., cells and cysts are transported outside the domain where cyst deposition will repopulate the GoM seedbeds). A big bloom (geographically) can lead to wide dispersal of cells and cysts. Efforts are underway to find a metric that correlates to the size of the cyst seedbed, and the most promising at this stage is with the cumulative amount of toxicity measured in shellfish during the preceding bloom season (D.M. Anderson, unpublished data). Unlike geographic extent, which only reflects areas where a toxicity threshold (80 µg saxitoxin equiv./100 g meat) has been exceeded, the cumulative toxicity more closely relates to the number of *A. fundyense* cells during the bloom.

Statistical analysis of cyst distributions. The expense and time required for cyst mapping surveys are significant, and need to be dramatically reduced if the *Alexandrium* model is to be used for operational forecasting of HABs in the region, as is planned. Statistical analysis of the nine large-scale cyst surveys conducted to date shows that the spatial distribution of *A. fundyense* cysts in the GoM exhibits a large-scale pattern that does not change from year to year, even though the overall cyst abundance varies inter-annually. Cyst abundance data are being used to develop and test a statistical model of distributional patterns and characteristics. The model appears to capture a large fraction of the observed inter-annual variability, suggesting that there is a generic or common relative distribution of cysts. In other words, each station tends to have a consistent proportion of the total cysts being mapped that year, with only the total number of cysts varying. The spatial pattern or relative distribution of cysts is thus relatively constant, but the magnitude or overall abundance varies year to year. This makes sense oceanographically, as the currents and manner in which cysts will be formed in the plankton, deposited in the sediments, and then reworked and re-deposited through time would be relatively similar between years in the large GoM system, whereas the overall abundance of cysts produced would vary. In principle then, it should be possible to sample a relatively small number of stations, determine the departure from the generic or common cyst distribution pattern at each of those stations, and then use the average departure to scale all stations to obtain a full or extrapolated cyst map. These extrapolated maps can then be used by the *Alexandrium* population dynamics model to simulate the bloom for the next year. In this manner, it should be possible to optimize the cyst sampling design with a significantly reduced number

of sampling locations. The objective is to identify the most informative locations and transects, and to design a sampling programme that would provide a realistic regional cyst map with a minimal expenditure for ship and personnel time.

HAB Index. A highly informative HAB index has been formulated that collapses huge amounts of toxicity data into a single measure indicative of annual severity in the GoM (D.M. Anderson et al., unpublished data). A current hypothesis is that the inter-annual and decadal patterns in toxicity reflect differences and trends in the distribution and abundance of *A. fundyense* resting cysts in the GoM. These distributions, plus the history of toxicity in the region, lead us to further hypothesize that beginning in 2005, the region entered a “new era” of frequent and intense toxicity in the region that may last 10-20 years.

Georges Bank toxicity. A series of surveys on Georges Bank document variability of *A. fundyense* populations on time scales ranging from synoptic to seasonal to inter-annual (D.J. McGillicuddy et al., unpublished data). Blooms of *A. fundyense* on Georges Bank can reach concentrations on the order of 10^4 cells l^{-1} , and are generally bank-wide in extent. Georges Bank populations of *A. fundyense* appear to be quasi-independent of those in the adjacent coastal GoM, insofar as they occupy a hydrographical niche that is colder and saltier than their coastal counterparts. In contrast to coastal populations that rely on abundant resting cysts for bloom initiation, very few cysts are present in the sediments on Georges Bank. Bloom dynamics must therefore be largely controlled by the balance between growth and mortality processes, which are at present largely unknown for this population. Based on correlations between cell abundance and nutrient distributions, ammonium appears to be an important source of nitrogen for *A. fundyense* blooms on Georges Bank.

Cyst germination rates and germling survival. A variety of techniques have been used in attempts to measure the *in situ* cyst germination rate. Using the plankton emergence traps (PETs) of Ishikawa et al. (2007), an average excystment percentage of 0.11% per day was estimated, excluding data from days where significant contamination of the PETs was likely from the high cell densities of vegetative cells in the surrounding bloom (E. Vahtera, unpublished data). These rates are 10-20 times lower than germination rates. Survival of germling cells in the dark (as would be the situation after excystment from cyst seedbeds at 100–150 m) was poor, with only 28% survival after seven days, the time needed to reach the euphotic zone in a 100 m water column. These mortality rates are generally lower than those used in the *Alexandrium* population dynamics model. These two results indicate that these critical aspects of bloom initiation need further study.

Resuspended cysts. Studies have been carried out to characterize the depth and extent of the benthic neph-

loid layer (BNL) and the number of resuspended *Alexandrium* cysts it contains (C.H. Pilskaln *et al.*, unpublished data). The benthic boundary layer (BBL) is the region encompassing the uppermost surface sediments and the overlying water column which is impacted by the presence of the sediment-water interface. The BBL is physically distinguished by the frictional influence of the sediment surface on the overlying water column flow and stratification and extends to a height above that surface where such an effect becomes essentially negligible. It is within the BBL that near-bottom particle resuspension layers or BNLs develop, representing a distinctive zone of increased suspended particle concentration. BNLs have been proposed as a possible source of inoculum for annual spring blooms of *Alexandrium*. The results presented herein from a gulf-wide study found BNLs to be pervasive throughout the GoM and adjacent Bay of Fundy, with maximum layer thicknesses of about 30 m in the regional basins. Topographic focusing and bathymetric control of the near-bottom resuspension layers was evident, as well as connections between the Bay of Fundy BNL cyst inventories, the Eastern Maine Coastal Current and the south-central region of the GoM. *Alexandrium fundyense* cyst abundance in the near-bottom particle resuspension layers varied spatially by three orders of magnitude and BNL thickness was not strongly correlated with BNL cyst inventories. Examination of time-series of sediment trap-measured, near-bottom cyst fluxes, surface sediment cyst abundance maps, and estimated BNL cyst inventories suggest that sediment-bound cysts in the eastern GoM have a shorter sedimentary residence time relative to those in the western GoM. The latter has implications for identifying the potential source of resuspended cysts to fuel periodic blooms in the southern GoM/Georges Bank region.

Future studies. These will aim to:

- Modify *Alexandrium* population dynamics model to simulate cyst formation;
- Couple the population model to a sediment transport model to simulate cyst transport, deposition, resuspension, and redeposition. In this way, an attempt will be made to close the entire life cycle with the simulation;
- Use statistical analysis of cyst deposition patterns to minimize the cost of cyst mapping surveys;
- Continue model refinement based on laboratory and field studies of encystment, and mortality factors such as grazing and parasitism. Our understanding of the timing and extent of encystment is limited, as is our ability to quantify the relative importance of multiple factors in bloom decline (e.g., encystment, grazing, parasite and viral mortality, dispersion);
- Obtain real-time cell and toxin data using *in situ* sensors (e.g., the Environmental Sample Processor, ESP) that will decrease model reliance on cyst mapping and improve accuracy of forecasts.

2. HAB Resting Stage Dynamics, Physiology and Life Cycles, with a Focus on Small-Scale Coastal Systems

2.1 Harmful Algal Blooms in Tropical Embayments Affected by Monsoons

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The Philippines, located in the tropics between 116°40' and 126°34' E longitude, and 4°40' and 21°10' N latitude, have several embayments with records of harmful algal blooms that are apparently related to the changing conditions of the bays, as affected by the different monsoons. Two study sites, Manila Bay and Sorsogon Bay (Fig. 4), which are part of the GEOHAB-endorsed programme entitled “Ecology and Oceanography of Harmful Algal Blooms in the Philippines” (PhilHABs), are discussed below, with a focus on the more-studied HAB dynamics in the country, with relevance to Southeast Asia. This programme was supported by the Philippines Department of Science and Technology – Philippines Council for Aquatic and Marine Resources Development (DOST-PCMRD) and the University of the Philippines, Marine Science Institute (UPMSI), which we gratefully acknowledge.

The dinoflagellate *Pyrodinium bahamense* var. *compressum* (Pbc) (Fig. 5), which can produce resistant cysts, has been recorded in more than 30 bays/areas in the Philippines since 1983 (BFAR Shellfish Bulletins, 1983-2012). PhilHABs and earlier studies (Bajarias and Relox, 1996; Azanza and Miranda, 2001; Azanza *et al.*, 2004) have shown that this organism generally blooms during the southwest (SW) monsoon (Fig. 6) characterized by relatively warmer water (29-32°C) with lower salinity (19-28 psu). The water column is strongly stratified during this season with freshwater from adjacent land area/rivers and rainwater bringing more nutrients into the embayments. Villanoy *et al.* (2006) showed that during this season, resuspended *Pyrodinium* cysts resulting from the trade winds/intermonsoon may germinate and produce blooms since conditions are more favourable than the preceding months. The blooms could last during the entire period of the SW monsoon (June to September in Manila Bay or July to October in Sorsogon Bay). Encystment, that is, early stages of hypnocyst formation and pellicle cyst formation, have been observed in the waters of Sorsogon Bay during the bloom maintenance (*i.e.*, SW monsoon period) (Dioneda and Azanza, 2010). Termination of the bloom generally comes at late SW or early Northeast (NE) monsoon. During the NE monsoon season (November to February in Sorsogon Bay or October to March in Manila Bay) water temperature drops (26-28°C) with a higher salinity (27-34 psu) and more turbulent water column (Table 1).

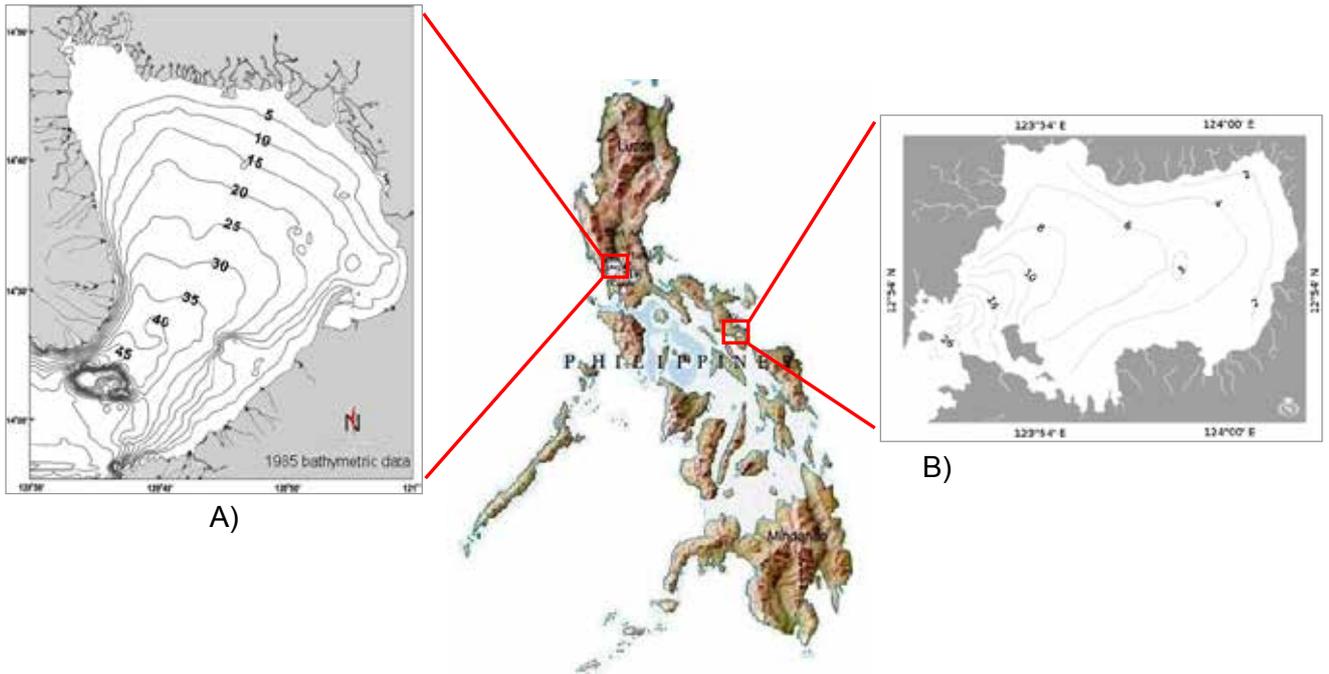


Figure 4. Map of the Philippines showing the two study areas, (A) Manila Bay (from Siringan et al., 2008, used with permission from Elsevier) and (B) Sorsogon Bay (references for bathymetry: Siringan et al., 2012).

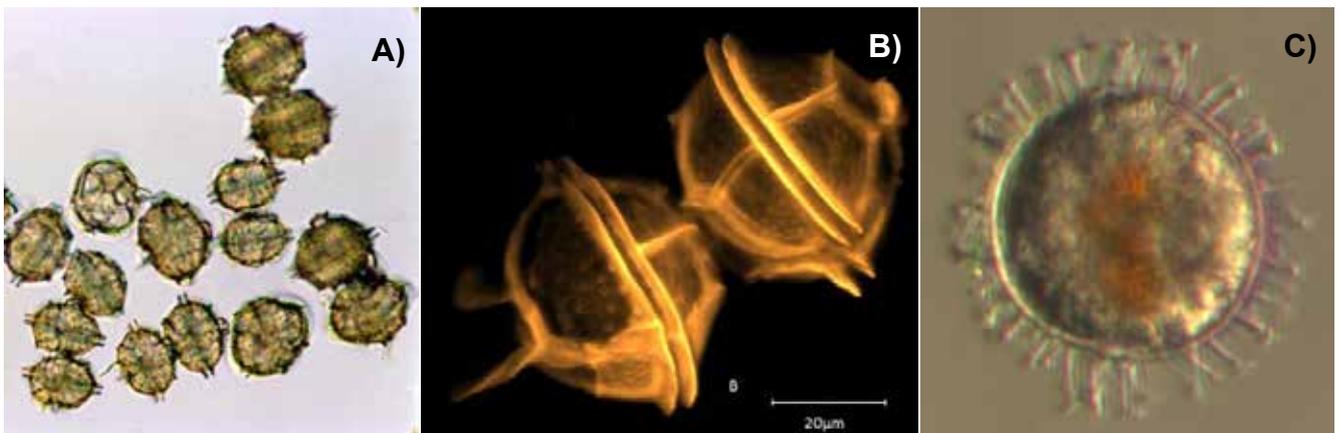


Figure 5. Photomicrograph (A) and lasergraph (B) of the vegetative cells and a live cyst from culture (C) of *Pyrodinium bahamense* var. *compressum*, the most common cause of Paralytic Shellfish Poisoning in Philippines/Southeast Asia (references for bathymetry: Siringan et al., 2012).

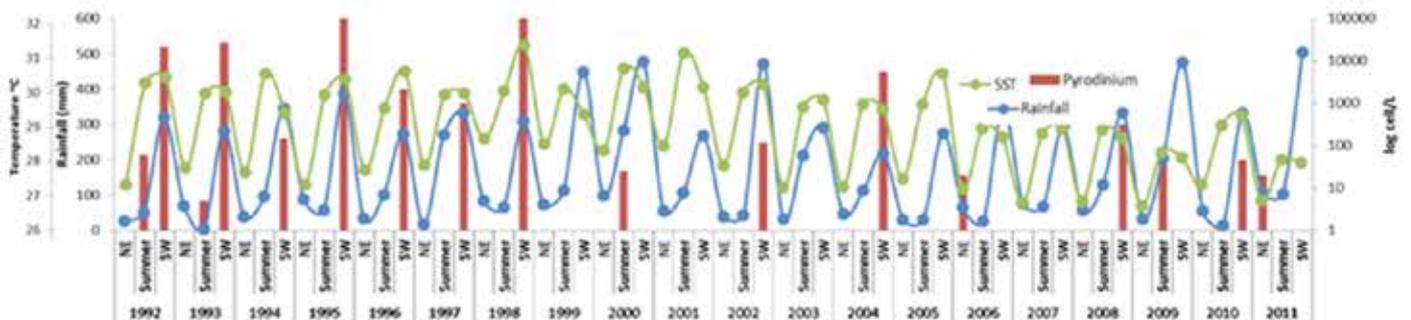


Figure 6. Rainfall (mm), sea surface temperature (SST, °C) (1992–2011) and Manila Bay *Pyrodinium* blooms (log cells l^{-1}) recorded from 1994–2011. (Figure from R.V. Azanza, unpublished, using data from various sources: rainfall, Philippine Atmospheric Geophysical and Astronomical Services Administration (PAGASA); SST, <http://oceancolor.gsfc.nasa.gov/>; *Pyrodinium* cell counts, Bajarias and Relox, 1996; Azanza and Miranda, 2001; Azanza et al., 2012).

Table 1. Summary of physico-chemical conditions in Manila and Sorsogon bays during different seasons and trends in *Pyrodinium* cyst and cell concentration. Downwards arrows indicate generally low, upwards arrows indicate generally high concentrations. Range of cyst concentrations: 40–450 cysts cm^{-3} (upper 2 cm), cell concentration: up to approximately 70,000–100,000 cells l^{-1} ; temperature: 25–32°C; salinity: 26–33 psu. For nutrients, concentrations in $\mu\text{moles l}^{-1}$ range from 0.3–4 for nitrate, 0.2–0.8 for nitrite, 0.4–0.6 for phosphate and 1.2–1.5 for ammonium. (References: Corrales and Crisostomo, 1996; Velasquez et al., 1997; Azanza et al., 2004; Villanoy et al., 2006; Dioneda and Azanza, 2010; Azanza et al., 2012).

Place	Season/Month	Cysts	Cells	Vertical Mixing	Stratification	Nut.	Temp	Sal
Manila Bay	NE (Nov-Feb)	↓	↓	↑	↓	↓	↓	mid
Sorsogon Bay	NE (Jan-Mar)	↓	↓	↑	↓	↓	↓	mid
Manila Bay	Summer (Mar-May)	↑	↑	↓	slightly	↑	↑	↑
Sorsogon Bay	Summer (Apr-May)	↑	↑	↓	slightly	↑	↑	↑
Manila Bay	SW (Jun-Aug)	↑	↑	↓	↑	↑	mid	↓
Sorsogon Bay	SW (Aug-Dec)	↑	↑	↓	↑	↑	mid	↓

Sampling during the different seasons in the two bays showed the predominance of diatoms during the NE monsoon and of dinoflagellates during the SW monsoon. The inter-monsoon or trade winds period (March to May) was characterized by almost co-dominance of dinoflagellate and diatom species. *Pyrodinium* high cell density and shellfish toxicity coincided during the SW monsoon in both bays (Bajarías and Relox, 1996; Azanza and Miranda, 2001; Azanza et al., 2012). Pbc blooms were recorded in Manila Bay during the SW monsoon from 1987 to about 2000. From 2001 to the present, the cell concentration of this dinoflagellate decreased with no bloom formation except in 2004 (Azanza et al., 2012). Pbc blooms in Manila Bay can be directly correlated with the cyst dynamics, as shown by both vertical (Siringan et al., 2008) and horizontal records (Corrales and Crisostomo, 1996; Azanza et al., 2004). Cysts were found in the upper sediments at various concentrations across seasons, with highest concentration during the SW monsoon (300–450 cysts cm^{-3}) apparently because of encystment processes. The lowest cyst concentration was found during summer and the NE monsoon, when cyst displacement was favoured due to water turbulence. Cyst beds have been found in both bays and modelling has shown that these beds could be sites for deposition because of sediment accretion (Siringan et al., 2012). Additionally, these could also be sites of possible cyst origin that seed the entire bay following the major currents (Villanoy et al., 2006).

Vertical core sampling has shown that *Pyrodinium* cysts, which are very resistant to environmental stress (Zonneveld et al., 2001), were present in the 1900s or even before (Siringan et al., 2008) in Manila Bay and in Sorsogon Bay (Siringan et al., 2012).

More recently *Noctiluca* blooms appear to have replaced *Pyrodinium* blooms in Manila Bay since 1999. Abundances of *Pyrodinium* cells in the water during the different seasons, even during the SW monsoon, have been very low and cysts in upper sediments much lower than the previous concentrations (0–20 cysts g^{-1}) (Azanza et al., 2012). *Noctiluca* feeding on *Pyrodinium* cells, as demonstrated in the laboratory (Hansen et al., 2004), could be one of the major reasons for this “take-over”, explaining the recent low Pbc cyst counts in Manila Bay.

Two other toxic dinoflagellates have been recorded in both bays: *Gymnodinium catenatum* and *Alexandrium* spp. These PSP-causative organisms were reported earlier in Manila Bay (Fukuyo et al., 1993; Azanza and Miranda, 2001), but it seems that only during recent years have they been occurring in high densities. *Gymnodinium catenatum* was more abundant during the NE monsoon together with *Alexandrium* spp. in Manila Bay, and also during the NE monsoon in Sorsogon Bay (Azanza et al., 2012). Cysts of *G. catenatum* have been found in Sorsogon Bay, whereas they still have to be confirmed (if present) in Manila Bay.

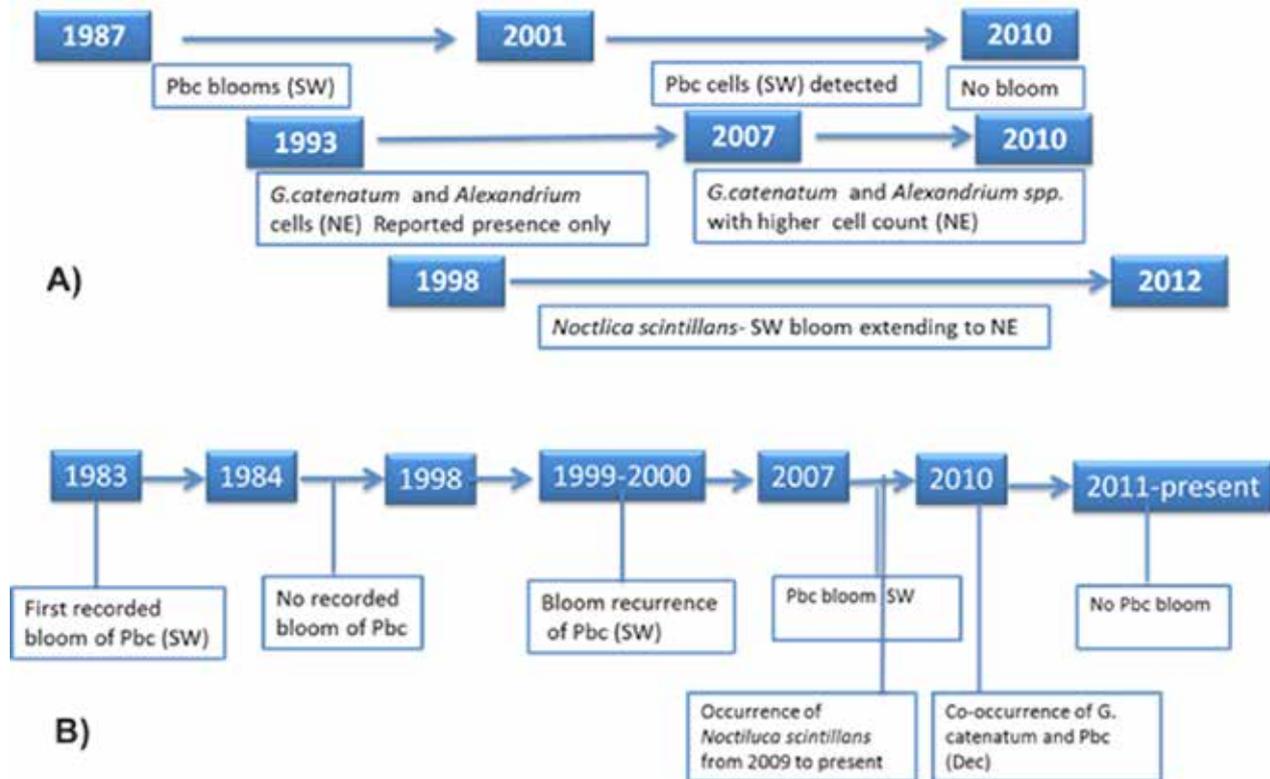


Figure 7. Timeline of HABs in (A) Manila Bay, Western Philippines and (B) Sorsogon Bay, Eastern Philippines (from R.V. Azanza, unpublished).

Table 1 summarizes the physico-chemical conditions during the monsoon periods while Figure 7 summarizes the timeline of HABs in Manila and Sorsogon bays. Smayda and Reynolds (2003) analysed the survival strategies of various HAB genera/species and hypothesized that *Pyrodinium bahamense* and *Gymnodinium catenatum*, being R-strategists, are able to withstand physically disturbed water masses and tolerate shear/stress force, thriving well into the typhoon season. *Alexandrium* spp., on the other hand, being C-strategists, are small fast-growing organisms able to proliferate after a period of higher nutrient concentrations. These dinoflagellates form blooms that collapse within a season. Such life cycle strategies have been observed for these organisms in Manila and Sorsogon bays. Analysis of more empirical data, however, could verify these observations.

Tropical embayments affected by monsoons, such as Manila and Sorsogon bays in the Philippines, undergo distinct physico-chemical changes that affect phyto-

plankton succession and dynamics in a species-specific way. Parameters primarily affected are the water stability, nutrient concentrations and water currents in the area.

Pyrodinium blooms in these bays can be considered cyst-based as evidenced by concentrations in horizontally and vertically sampled sediment. *Pyrodinium* vegetative cells and cyst concentration/cycling are apparently governed by previous and prevailing conditions, as affected primarily by the monsoons. The incidence and magnitude of *Pyrodinium* blooms also seem to coincide with ENSO events, although analysis is still underway to substantiate this relationship (Azanza *et al.*, 2012; Azanza *et al.*, unpublished). Variations in the species bloom dynamics are site-specific, dependent upon factors such as bay morphology/hydrography and water residence time. More studies in other bays similar to those in the Philippines would provide further information and verify observations from the present inter-basin analysis of HABs.

B. CHEMICAL ECOLOGICAL INTERACTIONS IN PLANKTON ASSEMBLAGES AND EFFECTS ON HARMFUL ALGAL BLOOM DYNAMICS AND BIOGEOGRAPHICAL DISTRIBUTION IN FJORDS AND COASTAL EMBAYMENTS

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Background. By definition, fjords and coastal embayments are partially constrained, semi-enclosed coastal ecosystems, with concomitant hydrodynamic, bathymetric and geomorphological features that shape the structure, dynamics and biodiversity of plankton assemblages. Hence, many models of HAB dynamics

are first predicated upon physical descriptions of water mass characteristics and then incorporate the biological components, but often imperfectly and with incomplete *a priori* knowledge of the dominant parameters. These relevant biological parameters comprise key factors such as growth rate, cell loss terms due to grazing, natural mortality, infection by parasites, bacteria, viruses or fungi, life history transitions, and behavioural responses, including swimming and buoyancy compensation. Collectively, the physical and biological functions will determine the net population growth rate and cell abundance within a defined water mass, and shape species interactions and co-evolution of HAB species.

Chemical interactions - a critical role for HABs in semi-enclosed coastal ecosystems. Often ignored in constructing the above scenarios is the nature of chemical interactions (other than macronutrients) on HAB dynamics, diversity and biogeography. Yet recent evidence suggests that chemical ecological interactions among planktonic members of marine food webs affect and may even regulate “top down” processes, such as competition, predator-prey relationships and chemical communication within and among certain species (Fig. 8).

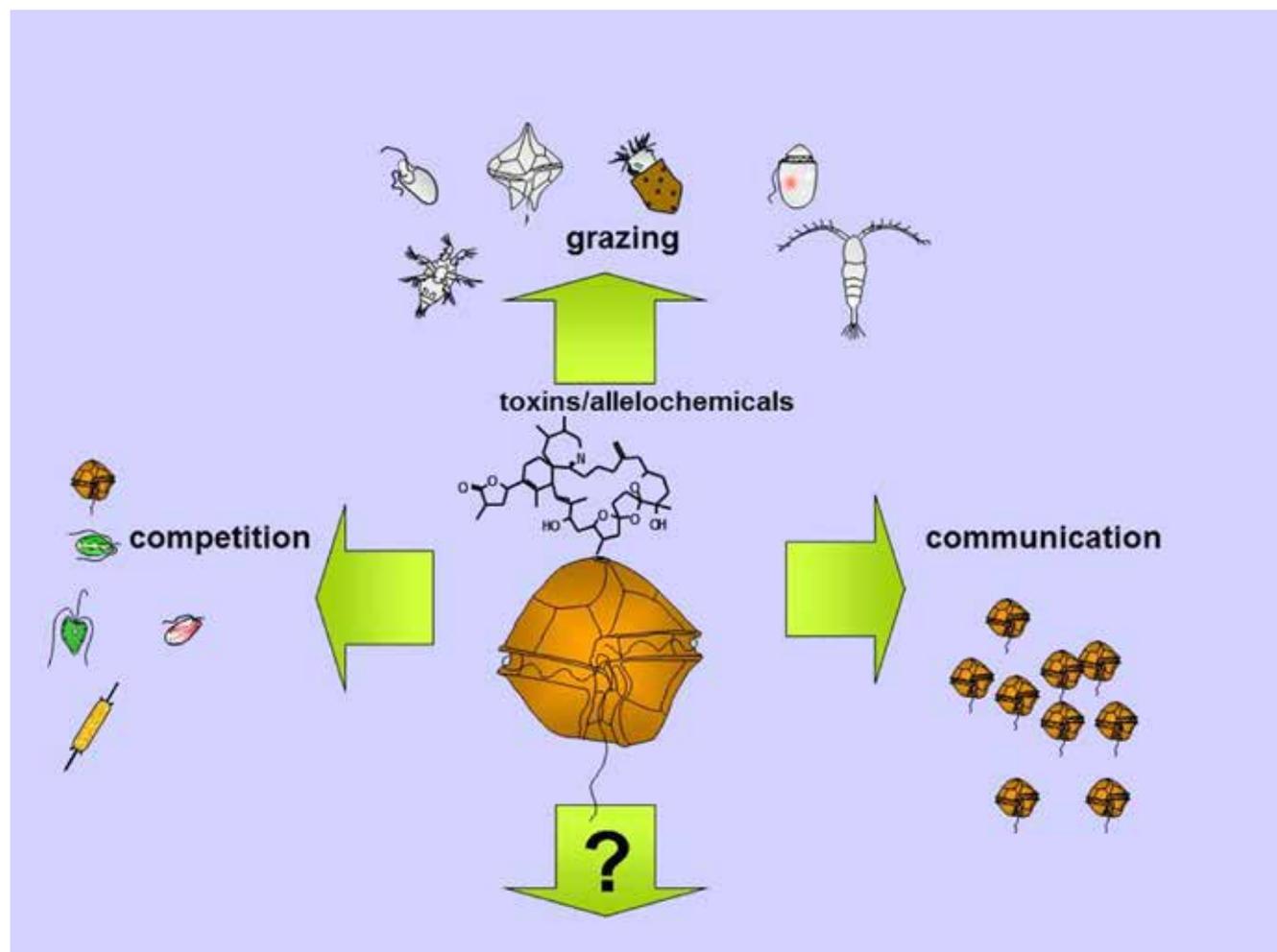


Figure 8. Schematic of chemical ecological interactions mediated by toxins/allelochemicals and potentially affecting growth, bloom dynamics and life history transitions (from A.D. Cembella et al., unpublished).

Members of toxigenic HAB taxa containing known phycotoxins were believed to produce these potent compounds as chemical defence against grazers or competitors in the “watery arms race” (Smetacek, 2001). This assumption was based upon the high potency of these compounds in humans and in mammalian cell model systems, combined with evidence of their effects on ion channels in cell membranes or on enzyme inhibition. The concept was simply extrapolated to the marine environment with the assumption that these compounds serve a defensive function in the bloom ecology and evolution of the toxigenic species. Nevertheless, experimental evidence often contradicts or fails to support this hypothesis as a general mechanism. Furthermore, many emerging allelochemicals show potent biological activity against co-occurring species, but are structurally and functionally unrelated to classic phycotoxins. Consideration of allelochemical interactions in the plankton (reviewed by Cembella, 2003; Legrand *et al.*, 2003) has revealed that chemically mediated effects of phycotoxin-producing HAB taxa are complex and often equivocal, but the evidence does not support a primary role for the known phycotoxins as defensive compounds against protistan or most metazoan competitors or predators.

The arguments for conducting field studies on chemical interactions in the plankton within fjords and coastal embayments are compelling and multivariate. As coastal features, these ecosystems are subject to direct influence of terrestrial run-off of complex dissolved organic matter and nutrients from anthropogenic and agricultural sources, as well as contributions from the natural environment. The geomorphological and hydrodynamic constraints limit bloom dispersion and reduce exchange with the adjacent coastal waters and thus promote bloom aggregation within the semi-enclosed system. This phenomenon thus maximizes the potential for chemical interactions.

Determination of the nature of allelochemical interactions requires a multi-disciplinary approach integrating knowledge on the behaviour and responses of organisms with sophisticated chemical analytical techniques and functional genomics – the *chemical ecology strategy* (Fig. 9). Most studies of toxic and allelochemical effects on growth dynamics have been conducted in very simple small enclosures (e.g., batch cultures) and have considered only bilateral species interactions. In a few cases, mesocosms containing natural assemblages supplemented with toxigenic test

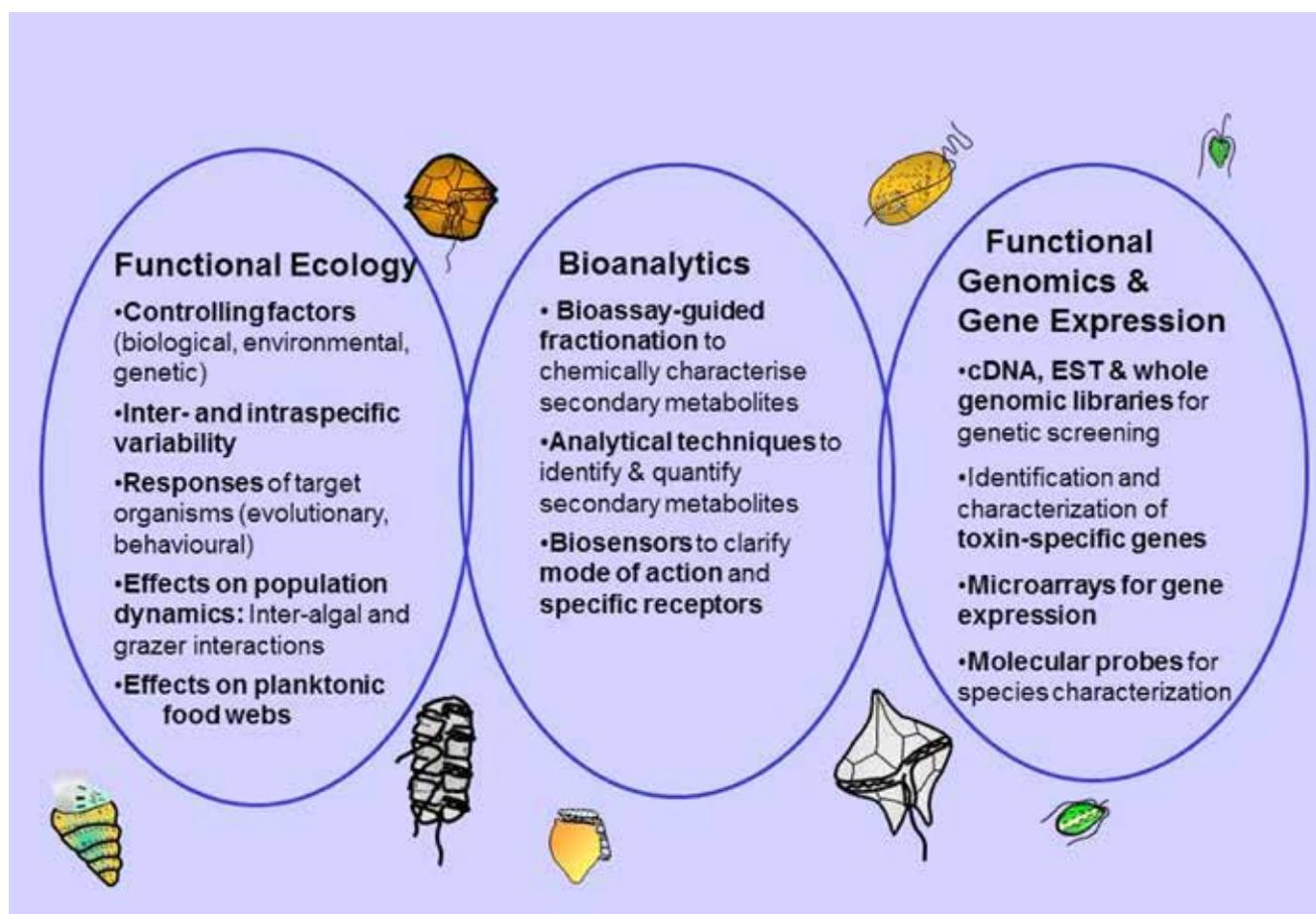


Figure 9. Chemical Ecology Strategy – determination of the ecological function of bioactive secondary metabolites from marine plankton by identification, characterisation, and quantification of toxins and allelochemicals and determining their mode of action and biosynthetic mechanisms (from A.D. Cembella *et al.*, unpublished).

organisms have served to explore species responses to chemical interactions, such as effects on survival and grazing. The disadvantages and limitations of flask experiments and artefacts developed in mesocosm systems are well known, and thus such experimental systems can only serve as preliminary indications of chemical ecological responses in natural communities. The physical constraints on advection and dispersion of blooms in semi-enclosed systems such as fjords and coastal embayments, offer maximum potential for understanding expression and transduction of chemical signals in natural plankton assemblages. Although the fine control of environmental variables must be sacrificed, studies of chemical mediation of HAB dynamics and diversity can be approached in comparative studies of mesoscale and microscale processes within such ecosystems.

Mode of action and mechanisms of allelochemical and toxic interactions. Smayda (1997) proposed that HAB species have evolved four major strategies to offset the ecological disadvantages of having low nutrient uptake capabilities: (1) vertical migration to reach deep nutrients; (2) mixotrophy; (3) allelochemically enhanced interspecific competition; and (4) allelochemical anti-predation defence mechanisms. To date, this general scheme has survived intact, but recent evidence suggests that these strategies are highly inter-linked rather than alternative mechanisms. Vertical migration patterns and aggregation behaviour, for example, at density gradients and in thin layers, may also be governed by organic nutrient concentrations, mixotrophy and allelochemical interactions. Furthermore, mixotrophy is frequently linked to allelochemical activity, particularly among species favouring coastal and brackish waters in embayments and lagoons. Allelochemicals are clearly involved in nutrient acquisition and feeding, as is well established for the mixotrophic prymnesiophyte *Prymnesium parvum*, which releases lytic compounds that immobilize or kill motile prey before ingestion (Skovgaard and Hansen, 2003).

The bewildering diversity of known phycotoxins produced among the phytoplankton – hundreds of analogues within more than a dozen structural groups – indeed complicates the study of their ecological significance and selective mode of action. The recent discovery of allelochemicals with high biological activity within the plankton must also be further considered with respect to the diversity of chemically mediated interactions, particularly those involving HAB taxa. The study of allelochemical interactions among coastal plankton has revealed not only high molecular diversity in production of known phycotoxins, even within a geographical population, but also the uncoupling of allelochemical potency against protistan targets from phycotoxin composition and cell content. The red tide dinoflagellate *Karenia brevis* produces growth inhibitors known to be active against certain diatoms, and

thus may affect competitive interactions and growth dynamics, but these substances are structurally and functionally unrelated to brevetoxins (Prince *et al.*, 2008). Attempts at total structural elucidation of these allelochemicals have not yet been successful, but at least one group comprises polar, unstable compounds of low molecular weight. Expression of “toxic” allelochemical activity by multiple clones of the dinoflagellate *Alexandrium tamarense* against the cryptophyte *Rhodomonas salina* and the predatory dinoflagellate *Oxyrrhis marina*, including loss of mobility and cell lysis, was also shown to be unrelated to the PSP toxin content or composition of *Alexandrium* isolates (Alpermann *et al.*, 2010). Preliminary characterization of the lytic toxins from *A. tamarense* (Ma *et al.*, 2009), which appear to target external cell membranes, indicated that these allelochemicals are macromolecular or large aggregates (>5 kDa). Further analysis indicated that these allelochemicals are neither proteinaceous nor primarily polysaccharide-derived, but can increase permeability of the target cell membrane for Ca²⁺ ions, without specifically binding to these ion channels (Ma *et al.*, 2011). The membrane-disruptive activity of the lytic compounds likely involves sterol components of membranes, but their high molecular weight (between 7 kDa and 15 kDa) precludes a direct analogy to the mode of action of karlotoxins.

The relationship (if any) between allelochemicals mediating chemical ecological interactions in the plankton and ichthyotoxicity remains to be determined. Significantly, many HAB species known to be responsible for fish kills also produce allelochemicals effective against contemporaneous plankton (Cembella, 2003; Anderson *et al.*, 2012). Furthermore, perhaps because of the high concentration of fish aquaculture activities in fjords and coastal embayments, most fish kills have been recorded from such environments. This suggests that semi-enclosed coastal ecosystems provide the best available natural systems for exploring linkages between toxicity at all trophic levels and discovering the mode of action of allelochemicals.

The karlotoxin-producing dinoflagellate *Karlodinium veneficum* is responsible for fish kills in estuaries and coastal embayments. This species provides perhaps the most comprehensive current model of the mode of action of allelochemical activity associated with a rather well-defined group of toxins. Grazer susceptibility to membrane lysis by karlotoxins is apparently due to the corresponding sterol composition of potential predators among the plankton; grazers containing predominantly desmethyl sterols are susceptible to membrane-disruptive attack by karlotoxins, whereas those with mainly 4- α methyl sterols are resistant (Adolf *et al.*, 2007). The mode of action of karlotoxins by membrane pore formation may also account for the known ichthyotoxicity of *Karlodinium* spp., as well as contributing to the success of *in situ* blooms against

competitors and predators. Such studies on toxin mode of action and target susceptibility could explain both eco-physiological “top down” regulation of harmful algal bloom dynamics and effects on higher members of marine food chains in fjords and coastal embayments.

Allelochemical and toxic interactions among planktonic organisms depend on threshold doses of bioactive substances. This is essentially analogous to the quorum sensing mechanism determined from bacteria but not yet clearly established for phytoplankton. In the case of intracellular allelochemicals, this exposure threshold can be reached by serial grazing upon toxigenic cells or alternatively by release of allelochemicals following bloom termination. For extracellular allelochemicals that may be excreted or leaked into the surrounding medium or remain associated to the cell within the phycosphere, the patch density of toxigenic cells is a critical factor. In contrast to terrestrial and airborne allelochemicals (e.g., insect pheromones), in the marine environment, dispersion of allelochemicals is limited by rates of molecular diffusion, turbulence and mixing interactions. With the exception of saxitoxin and analogues associated with PSP and the neurotoxin domoic acid produced by certain pennate diatoms, the known phycotoxins tend to be lipophilic polyether compounds with little solubility in seawater. Hence, when leaked or excreted from cells, they are expected to remain rather closely associated with the producing cells, perhaps even associated with the external membranes. For maximal effectiveness, as chemical defence weapons, pheromones, chemical communication agents, or other threshold-dependent functions, the response can be best expressed, transduced and elicited in the target cells if a critical “patch density” or cell concentration is maintained. One can then envisage a “chemical cloud” circumscribing the plankton patch that may serve as an exclusion zone for competitors or grazers.

A few studies have actually demonstrated an elicited behavioural response of exposure to allelochemicals, even in the absence of ingestion by grazers, as mediated by waterborne cues. Significantly, some of these responses are not just manifest by the target grazers,

such as copepods or tintinnids, but rather are elicited in allelochemical- or toxin-producing cells, when exposed to a perceived threat. In one such example, *A. tamarense* cell chains were shown to reduce encounter rates with grazers by splitting into single cells or shorter chains and slowing down swimming speed when exposed to waterborne copepod cues (Selander *et al.*, 2011). Furthermore, following exposure to waterborne cues even at naturally occurring concentrations of copepods, a shift up of >25-fold in cellular PSP toxin content may be induced in the toxic dinoflagellate *Alexandrium minutum*, and thus has been shown to correlate with increased resistance to copepod grazing (Selander *et al.*, 2006). In a similar fashion, exposure of *A. tamarense* cells to three copepod species and their corresponding waterborne cues also substantiated the potential for a rapid increase in PSP toxin content in the dinoflagellate (Wohlrab *et al.*, 2010).

The advent of molecular technologies for studies of functional genomics and gene expression profiling has provided further insights into such allelochemical interactions. Waterborne cues of copepods have been shown to induce changes in both cell PSP toxin content and gene expression profiles in *Alexandrium* spp. (Wohlrab *et al.*, 2010; Yang *et al.*, 2011). A transcriptomic model study of copepod-induced shift-up in cell PSP toxin content in *A. minutum* based upon a DNA microarray (Yang *et al.*, 2011) demonstrated that at least 14 genes were differentially regulated by exposure to water-borne cues from copepods. The functional genomic approach (Wohlrab *et al.*, 2010), based upon an expressed sequence tag (EST) library, indicated that regulation of serine/threonine kinase signalling pathways has a major influence in directing the copepod-cues into different intracellular cascades and networks in *A. tamarense*. Bidirectional allelochemical interactions thus provide a plausible basis for co-evolutionary mechanisms between HAB species and their predators and competitors in natural bloom populations. Studies of such chemically mediated phenomena in the GEO-HAB comparative framework will assist in determining the magnitude of the effect on HAB dynamics and co-evolutionary processes.

C. GENETIC DIVERSITY AND POPULATION HETEROGENEITY: RELEVANCE TO HABs IN SMALL-SCALE SYSTEMS

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Small-scale coastal systems, such as bays and fjords, are characterized by geographical constraints on water exchange and bloom retention, and are often impacted by harmful algal blooms. HAB species belong to various phylogenetic lineages, produce different toxins and secondary metabolites, and have different physiology, life cycles and ecological requirements. Within this broad ‘biodiversity’ background, it is crucial to acquire sound species-specific information on the biological traits of the organisms responsible for HABs. The necessary prerequisite is to achieve a proper definition of the units of interest (species or populations). In the past decade, research has provided important advancements on three different levels of ‘diversity’ that have important bearings for HAB research and for ecological research in general: (1) integrated approaches to species circumscription and evidence for cryptic diversity in many microalgae lineages; (2) intraspecific genetic diversity and evidence for the organization of species into distinct populations; (3) genotypic diversity and phenotypic variability.

Species circumscription and cryptic diversity. The taxonomy of phytoplankton is largely grounded on the ‘morphological species concept’: species are defined based on morphological characters that are recognizable in light and/or electron microscopy. The increased application of molecular approaches, such as sequences of ribosomal, chloroplast or mitochondrial markers, challenge, in several instances, the taxonomy of phytoplankton organisms. Cryptic (morphologically identical but genetically different) or pseudo-cryptic (genetically different and with minor morphological differences) species have been described for many phytoplankton taxa. It is almost 20 years ago that Scholin et al. (1994) provided evidence for cryptic diversity in the ‘*Alexandrium tamarense* species complex’; the analysis of larger sub-unit (LSU) rDNA sequences of strains of *A. tamarense*, *A. fundyense* and *A. catenella* (the morpho-species grouped in this species complex) collected in different locations worldwide did not cluster according to the ‘morphological species concept’, but rather grouped into five distinct clades. Two of these ribotypes comprise toxic strains: type I distributed along the North American and north European coasts and type IV recorded mostly in Asia. The other ribotypes group non-toxic strains; a new

non-toxic Mediterranean clade has been added to this group (John et al., 2003). Genetic diversity has been detected also within the morpho-species *A. minutum*, where toxic and non-toxic strains coexist within a Pacific clade and a clade grouping isolates with a broader geographic origin (Lilly et al., 2005). Similar findings have been obtained with other *Alexandrium* species (e.g., Kremp et al., 2009; Menezes et al., 2010). Cryptic diversity has been recorded also within the benthic dinoflagellate genus *Ostreopsis* that produces palytoxin or its derivatives; while Mediterranean and Atlantic strains of *Ostreopsis* cf. *ovata* seem to belong to the same genotype (Penna et al., 2010b), five distinct ribotypes, all toxic but one, have been recently identified along the Japanese coast (Sato et al., 2011). Cryptic and pseudo-cryptic diversity are also common features amongst diatoms, for which ‘species complexes’ have been described within various morpho-species (e.g., *Pseudo-nitzschia delicatissima* complex, *P. pseudodelicatissima* complex, *P. pungens*). The possibility to induce sexual reproduction in laboratory conditions allowed for testing the matches among morphological, phylogenetic, and biological species concepts, that is, to test reproductive compatibility amongst the different genotypes in sympatry, thus providing further support for species circumscription in this genus (Amato et al., 2007). A similar approach has been carried out by co-culturing the toxic *A. tamarense* ribotype I and the non-toxic ribotype III (Brosnahan et al., 2010). Cysts were formed in the breeding tests, proving that conjugation is still possible between the two genotypes; however, the F1 generation originating from the germination of the ‘hybrid’ cysts was not viable, proving that post-mating barriers exist and supporting the hypothesis that the two ribotypes might well be true biological species.

The examples mentioned above have various implications for HAB research and monitoring. The capability to model population dynamics and predict HAB events are based on our knowledge of the temporal and spatial distribution patterns of the species. In some cases, toxic and non-toxic cryptic species co-exist in the same area (e.g., Touzet et al., 2010a), although different photo-adaptation may lead to spatial segregation (Garcés et al., 2006). It is therefore important to foster integrated approaches for a better delineation of HAB species. Morphological investigations should be coupled with the use of different molecular markers, with investigations on physiological characters including the production of toxins or other secondary metabolites. Comparative studies should be carried out at a broad geographic scale. These kinds of studies will provide the required information to design molecular probes and/or identify suitable primers for rapid and reliable species identification.

Intraspecific diversity at the population level. The application of highly sensitive molecular markers to assess genetic diversity in marine microalgae at the

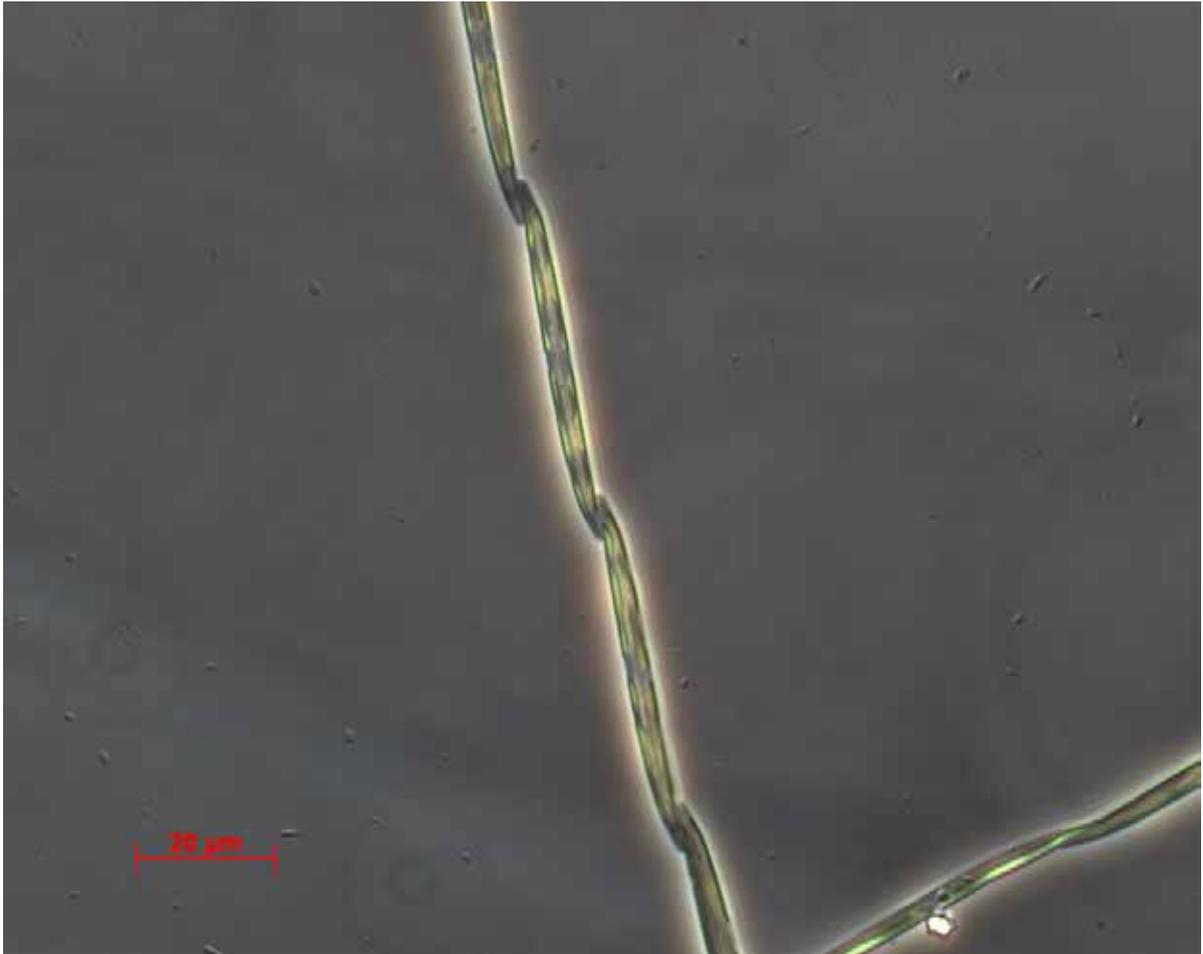


Figure 10. A light micrograph of *Pseudo-nitzschia multistriata* in confocal microscopy (the red is chlorophyll), cells are dividing and nuclei are stained with SYBR green (M. Montresor, unpublished).

intra-specific level, pioneered by Rynearson and Armbrust (2000), showed that: (i) a high level of genotypic diversity is present even within strains isolated in the same phytoplankton sample, and (ii) these different genotypes cluster into distinct populations structured at various spatial scales. Clade 1 of the diatom *Pseudo-nitzschia pungens* was considered cosmopolitan; however, when isolates obtained from various locations at a global scale were analysed with DNA microsatellites, different geographically distinct populations were detected (Casteleyn *et al.*, 2010). While genetic structure is evident at a large scale, no genetic structure was detected at the smaller scale of the southern North Sea Bight, notwithstanding the fact that strains were isolated in environmentally different locations (Casteleyn *et al.*, 2009). Three different populations have been instead recorded for *P. multistriata* in the Bay of Naples (Mediterranean Sea, Fig. 10), distributed with different ratios over a 3-year study (S. Tesson, unpublished data).

Alexandrium catenella, belonging to the toxic Asian ribotype IV, blooms in the Thau Lagoon (French Mediterranean Sea) and a recent introduction of the species was hypothesized. However, genetic characteriza-

tion of both Mediterranean and Japanese strains with microsatellite markers shows a finer level of genetic structure, with the Mediterranean population distinct from the Japanese one, which, in turn, was subdivided into two subpopulations. A distinct genetic pattern was detected at a relatively small scale for *A. tamarense*, when strains isolated from many coastal bays along the Japanese coast were analysed. The pattern was consistent with the geographical distances that separate the bays; in some instances, genetic flow amongst populations from different locations was detected, suggesting human-mediated translocation (Nagai *et al.*, 2007).

Two main hypotheses have been put forward to explain the recent spreading of the fish-killing dinoflagellate *Cochlodinium polykrykoides* along the Japanese and Korean coasts: either local populations bloom independently in coastal sites, or blooms are linked to the gradual dispersal of a single population by the Tsushima Current. The results of genetic analyses seem to support the second hypothesis, since the same population has been recorded along the western Japanese and the eastern Korean coasts, whereas a different population is present along the southern coast of Japan (Nagai *et al.*, 2009).

The diatom *Skeletonema marinoi* is responsible for spring and autumn blooms in the fjords along the Swedish coast and in the adjacent waters, but the two systems are inhabited by genetically distinct populations (Godhe and Härnström, 2010). In the fjord, the isolates collected in the plankton and those obtained from the resting stages in the sediments share the same genetic fingerprint, and sporadic intrusion of open sea populations seem not to affect the benthic reservoir over a long time scale. In fact, the analysis of strains obtained from a laminated core up to 100 years old, showed an almost stable population structure (Härnström *et al.*, 2011).

Microalgal species are constituted by different populations, possibly linked by a dynamic meta-population structure. Genetic structure can be detected at various spatial scales, often providing support to interpret population dispersal, colonization routes and biogeographic patterns. Particularly interesting are studies at the small spatial scale, where connectivity and/or isolation between different locations can be detected and linked with physical structures of the environment. A further expected outcome of these approaches is to shed light on the selective forces that act at the population level, on the specific adaptations of the different populations, on the mechanisms that regulate diversification and eventually speciation in unicellular planktonic organisms.

Genotypic diversity and phenotypic variability. Genetic and phenotypic variation in phytoplankton has

been acknowledged for a long time (Gallagher, 1982; Brand, 1989); however, there are few attempts to explore and quantify the links between the two traits at the population level. The analysis of a large number of isolates from a bloom of the toxic *A. tamarense* along the Scottish coast with two fine-scale molecular markers showed considerable heterogeneity; notable variation was also detected in two phenotypic characters, PSP toxin profiles and allelochemical properties, but without correlation with the genetic pattern (Alpermann *et al.*, 2010). A broad variability in various physiological traits, including autotrophic growth rates and ingestion rates, was detected amongst strains of the mixotrophic dinoflagellate *Karlodinium veneficum* isolated from a single bloom (Calbet *et al.*, 2011). High intra-specific diversity might be a winning strategy for unicellular microalgae living in an ever-changing physical, chemical and biological environment, where temporal variability in selecting pressures can favour the maintenance of diversity.

Our challenge is to explore and cluster the different levels of diversity into meaningful categories. Phenotypic plasticity somehow corresponds to the theoretical niche and it is important on the one hand to quantify it and on the other to infer the realized niche in the natural environment, also considering that the environment is changing. Coastal semi-closed ecosystems represent the ideal setting to test fine-scale population structure and diversity, offering a less complex system amenable to small scale investigations in time and space.

D. THE INFLUENCE OF PHYSICAL VARIABILITY ON HAB PATTERNS AND PERSISTENCE IN BAYS

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In the ocean, physical variability occurs on spatial scales ranging over 11 orders of magnitude, from the scale of an entire ocean basin (~10,000 km) to the smallest turbulent scales (~0.1 mm). The spatial patterns and temporal persistence of HAB events in bays and along the coast are influenced by much of this spectrum of physical forcing. Given that there is also significant interaction across different scales and significant biological/physical interactions at small scales, it is no surprise that general patterns of HAB events are so difficult to resolve. Even with the advent of high-resolution numerical models of coastal flow fields, prediction of HAB events in bays and along the coast remains an elusive goal.

The range of physical dynamics that influence pattern and persistence in coastal and bay HAB events is reviewed here. While not exhaustive, our summary is intended to clarify the physical forces that drive commonly observed HAB patterns and persistence in bays and in coastal waters. We emphasize the importance of field observations and see hope in new approaches for gathering biological and physical data at small spatial and temporal scales – and we suggest areas for future research.

Mesoscale influences (>100 km) Formation and advection of gradients in HABs

Mesoscale physical variability, most commonly observed in the energetic eddy field associated with large-scale oceanic currents, has a profound influence on the horizontal and vertical distribution of phytoplankton. Mesoscale variability is typically driven by large-scale flow instability, which often occurs due to an interaction of flow with large-scale coastal topography (e.g., headlands and ridges). Such mesoscale variability is essentially geostrophic (represents a balance between pressure gradient and effect of Earth's rotation), has no significant vertical circulation, and varies on large spatial and temporal scales. However, stirring by mesoscale flow can create variability in tracers (e.g., chlorophyll *a* or temperature) on scales smaller than the flow. In satellite images of chlorophyll *a* concentration and sea surface temperature, one can often see a turbulence-like array of scales within these mesoscale features. This is due to the fact that the shear (flow gradients) is primarily responsible for both the redistribution of

tracers and for enhancing spatial gradients in tracer concentration (Smith and Ferrari, 2009). In general, the horizontal scales of variability of shear are smaller than the horizontal scales of the mean flow, leading to an enhancement of gradients in tracers. Moreover, this process explains the tight spatial correlation found in satellite images between chlorophyll and other tracers such as temperature (Bracco *et al.*, 2009). The advection of these sharp shear-induced gradients by the mean flow can cause large, rapid changes in the local concentration of phytoplankton biomass, at times seen as a sudden onset of a HAB event in coastal waters.

Rossby-scale influences (~10 to 50 km) Water mass boundaries, frontal accumulation, and mixing refugia

The balance between baroclinic pressure gradients (due to horizontal gradients in density) and rotation occurs at smaller scales, the baroclinic Rossby radius of deformation, which is roughly between 10 and 50 km in the coastal ocean. This scale characterizes the curvature of the pycnocline and the scale at which strong vertical differences show up as significant horizontal differences in nutrient or phytoplankton concentrations. The outcropping of pycnoclines and sub-surface structure at the surface are seen as fronts, commonly found in association with wind-forced upwelling and at the seaward edge of freshwater or estuarine plumes in the coastal ocean. Fronts at this scale typically separate regions with distinct biological and physical signatures and may form a barrier to exchange between the water masses. These fronts and associated physical isolation are often found in association with bay-scale coastal topography, as is the case in upwelling shadows (Graham and Largier, 1997; Ryan *et al.*, 2008; Woodson *et al.*, 2009) and upwelling traps (Castilla *et al.*, 2002; Pitcher *et al.*, 2008). Physical isolation by a front and underlying pycnocline allows for the development of intense blooms by providing refuge from both advective and mixing losses and allowing for high growth rates. Mixing refuges are also found within fronts, where motile phytoplankton species may take advantage of convergent circulation to accumulate (thus not only countering dispersion, but actually re-concentrating plankton).

Sub-mesoscale influences (~1-10 km) Patchiness in nutrients and phytoplankton

As with larger scales, structure at this scale may be due to the interaction of coastal flows with topography, yielding eddies, jets or retention zones (e.g., Roughan *et al.*, 2005, 2006). Further, at this scale, meanders can develop on fronts, driving strong ageostrophic circulation (Capet *et al.*, 2008; Nagai *et al.*, 2008; Lévy *et al.*, 2009; Mahadevan *et al.*, 2010). Typically driven by changes in potential vorticity induced by frontal meanders, this ageostrophic circulation has a significant vertical component and, in numerical models, it has been shown to drive significant new production. Moreover, variability in frontal position and degree of horizontal

convergence, both influenced by sub-mesoscale processes, will affect the concentration and location of high biomass as described in the preceding section, and also the distribution of toxins. For examples of the impact of sub-mesoscale frontal variability in the distribution of HABs, see Fig. 15 in Ryan *et al.* (2010) and Fig. 10 in Fawcett *et al.* (2007). Understanding the role of sub-mesoscale processes on the pattern and persistence of high-biomass blooms and HAB events is hindered by the difficulties to-date in collecting *in situ* physical and biological data at sufficient resolution to test the hypotheses posed by numerical models (e.g., Lévy *et al.*, 2009). Nevertheless, the ubiquitous presence of sub-mesoscale variability in satellite images and the growing evidence for the importance of such processes in numerical models indicate that this is an important scale in HAB patterns and dynamics, and that *in situ* experimental approaches at this scale should be a focus of HAB research.

Pulsed cross shore transport of a Lingulodinium polyedrum bloom off San Diego by the internal tide, October 29/11 (A.J. Lucas, unpublished)

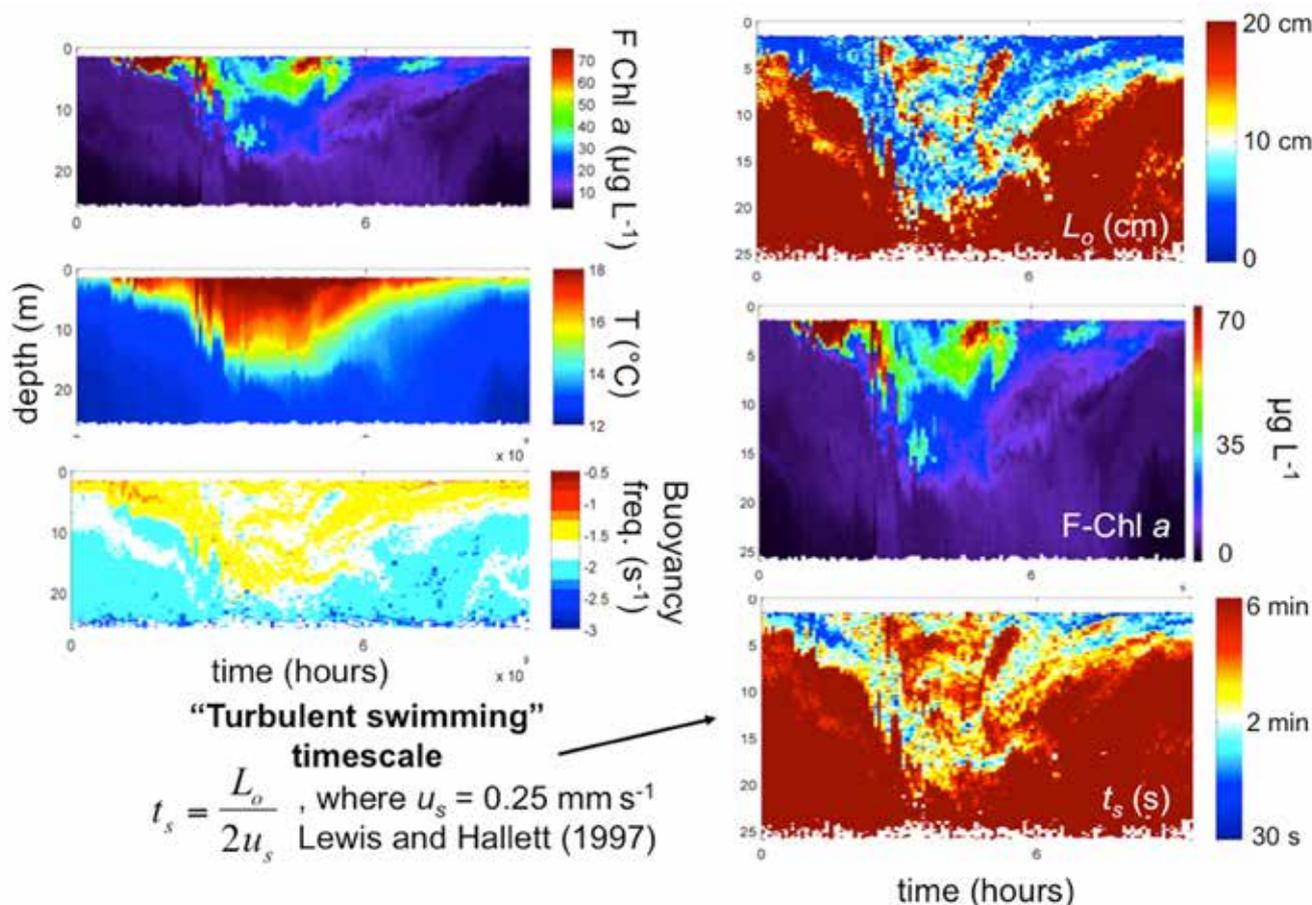


Figure 11. Approximately 12 hours of density and chlorophyll a fluorescence from a wave-powered profiling vehicle during an intense *Lingulodinium polyedrum* bloom off San Diego, California. The variability in temperature, buoyancy frequency, and chlorophyll are dominated by the oscillatory flow driven by the internal tide. The *L. polyedrum* distribution is extremely patchy vertically and horizontally and highly correlated with the physical variability. The length scale of turbulent scales can be estimated by the Ozmidov length scale, and assuming a constant, laboratory determined swimming speed, a time scale for a single phytoplankton cell to swim the Ozmidov length scale. Such high-resolution observations of small-scale spatial distribution are critical for HAB prediction.

High-frequency flow scales (~0.1-1 km) Vertical fluxes due to high-frequency motions

In coastal regions, circulation patterns at diurnal and higher frequencies are dominated by oscillatory flow, such as tides, inertial motions, diurnal winds and internal waves (e.g., Sharples *et al.*, 2009; Lucas *et al.*, 2011a,b; Lucas *et al.*, in press). Such flows can create strong transient horizontal and vertical gradients in blooms (Fig. 11), as well as drive vertical and horizontal nutrient fluxes that can maintain high-biomass events. The timescales of these high-frequency flows are of the same order or shorter than the time scales of physiological response in phytoplankton, photosynthetic variability, and population growth rates. When such variability is embedded within lower frequency forcing that alternatively favour high- and low-biomass events (e.g., upwelling/relaxation transitions), mixing due to these high-frequency flows

account for nutrient fluxes that can maintain high phytoplankton growth rates even during periods where the primary forcing (e.g., wind-forced upwelling) is absent (Lucas *et al.*, in press). These high-frequency flows are typically predictable, due to deterministic relations to tidal or diurnal forcing, suggesting that patterns in the distribution of phytoplankton driven by this forcing should be consistent between events and in principle amenable to prediction as fundamental understanding of the interaction of phytoplankton with high-frequency flows is developed.

Stratification and turbulence scale influences (~0.01-1 m) Interactions between physical and biological motions

There has been persistent recent interest in the generation of strong vertical gradients in phytoplankton concentration (i.e., “thin layers”). It is clear that both physical and biological mechanisms can cause such vertical organization, independently or acting together, depending on the physical setting and the phytoplankton taxa involved. Recent work has focused on understanding small-scale gradients in regions of elevated turbulence (as opposed to thin layers in quiescent waters), and it is now evident that spatially variable turbu-

lence can drive the accumulation of motile phytoplankton (e.g., gyrotactic trapping; Thorn and Bearon, 2010; Durham *et al.*, 2011; Hoecker-Martínez and Smyth, 2012). *In situ* studies are needed to assess the importance of this in HABs and phytoplankton blooms in general. High-resolution measurements during a dense *Lingulodinium polyedrum* bloom in southern California, where internal tide mixing controls cross-shore nutrient fluxes and phytoplankton transport, indicate that very different vertical stratification (and presumably turbulence characteristics) exists at different phases of the internal tide and in different vertical locations (Fig. 11). Thus, phytoplankton motility would be of variable effectiveness in such features. An analysis of “turbulent swimming timescales” (the time for phytoplankton to swim the length of a typical turbulent overturn) indicates that swimming will only be an effective strategy for controlling water column position in areas of high stratification, although benefits to the population may be seen in less stratified waters, given typical distributions of turbulent scales and swimming speed (Lucas and Largier, *unpublished*). These small-scale bio-physical interactions are clearly important in HAB ecology in general, particularly in the case of motile taxa, and deserve more attention (Fig. 12).

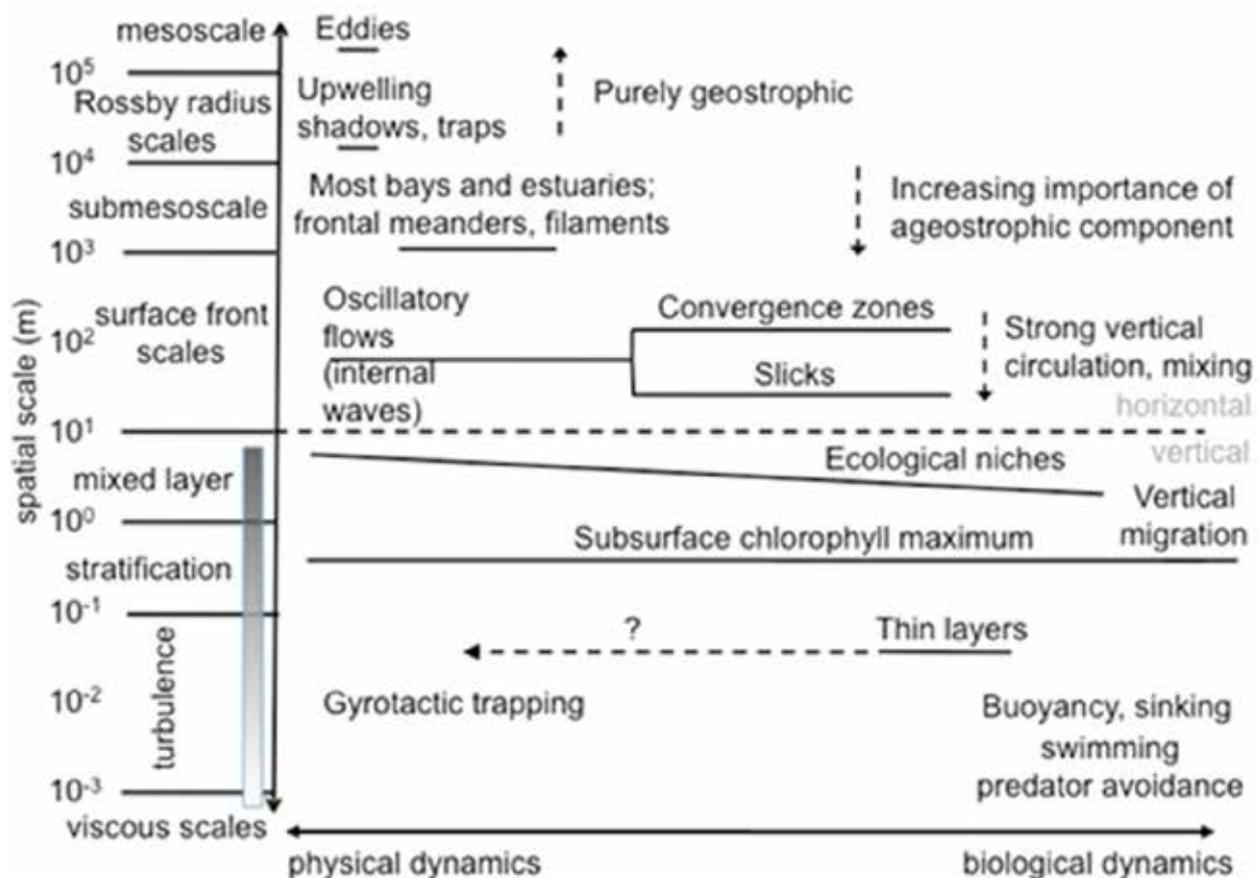


Figure 12. Time and space scales of the physical and biological dynamics that control phytoplankton pattern and persistence in coastal and embayment settings (from A.J. Lucas, unpublished).

Suggested priorities for future bay and coastal HAB research:

1. Emphasize sub-mesoscale horizontal scales

Even in open-coast settings, pernicious effects of HABs can be much localized. We need a better understanding of what sets horizontal scales of biomass (and toxicity) patchiness on scales of ~1-10 km.

2. Emphasize high-frequency flows (internal waves, tides, wind forcing)

High-frequency flows appear to play a primary role in HAB events. We require small-scale, finely-resolved, physical/biological measurements to assess

the importance of these flows to bloom maintenance (i.e., nutrient flux), bloom advection, and bloom termination (strong mixing, shearing, straining, shredding of blooms).

3. Emphasize concurrent *in situ* measurements of swimming and turbulence

From models it is evident that swimming strongly affects distribution (accumulation) and productivity (migration) of phytoplankton. There are very few instances of concurrent *in situ* measurements of turbulent microstructure and chlorophyll distribution – measurements needed to validate the role of swimming at ecological scales.

V – Update on Research Priorities for the Next Decade

Future research priorities should focus on improving our understanding of population dynamics of the most important HAB species. This will rely on the development of tools needed to detect and quantify different life stages (gametes and zygotes) in the natural environment, site-specific differences in sexual cycle strategies, and improved understanding of the role of cysts in the life cycle, as well as factors affecting the formation, deposition, transport and resuspension of cysts. When appropriate, models should be developed that simulate the entire life cycle, including the various life stages in the water and in the sediment. We need a better understanding of factors affecting bloom decline, including encystment and mortality factors such as grazing and parasitism. The putative role of allelochemicals, toxins and other secondary metabolites on the various stages of the life cycle

needs to be clarified. We need to continue exploring fine-scale population structure and diversity, in relation to small-scale environmental heterogeneity. In terms of physics, the sub-mesoscale horizontal scale needs more attention, since HAB events are often very localized and spatially constrained, particularly in fjords and coastal embayments. Future efforts should focus on high-frequency flows such as internal waves, tides and wind forcing, as these affect the small-scale coupling of physical and biological parameters. Finally, major efforts should be made to obtain *in situ* measurements as much as possible, rather than merely laboratory simulations. This applies to physical factors (e.g., turbulence) as well as to biological factors (rates of growth, cell swimming, encystment and excystment, etc.).

VI – Implementation Plan for these New Goals and Recommendations for the HAB community

Following the plenary discussion with all OSM participants, a consensus emerged that there is still a need for international coordinated research on the ecology and oceanography of harmful algal blooms: our understanding has progressed, but we are still far from being able to predict the occurrence/severity of these blooms or even to provide generally applicable causal explanations for bloom mechanisms and dynamics. Accordingly, there is also a perception that international cooperation based on a research agenda is needed more than ever and that GEOHAB and related initiatives are helping several countries to collaborate and better understand HABs, especially in water bodies shared by more than one country. GEOHAB remains the only global programme that provides an international scientific framework that addresses bloom dynamics and mechanisms rather than only focussing on monitoring, ecological consequences and human health effects. Hence, we recommend that international activities on the ecology and oceanography of HABs be maintained in one form or another after 2013.

Furthermore, we propose that a future agenda should focus on key questions, which should lead to more clearly identifiable deliverables. During the second OSM of the Fjords and Coastal Embayments CRP, we identified several major questions, which emanate from the general research themes identified in the first OSM in Chile, but where research presently indicates impediments or lack of knowledge that block progress in understanding HAB dynamics, with particular emphasis on coastal systems including embayments. Via this iterative process we identified actions that could help find answers to these questions in a relatively short time span (e.g., the next five years):

1. The “Cyst Connection”: the rates of cyst formation and of cyst germination need to be determined in the field, with proven methods, and factors affecting the viability and abundance of these life stages need to be better identified. Excystment and encystment are two key processes that deserve novel approaches and/or a re-thinking of what has been done up to now. A lot of information has been gained but it is also time to discuss if and how new technologies and approaches will help to address the same questions in a slightly different way. We recommend two action items:
 - a. A first workshop on methods to determine cyst germination rates, including a side-by-side comparison of existing tools in the field, with the eventual development of new tools to improve on the presently-available methods which are not considered satisfactory;
 - b. A second workshop on rates of encystment and on factors affecting the formation of cysts. Recent research suggests a much more complicated pattern than previously considered (SEED programme).
2. Models need to be developed that are more appropriate to small-scale environments generally characteristic of fjords and coastal embayment systems. These models should be coupled biological-physical-chemical models that incorporate the role of allelochemicals and toxins on cell interactions and terrigenous components other than limited to macronutrients. The models should also examine the role and influence of the benthic nepheloid layer on the availability of germinating cysts, either as a concentration mechanism favouring cell germination in an oxygenated layer, or preventing cells from reaching the upper layers where blooms develop. The following action item is proposed:
 - a. Discuss with the HAB modellers on the need to organise a workshop on small-scale models dealing specifically with coastal embayments and including pelagic and benthic coupling components.
3. Aquaculture is generally more prevalent in coastal than offshore environments, but the influence of aquaculture activities on the development of HABs is poorly known. One of the consequences of several aquaculture practices is to move the benthos up from the bottom to the water column (e.g., mussel lines) or to increase local eutrophication, with unclear consequences for the development of harmful algal blooms. We would like to initiate discussion with the CRPs on Benthic Algae and on Eutrophic Systems, to propose an eventual workshop on the changes that occur following the development of aquaculture activities in coastal environments and try to develop predictive capabilities regarding consequences to HABs in these environments.
4. We also recommend the continuation of research devoted to life history stages, particularly with respect to fish-killing algal species that cause

particular damage in coastal environments. Most of these are flagellates for which life stages have been incompletely described, hampering our understanding of the dynamics of these populations. Even for diatoms, understanding of the “resting” phase is still in need of research.

5. Finally, we recommend that emphasis be placed on climate change wherever appropriate for the

above recommendations, since the environmental modifications associated with climate change may be exacerbated in coastal environments. Long-term ecological research should be encouraged in this respect, in order to better identify the ongoing and historical changes, but with the view to providing the scientific basis for more efficient and cost-effective programmes.

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APPENDIX I – Open Science Meeting Programme

Tuesday 29 May 2012

Morning

Time	Speakers	Titles of Talks or Posters
8h30 – 9h00	Registration Suzanne ROY & Vera POSPELOVA	Welcoming Address & Scope of the Meeting
9h00 – 10h00	Esther GARCÉS (invited)	Diversity and complexity of the life histories of harmful algal species and the impact on their ecology (outcomes of the SEED project)
10h00 – 10h30	Break & Posters	Nicky HAIGH Monitoring HABs in the fjords and embayments of the west coast of Canada 1999 - 2011: the Harmful Algae Monitoring Programme and the BC salmon farming industry Faiza AL-YAMANI Assessment of harmful algal blooms (phytoplankton and phytobenthos) in Kuwait's marine environment Julia A. Busch, Allan D. CEMBELLA, Margarita Fernández-Tejedor, Jorge Diogéne, and Oliver Zielinski Comparative bio-optical studies and <i>Karlodinium</i> spp. at GEOHAB sites in the Ebro Delta, NW Mediterranean
10h30 – 11h30	Don ANDERSON, B.A. Keafer, K. Norton, D.J. McGillicuddy, R. He, C.H. Pilskaln, D. Couture, J. Martin and E. Vahtera (invited)	<i>Alexandrium fundyense</i> cyst dynamics in the Gulf of Maine: results from the ECOHAB-Gulf of Maine and GOMTOX programs
11h30 – 12h00	Paul J. HARRISON, J. Xu, K. Yin	Is there a link between N:P ratios and red tides in Tolo Harbour?
12h00 – 13h30	Lunch	
Afternoon		
13h30 – 14h30	Allan CEMBELLA (invited)	Allelochemical and toxic interactions: Effects on bloom phases and growth dynamics of HABs in small-scale coastal systems
14h30 – 15h30	Drew LUCAS & J. Largier (invited)	Transport and mixing: the role of physical forcing in coastal HAB dynamics
15h30 – 16h00	Break & Posters	
16h00 – 16h30	Hak Gyoon KIM, Chang Kyu Lee, Wol Ae Lim, Young Sang Suh	The change of dinoflagellate <i>Cochlodinium polykrikoides</i> bloom in association with oceanographic properties in Korean waters
16h30 – 17h00	Arielle KOBRYN and D. Varela	How to make a red tide harmful: the development of oxygen depletion during blooms of <i>Akashiwo sanguinea</i> in a Vancouver Island lagoon
17h00 – 17h30	Suzanne ROY, M. Parenteau, O. Casas-Monroy & A. Rochon	Introduction of harmful dinoflagellates through ship traffic: differences between the West and East coasts of Canada
19h	Dinner	

School of Earth and Ocean Sciences, University of Victoria, Victoria, Canada

Wednesday 30 May 2012**Morning**

Time	Speakers	Titles of Talks or Posters
8h30 – 9h30	Marina MONTRESOR (invited)	Genetic diversity and population heterogeneity: relevance to HABs in small-scale systems
9h30 – 10h00	Break & Posters	Deana L. ERDNER, M. Richlen & D.M. Anderson Diversity and dynamics of a widespread bloom of the toxic dinoflagellate <i>Alexandrium fundyense</i> Manuel BRINGUÉ, V. Pospelova & D. Pak Sediment trap study of dinoflagellate cyst production in the Santa Barbara Basin: implications for paleoenvironmental reconstructions and harmful algal blooms Stéphanie GRACIA, S. Roy & M. Starr Cyst mapping following a major bloom of <i>A. tamarense</i> in the St. Lawrence Estuary, Quebec, Canada Andrea PRICE & V. Pospelova Potentially toxic dinoflagellates and their cysts from Saanich Inlet, BC (Canada): a sediment trap study
10h00 – 11h00	Rhodora V. AZANZA (invited)	Harmful algal blooms in tropical embayments affected by monsoons
11h00 – 11h30	Cheryl GREENGROVE, S. Moore, J. Masura, B. Bill, L. Hay, E. Salathe Jr., N. Banas, N. Mantua, D. Anderson, V. Trainer & J. Stein	<i>Alexandrium catenella</i> in Puget Sound, WA USA: Cyst distribution and germination and cell growth rates and toxicity
11h30 – 12h00	Lincoln MACKENZIE	<i>Alexandrium catenella</i> blooms: a new problem for the aquaculture industry in the Marlborough Sounds, New Zealand
12h00 – 12h30	Vera POSPELOVA, S. Esenkulova, A.M. Price & K.N. Mertens	Insights on ecology of potentially toxic dinoflagellates and their cysts in British Columbian estuarine waters
12h30 – 13h45	Lunch	

Afternoon

13h45 – 14h45	All participants	Future Comparative Research Highlights & Recommendations
14h45 – 15h00	Hak Gyoon KIM	Announcing the upcoming 15 th ICHA Conference in Korea
15h00	End of Meeting	
15h30 – 17h30	GEOHAB committee	Closed Meeting for GEOHAB Report

APPENDIX II – Meeting Participants

Faiza AL-YAMANI

Kuwait Institute for Scientific Research, Salmiyah, Kuwait

Donald M. ANDERSON

Woods Hole Oceanographic Institution, Woods Hole, MA, USA

Rhodora V. AZANZA

The Marine Science Institute, University of the Philippines, Diliman, Quezon City, Philippines

Manuel BRINGUÉ

University of Victoria, B.C., Canada

Allan CEMBELLA

Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

Julie CORRIVEAU

Institut des Sciences de la Mer, Université du Québec à Rimouski, Rimouski, Québec, Canada

My Ha DAO

Singapore-MIT Alliance for Research and Technology (SMART), S16-05-08, 3 Science Drive 2, Singapore 117543

Deana L. ERDNER

University of Texas Marine Science Institute, Port Aransas, TX, USA

Svetlana ESENKULOVA

University of Victoria, Victoria, B.C., Canada, and Harmful Algae Monitoring Program, Vancouver Island University, Nanaimo, B.C., Canada

Esther GARCÉS

Institut Ciències del Mar, CSIC, Barcelona, Spain

Cheryl GREENGROVE

University of Washington, Tacoma, WA, USA

Nicky HAIGH

Vancouver Island University, Nanaimo, B.C., Canada

Paul J. HARRISON

University of British Columbia, Vancouver, B.C., Canada

Hak Gyoon KIM

Pukyong National University, 599-1, Daeyon-Dong, Nam-Gu, Busan, 608-737, Republic of Korea

Arielle KOBRYN

University of Victoria, B.C., Canada

Andrew J. LUCAS

Scripps Institution of Oceanography, La Jolla, CA, USA

Lincoln MACKENZIE

Cawthron Institute, Nelson, New Zealand

Julie MASURA

University of Washington, Tacoma, WA, USA

Marina MONTRESOR

Stazione Zoologica Anton Dohrn, Villa Comunale, Napoli, Italy

Vera POSPELOVA

School of Earth and Ocean Sciences, University of Victoria, Victoria, B.C., Canada

Andrea PRICE

University of Victoria, B.C., Canada

Suzanne ROY

Institut des Sciences de la Mer, Université du Québec à Rimouski, Rimouski, Québec, Canada

Diana VARELA

University of Victoria, B.C., Canada

APPENDIX III – List of Abstracts (in alphabetical order)

Faiza AL-YAMANI (poster)
Kuwait Institute for Scientific Research, Salmiyah, Kuwait

Assessment of harmful algal blooms (phytoplankton and phytobenthos) in Kuwait's marine environment

Microalgal blooms occur in Kuwait's waters year round. The ecology and taxonomy of phytoplankton as well as phytobenthos in Kuwait's waters including potentially harmful species have been studied during the past decade. Potentially toxic microalgae were found in the intertidal sediments of Kuwait. A total of 62 identified taxa can be categorized as potentially harmful species in the collected samples from Kuwait's waters and intertidal flats. Among them, 43 taxa are potentially toxic to humans and marine biota, and 10 taxa are potentially harmful to fish and invertebrates. Potentially toxic species are usually recorded in low densities in Kuwait's waters. However, the presence of a significant number of potentially harmful species in its phytoplankton can be regarded as a significant finding with potential hazards for humans and marine ecosystems. Documentation of this sporadic high abundance, together with significant species richness of the potentially toxic phytoplankton, requires more intensive and comprehensive studies of Kuwait's marine environment.

Donald M. ANDERSON¹, B.A. Keafer¹, K. Norton¹,
D.J. McGillicuddy¹, R. He², C.H. Pilskaln³, D. Couture⁴,
J. Martin⁵ and E. Vahtera⁶ (plenary speaker)

¹Woods Hole Oceanographic Institution, Woods Hole, MA USA

²North Carolina State University, Raleigh, NC USA

³University of Massachusetts Dartmouth, MA USA

⁴Maine Department of Marine Resources, Boothbay Harbor, ME USA

⁵Fisheries and Oceans Canada, St. Andrews, N.B., Canada

⁶City of Helsinki Environment Centre, Helsinki, Finland

***Alexandrium fundyense* cyst dynamics in the Gulf of Maine: results from the ECOHAB-Gulf of Maine and GOMTOX programs**

Cyst-forming dinoflagellates and other phytoplankton species with resting stages are responsible for HABs throughout the world. Some studies have examined linkages between cyst abundance and bloom timing and location, but these have typically been over small areas due to the difficulties and expense of mapping cysts over larger regions. Here we present the results

of more than a decade of studies of living *Alexandrium fundyense* cysts in the Gulf of Maine where seedbeds extend over hundreds of kilometres in the alongshore direction, and 50–100 km in the offshore. This talk will review interannual variability in cyst abundance and distribution based on a nine-year time series of regional cyst maps. We will highlight the strong relationship between the total numbers of cysts in the top centimetre of sediment with the extent of the *A. fundyense* bloom the subsequent season, and the lack of a relationship between the size of the regional bloom and the abundance of cysts present in sediments later that year. We will review studies of resuspended cyst abundance and dynamics, data on the erosion of cysts from surface sediments during storms, direct measurements of germling cell emergence rates, and numerical model results (hindcasts, nowcasts, and forecasts of *A. fundyense* population dynamics) based on cyst abundance and distribution. We also describe a "HAB Index" used to characterize the severity of PSP toxicity in two regions of Maine on a yearly basis and explore linkages between that variability and long-term patterns in the abundance of *A. fundyense* resting cysts. A relationship emerges that not only explains decadal-scale patterns of toxicity, but that also leads to a hypothesis that a regime shift recently occurred and that now the southwestern region has entered an era or interval that will have frequent, widespread, and high levels of toxicity, possibly for a decade or more. These and other studies relating to quantitative cyst dynamics were conducted through the ECOHAB-Gulf of Maine and GOMTOX research programs, each 5-year, multi-investigator studies of the large scale *Alexandrium* blooms in the region.

Rhodora V. AZANZA (plenary speaker)
The Marine Science Institute, University of the Philippines,
Diliman, Quezon City, Philippines

Harmful algal blooms in tropical embayments affected by monsoons

Harmful Algal Bloom (HAB) dynamics are less studied in tropical ecosystems/embayments. Most of the published works on HAB causative organisms in the area have dealt on their taxonomy, genetics, toxicity and bloom occurrences. From among the reported HAB organisms, *Pyrodinium bahamense* (var. *compressum*), which has caused a number of Paralytic Shellfish Poisoning (PSP) cases particularly in Southeast Asia,

has been the subject of several studies including HAB modeling. The dynamics of the bloom of other HAB organisms in the tropics like *Alexandrium* spp., *Gymnodinium catenatum*, among others, have received relatively little attention. Central to the understanding of the recurring blooms of dinoflagellate species are studies on the resting cysts in the sediments since this life stage can initiate the bloom in the affected areas. This paper will present the highlights of several studies done on the bloom dynamics of *Pyrodinium* and *Alexandrium* in areas where horizontal and vertical sediment/cyst studies have been done. The possibilities of seeding population coming from outside the embayments have also been considered. Evidences show that life cycle/strategies of these toxic dinoflagellates seem to fit the environmental changes in these monsoon-driven areas.

Manuel BRINGUÉ, V. Pospelova & D. Pak (poster)
SEOS, University of Victoria, B.C., Canada

Sediment trap study of dinoflagellate cyst production in the Santa Barbara Basin: implications for paleoenvironmental reconstructions and harmful algal blooms

A fortnightly sediment trap record spanning from May 1995 to March 1997 provides insights on the production of organic-walled dinoflagellate cysts in the highly productive waters of the Santa Barbara Basin (SBB), offshore Southern California. Marine productivity in the SBB is greatly influenced by wind-driven coastal upwelling, particularly intense from spring to early summer. During periods of active upwelling, dinoflagellate cyst export to the bottom waters are higher (up to 239,696 cysts m⁻² day⁻¹) compared to conditions of highly stratified surface waters (~ 60,000 cysts m⁻² day⁻¹). The assemblages are dominated by cysts of heterotrophic dinoflagellates *Brigantedinium* spp. (overall relative abundance of 62.4%) and *Echinidinium* spp. (13.7%). In total, 41 dinoflagellate cyst taxa are identified. Palynological and multivariate analyses show that *Brigantedinium* spp. is associated with active upwelling conditions, whereas *Lingulodinium machaerophorum* indicates “relaxed” upwelling conditions. Potentially toxic dinoflagellate species have been recovered in both thecal (e.g., *Prorocentrum micans*, *Lingulodinium polyedrum*) and encysted forms (*Lingulodinium machaerophorum*). The latter accounts for 5.0% of the total assemblage. *Prorocentrum micans* fluxes exceed 80,000 thecae m⁻² day⁻¹, typically in association with highly stratified, nutrient-depleted waters. These results have important implications for reconstructing HAB occurrences and climate history of the SBB from the underlying laminated sediments.

Julia Busch^{1,2}, A.D. CEMBELLA², M. Fernández-Tejedor³, J. Diogéne³ and O. Zielinski¹ (poster)

¹University of Oldenburg, Institute for Chemistry and Biology of the Marine Environment, 26382 Wilhelmshaven, Germany

²Alfred Wegener Institute for Polar and Marine Research, 27570 Bremerhaven, Germany

³IRTA, Ctra Poble Nou km 5,5, 43540 Sant Carles de la Rapita, Tarragona, Spain

Comparative bio-optical studies and *Karlodinium* spp. at GEOHAB sites in the Ebro Delta, NW Mediterranean

The two semi-enclosed embayments Alfacs and Fangar Bay in the Ebro Delta system, NW Mediterranean, are the major aquaculture sites in Catalonia. Due to the presence of phycotoxins, both bays are subject to occasional harvesting closures. In spite of their proximity and similar climatic conditions, Alfacs and Fangar Bay profoundly differ in Harmful Algal Bloom (HAB) dynamics. Circulation patterns and retention time of water in both bays are differently affected by winds, coastal currents and freshwater inflow from agriculture. Comparison of environmental forcing functions and bloom characteristics in both bays therefore provides the opportunity to improve our understanding of the key elements that drive bloom dynamics in time and space as a GEOHAB site. Harmful algal taxa and phycotoxins are monitored routinely within a governmental programme based upon weekly field sampling at representative stations in each bay. As yet, however, in the Ebro Delta there is no observational system for spatio-temporally enhanced monitoring of potentially harmful blooms. A sensor system based upon hyperspectral light-field measurements was evaluated in 2010 and 2011 as a tool for continuous monitoring of phytoplankton blooms in this semi-constrained environment.

Allan CEMBELLA¹, B. Krock¹, U. John¹, U. Tillmann¹, S. Wohlrab¹ & C. Legrand² (plenary speaker)

¹Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

²School of Natural Sciences, Linnaeus University, Kalmar 352 52, Sweden

Chemical ecological interactions in plankton assemblages affect bloom dynamics and biogeographical distribution – a critical role for HABs in semi-enclosed coastal ecosystems

Many models of HAB dynamics are predicated as physical descriptions of water mass characteristics and then incorporate biological parameters (growth rate, loss terms, life history transitions, behaviour). However, recent evidence suggests that chemical ecological interactions among planktonic members of marine food webs may also affect and even regulate “top down” pro-

cesses such as competition, predator-prey relationships and chemical communication within and among certain species. Among HAB taxa, members producing known phycotoxins were originally believed to produce these potent compounds as chemical defence against grazers in the “watery arms race”. Nevertheless, experimental evidence often contradicts or fails to support this hypothesis as a general mechanism. Furthermore, many emerging allelochemicals show potent biological activity against co-occurring species, but are structurally and functionally unrelated to classic phycotoxins. Here we explore the diversity of chemically mediated interactions in the plankton, in selective case studies with HAB taxa. We argue that the physical constraints on advection and dispersion of blooms in semi-enclosed systems such as fjords and coastal embayments offer maximum potential for expression and transduction of chemical signals in natural plankton assemblages. Studies of such chemically mediated phenomena in the GEOHAB comparative framework will assist in determining the magnitude of the effect on HAB dynamics and co-evolutionary processes.

Deana L. ERDNER¹, M. Richlen² & D.M. Anderson²
(poster)

¹University of Texas Marine Science Institute, 750 Channel View Dr., Port Aransas, TX 78373 USA

²Woods Hole Oceanographic Institution, MS#32, Woods Hole, MA 02543 USA

Diversity and dynamics of a widespread bloom of the toxic dinoflagellate *Alexandrium fundyense*

Widely distributed phytoplankton species were long considered to represent large unstructured populations. However, recent studies have shown that phytoplankton blooms contain an enormous amount of genetic diversity and that population structure exists over local to global scales. In this study, we focus on both temporal and spatial changes in the population structure of an extensive bloom of the toxic dinoflagellate *Alexandrium fundyense*. The bloom occurred in the north-eastern USA in 2005 and was notable for its intensity and duration, covering hundreds of kilometres and persisting for almost two months. Results indicate that this region harbours a single population of *A. fundyense* that includes at least two genetically distinct sub-populations. These subpopulations are associated with both temporal (early vs. late bloom) and spatial (northern vs. southern) stages of the bloom. Our results indicate that succession, presumably driven by environmental selection, occurs on the timescale of weeks during a continuous bloom. The effects of selection on population composition would be amplified if sexual reproduction were likewise influenced by environmental conditions. Differential growth and reproductive opportunity would synergistically reduce gene flow between the

sub-populations, thereby reinforcing population structure while maintaining the diversity of the overall regional population.

Esther GARCÉS¹ & D.M. Anderson² (plenary speaker)

¹Institut Ciències del Mar, CSIC, Barcelona, Spain

²Woods Hole Oceanographic Institution, MS#32, Woods Hole, MA 02543 USA

Diversity and complexity of harmful algal species' life history strategies and the impact on their ecology: outcomes of the SEED project

The SEED project was designed to increase our understanding of the extent to which environmental and physiological factors influence the non-vegetative life history stages of harmful algal species and the transitions between these and other stages, thereby contributing to the dynamics of harmful algal blooms (HABs) in marine, fresh, and brackish waters. The project focused on the life histories of some of the most important HAB species including freshwater (Raphidophyceae); estuarine (Cyanophyceae) and marine (Dinophyceae and Bacillariophyceae) examples and drawing on a wide range of locations (Western Mediterranean, Atlantic Ocean, North Sea, Baltic Sea and Swedish Lakes). All of these regions have heavy anthropogenic influences: fisheries, urban development, aquaculture and tourism, and are subject to the frequent occurrence of HABs, with a variety of detrimental impacts. SEED demonstrated that harmful algal events are widely divergent with regard to the life cycle mechanisms involved, and that the life cycles of several congeneric species show unexpected complexities. In this presentation, attention will be placed on singular and common patterns of response among species, the impact that life cycles have on the ecology of bloom events for a range of phylogenetic types, and the development of conceptual and numerical models of cyst-or spore-forming HAB species in coastal systems.

Stéphanie GRACIA¹, S. Roy¹ & M. Starr² (poster)

¹ISMER, Université du Québec à Rimouski, Rimouski, Québec, Canada

²Fisheries and Oceans Canada, Institut Maurice-Lamontagne, Mont-Joli, Québec, Canada

Cyst mapping following a major bloom of *A. tamarense* in the St. Lawrence Estuary, Quebec, Canada

In August 2008, a 600 km² large bloom of the toxic dinoflagellate *Alexandrium tamarense* caused the mortality of ten beluga whales, hundreds of seals and thousands of fishes, invertebrates and sea birds in the St. Lawrence estuary. The development of toxic blooms of this dinoflagellate species is linked to the presence of accumulation zones of resting cysts in sediments thus it has been hypothesized that cyst mapping can help

predict future blooms. The objectives of our study were to (1) determine the spatial distribution of *A. tamarensis* cysts in the coastal sediments of the St. Lawrence lower estuary in early summer 2009 and compare it with the spread of the vegetative bloom in August 2008 and with cyst maps determined 20 years ago in the same region, and (2) try to identify factors (including cyst viability) that can explain the observed cysts abundance. Our results show that cyst concentrations were negatively correlated with PSP levels from the same region, suggesting that cysts were formed and deposited mostly near the end of the bloom. The major bloom from August 2008 was not followed by particularly large cyst deposition or by any major bloom in 2009 in this region, calling for further tests of the cyst mapping hypothesis.

Cheryl GREENGROVE¹, S. Moore², J. Masura¹, B. Bill², L. Hay², E. Salathe Jr.³, N. Banas⁴, N. Mantua³, D.M. Anderson⁵, V. Trainer² & J. Stein² (talk)

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⁴University of Washington, Applied Physics Lab (APL), Seattle, WA 98105 USA

⁵Woods Hole Oceanographic Institution, MS#32, Woods Hole, MA 02543 USA

***Alexandrium catenella* in Puget Sound, WA USA: Cyst distribution and germination and cell growth rates and toxicity**

The Puget Sound *Alexandrium* Harmful Algal Bloom (PS-AHAB - <http://www.tiny.cc/psahab>) project is designed to: (1) map *A. catenella* cyst distributions in Puget Sound; (2) quantify the rates and timing of cyst germination; (3) quantify the growth rates and toxicities of vegetative cells; and (4) integrate the results from these three objectives into a hydrodynamic model forced by a downscaled climate model to determine current and future favourable habitat areas for *A. catenella*. Highest cyst abundances have been found in Bellingham Bay (northern) and Quartermaster Harbour (southern) in Puget Sound. Compared to a 2005 survey, the Bellingham Bay "seed bed" is new, whereas Quartermaster Harbour cyst concentrations have decreased by an order of magnitude. Preliminary results show no evidence for an endogenous clock controlling cyst germination. For salinities typical of Puget Sound, *A. catenella* growth rates are greatest over a broad range of temperatures. The upper end of this temperature range is much higher than the 17°C limit that was previously determined. Favourable habitat areas identified from the model match historical records of shellfish toxicity. Future climate scenarios indicate that blooms may occur earlier in the year and persist for longer. Future directions for PS-AHAB will be discussed.

Nicky HAIGH (poster)
Vancouver Island University, Nanaimo, B.C., Canada

Monitoring HABs in the fjords and embayments of the west coast of Canada 1999 - 2011: the Harmful Algae Monitoring Programme and the B.C. salmon farming industry

British Columbia's Harmful Algae Monitoring Programme has worked with the salmon aquaculture industry since 1999 to monitor HABs in the inshore areas of the west coast of Canada. In the past 13 years HAMP has accumulated a database of algal species and abundances, including harmful algae species concentrations, from weekly samples taken at 12-28 coastal sites around B.C.; these sites are generally at or near aquaculture operations, in protected channels and bays. During this time over 60 different sites were monitored, with nine sites monitored for eight years or more. HAMP has also increased the knowledge of ichthyotoxic algae species on the west coast: we can now identify at least 11 different species responsible for killing salmon at B.C. fish farms.

Paul J. HARRISON¹, J. Xu², K. Yin³ (talk)

¹University of British Columbia, Dept. Earth & Ocean Science, Vancouver, B.C., Canada

²Div. of Environment, Hong Kong University of Science & Technology, Hong Kong

³Rivers Institute, Griffith University, Nathan, QLD 4111, Australia

Is there a link between N:P ratios and red tides in Tolo Harbour?

It has previously been reported that the N:P ratio decreased from 20 to 11 while the number of red tide events increased from 10 to 20 from 1982 to 89 in Tolo Harbour, Hong Kong. When this time series was extended for another 18 years (1990 to 2007), no significant relationship was found between ambient N:P ratio and the occurrence of red tides. When this period was divided into pre- (before 1998) and post (after 1998) sewage treatment, the pre-treatment period was potentially Si limited since the sewage discharge is P-rich (~10N:1P) and has little SiO₄. This may be responsible for the increase in dinoflagellates compared to diatoms observed in the 1980s. Post-treatment, there was a 75% reduction in P and a 40% reduction in DIN which led to a significant increase in the N:P ratio (~10 to 30). The inner harbour is now potentially P-limited, but there was no significant change in the number of red tides during this pronounced increase in the N:P ratio from 1998-2007. In fact, the number of red tides started to decrease in 1991 for unknown reasons and have remained relatively constant to 2005.

Hak Gyoon KIM¹, Chang Kyu Lee², Wol Ae Lim²,
Young Sang Suh² (talk)

¹Pukyong National University, 599-1, Daeyon-Dong, Nam-Gu, Busan, 608-737, Republic of Korea

²National Fisheries Research & Development Institute, 409-1, Shirang-Ri, Gijang-Up, Gijang-Gun, Busan, 619-902, Republic of Korea

The change of dinoflagellate *Cochlodinium polykrioides* bloom in association with oceanographic properties in Korean waters

Cochlodinium polykrioides, a fish killing dinoflagellate bloom has been initiated in the central part of the South Sea, Narodo. This is the offshore region where the Tsushima warm current and eutrophic coastal waters are mixing and this lessens stratification. The subsequent bloom spread to neighbouring waters, oriented by winds and tidal currents mostly. This widespread bloom patch has been transported eastward in the same direction of Tsushima warm current, and then extended to the coastal waters of the East Sea. The dispersion has been affected by the oceanographic properties according to the year. Decadal results indicate that this eastward extension has been associated partly with the magnitude of Tsushima warm currents, and partly with the stretch of upwelling cold water plumes along the south-eastern coast of the East Sea of Korea. To clarify initiation, subsequent bio-geographical distribution and transport route of *C. polykrioides*, we need to understand the strength of Tsushima warm currents and subordinate oceanographic properties. In recent times, *C. polykrioides* blooms have become weaker and we are studying the reason why?

Arielle KOBRYN & D. Varela (talk)
University of Victoria, B.C., Canada

How to make a red tide harmful: the development of oxygen depletion during blooms of *Akashiwo sanguinea* in a Vancouver Island lagoon

Esquimalt lagoon is a shallow, tidally-influenced water body near to Victoria, B.C. that experiences a reoccurring red tide dominated by *Akashiwo sanguinea* (K. Hirasaka) (syn. *Gymnodinium sanguineum*). This species is not generally considered to be toxic, but in Esquimalt lagoon blooms of *A. sanguinea* are linked with oxygen depletion that is periodically severe enough to cause death of fish and benthic invertebrates. Blooms of *A. sanguinea* in Esquimalt Lagoon occur at the end of the growing season in a unique physical and chemical environment that has been shaped by the summer heat and a succession of phytoplankton communities that begins in the spring. This presentation will investigate the relationship between phytoplankton succession, nutrient uptake, and nutrient dynamics in Esquimalt Lagoon, focusing on the anomalous red tide that occurs when nutrients are very low. To conclude, we will dem-

onstrate how a temporal coincidence of specific tidal patterns, temperatures, and circulation/mixing regimes with the autumn red tide can create oxygen depletion events.

Andrew J. LUCAS & J. Largier (plenary speaker)
Scripps Institution of Oceanography, La Jolla, CA, USA

Transport and mixing: the role of physical forcing in coastal HAB dynamics

The physical flow field has a profound impact on the phenomenology and dynamics of harmful algal blooms (HABs) in coastal environments. The flow field in which HABs are embedded can be separated into advective and diffusive components (i.e., mean transport and mixing), each of which can impact blooms in a number of ways. The proximity of coastal and bottom boundaries introduce physical dynamics that are very distinct from those in the open sea. In particular, flow fields near the coast tend to be strongly sheared, both vertically and horizontally, and influenced by topography – lending a great deal of small-scale complexity to the nature of the flow and the distribution of tracers. The presence of larger coastal features can lead to retentive zones where flow residence times increase relative to the open coast (e.g., upwelling shadows, upwelling traps) or, with increased topographic enclosure, effectively isolate those waters from the open sea (semi-enclosed bays, fjords). In the latter case, HAB events can be of very long duration, and the pernicious effects of toxin accumulation and bloom-related anoxia can be extreme. Further, these retentive bays can act as refuges for HAB populations, which can expand rapidly into open coastal waters when the offshore conditions are suitable. In all cases, these shear-induced modifications of advective HAB pathways by the coastal and bottom boundaries are extremely sensitive to the vertical and horizontal position of the bloom in the water column. It is therefore true that even the weakest swimming behaviour can have a large effect on the distribution and accumulation of HAB-forming taxa. Further, frictional forces are large in systems with strong shear and may overwhelm the tendency of the fluid to remain stably stratified. Mixing then occurs, leading to irreversible fluxes of nutrients, phytoplankton, oxygen and other water properties. This vertical mixing is obviously important in nutrient and dissolved oxygen dynamics during HAB events. Although the swimming behaviour of some phytoplankton makes the understanding of small- and large-scale dispersal complex, it is becoming clear that resolution and quantification of vertical mixing and swimming are essential to understanding bloom dynamics and distribution. We will present the current state of understanding of the role of physical dynamics in bloom formation/maintenance/demise, point to new observation techniques that promise to increase our understanding of HAB dynamics, and outline a

box model framework for understanding the impact of transport and mixing on HAB dynamics in a variety of coastal embayments.

Lincoln MACKENZIE (talk)
Cawthron Institute, Nelson, New Zealand

***Alexandrium catenella* blooms: a new problem for the aquaculture industry in the Marlborough Sounds, New Zealand**

In early March 2011, for the first time in 18 years of intensive routine phytoplankton and shellfish toxin monitoring, saxitoxins were detected in mussels from Tory Channel, Queen Charlotte Sound. This signalled the beginning of a major bloom of *Alexandrium catenella*, which over the next 2 months spread throughout the Sound and resulted in lengthy shellfish harvest closures. *A. catenella* had never previously been identified in this region and the event appeared to be due to a new invasion. As a result of the bloom *A. catenella* resting cysts became widespread around Queen Charlotte Sound and were responsible for a repeat of the bloom at the same time of year in 2012. These blooms have been a good test of the newly established chemical PSP-toxin analysis programme (based on the Lawrence method) for saxitoxins, officially sanctioned and introduced for routine monitoring in 2010. It is feared that *A. catenella* will spread from Queen Charlotte Sound and become established in the main mussel growing regions of Pelorus Sound and Port Underwood which currently support a \$300 million/year aquaculture industry. There is an urgent need to improve current monitoring technologies, understand the autecology of *A. catenella* in the sounds and develop bloom prediction and tracking tools to enable management and mitigation of its effects in the future.

Marina MONTRESOR (plenary speaker)
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Genetic diversity and population heterogeneity: relevance to HABs in small-scale systems

In the last decade, molecular data provided evidence for the presence of cryptic or pseudo-cryptic species in many planktonic microorganisms, including taxa responsible for harmful events. Morphologically identical but genetically distinct strains have been reported for various ‘morphospecies’ and these results stimulated a more integrated approach to species circumscription. Phytoplankton species were considered to be con-

stituted by huge and largely unstructured populations, but the use of high resolution genetic markers revealed extensive genetic diversity also at the intra-specific level. Although information is still restricted at a handful of species belonging to distant lineages and characterized by contrasting life strategies, there is evidence for genetic structure at various spatial and temporal scales. As ecologists, we are concerned with the interaction between species/populations and their biotic and abiotic environment. It is therefore important to achieve a proper understanding of these biological units, in terms of their genetic fingerprint, their physiological and functional properties and their ecologically relevant traits. These studies will provide insights into speciation mechanisms, geographic patterns and possible dispersal routes of protists.

Vera POSPELOVA¹, S. Esenkulova^{1,2}, A.M. Price¹, & K.N. Mertens^{3,1} (talk)

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Insights on ecology of potentially toxic dinoflagellates and their cysts in British Columbian estuarine waters

We present results of the ongoing extensive investigation of the diversity and seasonality of dinoflagellate production in coastal and estuarine waters of British Columbia, Canada. Surface sediment and trap samples from the Strait of Georgia, as well as from Effingham and Saanich Inlets are examined in this work. Multi-year deployments of the traps resulted in the collection of high-resolution (bi-weekly) sequences of sediments which allows us to identify the seasonal and inter-annual variability of dinoflagellate cyst production in the Strait of Georgia and the Inlets. We document the composition, diversity, abundance and seasonal succession of dinoflagellate cyst taxa and examine these in relation to changes in freshwater input, sea surface temperature, salinity, and biogenic silica, based on the availability of such data. Toxic and potentially toxic dinoflagellate cysts and organic remains of the motile dinoflagellates are also recorded in the sediment trap samples. These remains included cysts of *Alexandrium* spp., *Protoceratium reticulatum*, *Gonyaulax spinifera*, as well as thecae of *Dinophysis acuminata* and *D. acuta*. Our sediment trap studies reveal valuable information on the duration and intensity of blooms of cyst-producing dinoflagellates, including toxic species.

Andrea PRICE & Vera Pospelova (poster)
University of Victoria, B.C., Canada

Potentially toxic dinoflagellates and their cysts from Saanich Inlet, B.C. (Canada): a sediment trap study

Dinoflagellates and their cysts were investigated in a high-resolution sediment trap study in Saanich Inlet (B.C., Canada) from November 2007 to February 2010. Samples were collected using a sediment trap deployed at ~97 m water depth. The sampling interval ranged from 0.5 to 19.5 days, allowing for a high-resolution study of dinoflagellate cyst production in relation to measured environmental parameters. Ninety-six samples were collected and a total of 42 dinoflagellate cyst taxa were identified. Cysts of toxic or potentially toxic *Alexandrium* spp. and *Protoceratium reticulatum* were found throughout the year, while cysts of *Gonyaulax* spp. showed greatest fluxes in winter. *Dinophysis* spp. were found predominately in the spring and summer, with fluxes reaching a maximum of ~410 000 thecae m⁻² day⁻¹. Seasonal and inter-annual variation in non-toxic dinoflagellate cyst species was also documented. Changes in cyst assemblages were found to reflect changes in environmental parameters such as sea-surface temperature, sea-surface salinity, solar insolation, river discharge, and biogenic silica flux.

Suzanne ROY, M. Parenteau, O. Casas-Monroy & A. Rochon (talk)
ISMER, Université du Québec à Rimouski, Rimouski, Québec, Canada

Introduction of harmful dinoflagellates through ship traffic: differences between the West coast and the East coast of Canada

We examined the diversity and abundance of dinoflagellates in ballast water from 63 commercial ships visiting the East coast and 71 from the West coast of Canada. Three categories of ships were compared, two which undertook ballast water exchange (BWE), trans-oceanics and coastal ships, and one category of coastal ships which is not required to do BWE because of the short distances covered. Results show differences between the two coasts: on the West coast, there are no significant differences for the concentration (cells per tank) and number of dinoflagellate taxa among the three categories of ships, but coastal exchanged ships carry more harmful species. On the East coast, ships with BWE show greater concentration and number of dinoflagellate taxa, particularly the trans-oceanics which bring more harmful species. Ballast water exchange seems to increase rather than decrease the abundance of these undesirable species. Coastal ship traffic should be of greater concern, as it may contribute to the spreading of harmful dinoflagellates notably from red tide coastal regions.

