GEOHAB

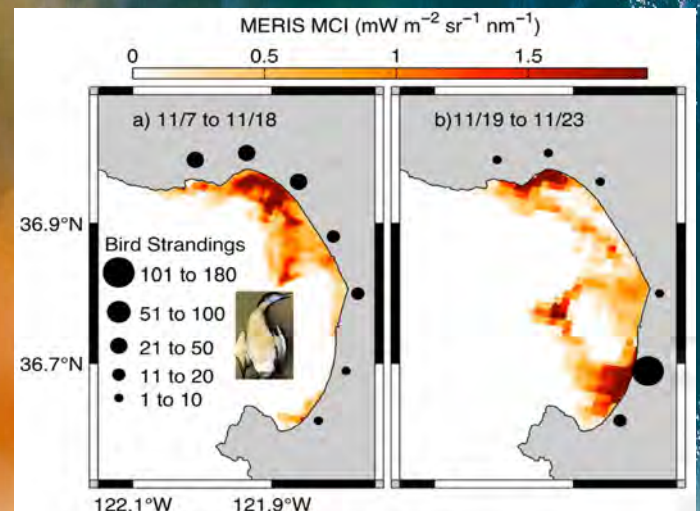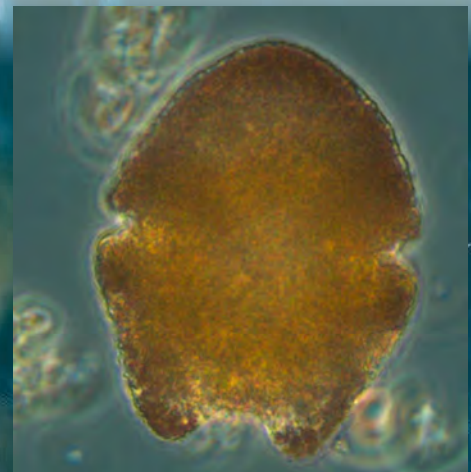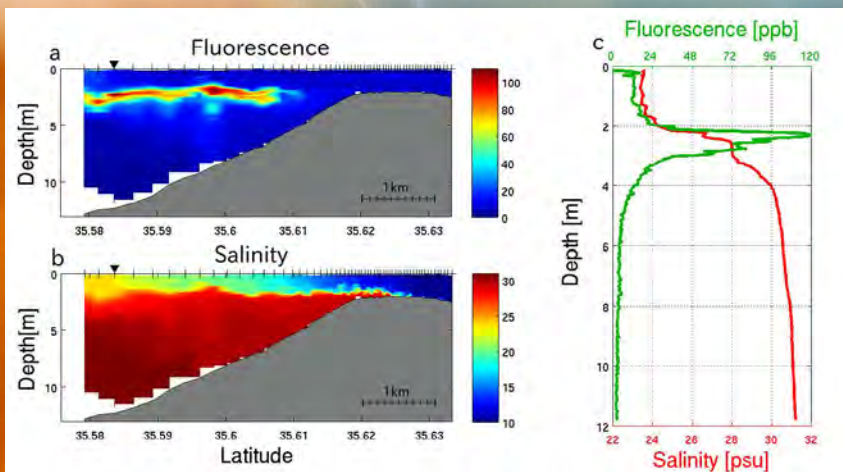## Global Ecology and Oceanography of Harmful Algal Blooms

GEOHAB CORE RESEARCH PROJECT:
HABs IN STRATIFIED SYSTEMS

"Advances and challenges for understanding physical-biological interactions in HABs in Stratified Environments"

A Workshop Report

International Council for Science
SCOR
Scientific Committee on Oceanic Research

UNESCO
United Nations
Educational, Scientific and
Cultural Organization

Intergovernmental
Oceanographic
Commission

GEOHAB

**GLOBAL ECOLOGY AND OCEANOGRAPHY
OF HARMFUL ALGAL BLOOMS**

**GEOHAB CORE RESEARCH PROJECT:
HABs IN STRATIFIED SYSTEMS**

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

**Workshop on
"ADVANCES AND CHALLENGES FOR UNDERSTANDING
PHYSICAL-BIOLOGICAL INTERACTIONS IN HABs IN
STRATIFIED ENVIRONMENTS"**

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This report is based on contributions and discussions by the organizers and participants
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http://www.geohab.info
http://ioc.unesco.org/hab
http://www.scor-int.org

Cover photos:
Background image shows clay being brought out in Jangsado Sea Park, South Korea, in an effort to control a local HAB outbreak. Some phytoplankton cells attach to the small clay particles and flocculate out of the water column to the seabed where the lack of light prevents further photosynthesis and growth. Courtesy of Oliver N. Ross.
Top left: Stratified conditions in Tokyo Bay, courtesy of Eiji Masunaga and Hidekatsu Yamazaki.
Bottom left: TurboMAP-G, courtesy of Hidekatsu Yamazaki.
Top right: Microphotograph of *Akashiwo sanguinea*, courtesy of Dr. Magda Vila (Institut de Ciències del Mar, CSIC).
Bottom right: Seabird mortality event linked to a senescent-phase bloom of *Akashiwo sanguinea* (adapted from Jessup et al., 2009).

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Workshop on "ADVANCES AND CHALLENGES FOR UNDERSTANDING PHYSICAL-BIOLOGICAL INTERACTIONS IN HABs IN STRATIFIED ENVIRONMENTS"

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EXECUTIVE SUMMARY

The overall objective of the Core Research Project (CRP) "Harmful Algal Blooms in Stratified Systems" of the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) programme was to determine the factors underlying the formation, maintenance and dissipation of harmful algal blooms (HABs) in stratified systems. In the last 20 years, investigations have been undertaken to further our understanding of the biological, chemical and physical mechanisms involved in the formation, maintenance, and dissipation of subsurface thin layers, which are often associated with stratified regions of the water column. Research has been focused on the relevance of physical structure for fundamental life processes of microorganisms (nutrient and light availability, reproduction, life cycle, ecologic interactions, etc.) and the relevance of thin layers for HABs. Advances in this area have depended heavily on the development of new and innovative instruments to observe and adequately sample these environments, as well as on improvements in numerical modeling techniques.

In August 2012, a workshop organized by the CRP "HABs in Stratified Systems" was conducted at the Monterey Bay Aquarium Research Institute (MBARI) to review our current understanding of the processes governing the structure and dynamics of HABs in stratified systems - related in particular to thin layers. Twenty-six scientists including engineers, physicists, biologists and modelers from all over the globe, working on the various aspects of phytoplankton dynamics in stratified systems, attended the meeting to provide an interdisciplinary understanding of this phenomenon.

This report summarizes the issues addressed by the participants during the workshop; these issues are structured in six main themes:

Theme 1) Physical Structure
Theme 2) Biological Structure: Rates and Interactions
Theme 3) Organism Behavior
Theme 4) Nutrients
Theme 5) Temporal Evolution of HABs in Stratified Systems and Thin Layers
Theme 6) Predictive Modeling

In addition to identifying the major scientific advances attained in the recent years, participants also identified gaps in knowledge, formulated open questions and elaborated on the priorities of these questions in order to orient future research for the improved modeling and prediction of HABs in stratified systems. Those questions constitute a 'roadmap' for the next 10 years of discovery, after the final meeting of GEOHAB (Paris, April 2013).

LIST OF ACRONYMS

|	
CRP	Core Research Project
GEOHAB	Global Ecology and Oceanography of Harmful Algal Blooms programme
HAB	Harmful Algal Bloom
IOC	Intergovernmental Oceanographic Commission
OSM	Open Science Meeting
SCOR	Scientific Committee on Oceanic Research
UNESCO	United Nations Environmental, Scientific and Cultural Organization
MBARI	Monterey Bay Aquarium Research Institution
EPS	Exopolymeric Substances

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 foster research on the ecological and oceanographic mechanisms underlying the population dynamics of harmful algal blooms (HABs). The ultimate goal of the GEOHAB research programme is to allow the development of observational systems and models that will enable prediction of HABs, thereby reducing their impact on the health of humans and marine organisms as well as their economic impacts.

To achieve its objective, the *GEOHAB Science Plan* (GEOHAB 2001) and the *GEOHAB Implementation Plan* (GEOHAB 2003) specified, among other activities, the formation of Core Research Projects (CRPs) to address comparative, integrative, multi-faceted and international research on HABs. Within the life span of the GEOHAB programme, five CRPs related to five ecosystem types (fjords and coastal embayments, upwelling, eutrophic, stratified, and benthic systems) were established. These CRPs were initiated through focused Open Science Meetings (OSMs) with wide international participation. At the OSMs, scientists discussed the state-of-the-art on the harmful events devel-

oped in each of the systems and highlighted the main questions that could be addressed in subsequent research efforts. The main outcomes from these meetings were research plans for each CRP, available in hard copy and electronic versions (see www.geohab.info). Once established, each CRP organized specific activities in order to implement the GEOHAB programme.

The CRP on HABs in Stratified Systems was initiated with the OSM held in Paris, 5-8 December 2005. Based on the contributions and the discussions among participants, a report (GEOHAB 2008) outlined the justification and research priorities for the study of the relationships between HABs and stratification. This cross-cutting CRP was focussed in the understanding of the small-scale hydrographic features which are encountered in upwelling and semi-enclosed coastal systems, affected by eutrophication or not. A particular emphasis was put on thin layers, where many harmful phytoplankton organisms can thrive. Furthermore, some approaches and available advanced instrumentation were identified during the meeting for their consideration in the following years. The key questions identified in that OSM (GEOHAB 2008) which have guided the research related to this CRP are listed in Box 1.

Significant progress has subsequently been made in evaluating the physical, chemical, ecological and bio-
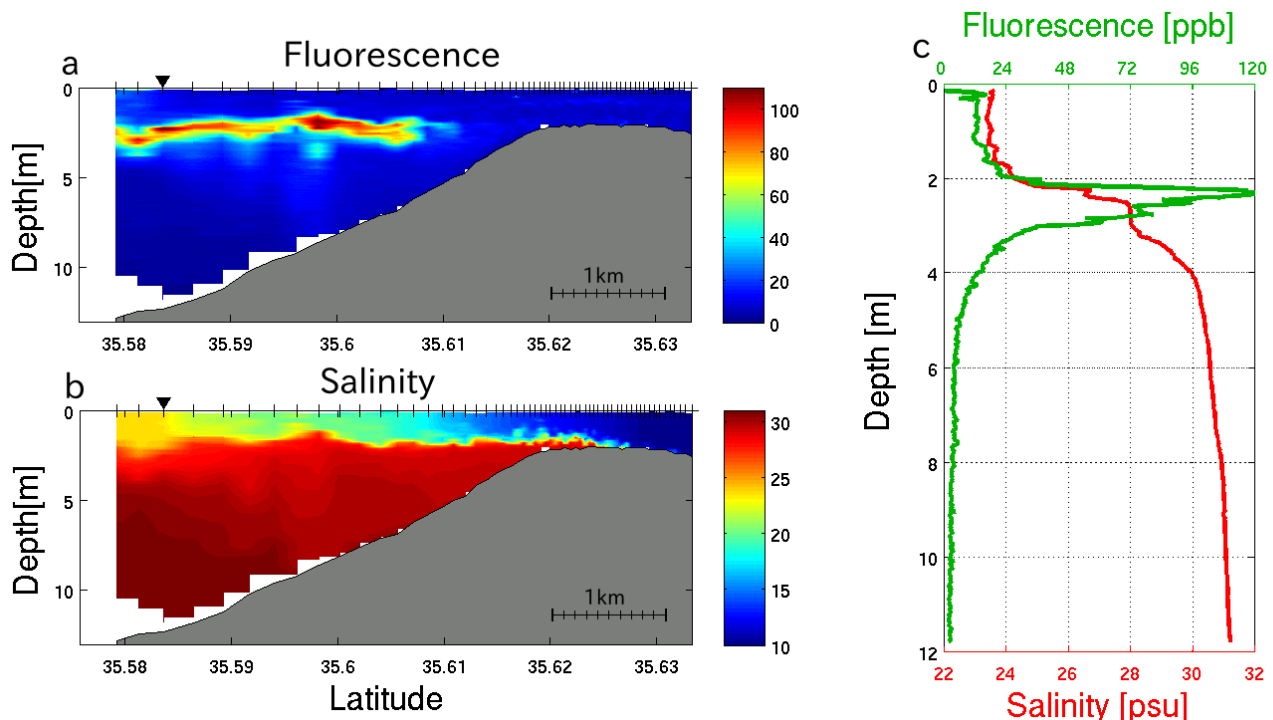
Representative profiles of fluorescence and salinity in a stratified system with a well-developed thin layer. Fluorescence (a) and salinity (b) observed on May 19, 2011 in Tokyo Bay. Panel (c) shows fluorescence and salinity profiles at the points marked by the dark triangle in a and b. From E. Masunaga and H. Yamazaki (2013).

logical processes that interact and operate over a large range of scales, and govern the structure and dynamics of HABs in stratified systems. This has been possible, in part, with parallel advances in technology and modeling tools. Indeed, in June 2009, during the GEOHAB Modeling workshop held in Galway (http://www.geohab.info), the participants discussed the progress and highlighted the scientific priorities that could be addressed using modeling tools. Outcomes of the workshop were written up in a new report (GEOHAB 2011) and a group of papers published in the *Journal of Marine Systems* 83 (special issue). More recently, as we approach the sunset of the GEOHAB programme, the Scientific Committee of this CRP organized a workshop to review the current understanding of HABs in stratified systems, and identify extant gaps in knowledge in order to orient future research towards improved modeling and prediction. With these aims in mind, a workshop was held at the Monterey Bay Aquarium Research Institute (MBARI), on 21-23 August 2012. The structure, list of participants and the content of the presentations can be found in Appendices I, II and III, of this report, respectively.

Box 1. Key questions synthesizing the scientific issues identified during the OSM in 2005 (GEOHAB 2008).

1. What are the turbulence length scales relevant to harmful phytoplankton and to the formation of thin layers? How do we measure turbulence at these scales?

2. What are the main processes controlling the population evolution of a given species, and how does their ranking vary over the time course of a bloom?

   2.1. Do HAB species migrate? Do they migrate vertically all the time or only at certain stages of the population growth or under certain hydrographical patterns?

   2.2. What are the gains of vertical migration? Acquisition of nutrients from deeper waters? Phototactic responses? Social behavior to promote sexual encounters? Aggregation around some unknown cues?

   2.3. Is the high cell density in the thin layer due to *in situ* division and passive accumulation in density discontinuities or does it result from aggregation?

   2.4. Is high density (aggregation) a pre-requisite for sexual recombination?

3. How can we quantify modifications in turbulence by phytoplankton through changes in the viscosity of its physical environment?

4. What nutritional opportunities do thin layers provide to phytoplankton, especially to the species selected within thin layers?

   4.1. Is growth rate in the thin layer higher due to a local enhancement in resources?

   4.2. What is the role of the microbial loop in thin layers?

5. What is the role of the retention of water bodies in the development of particular assemblages in the thin layers?

The purpose of this document, focused on HABs in stratified systems and thin layers in particular, is three-fold:

1) To summarize the main advances regarding HABs in Stratified Systems since the OSM in 2005. Our review, based on the scientific questions identified in Box 1, is presented in section III;

2) To compile scientific questions to be pursued within the next 10 years of research. The ideas that arose during the discussions in the 2012 workshop are presented in section IV; and

3) To show, in more detail, some of the most current research that has contributed to both the advances and the formulation of the future research steps. The abstracts and extended abstracts of the presentations given during the workshop are included in Appendix III.

The organizing committee acknowledges the contributions from scientists who participated in the Workshop (Appendix II) and who helped develop the ideas contained herein. The GEOHAB Science Steering Committee is also grateful to the organizations that contributed financially to the meeting, specifically the Scientific Committee on Oceanic Research (SCOR), the Intergovernmental Oceanographic Commission (IOC) of UNESCO, and the Monterey Bay Aquarium Research Institution (MBARI).
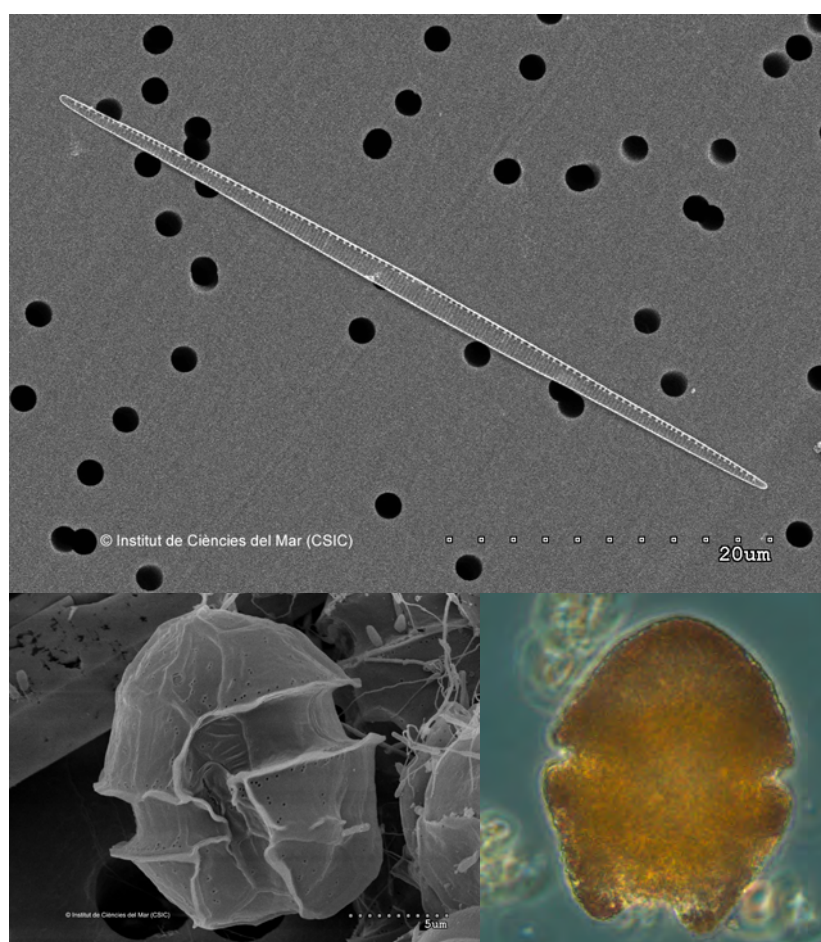
Three harmful taxa, Pseudo-nitzschia*,* Alexandrium *and* Akashiwo sanguinea*, often found in stratified systems and forming thin layers. Microphotographs provided by Dr. Lluïsa Cros, Dr. Magda Vila and J.M. Fortuño (Institut de Ciències del Mar, CSIC).*

II. THE GEOHAB APPROACH TO THE STUDY OF HABs IN STRATIFIED SYSTEMS

The overall strategy of GEOHAB is to apply a comparative research approach (GEOHAB 2001; Anderson et al. 2005). The comparative approach is the method of choice when controlled experimentation is not practical. The comparative method assembles observations and hypotheses needed for scientific inference by recognizing naturally occurring patterns, and temporal and spatial variations in existing conditions and phenomena. A comprehensive understanding of the population dynamics of HABs may be reached by comparing studies on the ecophysiology, biology, and spatio-temporal distribution of the main taxa involved in the harmful outbreaks, as well as the physico-chemical conditions accompanying and modulating them. The results from field and laboratory studies should be combined, if possible, with the application of models of comparable ecosystem types.

In accordance with the GEOHAB strategy, the approach of the HABs in Stratified Systems CRP has been comparative from the cellular to the ecosystem level. In the coming pages, the collected information is based on the general application of the comparative approach, including the identification of eventual divergences from predicted responses.

Application of the comparative approach highlighted the importance of stratified conditions in the occurrence of harmful algal outbreaks. Stratification may occur in a variety of ocean systems with different degree of enclosure, in conjunction with diverse nutrient and light availability conditions. The persistence and strength of stratification often appears as one of the most important conditions favoring phytoplankton development and in some cases the selection of noxious taxa as different as *Karenia* and *Pseudo-nitzschia*.

In addition, recent advances in technology have shown that the small density discontinuities supporting the existence of sub-surface biological layers, thin layers, are common in many different ecosystems. The organisms seem to respond to physical structure with shared living strategies that favor their proliferation within the thin layer. We now know that many HAB species exist in these sub-surface thin layers, which results in many challenges for the detection, monitoring and observation of such species.

III. RESEARCH PRIORITIES FOR UNDERSTANDING HABs IN STRATIFIED SYSTEMS:
WHAT HAS BEEN ACCOMPLISHED SINCE THE FIRST OSM IN 2005?

Generalities

As described in detail in GEOHAB (2008), the vision of HABs dynamics changed when advances in sampling and observation methods revealed that thin layer structures might be important to HAB ecology in many coastal environments. Discontinuities in the vertical structure of the water column exhibit distinct physical, chemical, and/or biological signatures from the surrounding water, with a significantly higher abundance of planktonic organisms compared to the water immediately above or below. Over the last 10 years, an increasing number of studies have revealed that harmful microalgae are often concentrated into thin layers (e.g. Gentien et al. 2005; McManus et al. 2008; Velo-Suárez et al. 2008). Thin layers have the potential to influence the transport of HAB populations, growth dynamics of plankton species, sexual reproduction (in particular gamete encounter rate in sexual cycles), organism behavior within the layer, and predation.

The horizontal scale of these layers can be of the order of kilometers, and they can persist for periods of days or longer (McManus et al. 2003; Churnside and Donaghay 2009; Cheriton 2010; Ryan et al. 2010; Sullivan et al. 2010b; Farrell et al. 2012). In the vertical, thin layers can be a few meters (<5m) thick (Dekshenieks et al. 2001; Sullivan et al. 2010a), although very high-resolution fluorometry has revealed even

thinner layers, at mm scales (Doubell et al. 2006, 2009, *in press*). Understanding the dynamics of HAB species in sub-surface thin layers has been difficult because traditional bottle samples at fixed depths often undersample or completely miss thin layers and it is not possible to monitor thin layers by traditional satellite remote sensing. Thin layers have usually been characterized on the basis of measurements of chlorophyll fluorescence, absorption, bioluminescence, acoustics and, more recently, direct water samples and cell counts.

With the instrumentation that is now available, it is possible to characterize the horizontal extent of thin phytoplankton layers in stratified environments. They have been quantified on scales of 1 to 100 km using tow-body systems like the Acrobat (SeaSciences) (Cheriton et al. 2010), autonomous underwater vehicles like the MBARI Dorado (Ryan et al. 2010) and, to a limited extent, gliders (Hodges and Fratantoni 2009). It is also possible to characterize thin phytoplankton layers on scales of thousands of kilometers by airborne LIDAR (Churnside and Donaghay 2009). LIDAR is not capable, however, of providing a concurrent measurement of the physical water column structure. Another approach to sampling thin phytoplankton layers in stratified environments over extended periods of time at a single location is through shipboard (Cheriton et al. 2009; McManus et al. 2012) and autonomous profiling (Sullivan et al. 2010b). Sullivan et al. (2010b) were
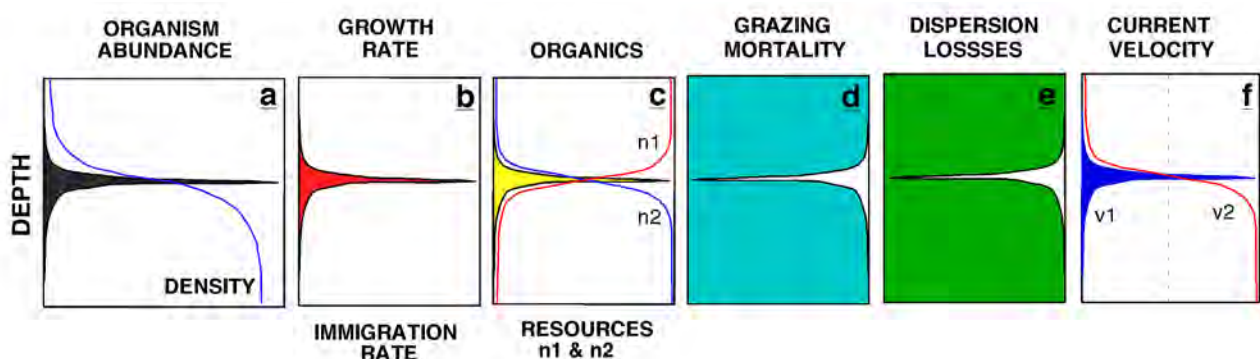

Figure 1. *General conceptual model of mechanisms controlling thin layers. Adapted from Donaghay and Osborn (1997).*

able to sample fine-scale vertical profiles (cm resolution) of biological, physical and chemical properties of the water column using an autonomous profiler over periods as long as three weeks, resulting in more than 1,000 profiles. The autonomous profiler data were supplemented with high-resolution ship based profiling and discrete water sampling for the identification of organisms.

The formation, maintenance, and dissipation of thin layers depend on a combination of physical, chemical, and biological processes (Figure 1). The physical factors most likely involved in the formation of thin layers are stratification, straining by shear, gyrotactic trapping and intrusions (Dekshenieks et al. 2001; Rines et al. 2002; Stacey et al. 2007; Ryan et al. 2008a; reviewed by Durham and Stoeker 2012). "Gyrotactic trapping" was suggested by Durham et al. (2009) as a mechanism driving thin layer formation by coupling cell motility with hydrodynamic shear. Regions of enhanced shear could disrupt vertical migrations of plankton cells and promote sharp-peaked cell accumulations. Biological processes promoting high cell concentrations include enhanced growth within the particular area near or at the thin layer, active aggregation by swimming (e.g. vertical migration towards the nutricline cf. Sharples et al 2001 and Ross and Sharples 2007), buoyancy control (through excretion of exopolymeric substances in some diatoms and physiological adaptations), grazer avoidance, suppression of grazing activity, and/or killing zooplankton and microzooplankton grazers within the layer (Derenbach et al. 1979; MacIntyre et al. 1995; Alldredge et al. 2002; Genin et al. 2005). A combination of migration and phototaxis may also create a thin layer (Yamazaki et al. *in press*). The production of allelochemicals—biologically active compounds eliciting specific responses in target organisms—has been identified as a chemical defense in some HABs species (e.g. Smayda 1997; Cembella 2003; GEOHAB 2013).

In the following sections, we summarize the recent findings regarding HABs in stratified systems, paying particular attention to thin layers. The points are grouped into six main themes that structured the workshop held at the MBARI in 2012:

Theme 1) Physical Structure

Theme 2) Biological Structure: Rates and Interactions

Theme 3) Organism Behavior

Theme 4) Nutrients

Theme 5) Temporal Evolution of HABs in Stratified Systems and Thin Layers

Theme 6) Predictive Modeling

Sections in each theme are headed by a key question identified during the OSM 2005 in Paris, that constituted the start point of the CRP "HABs in Stratified Systems". These key questions are denoted by bold italics.

Theme 1) Physical Structure

What are the turbulence length scales relevant to harmful phytoplankton and to the formation of thin layers? How do we measure turbulence at these scales?

From a physical point of view, the existence of an oceanic microstructure in the form of small-scale temperature and velocity variations has been known for several decades. It has been only recently, however, that the scientific community has linked their knowledge of small-scale physics to thin layers of plankton in the ocean. One way to infer oceanic turbulence is to use shear probes that are mounted on a free-fall profiler. Until recently, these instruments were only available to those people actually building the instrument. At present, commercial versions that exist in the community are the MSS (ISW Wassermesstechnik), MVP (Rockland scientific) and TurboMAP (JFE Advantech). Dissipation rates can also be calculated from measurements made by the Self-Contained Autonomous Microstructure Profiler (SCAMP, made by Precision Measurement Engineering) that measures temperature, salinity and pressure at 100 Hz. Recently, Yamazaki developed a free gridding quasi-horizontal profiler (TurboMAP-G, Yamazaki, pers. comm.) in order to sample more biological and physical data from thin layers (see the cover page). The wider availability of microstructure technology has allowed some advances in the understanding of thin layers within the context of fine-scale physical structure and dynamics. Some of these advancements are illustrated in the following paragraphs.

Steinbuck et al. (2009) investigated the dynamics of a phytoplankton thin layer in the context of vertical turbulent mixing. They detected a thin layer in the thermocline of a 20.5m water column between a strongly turbulent surface mixed layer and a weakly turbulent stratified interior. The differential mixing in combination with directed swimming established an asymmetric layer with a stronger Chl a gradient at the base of the layer than at the top. Steinbuck et al. (2009) applied a Eulerian advection-diffusion model and a Lagrangian particle-tracking model to explain the mid-column convergence needed to maintain the thin layer. They concluded that it was most likely swimming (by a motile dinoflagellate *Akashiwo sanguinea*) that balanced the diffusion by turbulent mixing on both sides of the layer and thereby maintained the observed Chl a gradients, as opposed to sinking or growth processes (see also Theme 2, for more examples on migration and thin layers). Ross and Sharples (2007) also examined the use of motility for creating and maintaining a layer of high cell concentrations in a tidally energetic shelf sea environment. They combined a Eulerian-Lagrangian approach where nutrients were modeled with a Eulerian advection-diffusion scheme with a Lagrangian random

walk model of the competition between directed motility and turbulence. The work showed that although both adjacent layers had high turbulent velocity scales, typical swimming capacities were sufficient to create and maintain a layer of high cell concentrations at the base of the thermocline. In a later study by the same authors (Ross and Sharples 2008), they found that the ability to swim is essential in stratified environments to maintain high cell concentrations in the thermocline, providing motile cells with a direct competitive advantage.

Yamazaki et al. (2010) conducted a 24-hour experiment at a station in Lake Biwa (Japan) in order to study small-scale biophysical structures. The surface water temperature remained at ~27ºC during the experiment, although slight warming/cooling took place during day/night (Figure 2a). The surface layer was well mixed down to approximately 12 m in depth (Figure 2b and c). The temperature below the surface mixed layer dropped sharply to < 10ºC at a depth less than 30 m (Figure 2a).
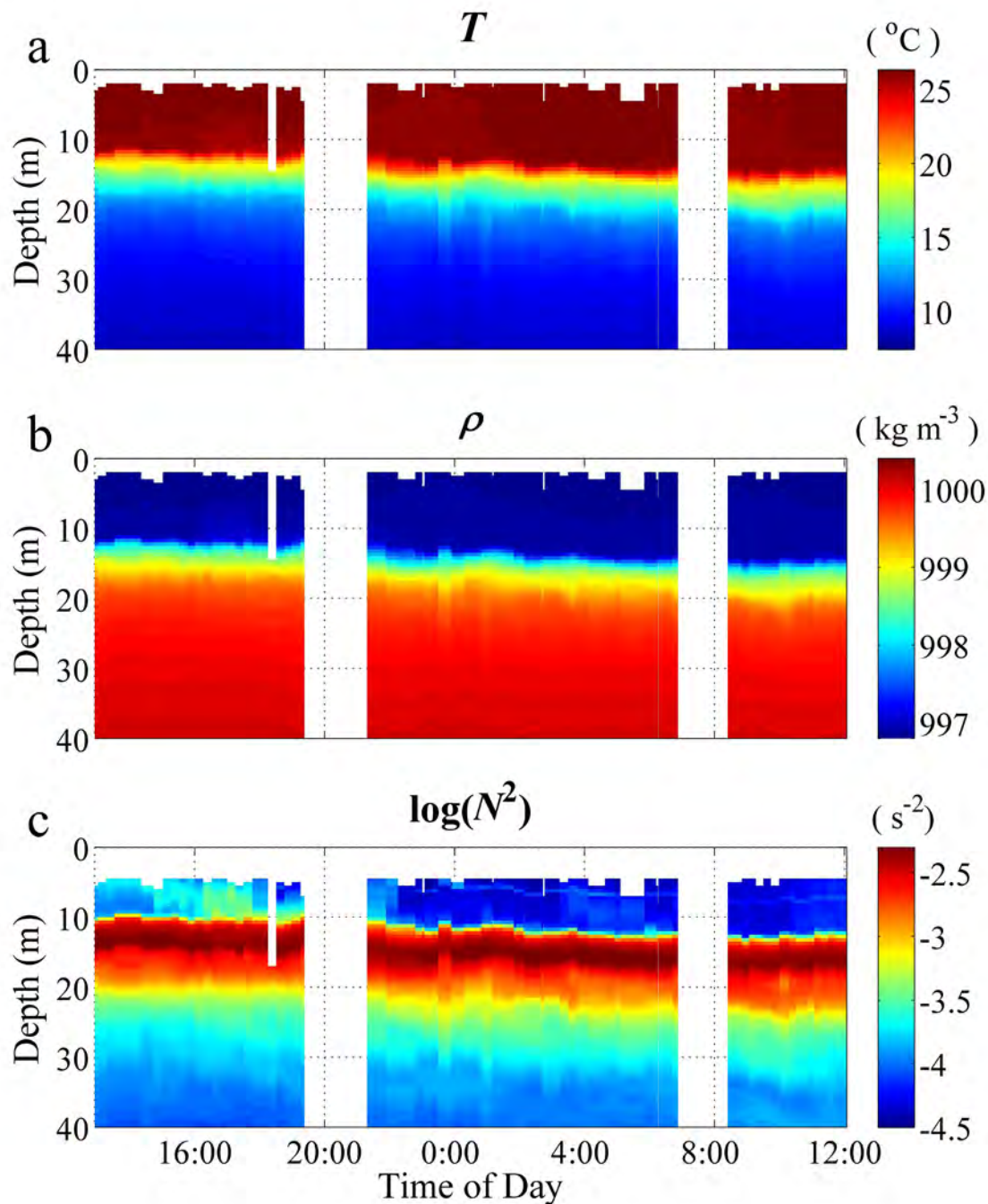

Figure 2. *Distribution of (a) temperature, (b) density , and (c) $\log_{10}$ of buoyancy frequency determined from TurboMAP-L profiling during the experiment. Profiles were obtained every 15 minutes. The surface mixed layer (epilimnion) is roughly 11 m at the bigginning of the experiment and deepened slightly toward the end of the experiment (redrawn from Yamazaki et al. (2010).*

Although the winds were weak, the surface mixed layer showed high turbulent intensities that formed an active surface mixing layer (Figure 3). The turbulence kinetic energy dissipation rate reached almost 10^{-6} W kg^{-1} during the night, consistent with nighttime convective mixing (Nagai et al. 2005; McManus et al. 2012). The turbulence level dropped after midnight, but still remained relatively high throughout the experimental period. Another strongly turbulent layer, the subsurface mixing layer, occurred below roughly 20 m depth.

According to the LED flourescence probe that was mounted on TurboMAP-L, the chlorophyll level exceeded 1 µg L^{-1} throughout the water column. A maxi-

mum occurred around 18 m depth, and the peak values increased during the night (Figure 4). This maximum occurred in a "thin" layer that did not exceed a few meters thickness. However, this layer does not meet the conventional definition of a "thin layer" which are typically associated with a 3 to 5-fold change in biomass (Dekshenieks et al. 2001). This may be due to the fact that the empirical definition of the thin layer is based on oceanic observations in which the background chlorophyll level is relatively low. In contrast, inland freshwater systems often exhibit high background chlorophyll concentrations, such as the current Lake Biwa case (see also Sullivan et al. 2010a).
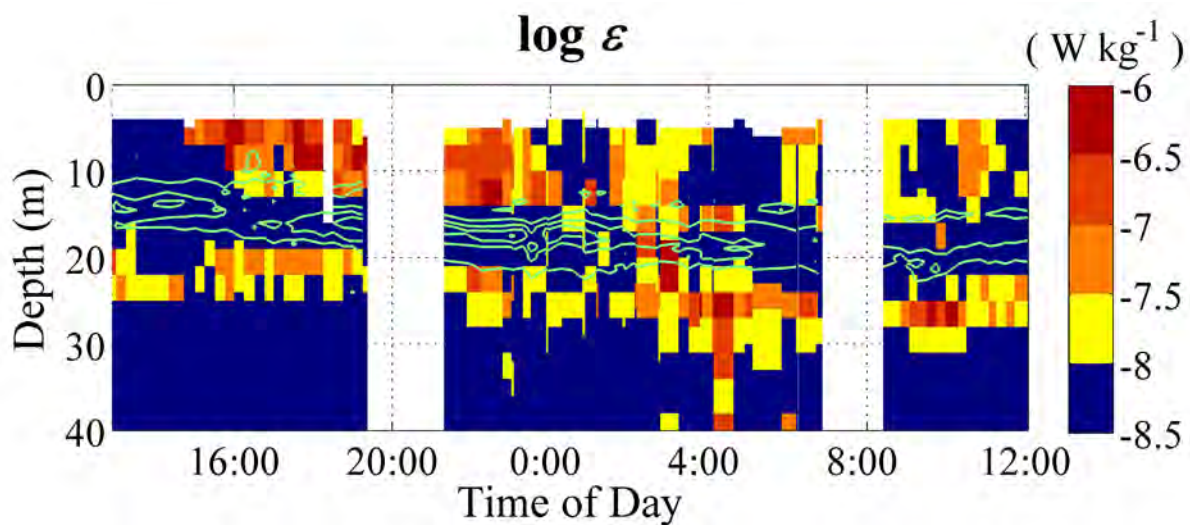
Figure 3. *The distribution of the rate of the kinetic energy dissipation (W kg⁻¹) is depicted with contours of chlorophyll concentration (1.5-2.8 µg•L⁻¹ range). The local peak in chlorophyll clearly appeared in the low dissipation rate region. All data were measured by TurboMAP-Ln (redrawn from Yamazaki et al. 2010).*
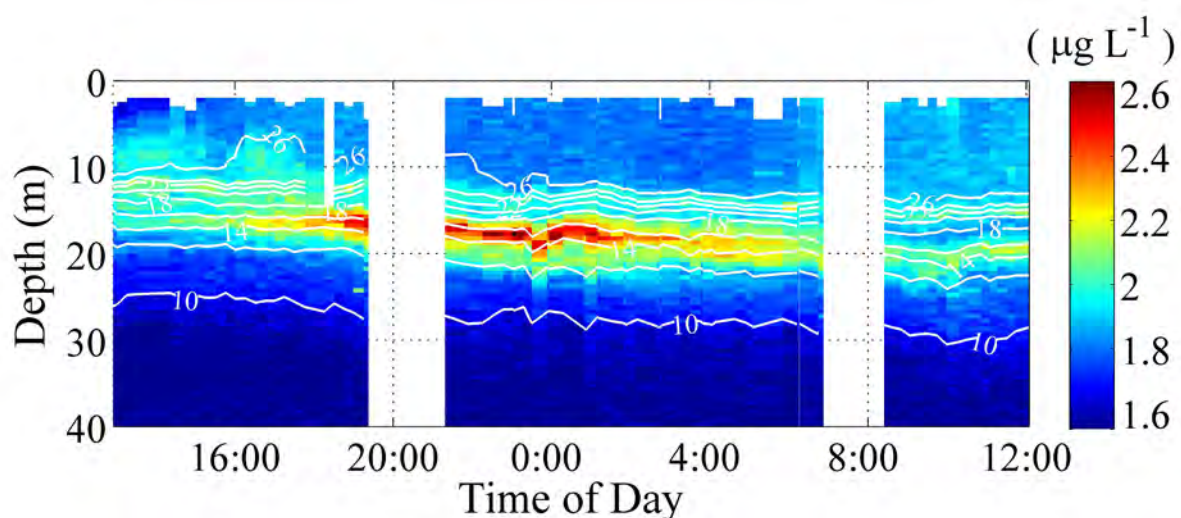
Figure 4. *The chlorophyll distribution (µg L⁻¹) and temperature structure (contoured in ºC) measured over the survey period. A pronounced chlorophyll peak layer appeared in the strongly stratified water region of the water column where the temperature dropped from 18 to 14º C. All data were obtained from TurboMAP-L deployed at 15 minute intervals (redrawn from Yamazaki et al. 2010).*
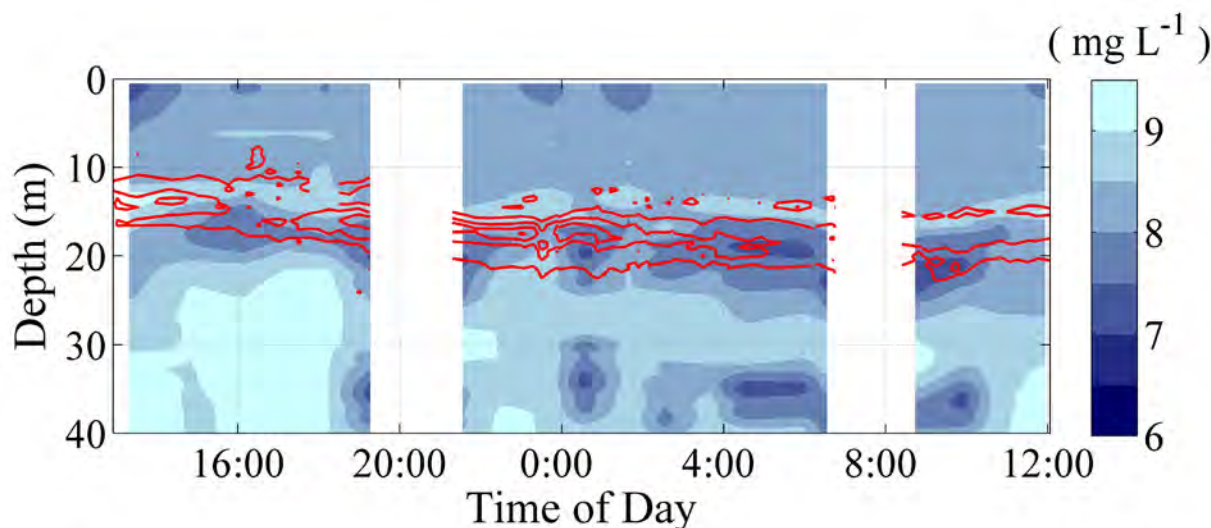
Figure 5. *The oxygen distribution depicted with chlorophyll contours. (1.5-2.8 µg•L⁻¹ range, as in Figure 4). The oxygen data were obtained from hourly F-Probe profiling and chlorophyll data were measured using TurboMAP-L (redrawn from Yamazaki et al. 2010).*

Three distinct layers appeared in the subsurface stratified layer (metalimnion). A local maximum oxygen layer was observed just above a local minimum oxygen layer (Figure 5).

How can we quantify modifications in turbulence by phytoplankton through changes in the viscosity of its physical environment?

During the last 25 years numerous studies have been devoted to the understanding of how viscosity and other rheological properties influence and are influenced by several aspects of plankton dynamics, including HABs (as reviewed by Jenkinson and Sun 2011). Seawater viscosity is comprised of a Newtonian, perfectly dispersed component contributed by the water and salts, plus a non-Newtonian, less well dispersed component due to more or less lumpy organic exopolymeric substances (EPS) derived mainly from phytoplankton. Dense phytoplankton patches are often associated with increased viscosity as well as elasticity of the seawater or lake water (Jenkinson and Sun 2011, and references therein; Seuront et al. 2010). Based on the gained knowledge including the few available measurements of rheological properties of some algal cultures and phytoplankton blooms (Jenkinson 1993; Jenkinson and Biddanda 1995), Jenkinson and Sun (2011) recently modeled how EPS could change pycnocline thickness. The authors emphasized the need for new measurements at natural oceanic concentrations as a function of length scale and future experimental and *in situ* investigations on the modulation by phytoplankton blooms of pycnocline dynamics. Comparison of viscosity at length scales from 0.35 to 1.5 mm in HAB cultures with that in reference medium have shown that viscosity in culture can vary with length scale. It can be increased in the presence of plankton, presumably due to EPS. However, Jenkinson and Sun (*in press*) showed that it can also be decreased in the presence of plankton, perhaps due to the presence of hydrophobic surfaces of the plankton or the EPS or both.

Other possible effects of biology on physics could be the generation of turbulence by organisms in the water column, turbulence which may potentially mix out fine-layered structures (Huntley and Zhou 2004; Kunze et al. 2006; Katjia 2012). This may be a key mechanism by which nutrients are periodically transported across the pycnocline of strongly stratified systems. Clearly, this mechanism depends upon the size of the organisms involved (Huntley and Zhou 2004; Visser 2007).

What is the role of the retention of water bodies in the development of particular assemblages in the thin layers?

Aggregations of plankton in the pelagic zone can be the result of a local reduction in horizontal and vertical dispersal. In the open waters off southern Ireland, a small patch of 7 km in diameter and ≈ 3m thickness at 20m depth was followed by researchers during one week in July 2007 and its trajectory was coherent with a narrow westward current (Farrell et al. 2012). This patch contained mostly *Dinophysis acuta* cells in high density (10^4-10^5 cells L^{-1}), which are usually ubiquitous throughout the coastal region of southern Ireland in summer but in much lower (10-10^2 cells L^{-1}) density.

In the Bay of Biscay, retentive structures in the form of gyres have been detected at mid-depth which correspond to a local accumulation of *D. acuminata*, in the pycnocline, (Gentien, unpublished data). These structures have been predicted by MARS3D simulations of the Bay of Biscay (Lazure et al. 2009). A prediction scheme for the onset of the Dinophysis season has been established, based on the existence of these eddies and their subsequent advection (Xie et al. 2007). Such patches may act as incubators for one population and their track will determine the delivery of toxins to the coast. This approach may be applicable to other species. The size of retentive structures may vary depending on the species and environments considered: in the case of *K. mikimotoi*, the patch size depends on the occurrence and magnitude of shear in the pycnocline.

In Alfacs Bay, a small semi-enclosed microtidal embayment in the NW Mediterranean Sea, recurrent HAB outbreaks have been associated with high-retention areas in the bay's interior, which are related to the flow regime and the meteorological forcing. Stratification, caused by freshwater runoff from the adjacent rice fields, competes with wind-induced vertical mixing to control the residence time of cells within the bay and eventually the occurrence or absence of HAB events (Berdalet et al. 2013; Artigas et al. *in press*). Retentive environments, in which residence time is locally enhanced, create distinct physical conditions, which in turn strongly influence the ecology of HAB species. One key physical condition often enhanced by retention is vertical density stratification.

Inshore areas of coastal upwelling systems in the lee of headlands have some of the important ecological consequences of retention and associated stratification. The process of coastal upwelling introduces destratification to coastal waters. Coastal geomorphology creates spatial heterogeneity in the exposure of coastal areas to the forcing and consequences of upwelling. 'Upwelling shadows' can develop in the lee of headlands and within bays, where surface wind forcing is relatively weak and retentive oceanic circulation develops (Graham and Largier 1997). Enhanced residence time within these locales affects not only the physical environment, for example, stratification caused by the cumulative heating from solar energy, but also the plankton populations, which can develop to relatively great abundance and maturity. These conditions permit incubation of phytoplankton blooms, including those of thin layer-forming HAB species (McManus et al. 2008; Jessup et al. 2009; Ryan et al. 2010). Further, HAB populations retained within such locales provide seed populations for subsequent blooms (Ryan et al. 2008b, 2009).

The toxic bloom of *Pseudo-nitzschia* that occurred in Todos Santos Bay (TSB), northwestern Baja California, Mexico, in April 2007 (García-Mendoza et al. 2009) would have also been favored by retention in that upwelling area. A numerical-modeling study of the water circulation dynamics (Rivas et al. 2010) showed that the factors triggering such a bloom had their origin in northern upwelling regions (Southern California Bight) about two weeks earlier. Thereafter, the bloom would have been transported by the circulation and wind regime and, accumulated in a retention zone of the eastern part of the Bay.

Theme 2) Biological Structure: Rates and Interactions

In order to understand the population dynamics of specific HAB species we need to be able to estimate changes of the cell populations, and in particular *in situ* growth rates (μ). When comparing the available methods for measuring growth, two features need to be considered: the cell number detection limit and the

species. The first of these does not present a problem in high-biomass harmful events such as those caused by *Pseudo-nitzschia* spp., *Noctiluca* spp., *Phaeocystis* spp.. Unfortunately, some of the most harmful organisms are often present in very low densities and constitute a small percentage of the overall community. For instance, toxicity is often detected in bivalves in the Ría de Vigo concurrently to very low cell abundances of *Dinophysis* spp. (10^2 cell L^{-1}) and *Alexandrium* spp. or *Gymnodinium catenatum* (10^3 cell L^{-1}). This introduces difficulties in quantifying both abundances of these species and their changes over time. Currently, the main challenge is to quantify cell abundance and μ in targeted species.

Quantifying Cell Abundance: To predict HAB population trajectories, it is important to characterize the spatial heterogeneity in cell abundance (patchiness). This requires methods that permit a synoptic description of the cell abundance of the targeted species. In particular, *in situ* imaging approaches can derive quantitative information about not only HAB phytoplankton populations, but also the zooplankton grazers involved in controlling bloom growth and transferring carbon and toxins into the food web.

As one example Jaffe et al. (1998) developed, deployed, and analyzed data from FIDO-Phi, a free descent autonomous profiler that was equipped with a Planar Laser Fluorescent Imaging system (Figure 6). Analysis of the fluorescent images of approximate size 10cm x 15cm gave particle size distributions as a function of depth. As a result of this analysis, Prairie et al. (2010) introduced the concept of "cryptic peaks" which are large increases in the fluorescent signatures from individual fluorophores, and assumed to be phytoplankton of sizes greater than 20 – 100μm. Such peaks would not be identifiable in the bulk fluorescent measurements, hence the label "cryptic".

Most recently, Jaffe's group has been developing *in situ* microscopes that are essentially long working distance microscopes that can be deployed underwater. More information can be found in the extended abstracts of this report (Appendix III).

Another recently developed imaging instrument is the LISST-HOLO (Sequoia Scientific). This holographic system provides detailed (4.4 micron pixel) images of plankton across the size range of approximately 25 to 2500 microns (Figure 7). This sensor has been deployed on an autonomous underwater vehicle to acquire densely sampled plankton images that define patchiness, and synoptic maps of the particle size distribution. For example, in a survey across an upwelling filament, the adjacent retentive locale in the bay's recess and the front between them, total particle concentrations were found to be maximal within the front, more than three orders of magnitude higher than in the upwelling filament. Further, the planktonic aggregation was evidently dominated by phytoplankton.
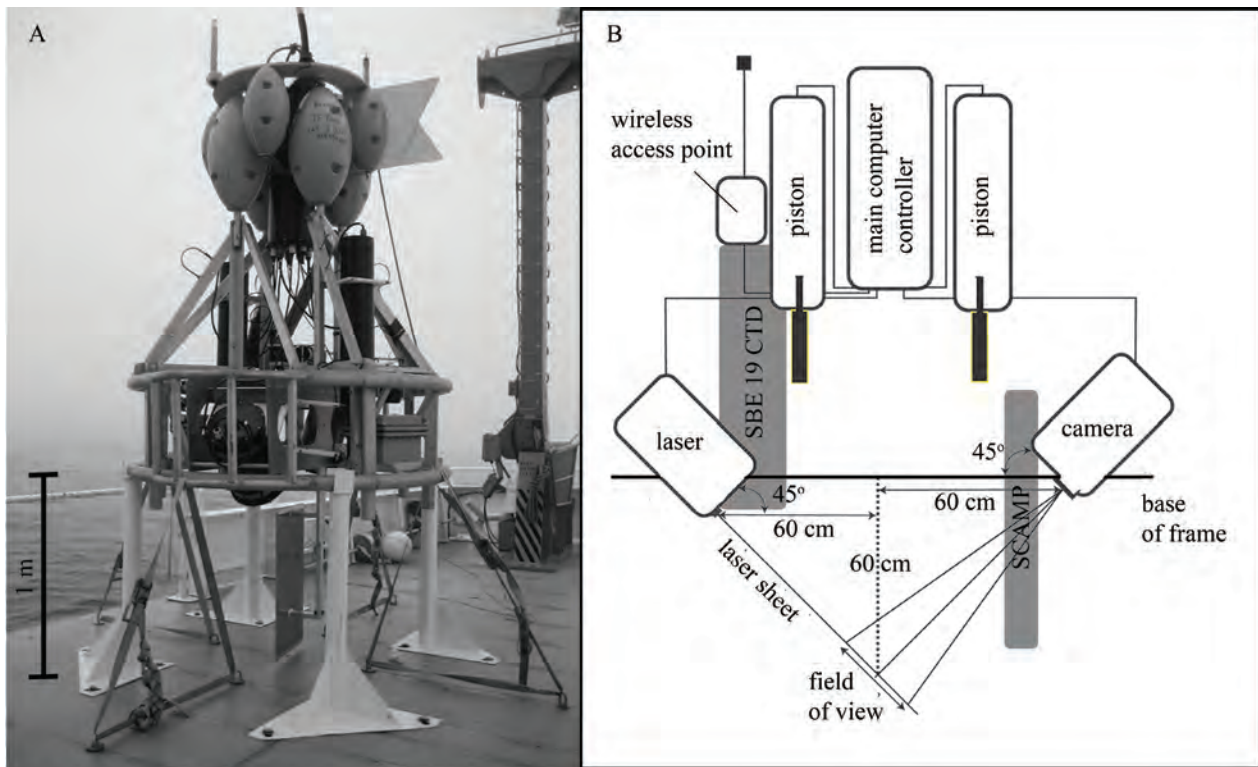
Figure 6. *(a) The FIDO-Phi on deck of the R/V Wecoma. (b) Schematic of the FIDO-Phi system showing the camera and laser housings and the region where the laser sheet is imaged. The placement of the attached WET Star fluorometer and SCAMP are also shown (from Prairie et al. 2011, with permission from the editor).*
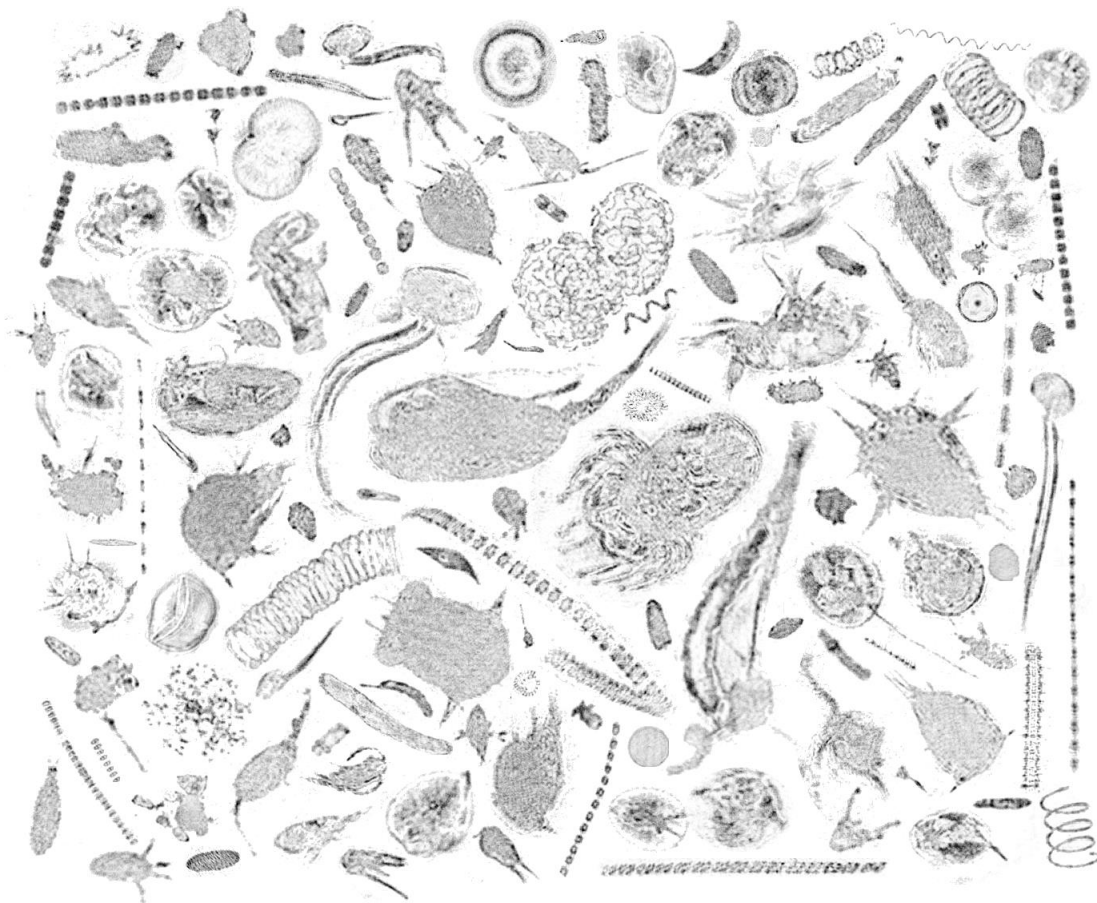
Figure 7. *Montage of planktonic diversity derived from images acquired by LISST-HOLO deployed on an AUV. The montage represents a small subset of images acquired in a single survey.*

Quantifying Growth Rate: Each species has a genetically controlled growth capacity that is modulated by environmental factors (e.g. light, nutrients, turbulence, temperature, salinity etc). Growth rates have been obtained in laboratory experiments under controlled conditions for those species that can be maintained in culture. In some cases such as *Dinophysis*, however, it has not been possible to grow the species in culture until recently, when its mixotrophic nature was demonstrated and its preferred prey identified (Park et al. 2006). While laboratory data help to understand nature, the challenge remains to quantify growth rates, µ, in the field.

At present, there is not a universal or recommended method to quantify specific µ. The mitotic index (McDuff and Chisholm 1982, modified by Carpenter and Chang 1988; see also Berdalet et al., extended abstract in Annex 3) has been successfully applied on organisms such as *Dinophysis* spp. (Reguera et al. 2003; Velo-Suárez et al. 2009; Campbell et al. 2010; Figure 8), given the morphological recognition of cytokinesis and sulcal list regeneration. For other species, namely, *Karlodinium* spp. or *Alexandrium* spp., the technique has been applied in combination with the microfluorometric analysis of the cellular DNA content (Garcés et al. 1999). A completely different approach lies in determining the RNA/DNA ratio that has proven to be correlated to µ in bacterial cultures, production rate in copepods and is also linked to the nutritional state in a variety of organisms (e.g. Berdalet et al. 2005 and references therein). Anderson et al. (1999) investigated the possibility of specifically determining µ for *Alexandrium fundyense* in natural samples using flow cytometry by combining antibody identification of the organism and a fluorometric staining of RNA. At that time, the available fluorochromes displayed some uncertainties regarding their fluorometric response. The recent advances in RNA and DNA fluorometric stains encourage this method to be reconsidered for further adaptions and new tests, possibly in combination with more sophisticated methods such as the Environmental Sample Processor (e.g. Greenfield et al. 2008).

Apart from a targeted harmful organism, there is often a requirement to determine the growth rate of the whole or some particular fraction of the phytoplankton community in order to understand its dynamics in the aquatic ecosystem. Estimates of growth rates are usually based on bulk chlorophyll and/or primary production (e.g. Bienfang and Takahashi 1983) or taxon-specific pigments (Latasa et al. 1997). In recent years,
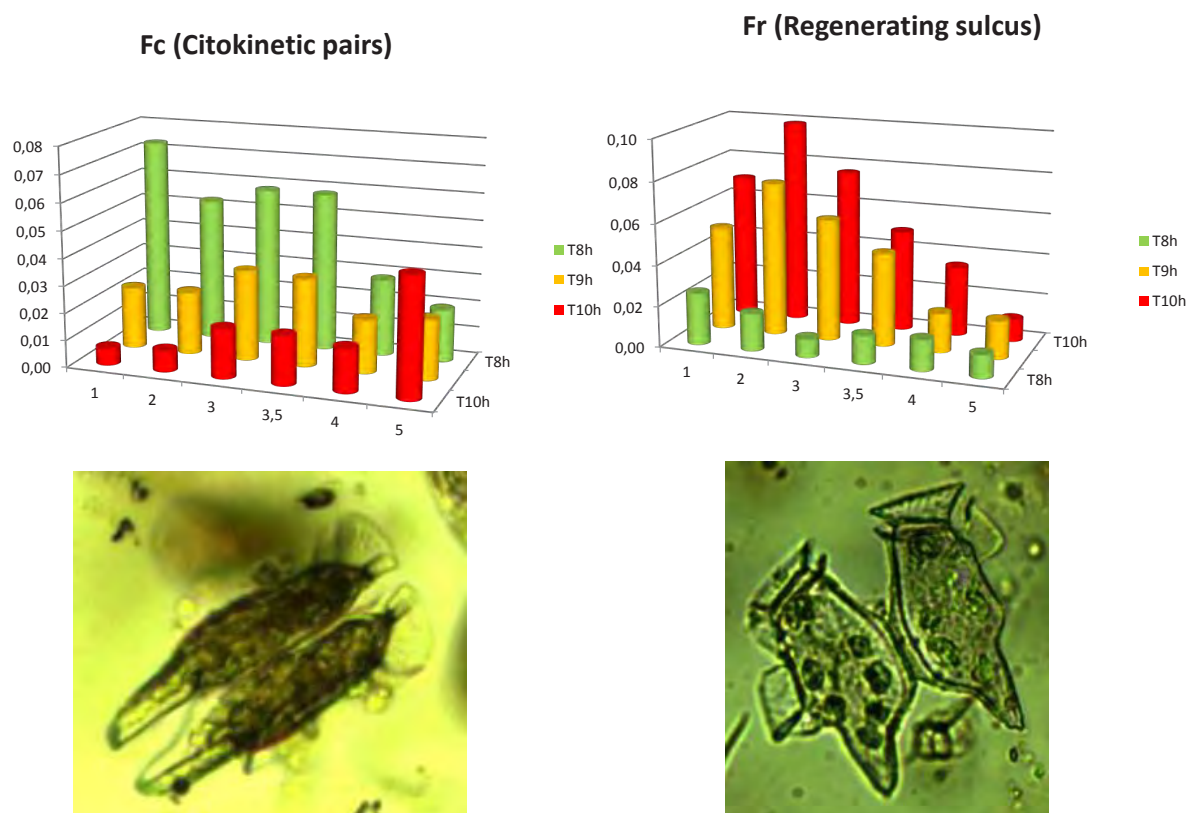
Figure 8. *Application of the mitotic index to characterize the vertical distribution of* Dinophysis caudata *growth rates in Alfacs Bay, an aquaculture site in the NW Mediterranean. Frequency of* D. caudata *cells undergoing cytokinesis (left), and in the process of sulcus regeneration (right). Samples were obtained in a 5 m water column in the center of this shallow micro-tidal estuary. The bay remains stratified most of the time, due to freshwater supply.* D. caudata *abundances were higher at the pycnocline (ca. 4m) and decreased markedly in the salty bottom waters. However, cell division processes occurred preferentially in the brackish upper layer, in the early light period. Mireia L. Artigas (unpublished).*

these methods have been combined with the dilution technique (Landry and Hassett 1982; Calbet and Landry 2004), where the microplankton community is incubated in clear bottles at a single depth or at a range of fixed depths for typically 24h. Ross et al. (2011) have shown that *in situ* point measurements, where the samples are suspended at a fixed depth during the incubation period, can have large errors associated with them. When trying to estimate the growth in a mixed layer from such point measurements, the error due to neglecting vertical mixing can be as large as 100% depending on the amount of mixing and the optical properties of the water column. They showed that these errors could be minimized by choosing an appropriate incubation depth or by incubating at several depths simultaneously. Errors associated with photoacclimation have also been discussed by Gutiérrez-Rodríguez et al. (2009).

The dilution technique can also provide measurements of grazing rates, a critical parameter for the evolution of phytoplankton, including the harmful species. In most studies, such measurements were applied to the whole community, to a fraction or functional groups based on pigment analysis, but not at a species level.

Is the high cell density in the thin layer due to in situ division and passive accumulation in density discontinuities or does it result from (biological) aggregation?

This overarching question, posed during the OSM in 2005 (GEOHAB 2008), requires answers to four fundamental questions: (1) What is the growth rate of the organism? (2) Does the organism passively settle onto a density interface to accumulate? (3) Is the organism actively aggregated by physical mechanisms? (4) Are the organisms actively behaviorally migrating into the layers? Methods to determine growth rate have been discussed previously in this document, physical convergence mechanisms are described in Theme 1, organism behavior is discussed in Theme 3. If these fundamental questions can be answered, it is possible to determine the dominant mechanisms of formation through modeling or theoretical studies, which are discussed in Theme 6.

Is high density (aggregation) a pre-requisite for sexual recombination?

There are currently no data available to answer this question. It could be speculated that because the characteristic time scale for the fusion of gametes is highly dependent on the local cell concentration (Wyatt and Jenkinson 1997), the local increase in cell density would increase sexual recombination rate. However, there are other factors involved in the induction of resting stages associated with gamete fusion, not necessary related to the presence of the organism within the thin layer. Likely, the eventual strategy will be species-dependent. In the particular case of chain-forming spe-

cies, where sexual recombination can occur more easily among the cells, living in a thin layer may not offer additional advantages other than a more physically stable environment.

Another aspect is that thin layers may facilitate some of the more subtle cellular processes occurring during sexual recombination. It may be speculated that these processes require relative stability, and it has been experimentally shown that high turbulence intensities interfere with cell division (e.g. Pollingher and Zemel 1981; Berdalet et al. 2007) and asexual cyst formation (Smith and Persson 2005; Bolli et al. 2007). If this were the case, thin layers with reduced turbulence would favour sexual recombination.

Theme 3) Organism Behavior

In the past 20 years, the oceanographic community has made tremendous strides in developing instruments to optically and acoustically detect thin layers (Holliday et al. 2003; Franks and Jaffe 2008; Doubell et al. 2009; Sullivan et al. 2010b) and quantifying the vertical and horizontal extent of thin layers in the coastal environment (reviewed by Sullivan et al. 2010a). Within this time frame, there have been very few studies that have sent back even still images of thin plankton layers from the field (Alldredge et al. 2002; Timmerman et al. *in press*). During the same 20 years, in parallel with the above mentioned progress, new insights were gained into the interactions between components of the planktonic community by observing the interactions directly (e.g. Bainbridge 1953; Strickler 1969, 1977, 1984, 1985; Strickler and Bal 1973; Kerfoot 1978; Hamner and Carlton 1979; Costello et al. 1990; Tiselius 1992; Paffenhofer et al. 1995; Yen and Strickler 1996; Doall et al. 1998; Kiørboe et al. 1999; Kiørboe 2010). These observations led to experiments (e.g. Hardy and Bainbridge 1954; Koehl and Strickler 1981; Costello et al. 1990; Marrasé et al. 1990; Fields and Yen 2002) and to fluid-dynamic simulations to understand the underlying principles governing the interactions between phyto- and zooplankton, zoo- and zooplankton, and biology and physics (e.g. Koehl 1983, 1996, 2004; Jiang et al. 2002a, 2002b; Jiang and Osborn 2004; Jiang and Paffenhofer 2004, 2008; Strickler and Balazsi 2007; Jiang 2011). A gap now exists between the results from these direct observations and the results obtained in the previously mentioned investigations on thin layers.

For instance, the ability of copepods to react to chemical cues such as phytoplankton exudates, conspecific and predator pheromones, or chemical pollutants has been well illustrated (Woodson et al. 2005; Woodson et al. 2007). Despite their likelihood under natural conditions, little is still known, however, about the interactive effects of different chemosensory stimulations on copepods, especially in the context of thin layers that may contain toxic and non-toxic microalgae and exhibit very specific rheological properties. One would expect that zooplankton like to feed in phytoplankton thin lay-

ers given that within the layer there is a higher concentration of food than in most parts of the water column. However, the other extreme where zooplankton are not active in the layer at all, may also be possible because we still do not know how these organisms react physiologically to physical structure and processes *in situ*. A clear need exists for instruments which allow us to directly observe zooplankton and phytoplankton behavior within and around the edges of thin layers in stratified systems. We are limited by the ability to directly observe plankton behavior and track physiological changes in response to the ambient physical structure and dynamics. The instrumentation to non-intrusively measure these small-scale behavioral responses to physical structure and processes *in situ* is needed.

Do HAB species migrate? Do they migrate vertically all the time or only at certain stages of the population growth or under certain hydrographical patterns?

Many HAB species are motile, others have a certain capacity to regulate buoyancy, and most exhibit a rather complex migratory behavior. Cell migration can be triggered by nutrient and/or light limitation (Eppley et al. 1968; Fauchot et al. 2005; Ault 2000), turbulence avoidance (e.g. Crawford and Purdie 1992; Sullivan et al. 2003, review by Berdalet and Estrada 2005), predator avoidance (see Smayda 2010 for a review), and phototaxis/geotaxis related to an endogenous rhythm (Ralston et al. 2007; Ji and Franks 2007). Some migrations are entrained by regular forcings such as solar or tidal cycles. Others depend on multiple physiological processes (Yamazaki and Kamykowski 2000), trophic interactions (predator-prey) and/or the stage in the cellular life-cycle (encystment, etc.), which complicates the characterization of the migratory strategy. Unveiling swimming strategies is further complicated because the order of magnitude of the turbulent velocity scales is often similar or greater than the swimming velocities and thus mask any deterministic behavior. Nevertheless, using a nutrient-light-based swimming strategy, Ross and Sharples (2007) could show that motility remains effective even in environments where the turbulent velocities may appear to exceed the swimming capabilities of cells. In addition, swimming patterns are
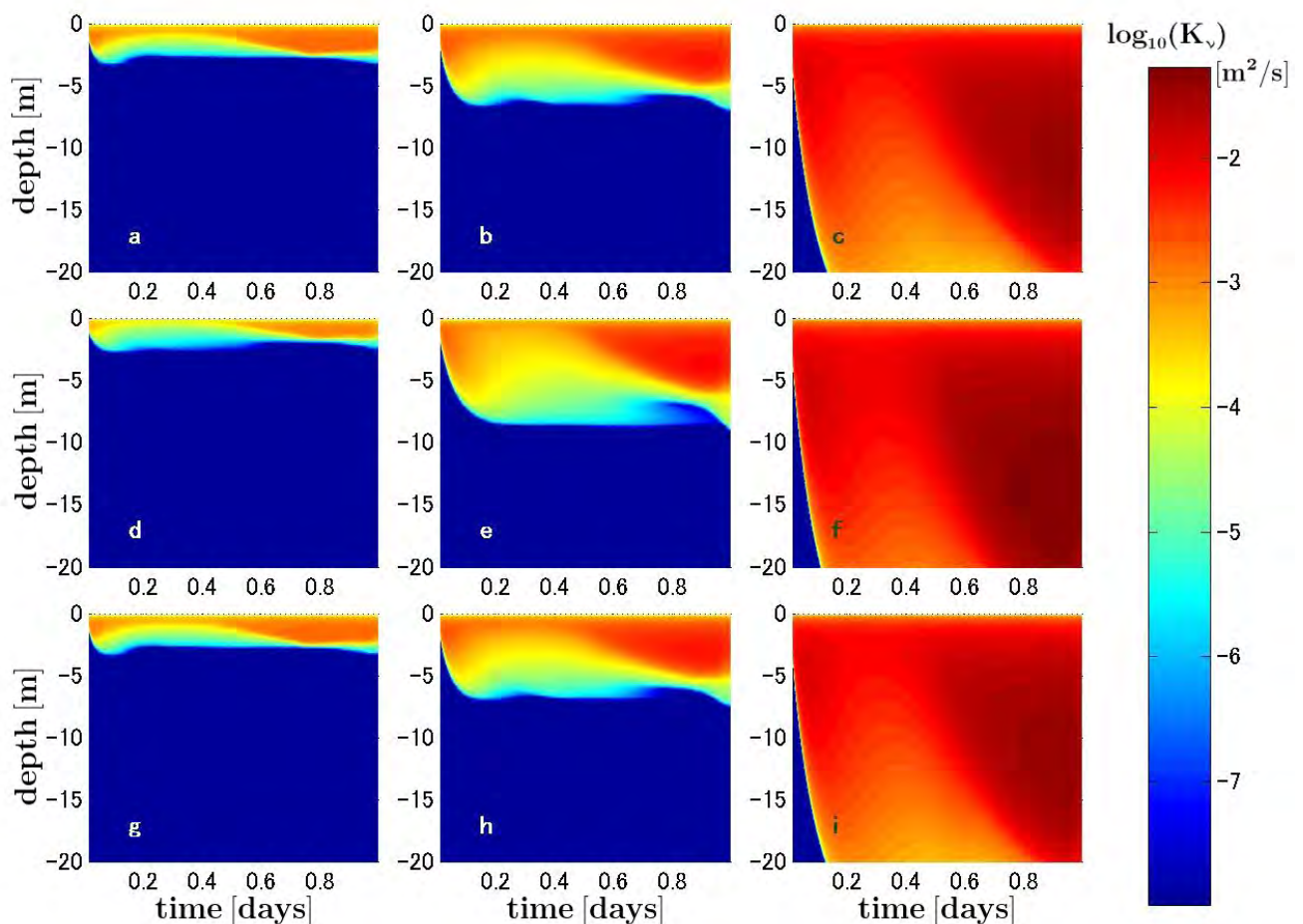
Figure 9. *Turbulent eddy diffusivity in terms of log10 (m^2 s^{-1}) during 24-hour simulations for three different wind conditions and three different water types. Coastal water type for 3 m s^{-1} (a), 5 m s^{-1} (b), and 10 m s^{-1} (c); Jerlov I water type for 3 m s^{-1} (d), 5 m s^{-1} (e), and 10 m s^{-1} (f); Jerlov III water type for 3 m s^{-1} (g), 5 m s^{-1} (h), and 10 m s^{-1} (h) (from Yamazaki et al. in press, with permission from the editor).*

species- and location-specific. Several species of *Dinophysis,* for instance, have been observed to migrate vertically (upwards or downwards; e.g. MacKenzie 1992; Villarino et al. 1995; Reguera et al. 2003). Concurrently, different species of the same genus, or even the same species in different locations, have been reported to remain stationary in the pycnocline or in the surface layer without exhibiting any diurnal migratory behavior (e.g. Carpenter et al. 1995; Maestrini 1998; Pizarro et al. 2008; Velo-Suárez et al. 2008).

Yamazaki et al. (*in press*) developed a numerical model to simulate thin layer formation due to phototaxis effect on vertical migration. The model was embedded in one-dimensional water column mixed layer model (GOTM) that produces realistic mixing and turbulent conditions (Figure 9). They showed that thin layer formation takes place when wind speeds are below 5 m/s (Figure 10).

Sullivan et al. (2010b) strove to elucidate the role that species-specific properties of phytoplankton play

in thin layers dynamics over a two-year period in Monterey Bay (California). Water samples were taken inside and outside optical features. Thin layers were observed in both years. In the first year, the dinoflagellate *Akashiwo sanguinea* formed intense thin layers near the pycnocline at night, and migrated to nearsurface waters at dawn. In the second year, layer composition was more complex, and related to the water mass present at the time of sampling. This was a comprehensive study, examining the biology, optics and physics of the water column.

What are the gains of vertical migration: acquisition of nutrients from deeper waters? Phototactic responses? Social behavior to promote sexual encounters? Aggregation around some unknown cue?

For motile phytoplankton, migration can provide the ability to outcompete non-motile species in environments with vertically opposing resource gradi-
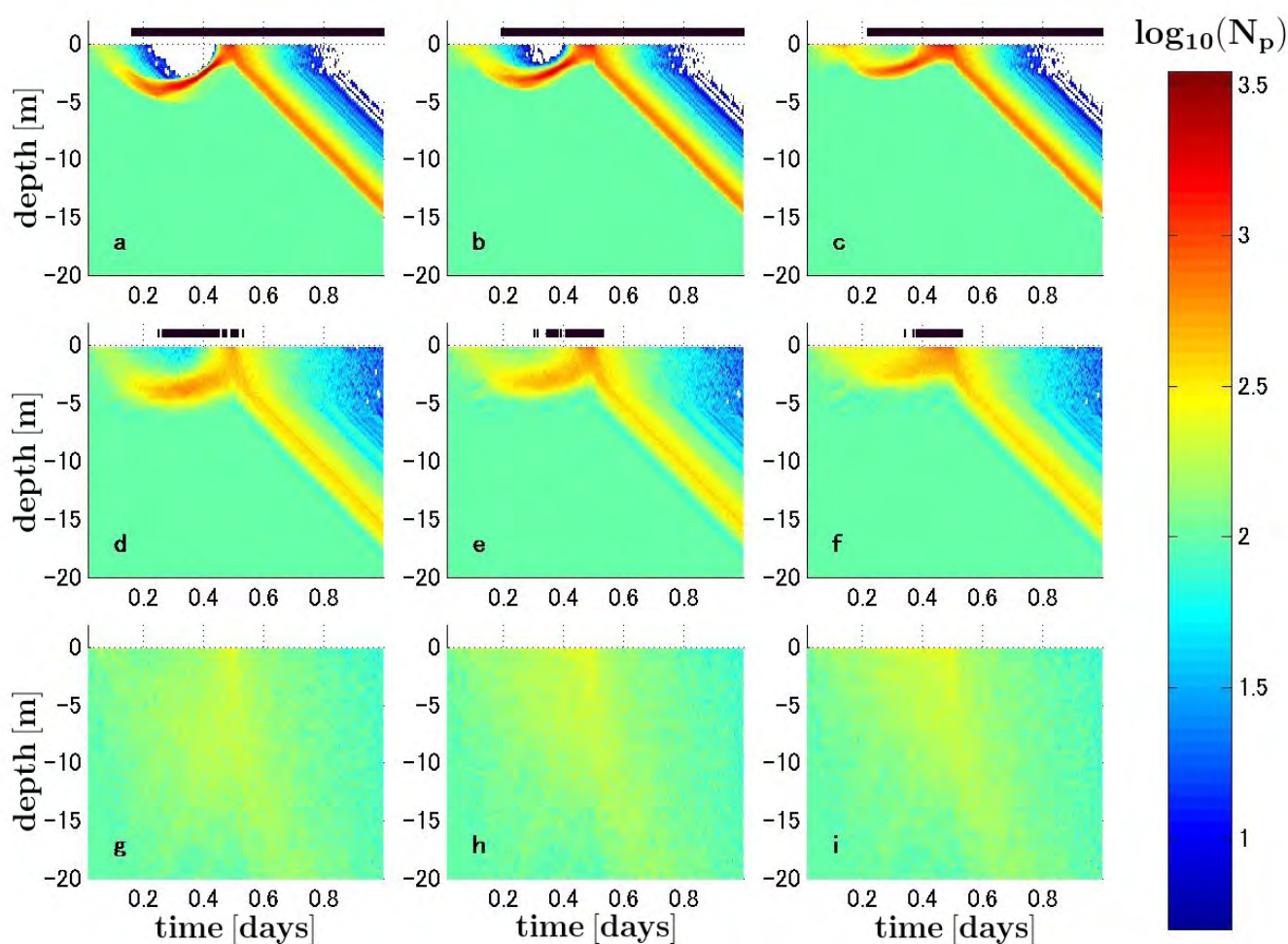
Figure 10. *Particle distributions -$\log_{10} (N_p)$- for coastal water types during 24 hour simulations. Particle density was computed for each 0.25 m depth interval. Three different winds are applied: Top row is 3 m s^{-1}, middle row is 5 m s^{-1}, and bottom row is 10 m s^{-1}. Also three different photoinhibition thresholds (Y_T a parameter that changes according to the cumulative light history of the cells) are applied: left column is 0.2, middle column is 0.5, and right column is 0.8. Thick black line at the top of each window show thin layer (from Yamazaki et al. in press, with permission from the editor).*

ents, namely, light vs. nutrients (e.g. Kamykowski and Zentara 1977; Klausmeier and Litchman 2001; Ross and Sharples 2007). Motility may also reduce the boundary layer limitation for nutrient uptake (e.g. Gavis 1976; Purcell 1977; Karp-Boss et al. 1996) in large microalgal cells (>50µm). According to Smayda (1997) the benefits of phytoplankton vertical migration depend on the physiological coupling among the photosynthesis metabolism during the day and the nocturnal nutrient uptake (and storage). In estuaries it has also been suggested that vertical migration in response to tidal forcing may increase the retention of cells within the coastal area (Crawford and Purdie 1992).

Swimming may facilitate sexual encounters through chemical processes (following a chemical plume over a short range) and through simply increasing their encounter rates (Visser and Kiørboe 2006). Other social behavior may include aggregation around some chemical cue (e.g. Kiørboe et al. 2004). Likely, all those processes may be facilitated within the thin layers.

Theme 4) Nutrients

Owing to the complexity and challenges in sampling, there have been fewer studies conducted on the role of nutrients in HABs in stratified systems than on the biological constituents within the layers. Nevertheless, one of the pioneer nutrient studies was conducted by Hanson and Donaghay (1998). Continuous vertical profiles obtained with a high-resolution profiler and a reagent-based profiling chemical analyzer in a small fjord in the US Pacific Northwest demonstrated that fine-scale chemical gradients and chemically distinct thin layers exist in stratified coastal environments. From these simultaneous measurements of the physical and chemical environment, rates of nutrient transfer across a thin layer boundary could be calculated.

Subsequently, Lunven et al. (2005) carried out a similar study in stratified water columns in the Loire River plume (Bay of Biscay, France) using a Fine Scale Sampler. The study identified periods of dissolved inorganic nutrient availability and limitation within the seasonal succession. Further, Ryan et al. (2010) were able to describe the nutrient supply processes relevant to blooms in stratified environments using optical methods for nutrient measurements deployed on an AUV. Specifically, internal tidal dynamics across a canyon-shelf environment pumped nitrate-rich waters from the deep canyon into the shallow shelf waters on short time scales of 1-2 d (Figure 11) in concert with a bloom of a vertically migratory dinoflagellate that can cause HABs (Ryan et al. 2010). Most recently, in the same research area, nutrient ratios and alkaline phosphatase activity, measured from bottle samples taken within and outside a thin layer, suggest that the *Pseudo-nitzschia* cells were phosphate stressed. Timmerman et al. (*in press*) suggest that this physiological stress led to increased toxicity of the bloom.
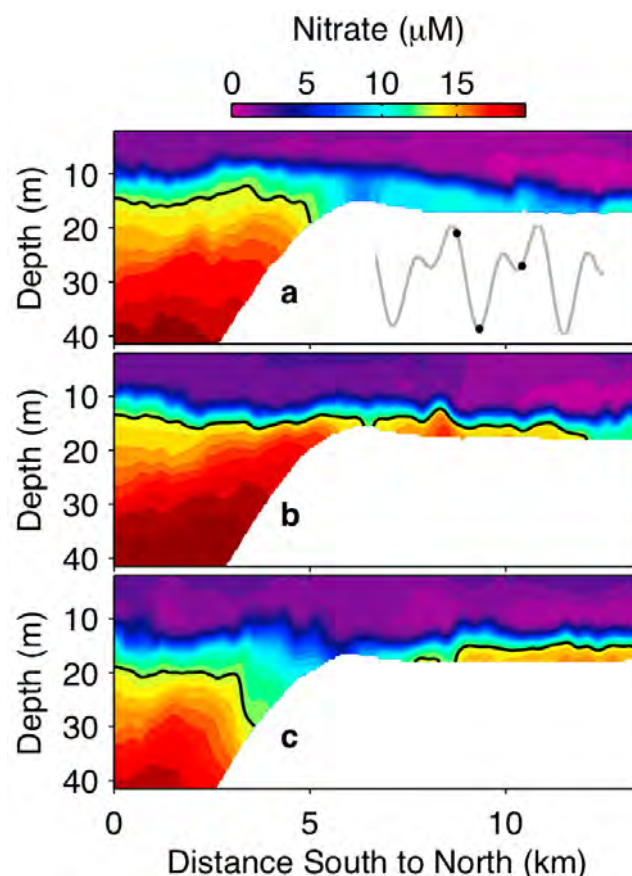
Figure 11. *Nutrient flux caused by internal tidal pumping from Monterey Canyon into the stratified 'upwelling shadow' of Monterey Bay, California. Consecutive vertical sections of nitrate were mapped on August 28-29, 2005. The black contour in all panels (13 µM) highlights the northward movemenhigh nitrate water below the thermocline. The inset in (a) shows bottom pressure from an ADCP on the shelf, illustrating the tidal oscillations (gray line) and the start of the consecutive AUV surveys (black circles). Adapted from Ryan et al. (2010).*

What nutritional opportunities do thin layers provide to phytoplankton, especially to the species selected within thin layers?

The last decade has provided increasing evidence on the broad range of nutritional strategies among phytoplankton. Although some HAB species are autotrophic, most of them incorporate organic molecules (including *Pseudo-nitzschia* spp., Loureiro et al. 2009) and also show mixotrophic capacities (e.g., *Dinophysis* spp. - Jacobson and Andersen 1994; Park et al. 2006; *Karlodinum* spp. – Li et al. 1999; Adolf et al. 2008). Thin layers may provide advantages to all kinds of nutritional metabolism: concurrent favorable light and nutrient conditions, if thin layers are located in the upper part of the nutricline (e.g. Cheriton et al. 2009); breakdown products from senescent cells can accumulate in the density gradient (pycnocline), thus favoring nutrient recycling and phytoplankton productivity (Le Corre

and L'Helguen 1993); and constitute high prey concentrations layers for mixotrophic species (e.g., *Dinophysis* spp., Velo-Suárez et al. 2008).

What is the role of the microbial loop in thin layers?

High concentrations of dissolved organic matter from phytoplankton excretion may be encountered at the thin layers, thus favoring the microbial loop, with all the associated processes (bacterial growth, phytoplankton-bacteria competition for nutrients, microzooplankton grazing, parasite infections). Encounter rates should also be modified within the thin layers compared to the adjacent layers. The particular (low) turbulent environment in the thin layer should influence the encounter rates among the different interacting components of the food web (Rothschild and Osborn 1988; Havskum et al. 2005; Llaveria et al. 2010). Maximum bacterial production rates were closely associated with thin layers of zooplankton and marine snow in a small fjord in the US Pacific Northwest (McManus et al. 2003). The high bacterial production rates may have been the result of increased dissolved organic matter (DOM) production in this layer, where concentrations of marine snow and zooplankton were highest. While some progress has been made on this topic, more investigation into the role of the microbial loop in thin layers is needed.

Is growth rate in the thin layer higher due to a local enhancement in resources?

To answer this question, we need appropriate methods to estimate the *in situ* growth rates of target (HAB) species at the depth of the thin layer (see Theme 2) and nutrient fluxes as well.

It is unclear at this time how significant the influences of thin layers are on distributions of inorganic and organic chemicals. The occurrence of underlying high nitrate concentrations does not necessarily mean that this nutritional source is used: the confinement of *Karenia mikimotoi* in the pycnocline is due to a higher survival rate in the layer rather than a nutritional advantage (Gentien et al. 2007). As mentioned earlier in this section, in a recent study, Timmerman et al. (*in press*) described a subsurface *Pseudo-nitzschia* bloom within a well-defined layer, containing high levels of domoic acid. Nutrient ratios and alkaline phosphatase activity (measured from bottle samples taken within and outside the thin layer) suggest that the *Pseudo-nitzschia* cells were phosphate stressed. Timmerman et al. (*in press*) suggest that this physiological stress led to increased toxicity of the bloom. Quantification of *Pseudo-nitzschia* abundance and toxicity using *in situ* molecular methods showed greater and more variable toxicity in association with exposure to suspended sediments (Ryan et al. 2011). Subsequent Lagrangian studies of a phytoplankton patch containing toxigenic

Pseudo-nitzschia revealed elevated toxicity within the portion of the patch affected by resuspended sediments (Ryan et al. *in press*). The hypothesis is that trace metals, known from lab studies to influence toxin regulation in *Pseudo-nitzschia* (Bates 1998; Rue and Bruland 2001; Maldonado et al. 2002; Rhodes et al. 2006) were contained in the resuspended sediments. However, trace metal measurements present an additional challenge, and the results of these studies are based on relatively few samples. It would be ideal to measure how these nutrients were distributed in space within the layer to further our understanding of how variations in nutrient gradients within the layer contribute to the development and persistence of the layer as well as to the potential toxicity of the layer. Understanding how frequently blooms such as these are under nutrient stress could improve our ability to predict when HABs will occur (Timmerman et al. *in press*).

Theme 5) Temporal Evolution of HABs in Stratified Systems and Thin Layers

What are the main processes controlling the population evolution of a given species, and how does their ranking vary over the time course of a bloom?

Population dynamics of phytoplankton species depend on the balance of biological processes that cause gains (e.g. cellular division, aggregation) or losses (e.g. senescence, grazing, dispersion and sedimentation) of individuals. In all systems, including stratified ones, these processes are strongly affected by the coupling of physical conditions with the life strategies of these species.

Recent advances in technology have provided insights into the physical and biological co-evolution of thin layers. The temporal evolution of thin layers dominated by a HAB dinoflagellate, *Akashiwo sanguinea*, was closely monitored during a study in Monterey Bay (California, USA) during which an AUV acquired nearly 7,000 profiles in a set of sections repeated almost continuously for a week (Ryan et al. 2010). Phytoplankton thin layer density doubled during a four-day period, in parallel with enhancement of stratification (Figure 12) and internal tide driven nutrient supply (Figure 11).

From the observed patterns, it is possible to estimate the overall and coarse *in situ* net growth rate of the whole phytoplankton community in terms of chlorophyll. However, more specific measurements on the target species or grazing are limited, as explained in Theme 2.

Of particular interest when dealing with harmful organisms is the ability to characterize their physiological status, that is, their capacity to thrive under given environmental conditions. Likely, along the studied period in Figure 12, the microplankton cells and hence

the harmful taxons experienced physiological changes over time. Tracking the changes in phytoplankton health over time is not straightforward. In part, there is still research to be conducted on indicators of the physiological or viability status in order to provide consistent results or reliable and general application *in situ*. Examples would include staining with vital fluorochromes to visualize cell viability or apoptosis (although rarely applied in natural phytoplankton, but see

Velhuis and Kraay 2000), membrane permeability (e.g. Agustí and Sánchez 2002), phosphorus incorporation (e.g. Dyrham et al. 2002), nutritional status (using e.g., RNA/DNA as proxy, Anderson et al. 1999) or prey ingestion (Sintes and Del Giorgio 2010).

The evolutionary stage of a bloom can influence the nature and degree of harmful effects. For example, the toxicity of *Pseudo-nitzschia* blooms may be heightened
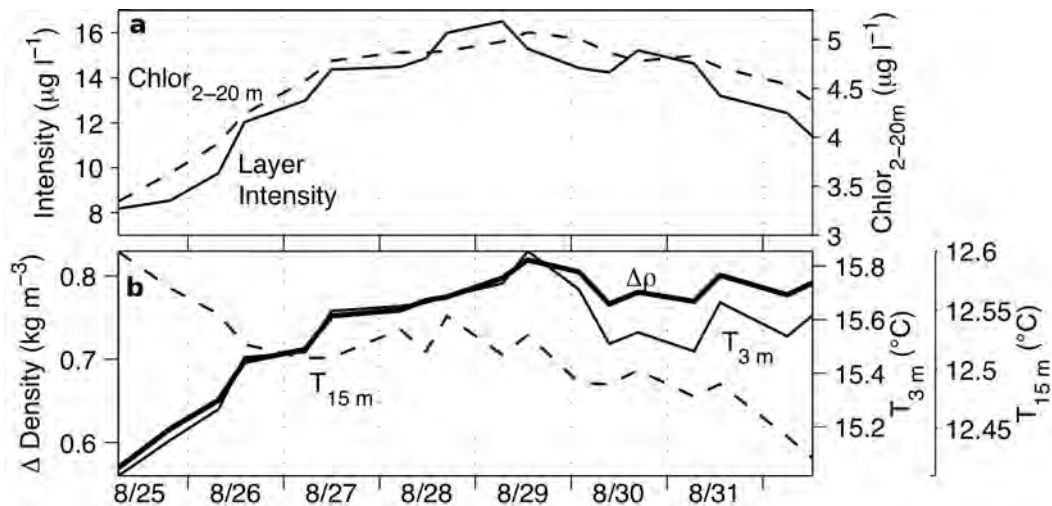
Figure 12. Temporal variability in thin layer attributes relative to stratification. Each point represents the average based on ca. 350 profiles over the northern shelf of Monterey Bay (California, USA). (a) thin layer intensity (above background) and average chlorophyll concentrations in the depth range 2-20 m; (b) temperature at 3 and 15 m depth, and the density difference between 15 and 3 m depth. Time series were smoothed with a 3-point running mean. Adapted from Ryan et al. (2010).
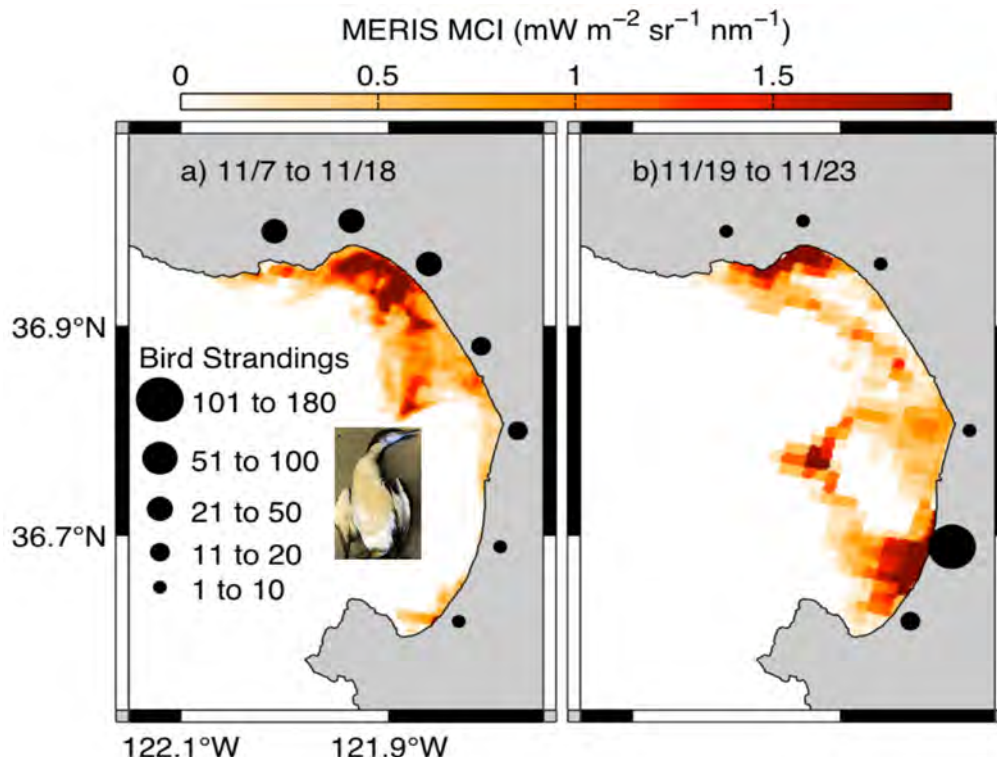
Figure 13. Seabird mortality event linked to a senescent-phase bloom of Akashiwo sanguinea *(adapted from Jessup et al. 2009). Much larger mortality events, linked to the same phytoplankton species, were subsequently observed along the greater northeastern Pacific.*

during the late stages of blooms, when certain nutrients (often nitrogen and/or silicate) have been depleted (e.g. Bates et al. 1998; Timmerman et al. *in press*; however, see also Pan et al. 2001). The senescent phase of very dense blooms can also accelerate harmful effects due to oxygen depletion. A recently discovered mechanism of harm, first documented in the stratification-enhanced upwelling shadow of Monterey Bay, was related to the late phase of dense blooms of *Akashiwo sanguinea* (Jessup et al. 2009; Figure 13 and 14). A surfactant-like protein in the organic matter released by a senescent-phase bloom coated birds that encountered bloom-generated foam. This caused loss of the insulating capacity of the birds' feathers and mortality by hypothermia. Since its discovery, this HAB mechanism has been observed along the coast of Oregon and Washington, associated with the same species (Phillips et al. 2011). For ecological purposes, it is also necessary to track toxin transfer within the food webs. This is, at present, one of the challenges we face.

Theme 6) Predictive Modeling

In June 2009, the GEOHAB community held a workshop to discuss strategies for using observations and models to both model and predict Harmful Algal Blooms (GEOHAB, 2011). This workshop provided a broad review of challenges and opportunities for modeling HABs in eutrophic, upwelling and stratified systems. A conceptual model balancing convergent and divergent biological and physical processes in stratified systems was discussed. The summary of the 2009 GEOHAB meeting concluded that the main needs for modeling HABs in stratified systems include: 1) recognition of the importance of scale, 2) identification and ranking of the dominant physical and biological processes driving the system, 3) inclusion of three dimensional processes and 4) resolution at cell scales (growth rates, behavior, etc.). These limitations were revisited in the workshop conducted at the MBARI in August 2012.

Coupled biological-physical oceanographic models are one set of tools that are increasingly being used to predict plankton abundance and dispersal (Cowen and Sponaugle 2009; Metaxas and Saunders 2009). Physical oceanographic models calculate water movement and physical attributes within the model domain. Biological models then calculate organism growth and loss rates, and can also incorporate organism behavior (Cianelli et al. 2004; Ross and Sharples 2007; McManus and Woodson 2012; Yamazaki et al. *in press*). In order to accurately model HABs in stratified systems, a three-dimensional (3D) circulation model capable of resolving fine-scale vertical structure is required. A first limitation of many 3D circulation models, however, is that they do not contain mixed-layer dynamics, and

an accurate representation of the vertical structure is needed to simulate HABs in stratified systems. A second limitation is due to the fact that 3D models often employ an Eulerian framework where phytoplankton are represented in terms of concentrations (e.g., g C·m^{-3}) rather than individuals. Such concentration-based approaches have a systematic weakness in that they cannot represent the strong biological gradients often present in stratified systems, and in particular in thin layers. Third, because physical flows become non-linear close to shore, many physical circulation models do not extend into the inner shelf and nearshore regions.

An additional limitation of the physical-biological models is that the biological components often do not incorporate species-specific organism growth and loss rates or behaviors (swimming and sinking) that contribute to distribution patterns. This can happen for a variety of reasons. As one example, many models of basin-scale processes produce daily-averaged output. These models cannot resolve higher-frequency processes like diurnal migration. Another reason that these coupled models rarely incorporate species-specific rates and behaviors is that they are simply not known. The scientific community should make an effort to understand and quantify these growth and loss rates, as well as behaviors, whenever possible. Without these capabilities, the calculated plankton abundance and dispersal patterns may be incorrect (McManus and Woodson 2012).

Finally, coupled models also need to take into account biomodification of water flow, including turbulence and both turbulent and laminar diffusion vertically. Such biomodification is brought about by: 1) differential solar heat absorption (Murtugudde et al. 2002) especially in thin layers; 2) changes in trubulence mediated by EPS (Jenkinson and Sun 2010, 2011).

Besides the indicated limitations, some approaches offer new possibilities to model HABs in stratified environment. Indeed, Lagrangian approaches where cells are represented by individual particles in combination with individual-based biological models (e.g. Ross and Geider 2009; Yamazaki et al. *in press*) allow for a more accurate characterization of both the light history and population dynamics. Furthermore, the new numerical approach of vertical grid adaptation towards strong vertical gradients (Hofmeister et al. 2010, 2011) allows high vertical resolution of down to a few centimeters in regions of nutriclines or thin plankton layers. With this method, it should be possible to use Eulerian models to simulate thin layer formation and its effects on the biogeochemical dynamics and budget, if the underlying relevant physical and biogeochemical processes are considered (see the extended abstract by Burchard et al. in Appendix III).
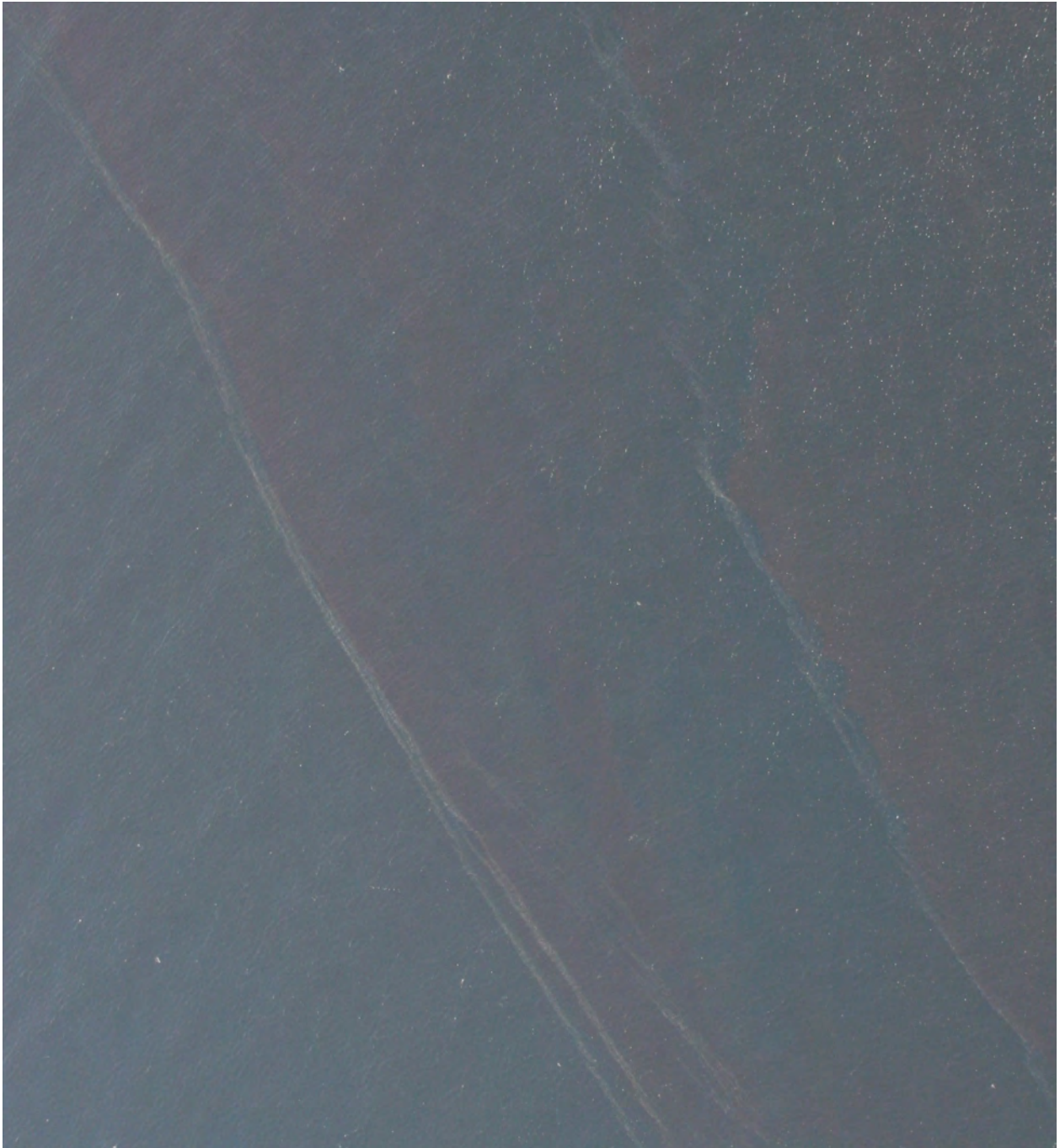
Figure 14. *This photograph, taken from 300 m above the surface of Monterey Bay (California, USA) on 6 October 2009, illustrates multiple aspects of HABs in stratified systems. Favored by stratification, dinoflagellates often bloom in this region during fall. The high visibility of the populations during mid-day is due to their motility-driven accumulation in a thin layer near the surface. The banded structure of bloom biomass is due to behavioral-physical interactions associated with internal waves. The foam lines represent a mechanism of harm only recently documented (Jessup et al. 2009). Saponification from bloom organic matter can result in mass mortality of birds via hypothermia. After being discovered in Monterey Bay (Figure 13), this mechanism of harm has subsequently been observed along the greater northeast Pacific, in Washington and Oregon.*

IV. FUTURE TOPICS TO BE ADDRESSED IN UNDERSTANDING THE ECOLOGY AND OCEANOGRAPHY OF HABs IN STRATIFIED SYSTEMS

Although the scientific community has made notable progress in understanding and quantifying HABs in stratified systems, some significant gaps still exist in our knowledge and methodology. From the presentations and the discussions during the 2012 workshop on "Advances and Challenges for Understanding Physical-Biological Interactions in HABs in Stratified Environments" we identified several outstanding questions and several gaps in our available methodology. These can be summarised within the six overarching themes developed in Section III:

Theme 1) Physical structure

- Can organisms modify the physical microstructure in ways that influence thin layer ecology?
- What are the viscosity and other rheological properties at the length scale of the phytoplankton cells, under natural oceanic conditions during the occurrence of blooms?

Theme 2) Biological structure: Rates and Interactions

- In the spatial dimensions: is the layer homogeneous? What are the fine-scale structures within the layer? For example, how are toxic phytoplankton and zooplankton distributed in space within the thin layer?
- How do these fine-scale spatial relationships influence trophic transfer of toxins?
- Temporally, does the layer composition and cell abundance change over time?
- How can be improved the methods to quantify cell abundance and growth and grazing rates in order to estimate these parameters within thin layers?

Theme 3) Organism Behavior

- How do organisms (including toxic and non-toxic phytoplankton, and zooplankton) behaviorally locate thin layers of HABs in stratified systems?

- We are still limited by the ability to directly observe plankton behavior in thin layers: How do organisms behave once they are within and in the vicinity of the thin layer?
- How do organisms react physiologically to physical structure and processes *in situ*?
- How does the fact that the environment is stratified favour the particular HAB species? Does the ability to swim, albeit weakly compared to the turbulent velocities, provide a competitive advantage which facilitates the occurrence of HAB events in the first place?

Theme 4) Nutrients

- How are a suite of nutrients distributed in space and with time within the layer?
- How do variations in nutrient gradients within the layer contribute to the development and persistence of the layer as well as to the potential toxicity of the layer?

Theme 5) Temporal Evolution of HABs in Stratified Systems and Thin Layers

- Methods to identify physiological and viability status of the phytoplankton cells need to be improved.
- Methods to quantify growth and grazing rates *in situ,* in near real-time, need to be improved.
- Methods to track toxin transfer within the food web need to be developed.

Theme 6) Predictive Modeling

- We need models with capacity to resolve and integrate physical and biological processes, that occur at different scales, involved in the dynamics of HABs in stratified systems, in order to understand and predict them.
- At present, biological models describing some processes at cell scale already exist. However, lack of *in situ* biological parameters (e.g. growth rates,

swimming behaviour) with high resolution on targeted organisms limit the capacity of these models to help to understand the dynamics of harmful blooms.

- Integration of 3D physical models and biological ones have shown to provide prediction capacity for management purposes in certain environments, although they are not appropriate to resolve stratified systems. Some recent advancements offer new possibilities of improvement.

- Specific modeling should be addressed to integrate HABs dynamics into biogeochemical processes as well as to provide future scenarios of HABs under a context of climate change.

V. CONCLUSIONS, NEXT STEPS

The Workshop on "Advances and Challenges for Understanding Physical-Biological Interactions in HABs in Stratified Environments" was the final activity organized by the CRP Sub-committee towards the sunset of the GEOHAB programme, which will end on 31 December 2013.

The CRP "Harmful Algal Blooms in Stratified Systems" of the GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms) programme facilitated the interaction of scientists from a variety of disciplines that have met during the GEOHAB life history and have made possible the advances in understanding of the global ecology of harmful algal blooms, in particular in stratified systems, as has been summarized in this report.

Multidisciplinary studies should continue beyond GEOHAB, because the open questions require a multidisciplinary approach. The key questions and gaps in methodology identified by the participants (section IV) can constitute the core for future research programs. International collaboration is encouraged, because it favors the application of the comparative approach from the organism to the ecosystem level, an approach central to the GEOHAB programme. A challenging future can then be addressed by joint efforts among scientists from a variety of disciplines, making an efficient means of providing scientific progress in a changing world.

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APPENDIX I – Open Science Meeting Program

Workshop on "Advances and Challenges for Understanding Physical-Biological Interactions in HABs in Stratified Environments"

Monterey Bay Aquarium Research Institute
Moss Landing, California, USA
21-23 August 2012

TUESDAY 21 AUGUST

8:45		Welcome and Logistics
	Session 1	**Physical measurements at small scale: instruments, measured parameters, obtained data, low-end versus high-end physical/ biological measurements**
9:00	Hidekatsu Yamazaki	Session Overview
9:10	**PLENARY** Jules Jaffe	The quest for biological and physical measurements of HABs: Progress and prospects
9:50	Rudi Strickler	Time budgets, transition matrices, and the temporal scales of water
10:15		Break Coffee and Refreshments. Time for viewing session posters.
	Rhodora Azanza[1]	Current patterns and residence times in Matarinao and Murcielagos bays, Philippines: Implications on the distribution of *Pyrodinium* blooms
10:40	Mary Carmen Ruiz de la Torre	Near surface temperature stratification and the wind transport of surface blooms
11:05	Hide Yamazaki	Fluorescent microstructures: quest for building block of planktonic ecosystem
11:30		Session Discussion
12:15		Lunch
	Session 2	**Biological-physical interactions across scales: the formation, maintenance and decay of thin layers**
1:20	Margaret McManus	Session Overview
1:30	**PLENARY** Tim Cowles	Planktonic thin layers as expressions of coupled physical, biological and chemical processes
2:10	Raphael Kudela	A regional comparison of upwelling, coastal land use patterns, and HAB hotspots along the California coast
2:35	Inga Lips	Bimodal distribution patterns of motile phytoplankton in the stratified Gulf of Finland

[1] Posters will be viewed during break. The author of the poster listed in the agenda should plan to stand with their poster during that time to address questions.

3:00		Break Coffee and Refreshments. Time for viewing session posters.
	Arturo Pedro Sierra-Beltran[1]	Toxic diatom blooms of the genus *Pseudo-nitzschia* along Mexico's northwest Pacific coast
3:25	Drew Lucas	The influence of diurnal winds on phytoplankton dynamics in a coastal upwelling system
3:50	John Ryan	Aspects of HAB phytoplankton ecology in a stratification-enhanced upwelling shadow
4:15		Session Discussion
5:00		**RECEPTION**

WEDNESDAY 22 AUGUST

	Session 3	**Living in a thin layer: calculations of biological rates**
9:00	Elisa Berdalet	Session Overview
9:10	**PLENARY** Jim Sullivan	Living in a thin layer: calculations of biological rates
9:50	Laurent Seuront	Thin layers, chemosensory stimulations and copepod swimming behavior: small-scale changes, broad implication
10:15		Break Coffee and Refreshments. Time for viewing session posters.
	Lourdes[1] Velo-Suarez	Dinoflagellate vertical migration and thin layer formation in laboratory experiments: preliminary results

10:40	Elisa Berdalet	Estimating phytoplankton growth rates in a stratified system: experimental and modeling approaches, open questions
11:05	Oliver Ross	The dilution method – a modelling study
11:30		Session Discussion
11:50		Lunch
	Session 4	**Integrating fine-scale measurements into a regional modeling approach**
1:00	Oliver Ross	Session Overview
1:10	**PLENARY** Hans Burchard	High-resolution 3D modelling of oceanic fine structures using vertically adaptive coordinates
1:50	Clarissa Anderson	The role of coupled physical-biological models for HAB prediction in California
2:15	Oliver Ross	Is Alfacs Bay a phytoplankton bloom incubator? *In situ* measurements and modeling approaches, open questions
2:40		Break Coffee and Refreshments. Time for viewing session posters.
	Ernesto Garcia-Mendoza	Toxic harmful algae blooms in Todos Santos Bay, northwestern Baja California, Mexico: I-environmental aspects that promote the growth of *Pseudo-nitzschia australis* in the region

[1] Posters will be viewed during break. The author of the poster listed in the agenda should plan to stand with their poster during that time to address questions.

	David Rivas-Camargo	Toxic harmful algae blooms in Todos Santos Bay, northwestern Baja California, México: II-circulation associated with *Pseudo-nitzschia australis* blooms
3:05		Session Discussion
3:25	Ian Jenkinson	Laminar-flow drag reduction found in harmful algae cultures: Is this the Lotus-leaf effect in phytoplankton?

THURSDAY 23 AUGUST

	Session 5	**Present gaps, future strategy**
9:00	Francisco Chavez	Session Overview
9:10	Gotzon Basterretxea	Lessons and gaps from last decades of research on nearshore microalgal blooms in the western Mediterranean Sea
9:35	Jaume Piera	Sampling requirements to characterize multiscale processes in HAB dynamics

10:00		Break: Coffee and Refreshments.
10:25		Session Discussion
10:45	Bridget Seegers	Coastal ocean dynamics and the subsurface seeding of surface harmful algal blooms in southern California
11:10		Tour of MBARI
12:00		Lunch
1:30		Open for group discussions for: • Identification of gaps in knowledge • Identification of future manuscripts • Identification of future international proposals

FRIDAY 24 AUGUST

Session 6: Meeting of the organizing committee to prepare the report

Elisa Berdalet, Francisco Chavez, Margaret McManus, Oliver Ross, John Ryan, Hide Yamazaki

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APPENDIX III – Abstracts and Extended Abstracts

THE ROLE OF COUPLED PHYSICAL-BIOLOGICAL MODELS FOR HAB PREDICTION IN CALIFORNIA

Clarissa R. Anderson[1], Raphael M. Kudela[1], Igor Shulman[2], Bradley Penta[3], Yi Chao[4], David A. Siegel[5], Claudia Benitez-Nelson[6]

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The use of optical signals to detect harmful algal blooms has proven successful for a variety of species and regions but shown limited application for remotely sensing toxic blooms of *Pseudo-nitzschia* along the California coast. Statistical models that incorporate satellite data are useful for detection and tracking of large plankton blooms but show reduced skill in remote detection of toxins. The latter requires knowledge of *in situ* nutrient distributions to constrain our inference of bloom physiological state. Regional ocean models accurately predict physical parameters for forcing statistical models of HABs and, when coupled to ecosystem models, provide simulations of chemical and biological fields that are critical for estimates of toxin production. Initial testing of previously developed statistical models parameterized with coupled physical-biological numerical model output shows promise. Despite error in modeled fields at regional scales, this approach generally captures seasonal patterns of toxic blooms but cannot currently replace environmental data. Future improvement requires coupled development of statistical and mechanistic models with numerical output to improve skill of short-term forecasts and allow for decadal analyses of forcing functions driving blooms and toxin production.

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CURRENT PATTERNS AND RESIDENCE TIMES IN MATARINAO AND MURCIELAGOS BAYS, PHILIPPINES: IMPLICATIONS ON THE DISTRIBUTION OF *PYRODINIUM* BLOOMS

Sanny David Lumayno[1], Cesar Villanoy, Aletta Yñiguez, Irene Alabia, Ian Quino Fernandez, Garry Benico and Rhodora Azanza

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This is the first report on hydrodynamic models to determine current and water residence time patterns for Matarinao and Murcielagos Bays (in Central and Southern Philippines, respectively) which have been experiencing prolonged Harmful Algal Blooms (HABs). Field surveys were conducted in Matarinao Bay in April 2010 and in Murcielagos Bay in February 2011. An SBE25 CTD was used in obtaining temperature and salinity data to characterize stratification across the bay areas. Hydrodynamic models of both bays were developed using Delft-3D-FLOW software with tides as forcing factor. Spatially explicit water residence times were estimated from the model based on rates of concentration decrease of a hypothetical pollutant within the bay due to advection out of the bay. Both bays are divided into two distinct areas – the mouth, with faster current flow and low residence time and the head area with slower current flow and higher residence time. Areas with long residence times correspond to areas that show higher concentrations of *Pyrodinium bahamense* var. *compressum* suggesting that in small and shallow embayments such as Murcielagos and Matarinao Bays, advection plays a major role in sustaining Harmful Algal Blooms. Further, the bay's residence time may determine the extent of HABs / *Pyrodinium* blooms.

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LESSONS FROM LAST DECADES OF RESEARCH ON NEARSHORE MICROALGAL BLOOMS IN THE WESTERN MEDITERRANEAN SEA

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Extended abstract

The paradigm of blue oligotrophic Mediterranean waters with modest increase in productivity as a response to seasonal enrichment produced by water column mixing or to mesoscale structures, such as fronts and gyres, is not widely applicable. The inner-shelf waters are relatively uncoupled from open ocean processes representing a well differentiated niche, where nutrient levels are relatively high and high-biomass microalgal blooms tend to occur (Flo et al. 2011). Several factors define this singularity including strong seasonal stratification, generally weak and variable currents, and a microtidal regime. The biogeochemical contrast between the culturally enriched inner-shelf waters and the oligotrophic conditions prevailing further offshore is particularly notable during summer, when surface oceanic waters are nutrient depleted and when nearshore waters in many coastal areas are particularly poorly renewed. Under these conditions, some harmful bloom species have a competitive advantage and indeed blooms are frequent and recurrent (Garcés and Camp 2012).

Monitoring data shows that nearshore blooms in the Western Mediterranean Sea are compositionally diverse, highly localized, and either recur annually or emerge in a seemingly arbitrary manner. Even though this variability, the diversity of the species causing harmful algal blooms in the area can be reduced to two main categories, the harmful algal blooms due to toxic or potentially toxic algae (e.g. *Alexandrium*, *Dinophysis*, and *Pseudo-nitzschia*), which can cause toxic symptoms in the marine fauna and humans, and high-biomass blooms producers (e.g. *Alexandrium, Gymnodinium*), which cause problems mainly because of the high biomass itself (cell abundances higher than 10^5-10^6 cells l^{-1} and the production of organic matter. Because of their relevance in this region, several species deserve mentioning:

- Among the toxic species of the genus *Alexandrium*, the most widespread species in the Mediterranean basin are the PSP producers *A. minutum* and *A. catenella*. Both are frequently reported in harbours, beaches and lagoons. Monitoring data suggest an increase in abundance and geographic expansion of these species in the Mediterranean Sea (Vila et al. 2001b; Lugliè et al. 2003; Collos et al. 2004; Penna et al. 2005; Turki and Balti 2007).

- Among the noxious species, *A. taylori* produces and maintains elevated biomasses (10^5 cells L^{-1}) and causes green-brown discoloration in marine coastal areas with the consequent water deterioration for recreational uses and beaches. Usually, the local authorities are alerted to the presence of the blooms because the seawater acquires a sewage polluted aspect. *A. taylori* blooms recurrently during the summer at highly frequented beaches along the Mediterranean Sea (Garcés et al. 1999; Basterretxea et al. 2007; Giacobbe et al. 2007).

- Several *Gymnodinium* species, as *G. impudicum*, *G. litoralis* or *G. instriatum* also produce high biomass blooms ($>10^5$ cell L^{-1}) in the Western Mediterranean Sea, affecting harbors, beaches and lagoons. Such proliferations usually appear during summer months, altering the water coloration and producing mucilages (Fraga et al. 1995; Vila et al. 2001a; Reñé et al. 2011).

Depending on atmospheric and oceanographic conditions, as well as on biological constrains, the high biomass proliferations produce water discoloration for time scales typically spanning from few days to weeks, although exceptionally prolonged episodes of up to two months have been observed. With some interannual variations, the number of HAB episodes in beaches and natural areas has remained relatively constant during the last decade in this region, however, in harbors and port areas the events are seemingly increasing. In the case of some dinoflagellates species, recurrence at these sites is been related to dormant cyst accumulation in the sediments and to bottom boundary resuspension processes (Anglès et al. 2010), an example of the importance of understanding species life strategies to explain bloom dynamics.

Blooms in the Western Mediterranean occur as small scale patches of increased biological activity in coastal and nearshore areas. This is, nevertheless, not unique to the Mediterranean Sea. Studies based on detailed surveys and high frequency measurements have shown that innershelf and nearshore regions often contain well differentiated ecosystems spatially structured as cross-shore, and often vertically thin gradients that present enhanced biological response. The existence of these ecotones of elevated diversity and productivity in coastal waters has been recently postulated by Ribalet et al. (2010). Some singularities distinguish the functioning of inner-shelf from open water systems. Principally, (1) the terrestrial influence (either natural or anthropogenic) is here a major driver (2) the benthic-pelagic

exchanges acquire more weight in the water column budgets, and (3) the geochemical (i.e. terrestrial and benthic nutrients) and biological factors are major regulators of bloom dynamics since physical processes (i.e. advection and diffusion) are attenuated. The delivery of terrestrial nutrient as diffuse groundwater discharges along the coast and the release of interstitial nutrients from the sediments have revealed as important factors in fueling microalgal blooms in areas with permeable sediments (Basterretxea et al. 2010; Basterretxea et al. 2011). Experimental evidence shows that even small discharges from unpolluted aquifers can induce notable changes in nearshore microbial communities (Garcés et al. 2011). Also, evidence shows that shorter scales of variability (often episodic) are here more important than in offshore waters due to the absence of significant tides. Comprehension of the mechanisms that regulate these processes has evident implications to the understanding of the onset and subsequent development of algal blooms but it is also a prerequisite for building reliable scenarios and predictions for future changes in drivers and pressures.

To conclude, the great effort posed into research and monitoring programs has yielded good results to the understanding of some process of these outbreaks such as recurrence, intensity and composition. However, while some aspects of these blooms seem solidly founded, wide gaps persist in the comprehension of the mechanisms that underpin their occurrence and that regulate their fate.

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ESTIMATING PHYTOPLANKTON GROWTH RATES IN A STRATIFIED SYSTEM: EXPERIMENTAL AND MODELING APPROACHES, OPEN QUESTIONS

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Extended abstract

The estimation of species-specific *in situ* growth rates (μ) is one of the fundamental parameters to understand population dynamics. The *in situ* growth rate is determined by intrinsic genetic factors, as well as by environmental conditions (e.g. light, turbulence, temperature, salinity). In the particular case of species involved in harmful events, such understanding is aimed to improve predictive capabilities to optimize management of the affected areas. Laboratory experiments have contributed in part to provide estimations on pure cultures under controlled conditions, but laboratory conditions can hardly mimic nature. Furthermore, some organisms of interest, like *Dinophysis,* had not been successfully maintained in cultures until recently. At present there is neither a universal nor a perfect method to estimate *in situ* μ. This presentation reviewed some commonly available techniques, proven useful to estimate μ for certain harmful species as well as for phytoplankton in general, and indicated their advantages and limitations. The mitotic index proposed by McDuff & Chisholm (1982) and subsequently modified by Carpenter & Chang (1988) has proven to be useful for the estimation of the species-specific *in situ* μ of several species, in particular when they represent a small fraction of the microplankton community. It is based on the es-

timation of the frequency of cells under the so-called "terminal events" within the cell cycle—e.g. nuclear division (s), cytokinesis (c) and regeneration of sulcal list/spines (r)—and their time duration (T):

$$\mu = \frac{1}{n(T_c + T_r)} \sum_{n=1}^{n} ((t_s)_i) \ln[1 + f_c(t_i) + f_r(t_i)]$$

For some HAB species, e.g. *Dinophysis* spp., cells undergoing these terminal events can be morphologically recognized by microscopic observation (e.g. Reguera et al. 2003 and references therein) (Figure 1). However, such morphological recognition is not so easy in most phytoplankton species. In certain scenarios, when the blooms are almost monospecific or the targeted species can be clearly differentiated from the rest of the assemblage, the analysis of the cellular DNA content stained with specific fluorochromes (in combination with flow cytometry or microfluorimetry) has allowed also the application of the mitotic index approach. That was the case estimating μ for *Karlodinium* spp. and *Alexandrium* spp. (Garcés et al. 1999) in Alfacs Bay (NW Mediterranean). In any case, for accurate estimations of μ, the mitotic index based method requires intensive samplings over 24 hours at very high temporal resolution with a minimum requirement of cell densities (e.g. Velo-Suárez et al. 2009). This poses severe limitations for its application using conventional sampling strategies and it often requires previous concentration of the samples. Recently, the autonomous FlowCytoBot sampler (Campbell et al. 2010), that combines video and flow-cytometry technologies, has provided a high resolution time series of both *Dinophysis* cell abundances and frequencies of cells undergoin mitosis during a bloom at the Port Aransas ship channel (Mission-Aransas, Gulf of Mexico).

Some promising technical advances have appeared over the last years, although they still require detailed tests for their application. Examples include, the estimation of the RNA/DNA ratio combining oligonucleotide and antibody probes (Anderson et al. 1999) or species-specific fluorescent staining of silicate uptake in diatom cells (Leblanc and Hutchings 2005).

For the estimation of the *in situ* μ of the whole phytoplankton community or of some functional groups, the dilution technique (Landry and Hasett 1982; Landry et al. 1995) is most commonly used. This method, based on *in situ* incubations at fixed depths allows the simultaneous estimation of grazing by microzooplankton on phytoplankton, another key parameter in the population dynamics equation. The main sources of errors of the method arise from the artifacts associated to sample manipulations and from the fact that incubations at fixed depths entrain photoacclimation problems that can rate estimates based on changes of chlorophyll (pigments) concentrations (e.g. Gutiérrez et al. 2009; Ross et al. 2011).
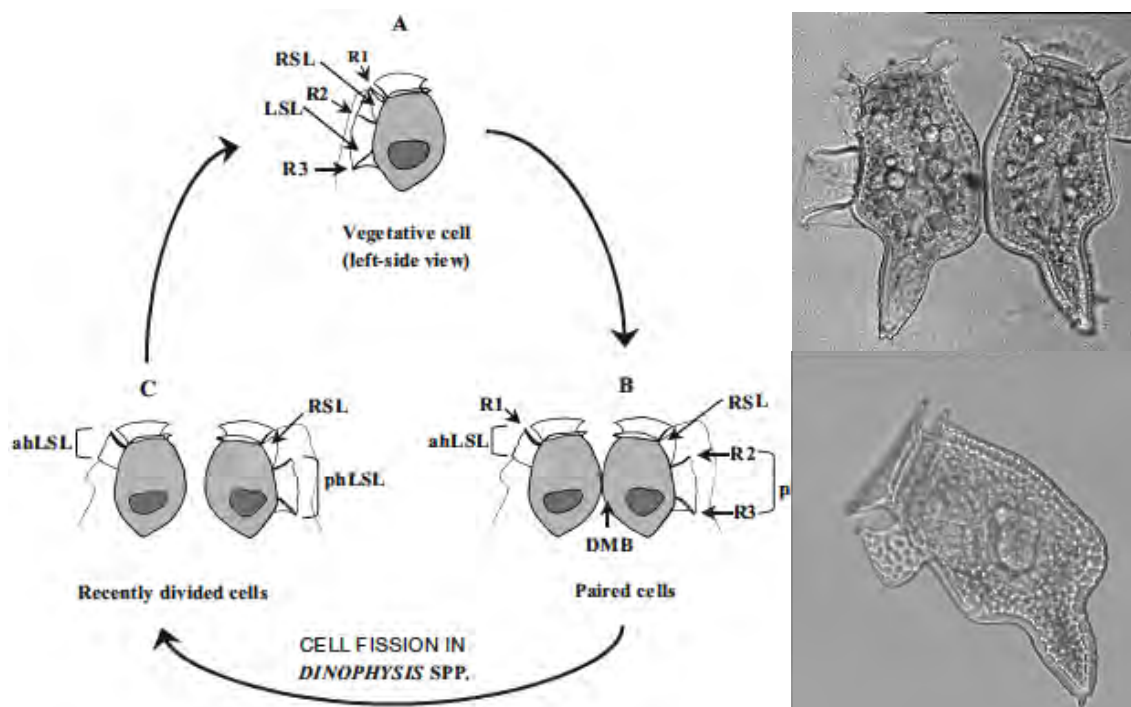
Figure 1. *Left: Simplified diagram of the* Dinophysis *cellular fission, showing the main morphological features used to estimate* in situ *μ by the mitotic index approach. A: Fully developed vegetative cells; B: paired daughter cells; C: recently divided cells. Right: Microphotographies of* D. caudata *recently divided cells: still remaining in pairs (top) and already individual (bottom). From Reguera et al. 2003, with permission.*

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HIGH-RESOLUTION 3D MODELLING OF OCEANIC FINE STRUCTURES USING VERTICALLY ADAPTIVE COORDINATES

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Extended abstract

There are various physical and biogeochemical mechanisms under debate which may be responsible for the establishment and maintenance of thin phytoplankton layers in the upper ocean. To understand their role and relative contribution to this environmentally critical phenomenon under complex realistic conditions, three-dimensional numerical modelling is an indispensible tool. However, application of conventional ocean models may be insufficient, since their vertical numerical resolution of typically above 1m will not resolve thin layers of a comparable vertical extent. In addition, numerical mixing (see Burchard and Rennau 2008, for
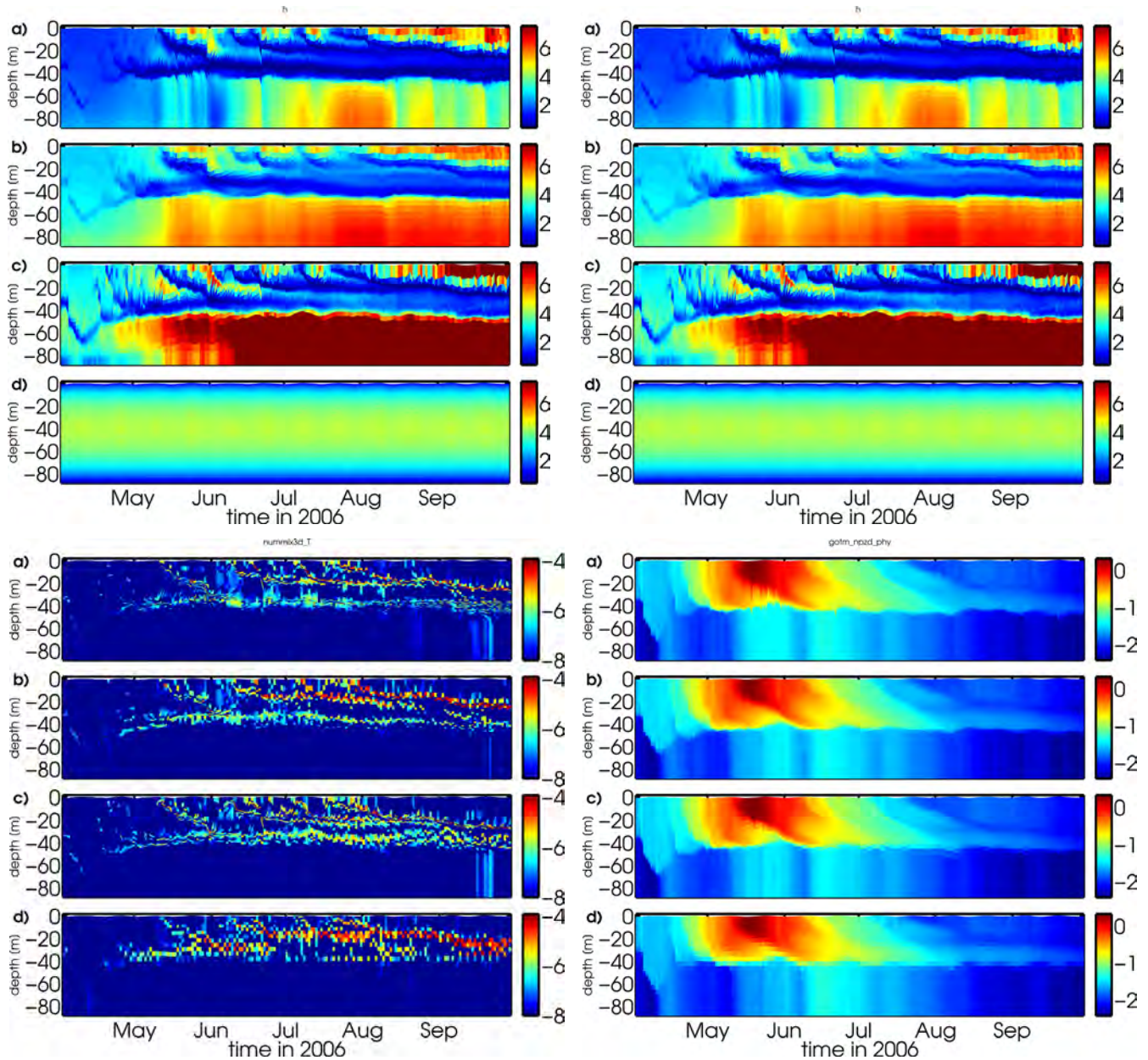
Figure 1. Mixed layer and plankton dynamics in the Central North Sea simulated by means of vertical coordinated adapted to physics and biogeochemical properties at a water depth of 80m. Four different coordinate definitions are used: a) 50 coordinate layers adapted to stratification and shear and to nutrient and plankton concentration; b) same as a, but for 30 layers; c) 30 coordinate layers adapted to stratification and shear; d) 30 layers of non-adaptive sigma coordinates. Four different variables are shown: upper left: potential temperature in [°C]; upper right: layer thickness in [m]; lower left: numerical mixing in $\log_{10}[D^{num}/(K^2/s)]$; lower right: phytoplankton concentration in $\log_{10}[P/(mmol\ N/m^3)]$.

an exact analysis method) would artificially erode thin layers moving up and down through fixed grid layers due to internal wave activity.

The aim of this presentation is to extend the modelling concept of *vertically adaptive coordinates* towards biogeochemical properties. This approach exploits the property of general model grid vertical coordinates of allowing redistribution of coordinate layers at each time step with great flexibility. Vertically adaptive coordinates are defined in a way that they accumulate in regions of large vertical gradients of selected state variables such as density or shear. This is obtained by solving a diffusion equation for the vertical layer position where the diffusivity is proportional to the squares or density or velocity gradients (Burchard and Beckers 2004; Hofmeister et al. 2010). Baltic Sea applications of these adaptive coordinates using the three-dimensional ocean model GETM (General Estuarine Transport Model, www.getm.eu, Burchard and Bolding 2002) have shown that the undesirable numerical mixing is strongly reduced and that saline inflows are smoothly propagating from the North Sea to the central Baltic Sea without significant artificial entrainment (Hofmeister et al. 2011).

In an experimental setup, the concept of adaptive vertical coordinates has been extended to accumulate at locations of biogeochemical gradients, in e.g. nutrient or phytoplankton concentrations. This would allow resolving moving thin layers also at locations where they do not coincide with layers of locally increased shear or stratification. In a first 3D experiment simulating the annual cycle of nutrients and phytoplankton in the North Sea using a simple NPZD model, this new approach is compared to fixed sigma coordinates and to adaptive coordinates that only adapt to the physical structure of the flow, see Figure 1.

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THE QUEST FOR BIOLOGICAL AND PHYSICAL MEASUREMENTS OF HABs: PROGRESS AND PROSPECTS

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Extended abstract

A fundamental impediment to understanding the formation, evolution, and ultimate dissipation of Harmful Algal Blooms has been a lack of suitable instrumentation for *in situ* observation. Spatial scales ranging from millimeters to tens of kilometers define both the micro and macroscopic features of the bloom, while temporal scales of cell growth, grazing, and physical transport can span the range of hours to weeks. Although shipboard sampling programs with traditional instruments like CTD-fluorometers and bottle casts can answer a variety of questions, increased sensing ability is paramount for sufficient understanding. In his talk, Dr. Jaffe documented both past, present, and envisioned work in developing ocean-sensing systems for sampling the euphotic zone. This includes the past development of a large autonomous profiler that was equipped with a laser imaging fluorometer used along with a host of other instruments (FIDO-Phi). Presently, his group is developing an inexpensive miniature vehicle, to be deployed in swarms, that has many of the properties of its predecessor, however, can be localized in 3-dimensions to track internal waves and mimic larval transport. Additional efforts in the acoustic tracking of zooplankton and the optical imaging of organisms from centimeters to microns are aimed at gaining a better understanding of the statics and dynamics of both plants and animals in the top 100 meters of the ocean. Examples of previous and recent work (performed in the last few months!), as well as intended future developments were described. One of such studies (Figure 1a) shows the result of counting diatoms from images (as shown in the smaller rectangles) obtained with an underwater microscope system. The standard fluorometer profile (Figure 1b) was obtained simultaneously from a CTD – fluorometer package that was co-located with the imaging system. As is evidenced, due to the increased information from the imaging system and the small volume of interrogation of the fluorometer, the diatom counts present a much less noisy view of the locations of the diatoms that were *in situ* at the time of data collection.

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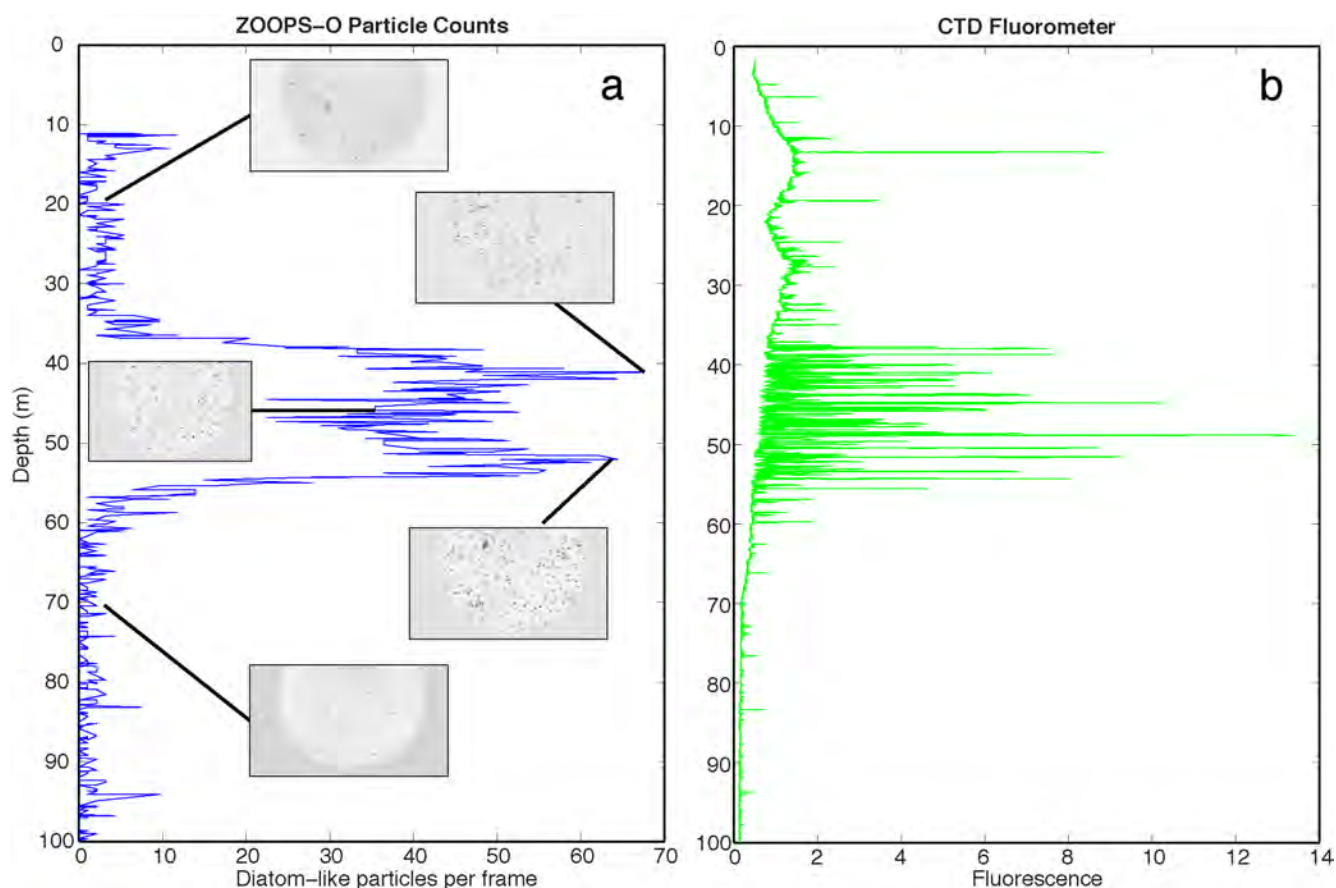
Figure 1. (a) A vertical profile that shows diatom counts as a function of depth along with the images from which the counts were derived. (b) The concurrent vertical profile as measured using a standard co-located fluorometer. (Reprinted with permission, Jaffe et al. 2013).

LAMINAR-FLOW DRAG REDUCTION FOUND IN HARMFUL ALGAE CULTURES: IS THIS THE LOTUS-LEAF EFFECT IN PHYTOPLANKTON?

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To validate a model of how *Karenia mikimotoi* blooms may control the stability of pycnoclines by increasing viscosity (Jenkinson and Sun 2011), we measured the viscosity of cultures of *K. mikimotoi*, other harmful algae and a bacterium. This was done in flow through capillary tubes of diameter 0.7 to 3.0 mm. Viscosity was generally higher than in filtered water at small diameters. We ascribe to polymeric thickening, already well documented. At large diameters, however, viscosity became smaller than water. This is called drag reduction (DR). This was not turbulent DR, as the Reynolds numbers of the flow were far too small to allow turbulence to occur. So it was laminar-flow DR (LDR). In the last 15 years, LDR has been found associated with self-cleaning and anti-fouling hydrophobic surfaces, that are rough at nm- to µm-scales, like the surfaces of Lotus leaves and now many industrial products. We suggest that the surfaces of phytoplankton cells and their exopolymers may produce a similar phenomenon. If this is correct, it provides another tool for phytoplankton to engineer its ecosystem, by increasing local flow at low Reynolds numbers and small scales. This would be in addition to the tool of reducing flow by polymeric thickening. Self-cleaning and anti-fouling may also be associated with the Lotus-leaf effect. DR in the larger capillaries interfered with measurement of polymeric thickening as a function of length scale. Our model thus remains unvalidated until further work can be done.

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A REGIONAL COMPARISON OF UPWELLING, COASTAL LAND USE PATTERNS, AND HAB HOTSPOTS ALONG THE CALIFORNIA COAST

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California represents approximately 1,000 miles of the Pacific coastline of the U.S. and major fractions of the coastal economy and environmental resources of our nation. Alarmingly, blooms of harmful and toxic algae have increased in frequency and severity along this coast during the past few decades. Although several HAB organisms are present, *Pseudo-nitzschia* (Domoic Acid Poisoning) is rapidly becoming the single greatest threat and problem for human and ecosystem health, potentially eclipsing PSP in severity due to the diverse impacts on the economy through commercial fisheries and tourism, as well as via direct impacts on marine birds and mammals. Our primary objective is to develop a better understanding of the ecophysiological conditions leading to bloom and toxin initiation for *Pseudo-nitzschia*, by simultaneously comparing two "hot spots", Monterey Bay and San Pedro, California. We hypothesize that large-magnitude blooms are associated with physical processes in California, similar to other regions of the U.S., and that the large bloom events spanning hundreds of kilometers over a period of weeks to months initiate offshore or in the subsurface where monitoring is sparse, allowing them to seemingly "appear" with little or no warning. We hypothesize that there are a unique set of environmental conditions leading from bloom initiation to toxicity that can be identified through a comparative approach, allowing us to contrast potential factors (such as stratification, nutrient load, nutrient type) between regions, and that blooms initiate both offshore and as subsurface layers. Here we present overall project goals and initial results from this 5-year program.

BIMODAL DISTRIBUTION PATTERNS OF MOTILE PHYTOPLANKTON IN THE STRATIFIED GULF OF FINLAND

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Field observations in the summers of 2009-2011 using autonomous and towed systems and adaptive sampling have revealed distinctive bimodal vertical distribution patterns of motile phytoplankton in the stratified Gulf of Finland (Baltic Sea). Thin phytoplankton layers, where chlorophyll *a* fluorescence values occasionally exceeded those in the upper layer, have been observed in the deeper part of the thermocline. The main species found in the deep maxima were the dinoflagellates *Heterocapsa triquetra* and (occasionally) *Dinophysis acuminata*. Vertical migration of the former species and different nutritional strategies of the two populations of the latter species are suggested as biological processes supporting the formation and maintenance of thin layers. The deep biomass maxima were the most intense in the areas of locally weaker stratification in mesoscale. We argue that the mesoscale dynamics favor successful vertical migration of *H. triquetra* between the surface layer and deep nitrate reserves. Significance of another physical mechanism – straining of phytoplankton patches by vertical shear can be proved by the observed tilt of phytoplankton layers across surfaces of constant density. Thin phytoplankton layers, as well as vertical migration leading to selective transport of nutrients, have to be taken into account in the regional ecosystem models, both to forecast harmful blooms and describe more precisely the seasonal dynamics of nutrients and primary production in the stratified estuaries.

THE INFLUENCE OF DIURNAL WINDS ON PHYTOPLANKTON DYNAMICS IN A COASTAL UPWELLING SYSTEM

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At a coastal upwelling zone near 30°S latitude, diurnal wind variability forced energetic inertial current oscillations (>0.5 m s^{-1}) that materially influenced phytoplankton distribution and productivity. The diurnal-inertial band resonance found at this latitude in

the Benguela upwelling system allowed rapid, efficient transfer of energy from counterclockwise rotating winds into anticyclonic currents upon the onset of the transition from relaxation to upwelling conditions. These inertial band oscillations caused regular pycnocline outcropping at the surface and the vertical advection of nutrient-rich waters in the coastal zone. Vertical pycnocline outcropping was coincident with the vertical redistribution of chlorophyll *a* fluorescence from a subsurface maximum to uniform distribution in the surface layer, in effect turning vertical phytoplankton gradients into horizontal ones. The shear caused by the vertical structure of the inertial oscillations during (and after) the onset of wind forcing was intense enough to erode the strong stratification established during a prior relaxation period, according to Richardson number and strain analyses. This diapycnal mixing also had the consequence of mixing heat and chlorophyll downwards and nutrient-rich water upwards, such that the surface nitrate concentration became non-zero. Chlorophyll concentrations thereafter increased in what qualitatively appeared to be a phytoplankton bloom. This diurnal-inertial resonance-driven mechanism for mixing-driven nutrient flux, embedded within the low-frequency advective vertical flux forced by Ekman dynamics, enhanced the efficiency of wind forcing to produce high phytoplankton productivity, and is likely to be of first order importance in bloom dynamics in the study area (including harmful algal blooms). Our results argue that, in general, high frequency physical dynamics should be considered when studying the bottom-up forcing of algal blooms and red tide events.

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TOXIC HARMFUL ALGAE BLOOMS IN TODOS SANTOS BAY, NORTHWESTERN BAJA CALIFORNIA, MEXICO: II- CIRCULATION ASSOCIATED WITH *PSEUDO-NITZSCHIA AUSTRALIS* BLOOMS

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Extended abstract

Here we study numerically the circulation in Todos Santos Bay area (31.88°N) and off Baja California during Spring and Summer 2007. This period is particularly interesting after an intense toxic algal bloom occurred in April 2007 in this area, which was most probably caused by environmental conditions associated with the wind-driven upwelling in the region. We carried out high-resolution, numerical model simulations to study dynamical features along the coast of the northern Baja California (BC) Peninsula and within Todos Santos Bay (TSB), and also to be used in a three-dimensional Lagrangian analysis which provides information about the origin and distribution of the waters present in the Bay during the occurrence of the toxic bloom. This study is the beginning of an interannual analysis of the dynamics in TSB and BC, which will involve also physical-biological interactions.

The analysis is based on the Regional Ocean Modeling System (ROMS) version 3.0 for the spherical-coordinated domain shown in Figure 1. The model is forced by realistic wind (IFREMER's MWF/Blended). At the open boundaries, daily-mean data from the regional model (Baja California domain) described in Rivas et al. (2010) are used.

Surface mean circulation in TSB shows an important influence by the flow seaward of the Bay, a persistent cyclonic gyre northwest of the Bay, and some recirculation in the eastern region (Figure 1a), which favors a modification (heating) of the water masses (Figure 1b). The transport into the Bay within the surface levels generally occurs via a near-surface net inflow through the northern section, which is compensated by a net outflow through the southern section. In the deeper levels, the volume supplied by the slope equatorward undercurrent is compensated by an outflow at mid-depth. The transport through the northern section presents an intensification during Spring and Summer. There are periods, however, when a vigorous transport through the southern section occurs (e.g., late February-early March and May). The mean net transport into the Bay is ~2,500 $m^3 s^{-1}$, this would renew the volume of the Bay (~$10^{10}\,m^3$) in 47 days.

Three-dimensional, Lagrangian advections, both backward and forward in time, were carried out in order to study the origin and distribution of the waters present within TSB by the end of April 2007, when an intense toxic *Pseudo-nitzschia* bloom occurred (see García-Mendoza et al. 2009). For details about the advections, see Rivas et al. (2010). The Lagrangian-advection results show that in spite of the chaotic character of the particle paths (evidenced by the important scatter of the paths), some coherent, meaningful patterns can be identified. One of these patterns shows that the particles cross the model's western boundary and travel westward to the Southern California-Baja California shelf, most probably advected by the so-called Ensenada Front, to ultimately flow southward and enter TSB (Figure 2a). Once the particles enter TSB, they get trapped within a persistent cyclonic eddy located in Salsipuedes Bay, northwest of the Bay, to ultimately
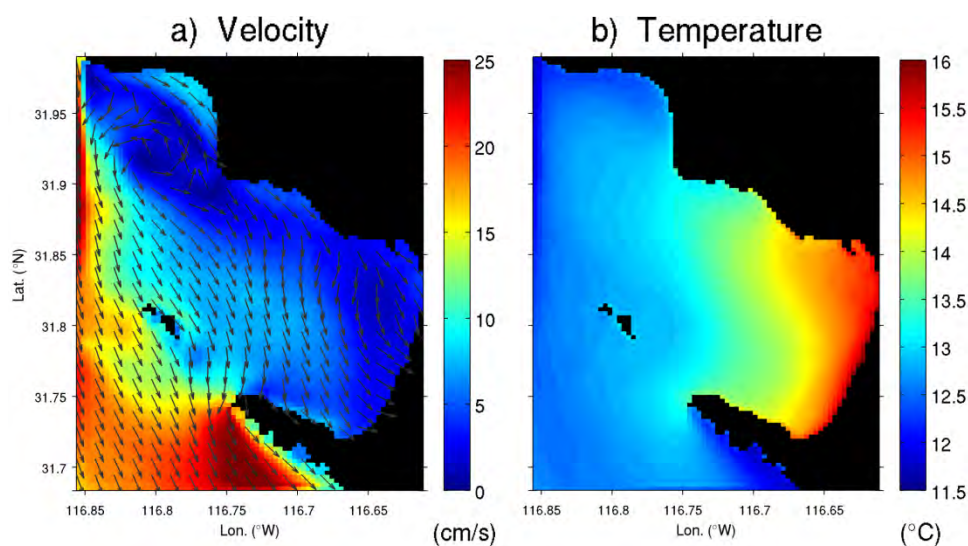
Figure 1. *Modeled Spring-mean surface (a) velocity and (b) temperature in TSB.*
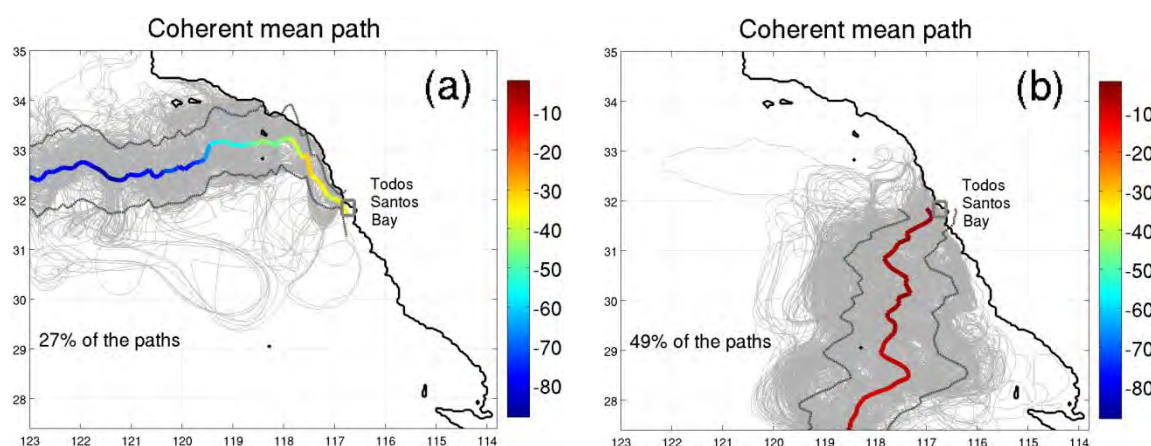
Figure 2. *(a) Particle paths with origin between the latitudes of 32°N and 33.5°N along the model's western boundary (27% of the total of 830 paths). (b) Paths leaving between the longitudes of 119.5°W and 118°W along the model's southern boundary (49% of the total paths). In both cases, a representative "mean" path is shown. Colorbar indicates the along-path depth.*

upwell to the surface levels and leave to the south. A residence time for the particles within TSB can be estimated by comparing the times at which they enter and leave the Bay, this is about one and a half months, consistent with the estimate from the net transport into the Bay. After the particles leave TSB they flow southward at surface levels and leave the model's domain through the southern boundary (Figure 2b).

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THE DILUTION METHOD - A MODELING STUDY

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The estimation of (species-specific) phytoplankton *in situ* growth rates (μ) is one of the fundamental parameters to understand population dynamics. As explained in the accompanying presentation (Berdalet et al. this workshop), estimating this parameter in the field is highly complex. One of the most accepted methods is the dilution technique (Landry and Hasset 1982; Calbet and Landry 2004) which has been designed to simultaneously estimate the growth rate and the grazing by microzooplankton on phytoplankton, another essential parameter to describe the population dynamics. The dilution technique involves the *in situ* incubation of organisms in bottles with particular nutrient enrichments at fixed depths.

We illustrate the limitations associated to this method and quantify the error associated with incubating the cells at a fixed depth, i.e. at fixed light conditions. By neglecting vertical mixing and the associated fluctuations in the ambient light levels, this incubation technique allows the organisms to acclimate their physiology to the ambient light level which results in different growth rates compared to freely mixing cells. Using a Lagrangian modeling approach we quantify the errors associated with this technique and suggest alternatives to minimize them (such as the yo-yo approach where the incubation models are cycled vertically through the water column, or the use of several incubation depth).

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IS ALFACS BAY A PHYTOPLANKTON BLOOM INCUBATOR? *IN SITU* MEASUREMENTS AND MODELING APPROACHES, OPEN QUESTIONS

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Extended abstract

Alfacs Bay, is a shallow microtidal estuary in the Ebre Delta, with a high productivity (compared to the adjacent oligotrophic NW Mediterranean waters), which has allowed the development of valuable aquaculture activities. Unfortunately, recurrent harmful phytoplankton outbreaks (caused mainly by *Alexandrium minutum*, *Dinophysis* spp., *Pseudo-nitzschia* spp. and *Karlodinium* spp.) threaten this industry. It is crucial to provide local policy makers with detailed knowledge and tools to minimize the socio-economic impact on the local community. With this final aim, our study focused on the exhaustive and continued study of the phytoplankton dynamics in relation to the physico-chemical forcings in the bay in order to better understand the occurrence of recurrent HAB events.

The productivity of the bay is due in part to its semi enclosed characteristics, and also to the nutrient supply through the freshwater inputs coming from groundwater seepage and specially from the runoff of rice field irrigation channels discharging from its northern coast. At seasonal time scale, the buoyancy associated with freshwater inflows dominates the tidal forcing and yields a strongly stratified two-layered system, with the surface and the bottom layers flowing in opposite directions (classical estuarine circulation). At shorter time scales, wind controls the physical behaviour of the bay. When wind-induced mixing is low, the water column stratifies showing the typical estuarine circulation.

Data have been collected for 6 years using synoptic cruises, time series of physical parameters from moored instruments (CT-loggers, ADCP, fluorometer) to obtain information on the general circulation, chlorophyll distribution, and stratification in relation to the meteorological conditions, and combining them with 3D modeling. Some cruises coincided with the occurrence of harmful outbreaks. The field data showed the existence of a preferential phytoplankton accumulation area in the inner NE side of the Bay (e.g. Figure 1), and a special vertical distribution, maybe linked to stratifi-
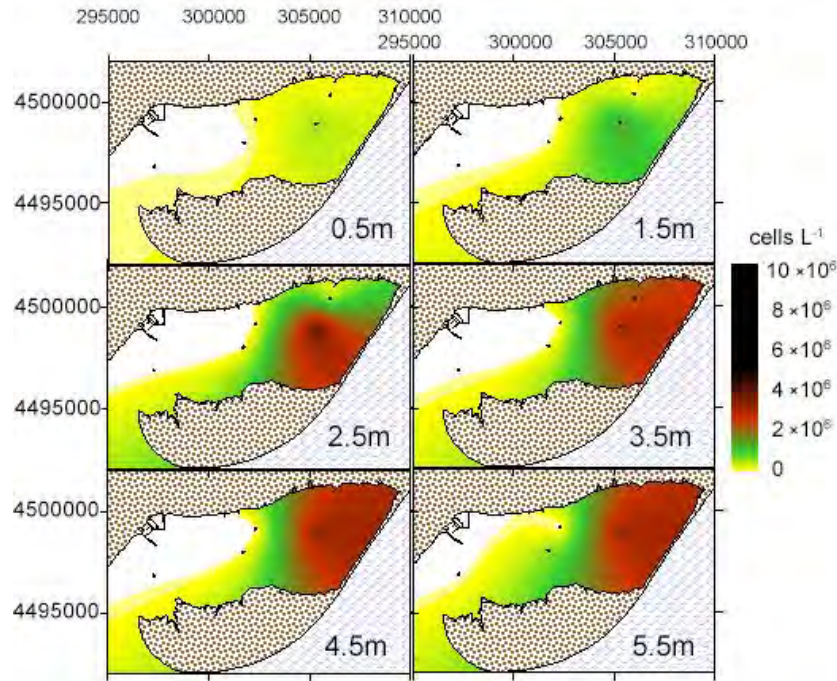
Figure 1. *Cell counts of Karlodinium spp. in June/July of 2007. Clearly visible is the preferential concentration in the NE interior of the bay and the lower part of the water column.*
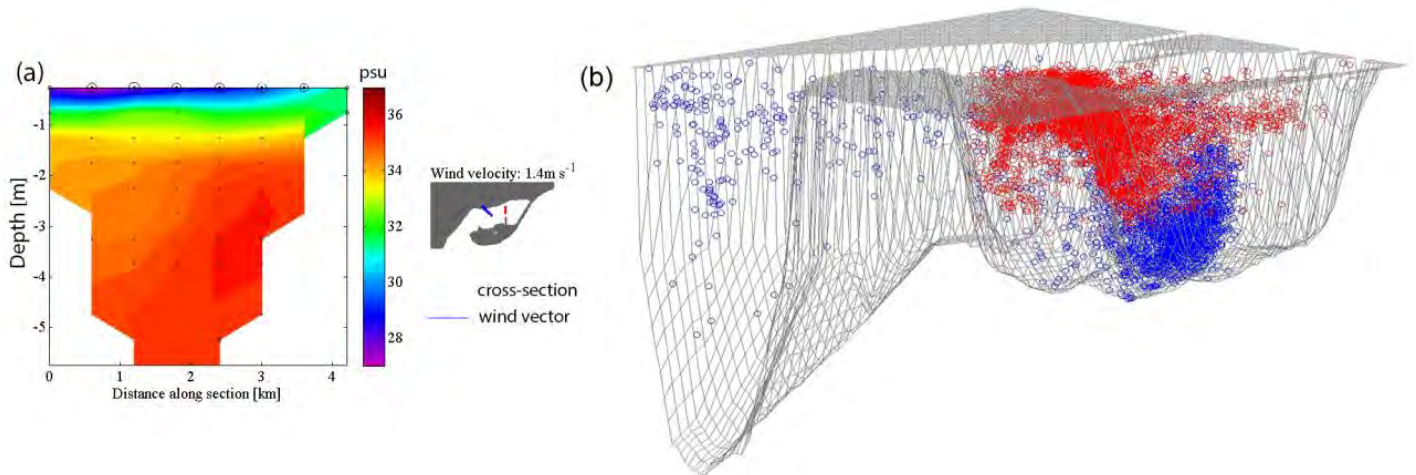
Figure 2. *Simulation result (a) the vertical salinity stratification during low wind intensities (the crosses and circles with dots inside them, represent the flow into and out of the bay respectively), (b) a snapshot of the coupled 3D hydrodynamic-particle tracking model including the bottom topography showing the particle retention in the NE interior.*

cation and/or biological behaviour. In addition to the nutrient supply, the hydrodynamic regime may explain the observed phytoplankton distribution patterns.

In particular the periodic suspension of the estuarine circulation due to wind mixing events, may facilitate bloom development in the bay's interior. This hypothesis was tested using new modeling approach featuring a 3D hydrodynamic model previously implemented and validated in Alfacs Bay (see detailed description in Llebot et al. accepted) in combination with a Lagrangian particle-tracking module (Ross and Sharples 2004; Ross et al. in preparation). Simulation experiments were performed for relevant periods for which cruise data was available, in order to compare the observed chlorophyll distributions with the modeled tracer concentrations. Two clouds (with 4000 passive tracers) were released, one in a vertically homogeneous distribution near the mouth of the bay and the other in the bay's interior. The estuarine circulation is particularly active when the water column is stratified and wind mixing is weak (Figure 2a), which drives the bottom particles towards the bay's interior, while flushing the particles in the surface layer out into the open Mediterranean. When wind-induced mixing is strong, the density stratification and associated estuarine circulation break down (not shown), and particles accumulate in the bay's interior (Figure 2b). When the freshwater inflow from irrigation channels is reduced and/or wind-induced mixing is high, the water column stratification decreases, resulting in a weakening of the estuarine circulation. Overall, this leads to increased residence times inside the bay.

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NEAR SURFACE TEMPERATURE STRATIFICATION AND THE WIND TRANSPORT OF SURFACE BLOOMS

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Extended abstract

The near surface thermal stratification produces a thin (~2 m thick) and warm near-surface layer. This buoyant layer is sufficiently decoupled from the layer below, that it can be transported efficiently by the wind stress.

Because in coastal upwelling areas the thermal wind is directed towards the coast during the day the buoyant layer is also transported towards the coast. During a surface bloom of *Lingulodinium polyedrum* on the northern Baja California coast (Oct. 2011) we measured near surface temperature stratification (NSTS) and drifter buoy trajectories (drogued at 1, 3, 5m). Temperature profiles during the bloom typically showed a gradient of about 0.2 to 0.5^{o}C between 1 and 3 meter depth. Generally NSTS took the shape of a continuous gradient and typically showed no marked discontinuity that would indicate a homogenous near surface layer (Figure 1). Temperature profiles inside and outside of the bloom showed differences in the upper 2.5 m; however, temperature gradients from 1 to 5 m for both cases showed similarities. Temperature differences are not simple to explain because the heat balance is strongly influenced by meteorological conditions with heat loss processes. We are still processing the temperature profiles to see if the high pigment concentration in bloom patches (> 80 mg m^{-3} chlorophyll) resulted in a significant increase in temperature due to high daylight attenuation at the surface. We expect that this mechanism would indirectly promote the transport of bloom patches towards the coast by thermal wind. The general pattern of drifter trajectories showed differences between surface (1m drogue), 3m and 5m drogue drifter trajectories. Drifter trajectories at 1 m were towards the shore following the wind direction whereas drifters at 3 and 5m depth showed trajectories parallel or away from shore. On three of the 6 days surface drifters did not have the same direction as the wind, which probably resulted from an interaction between wind and current forcing, but the differences in trajectory direction between 1, 3 and 5m drifters were maintained. Before the bloom condition, on three days we did a comparison of ADCP and drifter data and found similar behavior with different current vector directions at different depth (Figure 2). This shear flow pattern in the top few meters observed by us resulted in spiral current vectors that could turn in either direction depending on the azimuth relation of surface and deeper water current. Since this flow spiral responds on short time scales to varying winds, it bears no resemblance to Ekman-like spirals which are steady end conditions. The observed temperature stratification in the top few meters is a typical phenomenon in this regional and we propose that it is common feature in many other subtropical and tropical areas. In this work we also propose that the movement of the near surface layer, containing the surface bloom, is largely responsible for sustaining the bloom near the shore. We could demonstrate that during eight hours of active thermal breezes, typical for upwelling areas, the surface layer constituents including blooms were transported toward the coast about 2.7 km. Additional constituents that will be transported include all dissolved and particu-
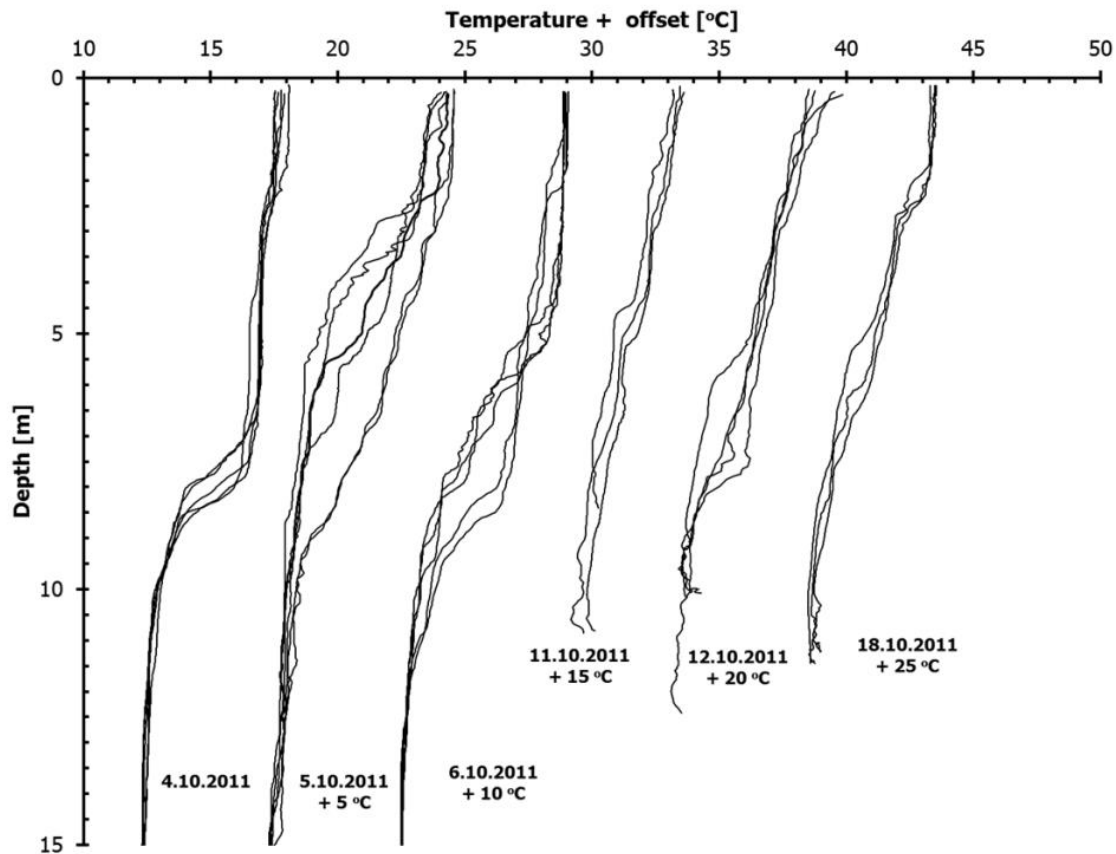
Figure 1. *Temperature profiles, CTD profiles on October 4, 5, 6, 11, 12, and 18, 2011 during a dense algal bloom in Todos Santo Bay, Mexico. Profiles of the different days are offset as indicated at the bottom below the dates. Modified from Ruiz-de la Torre et al. 2013.*
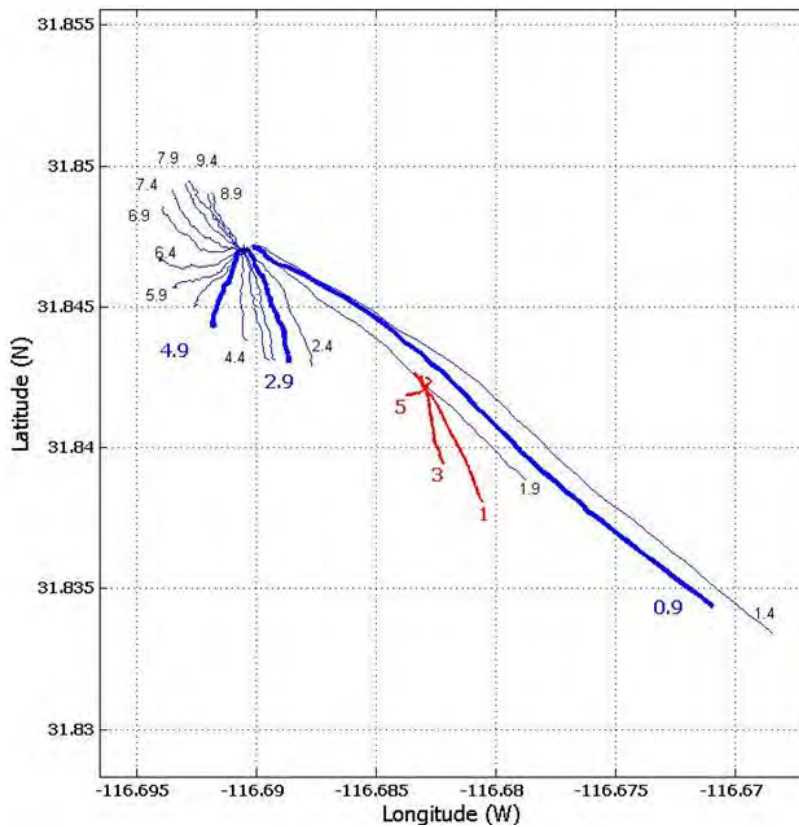
Figure 2. *Virtual displacements from ADCP (Aquadopp, Nortek) (heavy blue) at 4.9, 2.9 and 0.9 m, and CODE type drifters trajectories (red) at 5, 3, and 1 m on September 21, 2011. ADCP trajectories are for each 0.5 interval (light blue). Taken from Ruiz-de la Torre et al. 2013.*

late material in the top meters, including larvae and contamination, which broadens the applicability of the described wind transport in coastal waters. For more details see Ruiz-de la Torre et al. 2013.

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COASTAL OCEAN DYNAMICS AND THE SUBSURFACE SEEDING OF SURFACE HARMFUL ALGAL BLOOMS IN SOUHERN CALIFORNIA

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The Bight '08 Project used multi-month (February – June, 2010) Webb Slocum glider deployments combined with MBARI environmental sample processors (ESPs), weekly pier data, and ocean color data provide a multidimensional view of the development and evolution of harmful algal blooms (HABs). This combined data approach was used in the central Southern California Bight to better understand the spring seasonal variation in phytoplankton blooms related to many factors including upwelled nutrients and subsurface seeding of surface blooms.

Results from the glider and ESP observations show that blooms of toxic *Pseudo-nitzschia* sp. can develop offshore and subsurface prior to their manifestation in the surface layer and/or near the coast. A significant surface manifestation of the blooms appears to coincide with periods of upwelling, or other processes that cause shallowing and surfacing of the pycnocline and subsurface chlorophyll maximum.

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THIN LAYERS, CHEMOSENSORY STIMULATIONS AND COPEPOD SWIMMING BEHAVIOR: SMALL-SCALE CHANGES, BROAD IMPLICATIONS

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The ability of copepods to react to chemical cues such as phytoplankton exudates, conspecific and predator pheromones and chemical pollutants has been well illustrated. Despite their likelihood on the wild, little is still known, however, about the interactive effects of different chemosensory stimulations on copepods, especially in the context of thin layers that may contain toxic and non-toxic microalgae and exhibit very specific rheological properties. This study experimentally simulates thin layers characterized by distinct biotic and abiotic properties, and investigates their consequences on the swimming behavior of the common calanoid copepod *Temora longicornis*. Specifically, I first illustrate the ability of *T. longicornis* (i) to locate and remain within a layer of non-toxic algae, and (ii) to avoid a toxic layer (due to harmful algae or hydrocarbon contamination). Second, I quantify the geometric and stochastic properties of *T. longicornis* swimming behavior inside and outside a thin layer, demonstrate that the observed changes are density-dependent and can be interpreted as optimal foraging strategies; their consequences in terms of encounter rates and energy optimization are numerically explored and discussed. Similarly, the behavioral consequences of biologically-increased seawater viscosity are both experimentally and theoretically explored, with a specific focus on trophic interactions. Finally, I assess the interactive effects of attractive (non-toxic algae exudates, conspecific pheromones) and repulsive (toxic algae exudates, hydrocarbon contamination, predator pheromones) chemosensory stimuli. It appears that both synergistic and antagonistic effects appear below and above critical concentration thresholds that are discussed in terms of evolutionary adaptation to complex environments.

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TOXIC DIATOM BLOOMS OF THE GENUS *PSEUDO-NITZSCHIA* ALONG MEXICO'S NORTHWEST PACIFIC COAST

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In Mexico, the first toxic event associated with domoic acid occurred in 1996. *Pseudo-nitzschia* blooms appeared every winter since. Generally associated with anomalous cold and fresh water from the California Current pushing toxic species southwards, these events add Amnesic Shellfish Poisoning (ASP) to the Paralytic Shellfish Poisoning (PSP) danger. Additionally, plankton responds rapidly to local forcing because a bloom occurred during spring-summer. Domoic acid (20.156 mg/g) was detected by high performance liquid chromatography in cultured Pacific oysters from 26 June to 10 July 2005, bringing the first harvest closure from domoic acid. At the time, optical microscopic examination of plankton samples reveled stepped colonies of *Pseudo-nitzschia* as multiple species populations dominated by *P. australis*. The rapid occurrence of the bloom and dense concentrations of *Pseudo-nitzschia* in Bahía Ballenas suggest an oceanic bloom transported to the coasts by relaxation of upwelling or friction in the bottom layers as a subsurface process. Previous reports of *Pseudo-nitzschia spp.* associated with domoic acid showed less diverse assemblages (*P. australis* from 1996-1998 and *P. pseudodelicatissima* in 2004). Using scanning and transmission electron microscopy up to six (seven) species were observed during the bloom reported here. *P. calliantha* and *P. heimii* are the first records for Mexico. Results from our analysis and a review of published records suggest that *Pseudo-nitzschia* recently expanded along the northeastern coasts of the Pacific in cold water masses of the California Current increasing ASP danger in Mexican coasts.

LIVING IN A THIN LAYER: CALCULATIONS OF BIOLOGICAL RATES

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Thin layers are ubiquitous phenomenon in stratified coastal ecosystems. As thin layers are regularly sites of intense biological activity and can often be dominated by harmful algae, understanding their ecology is critical to numerous scientific disciplines, as well as public health and water management concerns. Quantifying biological rates within thin layers is at the heart of truly understanding their ecological dynamics. However, measuring rates within thin layers is not a trivial problem. This presentation will review strategies and approaches to measuring rates in thin layers, with examples of results from field studies. In addition, current and emerging technologies that can be applied to the problem will be discussed.

DINOFLAGELLATE VERTICAL MIGRATION AND THIN LAYER FORMATION IN LABORATORY EXPERIMENTS: PRELIMINARY RESULTS

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Dinoflagellates demonstrate a variety of vertical migration (VM) patterns that presumably give them a competitive advantage in stratified waters. The interaction between harmful algal bloom (HAB) dinoflagellates with their chemical-physical environment is a key aspect to understand their VM and thin layer (TL) development. However, at present, one of the major challenges lies in developing non-invasive instruments to measure these processes at small scales in the field and/or recreate them in laboratory experiments. In this work, VM behavior by HAB *Dinophysis caudata* was investigated using vertically stratified laboratory columns. Video and high-resolution image-analysis were used to quantify dinoflagellate vertical distributions and movement behavior. Several laboratory assays were designed to determine (1) the accuracy of the observation tools; (2) *D. caudata* ability to swim across several density gradients and (3) their capacity to form TL in small water volumes. Preliminary results will be

presented and highlight the next methodological steps to tackle before studying the *Dinophysis* sp. behavior at small scale.

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FLUORESCENT MICROSTRUCTURES: QUEST FOR BUILDING BLOCK OF PLANKTONIC ECOSYSTEM

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Extended abstract

Micro-scale aquatic ecosystems are the engine for earth's biogeochemical cycles. Phytoplankton fix inorganic carbon to organic carbon through the photosynthetic process. Although phytoplankton are single-cell organisms, they often appear in an aggregated form that elevates local fluorescence signal intensity. How intermittent are these features? We have developed a new free-fall microstructure profiler (TurboMAP-L) that carries sensors for turbulent shear and temperature gradient, small-scale fluorescence and turbidity as well as standard hydrographic parameters (conductivity, temperature, depth). The new profiler also carries a new laser fluorescence probe that resolves millimeter scale fluorescence fields, as well as a Digital Still Logger (DSL) CMOS camera system that records a 1024´1280 pixel image at 5Hz time interval with a pixel resolution of 330mm (Doubell et al. 2009).

Fluorescence profiles measured by TurboMAP-L and a conventional fluorescence probe are in good agreement at one-meter scale average. However, the fluorescence signals revealed by the LED fluorescence probe are intermittent at cm scale. Millimeter scale fluorescence signals obtained from the laser probe are even more intermittent than the cm scale LED signals (Figure 1). The source of the millimeter-scale strong signals identified from the DSL images are coagulated discrete material ranging between a few 100 mm and a few millimeters scale. Unfortunately, the DSL images are not well focused, so the details of the coagulated matter are not clear. Therefore, a recently developed holographic imaging system was combined with the TurboMAP-L operation in order to identify the detail of the millimeter
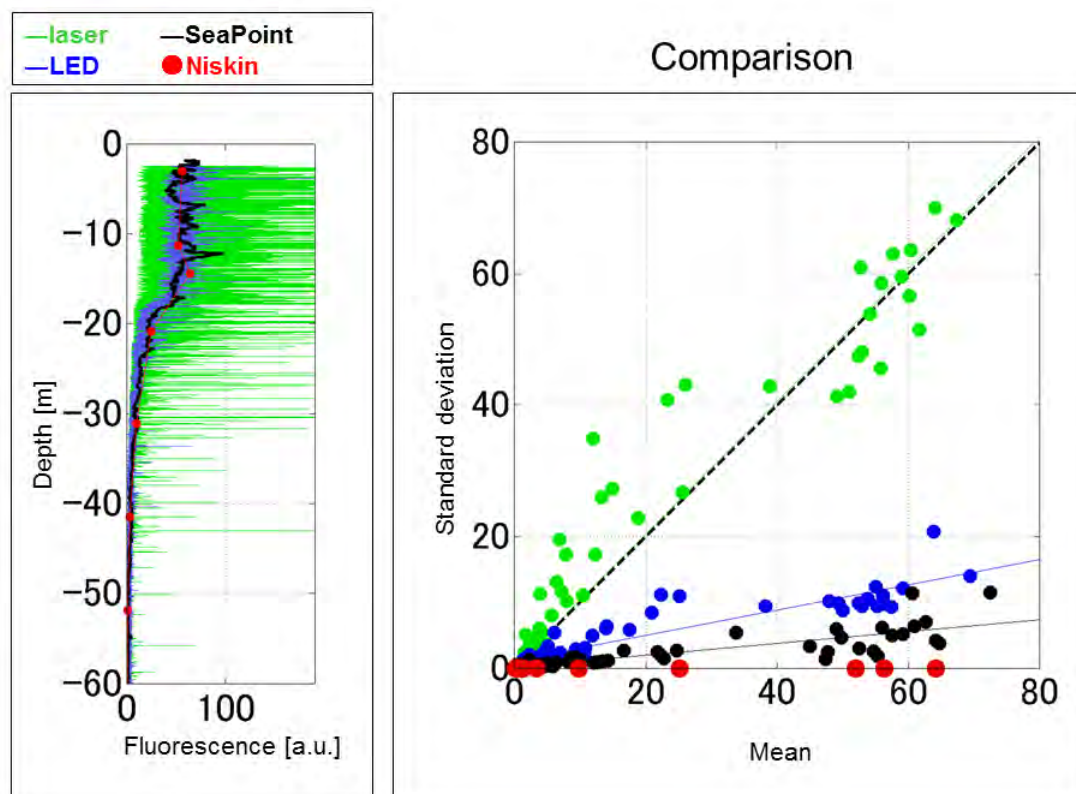
Figure 1. *Fluorescence signals from laser probe and LED probe mounted on a microstructure profiler TurboMAP-L are plotted again depth. Also shown are signals from SeaPoint probe mounted on a conventional CTD as well as the water sample data from Niskin bottle. The corresponding mean and standard deviation for one-meter interval are shown in the right hand side.*

scale coagulated material. We show that fluorescence signals at millimeter scale exhibit high values of coefficient of variation and the signals are no longer a Gaussian process. We found a transition scale that separates a continuous Gaussian process to a discrete event series. We are also developing a new NPZ ecosystem model based on our finding. We will present the consequence of our new model that may alter the way in which the global biogeochemical cycle should be treated.

References

Doubell, M.J., H. Yamazaki, H. Li, and Y. Kokubu. 2009. An advanced laser-based fluorescence microstructure profiler (TurboMAP-L) for measuring bio-physical coupling in aquatic systems, *Journal of Plankton Research* 31: 1441-1452.

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