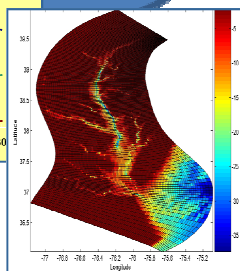# GEOHAB Modelling

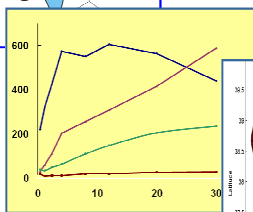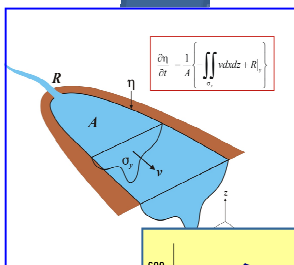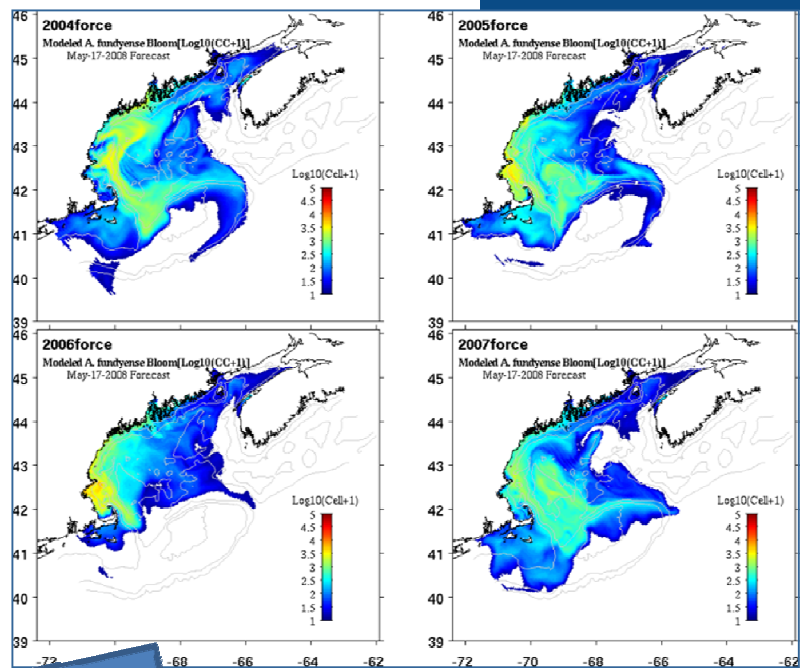## *Linking Observations to Predictions*

A Workshop Report

GEOHAB

Global Ecology and Oceanography of Harmful Algal Blooms

International Council for Science — Scientific Committee on Oceanic Research — SCOR

UNESCO
United Nations Educational, Scientific and Cultural Organization

Intergovernmental Oceanographic Commission

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Cover images, counterclockwise: Sampling in the Gulf of Maine, model constructs of estuarine processes; model runs of *Alexandrium fundyense* concentrations for 2004, 2005, 2006, and 2007.

GEOHAB Modelling:
Linking Observations to Predictions
A Workshop Report

Edited by Dennis J. McGillicuddy, Jr.,
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Based on contributions of the participants of the
GEOHAB Modelling Workshop

Galway, Ireland, June 2009

January 2011

GEOHAB Modelling:
Linking Observations to Predictions
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Dedication

Photo: Sonsoles González Gil

It was with great sorrow that our community learned of the death of Patrick Gentien on May 9, 2010. His sharp intellect and keen intuition afforded him a deep understanding of oceanic plankton populations, and his curiosity about marine systems was infectious. Patrick's generosity with ideas and keen sense of humor made him a wonderful collaborator. He was exceptionally dedicated to advancing the field, having served as chair of the ICES-IOC Working Group on HAB Dynamics (1996-1998), and French delegate at the Intergovernmental Panel on Harmful Algal Blooms (IPHAB). He was involved with the GEOHAB Programme from its inception, serving as the first chair (1999). Patrick played a major role in the organization, execution, and follow-up to the Galway modelling workshop. For all of these reasons, we dedicate this report to our treasured colleague and friend.

An Introduction to GEOHAB

Now is an historic time in the field of harmful algal bloom (HAB) science. HAB problems are growing worldwide, and society's need for understanding these phenomena is more pressing than ever. Technological advances have expanded our capabilities for observing the ocean, providing unprecedented opportunities not only for the detection of blooms, but also for observing with more accuracy the physical, chemical, and biological factors that trigger their initiation, development, and ultimate demise. However, despite these rapidly expanding observational capabilities, HAB processes will continue to be undersampled for the foreseeable future, owing to the wide range of space and time scales relevant to these oceanographic phenomena. As such, we must rely on models to help interpret our necessarily sparse observations. Such models can take many forms, ranging from conceptual models, to simple analytic formulae, or to complex numerical models that assimilate data (Franks 1997). Of course, the topic of HAB modelling is embedded within, and benefits from, the accomplishments of the broader field of physical-biological interactions generally (Franks 1995, Hofmann and Friedrichs 2002, Blackford et al. 2007, Lynch et al. 2009).

GEOHAB, the Global Ecology and Oceanography of Harmful Algal Blooms Programme, sponsored by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO, is an international programme to foster and promote cooperative research directed toward improving the prediction of HAB events. GEOHAB has recognized the impacts of HABs throughout all waters of the world, but has emphasized events in marine and brackish waters because of the global significance of these problems and the need for collaborative, international studies to address them.

HABs have been associated with fish and shellfish kills, human health impacts, and ecosystem damage throughout the world. Concurrent with escalating influences of human activities on coastal ecosystems, the environmental and economic impacts of HABs and consequent challenges for coastal zone management have increased in recent years.

GEOHAB is an international programme to coordinate and build upon related national, regional, and international efforts in HAB research. The GEOHAB Programme assists in bringing together investigators from different disciplines and countries to exchange technologies, concepts and findings. GEOHAB is not a funding programme per se, but instead will facilitate those activities that require cooperation among nations and among scientists working in comparative ecosystems. The central challenge is to understand the key features and mechanisms underlying the population dynamics

> **The mission of GEOHAB** is to foster international co-operative research on HABs in ecosystem types sharing common features, comparing the key species involved and the oceanographic progresses that influence their population dynamics.
>
> **The scientific goal of GEOHAB** is to improve prediction of HABs by determining the ecological and oceanographic mechanisms underlying their population dynamics, integrating biological, chemical, and physical studies supported by enhanced observational and modelling systems.
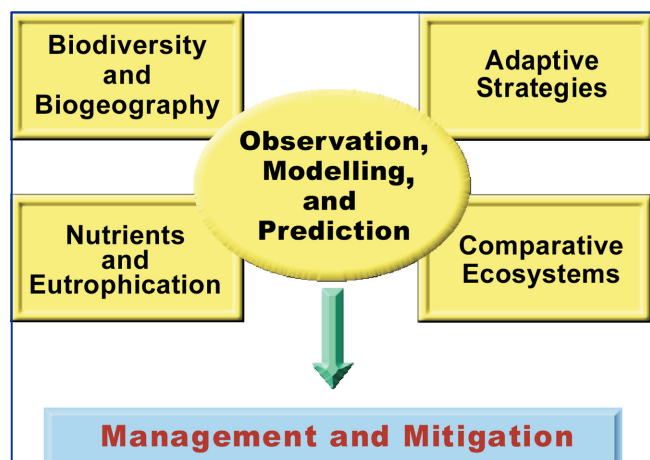
The goals of GEOHAB can be achieved through a tight link between its five Programme Elements. Improved modelling can foster the integration of research, improve predictive capabilities and advance forecasting for management and mitigation of HABs.

of HABs in a range of oceanographic regimes and influences by a range of natural and anthropogenic factors. The underlying mission and scientific goal of GEOHAB have been identified to reflect these needs.

The overall strategy of GEOHAB is to apply the comparative approach. The comparative method assembles the separate realizations needed for scientific inference by recognizing naturally occurring patterns, and temporal and spatial variations in existing conditions and phenomena (Anderson et al. 2005, GEOHAB 2005). Understanding the responses of harmful algae to the increasing anthropogenic perturbations of the world's coastal zones will assist in predictions of future patterns as well.

The GEOHAB *Science Plan* (2001) outlines five Programme Elements that serve as a guide to establish the programme's research priorities. These elements and their overarching questions include:

Examples of some of the GEOHAB reports published.

Biodiversity and Biogeography. What are the factors that determine the changing distributions of HAB species, their genetic variability, and the biodiversity of associated communities?

Nutrients and eutrophication. To what extent does increased eutrophication influence the occurrence of HABs and their harmful effects?

Adaptive strategies. What are the unique adaptations of HAB species and how do they help to explain their proliferation or harmful effects?

Comparative ecosystems. To what extent do HAB species, their population dynamics, and community interactions respond similarly under comparable ecosystems?

Observation, modelling and prediction. How can we improve the detection and prediction of HABs by developing capabilities in observation and modelling?

For the purposes of implementation, GEOHAB has adopted a 3-category system for defining and endorsing research.

Core Research is comparative, multidisciplinary, and international, and directly addresses the overall goals of GEOHAB as outlined in the *Science Plan.* Core research comprises oceanographic field studies conducted in, and application of models to, comparable ecosystems, supported by identification of relevant organisms, and measurements of the physical, chemical and biological processes that control their population dynamics. To date, GEOHAB has developed Core Research Project (**CRP**) Reports on Upwelling Systems, Eutrophic Systems, Stratified Systems and Fjords and Coastal Embayments.

Targeted Research addresses specific objectives outlined in the *Science Plan*. Targeted Research may include, but is not limited to, the development and comparison of specific models and observational systems, studies on the autecological, physiological, and genetic processes related to HABs, and studies on sub-grid formulations of physical, chemical and biological interactions affecting HABs. Targeted Research differs from Core Research in scope and scale. Whereas Core Research is expected to be comparative, integrative, and multi-faceted, Targeted Research activities may be more tightly focused and directed to a research issue or element. It is expected that such research activities will facilitate wider and larger-scale studies.

Regional/National Projects are those research and monitoring activities relevant to the objectives of the *Science Plan* and which are coordinated at a regional or national level. GEOHAB has developed a Regional Comparative Programme on HABs in Asia.

This report describes the approaches, needs and ongoing challenges required to incorporate modelling into all phases of GEOHAB Core Research.
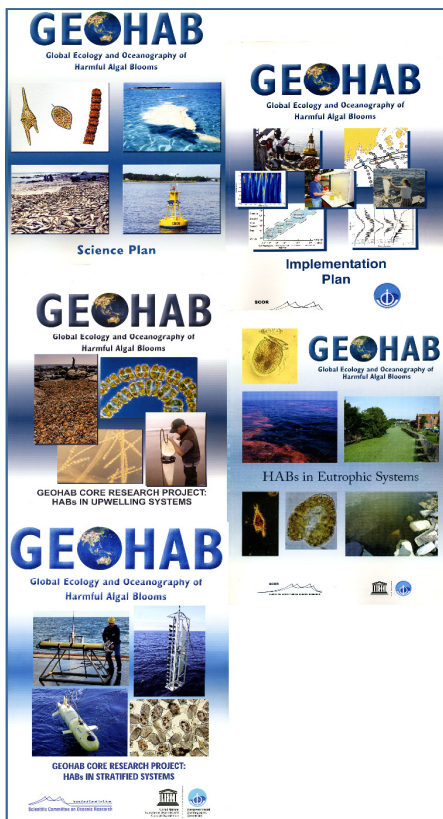
Overview of the
GEOHAB Modelling Workshop

In June 2009, a workshop was convened under the auspices of the GEOHAB programme to develop strategies for using observations and models to address the science questions articulated in the Open Science Meeting Reports for each of the GEOHAB Core Research Projects (Cembella et al., 2010; Gentien et al., 2008; Glibert, 2006; Pitcher et al., 2005). A total of 80 participants from 26 nations, including 20 students and postdocs met for one week at the National University of Ireland in Galway (McGillicuddy et al., 2010). Participants were selected by invitation and also via an application process in which the organizing committee attempted to achieve balance in three respects: ilk (modelers, observers, laboratory experimentalists), age (established researchers, postdocs, students), and application area (all 4 CRPs plus relevant related efforts such as GLOBEC, IMBER, etc).

The goals of the workshop were to:

- Develop strategies for using observations and models to address GEOHAB Core Research Project science questions

- Train students

- Provide publications in the form of this report and a special journal issue

The workshop was structured around four connected elements:

- Plenary talks comprised of (a) invited reviews on HAB modelling and other relevant approaches (ecosystem modelling, population dynamics modelling, cell biology moderization), and (b) contributed talks on models and observations in support of the CRPs.

- Dialogue seminars given by HAB observationalists and modelers. Specific modelling needs of the CRPs were identified; implementation plans were developed, utilizing existing modelling infrastructure where practical, and identifying needs for additional model development where gaps exist.

- Tutorials and training on model design and application of models (geared toward students involved in CRPs).

- Student project: participants built a model, conduct test runs, and described the results and in a report / presentation.

Appendices to this report include a participant list, detailed agenda, student-mentor pairings, and abstracts.

Participants of the GEOHAB Modelling Workshop.

Journal of Marine Systems:
Special Issue on GEOHAB Modelling

A key product of this effort was a special journal issue comprised of a set of papers conceived at the workshop (McGillicuddy, 2010). Collectively, these contributions illustrate the wide variety of approaches being brought to bear on harmful algal bloom phenomena, spanning conceptual, empirical, and numerical approaches.

Conceptual models are not only useful in their own right, but also form the foundation of all other types of models. As such, conceptual models figure prominently into each of the papers contained herein. One paper in particular provides a pedagogical guide to conceptualization of phytoplankton life cycles in both Eulerian and Lagrangian frameworks (Hense 2010). Because many HAB species have complex life cycles that can include resting stages, vegetative growth, and sexual reproduction, explicit representation of these biological aspects can be essential to accurate modelling of their bloom dynamics.

Empirically-based algorithms are playing an increasingly important role in HAB modelling, providing an important link between conceptual and dynamical modelling approaches. For example, Blauw et al. (2010) use fuzzy logic to relate nuisance foam events in Dutch coastal waters to *Phaeocystis globosa* blooms, quantifying their relationships with environmental parameters such as mixed layer irradiance and nutrient availability. Anderson et al. (2010) adopt a different mathematical framework – a logistic Generalized Linear Model (GLM) – to predict potentially toxigenic *Pseudo-nitzschia* blooms in the Chesapeake Bay as a function of time of year, location, temperature, salinity, light, nutrients, and freshwater discharge. Yet another analytical approach is offered by Wang and Tang (2010), who use Empirical Orthogonal Function analysis on satellite-based ocean color data to identify winter phytoplankton blooms south of Luzon Strait, relating their causes to subsurface upwelling and mixed layer entrainment via statistical analysis of both remotely sensed and *in situ* observations. Raine et al. (2010) identify a chain of observable events that lead to HAB events in a coastal embayment in southwestern Ireland: easterly winds tend to accelerate the coastal current, delivering *Dinophysis acuminata* blooms from the continental shelf to the mouth of Bantry Bay; subsequent southwest winds can then transport the blooms into the Bay. By encapsulating this sequence of wind forcing conditions into a single index, Raine et al. evaluate the skill of harmful algal event predictions in both hindcast and forecast modes. Each of these examples illustrates how empirically-based approaches provide a valuable framework for formulating and refining conceptual models underpinning HAB phenomena, setting the stage for future development of dynamical models. In some cases, such advances have turned out to be surprisingly useful and practical for prediction purposes.

Aggregated box models, sometimes referred to as zero-dimensional models, have tremendous utility for a variety of purposes, ranging from exploratory theoretical and conceptual model development to applications in real systems with HAB phenomena. Flynn and Mitra (2010) provide an excellent example of the former in their investigation of mixotrophy. Although few data are available to test such models, their numerical simulations offer a framework for initial evaluation of various mixotrophic formulations. Their findings could help inform the design of future experimental work to be used in more rigorous testing of such models. Similarly, Flynn (2010) uses detailed physiological models to examine how internal cellular nutrient stores respond to external nutrient availability, illustrating the complex nonlinear processes involved in phytoplankton response to varying environmental conditions. Such information is directly relevant to devising effective management strategies for HABs and eutrophication. Chapelle et al. (2010) describe species-specific physiological models for phosphorus-limited growth of *Alexandrium minutum* and *Heterocapsa triquetra*, testing them with laboratory experiments comprised of both pure and mixed semi-continuous culture. Such models yield insight into nutritional regulation of blooms of these harmful species, which is of course useful information in and of itself. In addition, such physiological formulations set the stage for more complete models of bloom dynamics that include controls such as light, temperature, predation, etc.

One framework in which to synthesize such a vast array of processes is provided by planktonic ecosystem models. Llebot et al. (2010) implement a zero-dimensional ecosystem model to explore nutrient supply processes fueling blooms in a Mediterranean coastal embayment. By comparing carefully constructed sensitivity experiments with available observations, they are able to assess the plausibility of a variety of nutrient sources and mechanisms for delivery. The results demonstrate the importance of dissolved organic phosphorus to bloom nutrition, despite the hydrodynamic simplifications inherent in the zero-dimensional formulation. In many cases, such models lend themselves to incorporation in three-dimensional circulation models, and Roiha et al. (2010) provide a striking example of how an ecosystem model with multiple phytoplankton functional types can be used to predict cyanobacterial blooms in the Black Sea. This is one of the first, if not the first, documented uses of ensemble methods of HAB forecasting. Such ensembles provide valuable information about forecast uncertainty and sensitivity, which are crucial in interpreting the results for use in management decisions. Moreover, ensemble forecasts can also be used to assess and refine observing systems used to drive HAB predictions. Another novel application of ecosystem models builds on the seminal work of Follows et al. (2007), who introduced the process of selection into such formulations. Simulations described by Goebel et al. (2010) start with a large number (78) of phytoplankton types for which physiological traits are randomly chosen. The plankton model is integrated forward in time within a high-resolution three-dimensional model of the California Current System, and this simulation of the natural selection process yields an autotrophic community with recognizable phytoplankton functional groupings, as evidenced by detailed comparisons with observations.

Three-dimensional models need not necessarily include complex biological components in order to be useful for HAB studies. Velo-Suárez et al. (2010) use particle tracking techniques to explain the disappearance of a *Dinophysis acuminata* bloom in the Bay of Biscay. Although biological processes may have contributed to decline of the bloom, results from a three-dimensional model seeded with passive particles suggest advection and dispersion processes were sufficient to provide a hydrodynamic termination mechanism. Hai et al. (2010) apply a similar approach to a *Phaeocystis globosa* bloom in the upwelling waters of south central coast of Viet Nam. Under strong southwest monsoonal winds, the population tended to be advected offshore, whereas in the absence of wind forcing the bloom was transported northward in the coastal current. These numerical experiments clearly illustrate the importance of wind forcing in determining transport pathways and exposure of HABs to coastal habitats.

Another major contributor to HABs in coastal environments is the process of eutrophication, which is a growing problem globally (Glibert et al. 2010). As with HABs in general, modelling approaches to HABs in eutrophic systems are quite diverse. For example, Xu et al. (2010) use primarily conceptual models to interpret time series data in two Hong Kong harbors to determine that differences in hydrodynamic circulation and mixing are the primary causes for differences in eutrophication impacts in those particular systems. At the other end of the spectrum of complexity lie global eutrophication models, which couple land use information with representations of the coastal ocean to assess the connection between nutrient loading and HAB occurrence (Glibert et al. 2010). A grand challenge for future progress in this area is integration of fully dynamic models of land use, watershed and coastal hydrodynamics, and HAB biology into a "system of systems."

This volume concludes with a review of rheological properties in marine systems (Jenkinson and Sun 2010). The potential importance of this topic to HAB studies stems from organic exopolymeric substances exuded by phytoplankton, which can have an impact on seawater viscosity. In turn, this could constitute a feedback mechanism relevant to thin layers of plankton in stratified systems.

The sixteen papers contained in the volume thus comprise a broad but incomplete survey of the field of HAB modelling. Future progress in this field depends heavily not only on the creativity and innovation of individual investigators developing new models and new approaches, but also on integration with the broader community of researchers dealing with physical-biological interactions of plankton populations. Interestingly, it was a HAB problem (on the west Florida shelf) that inspired one of the earliest coupled physical-biological models of plankton dynamics, which dealt with the competing effects of growth and diffusion (Kierstead and Slobodkin 1953, Skellam, 1951). Other key opportunities for this field abound in partnership with the emergent global ocean observing system, which has been in part justified by the need to observe, understand, and predict HABs in the coastal ocean (Nowlin et al. 1997).

Charge to Working Groups

Working groups were organized according to the three GEOHAB Core Research Projects for which Open Science Meeting Reports were available: HABs in Upwelling Systems (Pitcher et al. 2005), Eutrophication and HABs (Glibert 2006), and HABs in Stratified Systems (Gentien et al. 2008). A draft of the report for HABs in Fjords and Coastal Embayments (Cembella et al. 2010) was available at the meeting, and attempts were made to address those themes to the extent possible.

The specific charge to the working group was to develop strategies for using models and observations to address science questions identified in the CRP Open Science Meeting Reports, with specific reference to the 11 objectives of the workshop:

– stimulate modelling activity in GEOHAB Core Research Projects (CRPs)

– entrain researchers at all levels (students, post-docs, faculty, etc.) into HAB modelling

– facilitate dialog between model developers and HAB researchers involved in process studies through joint training sessions

– improve understanding of HAB processes through linkage of models, in situ observations, and remote sensing

– foster linkage between HAB modelling and the broader community of biogeochemical, ecosystem, and population dynamics modelling

– highlight species-specific aspects intrinsic to HAB modelling: autecology, behavior, species interactions, toxin production, etc.

– improve capabilities for prediction of HABs and quantitative assessment of their skill

– encourage the use of advanced data assimilation techniques in HAB modelling

– encourage the use of observing system simulation experiments (OSSEs) in array design

– improve forecast products and their dissemination to maximize their benefit to the user community

– develop a written glossary for terminology

The backdrop for these objectives is the key science questions for each of the CRPs.

Eutrophic Systems

- What HAB species are indicative of global nutrient increases?

- How do physical processes impact the relationship between HABs and nutrients?

- How do HABs interact with other members of the food web in eutrophic environments?

- How do overfishing and aquaculture activities impact HABs?

- How do land use and other anthropogenic changes impact HABs?

- How does climate change and variability interact with nutrients in promoting HABs?

Stratified Systems

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

- 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?

- Do HAB species migrate and if so, what are the cues and what are the gains?

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

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

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

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

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

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

- To what extent does the existence of thin layers –and the implication for the retention of water bodies- play a role in the development of particular assemblages?

Upwelling Systems

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

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

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

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

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

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

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

- Are climate indicators predictive of HAB events in upwelling systems?

These questions were developed, within the frame of modelling, by each working group. The fruits of their particular discussions are the Working group reports that constitute the following chapters. Although organized by according to the CRP structure, the many needs and applications of models cross-cut the general research project areas. Moreover, there are many modelling tools that have proven to be useful and can be applied in more than one research area.

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Modelling of HABs in Eutrophic Systems

Introduction

The term "eutrophication" has been defined in various ways (e.g., Nixon 1995, Richardson and Jørgensen 1996, Anderson et al. 2006). Central to all definitions is the concept that the enrichment of water by nutrients causes an enhanced biomass and/or growth rate of algae, which, in turn, leads to an undesirable disturbance in the balance of organisms present in the water and to the quality of the water body concerned. The result of eutrophication is often seen as an increase in total algal biomass, frequently dominated by a single species or species group. By definition, these deleterious growths often form harmful algal blooms (HAB) (Hallegraeff 1993, Anderson et al. 2002, Glibert et al. 2005, Glibert and Burkholder 2006, Heisler et al. 2008). The effects of such HABs include overgrowth and shading of sea grasses, oxygen depletion of the water from algal and bacterial respiration (especially on death of the algal biomass), suffocation of fish from stimulation of gill mucus production, direct toxic effects on fish and shellfish, and mechanical interference with filter feeding by fish and bivalve mollusks (Anderson et al. 2002, Landsberg 2002, Backer and McGillicudy 2006). Of additional concern with the development of high-biomass algal blooms, and more than likely a factor in their development, is a reduced transfer of energy to higher trophic levels, as many HAB species are not efficiently grazed, resulting in a decreased transfer of carbon and other nutrients to fish stocks when HAB species replace more readily consumed algal species (Irigoien et al. 2005; Mitra and Flynn 2006). For example, some HAB species secrete allelopathic sub-

stances that inhibit co-occurring species (Pratt 1966, Gentien and Arzul 1990, Granéli et al. 2008) and suppression of grazing occurs above a certain concentration of the HAB species (Tracy 1988).

Although eutrophication is occurring globally, nutrient export from coastal watersheds is not evenly distributed (Seitzinger et al. 2002, 2005, Howarth et al. 2005, Glibert et al. 2006). Eutrophication and nutrient pollution is occurring due to the increase in human population, the increasing demands on energy, increases in nitrogen (N) and phosphorus (P) fertilizer use for agriculture, changes in diet, leading to more meat production and animal waste, and expanding aquaculture industries (e.g., Smil 2001, Galloway and Cowling 2002, Galloway et al. 2002, Howarth et al. 2002, Wassmann 2005; Fig. 1). Global inorganic nitrogen export to coastal waters is estimated to be highest from European and Asian watersheds, although significant discharge also occurs from the United States and other parts of the world (Seitzinger and Kroeze 1998, Dumont et al. 2005, Harrison et al. 2005a,b, Van Drecht et al. 2005). This rate of nutrient export to coastal waters has increased dramatically in recent years in some parts of the world. For example, China, which used less than 5 million metric tonnes of N fertilizer annually in the 1970's now uses more than 20 million metric tonnes per year, representing 25% of global N fertilizer consumption (Glibert et al. 2006), leading to significant increased N pollution of its coastal waters. Crop uptake commonly amounts to only 50% of the fertilizer N applied (Peoples et al., 1995). The remainder is lost via various pathways, including ammonia volatilization, denitrification, runoff and leaching, or accumulates in the soil. The importance of the different losses depends on various factors, such as the timing of application, weather, soil temperature and pH and other factors (Bouwman et al., 2002, Khakural and Alva 1995 ,Wali et al. 2003, Glibert et al. 2006). In some regions excess N loading has skewed the nutrient ratio away from that normally considered suitable for phytoplankton growth towards P limitation (e.g., Matson et al. 1999). Phosphorus loading, however, is often cited as the major cause of HABs in freshwaters (e.g., Oliver and Ganf 2000,
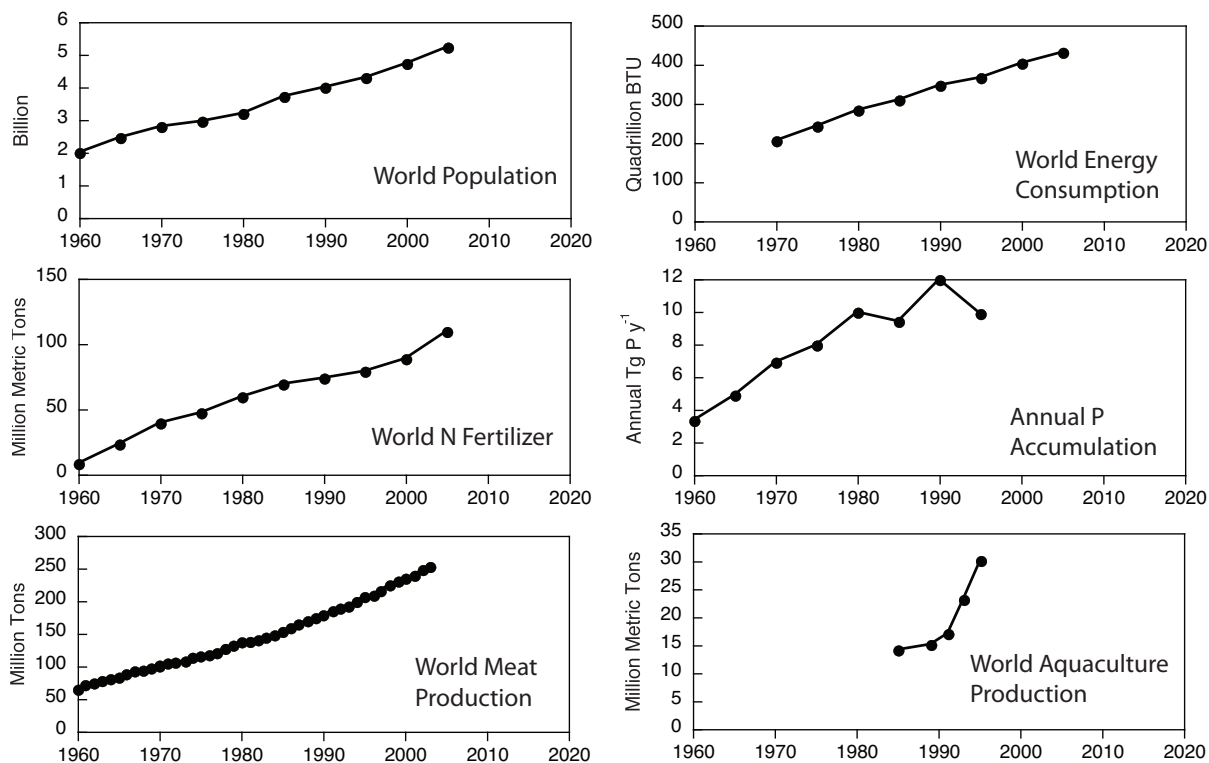
Figure 1. General trends in population, energy consumption, fertilizer use and accumulation, meat and aquaculture production from 1960 to present. Data compiled from www.census.gov/ipc/www/img/worldpop.gif, Global Fertilizer Industry, www.fertilizer.org, and the Food and *Agriculture Organization* (FAO) of the United Nations (2007).
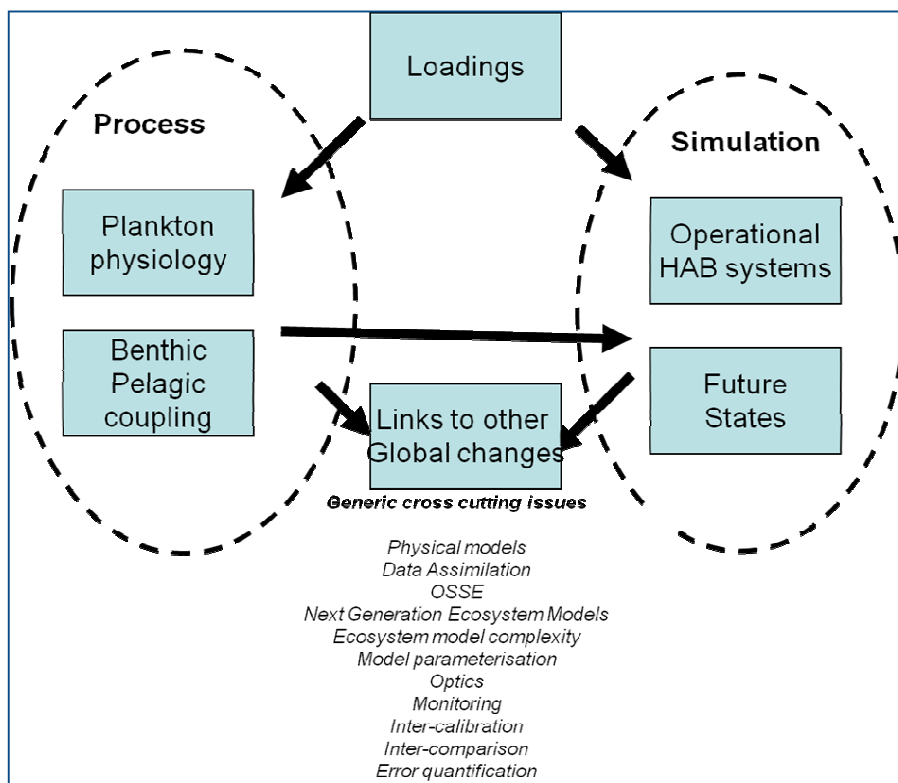
Figure 2. Modelling HABs in eutrophic systems requires a range of model types, but each type of model is ultimately coupled to the other and all share many cross-cutting issues. Models of loadings are linked to models of processes, and they both are linked to simulation models. All of these must also be coupled to models that estimate other global changes.

Schindler et al. 2009) where N_2-fixing algae often dominate, compensating for any deficit in N.

Nutrients can stimulate or enhance the impact of toxic or harmful species in several ways (Anderson et al. 2002). At the simplest level, harmful phytoplankton may increase in abundance due to nutrient enrichment, but remain in the same relative fraction of the total phytoplankton biomass. Even though non-HAB species are stimulated proportionately, a modest increase in the abundance of a HAB species can promote noticeable differences in the ecosystem because of its harmful or toxic effects. More frequently, a species or group of species dominates in response to nutrient enrichment or a change in the ratios of nutrient enrichment.

Natural resource managers and public health officials need better tools to forecast HAB events and to predict the composition of algal species and assemblages that may occur under conditions of changing nutrient loads. The requirements for models for understanding HABs in eutrophic systems are not only great, but also complex. This complexity ranges from the need for accurate estimates of nutrient loading rates, well parameterized physiological models, and mechanistic and integrated ecosystem models. Conceptually these needs can be viewed as components of a nested suite of models (Fig. 2). Herein we provide a broad review of the types of models and approaches for understanding HABs that are required in eutrophic systems, recent advances that have been developed, and recommendations for how these modelling approaches can and should be advanced to lead to better predictive capacity of HABs in eutrophic systems.

Nutrient Loading Models

Types of Models and Recent Advances

One of the core needs for modelling HABs in eutrophic systems is an estimate of nutrient loads. Nutrient loads, which reflect a rate of delivery of nutrients from water- and air-sheds, are not estimated from nutrient concentration data, which are static measures at a given point in time. Various hydrological models, such as the Spatially Referenced Regressions on Watersheds (SPARROW), Soil and Water Assessment Tool (SWAT), and Nutrient Export from Watersheds (NEWS), estimate nutrient loading, taking into account the broad range of nutrient sources and their alteration across the landscape. The SPARROW model has been used extensively in the USA to estimate nutrient loads to receiving waters, such as the Gulf of Mexico (Robertson et al. 2009, Hoos and McMahon 2009). SPARROW uses statistical relationships to relate water-quality monitoring data to upstream sources and watershed characteristics that affect the fate and transport of nutrients (e.g., Smith et al. 1997).

Another such empirical model is the Global Nutrient Export from Watersheds (NEWS) model. The NEWS system of models is unique in that it can be used to estimate magnitude and sources of different elements (carbon (C), N, and P) and different forms (particulate, dissolved inorganic and organic) (Seitzinger et al. 2005a). This suite of models, based on data from more than 5,000 exoreic basins, includes natural sources such as N_2 fixa-

tion and P weathering, and anthropogenic sources (non-point inputs from fertilizer by crop type, N_2 fixation by crops, atmospheric N deposition, and manure by animal species; point sources from sewage, as estimated by human population and treatment level) (Seitzinger et al. 2005a). The models also account for hydrological and physical factors including water runoff, precipitation intensity, land use and slope, as well as in-water removal processes such as dams and reservoirs and consumptive water use (Fig. 3). The models were validated as described by Dumont et al. (2005) and Harrison et al. (2005b). The input data bases are at a resolution of 0.5^{o} x 0.5^{o} and the resulting maps represent nutrient export for mid-1990s conditions, using units of nutrient yield (kg N or P km^{-2} of watershed yr^{-1}), dominant watershed source, and percent contribution from anthropogenic sources.

Global comparisons of NEWS- estimated nutrient loadings, by form, and one HAB species, *Prorocentrum minimum* have recently been made (Glibert et al. 2008). This HAB species is associated with regions of high dissolved inorganic nitrogen (DIN) and phosphorus (DIP) exports that are strongly influenced by anthropogenic sources (such as fertilizers and manures for DIN). Blooms of this species were also linked to regions with relatively high anthropogenic contributions to dissolved organic N and P export. Yet, these relationships should be viewed as only an initial step in associating individual species with global nutrient changes as nutrient yields do not necessarily reflect the nutrient that the cells may "see" at any particular point in time. Nutrient yields estimated by NEWS are annual averages whereas HABs frequently are ephemeral events, and little or no effort has been made to incorporate the event time scales. Thus, there may be a temporal mismatch. Furthermore, as described below, the likelihood for a species to bloom depends on a complex suite of factors, not just single nutrient forms and supply levels. Thus, much more rigorous quantification of these relationships is required, and global relationships need to be developed for many more HAB species.

Another important application of nutrient loading models is in estimating the potential change in loads due to predicted changes in anthropogenic practices on land use nutrient discharge. An integrated modelling approach connecting socioeconomic factors and nutrient management to river export of N, P, C and silica (Si) was undertaken using an updated version of the *NEWS* model. Past (1970-2000), and future trends (2000-2030-

2050) in river nutrient export globally based on four Millennium Ecosystem Assessment (MEA) scenarios were analyzed (Bouwman et al. 2009). The MEA scenarios were based on storylines developed by the Intergovernmental Panel on Climate Change (IPCC) and translated into changes of the main anthropogenic drivers, i.e. demography, economic development and agricultural production (Alcamo et al. 2006). The four MEA scenarios differ in terms of environmental management and in degree and scale of connectedness among and within institutions across country borders (Alcamo et al., 2006). The *Technogarden* and *Adapting Mosaic* scenarios were developed assuming pro-active environmental management, while *Order from Strength* and *Global Orchestration* scenarios assume re-active environmental management. *Global Orchestration* and *Technogarden* reflect trends towards globalization, while regionalization is assumed in *Order from Strength* and *Adapting Mosaic*. Scenarios with reactive approaches to environment management had higher river nutrient export; however, even in the scenario assuming a pro-active approach,

continued increases in river export of nutrients is projected in many world regions as a result of population growth, urbanization and economic development (Fig. 4). Continents with primarily industrialized countries, low-income countries, and countries in rapid economic transition differed in nutrient export trends and relative contribution of watershed nutrient sources. The most dramatic changes in nutrient export for all scenarios were in South Asia. Risks for coastal eutrophication will likely continue to increase in many world regions for the foreseeable future.

Fertilizer use is an important driver. Fertilizer use is at the beginning of the N cycle in the complex agricultural system, with N in animal feed being converted to animal manure that is recycled in the system. During this recycling of N various loss pathways lead to emissions (mainly ammonia) and re-deposition. The N surplus represents the actual N loss to the environment. N surpluses are the difference between the N inputs and the export in harvested crops, grass and grazing. This surplus is determined by agricultural efficiency. For the global system as a whole, this efficiency is 54%,
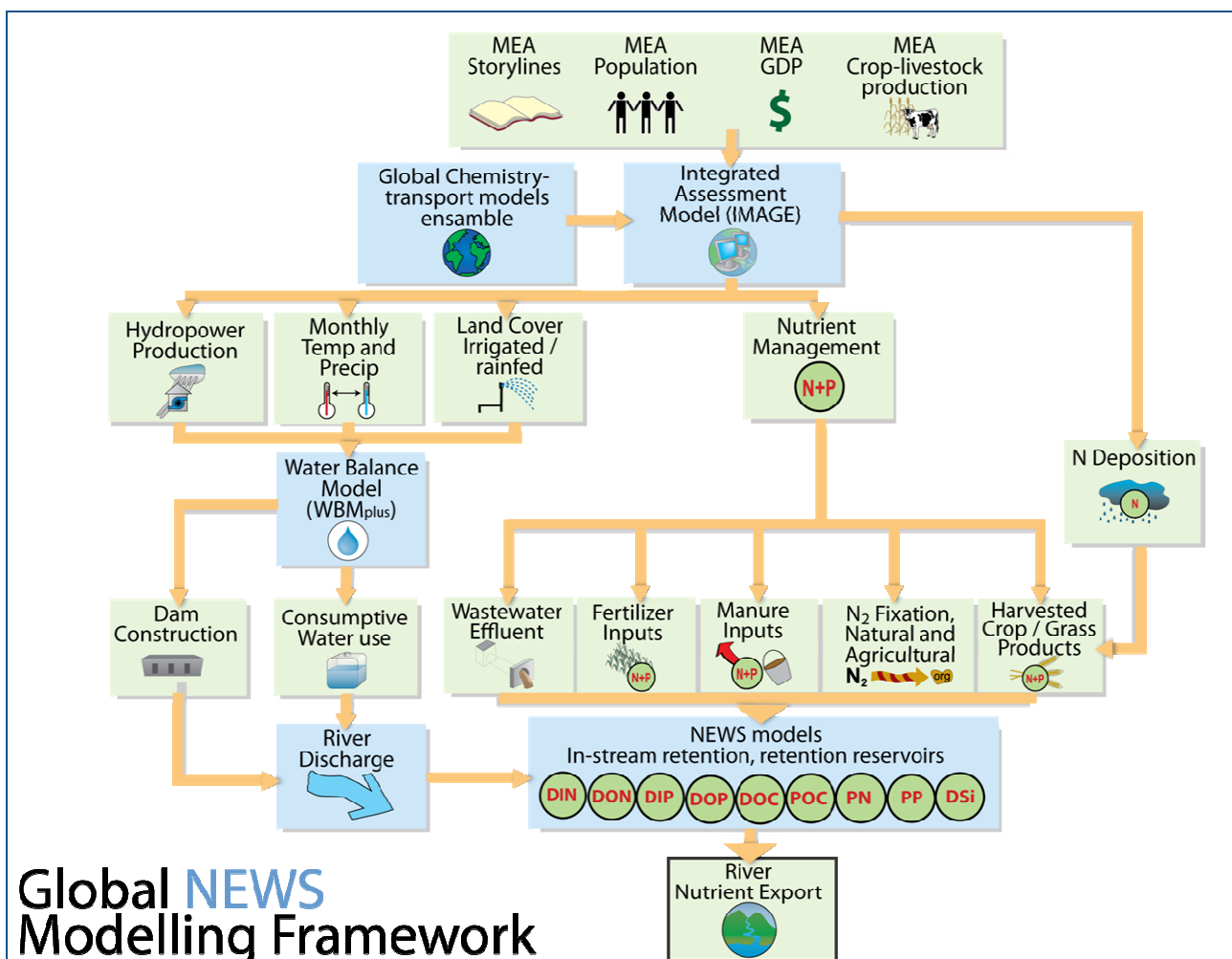

Figure 3. Conceptual diagram of the Global NEWS model construction, submodels and parameters used in developing the spatially explicit Global NEWS nutrient maps. Modified from Seitzinger et al. (2009).

implying that 46% of all inputs are lost to the environment. This efficiency has actually decreased in the past decades as a result of increasing N fertilizer use in low-input countries. In industrialized countries and several high-input agricultural systems in developing countries, there have been important increases in the N use efficiency due to improving agricultural management. The potential effects of such changes on nutrient export are difficult to quantify, but simple dilution in the ocean is not necessarily harmless and, as shown in more detail below, altering nutrient loading, ratios or forms can have effects on algal populations and succession.

Challenges and Opportunities for Advancement

A number of issues must be considered when dealing with spatially explicit nutrient loading models and advancement in many areas of these will lead to improvements in the prediction of nutrient loads and ultimately the relationships between these loads and HAB outbreaks. Not all models are equally robust in estimating all nutrient types or forms. In relating nutrient export or loadings to individual species the specific nutrient forms and/or nutrient ratios may relate more specifically to individual species as compared general algal biomass which relates more generally to total nutrient input. Too often that algal biomass is described in units of chlorophyll, or worse as chlorophyll fluorescence, neither of correlate well with actual C-
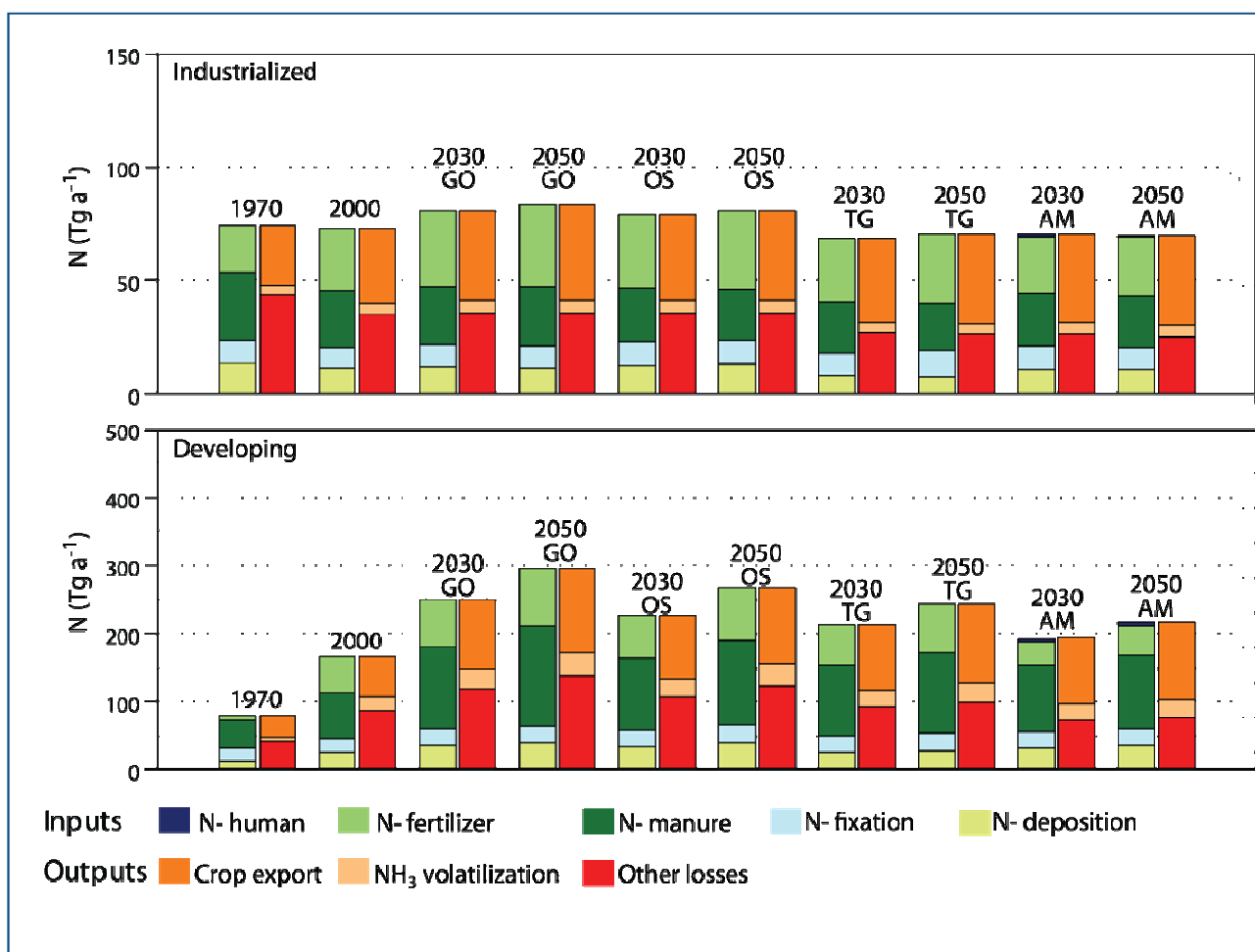
Figure 4. Global nitrogen surface balance for 1970 and 2000, and for 2030 and 2050 for the four Millennium Ecosystem Assessment scenarios for industrialized and developing countries. *Global Orchestration* (GO) portrays a globally connected society that focuses on global trade and economic liberalization and takes a reactive approach to ecosystem problems, but also takes strong steps to reduce poverty and inequality and to invest in public goods, such as infrastructure and education. In contrast, *Order from Strength* (OS) is a regionalized and fragmented world, concerned with security and protection, with the emphasis primarily on regional markets, paying little attention to public goods, and taking a reactive approach to ecosystem problems. *TechnoGarden* (TG) is a globally connected world, relying strongly on environmentally sound technology, using highly managed, often engineered, ecosystems to deliver ecosystem services, and taking a proactive approach to the management of ecosystems in an effort to avoid problems. In *Adapting Mosaic* (AM), the fourth scenario, regional watershed-scale ecosystems are the focus of political and economic activity. Local institutions are strengthened and local ecosystem management strategies are common; societies develop a strongly proactive approach to the management of ecosystems based on simple technologies. The four MEA scenarios indicate that major changes are expected in the developing countries. Based on data from Bouwman et al. (2009).

biomass (Kruskopf and Flynn 2006). Chlorophyll is also an unfortunate measure when so many HABs are mixotrophic.

Data availability on nutrient export and loading is an important issue in many parts of the world. For many regions there are good measurements and models; for other regions the data are poor. As noted above, data on changes in anthropogenic activities that may result in changes in nutrient loadings or rates, such as changes to sewage discharge, agricultural or aquacultural practices (fertilization form, feed used in aquaculture), laws that cap nutrient inputs, and many others are very difficult to obtain for many regions. Another issue is the scale of the model - from regional to global. Spatial dimension of the loading model is an important consideration. Dispersal of the nutrient and the interaction with the physical dynamics of the receiving water are difficult to quantify. While river plume dynamics may be understood, plumes of nutrients from nonpoint sources are still largely difficult to resolve.

Temporal issues are also of key importance. Temporal issues range from the scale of cellular physiology to bloom dynamics, to seasonal and interannual variability, and to the scale on which climate or regime shifts occur. Many loads are highly pulsed and episodic, resulting from storms, landslides or even volcanic eruptions (Heisler et al. 2008). Many loads also follow very specifically the period of time when fertilization of fields has seasonally occurred (Glibert et al. 2001, 2006). Seasonality is of particular importance in monsoonal regions where the load can shift dramatically. For example, the central west-coast of India is a dynamic aquatic ecosystem exhibiting a strong seasonal gradient, both in environmental variables and plankton assemblages. This area is strongly influenced by the southwest monsoon during June to September and the changes associated with its onset have marked effects on the phytoplankton community, food-web and production. Occurrence of phytoplankton blooms during southwest monsoon in tropical estuaries is a common phenomenon (e.g., Villanoy et al. 2006).

Process Models

Types of Models and Recent Advances

The goal of developing process-oriented models for eutrophic systems is to describe the emergent properties of such systems and hence have an explanatory predictive capacity for individual spe-

cies responding to various known and predicted nutrient conditions. "Emergence" is a term used to describe the appearance of new properties which arise when a system exceeds a certain level of size or complexity (Davies 2004). The development of process models often requires the use of functional-type approaches. There are multiple constructs of process oriented models. At the most basic level these are represented by single-nutrient based nutrient-phytoplankton-zooplankton (NPZ) models (Fasham et al. 1990), and perhaps at the extreme, even of single species models. However, such approaches may be inadequate as a base for models with emergent properties because of the interconnectivity in ecosystems typically subjected to eutrophication. Some of the salient aspects of process models as related to eutrophic systems are considered here.

Ecophysiology

Physiological models take one of a variety of forms. Traditional biomass- based models (often either single nutrient, N or C) are relatively simple, have few variables as they assume fixed stoichiometry (invariably Redfield) and operate using Monod kinetics. These models are unsuitable, and indeed are considered as dysfunctional for descriptions of algal growth under variable nutrient conditions (Goldman and Glibert 1983, Flynn 2005, 2009b). Further, such models are incapable of describing trophic interactions correctly because of the implications of variable stoichiometry and, for HAB species, the implications of the accumulation of noxious chemicals during nutrient stress (Mitra and Flynn 2005, 2006). A common use (and, in some cases, misuse) of such models in the context of eutrophication and HABs is the resource-ratio theory (Tilman 1977, 1982), which links the ratio of nutrients (such as N:P, P:Si, N:Si) to species succession (Flynn 2010). Physiologically-based mechanistic models contain explicit descriptions of biochemical processes. Such descriptions may operate within variable stoichiometric biomass-based models (Flynn 2001, 2003), or may be allied to individual based model (IBM) descriptions. IBMs offer the opportunity to describe allometric and cell-cycle processes but are thus more complex. It may be expected that IBM strategies will be given wider prominence in models of eutrophic processes, as this facilitates interfacing biological descriptors with the new generations of abiotic descriptors. However, certain groups, most notably bacteria, filamentous cyanobacteria, and colonial species such as *Phaeocystis*, are not readily amenable to such a treatment.

Multiple currency models (C vs N vs P vs Si for example) are particularly useful in physiological descriptions as stoichiometry is a reflection of the nutrient status of the cell. In typical eutrophic conditions the minimum configuration of multiple currency models is expected to consider C:N:P. Many systems will also require inclusion of Si, and some (especially those associated with deforested areas) may require inclusion of iron (Fe). Variable elemental stoichiometric models should become the norm. Multi-element descriptions in such stoichiometric models, as opposed to Redfield constructs, provide a basis for the development of mechanistic models that contain functional response descriptors with recognized physiological bases. They also support bioenergetic descriptions, which may be important for predicting the survival or organisms under unfavorable conditions.

Adding to the complexity of the formulation of relationships between nutrient availability and uptake, production, growth or biomass (reviewed in Flynn 2003), is the now widely-recognized understanding that a range of nutrient forms, including organic, and in some cases, particulate nutrients, are involved in the ecology of HABs, and at the biomass densities associated with eutrophic conditions any such interactions may be expected to be strengthened (e.g. Berman 1997, Carlsson et al. 1999, Glibert et al. 2004, Glibert and Legrand 2006, Burkholder et al. 2008). In eutrophic habitats phagotrophic mixotrophs, in particular, have been shown to attain higher growth than when in phototrophic mode alone (e.g., Adolf et al. 2008,

Glibert et al. 2009a). Yet for many HABs, quantitative data about the role of mixotrophy in nutrition, growth, and blooms are lacking, especially relating laboratory information to natural field assemblages, so that the relative importance of photosynthesis, dissolved organic nutrients, and ingestion of prey remain unknown (Burkholder et al. 2008). Indeed, modelling mixotrophy is an extreme challenge in plankton physiology because of the complexity of the physiology (Flynn and Mitra 2009; Raven et al. 2010; Fig. 5). It appears also that great care needs to be taken in attempting to simplify the description of mixotrophs, especially in the absence of data for rate processes (Mitra and Flynn this issue).

Our ignorance of the identity, concentration and flux of dissolved organics is exceeded only by our weakness in modelling such processes (Flynn et al. 2008). This problem extends also to the best studied organic nutrients, such as urea, amino acids and vitamins. Added to all the above is the problem of determining the nutrient concentration actually perceived by the organisms, as affected by diffusion gradients and other processes. This is a function not only of physical processes, but also of the biological processes that affect motility (sinking and swimming) and the release of mucus and other colloidal materials. As the latter is typically a reflection of nutrient-limited phototrophy, there is potential for a positive feedback process. This feedback may also be associated with a lessening of grazing (which in turn restricts nutrient regeneration) and with toxin accumulation (Mitra and Flynn 2005).
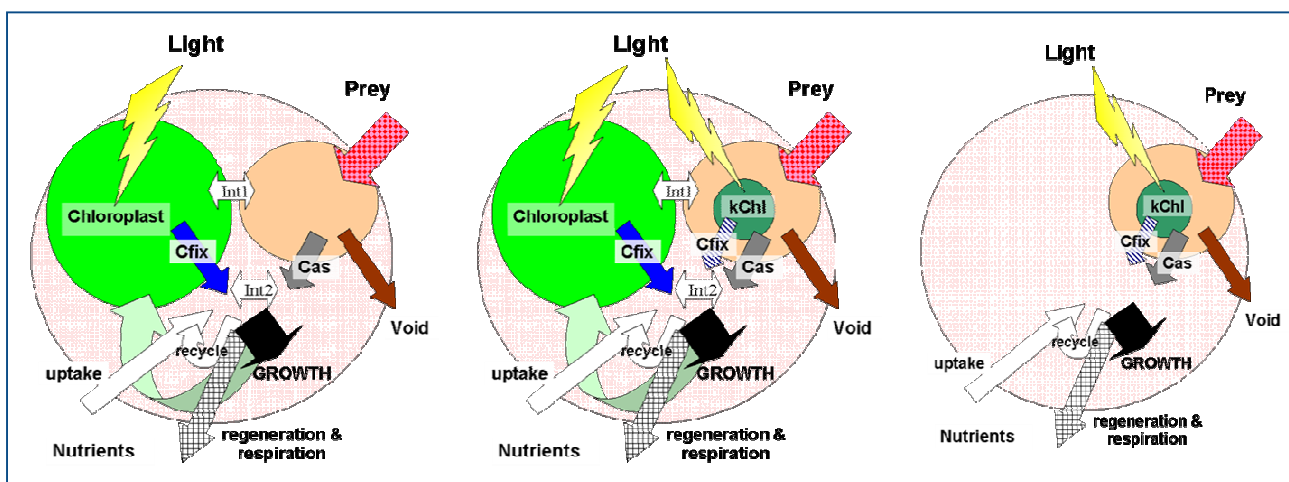
Figure 5. Different configurations of mixotroph physiology achieved using the model of Flynn and Mitra (2009). Left: phototrophic mixotroph obtaining additional nutrition by prey consumption - Int1 indicates competition for space within the cell between chloroplasts and food vacuole (only for phagotrophic species); Int2 indicates interactions between biosynthesis based upon new C-fixation and from prey digestion. Middle: combination of interactions from mixotroph and kleptochloroplastic C-fixation and prey digestion. Right: mixotroph performing photosynthesis using kleptochloroplasts from captured prey - digestion of the chloroplasts is restricted by products of C-fixation; when the kleptochloroplasts fail they are replaced. Adapted from Raven et al. (2010).
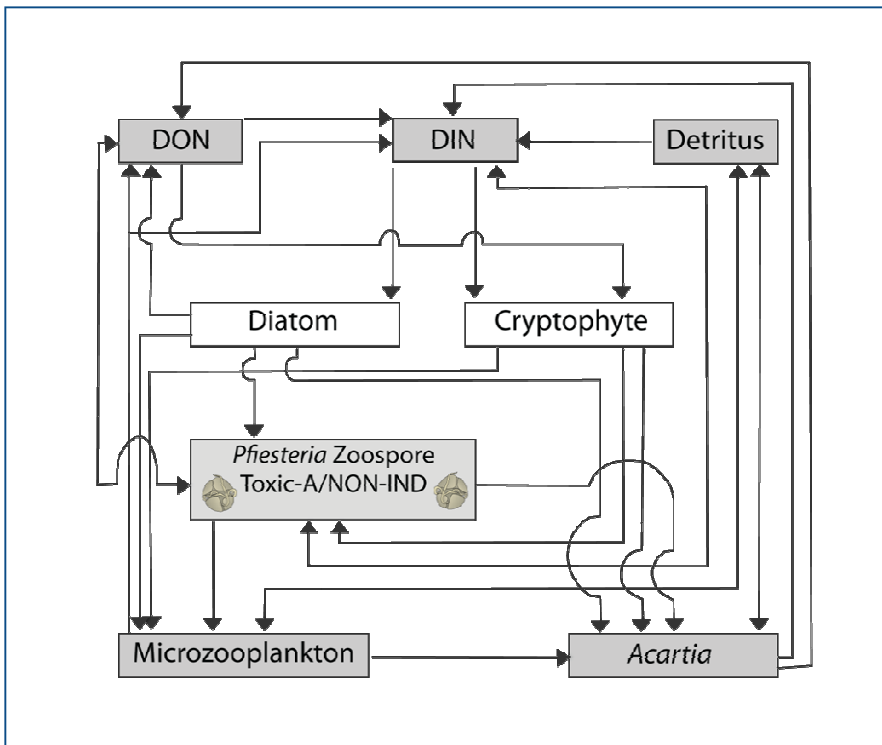
Figure 6. Generalized schematic of the 8-compartment *Pfiesteria* model. Reproduced from Zhang et al. (2004) and Hood et al. (2006) with permission.

The ecophysiology of the component organisms present in the ecosystem affects not only their own growth potential but the activities of others. This linkage to other organisms is either expressed explicitly through direct trophic linkage or through spatially and/or temporally indirect mechanisms. Inasmuch as studies of ecophysiology are logistically demanding even in the laboratory, and the matrix of conditions for experiments extensive, the full range of effects of all physico-chemical parameters (temperature, salinity, pH, nutrient concentrations, turbulence, light etc.) are not known even for a single species (Flynn 2005). For example, nutrient uptake processes are a function not only of factors such as temperature, salinity and pH, but also of the nutritional or growth state of the organism at the time of nutrient delivery (Flynn et al. 1999, Glibert and Burkholder 2006). The range of nutritional capability of many HAB species also adds to the complexity of adequately parameterizing nutrient acquisition.

One approach to modelling HAB physiology within a complex ecosystem is to represent the HAB species with a detailed model, but to describe other groups by aggregate models (e.g., "other flagellates"). This approach has been termed a rhomboid strategy (de Young et al. 2004, Mitra and Davis 2010). Allometric approaches may be appropriate for descriptions of general trophic interactions (e.g., Chisholm 1992), though there are important exceptions to such allometric "rules". Most notably, large diatoms often have maximum growth rates far in excess of the growth rates of smaller non-diatoms. A detailed description of non-HAB species may be warranted, for example for descriptions of prey growth dynamics in support of mixotrophic HABs, of specific predators, or of indicator species that may not even have a close trophic association with the HAB.

One such model is that of the heterotrophic dinoflagellate *Pfiesteria* sp. (Zhang et al. 2004, Hood et al. 2006; Fig. 6). This model is composed of *Pfiesteria* zoospores, microzooplankton, the zooplankter *Acartia*, dissolved inorganic nitrogen (DIN), organic nitrogen (DON), diatom, cryptophytes, and detritus. In addition to modelling the total biomass of *Pfiesteria*, this model followed the time dependency of *Pfiesteria* zoospores' cell size and abundance. In this model two forms of *Pfiesteria* were represented in an idealized way, a form in which the toxin is not inducible "NON-IND", and one in which toxin is present, "TOXIC-A". In the model, "NON-IND" *Pfiesteria* is kleptoplastidic, does not utilize DON, and has a relatively fast growth rate. In contrast, "TOXIC-A" is not kleptoplastidic, utilizes DON, and has a slower growth rate. This model was subsequently used to simulate effects of physical, chemical, and biological conditions and processes on *Pfiesteria* population dynamics (Zhang et al. 2004, Hood et al. 2006). An important lesson from the operation of this model, and from others such as Flynn (2008) and Flynn and Irigoien (2009), is the sensitivity of the system to the activity of the grazers of the HAB species and their competitors. Modelling HABs requires far more than modelling just the HAB species itself. For mixotrophic species, clearly a thorough understanding, and hence competent model, of prey species is required. Physiologically-based models are likely to be overly complex for routine usage but may be useful as drivers for Turing tests in which complex models are used to generate a reality. By this means a data series can be generated of detail exceeding that which may be determined from real sampling methods, and free from

the errors associated with such methods (notably enabling instantaneous, perturbation-free "sampling"). Critically, of course, it requires that the models used for generating the "reality" in this analysis are widely accepted as representing the state-or-the-art in their construction and operation. This approach may be used to a) develop more simple models, and b) to determine which processes are most important in nature (aided by reference to field data). This has been used by Mitra and Flynn (this issue) in an attempt to identify a simplified description of mixotrophy.

Organismal Life cycles

In the systems most likely impacted by eutrophication a close coupling between life cycle stages of organisms is likely. This is important not only for HABs species but also for other components of the system. Eutrophication (either direct from nutrient availability, or indirect via trophic interactions) can stimulate the formation of temporary or long-term resting stage (e.g. encystment, and/or excystment) (e.g., Steidinger and Garcés 2006). Germination and subsequent migration of organisms provides a route for the transference of nutrients as from sediments into the water column. This is a general issue, not just for HABs, but for other species in the system that may, or may not, interact directly with the HAB species. These processes are important because they affect the removal and transformations of elements (nutrients) for HAB development, as well as predator-prey interactions. There is a strong linkage between these processes and climatic/meteorological events, affected by inter-annual variability, seasonality and lunar cycles that requires attention. Although life cycle and other events are often described using an IBM approach, not least because it enables a description of the cell-cycle, allometric and behaviour issues related to it, and because of the importance of geographic and depth location in the water column, other approaches may also be appropriate (Hense 2010).

Some of these changes in behaviour have potential for promoting synergistic feedbacks in trophic dynamics. For example diel vertical migration in response to light-nutrient gradients may drive all cells to the surface at high densities due to self-shading; this would be exacerbated by advective processes, promoting sexual behaviour and transmission of viruses and pathogens. Dense accumulations formed by such behavior shades competitive phototrophs. The development of prey

rejection through nutrient-stress has been suggested, via promotion of anti-grazing activity, to offer a route for the establishment of an ungrazed HAB (Mitra and Flynn 2005).

Benthic-Pelagic Coupling

While most HABs are associated with active growth and activity, and advection within the water column, eutrophic events are typically associated with shallow coastal areas, such as lakes and estuaries. As a consequence, biogeochemical and trophic interactions between the water column and benthos are important. At the least this warrants inclusion of model descriptions of biogeochemistry processes. Typically such processes, driven by bacteria, are described empirically but the drivers for these processes need a closer association with those affecting HABs. Beyond the empirical description of generic benthic biogeochemical processes, there are a series of trophic and life-cycle interactions such as bioturbation as well as abiotic events that may promote fluxes of nutrients in and out of the benthic zone, and transformations of nutrients that originally entered during the primary eutrophication event. Historically far less emphasis has been placed on modelling benthic processes compared with pelagic, however there are a few models which attempt to capture the range of processes required (e.g. Ebenhöh et al. 1995, Ruardij and van Raaphorst 1995).

While most benthic processes may be best considered through empirical approaches, detailed descriptions of the growth and trophic dynamics of benthic organisms that graze the plankton, such as bivalves, are warranted. This is because the activity of these organisms can directly affect plankton community (for example removing planktonic prey that may also be prey for mixotrophic HABs, or competitors for common nutrients), the meroplanktonic stages may be subjected to interactions with HAB species, and of course these organisms often form an important interface between humans and HABs through accumulation of shellfish toxins.

The importance of attached and floating macroalgal and rooted macrophyte growth in some systems also should not be ignored. While these may usefully remove eutrophically released nutrients, and shade light from planktonic forms, on their collapse and decay these growths may conceivably provide an organic loading that may promote the growth of mixotrophic HABs. One such example comes from Florida Bay, USA, where the Sea-

grass Ecosystem Assessment and Community Organization Model (SEACOM) was developed. SEACOM is a mechanistic simulation model of seagrass-water column interactions on an ecosystem scale describing the biomass, production, composition and distribution of submersed aquatic vegetation (SAV)- *Thalassia* (turtle grass), *Halodule* (shoal grass), and *Ruppia* (widgeon grass)- as well as phytoplankton in the water column (Madden and McDonald 2007). A focus of model development is the effects of hydrologic and salinity restoration on the SAV and phytoplankton communities as managed adjustments of the timing and amount of freshwater discharge are implemented. This model (Fig. 7) is being used to refine Minimum Flows and Levels (MFLs) calculations of the freshwater input from the Everglades watershed required to maintain the SAV community and ecosystem health in Florida Bay. The model is also used to test hypotheses about various flushing rate and P recycling rate scenarios, response of the algal community, the impact on the water column light regime, and ultimately the SAV community. Blooms of algae have been a frequent occurrence in Florida Bay in recent years with considerable negative economic and ecological consequences (Fourqurean and Robblee 1999, Glibert et al. 2009b).

Challenges and Opportunities for Advancement

It is now widely recognized that descriptions of variable elemental (if not chemical, e.g., fatty acid) stoichiometry within organisms are essential in models of ecosystem functionality. This is particularly so for primary producers (including mixotrophs), not only because phototrophy lends itself to significant variability in C:N:P(:Si):Fe, but because changes in nutrient physiology associated with such variations in stoichiometry are linked to accumulation of noxious and toxic compounds (Granéli and Flynn 2006). Coupled with the above is the difficulty in modelling loss processes associated with viral and pathogenic attack, infauna activity and burial/exposure of resting stages in sediments. The importance of so-called programmed cell death, and programmed sexual cycles (after so-many vegetative cycles) remain poorly understood, but has clear potential for affecting dynamics. The largely qualitative understanding of organism life cycles needs quantification particularly in eutrophic systems. The role of density-dependent processes, which are most likely to be exacerbated in eutrophic systems, requires parameterization. Changing organism behavior has the power to shape and reshape ecosystem dynamics. The high biomass potential of eutrophic waters offers the capacity to exaggerate behavioral responses through enhanced biomass levels which increase the frequency of organism-organism interactions, decrease between-contact periods (thus minimizing respiratory costs), and increasing chemical concentrations.

Switching between nutritional modes can affect the growth rate of the organism and have a cascading ecosystem response (e.g. Adolf et al. 2008, Glibert et al. 2009a). These behavioral responses typically reflect biochemical (physiological) responses and
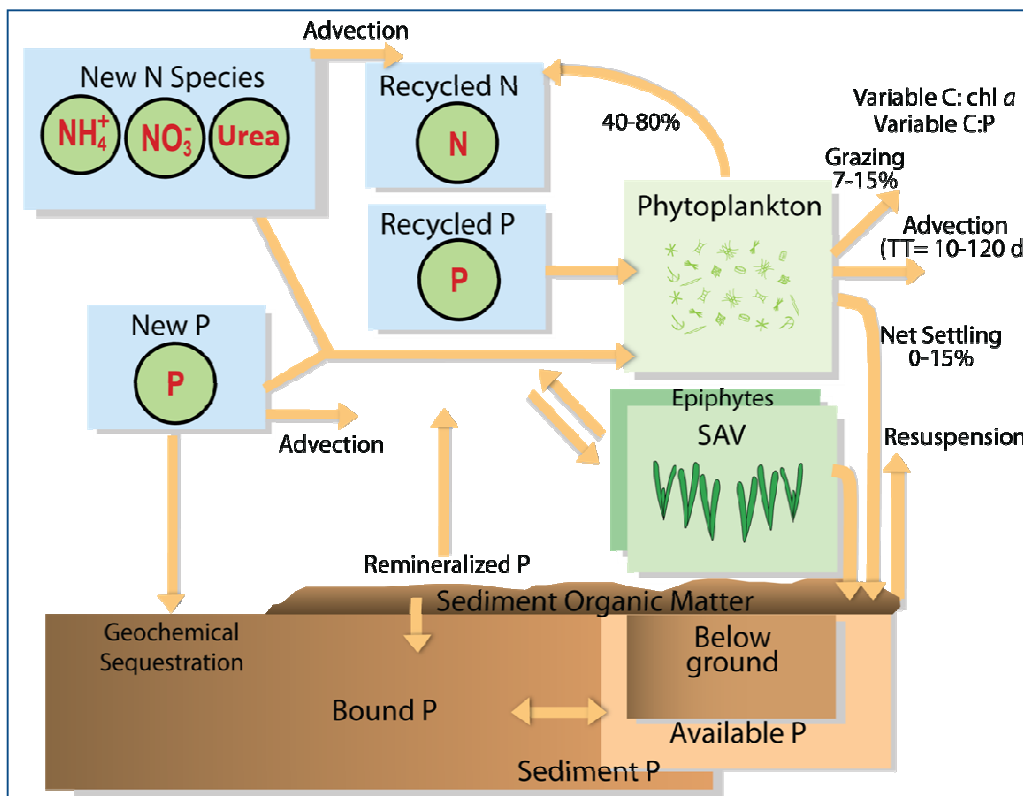

Figure 7. Conceptual model of the Florida Bay, USA, SAV-phytoplankton ecosystem numerical model.

include nutrient switching, prey switching, and for mixotrophy switching between nutritional modes. Responses more typically termed behavioral, associated with swimming for mating and diel vertical migration, are also associated with nutritional triggers but have not been well characterized in eutrophic systems, or indeed in others. Modelling of such switches is often crude, and sometimes flawed (Mitra and Flynn 2006b), but critically affects the dynamics (e.g., HAB development – Mitra and Flynn 2006a; mixotrophy nutrient switching – Flynn and Mitra, 2009).

A primary challenge for describing behavior is that of identifying and parameterizing functional response curves relating the stimulus to the response; typically these take the form of Michaelis-Menten type curves describing nutrient uptake as a function of nutrient concentration, or grazing rates as a function of prey concentration. Description and placement of these response curves within models is relatively easy, using sigmoidal curves which are typical of biochemical allometric interactions. Response curves are thus required relating stimuli for behavior to the response. As far as possible a mechanistic basis should be developed for such responses because the multitude of potential interactions will likely preclude the complete parameterization of the stimulus-response matrix. Modelling the growth of HABs requires that attention is also given to modelling those species that share the common environment. These organisms are important for the conditioning of the environment through removal and/or addition of nutrients and other chemicals, through grazing and other such interactions. For example, modelling *Dinophysis* may be expected to require modelling effort to also be directed towards *Myrionecta* and cryptophytes because these groups are involved in a kleptochloroplastic exchange (Johnson et al. 2006, Kim et al. 2008).

Important challenges include studying the cycling of nutrients, and of the positive feedback processes that may exacerbate or minimize interactions. Some of these are relatively simple (stoichiometric) but many may relate to processes that are synergistically related to changes in nutrient status, such as toxin, allelopathic and anti-grazer impacts. Even the simple stoichiometric interactions require careful consideration, particularly as eutrophication is usually associated with shifts in nutrient (elemental) ratios and nutrient forms in the incoming nutrient stream which may ultimately affect C:N:P within the primary producers (but see Flynn this issue).

The impacts of eutrophication upon toxin production act through two routes; the enhancement of biomass and hence of overall toxin burden in the water, and secondly the enhancement of per capita toxin content through nutrient stress associated with disturbed elemental ratios in the water column and thence in the organisms. Because eutrophic systems are often associated with coastal areas used for shell and/or finfish harvesting, the primary concern has been of toxins that affect humans (e.g., shellfish or ichthyotoxins). These are chemicals for which we typically have analytical techniques which may be applied also to experimental studies and as aids to model development (e.g. John and Flynn 2002). However, there is a more insidious class of toxins, and other processes, which are important for the biological warfare waged within the ecosystem, and for which we have relatively little knowledge. This group includes not only antigrazer compounds and processes such as spines and mucus, and allelopathic chemicals (Mitra and Flynn 2005, Pohnert et al. 2007). For many of these we have little direct knowledge, and hence few data (even qualitative data) for modelling. Eutrophication, however, may be expected to enhance the role of these processes for the same reason as given for shellfish toxins (Granéli et al. 2008). One of the best studied of these chemical classes is polyunsaturated aldehydes, and while the value of these chemicals as defense toxins produced by diatoms against their copepod grazers has been called into doubt, there is no question as to the potential damage that a eutrophic-enhanced bloom of diatoms could cause on copepods through such a mechanism (Flynn and Irigoien 2009). Allelopathy is clearly a density-dependent process, linked to the accumulation of chemicals in the water column, and may be expected to be enhanced in eutrophic waters.

Studying, and then parameterizing, models describing the involvement of anti-grazer and anti-competitor processes is complex, requiring an understanding of the ecophysiology of several members of the ecosystem. In turn this generates an experimental matrix of conditions that is typically logistically challenging, especially when the interacting organisms cannot be physically separated prior to chemical analysis. While most emphasis is often placed on the synthesis of toxins, modelling the deterioration and loss of toxins is a topic that warrants further investigation (John and Flynn 2002). Studies in which naturally occurring groups of organisms are brought together under controlled quasi-natural conditions are required, recognizing that these are very difficult experi-

ments to conduct well. In this context, a critical question is why the microzooplankton fail to control the growth of the phytoplankton (Irigoien et al. 2005). Understanding the failure of top-down control is as important as understanding factors relieving bottom-up control for HAB development (Stoecker et al. 2008). In large measure this may be related to the more complex behavioral and life cycle of higher trophic levels that in turn control the microzooplankton. Certainly the age structure of copepods (Flynn and Irigoien 2009, Flynn 2009a) and the operation of intraguild cannibalism (Mitra 2009) all operate to affect the dynamics significantly. The effects of temperature in these dynamics are also important, especially given the differential effect on heterotrophy (Rose and Caron 2007), that mixotrophy is important in many HABs, and that bloom development itself raises local water temperature in blooms.

Forecast Models

Types of Models and Recent Advances

HAB forecasts provide an estimate of the likelihood of occurrence, abundance, or both, of a HAB species at a given location and time in the future. The time scales of forecasts range from short- (days to seasons) to long-term (years to decades). Short-term forecasts - termed predictions here - carry the expectation of accurately reproducing future events, while longer term forecasts - termed projections here - are considered to possess a high degree of uncertainty. Both have relevance in terms of understanding the relationships between HABs and eutrophication.

Both short- and long-term HAB forecasts provide a bridge between research and management, linking research on HAB causes and impacts to applications that can lead to management outcomes (e.g. advanced management knowledge; changes in management strategies; improved environmental conditions; societal benefits). Short-term predictions provide advance warnings that can alert local, state and federal agencies and individuals to prepare for and respond to HABs in a timely fashion and alleviate the deleterious effects of the HAB presence on human and ecosystem health, as well as provide a means to assess the effectiveness of alternative management strategies on HAB prevention. The predictions may also supply information on bloom sources (e.g. cyst beds, eddies), triggers (e.g. nutrients, water column stratification), trajectory (e.g. landfall), duration, decline, toxicity, and impact risk analysis. The

longer-term projections offer a tool to evaluate the response of HABs — their intensity, frequency, distribution, and impacts — to proposed management and land-use/land-change policies and climate change. In regards to eutrophication, projecting the long-term effects of nutrient loading on HABs will enable management actions to reduce loads and minimize HABs, leading to multiple benefits, such as planning for restoration and aquaculture facilities, the reduction in drinking water contamination, and a reduction in an excessive monitoring burden on state and local agencies.

HAB forecasts will likely be most effective when applied through a regional ecosystem-based management approach where physical, chemical, biological, economic, and socio-economic data about the present condition of the coastal environment and expected future conditions are integrated and considered together. An important use of HAB forecasts is in goal-setting – e.g., determining the amount of nutrient abatement required to decrease HAB magnitude, frequency, extent, and/or impacts. This includes an adaptive management approach (Holling 1978), where it is critical to validate and reassess goals according to any new and improved understanding of the ecosystem effects and changing conditions (from management actions, climate change, regime changes, etc). Short-term predictions and long-term projections both rely on the application of our basic knowledge and understanding of HABs and their interaction with the environment. HAB forecasts employ information from empirical and process/mechanistic models to develop a predictive relationship between causative factors and HAB parameters, and their impacts.

Forecast models can be simple (involving a limited number of variables or one or few species) or complex (system-scale). The complexity of models is limited by our understanding of ecosystem dynamics, and so various process-level models are often not fully developed. Therefore, simple models are often the strategy employed, whether they are appropriate or not. The model and supporting data requirements for HAB forecasts vary with region and HAB species. Forecast approaches include use of: a) observations coupled with transport models; b) mechanistic models; c) empirical statistical models; d) hybrid mechanistic and statistical models; e) coupling of b, c, and d with real-time observing systems, and f) food web models. Typically, operational forecast systems will couple circulation models (which may be linked to transport models), population dynamic models (process models), and ecological conditions models (e.g.

nutrient loading models). For instance, the system that forecasts "red tide" blooms of the dinoflagellate *Karenia brevis* on the west shelf of Florida detects probable blooms in satellite ocean color imagery and uses a simple transport model to predict the likely movement and location of landfall (Stumpf et al. 2003).

HAB forecast systems in the U.S. are in various phases of development (Stumpf 2008), and only that for *Karenia brevis* in the Eastern Gulf of Mexico is in operational status (www.csc.noaa.gov/crs/habf/). Nutrient loading/availability is incorporated in all of these as a triggering factor (e.g. Lake Erie, Chesapeake Bay, California) or a factor in bloom duration/prolongation. For example, the HAB prediction system in the Chesapeake Bay (http://155.206.18.162/cbay_hab/index.php) uses or will use real-time and forecast data acquired and derived from a variety of sources to drive multi-variate, habitat suitability models of HAB species, such as *Karlodinium veneficum and Prorocentrum minimum,* in order to generate daily nowcasts and 3-day forecasts of their relative abundance and bloom probability. The empirical habitat models for three HAB species in the Chesapeake Bay, including the two species mentioned above and the diatom *Pseudo-nitzschia* (Anderson et al., 2009), require estimates of dissolved inorganic N, particulate N, or P. Other variables used in the habitat models include chlorophyll concentration and dissolved oxygen, both of which will likely be affected by changes in regional nutrient loading, and the ecophysiology of the organisms and whole system. At the seasonal scale, forecasts on the likelihood of occurrence and intensity of *Microcystis aeruginosa* in the Potomac River and *P. minimum* in the Maryland region of Chesapeake Bay during the summer are generated based on flow and nutrient loading conditions through mid-May (www.eco-check.org/forecast/chesapeake/2009/).

HAB prediction systems are also being developed and implemented around the world. Most of these focus on short-term predictions. Examples include *Cochlodinium polykrikoides* predictions based on temperature in Korea (Kim et al. 2003), predictions of diatoms (various species) red tides based on rain and river discharge in Japan (Ishizaki et al. 2006), and predictions of *Gymnodinium catenatum* blooms based on downwelling conditions in Portugal and Spain (Moita et al. 2003). The Harmful Algal Blooms Expert System (HABES) project uses fuzzy logic models to predict conditions favoring blooms and harmful effects from 7 species from various European waters, including *Phaeo-*

cystis globosa and *Dinophysis* spp. in the Dutch coastal zone (Blauw et al. 2006).

Longer-term projections are also needed and forecast models are being developed to examine how anthropogenic activity, eutrophication and HABs may be accelerated due to climate change, including influences from the circulation and temperature structure of the ocean. Concurrently, increasing population, likely to be centered on the coast (e.g., NOAA 2004), and changes in land-use will lead to increased nutrient loading to coastal waters. These and other factors, such as invasive species, ocean acidification, overfishing, and pollution, will impact HAB distribution and abundance on a regional and to global basis. In the context of climate change the focus of marine ecosystem model modelling activity has largely been on C cycling at a global scale (Le Quere et al 2005, Moore et al. 2002, Aumont 2001).

Data analysis only allows one to look at the current state; modelling will allow exploration of the consequences of these changes on HAB distribution beyond the climate envelope. Models can be used to attribute the various factors, identifying the important factors causing these distributional changes. Numerical models with feedbacks are the only way to explore ecosystem response beyond the current climate envelope. In the Chesapeake Bay, for example, a regional earth system model, which consists of a coupled atmospheric, land, and ocean model, complete with biological and geochemical components, is being implemented with dynamic downscaling of the seasonal to interannual and climate forecasts and IPCC projections for the Chesapeake watershed to routinely generate seasonal predictions and decadal projections of HABs and other organisms, e.g. pathogens, and ecological conditions www.climateneeds.umd.edu/chesapeake/).

The role of such models is very different, however, from that of models required for HAB research, and the constructional detail of the biological descriptions are inadequate. These models also do not resolve the loadings of coastal zone spatially, temporally, or in terms of key processes. At the same time, shelf seas modelers have focused primarily on eutrophication and nutrient cycling resulting in numerous medium-to-high resolution regional models, ranging from simple nutrient-phytoplankton-zooplankton-detritus (NPZD) models (Fasham et al. 1990) to highly complex, coupled physical – biogeochemical ecosystem models (e.g. Allen et al 2001; Schrum et al. 2006). Such models are used routinely, and are begin-

ning to be applied in a climate context. For example, the European framework project Marine Ecosystem Evolution in a Changing Environment (MEECE; www.meece.eu) seeks to address the broad range of ecosystem responses to climatic and anthropogenic drivers at a regional scale. Parameterization to study ocean acidification and end-to-end ecosystem models (e.g. those simulating the response of trophic levels from phytoplankton to top predators) are being rapidly developed and implemented. Simulation strategies are required to make reliable hindcasts, including re-analysis simulation and error quantification. A reliable hindcast means making the best available simulation of the current state of the system in question, using the best available external forcing (e.g. meteorology, land derived inputs), whose skill has been assessed against observations.

A challenge is to get emergence from ecosystem models in the sense of allowing model organisms to evolve and adapt to their environment rather than just occupy niches. Bedau (1997) highlights two "vague but useful hallmarks of emergent phenomena": that emergent phenomena are somehow constituted by and generated from underlying processes and that these processes are somehow autonomous from these underlying processes. Follows et al. (2007) used such an approach towards generating biogeography; a marine ecosystem model was seeded with many phytoplankton types, whose physiological traits were randomly assigned from ranges defined by field and laboratory data. Global scale simulations generated an emergent community structure and biogeography consistent with observed global phytoplankton distributions. This is a model of selection not adaption. Further, emphasis was placed upon bottom-up phytoplankton dynamics, with scant effort directed to the predators, and none directed to mixotrophy. The methodologies used by Follows et al. (2007) provide a conceptual framework within which we can create emergent ecosystems combining generic cells with food web interactions, but requires significant upgrading in scope to be of utility. To address issues such as physiological adaption to ocean acidification or the plasticity of response in food web dynamics requires a theoretical framework which allows processes to adapt. The system of infinite diversity (SID) approach (Bruggeman and Kooijman 2007) simulates biodiversity by describing the ecosystem with one generic population model and species characterising parameters and models phytoplankton succession as evolution of the parameter value distribution and may provide one starting point.

Challenges and Opportunities for Advancement

The interdisciplinary nature of the multiple challenges for modelling the suite of interactions between eutrophication and HABs, the development of reliable short-term forecasts for managers and the understanding of the interactions with long-term changes such as climate, have many cross-cutting issues.

There is an ongoing quest for better models of nutrient loading, transport and mixing. The current models are adequate for many applications, but our needs are for higher resolution nutrient loading models and hydrodynamic models and for better coupling between the two. On multi-year scales, there is much to be learned from the interactions of nutrient loading and other environmental factors, such as changes in temperature and precipitation that may occur due to regime shifts and/or climate change (Najjir 1999, Najjir et al. 2000, Howarth et al. 2006, Howarth 2008). Spatially explicit modelling will be of importance in advancing this understanding. For example, estimates of the net anthropogenic nitrogen input to 16 major watersheds of the northeast USA show that increases of up to 45% are expected in watersheds where precipitation is expected to increase, but that in drier regions, decreases of only 10-20% are expected (Howarth 2008). Clearly, linking climate and nutrient loading estimates is a significant challenge, but an even greater challenge will be predictions of how such changes may affect the relationship between nutrients and HABs, as not only will loading rates changes, but so too will water temperature and trophodynamics among other factors. In addition to determining trends in environmental conditions, such as temperature, there is a need to understand the consequences of climate variability and possibility/probability of increased extreme events, both in frequency and magnitude. Current models provide possible realizations of future states on a regional and global basis, but are insufficient to address the response of HABs to climate change that we face. The development of integrated ecosystem models that couple the atmosphere, land, and coastal ocean to enable the quantitative estimation from air-shed to the ocean is required to investigate ecosystem response to climate. This activity is beginning but will require considerable computation capabilities to run routinely at the time and space resolutions required.

An assessment of the confidence that can be placed on model results (known as model validation) must take into account the complex combina-

tion of model and observational uncertainties. Model errors derive from inaccuracies in the model structure itself, process descriptions, parameterisation, initialisation and forcing functions. Errors in observations arise from basic measurement error, inadequate sampling of a process (i.e. aliasing of small scale signals to large scales due to under-sampling) or lack of replication in highly heterogeneous systems and issues of methodology. A crucial issue is balancing precision (how well the model fits each data point) with trend (i.e., how well it reproduces the observed seasonal cycles). For example, even when the trend is well reproduced small differences in the timing of an event can lead to large errors in precision. The choice of error statistic is crucial and a comprehensive validation process must consider several. A variety of univariate and multivariate methods are now being used to assess model skill (e.g. Stow et al. 2009; Allen and Somerfield 2009, Joliff et al., 2009), the choice of which is dependent on the questions being asked and the data available for confronting the model.

High model skill depends on the fidelity of all model components, and also upon the adequacy of the data used for its parameterisation and validation. Models depend on parameters that are not always easily measured or available and knowledge of fluxes, dynamics or physiological variable is often not adequately captured in models. In many cases, also, data on a relevant process may be obtained using multiple methods, but such techniques may not be inter-comparable, and such subtleties are not well captured in models. One such example is the measurement of productivity, which may be by use of ^{14}C, ^{18}O, or variable fluorescence. Whereas ^{14}C measurements determine the rate of incorporation of C, ^{18}O experiments measure the water splitting reaction and non-cyclic electron transport, and variable fluorescence instruments (e.g. FRRF, PAM) measure photochemical efficiency of the photosystem II pathway; these rates are not equivalent (Suggett et al. 2009). There are many other examples of methodological issues where data from one method are not equivalent to data obtained via another method, yet used inter-

changeably in models. The estimation of rate processes can be critical; models tuned only against the usual state variables of nutrients and biomass can fit data using erroneous or dysfunctional descriptions of rate processes, two wrongs making a right, so to speak (Mitra et al. 2007, Mitra and Flynn 2010). As rate process data invariably carries wide ranges of error, and empirical fits to data can be so misleading, it is imperative that model structure is fit for purpose (Flynn 2009b).

All ocean models have some biases with respect to observations. Data assimilation offers a way to reduce these biases and improve a model's representation of the observed state of the system in question. In particular, these kinds of simulation allow us to make the best possible model quantification of key biological processes over the periods which have suitable data). The application of data assimilation has demonstrated the value of constraining the physical environment; improved descriptions of physical mixing lead to better estimates of the C cycle at a global scale. The next stage is to develop complementary assimilation techniques to constrain the biological models. There are three main limitations to this approach; it is computationally expensive; the availability of suitable data sets at a global scale is currently limited to ocean color, and, as data assimilation limited to hindcasts, we cannot make simulations which project future ecosystem states. Multiple models ('ensembles') are the preferred approach to develop a range of future predictions and hence an idea of the range of future ecosystem responses (Fig. 8). Ideally such ensembles would
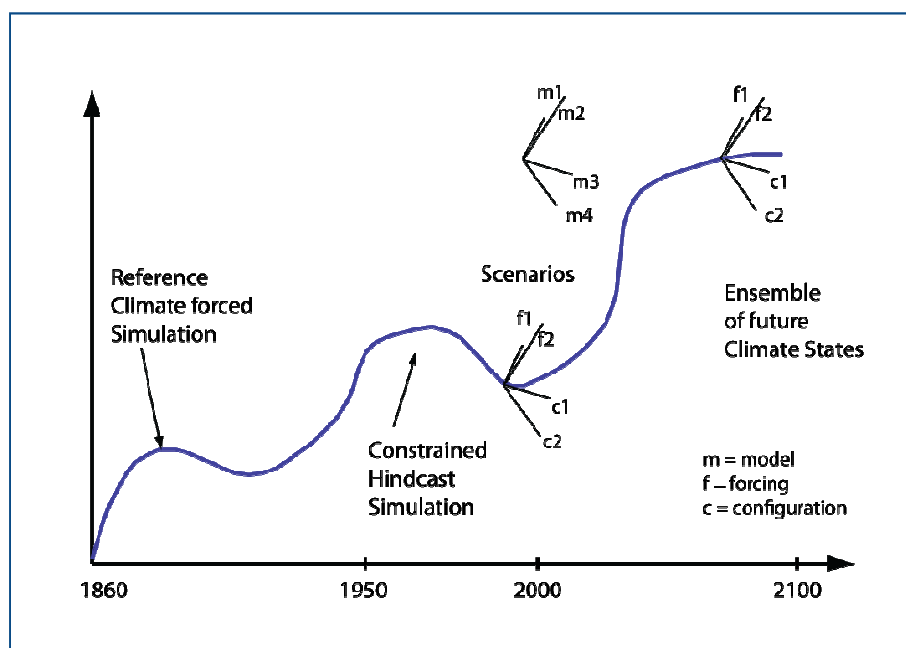

Figure 8. Schematic diagram of the simulation strategy for future climate scenarios (modified from Jason Holt, Proudman Oceanographic Laboratory, UK).

be derived from multiple combinations of different biological and physical models which are then are assessed to decide which outcomes are more likely (probable) than the others and which then explore the uncertainties introduced by parameter and driver choices. This is important, for example, when assessing the sensitivity of biological models to changes in hydrodynamic environments. Again, robust validation of hindcast simulations is required to underpin this activity and where necessary to help weight the ensembles.

In Summary

Understanding and quantifying the relationships between eutrophication and HABs, and developing both short and long term predictive capabilities will require a suite of modelling approaches. Loading models draw on the complexity of nutrient sources from individual water- and air-sheds and how they are modified by human population, agricultural and aquacultural practices, precipitation, land use and slope and many other factors. Coupling nutrient discharge to the response of a single species or group of species requires models of hydrologic properties of the receiving water for estimating retentiveness of the nutrient, as well as knowledge of the rates and pathways by which nutrients are consumed and recycled and how such rates and pathways are affected by physicochemical factors. The plasticity of nutritional pathways, as well as the plasticity of food web interactions, including grazing, allelopathy, symbioses and other interactions, creates immense challenges for model constructs. Capturing dynamic behavior, including adaptation will continue to be a challenge. Ultimately forecast models must be robust, but must be simple enough to be operational and affordable to managers. Ensembles of models and integrated ecosystem models that couple the atmosphere, land, and coastal ocean are required to enable the quantitative estimation from air-shed to the ocean and to investigate ecosystem response to climate changes and to further explore the changes in HABs that are to be expected in the future as eutrophication impacts increase. The HAB modelling community will need to engage with climate scientists, for climate change scenarios and model uncertainty analysis; plankton and marine ecologists to improve the description of physiology and ecology in the models; invasive species experts to characterize and parameterize such changes; watershed modelers and hydrologists to estimate future changes in the land derived inputs; socio economists, managers and policy makers, to help define future land use scenarios and to interpret results in a policy context.

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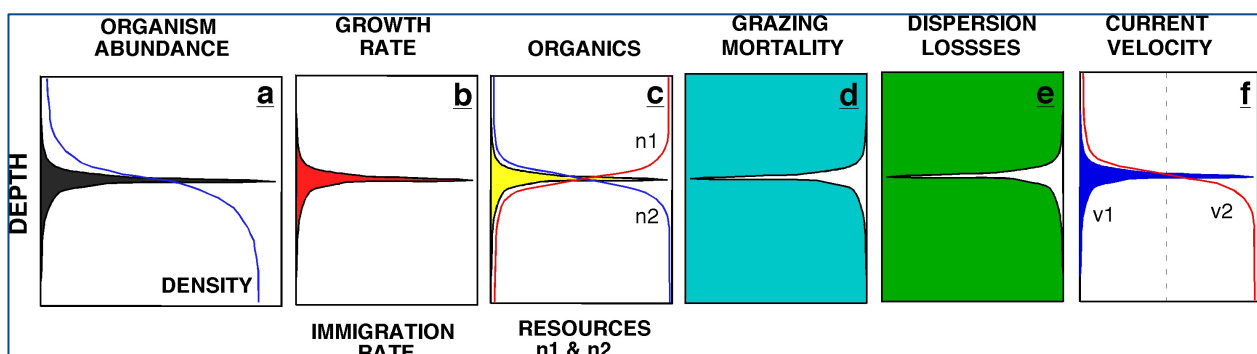
Modelling of HABs in Stratified Systems

HABs in Thin Layers - Definitions

Often, the occurrence of HABs is linked to marine stratification. The term "stratification" means "layering", which in the case of coastal and shelf seas indicates that their vertical structure is typically composed of a wind-mixed surface layer (SML) and a tidally-mixed bottom layer (BML), separated by a pycnocline. However, within the SML, several small discontinuities are often found: the so-called "thin layers". These are structures that exhibit physical, chemical, and/or biological signatures that are different from the surrounding water, in particular with a significantly higher abundance of planktonic organisms compared to the water immediately above or below. Sustained interest in thin layers started when it became clear that the mean concentrations of phytoplankton alone could not provide for the energetic and growth requirements of fish larvae (Lasker 1978). More recent interest in thin layers stems from the recognition that some species of harmful algae are often confined to narrow parts of the water column. The vertical extent of a thin layer can range from several metres to centimetres, depending on author, study site, and sensor (Haury et al. 1978).

Thin layers are usually characterized on the basis of measurements of chlorophyll fluorescence, acoustics, bioluminescence, and - more recently - cell counts. Cell and chlorophyll concentrations in a thin layer can be 1 to 3 orders of magnitude higher than bulk concentrations (e.g., Kils 1993 for *Prorocentrum minimum*; Bjørnsen and Nielson 1991 for *Gyrodinium aureolum (Karenia miki-motoi)*; Alldredge et al. 2002 for several diatom species; Rines et al. 2002 and Velo-Suárez et al. 2008 for *Pseudo-nitzschia*; McManus et al. 2003 for *Chaetoceros socialis*; revision in Gentien et al. 2005). The horizontal scale of these layers is of the order of kilometres, and they can persist for periods of days or longer. Very high resolution fluorometry has revealed even thinner layers, at mm scales (Doubell et al. 2006). Focussed attention on the biology of these thin layers is quite recent, only a few examples have been studied in detail, and their significance is poorly understood. Perhaps the least known biological thin layer is that at the air-sea interface comprising the neuston. Within the context of HABs, thin layers are important as they 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, cell behaviour within the layer, predation, and shellfish resource intoxification ("a toxic carpet").

Figure 1: General conceptual model of mechanisms controlling thin layers. Modified from Donaghay.

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Conceptual Model

Understanding the dynamics of HAB species in sub-surface thin layers is highly constrained by the difficulty in the detection of the layer which is not possible by remote sensing and limited in the case of the instrumentation deployed at fixed depths. As a general framework, the conceptual model in Figure 1 indicates that a combination of physical, chemical, and biological processes are involved in the formation, maintenance, and destruction of thin layers.

Numerically, this conceptual model can be expressed in the following form:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = r \cdot P$$

with $r = \mu + I - E - g - m$

The net growth, r, i.e. the numerical increase/decrease of a population P with time, is the balance between gains (cell division, aggregation and physical advection) and losses (natural mortality, grazing, dispersion and sedimentation), where μ is the intrinsic division rate, I and E represent physically driven imports and exports, g is grazing and m is mortality (cell lysis, infections, sedimentation). The different rates can depend on the dynamics of state variables other than growth rate, such as nutrients and zooplankton (grazing). Given the wide range of environmental conditions and species associated with the development of thin layers, it is unlikely that a single mechanism is responsible for all observed layers.

Among the **biological processes** promoting a positive r are: enhanced growth in a particular area, active aggregation by swimming (e.g. vertical migration of dinoflagellates) and/or buoyancy control (through excretion of exopolymeric substances in some diatoms), and physiological adaptations, grazer avoidance, suppression of grazing activity, and/or killing zooplankton and micro-zooplankton grazers within the layer (e.g., Deren-

bach et al. 1979; MacIntyre et al. 1995; Alldredge et al. 2002; Genin et al. 2005).

The production of allelochemicals—biologically active components eliciting specific responses in target organisms—have been invoked as agents of chemical defence in some HAB species.

The important **physical factors** potentially involved in the formation of thin layers are vertical shear, density steps and gradients in turbulence (Dekshenieks et al. 2001; Rines et al. 2002; Ryan et al. 2008; Birch et al. 2008; Durham et al. 2009, Churnside and Donaghay 2009). Thin layers can be formed by vertical shear (Fig. 2). If a patch of phytoplankton exists, the vertical shear will tend to tilt and stretch this patch as one part is moved horizontally relative to another part deeper down. This shearing will create interleaved layers whose vertical extent is determined by the initial patch characteristics, and the temporal and spatial structure of the shear. This shearing mechanism may be ubiquitous, and will interact with other layer-forming mechanisms in determining the layer structure at any time. If mixing with the surrounding water is small, resulting in the volume of layer remaining constant, the type of shearing in Figure 2 results in the layer becoming thinner vertically as it extends horizontally.

Durham et al. (2009) have recently suggested a new thin layer formation mechanism based on "gyrotactic trapping" (see also Kessler 1984). Thin layers can be generated by coupling the action of a population of active swimming cells and hydrodynamic shear. This study suggests that regions of enhanced shear can disrupt vertical motility of plankton cells and promote sharp-peaked cell accumulations in this area.
Finally, eddies have been suggested to operate as traps that minimize lateral dispersion of plankton populations. Furthermore, the circulation and vertical physical structure within these eddies can reduce vertical mixing, so allowing thin layers to develop and persist (Churnside and Donaghay 2009).
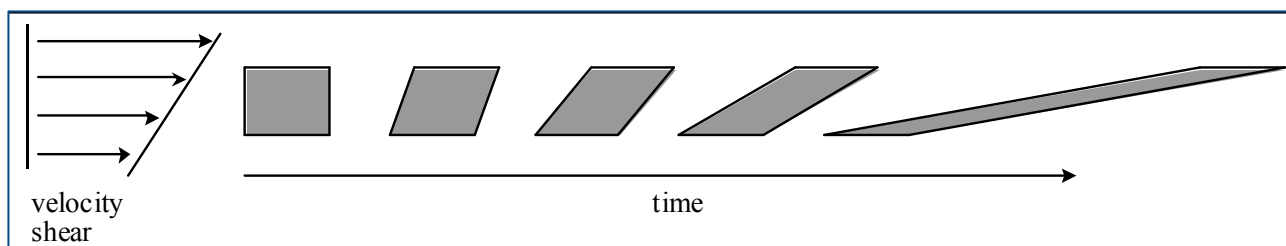

Figure 2: Thin layer formation from velocity shear (redrawn after Stacey et al. 2007).

Key Questions

Question 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?

The existence of ocean microstructure is well known from the physical viewpoint, at least in terms of temperature, and has been for several decades. Vertical profiles of the ocean characteristically reveal step-like structures at all scales. Turner (1973) describes turbulence in the ocean interior confined to thin elongated patches which occur intermittently in space and time. He notes that records of temperature and velocity fluctuations reveal regions of small scale turbulence separated by others which are laminar, plus regions that contain 'fossil turbulence', i.e. temperature microstructure which remains after turbulence has decayed. Some of the non-uniformities observed are due to internal waves. Federov (1978) described "laminae", tens of metres to centimetres thick, with abrupt changes in thermodynamic properties on vertical and horizontal scales of the order of 10cm and 200m respectively, and degradation times of inversions of the order of 10h with initial inversion thicknesses of 1m and temperature differences of approximately 0.1°C.

The upper end of the biological size spectrum is typically larger (up to 5m) than physical microstructure, while the lower end (centimetre scale or smaller) might coincide with it. This raises questions about whether and to what extent the same processes which generate and maintain the physical structures are also responsible for thin layers of phytoplankton. Particularly at large scales, salinity or temperature may be strongly coupled with fluorescence distributions, and in those cases chlorophyll has been considered as a passive tracer (but see Strutton et al. 1997). However, species distributions can be very distinct from chlorophyll profiles, e.g. thin layers of a particular species in the same water column at the same moment do not match the chlorophyll. This leads to the conclusion that biological processes must actively contribute to thin layer formation. In any case, the similarities of the power spectra of turbulence and chlorophyll do not extend to scales below 1 meter (Mitchell and Furhman 1989, Waters and Mitchell 2002, Doubell et al. 2006).

In Lasker's original formulation (Lasker 1978), thin layers of phytoplankton become possible if wind velocities remain below 4m s^{-1} during 4 consecutive days (these are called Lasker events in the fisheries literature): decreased mixing rates at low wind velocities allow accumulation at restricted depth ranges by vertical migration or prevent the dispersion of localised production. Such thin layers are thus the result of physical-biological interactions. Some physical thin layers are caused by lateral intrusions (Osborn 1998); if such intrusions are accompanied by high cell concentrations, a biological component of layer formation is clearly not necessary. Similarly, passive particles can be concentrated into thin layers in shear fields. But in other cases, biological thin layers can form independently of the physical dynamics, by buoyancy regulation, vertical migration, and other taxes including social aggregation. Layers, once formed, might then be stabilized, e.g., by polymer secretion or by heat absorption. Nevertheless, with persistent high turbulence, fine scale biological structures must be destroyed.

Although turbulent flow is complex, there are a few successful theories that generalize the nature of the flow. The most important one, the inertial subrange theory of Kolmogorov (1941a), predicts a universal spectral slope in the wavenumber range,

$$L_o^{-1} << k << L_k^{-1}$$

where L_o is the spatial scale of external forcing and L_k the Kolmogorov microscale (Table 1). Since the separation between these two scales has to be large by the definition of the inertial subrange, the associated Reynolds number also has to be large (Kundu and Cohen 2002) and the velocity power spectrum follows a $k^{-5/3}$ universal shape.

The Kolmogorov length scale is defined from a simple dimensional argument, namely that the smallest eddy should be determined from a combination of the kinetic energy dissipation rate, ε, and the kinematic viscosity of the fluid, v:

$$L_k = (v^3 / \varepsilon)^{1/4}$$

The rate of the kinetic energy dissipation ε, is the most important observable parameter describing the dynamics of turbulence. When turbulence is in an isotropic condition, we can estimate ε from a cross-stream shear component, such that:

$$\varepsilon = 7.5v \left\langle \left(\frac{\partial u}{\partial z} \right)^2 \right\rangle$$

where z is vertical coordinate and u is a horizontal turbulence velocity component. The Reynolds number Re_o, based on the external forcing scale, L_o, is usually large for geophysical flows. On the other hand, the Reynolds number based on the Kolmogorov scale is always 1 by definition.

Thorpe (1977) proposed a length scale l_T (Table 1), which characterizes the energy-containing eddy size based on a sorted density profile, whereby observed densities are exchanged vertically until a stable density profile is obtained. The Thorpe scale is a good length scale to describe the size of an overturning eddy for a stratified fluid. The intensity of stratification is expressed in terms of a buoyancy frequency,

$$N = (-g\rho^{-1} \frac{\partial \rho}{\partial z})^{1/2}$$

where g is gravity acceleration and ρ the density of the fluid. When an eddy scale exceeds l_T the eddy is no longer free from the effect of gravity. A combination of ε and N provides another length scale characterizing an over-turning eddy size, namely the Ozmidov scale (Table 1), $l_O = (\varepsilon/N^3)^{1/2}$. These two scales correlate closely with each other. The Thorpe scale l_T does not require ε but requires a sorting process. On the other hand, l_O requires ε and the density profile for N. Since both these scales estimate the over-turning scale of individual mixing events, the external length scale L_o is usually larger than these scales. A reasonable estimate for L_o is the turbulent patch size L_P (Table 1).

Stacey et al. (2007) derived three different thin layer scales based on diffusion, swimming, and buoyancy: a balanced length scale between diffusion and shear strain:

$$l_{strain} = \sqrt{\frac{K}{\alpha \theta}}$$

a balanced length scale between diffusion and swimming:

$$l_{swim} = \frac{K}{w_s}$$

a balanced length scale between diffusion and buoyancy:

$$l_{buoy} = \sqrt{\frac{18 K \upsilon}{N^2 D^2}}$$

where K is the turbulent diffusion coefficient, α a shear rate, dU/dz the velocity gradient, θ a patch angle, w_s swimming speed of cell, D the particle diameter. The turbulent diffusion coefficient is usually estimated from the following equation (Osborn 1980):

$$K = 0.2 \frac{\varepsilon}{N^2}$$

Clearly, the most important physical parameter to define thin layer scales is the turbulent kinetic energy dissipation rate, ε (Table 2). Yamazaki et al. (2010) observed a thin layer at the base of surface mixed layer in a large fresh water lake (Lake Biwa). The layer thickness is about 1 m (Fig. 3) and the observed ε did not exceed 10^{-8} W Kg^{-1} (Fig. 4). So a swimming velocity scale of a cell can be as small as 10^{-8} m s^{-1} (0.01 μm s^{-1}) to maintain the layer thickness against turbulent diffusion. Swimming scales of phytoplankton can exceed 100μm s^{-1} and thus the behavioural aspect becomes important for the observed layer thickness.

In order to obtain the turbulent kinetic energy dissipation rate, one needs to use a shear probe that is mounted on a free fall profiler, such as Turbo-MAP-L (Doubell et al. 2009). Another way to estimate ε is to use a 3D particle tracking system (Nimmo Smith 2008) which requires a stable platform, making this method unsuitable to obtain profile data. Scalar fields, such as temperature, may be used to infer the turbulent kinetic energy dissipation rate, but it is an indirect estimate and requires a careful interpretation. At the moment, the shear probe may be the best suited instrument to estimate ε.

Question 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?

Population dynamics of phytoplankton species depend on the balance of biological processes that cause gains (e.g. cellular division, aggrega-

Table 1. List of turbulence length scales. In general, the following inequality is true: $L_p \approx L_o \geq l_T \approx l_o \geq \eta$

L	Characteristic length scale
L_o	External forcing scale
L_p	Turbulence patch size
l_T	Thorpe scale
l_O	Ozmidov scale
η	Kolmogorov scale

tion) or losses (e.g. senescence, grazing, dispersion and sedimentation) of individuals. In stratified systems, these processes are strongly affected by the coupling of the physical conditions with the life strategies of these species. The use of hybrid models, which integrate both mathematical (numerical) and rule-based models, would provide an understanding of both the relative importance of biological and physical processes controlling the population evolution of a given HAB species and the interaction of these processes (Fig. 5).

Question 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 hydrographic patterns?

Many HAB species are motile (in which we include the ability of buoyancy regulation) and most exhibit a rather complex migratory behaviour. While some migrations seem to follow a very regular pattern (e.g. related to the solar or tidal cycle), other strategies are much more difficult to grasp as they depend on a multitude of physiological parameters, trophic interactions (predator-prey) and/or the stage in the cellular life-cycle (encystment). In such situations, the task of explaining an observed migratory strategy often becomes impossible as it would require resolution of too many factors ranging from cell physiology to
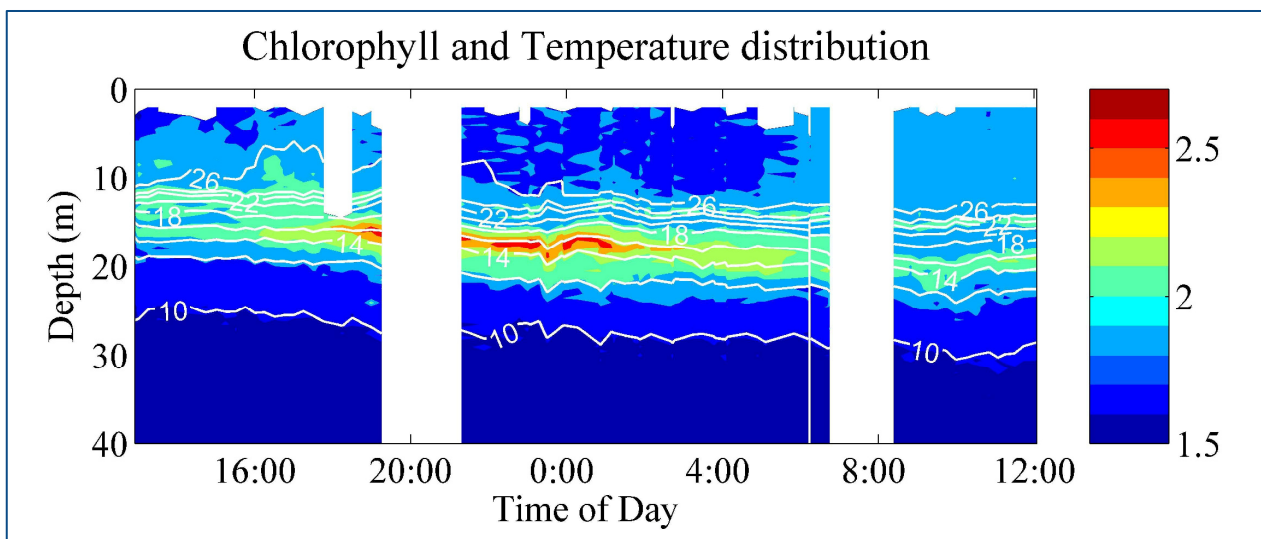
Figure 3. Plot of the chlorophyll distribution (colours in µg L^{-1}) and temperature structure (contoured in °C). A pronounced chlorophyll peak layer appeared in the strongly stratified region of the water column where the temperature dropped from 18 to 14°C. All data were obtained from TurboMAP-L deployed at 15 minute intervals (Yamazaki et al. 2010).
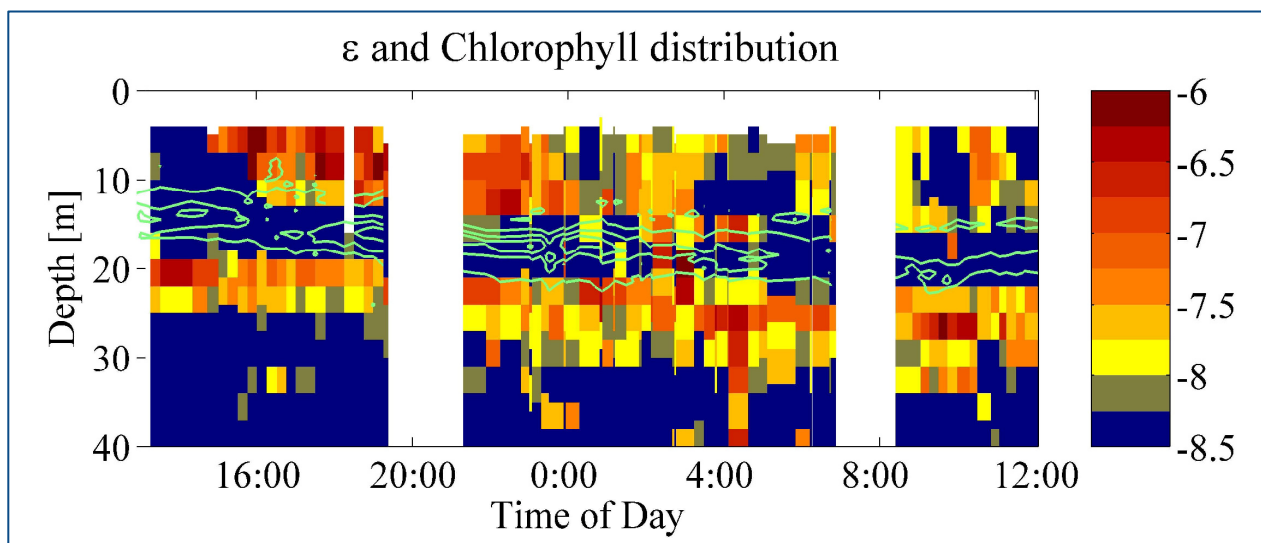
Figure 4. The distribution of the rate of the kinetic energy dissipation (colours in W kg^{-1}) with overlying chlorophyll concentrations (green contours). The local peak in chlorophyll clearly appeared in the low dissipation rate region. All data were measured by TurboMAP-L (Yamazaki et al. 2010).

Table 2. Turbulent kinetic energy dissipation rates and Kolmogorov scales, for kinematic viscosity $\eta = 10^{-6}$ m^2 s^{-1} with the Kolmogorov velocity scale $u_k = (\varepsilon V)^{1/4}$ and the Kolmogorov time scale $\tau_k = (v / \varepsilon)^{1/2}$

ε (W kg^{-1}) or (cm^2 s^{-3})	η (m)	V_k (m s^{-1})	τ_K (s)
10^{-4} (1)	3.16×10^{-4}	3.16×10^{-3}	1.0×10^{-1}
10^{-5} (10^{-1})	5.62×10^{-4}	1.78×10^{-3}	3.16×10^{-1}
10^{-6} (10^{-2})	1.0×10^{-3}	1.0×10^{-3}	1.0
10^{-7} (10^{-3})	1.78×10^{-3}	5.62×10^{-4}	3.16
10^{-8} (10^{-4})	3.16×10^{-3}	3.16×10^{-4}	10.0
10^{-9} (10^{-5})	5.62×10^{-3}	1.78×10^{-4}	31.6
10^{-10} (10^{-6})	1.0×10^{-2}	1.0×10^{-4}	100.0

the ecosystem. The observation of a swimming strategy is further complicated by the fact that the turbulent velocity scales may often be of a similar or greater order of magnitude than the swimming velocities and thus camouflage any deterministic behaviour. In addition, the swimming behaviour may be a combination of species- and location-specific factors which are difficult to separate. 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), but 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 behaviour (e.g., Carpenter et al. 1995, Maestrini 1998, Pizarro et al. 2008, Velo-Suárez et al. 2008, Gonzalez-Gil et al. 2010).

A non-exhaustive list of possible factors that have been suggested to trigger cell migration includes

- Nutrient limitation
- Light limitation
- Turbulence avoidance
- Predator avoidance
- Phototaxis/geotaxis related to an endogenous rhythm

Nutrient and light limitation strategies are often observed in concert, typically resulting in semi-diurnal migrations (Eppley et al. 1968; Fauchot et al. 2005; Ault 2000). Although this is one of the simplest strategies, these two driving factors are sufficient to explain some rather complex distribution patterns (Ralston et al. 2007, Ji and Franks 2007). Turbulence avoidance strategies (e.g. Sullivan et al. 2003) have also been observed both in the field (Crawford and Purdie 1992) and in laboratory set-ups (e.g. reviewed in Berdalet and
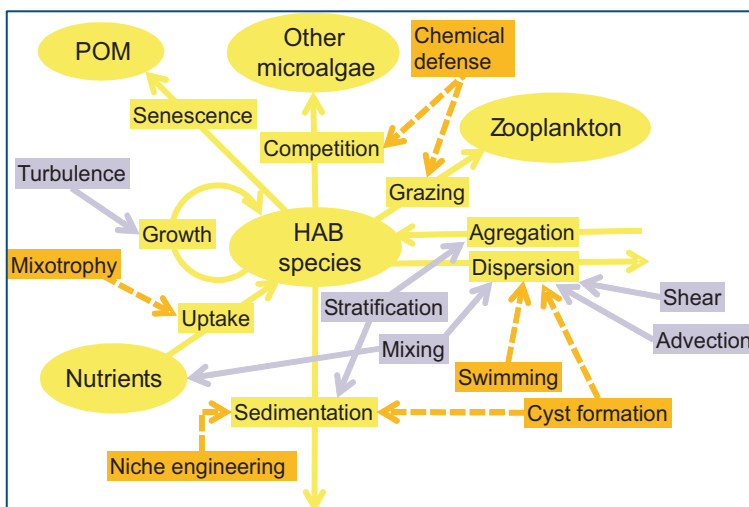

Figure 5. Conceptual model showing interactions between main biological (yellow rectangles) and physical (lilac rectangles) processes on population dynamics of HAB species. Orange rectangles correspond to biological strategies that interact with some of these processes. The graph shows only the main linkages among the illustrated components-- not all of them.

Estrada 2005). Phototaxis and geotaxis related to endogenous rhythms (Heil 1986) are also key processes that are of outmost importance for HAB species having a benthic stage (e.g. *Alexandrium sp.* cysts). It may be possible that within a thin layer the cells typically exhibit less of a migratory behaviour.

Question 2.2) What are the gains of vertical migration: acquisition of nutrients from deeper waters?, phototactic responses?, social behaviour to promote sexual encounters?, aggregation around some unknown cue?

Possible benefits include the ability to outcompete a non-motile species in environments with vertically opposing resource gradients: the phytoplankton dilemma consists in that light is abundant near the surface while nutrients are typically more abundant at depth (e.g. Kamykowski and Zentara 1977; Klausmeier and Litchman 2001, Ross and Sharples 2007). Other uses for motility that have been brought forward in the literature are the reduction of the boundary layer limitation for nutrient uptake (e.g. Gavis 1976; Purcell 1977, Karp-Boss et al. 1997), although this has only been found to be effective for larger cells (>50µm). Some experimental studies seem to confirm a tendency of phytoplankton to migrate upward into the euphotic zone during day time (phototaxis) to photosynthesise and downward to lower regions in the water column at night time (geotaxis) where they find more nutrient-rich waters (e.g., Kamykowski 1995; Levandowski and Kaneta 1987; Margalef 1978; Kamykowski and Zentara 1977). According to Smayda (1997) they exhibit a metabolic coupling between daylight photosynthesis and nocturnal nutrient uptake (and storage). The capacity for vertical migration may thus only be beneficial to the cell if several physiological parameters are adapted to this ability such as the capacities for nutrient storage and mixotrophy for instance.

Passow (1991) found that apart from showing a positive phototaxis, some species that were monitored over two 27 hour periods in the Baltic Sea use their motility to avoid light saturation, following an isolume of approximately 100 µmol photons m^{-2} s^{-1} (a value which very much depends on the light history of the cells). 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).

Through their capacity to swim, the cells may be able to promote their 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 behaviour may include aggregation around some chemical cue (Kiørboe et al. 2003).

Question 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?

This question assumes that physical conditions in the water column allow for the maintenance and development of a thin layer by the biological processes of cell division and/or aggregation and the appropriate dynamic stability (characterized by the Richardson number) would warrant the persistence of gradients. Then, the differential growth of the target population at particular depths may lead to thin layer formation. Some of the possible scenarios are illustrated in Figure 6.

However, even with a positive *in situ* growth rate, cells can be lost by horizontal dispersion or extruded through a shearing process. Another factor that may contribute to a population increase is lateral advection.

At present, one of the main challenges lies in overcoming the technical difficulties associated with being able to distinguish *in situ* division and accumulation or dispersion. Velo-Suárez et al. (2009) approached this question by combining a simple population model and the estimation of the *in situ* growth rate of *Dinophysis acuminata* by the mitotic index approach at the depth of the population maxima combined with a simple model. They concluded that this species aggregated at the particular depth with no growth, over a 24 hour period (although lateral advection could not be discarded). Also, Pizarro et al. (2008) found that the maximum concentrations of *D. acuta* were the result of active swimming and aggregation with no cell division. In those two studies, the organisms did not form thin layers, but the method could also be applied in those systems. Unfortunately, this technique, which is based on optical microscopy, can only be applied to cells whose division phases (in particular, the recently duplicated cells) can be clearly identified.

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

In general, the characteristic time scale for fusion of gametes is highly depending on the local cell concentration (Wyatt and Jenkinson 1997): in that sense, the simple local increase in cell density would increase sexual recombination rate. At present, there are not data available regarding this question and anyhow, for organisms that form resting stages their answer should be species-dependent. Furthermore, in the case of chain-forming species, this situation may not be necessary.

The question can be also seen from the perspective that thin layers may also facilitate the 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 intensity interferes with cell division (e.g. Pollingher and Zemel 1981, Berdalet et al. 2007) and asexual cyst formation (Latz et al. 1984, Smith et al. 2004, Bolli et al. 2007). If this was the case, thin layers with reduced turbulence could favor sexual recombination.

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

The rheological properties of seawater have been reviewed by Jenkinson and Sun (2010a). After observations that bubbles of 0.1 to 0.5 mm diameter were trapped in a *Karenia mikimotoi* bloom, Jenkinson (1986) measured the rheological properties of some algal cultures and found that their rheological properties corresponded to a "solution" viscosity η_W on which was imposed an excess viscosity, η_E, yielding a total viscosity,

$$\eta = \eta_W + \eta_E \qquad [\text{Pa s}]$$

where η_W is the viscosity of the water with small molecules of dissolved salt, and it is Newtonian, meaning that it is independent of shear rate, and depends only on the temperature and salinity. In most natural waters, (temperatures from 0 to 30° C, salinities from 0 to 40 psu), η_W varies by no more than a factor of 2 from 1 mPa s (Miyake and Koizumi 1948). η_E, on the other hand, varies with γ_t [s^{-1}], and is mostly shear thinning, meaning that it is a negative power P of shear rate γ_t. Corresponding with the finding of rheologists working on many other polymers, the value of P was found to vary both between cultures and with γ_t, probably reflecting the molecular structure of the phytoplankton-secreted expolymeric substances (EPS). Based on these data, using the zero-dimensional Kolmogorov model of turbulence, Jenkinson (1986) suggested how this biorheological modification of natural waters by phytoplankton might change the characteristics of turbulence, in particular increasing the length scales and time scales of Kolmogorov eddies for any given value of turbulent dissipation rate ε. This is treated further below.

Subsequent measurements of rheology were made (Jenkinson 1993, Jenkinson and Biddanda 1995) at γ_t val-

Exercise 1:
Homogeneous growth rate

Exercise 2:
Ramdom growth rate values

Exercise 3:
Heterogeneous growth rate
No growth in the water column
Active growth in the thin layer

Exercise 4:
Heterogeneous growth rate
Active growth in the water column
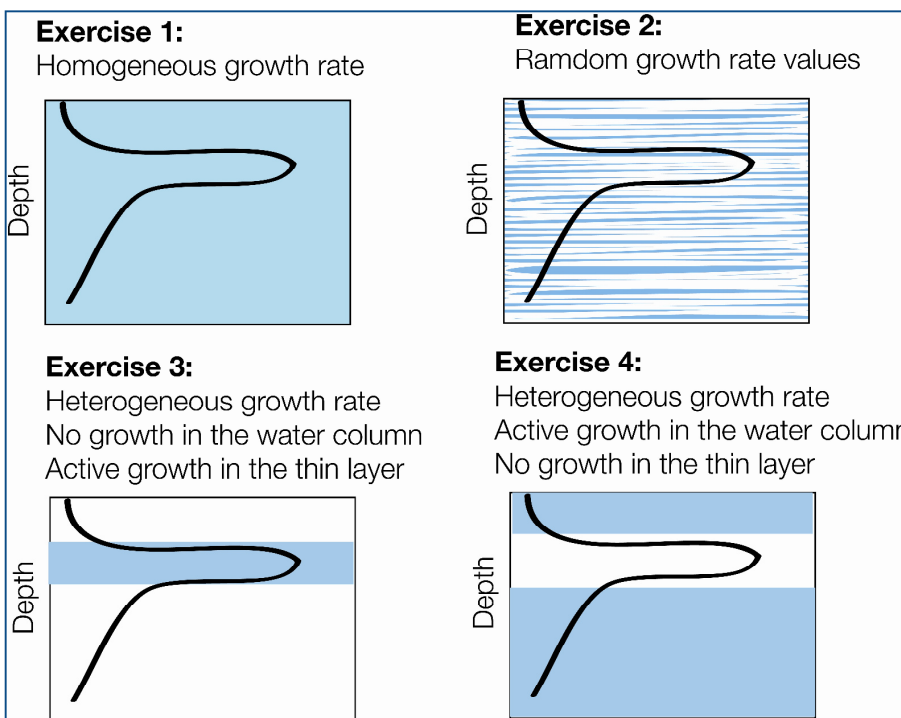No growth in the thin layer

Figure 6. Different scenarios that could be tested to determine the mechanisms that contribute to thin layer formation . From L. Velo-Suarez (unpublished).

ues ranging from 0.002 to 1 s^{-1} on phytoplankton-poor Mediterranean seawater and on seawater from the North Sea during blooms of *Phaeocystis* and *Noctiluca*. Like in most of the previously measured algal cultures, the water was found to be shear-thinning with *P* between -1.1 and -1.5. η_E was also a positive function of chlorophyll concentration (Fig. 7). Note how at γ_t values < 0.004 to < 0.06 s^{-1}, mean values of η_E exceeded η_W, meaning that the total viscosity was doubled or more. The effect is thus *not trivial,* as some other published studies have indicated because they used measurements performed at undefined or inappropriate scales of length or shear rate.

The above measurements by Jenkinson and Jenkinson and Biddanda are inter-comparable because they were made with rheometers using a Couette (concentric cylinders) geometry with the same inter-cylinder measuring gap of 0.5 mm, and a general relationship was found by Jenkinson and Biddanda (1995) for the excess complex modulus G^*_E [Pa] (essentially the viscosity at 1 s^{-1})

$$G^*_E = 2.0 \cdot chla^{1.3} \qquad [\mu Pa]$$

where *chla* is chlorophyll *a* concentration [mg m^{-3}].

Seuront's team (Seuront et al. 2006, 2007, Kesaulya et al. 2008) have measured the viscosity in *Phaeocystis* blooms and found viscosity up to 4 times that of "clean" seawater. Their data mostly confirmed the positive correlation between viscosity and chlorophyll concentration, except at certain stages of the blooms, when the relationship can become negative, probably as the motile flagellates of *Phaeocystis* leave the shelter of their mucus. While the length scales and shear rates of these measurements were not defined in the publications, from the manufacturer's specifications of the viscometers used it can be deduced that shear rates were of the order 1 s^{-1} and length scales 0.23 mm, both within the range used by Jenkinson and Biddanda. The length scales between the samples, close to those used for making correlations, however, were different, cm to dm in Seuront et al.'s work but m vertically to km to 1000 km horizontally in Jenkinson and Biddanda's work. In Antarctic waters in summer, Seuront et al. (2010) have recently shown the familiar positive relationship between viscosity and chlorophyll a in the deep chlorophyll maximum, but this correlation was absent in low-chlorophyll, low-nutrient subsurface layers, where viscosity was correlated to bacterial abundance. This suggests two distinct and
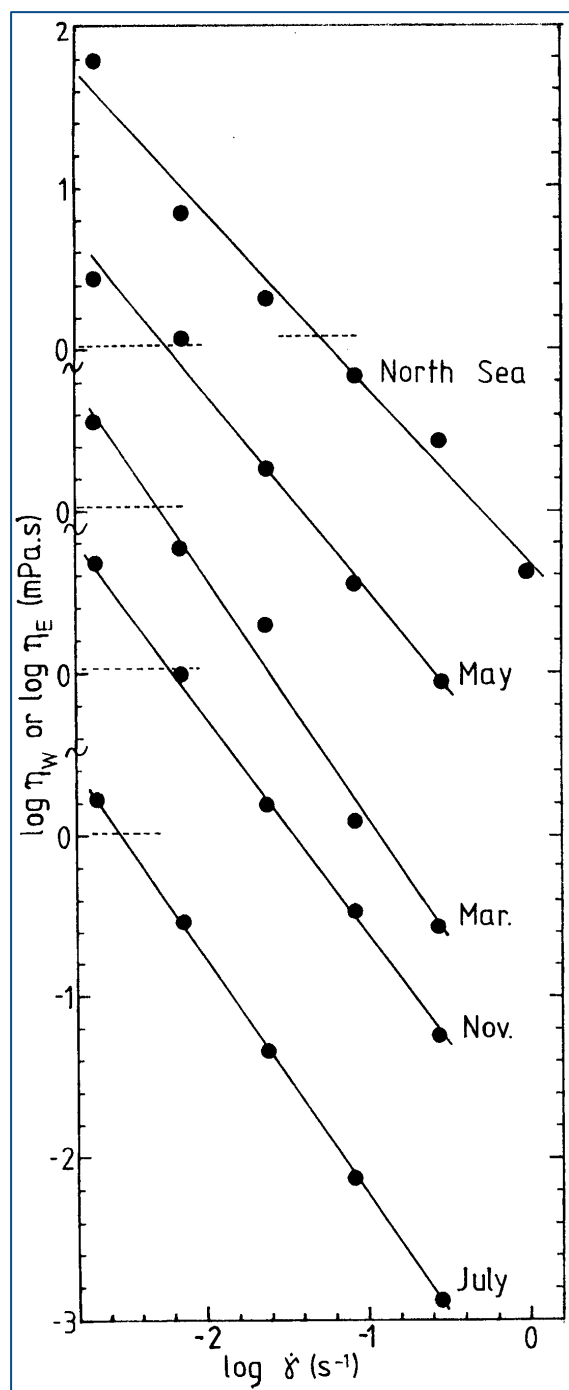
Figure 7. Mean measured values of excess viscosity η_E vs. shear rate γ_t (gamma dot) for the North Sea (uppermost curve) and the Mediterranean (4 lowest curves). From bottom to top, successive curves for the Mediterranean (July, November, March, May) are offset by one decade, but not the top curve (North Sea). Horizontal dashed lines give viscosity of aquatic phase η_W for comparison with η_E. The slope of the lines showing the relationship between log(η_E) and log (γ_t) varies from -1.1 to -1.5.

significant sources of thickening EPS from plankton, autotrophic phytoplankton and heterotrophic bacteria.

The results from seawater and algal cultures led to attempts to improve the Jenkinson (1986, 1993) model of rheological modification of Kolmogorov

turbulence at oceanic scales of shear rates by adding new ideas of intermittency in both turbulence and rheological thickening. The idea was to then test this model, initially in the laboratory, by generating turbulence at different values of ε with and without phytoplankton, and by calibrating the effect when phytoplankton was replaced by dissolved sugar (increasing viscosity by a factor of 10 at all γ_t values, the solution thus remaining Newtonian) (Jenkinson 2004a,b). Disappointingly, no significant effect of changing the viscosity with sugar could be discerned on the turbulence characteristics. This may have been due to stable harmonic circulation cells forming in the apparatus (Solomon and Mezic 2003). In any case the hypothesis that phytoplankton EPS would change characteristics in isotropic ocean turbulence could not be tested, the question remains open and more work is required (Jenkinson and Sun 2010a).

In work carried out to measure the effect of excess viscosity produced by HABs (Jenkinson and Arzul 1998, Jenkinson et al. 2007b) and intertidal organic fluff (Jenkinson et al. 2007a) on the ventilation of fish gills, the appropriate length and time scales were difficult to discern, and are probably different from those acting on isotropic turbulence. Therefore an ichthyoviscometer was invented, using a dead fish as a model for a live one, thus, it was proposed, getting the scales of flow right.

The science of Rheology developed in the 1940s, and in the beginning dealt with models and measurements of soft matter based on continuum models (Barnes et al. 1989). More recently, however, Rheology has come to embrace flows in powders, granular matter (Coussot 2005) and soft, wet matter using both continuum and 'granulocentric' models (Clusel et al. 2009). The yield stress [Pa] of sewage sludge in capillary tubes is proportional to 1/(tube diameter)² (Fig. 8) (Spinosa and Lotito 2003, Jenkinson and Wyatt 2008), graphically illustrating a strong effect of length scale. Like sewage sludge but more dilute, seawater is a suspension of partially flocculated EPS.

Jenkinson's (1986, 1993b) model of biomodification by phytoplankton EPS of isotropic turbulence thus now needs matching between the length scale of rheometry (so far mostly 0.5 mm) and that or those acting

on turbulent energy dissipation. If complete matching is not possible, rheometry at a series of length scales could allow extrapolation of measured viscosity and elasticity to the length scale(s) of the process of interest. Based on published measurements of the rheological properties of *Karenia mikimotoi* cultures, a model has been published of how phytoplankton EPS may change the dynamics and the thickness of pycnoclines (Jenkinson and Sun 2010b). The model predicts that the degree of modification will be extremely dependent on the relationship between excess viscosity and length scale, which will itself be a property of EPS lumpiness.

Further energy may be extracted from turbulent flow by the flocculation (Squires and Yamazaki 1995, Passow 2000, Alldredge et al. 2002), viscoelastic deformation and breakup (Alldredge et al. 1990, Jenkinson et al. 1991) of EPS (marine snow and marine organic aggregates), and more work is required in studying the energetics of how these processes affect turbulence.

From the viewpoint of isotropic turbulence, an obvious length scale to target for measurements of viscosity (and elasticity) is the Kolmogorov length L_k. From the viewpoint of thin-layer dynamics, vertical length scales of layer thickness and step thickness should be targeted. For processes taking place around organisms, such as diffusion in shear of nutrients, toxins or dissolved allelopathic substances, encounter dynamics and patch dispersal, Deborah numbers would be useful in iden-
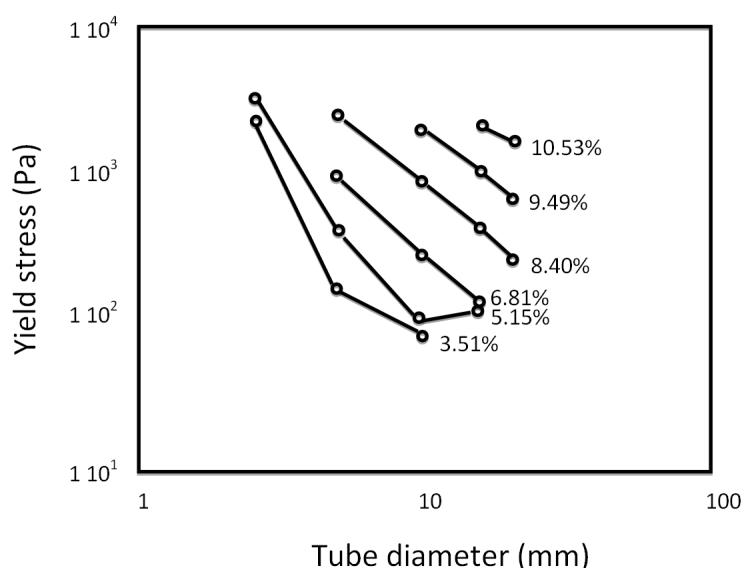

Figure 8. Log (yield stress) [Pa] vs log (tube diameter) [mm] for different dilutions of sewage sludge from the same batch. Note how for a given sludge concentration yield stress is a negative function of tube diameter (from Jenkinson et al 2007a, drawn from data in Spinosa and Lotito 2003).

tifying the relevant length and time scales (Jenkinson and Wyatt 1992). For allelopathic action by harmful algae that use megadalton protein-polysaccharide complexes for cell-cell recognition and adhesion (Yamazaki et al. 2009), the development, dynamics and strength of adhesion are important, as they are in similar mechanisms in higher organisms. Atomic force microscopy (AFM), a tool widely used by micro- and nano-rheologists, will be likely useful to investigate cell-cell attraction, repulsion and adhesion forces in flow fields, not only in such allelopathic action, but also in processes such as flagellate grazing and mating (Schmid 1993). AFM and hanging-drop electrochemistry are already being used (Svetlicic et al. 2006) to study EPS mechanics and molecular dynamics.

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

It is important to note the broad range of nutritional strategies present in the phytoplankton world, including the HAB forming species. Interestingly, some HAB species rely solely on inorganic nutrients, but most of them have in addition the capacity to feed through osmotrophy or phagotrophy. Examples of mixotrophic species are *Dinophysis acuminata, D. norvegica* or *Karlodinum armigeri* (e.g. Adolf et al. 2008, Berge et al. 2008, Carvalho et al. 2008, Nishitani et al. 2002).

The nutritional advantages enhanced in thin layers can be summarized as follows:

- The location of the thin layer in the upper part of the nutricline provides both favorable light conditions and high nutrient concentrations to phytoplankton.

- The accumulation of breakdown products from senescent cells in a density gradient such as a pycnocline can increase the local concentration of recycled nutrients, enhancing phytoplankton productivity.

- The high concentration of small prey distributed in thin layers can be an advantage for mixotrophic species.

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

The correct response to this question depends on the availability of the appropriate methods (see Question 2.3) to measure the *in situ* growth rates of target (HAB) species with fine resolution at the depth of the thin layer. Often, the toxic species (*Dinophysis* spp., *Alexandrium* spp.) are present at very low concentrations and constitute a small percentage of the overall community. Thus, measurement of growth rates through the estimation of bulk chlorophyll or primary production would correspond to the whole phytoplankton population but not to the harmful species. Further measurements of nutrient fluxes are required to understand the formation of these structures (Lunven et al. 2005). Difficulties limiting fine scale sampling of chemical tracers and phytoplankton need also to be overcome in order to detect such gradients and relate them to phytoplankton layering.

Apart from the technical limitations, it can be stated that the growth in the thin layer may be due to the local enhancement in resources. Some thin layers can appear in the upper part of the nutricline, where both nutrients and light levels are optimum for growth (Cheriton et al. 2009). Vertical turbulent fluxes of nitrate into shelf sea thermoclines should provide the mechanism for the higher production rates and biomass concentrations at these layers (Sharples et al. 2001). The decoupling of the thermocline and the nitracline can be understood in terms of uptake by the phytoplankton removing much of the nitrate from regions of high cell concentrations and thus both deepening and sharpening the nitrate gradient (Hanson and Donaghay 1998). It should be noted that in some cases, the layered population does not benefit from nitrate upward flux, but simply from ammonium regeneration occurring in the pycnocline (Le Corre and L'Helguen 1993). 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 to a nutritional advantage (Gentien et al. 2007).

For species with special nutritional strategies, like the mixotrophic *Dinophysis* spp. the high densities of prey cells in thin layers can be a nutritional advantage that increases the growth rate (Hansen 1991).

Furthermore, high cell concentrations may chemically modify the local environment of the populations. For instance, the thin layer formed by *Chaetoceros* spp. appeared to create a favourable microenvironment for the development of other species, such as *Pseudo-nitzschia* spp. (Rines et al. 2002). These favourable growth conditions could be nutrient-related. However, in this latter study vertical distribution of cells was not simply a function of *in situ* growth processes in the euphotic zone, but also of advection by physical oceanographic events (e.g. lateral transport as indicated in Question 2.3).

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

Certainly, thin layers should constitute hot points for the microbial loop to develop. The elevated phytoplankton concentrations in the thin layers should produce increased dissolved organic matter (DOM), which will stimulate bacterial growth. New results (Donaghay, pers. comm., unpublished data) show bacterial reduction in thin layers. The capacity of bacteria to overcome phytoplankton may depend on the availability of the main nutrients for phytoplankton (nitrogen, phosphorus, silicate, micronutrients) in the suitable form (organic or inorganic), their physiological state along the succession and the grazing pressure. NPZ models would be useful in order to evaluate the importance of DOM, especially DOC, and nutrient availability on some microbial loop processes in thin layers (e.g. bacterial growth, competition between phytoplankton and bacteria, microzooplankton grazing).

Further, parasite-host encounters should also be important within the thin layers. The particular (low) turbulent environment there, should influence the encounter rates among the different interacting components of the food web (Rothschild and Osborn 1980, Havskum et al. 2005, Llaveria et al. 2008).

Question 5) To what extent does the existence of thin layers –and the implication for the retention of water bodies- play a role in the development of particular assemblages?

Any biomass build-up in the pelagic environment is the result of either an increased growth or a local reduction in horizontal and vertical dispersal. This report focused mainly on vertical structures. There is however a need to embed these 1-D

models into a larger 3-D framework. Lateral (horizontal) fluxes affect the extent and duration of these structures which in turn determine the net growth of any confined population. The characteristic time scales for a phytoplankton species or a specific phytoplankton assemblage can be on the order of 10 km and 10 days.

Off the south of Ireland, a small patch of 3km in diameter and ca. 1m thickness at 20m depth was followed during one week and its trajectory was coherent with the westward drift current (Farrell et al. 2009). In July 2007 this patch contained mostly *Dinophysis acuta* cells which are ubiquitous throughout the South Ireland waters. In the Bay of Biscay (Gentien, unpublished data), retentive structures have been detected at mid-depth, in the pycnocline which corresponded to a local accumulation of *Dinophysis acuminata*. These structures have been identified in the MARS3D simulations of the Bay of Biscay (Lazure et al. 2009). A prediction scheme for the beginning of the *Dinophysis* season has been established, based on the existence of these eddies and their subsequent advection (Xie et al. 2007).

It can therefore be concluded that such patches act as incubators for one population and that their track will determine the delivery of toxins to the coast: this is especially true for *Dinophysis* but could be adapted for other species. The size of retentive structures may vary depending on the species considered: in the case of *K. mikimotoi*, the patch size depends on the geographical distribution of shear rate in the pycnocline.

Modelling Needs

Modelling needs on HABs in Stratified Systems include

- Recognition of the importance of the scales of approach. Models should deal with the physical and biological scales that are observed in nature. In stratified systems, processes occur on multiple scales. In some cases, it will be possible to resolve them in a single model, while in others it may not.

- Identification of the ranking of the processes. Models become easier to set up if there is a particular physical or biological forcing which dominates. Identifying those forcings is critical for the prediction and model selection.

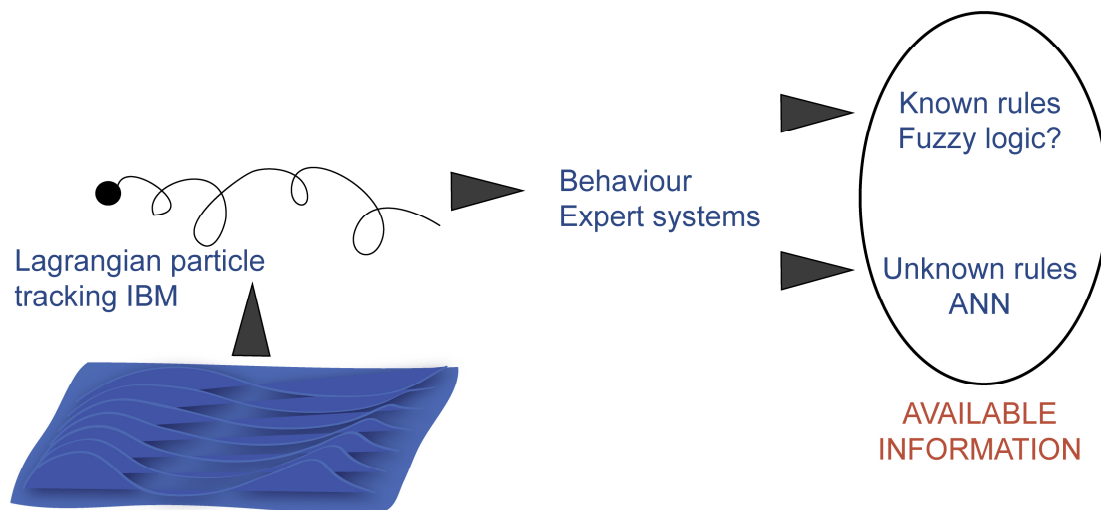- Resolution at cellular scales. For biological

Figure 9. Possible approach to model different swimming strategies. From L. Velo-Suarez (unpublished).

models, there is some information available (growth rate, behaviour, photosynthesis, photo-acclimation, mixotrophy, respiration, gene expression). In some cases, cellular scale models need to be incorporated into larger scale models.

- Inclusion of 3D processes such as advection and intrusion. The integration of 3D physical models and of the biological ones containing the available information on the species of interest can provide an "engineering" (prediction for managers) kind of model to have a probability "scenario" on the occurrence of a HAB event.

- Consideration of statistical climatological "heuristic" models for blooms, such as the fuzzy logic approaches.

Two different approaches are necessary: a more pragmatic one (prediction for managers), and another one concerning scientific understanding of bloom dynamics. These can be synergistic. Indeed, the previous chapter on HABs in Eutrophic Systems illustrates this as well.

Regarding Question 1, there is a clear need to appropriately formulate mixing. Good mixing representations have been achieved with turbulence closure schemes implemented in 1D models such as GOTM (www.gotm.net). A priori, 1D and 3D models should be combined to study the formation of thin layers. Destruction and maintenance of the layer are balanced by the swimming capability of the cells and stirring motion due to turbulence. Individual based 1D models are probably worth-

while to simulate systems like the vertically migrating *Rhizosolenia* mats studied by for instance Singler and Villareal (2005).

Regarding 3D models, some participants questioned the real use of them. They may be feasible for layers which are metres thick, but to model thin layers on centimetre scales may be a serious technical challenge. 2D models may be appropriate for environments like fjords and estuaries, where the physical forcing and biological behaviour are combined to create thin layer trajectories for comparison with field data. Finally, Direct Numerical Simulation (DNS) should be applied to study fluid motions and single cell interactions in detail.

Regarding the migration discussion (Questions 2.1. and 2.2), there are contradictory observations on the vertical migrations of a particular species. Under different circumstances the same species may or may not perform vertical migrations. Indeed, different factors may have been involved in the observed responses. In order to progress further in answering questions for a particular species and in a particular location, it is imperative to test several types of migratory behaviour in coupled biological/physical models to evaluate the importance of each process through a validation with observed vertical distribution data. Many modelling studies on the migratory behaviour in response to environmental cues have been carried out which may serve as a theoretical framework (Ji and Franks 2007, Ralston et al. 2007, Ross and Sharples 2007). However, the actual

swimming strategy is often unknown. One way to proceed to determine which strategy is responsible to explain particular observations (i.e. the depth and/or frequency at which aggregations occur) may be to use models which are initialized with tens or hundreds of species, or identical clones of the same species that only differ in, for instance, the swimming strategy (different responses to environmental cues). This may not necessarily result in a single emerging strategy but will produce a small subset of strategies which the cells use in order to form the observed aggregations.

Questions regarding the swimming behaviour can be addressed through modelling exercises using individual based Lagrangian models (e.g. Ross and Sharples 2004) in combination with other sub-models on turbulence and behaviour (cf. Fig. 9). By applying a 1D IBM to a thin layer scenario and individually switching off the different processes considered responsible for the layer formation (growth rate, immigration, opposing resource gradients, high grazing outside the layer, dispersion losses, current velocity, etc.) it should be possible to determine the relative importance of each process and eventually exclude those that are not relevant.

The retentive structures described in Question 5 may be of small size. Thus the 3D models used in that study to identify their presence and determine their locations should work at a mesh size compatible with the retentive structures (mesh size = scale/ 3 to 10). These retentive structures may occur anywhere in the 3D block diagram of simulated variables: it will become necessary to automatically identify retentive structures within the scalar or vector field. Eulerian and Lagrangian methods may be used to this effect. Eulerian methods allow for the estimation of hydrodynamic parameters like the local e-flushing time which is the time required to reach a local grid mesh concentration of 1/e from a previous step (Jouon et al. 2006). Lagrangian methods basically imply:

- tracking of passive particles mimicking fish eggs (Petitgas et al. 2006)
- particles with aggregation behaviour (ant algorithm, Segond et al. 2004)
- particles with behavioural rules (Ross and Sharples 2007, Sourisseau et al. 2008).

Finally, some open questions concerning thin layers in general are:

- Could large 3D hydrodynamic models identify areas where thin layers are likely to be present?
- Can we use the macroscale models to identify stratification conditions that favour blooms development or termination?
- Can existing large-scale 3D models reproduce the advection and/or dispersion of retentive structures that may be horizontally advected?

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Modelling of HABs in Upwelling Systems

Introduction

In the past few decades, numerical models have been used with increasing resolution to resolve physical processes related to the dynamics of eastern boundary current systems. Initial efforts included the resolution of the wind-forced coastal jet and the secondary ageostrophic circulation associated with coastal upwelling. Increasing precision in numerical schemes as well as increased resolution allowed for the simulation of instability processes, topographical effects and ocean turbulence. These processes play a significant role in cross-shelf exchanges of material and energy. Large time- and space-scale modulations of the thermocline, alongshore currents and surface forcings, affecting these processes are now addressed by numerical models.

In the context of HABs, high resolution and high frequencies in the forcings (winds, tides, freshwater flows, topography) are essential to capture the salient dynamics. Further increase in resolution and new physics (e.g. non-hydrostatic) in models will allow for the exploration of the submesoscale and internal wave-driven dynamics. Continual developments in gridding schemes such as nesting capabilities, open boundaries [implementation], unstructured grids and adaptive gridding as well as improvements in the numerical schemes themselves will facilitate advances in small-scale modelling.

Background

A common feature of all upwelling systems is the tendency for blooms to be advected equatorward and offshore by the mean geostrophic currents. Despite this, high bio-

mass red tides are frequently observed in these systems, particularly at sites of local retention (e.g. at capes, bays, rias). Of particular interest are the "extreme" blooms that have been documented in the past few years: in the California Current System, red tides of *Ceratium* spp. and *Akashiwo sanguinea* have approached concentrations of 1,000 mg/m^3 chlorophyll (Fig. 1, Ryan et al., 2008; Jessup et al. 2009). In 2009, a bloom of *Ceratium dens* achieved biomasses >2,000 mg/m^3 in the Benguela Current. In the Humboldt Current a recent red tide of *Akashiwo sanguinea* (=*Gymnodinium sanguineum*; Kahru et al. 2004) achieved similar densities, causing ecological and economic disruption. Some obvious questions arise concerning how these blooms form and are maintained. Given the moderate growth rates of these organisms, there must be some form of physical and/or behavioural aggregation involved. Similarly, there must be an equally large source of nutrients to support such large blooms.

Comparative modelling could be used to address these questions. Beginning with only physical transport models, it would be possible to determine whether advection alone (or advection coupled with growth) could achieve the observed bio-

Figure 1. Sampling an *A. sanguinea* bloom in Monterey Bay, CA during 2006; peak bloom concentrations reached ~1,100 mg/m^3 Chl-a.

mass distributions. If physical transport alone is an insufficient explanation, addition of behaviour would likely be necessary. Inclusion of growth processes may also be necessary, requiring specification of the external nutrient fields. Simple transport models could be coupled to nutrient fields to determine the relative importance of pre-existing nutrients in the mixed layer, the importance of advective and diffusive fluxes, the role of exogenous sources (i.e. riverine inputs, groundwater discharge), and again the potential role of vertical migration (behaviour). Finally, these relatively simple models can address the role of dispersion, advective loss, and mixing in the dissipation of these blooms. If physical processes alone are not sufficient to cause bloom demise, then biological explanations such as enhanced grazing, allelopathy, mortality due to viral lysis, etc. must be invoked. A comparative modelling approach would allow the similarities and dissimilarities across systems to be identified, enhancing our understanding of where and why these high biomass events occur globally.

Specific Issues

Synthesizing and comparing physical-biological dynamics among upwelling systems must include an investigation of the commonalities among the HAB species. Based on available observations, some tendencies can be identified among blooms of both toxic diatoms and dinoflagellates, and these are described below.

Species Adaptations

In an upwelling event, toxic diatoms (*Pseudo-nitzschia* spp.) follow centric diatom blooms (intermediate turbulence, lower silica levels); they often form thin layers at the depth of minimum shear. The higher their division rate, the sooner they reach the critical small size that triggers sexuality and formation of auxospores. However, we have limited knowledge concerning the mechanisms by which these species seed themselves in the upwelling system to cause recurrent blooms.

Harmful dinoflagellate species that thrive in upwelling systems benefit from having more "flexible" life cycles, with multiple pathways that allow switching from one life stage to another. For example, the PSP producer *Gymnodinium catenatum* and the yessotoxin producers *Lingulodinium polyedrum* and *Protoceratium reticulatum* produce resting cysts with very short mandatory periods (1-2 weeks); they can have intermittent encystment and germination pulses within the same bloom. Despite their capability to produce resting cysts, they may rely very little on this stage as a seeding mechanism. The local selection of species in the community appears to be determined by water column structure (e.g., stratification) and
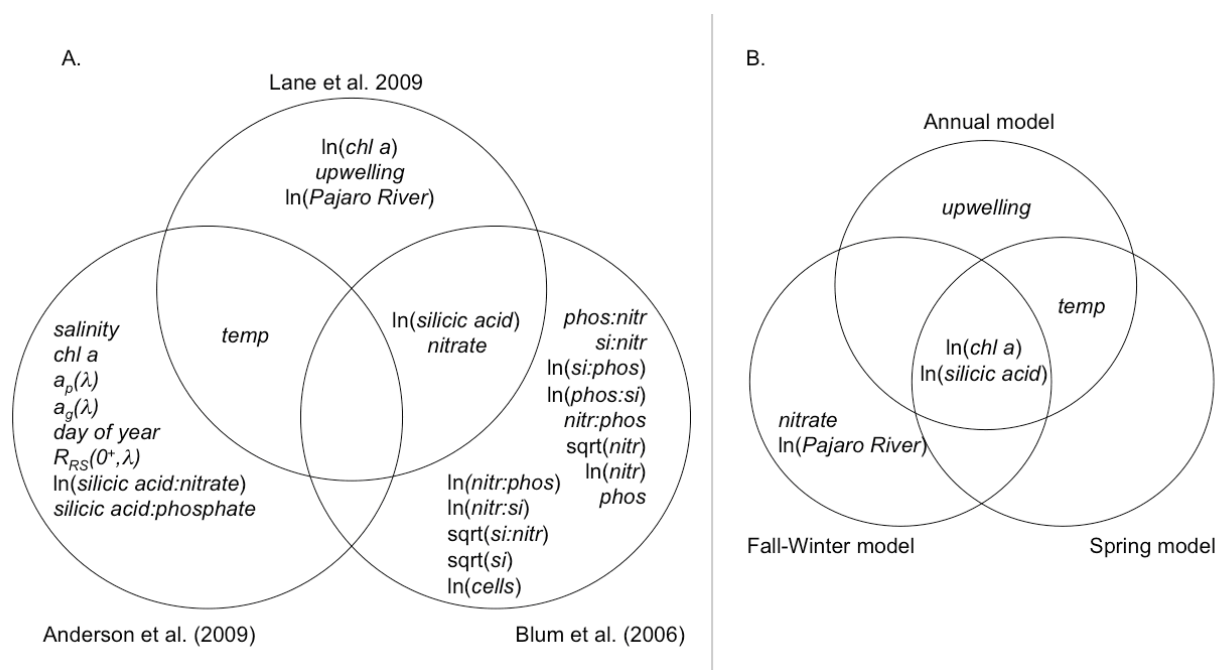
Figure 2. A comparison of statistical prediction models developed for *Pseudo-nitzschia* blooms in the California Current Upwelling System (Lane et al., 2009). Nutrient concentrations and ratios of macronutrients are common variables related to *Pseudo-nitzschia* bloom dynamics in all models. Upwelling processes clearly deliver the majority of nutrients that support spring and summer bloom development. In fall/winter riverine-derived nitrate supply is more important for the Monterey Bay (Panel B).

event pattern. For blooms of these species there is a need to identify the physical forcings that trigger different life cycle transitions (vegetative stage, sexual stage, temporary cysts).

Nutrient Species, Ratios, Fluxes

Toxigenic *Pseudo-nitzschia* species are present in all of the major eastern boundary upwelling systems. Since discovery of the effects of domoic acid in the early 1990s, many potential triggers for domoic acid production have been described, but the most frequently cited are related to nutrients, both macro- (particularly Si and P) and micro (Fe, Cu). Associated with this, riverine discharge has been invoked (Trainer et al. 2000, Lane et al. 2009) as a potential triggering mechanism for toxic bloom events. Despite these assertions, field results are conflicting at best, and there are very few clear examples of nutrients and/or riverine discharge being directly related to toxicity of field populations (Velo-Suarez et al. 2010).

Recent statistical (empirical) modelling approaches have begun to elucidate these conflicting results. Lane et al. (2009) and Anderson et al. (2009), using similar approaches, developed models for the prediction of toxigenic blooms and toxin production, respectively, for the Monterey Bay and Santa Barbara Channel regions of the California Current. The models identified Si, N, and the Si:N ratio as important factors in predicting bloom events. Lane et al. (2009) went one step further by adding a seasonality component, and identified riverine discharge (assumed to be related to nutrients) as important, but only during non-upwelling periods (Fig. 2). These simple statistical approaches can be applied in any region where sufficient data sets exist, and can help to identify common factors (such as nutrient ratios) and previously overlooked subtleties related to nutrient sources in upwelling systems (such as seasonal influences of riverine discharge) that should be explored further in other regions and/or with numerical modelling approaches.

Mixing in Ocean Models

Mixing in the ocean results from a variety of complex processes, including internal shear instability, convective overturning, and boundary stress-driven turbulence. Understanding and modelling of oceanic mixing processes and their implications has been for decades and currently remains at the forefront of physical oceanographic research.

Ocean models that are used in coastal upwelling scenarios already incorporate among the most advanced subgridscale parameterizations for mixing such as the K-profile parameterization (Large et al. 1994) and the generalized length-scale parameterization (Umlauf and Burchard, 2005). Though imperfect, such parameterizations enable very good representation of many physical properties and features that characterize the coastal upwelling system. For example, the basic upwelling circulation, surface and bottom boundary layers, surface eddy kinetic energy, and mean horizontal circulation exist with reasonable statistical comparison to observations (Gan and Allen 2002, Marchesiello et al. 2002, Veneziani et al. 2009). Properties that are more sensitive to mixing in coastal upwelling systems are the position of the inner/outer shelf boundary, the strength and position of the main and seasonal thermocline, and restratification processes that occur during upwelling wind relaxation events. Recognizing that there are shortcomings in present ocean models, the representation of physical processes is sufficient to provide the foundation for coupled biological-physical interactions.

Small-Scale Physical Dynamics

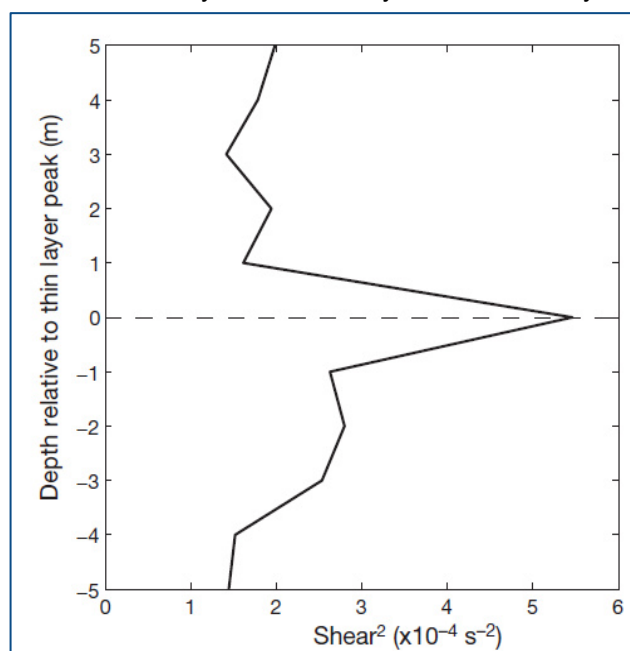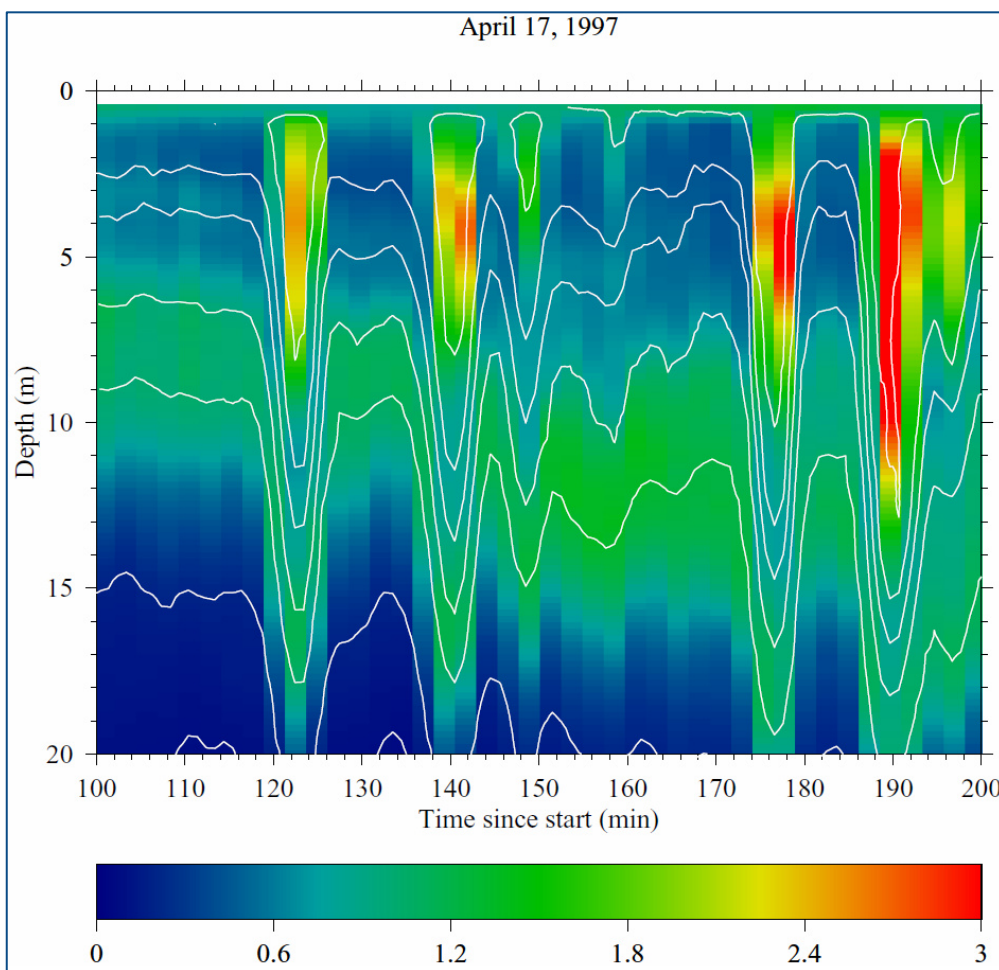Thin (<5 m vertical scale) phytoplankton layers occur in many coastal ecosystems. Such layers

Figure 3. Median shear squared profile computed in the layer frame of reference (0 m is the center of the thin layer) from all velocity profiles coincident with thin phytoplankton layers (n=36). From Ryan et al. (2008).

can be enhanced by biological processes such as growth and swimming, and can persist for days in the face of physical mixing. These thin, intense subsurface features are often invisible to normal sampling methods, but may represent the dominant source for subsequent HAB delivery to the nearshore and surface in upwelling systems. Vertical shear in the water column has the potential of creating thin layers of plankton, by tilting and elongating existing patches (Franks, 1995; Stacey et al., 2007; Birch et al., 2008, 2009). The shear-induced straining mechanism for phytoplankton thin-layer formation proposed by Franks (1995) was supported by observations in Monterey Bay (Fig. 3).

Thin layers containing the toxin-producing diatom *Pseudo-nitzschia* have been observed in Monterey Bay, California near the base of the thermocline (McManus et al., 2008). The thin layers persisted for a week, with chlorophyll concentrations exceeding 150 µg/l. Concentration of toxic populations in thin layers has significant implications for

harmful effects though trophic transfer. Thin layers of *Pseudo-nitzschia* have also been observed in East Sound, Washington (Rines et al., 2002) and in the Galician Rias (Velo-Suarez et al. 2008). *Akashiwo sanguinea* (*Gymnodinium sanguineum*) has been observed to form vertically migrating thin layers in Monterey Bay (Sullivan et al., 2009), where their intensity, thickness and frequency were influenced by frontal dynamics (Ryan et al., 2009). A bloom of this species during fall 2007 revealed a previously unknown mechanism of harm - external coating of seabird feathers that impaired insulation and led to hypothermia (Jessup et al., 2009).

Linear and nonlinear internal waves have the potential to concentrate swimming organisms into patches, and transport them across the shelf. This was first demonstrated by Kamykowski (1974), and formalized in theory and models by Franks (1997), Lennert-Cody and Franks (1999) and Lamb (1997).

Figure 4. Patches of the dinoflagellate *Lingulodinium polyedrum* that formed in the troughs of high-frequency internal waves. A depth-keeping swimming behavior of the dinoflagellates allowed them to form patches through the horizontal convergence and divergence driven by the internal waves. From Lennert-Cody and Franks (2002).

Swimming plankton such as dinoflagellates that have behaviors that allow them to swim against the ambient vertical flows will tend to accumulate over the troughs of internal waves in the surface layer. These studies showed that while linear waves could form patches no greater than twice the background concentration of organisms, the organisms were not transported with the wave. A nonlinear wave, however, could form patches that were considerably more concentrated, and those patches could advect with the wave. Such patches were demonstrated in the field in a study by Lennert-Cody and Franks (2002, Fig. 4), in which the dinoflag-

ellate *Lingulodinium polyedrum* formed dense patches in the troughs of nonlinear waves propagating onshore. These patches had across-shore scales of a few hundred meters, and alongshore scales of kilometers.

Cross- and Alongshore Advection

Cross-shore and along-shore advection in upwell-

ing systems is highly variable at the scale of wind events (upwelling, downwelling and their relaxation). Many HAB populations experience conditions favorable for their presence in shelf offshore areas. Their appearance at the coast thus requires mechanisms for transporting them across the shelf.

Cross-shore transport forces populations towards
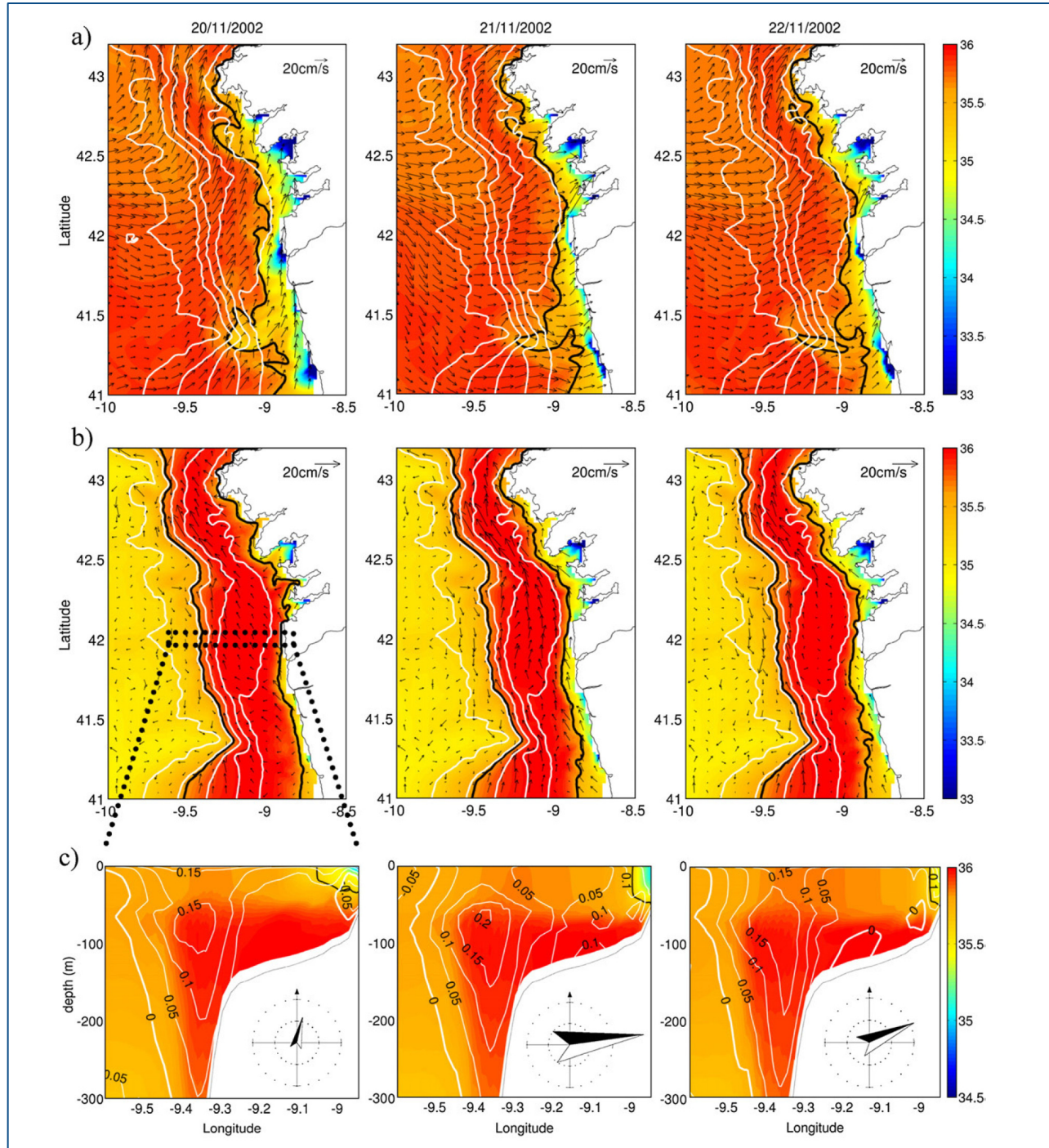
Figure 5. Expansion by upwelling favourable winds during 5, 6 and 7 December (Case 3). Daily distributions of surface current and salinity (a), bottom current and salinity (b) and salinity and along-shore velocity (positive northwards) sections at 42°N (c) are shown. Note that the reference current vector is half in surface maps than in bottom maps. Current arrows are displayed each three cells in the model. The 35.6 isohaline (coarse line) is marked as reference of the limit of the buoyant plume in all maps. In vertical sections, the salinity scale is different and goes from 34.5 to 36.0. Mean daily wind stress from MM5 is displayed in (c) with 0.2 Pa as the length of the semi-axis. Marked isobath lines are 100, 200, 500, 1000 and 2000 m. From Otero et al. (2008).

Influence of capes:
The influence of Cape Roca on the development of HABs in Lisbon Bay

Capes modulate the upwelling process by influencing across-shelf structure in alongshore flow, creating zones of retention favourable to the development of HABs. Ocean simulations performed by Oliveira et al. (2009) using ROMS-AGRIF clearly depict these physical processes. Model solutions include realistic evolution of sea surface temperature and advective patterns; reproducing strong along-slope flows, shadow areas downstream of capes, and the rapid onset of coastal counter currents during relaxation (Figure 6a). The formation of cyclonically rotating pools of dense water inshore was reflected by the depression in surface elevation and the upward displacement or doming of isopycnals (Figure 6b). The doming of isopycnals corresponded to a shallowing of the mixed layer depth, which in turn tends to correspond to higher phytoplankton biomass.

These model results suggest that the simulated physical conditions not only favour the accumulation of phytoplankton through patterns of retention, but the depth of the mixed layer plays a major role in setting the physical conditions favouring phytoplankton growth (specifically dinoflagellates).
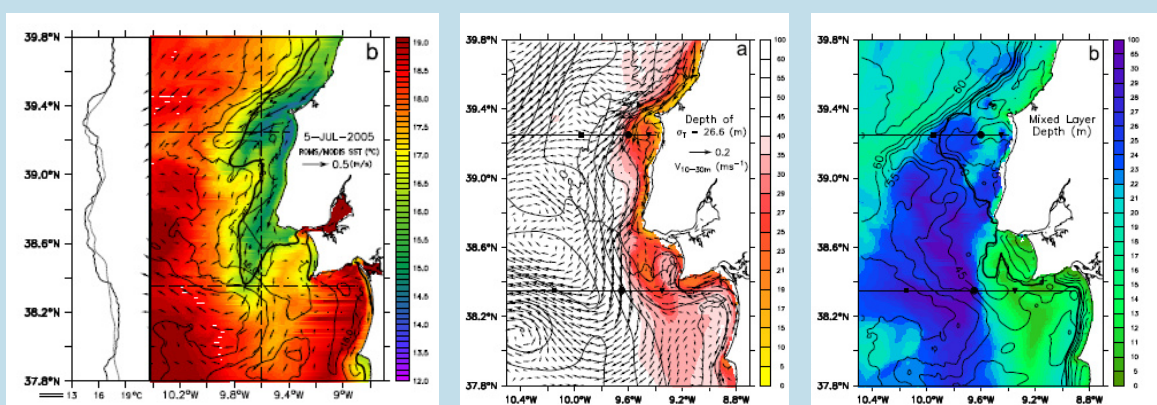

Figure 6(a) Modeled SST and surface velocity vectors, (b) isopycnal topography (representative of the top of the thermocline) and upper surface velocity vectors, and (c) mixed layer depth off Central Portugal.

(or away from) the coast. Downwelling events can introduce HAB populations present in shelf waters into coastal embayments, estuaries, rias, beaches, etc., where their socio-economic impact is higher. Along-shore advection in upwelling systems is dependent on the coastline configuration (presence of capes or embayments, for example) and bottom topography, as well as variations in the wind field. Spatial variations in wind patterns have been shown to induce variations in along-shore advection in zones where upwelling intensity is reduced (upwelling shadows) where conditions favorable for HABs occur (Ryan et al. 2008). Shelf circulation varies strongly in response to wind variations (upwelling, downwelling, relaxation) at short time scales (e.g., Fig. 5). Strong along-shore transport has been described in different upwelling systems as a result of the development of inner shelf currents during periods of upwelling relaxation (Kosro, 1987).

Current numerical models have been shown to be able to capture the variability in shelf and slope currents and hydrography in upwelling systems at the relatively small spatial and temporal scales

(Gan and Allen 2002, Otero et al. 2008, Kirincich and Barth 2009, Ruiz-Villarreal et al. 2009) in upwelling systems. Therefore, they can be used as a tool for process studies that give insight on the coupling of HAB populations to environmental variability (MacFayden et al. 2005). Additionally, they can be used in forecast mode for predicting the coastward transport of HAB populations that proliferate in offshore waters. If coupled to nutrient models, they can provide also the variable environment of nutrient distributions in upwelling systems, although the skill of nutrient models is usually relatively low relative to physical models (see also Eutrophic Systems chapter).

Interdecadal Fluctuations and Climate Time Scales

Interannual fluctuations related to the El Niño-Southern Oscillation (ENSO) and longer-term cycles, such as the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO), affect coastal upwelling systems through modification of seasonal upwelling-downwelling strength. There is a need to apply models to determine the

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influence of these changes on the presence of HABs in order to assess the possible use of climate indicators as predictors of HABs in upwelling systems.

Modelling Needs

The fundamental need identified for improved modelling of HABs in upwelling systems is the development of improved biological models. Because of the strong physical forcing in these systems, a great deal of understanding can be gained from physical models with passive tracers representing HAB populations. However, the subtleties of couplings among the physics, ecosystem, and HAB populations will only be revealed with carefully parameterized biological models, including swimming (sinking, floating) behaviors.

Many dinoflagellates have been shown to be facultative mixotrophs. Assuming heterotrophic behavior of mixotrophic dinoflagellates leads to optimum division rate, we need to model intermittent predator-prey encounters assuming they occupy different niches, and we need to model survival strategies (photosynthesis, supplementary organic sources) between feeding pulses.

Future directions that would greatly benefit our understanding of nutrient supply on HAB dynamics are models on riverine discharge delivery to coastal upwelling regions and physical models capable of resolving river plume effects, alongshore transport of plume constituents, and the differentiation of the nutrient sources dominated by upwelling processes.

More adaptive sampling strategies guided by current modelling exercises are necessary for capturing nutrient stoichiometric shifts between upwelling and downwelling transitions that are often key drivers of phytoplankton succession and HAB initiation.

While simple analytical models have proved accurate in predicting and describing small-scale features such as thin layers and internal wave-driven patches, such dynamics are difficult to include in

Interdecadal fluctuations in HABs:
Long-term trends in the flushing of Rías Baixas and HABs

A decrease in the extent and intensity of the upwelling season on the Iberian coast over the last 40 years has resulted in an increase in the calculated flushing time of the Rías Baixas which has in turn caused an increase in the occurrence of HABs in these systems (Alvarez-Salgado et al., 2008). Over the last 40 years a significant decrease is seen in calculated values of Ekman transport ($-Q_X$), which serves as an index of upwelling, with the annual average $-Q_X$ declining from an upwelling favourable index in the early 1960s to a slightly downwelling favourable value in the early 2000s (Figure 8A). Superimposed on this declining trend are two cycles with periods of 15-20 years, consistent with the North Atlantic Oscillation (Visbeck et al., 2001). Analysis of this data set has revealed a decrease in the intensity of upwelling during the upwelling season, an increase in the intensity of downwelling during the downwelling season and a shortening of the upwelling season. As a result, flushing rates of the Rías Baixas, determined from the inverse of the offshore Ekman transport, and the volume and length of the mouth of the Rías, indicate an increase in flushing time of 240%.

Associated with the increased flushing time is an increase in the number of days that mussel rafts are closed to harvesting owing to the increased presence of harmful algae (Figure 8B). Residual circulation patterns are considered to determine the microplankton composition in the Rías Baixas during the upwelling season. Upwelling enhances positive residual circulation and transports dinoflagellates to the shelf leaving the Rías Baixas dominated by diatoms. Conversely, during downwelling dinoflagellates are advected to the inner parts of the Rías Baixas, where species of *Dinophysis* are most often responsible for the suspension of mussel harvesting (Alvarez-Salgado et al., 2008).
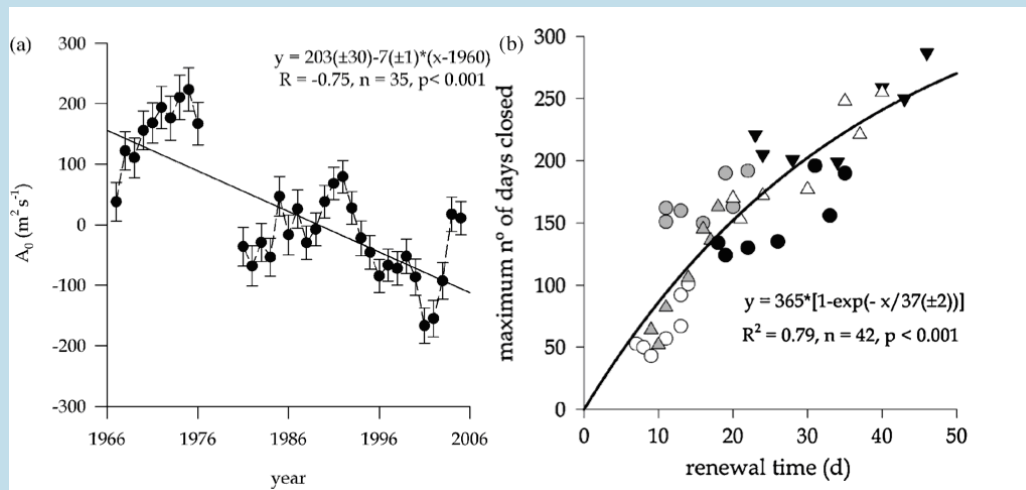
Figure 8 (a) A 40-year time series of offshore Ekman transport, $-Q_X$ (where A_0 is the annual average $-Q_X$) on the Iberian coast, and (b) the number of days per year for which a given mussel cultivation area in the Rías Baixas is closed to harvesting in relation to the renewal time for each area. Modified from Alvarez-Salgado et al. (2008).

most numerical models. This is due to the limitations in vertical resolution of the numerical models, as well as the difficulty in representing swimming in an Eulerian framework. To include these small-scale processes in Eulerian numerical models might require the coupling of a Lagrangian particle-tracking model with the Eulerian model. Such coupled Lagrangian-Eulerian models exist (e.g., ROMS), but have not been widely applied to HAB problems.

To validate models and their capacity to forecast HAB events, hindcast simulations are a useful approach. Two sources of past information may prove useful for hindcasting HABs in upwelling systems: 1) reported anoxia events and 2) toxic events. It will be necessary to convert these observations (for instance, volume of anoxic waters, tons of fish kills or concentrations of toxin in dead

material) to values that may be comparable to models outputs (total biomass, biomass of toxic algae, their concentration in cells per liter or in toxin content). Knowledge of the associated error in the data is necessary for model-data comparisons.

In upwelling systems, which are very productive, an adverse effect, not directly linked to HABs is the potential resulting anoxia. In those cases, a relatively common biological model coupled to a physical model, providing estimates of total biomass, will provide useful knowledge on the production and its decay, with the related oxygen consumption.

In a number of cases, however, it appears that the HAB biomass, causing adverse effects, is uncorrelated with total phytoplankton biomass. There is

then a need for models focusing on the biological dynamics of particular HAB species.

Data assimilation will be an important tool for combining models and data in the investigation of HABs in upwelling systems. These techniques require quantification of both observation errors and model error statistics which particularly for biological models is a challenging task. Assimilation of physical information such as temperature and salinity alone should improve transports of embedded ecosystem state variables and, in turn, improve modeled ecosystem response. Direct assimilation of biological data (e.g., nutrient or chlorophyll) is at the forefront of the field but being pursued actively and should significantly impact practical HAB modelling and prediction.

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Recommendations and Programme Advancement

Numerous recommendations for advancement arose from the deliberations of the GEOHAB Modelling Workshop.

In addition to the specific modelling needs and challenges highlighted in the previous chapters, some of the cross-cutting scientific needs include:

- Good sampling, i.e. high (technological) resolution sampling of the appropriate parameters is required for model parameterization and validation. This is particularly the case for the occurrence of HAB species occurring at very small spatial scales such as thin layers.
- Better visualization tools are needed, especially *in situ.* This includes improvements in the detection of toxins and chemical cues.
- Observing systems are needed that are able to detect thin layers and to identify also the minor constituents of the plankton community. This requires the development of new technologies and instrumentation.
- Scale dependent rheological measurements are needed to detect layer reinforcement and allow realistic modelling of hydrodynamics and water deformation (at a range of scales from µm to m).
- Support from the coastal observing system community is needed to develop the next generation of HAB models and data assimilative systems that will provide improved state estimates of critical nutrient fluxes and HAB dispersion.

To accomplish the continued incorporation and advancement of modelling in all aspects of GEOHAB, some of the recommended framework activities include:

- A proactive effort to weave modelling into all aspects of GEOHAB CRP activities.
- Continued training researchers at all levels (students, postdocs, faculty, etc.) via any number of mechanisms: personal communication, CRP working meetings, follow-up modelling workshop(s), and representation of modelling aspects on the GEOHAB SSC.
- Future joint training sessions for experimentalists and modelers. Among the array of possible topics are:
  - Species-specific aspects intrinsic to HAB modelling: autecology, behavior, species interactions, toxin production, life cycles, etc.
  - Linkage of models, *in situ* observations, and remote sensing via data assimilation
  - Quantitative skill assessment of HAB models
  - Use of observing system simulation experiments (OSSEs) for array design
  - Evaluation of forecast products to maximize their benefit to the user community
- Foster engagement between the HAB modelling community and the broader community of biogeochemical, ecosystem, and population dynamics modelling
- Actively engage leadership of the emerging global ocean observing system. The need for such a system has been in part justified by the need to observe, understand, and predict HABs in the coastal ocean. As such, it in incumbent upon the HAB community to articulate the specifications of the observing system required to meet these needs.
- Maintain an active GEOHAB web site on modelling issues.

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Appendix B: Workshop Agenda

Note: an archive of presentations is available at:
http://science.whoi.edu/users/mcgillic/
GEOHAB_modeling_workshop_presentations

Monday 15 June – primarily for students and instructors; others attendance optional

9:00	Kevin Flynn – Phytoplankton Competition, Succession; Nutrient Competition Versus Predator Avoidance
10:00	Peter Franks – Biological and Ecological Dynamics of HABs
11:00	Break
11:30	Wolfgang Fennel – Construction of Models
12:30	Lunch
2:00	Hans Burchard and Inga Hense – Generalized Ocean Turbulence Model (GOTM)
3:00	Break
3:30	Tim Wyatt – Shifting Control Mechanisms–A Manifold Model
4:30	Discussion
5:00	Adjourn – Informal Student/Instructor Interactions

Tuesday 16 June – workshop convenes with all participants

9:00	Overview and Objectives Mentor – Student Introductions
9:30	Marc Sourisseau – Life Cycles/Population Dynamics of Copepods and Dinoflagellates
10:00	Marina Levy – High-resolution Plankton Ecosystem Modeling
10:30 of	Marcel Babin and Maéva Doron – Monitoring Harmful Algal Blooms Using Ocean Color Remote Sensing: Mature Methods and Promising New Avenues
11:00	Break
11:30	Ted Smayda – Harmful Algal Bloom and Red Tide Species in Narragansett Bay: The Diversity,Varieties, and Ecological Drivers of Their Multidecadal Variations
12:00 at	Ian Jenkinson – Identifying Appropriate Scales at Which to Measure Rheological Properties Important to HAB Dynamics: Designing the Right Rheometer
12:30	Lunch

GEOHAB Core Research Project: Eutrophication

2:00	Pat Glibert (Chair) – Eutrophication and HABs: Recent Modeling Advances, Continuing Challenges
2:30	Icarus Allen – Models of Eutrophication
3:00	Break

3:30	Lex Bouwman – Exploring Changes in Water shed Nutrient Sources, Forms and Exports: a Global News Implementation of the Millennium Ecosystem Assessment Scenarios
4:00 ing,	Alan Lewitus – Plans for a Regional Monitor-Alert, and Response Network and a Regional Forecasting System for Coastal California, Oregon, and Washington
4:30	Discussion
5:00	Working Group Icebreaker – working group introductions and discussion of their Charge

Evening Reception and Posters

Wednesday 17 June

GEOHAB Core Research Project: Stratification

9:00	Patrick Gentien (Chair) – CRP Overview
9:30	Hide Yamazaki – Oceanic Turbulence and Phytoplankton Dynamics
10:00	Beatriz Reguera – Biological Observations of Relevance for Species-Specific Models
10:30	Break
11:00 be	Hans Burchard – What are the Unknowns to Resolved at Small Scales?
11:30 ton	Elisa Berdalet – Ecophysiology of Phytoplank-Under Small Scale Turbulence: From the Laboratory to the Modulation of Natural Blooms
12:00	Ian Jenkinson – Deborah Numbers Revisited: How They May Apply to Harmful Algae and Other Plankton in Thin Layers
12:30	Lunch

GEOHAB Core Research Project: Upwelling

2:00	Grant Pitcher (chair) – Modelling Harmful Algal Blooms in Upwelling Systems: The Value of Hydrodynamic Models
2:30 in	Pierrick Penven – Regional Ocean Modelling the Benguela
3:00	Manuel Ruiz Villareal – Oceanographic Conditions Affecting Autumn Dynoflagellate HABs off Western Iberia
3:30	Break
4:00	Amy MacFayden – Numerical Modeling of the Juan de Fuca Eddy – an Initiation Site for Toxigenic *Pseudo-nitzschia* Blooms in the Northern California Current System
4:30	Chris Edwards – Modeling Biocomplexity in the California Current System with a Self-organizing Ecosystem Model
5:00	Discussion

Evening Reception and Posters

Thursday 18 June

9:00	Review Charge to Working Groups; Working Groups Convene
10:30	Break
11:00	Working Groups Reconvene
12:30	Lunch
2:00	Working Group Status Update in Plenary

Future Directions

2:30	Anouk Blauw – Alternative Model Approaches to HAB Prediction
3:00	Changsheng Chen – US Northeast Coastal Ocean Forecast System (NECOFS): Applications to Simulate Multi-Scale Estuarine-Coastal Interactions
3:30	Break
4:00	Rick Stumpf – Integrating Models and Observations to Forecast Harmful Algal Blooms
4:30	Dennis McGillicuddy – Toward an Operational Model for *Alexandrium fundyense* in the Gulf of Maine
5:00	Discussion
Evening Reception and Posters	

Friday 19 June

9:00	Working Groups Convene
10:30	Break
11:00	Working Groups Convene
12:30	Lunch
2:00	Working Group Reports and Discussion
3:30	Break
4:00	Student/Postdoc Presentations (5 min each)
5:30	Final Wrap-up

Appendix C: Student-Mentor Pairings

Albert, Aurélie	Grant Pitcher
Alves de Souza, Catharina	Beatriz Reguera
Anderson, Clarissa	Rick Stumpf
Artigas, Mireia Lara	Hans Burchard / Inga Hense
D'Silva, Maria Shamina	Tim Wyatt
Francé, Janja	Ted Smayda
Frolov, Sergey	Chris Brown
Garcia, Marcos Cobas	Pierrick Penven
Kehoe, Michael	Kevin Flynn
Kroll, Alexandra	Ken Furuya
Li, Ji	Alan Lewitus
Llebot Lorente, Clara	Patrick Gentien
Pawlowski, Marcin	Pat Glibert
Ross, Oliver	Marcel Babin
Vahtera, Emil	Ian Jenkinson
Veitch, Jennifer	Marina Levy
Velo Suárez, Lourdes	Peter Franks
Wang, Jiujuan	Raphe Kudela
Xu, Jie	Icarus Allen

Appendix D: Abstracts

A MODELING STUDY ON THE NUTRIENT ENVIRONMENTS OF THE EASTERN SETO INLAND SEA, JAPAN

Katsuyuki Abo, Toshinori Takashi and Tateki Fujiwara

Eastern area of the Seto Inland Sea is one of the most important nori (Porphyra) aquaculture fields in Japan. However, in recent years, the production is getting lower because of the bleaching of nori which is caused by the deficiency of nutrient in the sea water. The bloom of diatoms such as *Eucampia zoodiacus* and *Coscinodiscus wilesii* absorb nutrients from sea water resulting in the nutrient deficiency. To elucidate and predict the occurrence of nutrient deficiency in the nori aquaculture fields, we developed a numerical model. Firstly, we developed a diagnosis model which can calculate the time-averaged current velocity field from observed temperature, salinity and meteorological data. The monitoring data obtained by local governments were used to calculate the velocity field and to analyze the effect of the flow field on the occurrence of the nutrient deficiency. The nutrient deficiency occurred initially in western side of the area and propagated to the east toward the nori aquaculture fields. The result suggested that the eastward current flow induced by seasonal wind affects the propagation and governs the initial timing and level of the nutrient deficiency. Secondly, we developed an ecosystem model to calculate the nutrient level in the sea water. We reproduced the fluctuation of nutrient level in the nori aquaculture season in the eastern Seto Inland Sea. Although the model still includes some problems for its practical application, it can be applied to predict short term fluctuation of the nutrient level in the nori aquaculture fields.

A MODELING APPROACH OF THE OXYGEN MINIMUM ZONE IN THE HUMBOLDT CURRENT SYSTEM

Aurélie Albert and Vincent Echevin

The Humboldt Current System is the most productive upwelling system in the world ocean. There, associated with the Eastern South Pacific Current System, a shallow Oxygen Minimum Zone extends offshore as far as 110°W off Peru and Northern Chile. Oxygen values can be lower than 10 µmol dm^{-3} at 20 m, and reach less than 1 µmol dm^{-3} in the OMZ core. Oxygen concentration is one of the key parameters for ocean biogeochemistry. A coupled dynamical-biogeochemical model is used to evaluate how the OMZ spatial and temporal structure can be driven by both physical and biological conditions. Indeed, the time and space variability is to a large extent dependant of remote equatorial variability in the form of coastally trapped and westward propagating Rossby waves. Furthermore, mesoscale eddies may transport low O$_2$ off-shore. Variations of the poleward Peru-Chile undercurrent may also induce fluctuations of the OMZ. Besides, high levels of organic production are associated with a strongly advective regime of waters rich in nutrients, gases, and trace metals and with an enhanced OMZ in the subsurface water column as a consequence of organic matter mineralization. We also investigate the respective role of the parameterized biogeochemical processes on the mean and variability of the OMZ..

MODELS OF HABS AND EUTROPHICATION

J Icarus Allen

Eutrophication can be defined as the enrichment of water by nutrients causes an accelerated growth of algae and higher forms of plant life, which leads to an undesirable disturbance in the balance of organisms present in the water and to the quality of the water concerned. This is often a consequence of increasing nutrient loading to coastal and enclosed or estuarine environments is a result of agricultural, aquaculture, industrial and sewage effluents. Numerical modelling tools allow the exploration and prediction of nutrient transport and cycling and its relationship to HABs. This paper will describe the major issues related to eutrophication modelling illustrated with examples from existing model systems.

FIRST REPORT OF TEMPORAL VARIABILITY OF DIARRHETIC TOXINS IN BIVALVES RELATED TO *DINOPHYSIS* SPP. ABUNDANCE IN SOUTHERN CHILE

Catharina Alves-de-Souza, Daniel Varela, Carlos García, Néstor Lagos and Humberto González

Southern Chile represents one of main area worldwide with endemic Diarrheic Shellfish Poisoning (DSP) intoxications, generating serious problems both for public health and fishery industry. However, little attention has been given to DST in this area. This study show the first report of temporal variability of concentrations of DSP toxins in bivalves, related to the abundance of *Dinophysis* species, in southern Chile. The study was performed in Reloncaví fjord (41º29' S; 72º18' W), between December 2007 and April 2008, with a temporal interval of 15-21 days between samplings. *Dinophysis* spp. showed very variables abundances and an evident tendency for cell accumulation in depths close to the pycnocline. In general, the species of this genus showed low to moderate cell concentrations (> 2000 cells L^{-1}), with exception of March 2008, when a bloom of *Dinophysis acuminata* Clarapède et Lachmann (38032 cells L^{-1}) was observed. A strong temporal variability in the diarrheic toxin concentrations in bivalves was recorded. In the two first sampling dates, it was observed the highest values of DST, which were above the above the international regulation and composed both by Dinophysistoxin-1 and -3. In the subsequent months, it was observed an abrupt decrease in the concentration of these two diarrheic toxins, which showed values lower than 1 ng/g hepatopancreas. The occurrence of low DSTs values simultaneously the bloom of *Dinophysis acuminata*, would be indicating that other

factors could also affect the accumulation of these toxins by bivalves.

A REMOTE SENSING AND REGIONAL DOWNSCALING APPROACH TO THE ECOLOGICAL FORECASTING OF POTENTIALLY TOXIC DIATOM BLOOMS IN THE CHESAPEAKE BAY AND SANTA BARBARA CHANNEL

Clarissa R. Anderson, Raghu Murtugudde, Raphael M. Kudela, Christophter W. Brown, Mathew Sappiano and David A. Siegel

Recent downscaling efforts for the Chesapeake Bay have led to an open source, hydrodynamic model currently being applied to empirical habitat models for various harmful algal bloom taxa, with a fully coupled regional Earth System Model in development. Statistical models for predicting the occurrence of rare, but potentially toxic algal blooms in the Bay were used to create hindcasts and forecasts of bloom probabilities with ChesROMS. Environmental parameters significantly associated with toxigenic blooms in the Bay have also been shown to be important for similar blooms off the coast of central California. The Santa Barbara Channel, CA (SBC) is a very different region where wind-driven upwelling and mesoscale eddies are important processes driving phytoplankton blooms. In recent years, the spring bloom has been dominated by the neurotoxin-producing diatom, *Pseudo-nitzschia* spp. Statistical models created for the SBC suggest that conditions most associated with high cellular toxin levels were those associated with local upwelling as well as with increased absorption by cDOM (412 nm), increased reflectance at 510/555 nm, and decreased particulate absorption at 510 nm., indicating that the detection of toxic blooms using satellite platforms such as MERIS, MODIS, and AVHRR is a possibility for the SBC. Future work will focus on collaborative efforts to merge satellite and regionally down-scaled forecasting products with these empirical habitat models to assess forecasting capabilities in the CA Current System and any potential connections to large-scale climate modes to explore the potential for extending the lead times for forecasts including the impact of climate change.

CHRYSOCHROMULINA cf. *LEADBEATERI* IN NORTHERN NORWAY 2008

Johanne Arff and Karl Tangen

A monitoring and forecasting service for the Norwegian fish farming industry has been in operation since 1987 with the aim to reduce potential losses caused by harmful plankton, extreme temperatures and sea states and acute pollution including oil spills. The service is run by SINTEF Fisheries and Aquaculture for insurance companies and their customers and is motivated by the empiric experience that economic losses have been reduced after early warning of harmful algal blooms and mass occurrences of harmful jellyfishes, specially adapted weather and sea state forecasts and actions taken during oil spill incidents. In May 2008 there was a situation with losses of cultured salmon in Northern Norway. Water samples from the area showed high densities of a potential fish toxic Prymnesiophyte, *Chry-sochromulina* cf. *leadbeateri*. A description of the bloom with focus on crisis management, including sampling and dissemination of the results, will be given.

HYDRODYNAMIC PROPERTIES AND SMALL-SCALE TURBULENCE RELATED TO DIFFERENT HAB EVENTS IN ALFACS BAY (NW MEDITERRANEAN)

Mireia L.Artigas, Elisa Berdalet, Rubén Quesada, Jaume Piera and Marta Estrada

Different laboratory experiments have shown the particular biological responses of many dinoflagellate species to small-scale turbulence. However, the relevance of these observations has been rarely tested in the field. In this work we characterized the environmental physical conditions during blooms of two different species, the ichthyotoxic dinoflagellate *Karlodinium veneficum* occurred on June-July 2007 and the diatom *Pseudonitzchia* spp. occurred in October 2007 in Alfacs Bay. Over the first bloom event, velocity data were almost continuously recorded by a 2MHz acoustic Doppler current profiler deployed on a fixed station (6 m depth). Additional physical (using a CTD and a SCAMP microstructure probe) and biological (chlorophyll concentration, phytoplankton species composition) parameters were obtained from several sampling points. Meteorological data were provided by a nearby station. During the *Pseudonitzchia* spp. bloom, only microstructure and biological data were collected along 5 days. We will show our preliminary results on the different scenarios under which both events occurred.

RELATIONSHIP BETWEEN TOXIC DINOFLAGELLATE ABUNDANCE, CYSTS AND ENVIRONMENTAL FACTORS IN SFAX COASTS (SOUTH OF TUNISIA)

Hamza Asma, B. Belhassen Malika, Fekiwafa, Bouain Abderrahmen

In phytoplankton monitoring survey in Sfax coasts, detection and study of dinoflagellate cysts is averred as much necessary as toxic species. Cysts can't only provoke blooms, but we also detected some toxic responses related for presence of these forms in our coasts as case of *Karenia selliformis and Alexandrium minutum*. Sfax coasts are characterized with tidal movement and that hydrodynamic condition can therefore produce high local cyst accumulations. The movement and turbulent mixing of the sediment lead possibly to vertical redistribution of the resting stages in the sediment cyst resuspension, their persistence in the water column and germination of the vegetative population.

In this study we try identify the relationship between those toxic dinoflagellates, their cysts, oceanographic parameters and environmental factor. The data were collected from ten years of phytoplankton monitoring in Sfax coasts coupled with a specific sampling in sediment and water in tide period in different season in 2006. The abundance of the species in the motile form and cyst encountered in the water column varied significantly. The variation in cysts and motile stage depend of tidal flushing. Our main results indicate that salinity and temperature determine when germination and encystment can occur. Contrary to the general accepted idea that the nutrient status plays a triggering role for encystment, we can suggested that phenomenon is a

naturally occurring stage in the dinoflagellate life history and environmental parmeters can only favoured optimum growth conditions.

THE BIOLOGY AND ECOLOGY OF *PYRODINIUM BAHAMENSE*: INPUTS INTO MODELING A TROPICAL TOXIC DINOFLAGELLATE

Rhodora V. Azanza

Pyrodinium bahamense var. *compressum* has been causing toxic blooms in the tropical world for more than three decades now. In the Philippines its bloom was first recorded in 1983 and to date, about one thousand eight hundred and twenty four (1,824) Paralytic Shellfish Poisoning (PSP) cases and one hundred and nine (109) deaths have been reported in about twenty six (26) areas/embayments. Modeling of the bloom dynamics of this tropical toxic dinoflagellate has been attempted for the first time in 2000 using data sets from the Philippines. With more observations and results from studies in the laboratory and the field, additional synthesis and modeling of the bloom dynamics of the organism are in order.

ECOPHYSIOLOGY OF PHYTOPLANKTON UNDER SMALL SCALE TURBULENCE: FROM THE LABORATORY TO THE MODULATION OF NATURAL BLOOMS

Elisa Berdalet, Gisela Llaveria, Mireia Lara, Rubén Quesada, Jaume Piera and Marta Estrada

Laboratory studies have shown that small-scale turbulence may interfere with different physiological processes on phytoplankton cells. Relevant observations include: 1) changes in the metabolite fluxes in and out of the cell, 2) changes in the morphology and cellular volume, 3) alterations of the cellular content of DNA, toxins or DMSP, 4) modifications of the cell division and live cycles (cyst formation) and of motility patterns, 5) interferences with predator-prey and parasite-host interactions, and 6) cell death. Altogether, these results point to the particular sensitivity of dinoflagellates to small-scale turbulence, although the fundamental mechanisms of these responses are not known. One challenge now is to ascertain to what extent experimental laboratory designs and setups approximate natural conditions and how the physiological capacities of the organisms interact with other biological factors, environmental forcings and water circulation at a variety of spatio-temporal scales, to determine the dynamics of dinoflagellate populations in nature. With this objective in mind, we are conducting a multidisciplinary study in the Alfacs Bay (Ebro Delta, NW Mediterranean). Velocity data have been almost continuously recorded during 2 years by a 2MHz acoustic Doppler current profiler deployed on a fixed station (6 m depth). Additional physical (using a CTD and a SCAMP microstructure probe) and biological (chlorophyll concentration, phytoplankton species composition) parameters have been obtained from several sampling points. Meteorological data are provided by a nearby station. We will show our preliminary results on the main scenarios under which several HABs have occurred during this period.

ALTERNATIVE MODEL APPROACHES TO HAB PREDICTION

A.N. Blauw

Models can be used to as a tool for ecosystem analysis and for prediction of harmful algal blooms. Several model approaches are available that all have their specific advantages and disadvantages. Both the level of understanding of the bloom phenomenon, data availability, the type of processes that are most controlling and the purpose of the model play a role when selecting the most suitable modelling approach. The most commonly used model approach is a process-based deterministic numerical model. Alternatively, data-based model approaches are available, such as statistical models and neural network models. These are useful is cases when the bloom phenomena are not sufficiently understood or too complicated to apply the deterministic approach. However, they require a lot of data and cannot predict what will happen under changing circumstances. As intermediate approaches between process-based and data-based model approaches combinations can be made that benefit optimally from available process knowledge and fill in the knowledge gaps with data-based submodels. An example of such an intermediate model approach is fuzzy logic modelling. Some examples of model approaches applied on HAB phenomena are evaluated to illustrate their applicability for specific situations.

EXPLORING CHANGES IN WATERSHED NUTRIENT SOURCES, FORMS AND EXPORTS: A GLOBAL NEWS IMPLEMENTATION OF THE MILLENNIUM ECOSYSTEM ASSESSMENT SCENARIOS

Lex Bouwman, Sybil Seitzinger, Carolien Kroeze, Arthur Beusen,Gilles Billen, Gerard Van Drecht, Egon Dumont, Balázs M. Fekete, Josette Garnier, Emilio Mayorga, Dominik Wisser and Wilfred M. Wollheim

The rapidly increasing global anthropogenic nutrient production on land and negative impacts on coastal systems due to export from rivers are extensively documented. According to the comprehensive Millennium Ecosystem Assessment (MA) the excessive nutrient loading of ecosystems and nutrient mobilization is expected to continue during the coming decades in response to economic and population growth. For developing a firm scientific basis for actions to reverse these trends and sustain riverine and coastal ecosystem health, quantitative models are needed for simulating changes in river loads of nutrients based on changes in watershed anthropogenic forcings at regional to global scales. Particularly, models are needed to predict changes in element ratios and nutrient forms (dissolved vs. particulate, organic vs. inorganic) which have been shown to modulate the impacts of nutrient loading on marine ecosystems. The Global Nutrient Export from Watersheds (NEWS) system of models was designed to meet these requirements. We will present preliminary results from an application to past (1970) and current (2000) conditions, and compare them four MA scenarios for the coming five decades. These scenarios integrate economic and social processes, changing climate, hydrology and water engineering, and land cover and

represent plausible futures with contrasting degrees of global cooperation and of sustainability of ecosystem services. Consistent global datasets of land nutrient fluxes (diffuse and point sources) and hydrological alterations were developed for this Global NEWS effort.

DEVELOPMENT OF A HARMFUL ALGAL BLOOM PREDICTION SYSTEM IN THE CHESAPEAKE BAY

Christopher Brown, R. Hood, W. Long, B. Michael, C. Wazniak, D. Ramers, P. Tango, J. Wiggert and J. Xu

A variety of harmful algal blooms (HABs) afflict the Chesapeake Bay, degrading the bay's health and jeopardizing the viability of this important natural resource. We are developing an operational system that will predict the likelihood of three important HAB species in Chesapeake Bay and its tidal tributaries: the dinoflagellates *Karlodinium veneficum* and *Prorocentrum minimum* and the cyanobacteria *Microcystis aeruginosa*. Warnings of these events will aid in mitigating their deleterious effects on human and ecosystem health. The approach uses real-time and 3-day forecast data derived from a variety of sources and techniques to drive multi-variate, empirical habitat models that predict the probability of blooms of these HAB species. A prototype prediction system generates daily nowcasts and 3-day forecasts of *K. veneficum* using environmental conditions simulated by the hydrodynamic Regional Ocean Modeling System (ROMS) configured for Chesapeake Bay and a habitat model constructed using an artificial neural network. The predictions, in the form of digital images, are available via the World Wide Web to individuals and interested agencies to help guide research, recreational and management activities. These predictions will be employed by the Maryland Department of Natural Resources to guide response sampling efforts for HAB monitoring.

WHAT ARE THE UNKNOWNS TO BE RESOLVED AT SMALL SCALES?

Hans Burchard and Lars Umlauf

Giving the fact that a comprehensive state-of-the-art report about the topic suggested by the title would fill various interdisciplinary text books, this presentation will be restricted to diapycnal mixing processes in the central Baltic Sea, with specific focus on surface mixed-layer dynamics. This is justified, because the semi-enclosed Baltic Sea represents an ocean in a nutshell, including overturning circulation mediated by internal diapycnal mixing. The overturning circulation is established by a freshwater surplus in the Baltic Sea catchment area, setting up a typical estuarine circulation, with an average inflow of saline water near the bed and outflow of relatively fresh water near the surface. This overturning circulation, which is characterised by episodic inflow events, is closed by a variety of diapycnic mixing processes: the inflowing dense water is diluted by entrainment of ambient water; turbulence in stratified waters generated near the sea bed due to internal wave shoaling and boundary currents leads to diapycnal mixing; coastal upwelling of dense water may lead to irreversible diapycnal mixing. The individual quantitative

contributions of these processes to the bulk salt flux are however largely unknown. The Baltic Sea near-surface region is complicated, because a seasonal summer thermocline establishes above the permanent halocline. Due to the relatively low salinity in the Baltic Sea, the winter surface temperature is typically below the temperature of maximum density, leading to most vigorous near-surface mixing in spring and autumn. Quantification of diapycnal mixing processes is essential for the understanding of massive cyanobacteria blooms which are typical for stable summer conditions.

GENERAL OCEAN TURBULENCE MODEL (GOTM)

Hans Burchard and Inga Hense

GOTM is a Public Domain water column model which is available via www.gotm.net since almost exactly 10 years. Assuming that horizontal gradients are either irrelevant or diagnostically prescribed, GOTM discretises the one-dimensional idealisation of the hydrostatic Reynolds-averaged equations for momentum, salt and temperature. The core of GOTM is a collection of turbulence closure models for calculating the vertical exchange of momentum and tracers. The specific focus is on two-equation turbulence models, with the dynamic turbulent kinetic energy (TKE) equation as the first and a dynamic length-scale related equation as the second. Examples for the latter are the dissipation rate of TKE (k-epsilon model), the turbulence frequency (k-omega model), or a generalised length scale. A number of algebraic second-moment closures are coupled to these two-equation models in a consistent way. This physical part of GOTM has been used in many estuarine, coastal and shelf seas application as well as for upper ocean studies. The turbulence module has been coupled to some of the most important ocean circulation models. In recent years, several biogeochemical and ecosystem modules have been interactively coupled to the physical part of GOTM: e.g. simple NPZD-type modules used for basic ecosystem investigations as well as complex ecosystem modules like ERSEM. Current activities comprise the implementation of phytoplankton life cycles into GOTM as well as inclusion of various chemical modules. GOTM is written in FORTRAN, but to allow for wide-spread use of GOTM, a Graphical User Interface (GUI) has recently been developed.

DYNAMICS OF TURBID BUOYANT PLUMES AND THE FEEDBACKS ON NEAR-SHORE BIO-GEOCHEMISTRY AND PHYSICS

Bronwyn Cahill, Oscar Schofield, Robert Chant, John Wilkin, Eli Hunter, Scott Glenn and Paul Bissett

The near-shore waters of the New York/New Jersey Bight in April 2005 exhibited distinct regions of turbid water with clearly differing optical properties associated with the Hudson River plume. We examined the effect of variable light attenuation on the hydrodynamics and ecological response of the Hudson River plume and its environs using field observations and a 3-dimensional biophysical model. Important feedback mechanisms between the attenuation of light and the resulting impact on the mixed layer depth were revealed from the model-

ing results. High concentrations of chlorophyll, detritus and colored dissolved organic matter in the upper water column as a result of enhanced stratification increase the attenuation of light and modify the buoyancy driven circulation. This further impacts the growth of phytoplankton in the model and subsequently modifies the vertical profile of the attenuation coefficient, which in turn feeds back into the overall heat budget.

MODELLING TOXIC *ALEXANDRIUM* BLOOMS IN PENZE ESTUARY

A. Chapelle, M. Sourisseau, R. Verney, J. Fauchot, C. Labry and A. Youenou

The harmful *Alexandrium* blooms are relatively recent in France, they occurred for the first time in the 1980[S] . The presence of *Alexandrium* in the Penzé dates back to 1988, and the first case of toxicity occurred in 1989 in the Bay of Morlaix and in 1993 in the Penzé estuary. In order to understand and predict the toxic events, 2 research strategies have been followed. A 20 years historical database was used to find links with *Alexandrium* toxic blooms and environmental data involving statistical analysis. This methodology allowed to determine the predictive potential of different environmental parameters, the main factors are : water temperature, tide and river run. Apart from this, we have drauwn up an *Alexandrium* model in the Penzé. First step was to calibrate *Alexandrium* growth processes in function of different environmental parameters against laboratory data. Then this ecophysiological model has been coupled to a 3D hydrosedimentary model of nitrogen and phosphorus cycles in water and sediment. This model enables diatom and dinoflagellate growth to be simulated over a year as well as *Alexandrium*. The model shows, as the statistical model, the importance of the dilution effect balancing growth which is also dependant of light and water temperature. This working experiments has shown some limits : the possible shift in the Penzé ecosystem , as the statistical model is not able to prdict the last years (2004 to 2006) and the sensibility of *Alexandrium* modelled to parameters of the general phytoplankton blooms (diatoms, dinoflagellates).

US NORTHEAST COASTAL OCEAN FORECAST SYSTEM (NECOFS): APPLICATIONS TO SIMULATE MULTI-SCALE ESTUARINE-COASTAL INTERACTIONS

Changsheng Chen and Robert C. Beardsley

A team of University of Massachusetts-Dartmouth and Woods Hole Oceanographic Institution researchers has developed the Northeast Coastal Ocean Forecast System (NECOFS). NECOFS is an integrated atmosphere-ocean model system in which the ocean model domain covers the northeast US coastal region (the New England Shelf, Georges Bank, the Gulf of Maine, and the Scotian Shelf) with a horizontal resolution of 10-15 km in the open ocean, 1-5 km on the shelf, and down to 20 m in estuaries, inner bays, inlets and harbors. The system includes: 1) two community atmospheric mesoscale models, WRF (Weather Research and Forecasting model) and MM5 (fifth generation NCAR/Penn State model), modified to incorporate the COARE 2.6 air-sea flux algorithm); 2) the unstructured-grid Finite-Volume Coastal Ocean Model configured for this region (FVCOM-GOM) with a nested higher-resolution FVCOM configured for Massachusetts coastal waters (FVCOM-MASS); 3) an unstructured-grid surface wave model (FVCOM-SWAVE); and 4) the FVCOM-based unstructured-grid sediment transport model. In its present initial stage, the forecast system is built based on WRF, MM5 and FVCOM-GOM/FVCOM-MASS. Both meteorological and ocean models have been tested through comparison with field data in hindcast experiments covering the period 1979 to present. The system produces 3-day forecast fields of surface weather, surface waves, surface wind stress and heat flux, and 3-D water temperature, salinity, and currents, with daily updating using hindcast data assimilated fields whenever field data are available. FVCOM-GOM and FVCOM-MASS are being upgraded with a new semi-implicit FVCOM code, which will allow regional and coastal as well as estuarine model runs with a significant reduction in computational power. The model-predicted flow, temperature and salinity fields have been validated by comparing with available hydrographic, CODAR, and current data in this region; some results will be discussed in this presentation. This system shows a great potential to be used to study the impact of estuarine-coastal interactions on harmful algal blooms.

SIMULATION OF THE OCEANOGRAPHIC CONDITIONS DURING THE AUTUMN 2005 HAB IN NORTH-WEST IBERIA

Marcos Cobas-Garcia, Manuel Ruiz-Villarreal, Pablo Otero-Tranchero, Laura Escalera and Beatriz Reguera

North-West Iberian waters are frequently affected by red tides during the autumn transition to downwelling-favorable winds. Different hypothesis have been considered to explain the development of these HABs: germination of resting cists, latitudinal progress in microplankton succession and transport from the south by means of an inshore poleward current. Although the Diarreic Shellfish Poison is a common toxin detected in these waters, during the autumn 2005 HAB, the dinoflagellate *Gymnodinium Catenatum*, responsible for the Parallitic Shellfish Poison toxin, was found in this area, after 10 years of absence in the Galician and Portuguese coasts.

This study focuses on the oceanographic conditions during the red tides episodes occurred in autumn 2005. During this period, the *Gymnodinium Catenatum* dinoflagellate was first detected in the coast of Obidos (Portugal) and in the following days it was reported in other sites located further north, up to the Galician coast 20 days later. We will present the results of a simulation of that period using the Regional Ocean Modelling System (ROMS), forced with atmospheric data from the HIRLAM model, and compared with data from oceanographic cruises. Sensitivity of the model to different parameters will also be presented. Comparison of mean modeled shelf circulation with the chronology of proliferation of toxic cells agrees with the hypothesis of the along-shore transport.

CRITICAL SCALES FOR UNDERSTANDING THE ROLE OF FINESCALE PHYSICAL-BIOLOGICAL INTERACTIONS IN CONTROLLING THE DYNAMICS AND IMPACTS OF THIN LAYERS OF HARMFUL ALGAL IN STRATIFIED COASTAL WATERS

Percy L. Donaghay, James M. Sullivan, Jan E.B. Rines, D. Van Holliday and Alfred K. Hanson

One of the major challenges in modeling the dynamics and impacts of harmful algal blooms is to determine the scales that control critical physical-biological interactions, and then develop techniques to measure those processes and incorporate them into numerical models. This problem is particularly challenging for harmful algae that form layers that are substantially thinner than the multi-meter scales that are typically resolved in physical models or easily sampled from ships. Herein we will first use field data to evaluate the vertical sampling scales needed to resolve the finescale biological, chemical and physical structure of thin layers, and then use those data to evaluate the importance of finescale physical-biological interactions in controlling the dynamics and impacts of such layers. We will consider both mighating and non-migrating HAB thin layers.

MONITORING OF HARMFUL ALGAL BLOOMS USING OCEAN COLOR REMOTE SENSING: MATURE METHODS AND PROMISING NEW AVENUES

Maéva Doron and Marcel Babin

Several approaches for monitoring harmful algal blooms using ocean color remote sensing have been recently proposed. We will first review those methods and assess them with reference to the capabilities and limitations of ocean color inversion. Second, we will show how ocean color data can be combined with other data sources (in situ and remote sensing) to constrain coupled physical-biogeochemical models. We will review the different data assimilation methods for optimally constraining a model using ocean color data. Results obtained for a large-scale physical-biogeochemical model will be presented, and promising avenues for HAB modeling evoked.

OCCURENCES OF HARMFUL ALGAL BLOOMS ALONG THE WEST COAST OF INDIA

Maria Shamina D'Silva and Arga Chandrashekar Anil

Harmful Algal Blooms caused by dinoflagellates are being reported with increasing frequency, with ill effects on human health and the ecosystem. The west coast of India is influenced by southwest monsoon coupled with moderate upwelling and reported to harbour large areas of severely hypoxic waters during September-October. An investigation to understand the ecology of dinoflagellates, many of which produce cysts as part of their life cycle was carried out along the west coast of India. Heterotrophic dinoflagellate cysts, mainly *Protoperidinium* spp., were the most diversified, predominating at most of the locations sampled. Earlier studies elsewhere have linked dominance of heterotrophic cysts to elevated nutrient concentrations and industrial pollution. Dominance of heterotrophic dinoflagellates can also be influenced by moderate seasonal upwelling and mon-

soon perturbations in these regions. Cysts of dinoflagellates capable of producing Paralytic Shellfish Toxin (PST) and yessotoxin were detected at some locations.

MODELING BIOCOMPLEXITY IN THE CALIFORNIA CURRENT SYSTEMS WITH A SELF-ORGANIZING ECOSYSTEM MODEL

Christopher A. Edwards, Nicole Goebel, Jonathan P. Zehr, Mick Follows

The California Current System (CCS) refers to the collection of poleward and equatorward surface and subsurface currents that extends along the west coast of North America and a thousand kilometers offshore where it merges with the larger Pacific circulation. It exhibits strong seasonal fluctuations and rich mesoscale variability and supports a productive and diverse ecosystem with geographically varying communities. We report on the development and evaluation of an interdisciplinary modeling effort for this region. Within an implementation of the Regional Ocean Modeling System (ROMS) for the CCS, we incorporate a relatively new type of ecosystem model that supports multiple functional groups and includes multiple phytoplankton types within each group. The model is seeded with 78 phytoplankton types with randomly assigned physiological traits. The resultant modeled functional groups, their biogeographic zones and seasonal variability that emerge resembles that observed in the CCS. In particular, the model captures the climatological seasonal structure in the coastal phytoplankton community, the robust spring bloom of coastal diatoms, and the offshore presence of *Prochlorococcus*-like organisms.

ADVANCES IN OPERATIONAL ECOSYSTEM MODELLING AND THE PREDICTION OF HARMFUL ALGAL BLOOMS AT THE UK MET OFFICE

Karen Edwards, Rosa Barciela, Ray Mahdon

The UK Met Office is applying coupled 3D carbon-cycle and biogeochemical models for both the open-ocean and UK shelf-seas which have been developed in collaboration with partners in the National Centre for Ocean Forecasting and the Met Office's Hadley Centre for Climate Research. For the UK shelf-seas, we use the MRCS (Medium-Resolution Continental Shelf – POLCOMS hydrodynamic model) coupled to the European Regional Seas Ecosystem Model (ERSEM). The shelf-seas ecosystem forecasts have been operational since March 2007 and are supplying users with operational products, providing ocean forecasts and serving as a basis for developing predictive capabilities.

One important application of our self-seas ecosystem model is providing support for the UK agencies responsible for ecosystem health, water quality monitoring and HAB prediction. In collaboration with the Plymouth Marine Lab and the UK Environment Agency, the AlgaRisk 08 project is designed to help focus monitoring efforts and develop a forecasting system for nuisance algal blooms, as well as enabling the EA to advise local authorities. Using operational data feeds, this project combines model output (including physical and biological parameters) with Earth Observatory data to create a forecasting system for nuisance algal blooms. This work

presents the AlgaRisk08 model design along with initial results. We also present recent model developments including a novel data assimilation scheme for ocean colour developed jointly by NOCS and the Met Office for the FOAM-HadOCC system (our open-ocean ecosystem model) and plans to nest our shelf seas ecosystem model within the HadOCC open ocean model.

HIGH RESOLUTION MODELS OF PHYSICAL AND BIOLOGICAL PROCESSES IN NORWEGIAN COASTAL WATERS
Ingrid H. Ellingsen

The SINMOD model system has been continually developed at SINTEF since 1987, and is well established for studies of physical, chemical and biological processes in the oceans and coastal waters of the North Atlantic and Eurasian Arctic. The hydrodynamic part of the model systezm is based on the primitive Navier-Stokes equations. The ecosystem module system includes nitrate, ammonium, silicate, diatoms, flagellates, micro-zooplankton, bacteria, heterotrophic nanoflagellates, fast sinking detritus, slow sinking detritus and *Calanus finmarchicus.* A present model setup covers the North Atlantic and the Arctic Ocean with a 20 km horizontal grid point distance. This model generates boundary conditions for higher resolution models using a nesting technique in several steps. High resolution models (horizontal resolution of 160m) have been established for simulations of physical and biological processes in Norwegian coastal waters. The coupled model system is, for instance, being used to simulate the spreading of nutrients from fish farms and and how this affects primary production, and how knowledge in turn can be exploited for mussel and seaweed production. The model will be developed further to simulate the spreading of harmful algae blooms. Preliminary model results will be presented for a case with a bloom of *Chrysochromulina* cf *leadbeateri* in northern Norway in 2008.

HABS IN MOROCCO: MONITORING AND MANAGEMENT
Btissam Ennaffah and Abdelghani Chafik

Records of HABs in Morocco have increased in this last decade. Natural events, as well as human activities have contributed to this increase. Toxic events are frequent on Mediterranean and atlantic coast and in some cases, can cause a serious losses for aquaculture projects and also for naturals beds of shellfish. Since 1996, a national program of Monitoring of HAB has been working, to predict HAB events in time and space, this program cover now the entire Moroccan coast (3500Km), there are 7 coastal laboratories, in who 7 scientists work with a weekly frequency. After many years in Monitoring, severals potentially toxic species was identified frequently, on Atlantic coast, we note *Dinophysis* genus, with *D.acuminata*, *D.caudata*, *D.sacculus*, *D.rotundata*, *D. hastata*, this presence cause the DSP outbreaks during the year and can close the shores for several months. *Alexandrium minitum* is also present, but never associated with PSP syndrome.

For toxics Diatoms, we identify P. *pseudodelicatissima*, *P.australis*, their presence are often correlated with the presence of ASP in mussels (*Mytilus galloprovincialis*). Morroccan Mediterranean coast develop always the *Gymnodinium catenatum* blooms, and then the PSP (Paralytic shellfish Poison) cause the contamination of cockles (*Acanthocardia tuberculatum*) and clams for many years and there are a several economic losses in the region. Recently some Rhaphydophytes has been included in the list of blooming species in our areas, like *Tetraselmis sp*. The national program of monitoring of HAB permit to detect, evaluate the impact of the proliferation of toxic algae on shellfish industries and consequently on consumers, and define year after year the shores which was very susceptible to develop more toxic events than others.

CONSTRUCTION OF MODELS
Wolfgang Fennel

At the outset, an introduction to the theoretical fundamentals of marine ecosystem modeling will be given to define and discuss state variables and model individuals as well as the dynamical relationships, which describe the interactions of physical, chemical and biological variables. The connection of different model approaches is demonstrated by means of the representation of plankton cells, zooplankton and fish as well as individuals, super-individuals, biomass concentration and abundance in an abstract phase space.

The relationships between model variables and process-descriptions as well as observations and experiments are highlighted and the predictive potential of models is explained. This involves also the discussion of limitations and opportunities of models.

Some specific aspects relevant for modelling HABs will also be addressed and example models will be provided that may help students to develop their own models adjusted to their research problems. The talk is focused on the chemical biological part of model construction and uses a strongly simplified description of the physical processes.

PHYTOPLANKTON COMPETITION, SUCCESSION; NUTRIENT COMPETITION VERSUS PREDATOR AVOIDANCE
Kevin J Flynn

Success of an individual phytoplankter depends on upon the growth rate, net of all positive and negative processes. Growth at the organismic level depends on competition for external resources, efficiency of internal resource allocation, and physical processes affecting position in the water column. Losses also depend on physical processes but also upon predation. Because of the coupling between predation, nutrient regeneration and the development of anti-predation measures, competition for resources between phytoplankton is far more complex than is apparent when studying the interactions in a piece-meal fashion. The interactions will be considered making use of models, examining the potential for the formation and dispersal of harmful algal

blooms through different mechanisms. The importance of the growth-loss processes of other, non-harmful, algae will also be explored, indicating why a holistic approach to HABs is required rather than concentrating on the HAB species itself.

HABs AND RECENT CHANGES IN PHYTOPLANKTON COMMUNITY STRUCTURE IN SLOVENIAN COASTAL WATERS

Janja Francé and Patricija Mozetiè

Shellfish growing areas in the Gulf of Trieste (Northern Adriatic) are subjected to HAB monitoring and shellfish toxicity tests that are carried out concomitantly. Up to date, the DSP species are currently the only ones presenting problems for the aquaculture in the area. PSP and ASP problems are to be expected as well due to the presence of *Alexandrium* and *Pseudo-nitzschia* species in the phytoplankton assemblage. Past data analysis (1995-2004) pointed out a marked seasonal succession of selected HAB species. However, occasional abundance outbursts of these species showed considerable inter-annual variations, making the prediction of possible harmful events difficult. Recently, the results of whole phytoplankton community of the past 25 years have been analyzed. Several statistical approaches, intended to map annual and multi-annual succession patterns and identify indicative phytoplankton assemblages, pointed out structural changes in phytoplankton community. The change that could affect future HAB events is the disappearance of the late spring-early summer dinoflagellates' dominated assemblage. Instead, a prolonged summer assemblage characterized by diatoms has established during the past three years. Changes in patterns of certain HAB species were detected as well. *Pseudo-nitzschia calliantha*, for example, that was continuously present in the community from March to December in the 1990's, established a bimodal dynamic with early summer and autumn peak during the past years. The ongoing monitoring of HABs will answer the question, whether the shift towards phytoplankton community with less dinoflagellates and more diatoms is indicative of less frequent DSP events and more probable ASP outbursts.

PHYSICAL-BIOLOGICAL MODELING OF HABS

Peter J.S. Franks

The interaction of the organisms forming HABs with their physical environment is often a critical aspect of bloom development. Here I will explore how we can quantify these interactions in the form of mathematical equations that we can solve on the computer. I will begin with individual-based models of organism swimming behavior, turbulence and advection. I will then move to continuum models and investigate their coupling to physical forcings. These relatively simple physical-biological models can form useful null hypotheses for exploring bloom dynamics in the field, and are the basis for building more complex physiological and ecosystem models of HAB dynamics.

EVALUATING OBSERVING TECHNOLOGY FOR ECONOMICAL HAB PREDICTION AND DETECTION: A PILOT PROJECT IN MONTEREY BAY

S. Frolov, J. Bellingham, F. Chavez, K. Rajan, Z. Kolber, J. Kildow, S. Ramp, J. Ryan, C. Scholin and Y. Zhang.

Our ability to issue forecasts of HAB landfall is increasing with recent advances in observing technology: such as the Environmental Sampling Processor, the FlowCytobot, autonomous underwater vehicles, and advanced numerical models. However, the cost of the advanced observing technology can easily surpass the potential economic benefit of a HAB prediction. To control the cost of the HAB observatory, we are designing CANON—an agile observatory that integrates multiple observation types into a HAB warning system. We propose to control the cost of the CANON observatory design (and inadvertently the prediction accuracy) using economic valuation model, which will quantify the economic value of improvements in the HAB prediction accuracy.

A notional framework for CANON includes: (a) a low-cost screening method for detecting incubation of HABs, (b) an observation targeting method for improvement in HAB models, (c) a landfall forecasting model, and (d) an economic valuation model for HAB forecasts. In our pilot study presented here, we study how the intrinsic timescales of the biological and physical variability in Monterey Bay (estimated from numerical models and historic observations) determine the mixture of observational platforms required for detecting bloom incubation and for tracking the bloom development. Comparing the costs of the evaluated observation scenarios with the potential economic benefits from the improved HAB forecasts allows us to prioritize technology development for the future HAB forecasting system.

GREEN *NOCTILUCA SCINTILLANS*, A SUCCESSFUL MIXOTROPH IN SOUTHEAST ASIAN WATERS

Ken Furuya and Paul J. Harrison

Noctiluca scintillans which possesses a photosynthetic endosymbiont *Pedinomonas noctilucae*, commonly called "green *Noctiluca*", is one of the most recurrent bloom species in the Southeast Asian waters, particularly in Manila Bay, the upper Gulf of Thailand, and JakartaBay. In Manila Bay, green *Noctiluca* forms perennial red tides throughout the year, occasionally covering almost the whole bay. Green *Noctiluca* exhibits two nutritional modes according to laboratory studies on isolated clones: one requiring an external food supply and the other one is an autotroph. The latter grows photoautotrophically for many generations, but it also feeds on food particles. Phagotrophy promotes faster vegetative growth than autotrophy, and provokes sexual reproduction. Recent field studies show that bloom formation of green *Noctiluca* depends on active phagotrophy, and that it survives primarily on photoautotrophy under food-limited conditions. These observations lead to the hypothesis that progressive eutrophication in Southeast Asia provides a competitive advantage to green *Noctiluca* over co-existing species by increasing food availability. Furthermore, once it becomes dominant, its active grazing is expected to prevent population growth of co-existing phytoplankton. With these potential ecological advantages, green *Noctiluca* is a unique model organism to determine why some

mixotrophic species bloom in eutrophic waters.

SCALES AND DISTANCES IN BLOOM DYNAMICS
Patrick Gentien

The major differences between a biogeochemical model and a specific model of population dynamics are based on the assumption that one average species exists and on the Baas-Becking hypothesis (1936). This old tenet, stating that "*Everything is everywhere, but the environment selects*" has been implicitly used in classical niche-assemble theories as well as in classical biogeochemical models but has been rejected by opposing biodiversity theories. It appears that two classes of models exist depending or not on the need to define initial conditions: some examples concerning mainly cyst producing species are presented and discussed. As a result, some *Alexandrium* blooms may be confined to some estuaries. During the vegetative stage, the "swarmers" and "swimmers" strategies separate two phytoplankton groups which both exploit two different sets of ecological trade-offs. Biomass layers are mainly formed by motile cells which aggregate and grow in restricted layers gaining momentarily some competitive advantages. Sometimes, these layers are even restricted to a few miles on the horizontal. These 1-2 meters thick layers appear to be stable for durations of the order of a population characteristic time: a feature which is not easily reproduced by hydrodynamical models. Furthermore, it is argued that locally, biology influence physics at small scale. Many control processes are due to cell crowding and related to the intercellular distances rather than to concentrations. Some examples are presented. It is clear that most processes operating at small scale need further description; however, they should be considered in most of the HABs modelling exercises.

INDIVIDUAL-BASED MODELLING OF THE TRANSPORT OF *KARENIA MIKIMOTOI* ON THE SCOTTISH CONTINENTAL SHELF
P.A. Gillibrand, K. Davidson and P.I. Miller

In 2006, a large and prolonged bloom of the dinoflagellate *Karenia mikimotoi* occurred in Scottish coastal waters, causing extensive mortalities of benthic organisms. We present an individual-based model that was used to track the development and progression of the bloom around the Scottish coast. The model includes growth and mortality of *K.mikimotoi* cells, and incorporates upward (phototactic) vertical migration during daylight hours. Cells are transported by physical processes of advection and turbulent diffusion, using current velocities extracted from operational simulations of the MRCS ocean circulation model of the North-west European continental shelf. Vertical and horizontal turbulent diffusion of cells are treated using a random walk approach. The coupled hydrodynamic-algal transport model was used to simulate *K. mikimotoi* during June – September 2006; predictions being compared to remotely sensed chlorophyll concentrations and cell counts from coastal monitoring stations. Model results captured the qualitative pattern of bloom development and transport. In order to achieve this agreement, initial sub-populations of *K. mikimotoi* cells were specified on the continental shelf at three separate locations. We interpret this as indicating that the source population was transported northwards by the Hebridean slope current from where cells were injected onto the continental shelf by eddies or other transient exchange processes. The dependence of modelled algal growth was sensitive to water temperature and cell mortality. Improved modelling of future blooms will require more accurate and finer resolution hydrodynamic models, and better understanding and parameterisation of the growth, mortality and behaviour of *K. mikimotoi.*

EUTROPHICATION AND HABs: RECENT MODELING ADVANCES, CONTINUING CHALLENGES
Patricia M. Glibert

There is no doubt that coastal and estuarine waters worldwide are becoming increasing enriched with nutrients from human population growth along coastal lands, development in coastal watersheds of intensive animal production and cropland operations that use ever-increasing amounts of fertilizer, burning of fossil fuels and resulting atmospheric deposition of nitrogenous compounds, and, in many parts of the world, intensification of aquaculture. HAB species can be directly and/or indirectly stimulated by nutrient over-enrichment, but chronic, subtle effects can be equally important or even more important in HAB proliferation than the obvious effects of increased nutrient loads. Understanding how nutrient enrichment leads to proliferations of specific algal species is a complex issue and creates many challenges for modelers.

In this talk, a review of the approaches that are needed to model eutrophication and HABs will be presented. Beginning with global modeling of nutrient export, better quantitative estimates of nutrient loads are now available. These models need to be coupled with models that describe the range of physiological responses by different phytoplankton species and functional groups, and the interactions of other dynamic factors such as physics and grazing in controlling responses to cultural eutrophication by HAB and other algal populations. It is particularly challenging to understand, quantify, and model the *dynamic* physiology of algae in a *dynamic* environment. Too often parameters are developed from single-species, static culture conditions that are not representative of natural conditions.

CONCEPTUAL MODEL OF DEVELOPMENT OF *PHAEOCYSTIS GLOBOSA* BLOOMS IN THE UPWELLING WATERS OF SOUTH CENTRAL COAST OF VIETNAM
Doan-Nhu Hai, Nguyen-Ngoc Lam, Joachim W Dippner

Blooms of haptophyte algae in the southern central coastal waters of Vietnam often occur in association with upwelling phenomenon during southwest monsoon. Sometime the blooms cause damage in wildlife and cultures while other time, with lower magnitude, could have been hardly seen an obvious affect on natural

communities. Base on data sets of two years investigation on biology, oceanography, and marine chemistry, the present study suggest a conceptual model of the haptophyte *Phaeocystis globosa* success in the waters. At the beginning of the blooms, the upwelling and early rain supply nutrient, especially nitrate, to the water column, and the lower sea temperature would favour development of diatoms. During the blooms, nutrient consumption of diatoms reduce nitrate and silicate in the waters, pulse supplying phosphate from upwelling activity and lower temperature make *Phaeocystis globosa* become the best competition to diatoms. At the end of the *Phaeocystis* bloom free cells of this species may be a good food supply to stimulating another bloom of other dinoflagellate species, *Noctiluca scintillans*. During the blooms, phytoplankton decay on sea floor leading to remineralisation of bacteria which reduce dissolved oxygen to a very low concentration, and this condition favouring growth of nitrate-reducing bacteria.

IDENTIFYING APPROPRIATE SCALES AT WHICH TO MEASURE RHEOLOGICAL PROPERTIES IMPORTANT TO HAB DYNAMICS: DESIGNING THE RIGHT VISCOMETER

Ian R. Jenkinson

Previous models of the effects of water deformation, turbulence and rheological thickening will be revisited in the light of recent data, ideas and rheological expertise concerning granular and lumpy materials. It is important to treat each problem in relation to the scales (length, deformation rate, deformation forces, perhaps time) associated with it. Measurement of deformation and rheological properties in such materials are also functions of scales, and so appropriate scales have to be chosen to design the geometry of the measuring apparatus. In recent years ichthyoviscometers have been used to measure rheological effect produced by HAB-produced exopolymeric substances (EPS) on flow through fish gills. The approach, however, needs to be generalised to other problems, and the scales identified more explicitly. Such problems are:

Encounter dynamics among soft, lumpy flocs or in media of variable viscosity, associated with secreted EPS; Energetics of swimming, feeding, etc. in media modified by EPS. Modification of thin-layer stability through EPS-induced modification of Richardson number, viscosity and turbulence.

Having identified the appropriate scales, a rheometer (that measures both storage and viscous moduli) or a viscometer (that is simpler but confounds viscous and elastic moduli) needs to be designed that can measure the appropriate rheological properties at the appropriate scales. Ultimately, experimental observations are then required to validate both the data produced and the models in which they are used.

DEBORAH NUMBERS REVISITED: HOW THEY MAY APPLY TO HARMFUL ALGAE AND OTHER PLANKTON IN THIN LAYERS

Ian R. Jenkinson

Back in 1992, Jenkinson & Wyatt (*J. Plankton Res.*, 14: 1697-1721) proposed the Deborah number *De* to characterise processes taking place in deforming continua. For any given process taking place in a continuum, the Deborah number,

$$De = \lambda \backslash t$$

where *t* is the characteristic time of deformation of the supporting medium and λ is the characteristic time of the process under consideration. *De* << 1 corresponds to a functionally solid support and *De* >>1 corresponds a functionally deforming one. Apart from in flowing mountains (Deborah & Barak, c. 1100 BC, *The Bible, Judges*, Chap. 5), *De* has been used to explore mini-models of the following process in shear fields in aquatic *milieux*: i) dispersion of the (immotile) daughter cells resulting from cell division; ii) microzones of increased or decreased concentrations of dissolved nutrients and metabolites around non-motile cells; iii) encounter. Scales investigated corresponded to laminar flow, ("real", modelled or imagined) fully turbulent flow, and intermediate conditions. The authors aimed to stimulate research into modelling how plankton adapts to, selects, or changes the water-deformation regime in which it operates. One way plankton changes the regime is by using exopolymeric secretions (EPS), through managing their rheological (biomechanical) and selectively adhesive properties. Since the structure of EPS is generally scale-dependent and heterogeneous, input to scale-related modelling requires that we measure the viscosity and other rheological properties of EPS over appropriate ranges of scales.

MODELLING THE EFFECTS OF TEMPERATURE CHANGE ON PRIMARY PRODUCTIVITY-IRRADIANCE CURVES FOR THE TOXIC CYANOBACTERIUM CYLINDROSPERMOPSIS RACIBORSKII

Michael Kehoe, Kate O'Brien, Michele Burford, Alistair Grinham

Cylindrospermopsis raciborskii is a toxic cyanobacterium found in an increasing number of freshwater systems world wide. While *C.raciborskii* has been the subject of many ecological studies, there is currently not enough information to model growth or primary productivity of this species as a function of light, temperature and nutrients. In this study, the effect of temperature on primary production was determined for samples from a reservoir dominated by *C.raciborskii* (Lake Borumba, Queensland, Australia). Primary production-irradiance (P-I) curves were determined for incubation temperatures ranging from 20 °C to 32 °C. Four models were fit to the data: a mechanistic and two empirical P-I model, and one machine function learners (Random Forest and Support Vector Machine). Incubation temperature had a similar effect on the P-I curve parameters of each model, but only the mechanistic model was able to explain the effect of temperature in terms of physiological

parameters (electron turnover time and PSU damage rate). This study also demonstrates how uncertainty of the P-I parameters can be quantified through the application of multiple models to a single data set.

MODELING THE LIFE CYCLE OF COASTAL AND SHELF SEA PHYTOPLANKTON: DYNAMICS ON SEASONAL AND INTERANNUAL TIME SCALES

Alexandra Kroll and Inga Hense

Mass occurrences of harmful algae regularly occur in coastal regions and shelf seas. Prominent examples include the North Sea where harmful species like *Phaeocystcis*, *Prorocentrum*, *Chattonella* with high biomass suddenly appear. In the past mainly external factors have been made responsible for the outbreaks of harmful algal blooms. However, the life cycle of dominant organisms as a regulating factor determining the magnitude and duration of harmful algal blooms has been only insufficiently taken into account. Numerical models generally neglect the life cycle of the dominant organisms and hence show deficiencies in the representation of the seasonal cycle and interannual variability. This PhD project aims at an improved understanding of life cycle processes on phytoplankton bloom formation. Life cycle models of key organisms will be developed and tested in 1- and 3-dimensional frameworks. The results will lead to a more comprehensive view on the role of internal dynamics, e.g. of seed population on bloom formation.

HARMFUL ALGAL BLOOMING EVENTS IN SOUTH CENTRAL COAST OF VIETNAM: BIODIVERSITY AND PLANKTONIC COMMUNITY STRUCTURE CONSEQUENCES

Nguyen Ngoc Lam, Doan Nhu Hai, Nguyen thi Mai-Anh, Ho Van The and Nguyen Ngoc Tuong Giang

Blooms of a haptophyte, *Phaeocystis globosa*, in coastal waters of Binh Thuan Province have been recorded in 2002, 2005, 2006 and 2007. About 90% of animal and plant species in tidal reefs of Phan Ri Bay were eliminated by the bloom in July 2002. Lost was estimated to be over VND10 billion (ca. $US 650,000). During this bloom, low diversities of both phytoplankton and zooplankton were reported. Density of *P. globosa* reached $320 \cdot 106$ cells·l-1, and chlorophyll-a at 45.6 ±7.6 µg·l-1 in the bloom in 2005. In the bloom in September 2007, phytoplankton community with low species number as well as extremely low Shannon diversity index (0.09, log2) was also recorded. Cumulative dominance (k) analysis showed that phytoplankton community was very old and at senescence stage in comparison with a pre-bloom period. Difference between phytoplankton communities in the areas with and without dominance of *Phaeocystis* was 65.2 %. Dinoflagelates were more diverse at stations without *Phaeocystis* dominance while it was vice versa for diatoms. During the pre-southwest monsoon month (June 2007) phytoplankton species richness (61 - 99 species/station) and biodiversity (H'=2.99) were much higher compare to months with bloom. Calculation on abundance central to pennate diatoms ratio (C/P) clearly indicated affect of

Phaeocystis dominance. After the bloom in September 2007, plankton communities have gained back the level of species richness but the structure has been much modified. The C/P ratio was averaged to 7 and at most station it was close to 1. Community analysis showed phytoplankton assemblages at the most southern transect was more stable while the northern transects with bloom of *Noctiluca* and middle transects with some domination of *Phaeocystis* were less stable.

DEVELOPMENT OF A LOGISTIC REGRESSION MODEL FOR THE PREDICTION OF TOXIGENIC PSEUDO-NITZSCHIA BLOOMS IN MONTEREY BAY, CALIFORNIA

J. Q. Lane, P. T. Raimondi and R. M. Kudela

Blooms of the diatom genus *Pseudo-nitzschia* have been recognized as a public health issue in California since 1991 when domoic acid, the neurotoxin produced by toxigenic species of *Pseudo-nitzschia*, was first detected in local shellfish. Although these blooms are recurring and recognized hazards, the factors driving bloom proliferation remain poorly understood. Contributing to this, and hindering the develoment of robust forecasting tools, has been a lack of long-term field studies and/or deficiencies in the scope of environmental data included with field observations. For this study, we successfully developed predictive logistic models of toxigenic *Pseudo-nitzschia* blooms in Monterey Bay, California from a multi-project dataset representing 8.3 years of sampling effort. Models were developed for year-round use (Annual model) or for seasonal use (Spring model and Fall-Winter model). Chlorophyll a and silicic acid emerged as significant variables common to all models, while model-specific inclusions of temperature, upwelling index, river discharge, and/or nitrate provided further model refinpement. Sensitivity (specificity) of the Annual, Spring, and Fall-Winter models was 77% (78%), 75% (75%), and 89% (89%) respectively. Predictive power for 'unknown' bloom cases (i.e. future blooms) was demonstrated at 75% for all models. Our models out-performed chlorophyll a anomaly models applied to our dataset and performed comparably to, or better than, previously described statistical models for *Pseudo-nitzschia* blooms or domoic acid. The models presented here are the first to have been developed from long-term (>1.5y) monitoring efforts, and the first to have been developed for bloom prediction of toxigenic *Pseudo-nitzschia* species.

MODELLING THE 2008 ST-LAWRENCE ESTURAY RED TIDE (CANADA)

Le Clainche Y. , M. Levasseur , S. Roy and M Starr

Blooms of the toxic dinoflagellate *Alexandrium tamarense* are recurrent in the lower St-Lawrence estuary (LSLE, eastern Canada). During the summer of 2008, an unusually large bloom of *A. tamarense* occurred in LSLE causing the death of many fishes, birds and of several marine mammals. Fisheries and Ocean Canada scientists monitored the evolution of the bloom during this event and successfully tracked the trajectory of the patch using a hydrodynamical model of the estuary and

gulf of St-Lawrence. A biological model of *A. tamarense* was previously coupled to this hydrodynamical model to study the impact of the river plume dynamics on an *Alexandrium* bloom that took place in 1998 (*Fauchot et al., 2008*). We are planning to use this coupled physical-biological model forced with the summer 2008 meteorological and hydrological conditions to simulate the 2008 red tide and assess the role of precipitations and wind conditions on this exceptional bloom.

HIGH-RESOLUTION PLANKTON ECOSYSTEM MODELING
Marina Lévy

This lecture will show how high-resolution ecosystem modeling can complement field data to gain knowledge on the seasonal and sub-mesoscale evolution of an ecosystem. It will be based on the example of the POMME experiment, which took place in 2001 in the Northeast Atlantic (special issue of JGR, vol 110, 2005). I will start by presenting the construction and the validation of the model built for POMME. Then, the model will be used to : 1) evidence spatial variability at the scale of a few tens of kilometers. This variability could hardly be detected with the resolution of the POMME observations; 2) interpret this variability in terms of the forcing physical mecanism, and 3) derive regional budgets of primary production, export and carbon fluxes.

PLANS FOR A REGIONAL MONITORING, ALERT, AND RESPONSE NETWORK AND A REGIONAL FORECASTING SYSTEM FOR COASTAL CALIFORNIA, OREGON, AND WASHINGTON
Alan Lewitus

HABs have had significant ecological and socioeconomic impacts on the California, Oregon, and Washington coastal communities for decades, and their prevalence and impacts on living resources in this region have increased markedly over the last 10-15 years. Paralytic shellfish poisoning from *Alexandrium catenella* and domoic acid poisoning from *Pseudo-nitzschia* spp. have been major threats to commercially, recreationally, and culturally important fisheries, protected species (marine mammals and birds), and human health, affecting coastal communities in all three states. Several other HAB species are also widespread along the U.S. West Coast, and recent observations suggest possible future impacts. Effective mitigation of the West Coast HAB problem will require a regional holistic approach to coastal ecosystem management, and depend on Federal and state collaboration and coordination. Recognizing the need for regional coordination in researching and managing HABs, NOAA and the states of California, Oregon, and Washington (on behalf of the West Coast Governors' Agreement on Ocean Health) convened the *West Coast Regional Harmful Algal Bloom Summit* on 10-12 February 2009 in Portland, Oregon. Among the *Summit*'s outputs were plans for a *West Coast Regional HAB Monitoring, Alert, and Response Network* that would be driven by end user informational needs, and a *West Coast HAB Regional Forecasting System* as an extension of the *Monitoring Network* de-sign. Overviews of these regional plans are presented, including their benefits for ecosystem HAB management.

THE EFFECT OF N:P RATIOS ON THE GROWTH AND NITROGEN UPTAKE OF *PROROCENTRUM* SPP. IN TURBIDOSTAT AND MODEL SIMULATION
Ji Li and Patricia M. Glibert

The harmful dinoflagellates *Prorocentrum minimum* and *Prorocentrum donghaiense* were grown respectively in turbidostat, a continuous culture system, at steady biomass and maximum growth rates. Nitrate was the nitrogen (N) source of in-flow medium at 80 µM. Phosphate was the phosphorus (P) source, but its concentration was set to vary from low to high to make the ratio in the medium a gradient which covered from P limitation to N limitation. Nitrogen (N) uptake experiments were conducted using ^{15}N tracer techniques at each N:P ratio to estimate N-specific uptake rates (V, h^{-1}) of substrates (NO_3^- and NH_4^+). Ambient nutrient concentrations, intracellular N: P ratios and cell maximum growth rates were also measured at each N:P ratio. Both N uptake rates and growth rates were correlated to the ambient N:P ratios. Supported by the parameters from the experiments, a numerical model was developed to simulate the nitrogen dynamics and cell growth in the turbidostat. This model is modified from Droop's model, and simulates the process in which N is taken up into the cell and subsequently assimilated. Ambient N:P ratio is the key variable in this model.

EFFECT OF SALINITY ON VERTICAL DISTRIBUTION OF *NOCTILUCA SCINTILLANS* WITH PHOTOSYNTHETIC SYMBIONTS UNDER LABORATORY CONDITIONS
Thaithaworn Lirdwitayaprasit, Pornthep Chuabkarnrai and Chareon Nitithamayong

Field studies on red tides of *Noctiluca scintillans* with the photosynthetic symbiont *Pedinomonas noctilucae* in the Upper Gulf of Thailand and Manila Bay showed that vertical maximum of *N. scintillans* often occurred under the halocline layer below 10 to 15 meter depths where salinity was in the range of 26 to 28. These observations suggest that salinity may influence the vertical distribution of this organism. Then, we examine influence of salinity on vertical distribution of *N. scintillans* under laboratory conditions. A two layer system was produced in 3 acrylic tubes of 60 cm in height and 10 cm in diameter, with saline water (salinity 30) at the bottom overlaid by less saline water (salinity 10). A control was prepared without *N. scintillans* cells to find physical diffusion of 1 cm d^{-1}. About 2,000 cells of *N. scintillans* were added at the surface of a tube, while another 2,000 cells were added at the bottom of another tube. Cell density was counted every two hours for one day. Both tubes were exposed to a light-dark cycle of 12:12 hrs under light intensity of 70µmol $m^{-2}s^{-1}$. A major portion of cells in both tubes aggregated at a mixed layer whose salinity was about 25, indicating their preference of salinity at around 25. Based on this observation, further experiment using bigger tubes of 1.5 m long

and 20 cm in diameter with more layers of different salinities are now in progress. Dependence of cell size of *N. scintillans*, and density of the endosymbiont as well as swimming velocity and salinity preference are under examination. Results of these experiments will be discussed with an aim to model vertical distribution and migration of *N. scintillans* in the sea.

MODELLING THE SEASONAL BEHAVIOR OF TWO FUNCTIONAL GROUPS OF PHYTOPLANKTON IN A MEDITERRANEAN BAY
Clara Llebot, Yvette Spitz, Jordi Solé, Marta Estrada

Alfacs Bay is an estuarine bay located in NW Spain, as part of the Ebro river Delta. It has great interest due to the importance of its fishery and aquaculture industries. However, during the last decades, episodes of Harmful Algal Blooms have been repeatedly observed. Analyses of 14 year-long time series have shown a clear seasonal behavior of the two main functional groups of phytoplankton in the bay. Diatoms present a population peak in autumn while dinoflagellates are more abundant in winter and spring. Factors affecting the variability of the different phytoplankton assemblages include inputs of freshwater into Alfacs Bay, which occur from April to October and influence the amount of nutrients and the stability of the water column. We used a zero-dimensional N-PP-Z D model with two phytoplankton functional groups to explore the relationships between physico-chemical variability and the behavior of the two main phytoplankton groups in the Bay, with the aim of defining scenarios that can explain the alternation between these groups.

NUMERICAL MODELING OF THE JUAN DE FUCA EDDY – AN INITIATION SITE FOR TOXIGENIC *PSEUDO-NITZSCHIA* BLOOMS IN THE NORTHERN CALIFORNIA CURRENT SYSTEM
Amoreena MacFadyen, Barbara Hickey, Vera Trainer and Mike Foreman

Domoic acid (DA) poisoning, caused by a neurotoxin produced by phytoplankton of the genus *Pseudo-nitzschia*, has been a persistent problem in the California Current System (CCS) for at least the last decade. A survey of DA and *Pseudo-nitzschia* along the U.S. West Coast in 1998 suggested a strong relationship between toxin concentration and mesoscale topographic features, which modify regional flow patterns. One such feature is the Juan de Fuca Eddy, located at the northern end of the CCS. This region was the focus of a recent multi-disciplinary study: ECOHAB-PNW. The eddy was found to be a toxic "hotspot"; DA was detected in the eddy during multiple cruises over the 4-year study period. The eddy may also be an initiation site for toxic blooms that impact coastal Washington shellfisheries. As part of ECOHAB-PNW, numerical models were utilized to simulate the ocean circulation during and after field surveys and to investigate pathways of regional scale transport of *Pseudo-nitzschia* to the coast. Model simulations illustrate the seasonal growth of the eddy, which results in a broad region of high nutrients reaching ~100 km offshore by midsummer. Retention or es-

cape of surface waters (and plankton) residing in the eddy is determined by prevailing wind conditions; during periods of typical intermittent upwelling/downwelling winds, the eddy is very retentive to surface particles. These retentive circulation patterns combined with persistent nutrient supply may favor the development of toxigenic blooms. Ultimately, the exact sequence of wind conditions in late summer determines whether blooms in the eddy pose a threat to coastal fisheries.

OBSERVATIONS AND MODELS OF HARMFUL ALGAL BLOOMS IN THE GULF OF MAINE: FROM CLIMATOLOGY TO FORECASTING
Dennis J. McGillicuddy, Jr., Donald M. Anderson, Ruoying He, Bruce A. Keafer

Throughout the global coastal ocean, harmful algal blooms (HABs) are a serious economic and public health problem. In New England, the most serious HAB issue is paralytic shellfish poisoning, a potentially fatal illness that occurs when humans eat shellfish that have accumulated saxitoxins as they feed on the dinoflagellate *Alexandrium fundyense*. This organism has a complex life cycle, including a resting cyst that overwinters in bottom sediments and a planktonic vegetative phase during which blooms occur.

Climatological distributions of *A. fundyense* have been simulated by incorporating its population dynamics into a model of the seasonal mean flow. A model that includes germination, growth, mortality, and nutrient limitation is qualitatively consistent with observations. Cells germinated from cyst beds in the Bay ofFundy and offshore of mid-coast Maine are advected from east to west in the coastal current. Growth of vegetative cells is limited by temperature from April through June throughout most of the region, whereas nutrient limitation occurs in July and August in the western gulf. These factors cause the center of mass of the bloom to shift upstream in the coastal current as the season progresses.

In 2005, the western Gulf of Maine and southern New England were hit by the worst *A. fundyense* bloom to occur in at least 30 years. Numerical models have been used to hindcast this historic bloom and to investigate its causes. Sensitivity experiments distinguish the roles of three major factors: 1) high abundance of cysts in western Gulf of Maine sediments; 2) several strong storms with prevailing downwelling-favorable winds; and 3) anomalously large fresh water discharge entering the gulf due to abundant rainfall and heavy snowmelt. Our results suggest that high abundance of cysts in western Gulf of Maine was the main cause of the 2005 bloom.

These results suggest that cyst abundance could be a first-order predictor of overall bloom severity in the coming year. Observations in the fall of 2007 indicate cyst abundance off mid-coast Maine was 30% higher than it was preceding the historic bloom of 2005. An ensemble seasonal forecast predicted a severe bloom in the western Gulf of Maine, which was confirmed by both *in situ* observations of cell concentrations and toxicity measurements from coastal shellfish.

BIOMASS, PRODUCTION AND ECOLOGICAL ROLE OF *NOCTILUCA SCINTILLANS* IN THE COASTAL WATERS OF SAGAMI BAY, JAPAN

Hideo Miyaguchi, Victor S. Kuwahara, Tetsuichi Fujiki,, Norio Kurosawa, Tomohiko Kikuchi, Satoru Taguchi and Tatsuki Toda

Biomass and production of heterotrophic dinoflagellate *Noctiluca scintillans* were examined in the coastal waters of Sagami Bay, Japan from 1997 to 2006. In order to estimate the biomass of *N. scintillans*, the relationship between the cell volume and the carbon content was obtained as; C = 0.24 X Loge V – 3.71, where C is the carbon content per single cell of *N. scintillans* (μg C cell^{-1}) and V is the cell volume (μm^3 cell^{-1}). The growth rates of *N. scintillans* (μ) were also measured in the laboratory under different chl. *a* concentrations from 0.2 to 20 mg Chl. *a* m^{-3}. The relationship between *N. scintillans* growth rate and chl. *a* concentration could be approximated as: μ = 0.21 - 0.03 Chl. *a* $^{-1}$. The production of *N. scintillans* was estimated using this relationship and the measured biomass. The highest biomass was 294 mg C m^{-3} in May 2000. The biomass in 2000 was extremely high compared with other years. During the bloom period in spring, the biomass of *N. scintillans* overwhelmed the other-zooplankton biomass. The production of *N. scintillans* in 2000 reached 48 mg C m^{-3} d^{-1}. The production in the period was not only considerably higher than that of dominant copepods such as *Calanus sinicus, Paracalanus parvus and Acartia steueri*, but also the production was occupied the half of primary production; 83.5 mg C m^{-3} d^{-1} in this study area. These suggest that *N. scintillans* plays an important role in the carbon flux in the coastal waters of Sagami Bay.

EFFECT OF ENVIRONMENTAL PERTURBATIONS ON THE OCCURRENCE OF PHYTOPLANKTON BLOOMS DURING SOUTH WEST MONSOON IN A TROPICAL BAY

Jagadish S. Patil and Arga Chandrashekar Anil

Occurrence of phytoplankton blooms during south west monsoon in tropical estuaries is a common phenomenon. Earlier studies have shown that the oscillations in freshwater discharge during monsoon have a bearing in determining the nature of phytoplankton blooms. Based on monthly observations it was found that the prevalence of low saline waters in the surface during onset and restart of monsoon after an intermittent break coincided with diatom blooms. The break period in monsoon coincided with mixed species bloom of large-sized diatoms and harmful dinoflagellates under high-saline, nutrient-poor and transparent water-column. In such environment phytoplankton blooms often lasts only a couple of days and signatures of such blooms can only be ascertained by high resolution sampling. Keeping this in mind we carried out observations from a fixed station in Dona Paula Bay at 24 hour intervals from 24th May to 30th September. Phytoplankton cells were analysed live using FlowCAM and this effort is first of its kind from India. The chlorophyll fluorescence revealed 6 peaks during the observation period. Based on fluorescence data it is possible to perceive the maximum length of a bloom to be 6 days. Salinity fluctuations did differ blooming species and the blooming species were *Skeletonema, Chaetoceros, Thalassionema, Leptocylindrus, Odontella, Ditylum* and flagellates. It appears that the suspended particles influenced bloom formation. This presentation provides a basis for evaluating the consequences of changes in the intensity and frequency of monsoons increasingly observed in the recent years.

ESTIMATING PAST AND FUTURE GLOBAL CONTRIBUTIONS OF NITROGEN AND PHOSPHORUS FROM SHELLFISH AND AQUATIC PLANTS AQUACULTURE

Marcin Pawlowski

Over the past 40 year, the aquaculture industry has been steadily growing and in 2004 as much as 43% of the total harvest of aquatic plants and animals has been produced by aquaculture. The amount of nutrients released by these activities to the waters can be substantial. N and P can be particularly harmful, as these nutrients can further increase the likelihood of Harmful algal Blooms occurrence. Aquatic plants have the potential to absorb some of these nutrients. Shellfish aquaculture on the other hand will contribute to the stocks of nutrients in water, owing to feeding regimes and transformation of the nutrients contained in seston into dissolved forms available to algae. This paper will estimate the net contribution of shellfish and aquatic plants aquaculture to global N and P stocks based on production data and nutrient conversion rates. Four scenarios consistent with the MEA scenarios were developed in order to estimate the potential future N and P emissions up to 2050.

REGIONAL OCEAN MODELLING IN THE BENGUELA

P. Penven, N. Chang, J. Veitch, F. Shillington and the Vibes/ Idyle group.

During the past decade, a modeling effort has been conducted in the Benguela region. This was done for a better understanding of fish recruitment in the Southern Benguela, in the context of collaborations between IRD, UCT and MCM. This presentation is an attempt to summarize what has been done during this period.

A peculiarity of the Southern Benguela system in comparison to the other major upwelling systems is the direct effect of the large scale ocean on the shelves due to the proximity of the Agulhas Current. The first model attempts were focusing on the local forcing of upwelling and the shelf circulation. Recent models developments, such as the possibility of nested models, allowed to take into account large scale effects explicitly, while resolving coastal processes. The chosen strategy was to resolve the mesoscale dynamics of the greater Agulhas Current System, from its sources in the Mozambique Channel, and to use higher resolution nested coastal models for the Benguela or the the Agulhas Bank. With such modelling structure, it is possible to test the effects of the Agulhas Current in the coastal regions. This facilitates also the downscaling of large scale climatic signals in coastal regions. These models are also coupled to biogeochemical and fishery models.

MODELLING HARMFUL ALGAL BLOOMS IN UP-WELLING SYSTEMS: THE VALUE OF HYDRODY-NAMIC MODELS

Grant Pitcher, Claudio Marangoni and Pedro Monteiro

The enrichment of surface waters of eastern boundary upwelling systems supports high productivity and a high frequency of harmful algal blooms (HABs). The incidence and distribution of HABs within upwelling systems is related to the dynamics of the surface boundary layer in that the upper mixed layer is important in effecting the composition of phytoplankton communities and in that the fields of flow determine bloom transport and concentration. These processes can be simulated using dynamic circulation models. Within the temporal framework of upwelling various mesoscale features are found to interrupt typical upwelling circulation patterns, and are critical in influencing the dynamics and distribution of HABs. In particular the influences of coastline orientation and discontinuities on HABs are considered important through their influence on water stratification and retention. The value of hydrodynamic models in describing and predicting processes of relevance to HABs is demonstrated over a spectrum of coastline orientation and configuration, including banks and canyons, headlands, capes, peninsulas, rías, bays and estuaries, representing systems of increasing isolation from the open coast and consequent increasing retention times.

OPERATIONAL FORECASTING OF HARMFUL AL-GAL BLOOMS IN IRELAND

Robin Raine, Aoife Ni Rathaille, Caroline Cusack, Kieran Lyons and Joe Silke

Most harmful algal events within Ireland come about through one of two ways. Either a population of toxin producing species is physically transported from the continental shelf into a site used for shellfish culture or else a chronic infestation of a toxic species recurs annually in a bay due to a combination of the bay's retentive nature and an overwintering cyst stage in the life cycle of the species. Wind-forced transport of harmful species such as *Dinophysis* and *Karenia,* amongst others, can be predicted for the bays of southwestern Ireland as the precise sequence of shifts in wind direction which both force the currents and cause these infestations is known. The prediction is therefore based on the weather forecast, albeit having a similar range, using a fuzzy logic style approach. There is a high degree of physical forcing, through tidal dilution, which controls the onset of annual blooms of *Alexandrium minutum* in Cork Harbour. Knowledge of excystment, and the effects of irradiance and temperature on the growth of this species, combined with the relationship between tidal range and tidal dilution in the bay can be used to successfully produce a simple model which can successfully predict the onset of these blooms.

ECOLOGY AND OCCURRENCE OF HARMFUL AL-GAL BLOOMS IN ABU DHABI WATERS

Anbiah Rajan, Rajasekhar Thankamony and Thabit Zahran Al Abdessalaam

Harmful Algal Bloom incidents have been increasing world wide and becoming a growing problem to human health and environment. Increasing incidents of HABs along the Abu Dhabi coast have forced the Environment Agency Abu Dhabi to initiate a survey on harmful algal blooms (HABs) in 2002. Due to rapid development of industries and urban areas in Arabian Gulf bordering countries the amount of nutrient entering in to the marine environment has been increased, that enriched the marine environment and increase the number of bloom incidences. Potentially harmful species were detected in Abu Dhabi waters and the blooms were produced by both dinoflagellates and Cyanobacteria. During 2008 this arid subtropical area has been witnessed for 8 incidents, among them 6 were created by the *Tricodesmium erythraeum.* The water samples collected within bloom areas showed significantly higher nutrient values than the non bloom areas. The hydrographic parameters such as salinity, water temperature, conductivity, pH, and dissolved oxygen exposed variation between sites. Increasing anthropogenic activities and sand storms have been found to be the main factor determining the bloom formations. The consequences, mechanisms of impact and management of blooms are discussed in detail.

AUTOMATED DECISION MAKING FOR A NEW CLASS OF AUV SCIENCE FOR UPPER OCEAN PROCESSES

Kanna Rajan, Frederic Py and John Ryan

AUVs are an increasingly important tool for oceanographic research. However, control of these platforms has relied on fixed sequences for execution of pre-planned actions limiting their effectiveness for measuring dynamic and episodic ocean phenomenon. At MBARI, we have developed an advanced Artificial Intelligence based control system to enable our AUV's to dynamically adapt to the environment by deliberating insitu about mission plans. It does so while tracking a dynamic feature of interest, dealing with mission failures by allowing re-planning and being cognizant of vehicle health and safety in the course of executing science plans. Mission plans are synthesized onboard allowing for the vehicle to be driven by scientific opportunity rather than prior knowledge on shore. Our software system the Teleo-Reactive EXecutive (TREX http://www.mbari.org/autonomy/TREX/index.htm) has been deployed on an MBARI Dorado AUV with a range of scientific instruments for water-column surveys in Monterey Bay and has successfully tracked estuarine plumes and Intermediate Nepheloid Layers (INLs). Our long term goal is to see a marine robot which can be unshackled by predetermined transects and is responsive to a range of environmental signals for resolution both spatially and temporally for accurate 4D (space + time) models to be generated.

BIOLOGICAL OBSERVATIONS OF RELEVANCE FOR SPECIES-SPECIFIC MODELS OF LOW BIO-MASS HABs

Reguera B. and L. Velo-Suárez

Before any attempt is made to model the population dynamics of a HAB species, a conceptual biological model of its annual cycle and behaviour is essential. The origin of the *inoculum* has been in some cases closely linked to previously established cyst-beds, but in many others is unknown, and may well come from dispersed or aggregated overwintering cells; the physical-biological interactions that favour inoculation are key processes which need to be identified. Growth of the free living population can be followed with *in situ* division rate estimates complemented by routine monitoring observations; the nutritional mode of species (phototrophic, mixotrophic) and their behavioural patterns (vertical distribution, adaptations) need to be described on a species and location basis. Observations on life cycle transitions are possible, so far, in species with polymorphic life cycles or other peculiarities that allow recognition of their different stages. Grazing and mortality rates are very difficult to measure, and studies to elucidate the causes of bloom termination (dispersion, natural mortality, parasitism) are still in their infancy. A mismatch between good conditions for bloom initiation and bloom development may account for large interannual variability and unexplained bloom failures. Despite the complexity of biological processes and the difficulties to develop full life cycle predictive models, there are fortunately population-growth situations where major simplifications can be made, and where numbers are overwhelmingly controlled by physical forcing. Here we examine a few examples focusing on *Dinophysis* spp.

ENSEMBLE FORECASTING OF HARMFUL ALGAL BLOOMS IN THE BALTIC SEA

Petra Roiha, Antti Westerlund, Tapani Stipa

Operational marine environmental modelling has been considered notoriously hard, and consequently there are very few operational ecological models. Operational modelling of harmful algal blooms is harder still, since it is difficult to separate the algal species in models, and in general, very little is known of HAB properties. We present results of an ensemble approach to HAB forecasting in the Baltic, and discuss the applicability of the forecasting method to biochemical modelling. It turns out that HABs are indeed possible to forecast with useful accuracy.

For modelling the algal blooms in Baltic Sea we used FIMR's operational 3-dimensional biogeochemical model to produce seasonal ensemble forecasts for different physical, chemical and biological variables. The modelled variables were temperature, salinity, velocity, silicate, phosphate, nitrate, diatoms, flagellates and two species of potentially toxic filamentous cyanobacteria *nodularia spumigena* and *aphanizomenon flos-aquae*. In this work we concentrate to the latter two.

Ensembles were produced by running the biogeochemical model several times and forcing it on every run with different set of seasonal weather parameters from ECMWF's mathematically perturbed ensemble prediction forecasts. The ensembles were then analysed by statistical methods and the median, quartiles, minimum and maximum values were calculated for estimating the probable amounts of algae. Validation for the forecast method was made by comparing the final results against available and valid in-situ HAB data.

LAGRANGIAN VS EULERIAN MODELLING OF PHYTOPLANKTON PHOTOSYNTHESIS AND PHOTOACCLIMATION: LESSONS FROM A NEW INDIVIDUAL BASED MODEL

Oliver N. Ross and Richard J. Geider

Most large scale models rely on the Eulerian representation of phytoplankton as a continuous entity where the time averaging takes place before the time integration. The Lagrangian approach first integrates over time and then averages over the ensemble. While only the latter approach is mathematically correct, the former has been used quite successfully to describe certain properties of phytoplankton dynamics in the ocean. We will present the results from our recent work where we developed a new phytoplankton photosynthesis and photo-acclimation model, for particular use in individual based modeling approaches. With the help of this model we can show that the Eulerian approach delivers significantly different growth rates and acclimation states in the cells, not only in the deep mixed layers which are characteristic of winter and early spring at moderate to high latitudes, but also in the more shallow mixed layers which can be observed during the spring bloom and in summer. This result is expected to be of interest to the large scale modeling community, who usually favours the computationally less expensive Eulerian approach, as it will have direct impacts on the carbon budgets derived from their models.

MULTIDISCIPLINARY OBSERVATIONS OF A PHYTOPLANKTON BLOOM INCUBATOR IN THE CENTRAL CALIFORNIA CURRENT SYSTEM

J.P. Ryan, C.A. Scholin, R.M. Kudela, J.F.R. Gower

Recent studies show that the 'upwelling shadow' of Monterey Bay, California functions as a incubator of extremely dense dinoflagellate blooms, including species that can cause harm via effects of toxins and high-biomass. Additionally, highly concentrated 'thin layers' of potentially harmful dinoflagellates and diatoms are observed in this relatively stratified environment. Lagrangian drifter studies show that this bloom incubator region regularly exports blooms along the coast in response to variable wind forcing. We examine biological variability and oceanographic dynamics of this bloom environment by integrating unique multi-scale, multidisciplinary observations. Orbital and suborbital remote sensing of high spatial and spectral resolution reveal climatological and synoptic patterns of 'red tide' bloom development. These observations also show a repeated pattern of bloom inception at estuarine and riverine outflow sites following the onset of seasonal rains, indicating a potential role for agricultural land drainage in bloom genesis. Time-series observations from a highly

capable autonomous underwater vehicle (AUV) describe the unique environment of the bloom incubator as well as physical forcing of bloom development. Monitoring of HAB species and toxins by the Environmental Sample Processor (ESP) reveals tremendous high-frequency variability related to oceanographic processes observed in situ by moorings and AUV, and by remote sensing. We apply extensive observational studies of Monterey Bay to define key observing and modeling requirements for advancing understanding and prediction of HAB phenomena in the central California Current System, and we extend these results to indicate similar requirements for regions of other eastern boundary upwelling ecosystems.

A COUPLED PHYSICAL-BIOLOGICAL PREDICTION SYSTEM FOR THE NORTH ATLANTIC AND THE ARCTIC OCEAN
Annette Samuelsen, Cecilie Hansen, and Laurent Bertino

As part of a European initiative to establish marine forecasting systems in the oceans and seas surrounding Europe a coupled physical-biological prediction system is set up for the Arctic and North Atlantic Ocean. The physical model used is the Hybrid Coordinate Ocean Model (HYCOM) and the ecosystem model is the Norwegian Ecological model system (NORWECOM). The ecosystem model includes three nutrients (nitrate, phosphate, and silicate), two phytoplankton functional groups (flagellates and diatoms), oxygen, detritus, and biogenic silica. The model does not include zooplankton as a separate group, but grazing mortality is included as a parameterization. This system is planned to be ready for operational demonstration mode in 2011. Here, results from a reanalysis for the spring and summer of 2007 are presented. The reanalysis was run online, restarting from analyzed fields (result after data assimilation) every seven days. The results were evaluated with respect to satellite-derived chlorophyll concentration and available in-situ data with focus on the North Atlantic and Arctic Ocean. The modelled winter-concentrations of chlorophyll were on the low side, while summer chlorophyll concentrations were too high. At the same time nutrients concentrations were generally too low during summer. This indicates that it is the lack of grazing rather than excess nutrients that is responsible for high summer chlorophyll concentration.

HABS AND SUCCESSION: WHAT HAVE LONG-TERM STUDIES REVEALED?
Ted Smayda

Succession is a term borrowed from terrestrial ecology applied to the replacement of phytoplankton species and functional groups by other species and functional groups. The use of the term succession as applied to the phytoplankton; the distinction between succession as a process vs. as a descriptor of species changes; and the problems encountered in quantifying succession and its underlying environmental drivers are discussed. The types and processes of phytoplankton species replacements that occur will be illustrated using long-term data sets, and tested against the various conceptual models of phytoplankton succession that have been proposed. The emergence of HAB species within coastal successional cycles is of special interest, and is contrasted with diatom species replacement behavior and strategies.

LIFE CYCLES/POPULATION DYNAMICS OF ZOO-PLANKTON AND DINOFLAGELLATES
Sourisseau M.

The zooplankton population dynamic is broadly known for several key species due to the observations and experimental processes measurements over the past 20 years. The well-developed copepods population dynamic models (PDM) converge to the same structure, with a life cycle divided into developmental stages more or less aggregated. These PDM succeed in several area to simulate the main spatial and temporal patterns of copepods dynamic. They permit to highlight the key role of the organisms behaviour and several critical steps in their life cycle. In comparison, dinoflagellates PDMs also divide the life cycle into stages depending on cells characteristics (temporary or resting cysts, haploid or diploid cells, sexual or asexual reproduction, gamets and planozygots, ...). These models however can not always include all the transfer processes and stages of the life cycle since some of them are still unknown for a lot of dinoflagellates species. Only few complete PDM for dinoflagellates species are available. Major part of models dealing on dinoflagellates should be indentified as vegetative cells growth model. The models structure is thus widely variable according to the considered species and its associated knowledge. A non-exhaustive review of the sensitivity of these PDMs to the behaviour cells and to several crucial processes indiquate the next biological observations required for a better understanding of their population dynamics.

INTEGRATING MODELS AND OBERVATIONS TO FORECAST HARMFUL ALGAL BLOOMS
R.P. Stumpf, M.C. Tomlinson, T.T. Wynne

NOAA has developed some operational and demonstration forecasts of HABs and their impacts. These include forecasts involving *Karenia brevis* along the eastern and western coasts of the Gulf of Mexico, and cyanobacteria in Lake Erie. Both of these HABs pose public safety concerns for recreational users, as well as for shellfish (*Karenia*) and drinking water (cyanobacteria). Nowcasts and forecasts involve a combination of strategies. *K. brevis* is capable of producing aerosols, and poses a particular risk when these aerosols reach the shore. Cyanobacteria pose a risk when it concentrates near the surface. Identifying when and wblooms that can be observed visually or from satellite, so ocean color imagery is an integral part of the detection system. Heuristic models incorporate additional data are used to identify and constrain the bloom field, and also to generate the forecasts. Forecasts include transport models (that may be coupled with numerical circulation models), and also models pertaining to the ecological conditions that indicate likelihood of harmful events or conditions. Creating a heuristic strategy leads to "standard operating

procedures" (SOPs) that are necessary to produce consistent forecasts that can be validated. Ultimately, these SOPs and the associated heuristic models may be automated through rule-based software systems.

APPLICATION OF SATELLITE DATA ON RESEARCH OF HAB OCEANIC DYNAMICS

DanLing Tang, XX Yang, JJ Wang

HAB is one of the most serous oceanic problems in China and in the western South China Sea (SCS). This paper review application of satellite data on research of HAB Oceanic dynamics. Satellite remote sensing data of ocean color, sea surface temperature (SST), wind data, and in situ observation of phytoplankton species and ocean condition were applied in the analysis. The results show that in the western SCS, upwelling along the coastal water can induce HAB by bringing nutrients from the deep ocean to the surface water in southwester wind season. In the coastal region of north SCS, nutrients from land and aquaculture are the major nutrient source inducing HAB. Typhoon could also induce HAB in some cases, by influencing temperature, nutrients distribution and other oceanic conditions.

A FUZZY LOGIC MODEL TO DESCRIBE THE CYANOBACTERIA *NODULARIA SPUMIGENA* BLOOMS IN THE GULF OF FINLAND, BALTIC SEA

J. Laanemets, M.-J. Lilover, U. Raudsepp, R. Autio,, E. Vahtera, I. Lips and U. Lips

A fuzzy logic model to describe the seasonal evolution of *Nodularia spumigena* blooms in the Gulf of Finland was built and calibrated on the basis of monitoring data. The model includes three phosphate sources: excess phosphate after the annual spring bloom and parameterised phosphate transport to the upper mixed layer by turbulent mixing and upwelling events. Surface layer temperature and wind mixing form the physical conditions controlling the growth of *N. spumigena*. Model simulations revealed that phosphate input caused by turbulent mixing and upwelling have to be taken into account to achieve the best fit with observed data. Testing the fuzzy model for early prediction of maximum *N. spumigena* biomass about a month before the usual occurrence of blooms, gave good results. The potential use of the model for prediction of bloom risk at a certain location along the Estonian or Finnish coast was tested. The bloom transport velocities used in the fuzzy model were pre-calculated by a 3D numerical circulation model for different wind regimes.

EQUILIBRIUM DYNAMICS OF THE NORTHERN AND SOUTHERN BENGUELA SYSTEMS

J.A. Veitch, P. Penven, F.A. Shillington

The Benguela system is one of the four major eastern boundary current (EBC) systems of the worlds oceans. It is unique among EBC systems in that, not only its equatorward, but also its poleward boundary is marked by a warm water regime. The Regional Ocean Modelling System (ROMS), forced with climatological QuikSCAT winds, is used in this study to improve the understanding of the equilibrium dynamics of the BCS. The BCS can be divided into northern and southern regimes, based on distinct dynamic as well as topographical differences. Topographically, the division between the northern and southern regimes coincides with an abrupt narrowing of the continental shelf at ~28°S. The dynamic manifestation of the divide is associated with an upwelling-favourable wind stress maximum, an alongshore offshore transport maximum and a stratification discontinuity on the shelf (i.e. more stratified in the south). A modeling experiment in which the coastline and continental shelf have been straightened suggests that the wind is a primary forcing mechanism for this divide. Characteristic of the northern Benguela system is a deep poleward current that is most intense between ~10-400 m and tends to follow the orientation of the shelf-edge. This poleward current advects water of tropical Atlantic origin into the northern Benguela system. A topographical control exists in the southern Benguela system such that the position of the upwelling front and the path of the Benguela Current closely follow the orientation of the shelf-edge. The distinct northern and southern areas of the Benguela provide a good platform for a comparative study of upwelling regimes within one system and one model simulation.

THREE MODELS OF DINOPHYSIS POPULATION DYNAMICS

L Velo-Suárez, B. Reguera, T. Wyatt, J.C. Gutiérrez-Estrada, P. Lazure and P. Gentien

Blooms of toxin-producing species of *Dinophysis* are recurrent events in Europe, SE Asia, New Zealand and in the Chilean Fjords. Models provide important tools for understanding their population dynamics and predicting blooms in shellfish exploitation areas. Here we describe three models of *Dinophysis* that have been developed in different contexts. i) Retention zones and other small-scale hydrodynamic structures on the Bay of Biscay shelf have been investigated as incubators for *Dinophysis acuminata* populations. The advection/dispersion of *Dinophysis* in the area has been analyzed with *Ichthyop*, a Lagrangian tool developed to study the influence of physical and biological factors on plankton dynamics. It uses three-dimensional fields of velocity, temperature and salinity archived from simulations of 3D hydrodynamic models run with realistic forcing. ii) The contribution of division rates to *Dinophysis* spp. population dynamics in the Rías Baixas (Spain) has been analyzed with a simple biological model which highlights the balance between gains and losses due to biological and physical processes. iii) Artificial neural networks (ANNs) have been successfully used to model *Dinophysis acuminata* blooms on the southwest coast of Spain. These models can be used as forecasting tools, which could complement HAB monitoring programs.

While deterministic models contribute to a better understanding of the population dynamics of *Dinophysis*, they have not yet provided potent predictive tools. Alternative modelling approaches, such as ANNs, are currently in progress as a valuable predictive tool in environmental sciences. Nevertheless, ANNs are "blackes boxes" and

do not provide information on the mechanisms involved in bloom development.

LONG TERM TRENDS IN COASTAL PRODUCTIVITY IN THE PHILIPPINES

Cesar Villanoy, Laura David, Aletta Yniguez

Harmful algal blooms are a regular occurrence in some parts of the Philippines. Such blooms have been attributed to increased euthrophication of coastal waters from nutrients discharged from the watershed either through surface and/or groundwater. Anthropogenic activities from agriculture to mariculture are also contributing to this nutrient loading. Satellite data for sea surface temperature and chlorophyll pigment concentration and possibly rainfall patterns over the past two decades will be analyzed for long term trends and patterns in variability. The objective is to classify the different coastal areas around the Philippines with regards to potential vulnerability to climate change. Nutrient loading and coastal hydrodynamics will be incorporated into a coastal ecosystem model focusing on the primary producers.

OCEANOGRAPHIC CONDITIONS AFFECTING AUTUMN DINOFLAGELLATE HABs OFF WESTERN IBERIA

Manuel Ruiz Villarreal

North-West Iberian waters are frequently affected by HABs during the autumn transition to downwelling-favorable winds. Different hypothesis have been put forward to explain the development of these HABs: germination of resting cists, latitudinal progress in microplankton succesion and along-shore northwards transport. Most of these hypothesis rely on inferences from scarce physical data. In this contribution, I will review the knowledge on circulation in the area during the autumn transition in this EBC area.

I will present hydrodynamical model simulations of the conditions on the shelf and slope during episodes of strong dynoflagellate HABs, when concentrations of toxic dynoflagellates are specially high. Specific oceanographic conditions shape a habitat favorable for dynoflagellate blooms, which can be characterized with numerical simulations. The results indicate the presence of stratification and northwards advection on the shelf, and strong variability of shelf circulation in response to wind events and variations of the shape and depth on the shelf. Comparison of mean modeled shelf circulation with the chronology of proliferation of toxic cells could support the hypothesis of a nothwards along-shore transport, while cross-shore transport is associated to detection of toxins in coastal monitoring stations.

PRELIMINARY ANALYSIS OF INFLUENCES OF PHYSICAL PROCESSES ON PHYTOPLANKTON COMMUNITY STRUCTURE AROUND THE LUZON STRAIT

Jiujuan Wang, Danling Tang, Yi Sui[2], XinFeng Zhang

The Luzon strait, connecting the Western Pacific Ocean (WPO) to the South China Sea (SCS), is an important channel with complex hydrological condition. This paper presents preliminary analysis of the community structure of phytoplankton using in situ observations and remote sensing measurements, and statistic models. The results indicated that phytoplankton biomass was closely associated with the oceanic conditions, the interaction of biological and physical process is vital to structuring the biological communities in the open ocean. The spatial heterogeneity of phytoplankton populations in the vicinity of Luzon Strait were regulated by the steering of physical processes (upwelling, internal waves, meso-scale eddies, etc.), which play a significant role together in providing nutrients below the thermocline throughout the euphotic zone, and consecutively influence the structure of phytoplankton communities. The present observations and explanations of the active area of high primary productivity in the southwest of Luzon strait may provide insight on the contribution of different physical forcings to biological processes in the ocean.

SHIFTING CONTROL MECHANISMS – A MANIFOLD MODEL

T. Wyatt

Logistic growth models lead to the expectation that changes in population numbers occur smoothly, and that there is only one stable positive equilibrium. Many reports of exceptional algal blooms indicate that population densities are sometimes very high, and that these high numbers are achieved more rapidly than elementary models allow. Such sudden changes in abundance have the appearance of what mathematicians call bifurcations, in which the dependent variable moves so far from one stable equilibrium that it can jump or escape to another. The logistic with its single equilibrium does not provide this option, but we can turn to a model in which local population dynamics are represented by an equilibrium *manifold*. In a simple manifold, we recognize two stable positive equilibria, which we can call endemic and epidemic respectively. The escape to epidemic numbers depends on the relative values and characteristic time scales of the regulatory processes, the growth and loss terms; any process which temporarily decouples them, such as a mixing event, can promote such an escape. The unstable equilibrium of the manifold is thus an escape threshold separating two domains of attraction.

ALGAL BLOOMS IN HONG KONG WATERS ARE REDUCED BY PHYSICAL AND CHEMICAL FACTORS

Jie Xu, Paul J. Harrison and Kedong Yin\

The Pearl River Estuary is a sub-tropical estuary, the second largest in China and the 13th largest in the world. It is a fascinating study site since processes vary along a spatial gradient from the estuary (eutrophic) to coastal (low nutrients) and temporally (monsoon driven wet vs dry season). In the wet season, the SW monsoon winds push the Pearl River estuarine plume into Hong Kong waters and hence eutrophication impacts are a combination of nutrient loads from the Pearl River plus local sewage discharge. Eutrophication is not as severe as one would expect from these very high nutrient loads. This estuary shows a remarkable capacity to cope with excessive nutrients. Physical processes such as river discharge, tidal flushing, turbulent dispersion, wind-induced mixing, estuarine circulation and a shallow water column play important roles in controlling the production and accumulation of very high biomass algal blooms (often > 25 µg Chl/L) and the subsequent potential occurrence of hypoxia. Superimposed on the physical processes of the estuary are the chemical and biological processes involved in the production of algal blooms. For example, the 100N:1P ratio of estuarine waters indicates that phosphorus potentially limits the amount of algal biomass (and potential biological oxygen demand) in summer. While extended periods of hypoxia are rare in Hong Kong waters, episodic events have been reported to occur during late summer due to factors such as low wind, high rainfall and river discharge which result in strong density stratification that significantly dampens vertical mixing processes.

OCEANIC TURBULENCE AND PHYTOPLANKTON DYNAMICS

H.Yamazaki, T.Nagai, M.Doubell and C. Locke

We present the nature of oceanic turbulence making use of observed data and how microscale fluid motions affect planktonic organisms. Then Lagrangian simulations are introduced to model phytoplankton dynamics in turbulent water column. In order to link the models we also introduce observed patterns between mixing and phytoplankton dynamics. Finally, we present recent development in microstructure instrumentation to measure micro-scale fluorescence field. In addition to the fluorescence field, we have successfully mounted a mini-camera system that resolves less than mm scale optical images. These new findings are presented with a potential future simulation approach.

OCEANOGRAPHIC PROCESSES AND RED TIDES IN HONG KONG WATERS

Kedong Yin

Hundreds of high biomass red tides have occurred in Hong Kong waters during 1983 to 2001, and show a clear spatial and temporal distribution. Most (74%) occurred in semi-enclosed northeast bays away from the Pearl River estuary, and fewer occurred in western estuarine waters. Most red tides (>70%) occurred between December and May, and fewer in summer. However, nutrients are high in the Pearl River estuary, whereas nutrients are generally low in the northeast bays and cannot support the high biomass of red tides. This suggests that the formation of red tides in Hong Kong waters is due to factors other than nutrients. The spatial and temporal distribution pattern of red tides was thought to be linked to the Southeast monsoon and Pearl River outflow induced physical processes which set up residence times of the semi-enclosed waters and nutrient regimes (nutrient concentrations and nutrient ratios). The residence time in the semi-enclosed bays is longer during northeast monsoon which induces downwelling and shorter during southwest monsoon which results in upwelling. In general, dinoflagellate red tides occur mostly in April when Si is low, whereas diatom red tides occur in June when Si increases due to the freshwater discharge. Deep oceanic water on the continental shelf is drawn into the NE bays during the upwelling; it is poor in nutrients, and hence does not favour the strategy of vertical migration by dinoflagellates for the acquisition of nutrients in deep waters.

STUDY ON HAB FORECASTING IN COASTAL WATER OF QINGDAO BY MULTIVARIATE GREY MODEL (MGM(1,N))

Yongquan Yuan and Zhiming Yu

According to research on pattern and trend of HAB in the typical coastal water of Qingdao by a long-term monitoring data from 1990 to 2007, some special species, such as *Skeletonema costatum* and *Mesodinium rubrum* are believed to be dominating species in most cases, meanwhile, abundance of dominating species in each HAB case is highly-correlated with some easily-quantified environmental factors obviously. Therefore, HAB cases in such area seemed to be possible forecasted basing on some significant factors that could be monitored in routine survey. In this paper, we initially use Canonical Correspondence Analysis (CCA) and Grey Relationship Analysis (GRA) to analyze the statistically relationship between *Skeletonema costatum* abundance and 17 environmental variables by HAB monitoring data in 2007, as a result, wind direction and PO4-P concentration are determined as significant variables. Provided by the results of CCA and GRA, a Multivariate Grey Model (MGM(1,N)) is established to forecast *Skeletonema costatum* HAB in the target area by significant variables mainly. According to the residual-revision predication precision test, this model is proved feasible and valid.

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Modeling of HABs in Eutropic Systems

Reproduced with permission from Glibert, P.M., Allen, J.I., Bouwman, A.F., Brown, C.W., Flynn, K.J., Lewitus, A.J. & Madden, C.J. (2010). *Modeling of HABs and Eutrophication: Status, Advances, Challenges. J. Mar. Systems doi:10.1016/j.marsys.2010.05.004. Elsevier.*

Modeling of HABs in Stratified Systems

Figure 2. Thin layer formation from velocity shear

Reproduced with permission from Stacey, M. T., McManus, M. A., & Steinbuck, J. V. (2007). Convergences and divergences and thin layer formation and maintenance. *Limnology and Oceanography, 52*, 1523-1532. American Society of Limnology and Oceanography.

Figure 3. Plot of the chlorophyll distribution (colours in µg L^{-1}) and temperature structure (contoured in °C).

Yamasaki, H., Honma, H., Nagai, T., Doubell, M., Amakasu, K., & Kumagai, M. (2010). Multilayer biological structure and mixing in the upper water column of Lake Biwa during summer 2008. *Limnology, 11*, 63-70.

Figure 4. The distribution of the rate of the kinetic energy dissipation (colours in W kg^{-1}) with overlying chlorophyll concentrations

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Modeling of HABs in Upwelling Systems

Figure 5. Expansion by upwelling favourable winds during 5, 6 and 7 December (Case 3).

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Figure 8. A 40-year time series of offshore Ekman transport, -QX (where A0 is the annual average -QX) on the Iberian coast, and (B) the number of days per year for which a given mussel cultivation area in the Rías Baixas is closed to harvesting in relation to the renewal time for each area.

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