REPORT OF THE

STUDY GROUP ON MODELLING OF PHYSICAL/BIOLOGICAL INTERACTION

La Rochelle, France
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1   INTRODUCTION

Modelling physical/biological interactions is a growing field which is at the centre of much of the fisheries oceanography research around the world and is a core topic of international programmes such as GLOBEC (Global Ocean Ecosystem Dynamics) and GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms). Even the new international programme SOLAS (Surface Ocean Lower Atmosphere Study) which focuses on the interaction between the atmosphere, climate and marine biogeochemical processes contains important elements of physical/biological interactions.

The Study Group on Modelling of Physical/Biological Interaction (SGPBI) was established at the 88th Statutory Meeting (September 2000) under Council resolution C.Res2000/2C02, and with the following terms of reference:

a) review capabilities of existing coastal models and to consider the incorporation of biological processes and the comparison with measurements of species specific distributions and small scale structures;

b) propose a strategy for continued model development for the understanding and forecasting of physical/biological/chemical interactions (e.g., single species blooms and contaminants);

c) review existing observational methodologies to support modelling and understanding of physical/biological interactions.

Shortly after the endorsement of this Resolution the Chair of the Group (F. Saucier, Canada) resigned. C. Hannah (Canada) agreed to act as interim Chair for this meeting. The Group agreed to him being formally installed as Chair for the next three meetings. This appointment will be ratified by the Oceanography Committee at the Oslo Statutory Meeting.

This is the report of the first meeting of the SGPBI in La Rochelle, France from March 5–7, 2001.

The report is structured as follows. The concrete recommendations are given in Section 2 and the conclusions derived from the discussions are presented in point form in Section 3. The discussions are summarized in Sections 4, 5 and 6 and some final comments are made in Section 7. A list of participants and the extended abstracts from the presentations are given in Annexes 1 and 2 respectively.

2   RECOMMENDATIONS

•   A major workshop in Summer/Autumn 2003 on 'Future Directions for Modelling Physical/Biological Interactions in the Ocean', possibly co-sponsored by GLOBEC and GEOHAB. The chairs, location and dates will be settled in time for a resolution at the 90th Statutory Meeting (2002).

•   The second meeting of the Study Group should be in March 2002 to review the strategy and plan the workshop. The location and other details will be settled in time for a resolution at the 2001 ICES Annual Science Conference.

•   The third meeting of the Study Group should immediately follow the workshop to review the results of the workshop and further develop the Strategic Plan.

3   CONCLUSIONS

1) For the purposes of this Study Group, modelling is restricted to organisms (such as plankton) where the behaviour is physiologically driven. We chose not to deal with complex-adaptive systems such as adult fish.

2) Priorities for R&D aimed at improving ecosystem models, which are designed to be useful in practical applications, depend on accurate analysis and ranking of the sources of errors in those models. The community needs to develop methodologies for estimating errors associated with approximations in physical/biological models.

3) Methodologies are required for dealing with multi-scale problems, such as interactions in thin layers (horizontal and vertical). Techniques, such as adaptive and embedded grids, should be borrowed from other fields, e.g., the stratospheric ozone problem and engineering combustion problems.

4) Methodologies are required for aggregating species into functional groups depending on the problem. These methods should account for the fact that as the biological and physical environment change the relative abundance of the species in the group may change and this will change the aggregated rate parameters.

5) Circulation models are required to provide 3D fields of velocity, temperature, salinity and nutrients as a background for the physical/biological interactions. Comprehensive 3D circulation models that include the full

tidal spectrum, meteorological forcing, and the 3D structure of the temperature, salinity, velocity and turbulence fields are required for serious study and application of physical-biological interactions on the continental shelf.

6) The present state-of-the-art in coupled 3D physical-chemical-biological models are very useful, although they are limited in many and varied ways. These types of models are providing a framework for research into physical/biological interactions and in some cases are providing useful information for management. The community has not yet pushed these models to their full potential and their continued development and application is encouraged.

7) Modelling physical/biological interactions is plagued by the 'microcosm effect' whereby models and parameters derived in the laboratory do not survive scaling up to the oceanic environment. There is a need for models (biological equations) which are sufficiently complete that the parameter values can be determined by laboratory experiment and used in the ocean. We call such models the 'Biological Primitive Equations'.

8) The details of the physical-biological interactions are the result of the interaction of individual organisms with their environment. Logically the model structure should also be based on individual organisms. This avoids the well know bias arising from $\overline{A \times B} \neq \overline{A} \times \overline{B}$. Therefore, a priori, we expect that individual based modelling will play a central role in the future of modelling physical/biological interactions at all scales.

9) Validation, both in the laboratory and the field, is an essential part of establishing model credibility. Comparative ecosystem studies are an important component of validation because it is impossible to study ecosystems under completely controlled conditions and there are biases that occur when extrapolating from mesocosm studies.

10) The ability of organisms to adapt to the local environment needs to be addressed in future models and experiments. Care should be taken that the experimental strain properly represents the population modelled.

11) The number of plankton species for which even rudimentary models can be constructed is only a small fraction of the total. There should be increased effort towards determining the basic equations and parameters, which govern the physiology and behaviour of a significant fraction of the planktonic species.

4   DISCUSSION

The meeting opened with comments from the Chair on the wide spectrum of topics that fall under the heading of modelling physical/biological interactions. He indicated that one of the goals of the meeting was to define a focus for the Study Group on Modelling Physical/Biological Interaction (SGPBI). The presentations and discussion covered an even wider range of topics than the Chair had imagined. Nevertheless the discussions were fruitful and general themes emerged.

This report on the discussions of the Study Group is organized by themes rather than by the chronology of the discussions.

4.1   The Physical Environment

The most basic theme was that the biological activity takes place in an environment dominated by physical processes (such as temperature, advection, and turbulence). Therefore accurate simulation of the physical environment is required: velocity, temperature, salinity, turbulence, large-scale nutrient fluxes, etc. The question of how accurate the physical simulations need to be, is an open question and clearly problem dependent. The errors associated with not modelling processes such as transient structures, meso-scale turbulence, and thin layers in the horizontal and vertical have not been quantified.

From the perspective of this Study Group, the present generation of 3-D shelf circulation models, while not perfect, are good tools for providing estimates of 3-D fields of velocity, temperature, salinity, and turbulence for the continental shelf and near-shore zones. The utility of these estimated fields is greatly enhanced if the circulation model is part of a operational system which uses all the available observations to provide the best possible estimates, via various forms of data assimilation. The system should include the full tidal spectrum, meteorological forcing, and the 3-d structure of the temperature and salinity fields. This type of system is the entry-level system for serious study and application of physical-biological interactions on the continental shelf.

The recent papers by Haidvogel and Beckmann (1998), Greatbatch and Mellor (1999) and Griffies *et al.* (2000) provide reviews of the capabilities of ocean circulation models for applications on the shelf and the deep ocean. There are many models suitable for incorporating biological processes and there is no need for this Study Group to provide a review.

4.2 Complex Adaptive Systems

Some species, such as humans, have the ability to change the rules that govern their behaviour when circumstances change. This makes it very difficult to model human dominated systems such as financial markets. These types of systems go by the name 'Complex Adaptive Systems'.

For a planktonic organism it seems reasonable to assume that behaviour is physiologically driven; the result of the interaction between the rules hard-coded into the organism's genes and the environment experienced by the organism. Thus for planktonic organisms it seems reasonable that the rules governing the behaviour are fixed and can be established through experiment.

There was a general consensus that the group would focus on planktonic organisms where the behaviour is physiologically driven. The line was drawn between larval and adult fish.

We note however that many of applications of models involving physical/biological interactions will involve adult fish in some fashion. For example, migrating mackerel are known to graze on larval cod and haddock on Georges Bank. How should this be included in an early life stage for larval cod? One of the large challenges will be developing modelling techniques to include grazing by juvenile and adult fish on various planktonic organisms.

4.3 Biological Primitive Equations

There was extensive discussion of the concept of the biological primitive equations (BPE). For a given phenomenon, or problem, the primitive equations are a set of equations for which the fundamental parameters can be determined by repeatable laboratory experiments. By definition the parameters are not tuned to field data, rather the data is used to test the model (the implementation of the equations), examine its limitations, and help refine the equations. Woods (2001) provides a comprehensive discussion of the BPE.

A example of an attempt to create a set of biological primitive equations is the larval fish trophodynamics models for cod and haddock which predict the growth and development of larval cod and haddock based on a detailed larval fish bioenergetics model, which includes metabolic costs (Laurence 1985) and feeding (Werner *et al.* 1996), the effects of turbulence on prey encounter and digestion (e.g., Rothschild and Osborn 1988; Mackenzie and Kiorboe 1995), light limitation, and temperature effects on physiology (Leising and Franks 1999; Buckely *et al.* 2000). The models are not perfect and providing the models with accurate representations of the prey fields is a serious problem (Werner *et al.* 1996; Lynch *et al.* 2000). However they represent a systematic attempt to create models where the equations and parameters are based on laboratory experiments and theory.

There was discussion of the form of the biological primitive equations and whether they could be problems dependent. The questions raised included:

- Are individual based models the correct building blocks?
- Are single species models the correct building blocks?
- Does an ecosystem model based on the BPE consist of single species models for every planktonic species in the ecosystem?
- What are the possible forms of an ecosystem model that would be consistent with the requirements of the BPE?
- Does it make sense for the BPE to be problem dependent or scale dependent?

There was no consensus on answers to these questions. The key to the BPE is that the equations and parameters can be determined by repeatable laboratory experiments. The consequences of this requirement for the mathematical form of the equations are not fully understood.

The discussion of the BPE leads to a broad discussion of the relationships among lab experiments, models and the ocean. The discussion highlighted the difficulties in doing laboratory experiments where physical/biological interactions are important, the limitations of the present generation of models, and the problems relating the experiments and the models. These points are illustrated by the following three examples:

- Many processes involving bacteria and small phytoplankton are mediated by shear at scales below the Kolmogorov scale (see the extended abstract by Peters) and turbulence at this scale is not well modelled.

- For lobster larvae, the temperature dependent growth relationships are derived from constant temperature experiments. The uncertainties associated with transforming these equations for use in field applications with varying temperature fields is unknown.

- Some organisms are known to adapt to local conditions. For example in the Bay of Biscay, two strains of the toxic phytoplankton species, *Gymnodinium mikimotoi* isolated from two stations 30 n.m. apart but in a different hydrodynamic environment, exhibited a difference of 3°C in optimal growth temperature for 2 months.

Examples of biological primitive equations that would be of direct interest to the ICES community are:

• A generic life history model for *Calanus finmarchicus* which when forced by local conditions (physical environment, prey, predators, etc.) reproduced the details of the different life history cycles observed in the North Atlantic.

• A model for *G. mikimotoi, which* includes physiological adaptation to local conditions so that the temperature for optimum growth is a function of the time history of the local environmental conditions.

In summary, the difficulties inherent in achieving the biological primitive equations are highlighted by the known difficulties and dangers in translating the results of microcosm and mesocosm experiments directly to the oceanic environment. However the concept of the biological primitive equations provides a framework for thinking about the type of models and experiments that are required to overcome these problems.

The task of establishing the BPE for even a single species is daunting because of their small size, the complexity of their physiology and behaviour, and the significant intra-species variability (for some species at least). However, the benefits of creating a system of equations that allowed the direct translation of laboratory experiments to the field, even for a limited number of species or a few restricted ecosystems, would be enormous.

4.4   Reduced Models

The discussion of the biological primitive equations leads naturally to questions about their form, in particular 'What are the fundamental building blocks?' A related problem is that of reducing a complex model to a more tractable one (the process of creating a reduced model).

We define a reduced model as one with fewer state variables, interaction terms and/or free parameters than the model from, which is it derived. The question is how to derive reduced models and understand the errors introduced. The chemical modelling community has proceeded using techniques such as adaptive model refinement, where the form of the equations changes depending on the local environment.

The details of the physical-biological interactions are the result of the interaction of individual organisms with their environment. This suggests that the basic model structure should be based on individual organisms. However there are species that cannot be cultured in isolation. This suggests that in some cases, the basic building blocks may not be individual models or even single species models, but community or ecosystem models.

Two natural methods for creating a reduced model from a more complex one are:

1) Individuals (or species) can be grouped together when their function is sufficiently similar (e.g., their biological primitive equations have the same form but different parameter values). Two examples are the collection of individual into a species and the aggregation of similar species into a super-species.

2) Individuals (or species) can be grouped when they are so tightly coupled that the group can be considered a single component for the problem at hand. Parameterizing the microbial food web as a nutrient recycling term in a nutrient-phytoplankton-zooplankton (NPZ) model is an example of this.

Both of these methods are in common use and have analogies in other fields. There are probably other methods.

At a recent meeting, the GLOBEC Focus 3 working group on modelling and predictive capabilities (GLOBEC Focus 3 Working Group, 2000) concluded that the appropriate modelling approach was to focus on detailed modelling of the trophic level of interest, and ±1 trophic level, with much simpler representations at ±2 trophic levels. This was borrowed from an earlier ICES Study Group on Spatial and Temporal Integration (Glasgow, 1993; ICES C.M. 1993/L:9). This is a specific proposal for a method of creating reduced models, which deserves consideration and testing.

The community requires methods for estimating the errors associated with particular choices of reduced model. This would provide a rational basis for choosing one reduced model over another. Developing such methods requires understanding the source of the errors and metrics for measuring model error.

4.5 The Ecological Turing Test

John Woods introduced the Ecological Turing Test (ETT) as a methodology for testing ecological models (Woods 2001). The basic idea is the famous 'Turing test' designed to discover whether one was talking to a person or a computer. The computer was deemed to have a mind if the human interrogator could not distinguish between a human and a computer based on the answers to questions asked by the interrogator.

The basic features of the ETT are (Woods 2001):

1. Selected features of the observations and the simulation are compared.
2. The model is verified if there is no statistically significant difference between simulation and observation, given the uncertainties in each data set.
3. In this case, it is impossible to claim that the simulation could not have been observed.
4. The model has survived to fight another day, until more challenging observations are available, either to repeat the test for that feature, or to perform a similar test for some other feature.

The basic philosophy of the ETT is common in model testing and verification in the physical sciences but is not common in ecological modelling in the ocean. One of the recommendations of Moll and Radach (2001) is:

Marine ecological modelling is advanced now so far that quantitative local and global measures should be applied for discriminating the validated, acceptable models from those that need further validation. For this purpose well accepted methods for validation should be routinely used, employing root mean square errors for the various simulated model quantities for which data are available.

The ETT places a substantial burden on the observations. Based on comparisons between SeaWIFS observations and simulations for an area north of the Azores (Lui *et al.* 2001), Woods (2001) concludes that:

1. The uncertainties in the observations are 'so large that only gross inadequacies of the model will be revealed by existing observations'.
2. There is an urgent need for 'new experiments that will yield observations that can be used for more stringent testing of ecosystem models'.

4.6 Errors and Models

The topic of model errors was discussed several times. There was general agreement that comparison of model output with observations was not a sufficient method for quantifying model errors because of the uncertainty in the observations, in the initial conditions and in the boundary conditions. Nevertheless, it is essential to identify the causes of errors in simulating the ecosystem. This can be done by a systematic approach to assessing the source of the errors in the modelling procedure.

Engineers analyse source errors in three broad classes described by the following equation (Gnanem and Knio 2001):

$$\varepsilon = \varepsilon^d + \varepsilon^h + \varepsilon^s$$

where:

ε the total uncertainty in a particular feature of the simulation.

ε^d the errors in the simulation arising form the inadequacies of the model equations and in the values of their parameters.

ε^h the errors arising from limitations of the method of integration.

ε^s the errors arising from uncertainty in the initial and boundary conditions.

This provides a useful framework for assessing the sources of model errors and understanding where to concentrate effort. Lui *et al.* (2001) and Woods (2001) provide an example of this approach in their analysis of the spring bloom error in their Virtual Plankton Ecosystem simulation near the Azores.

4.7 3-D Coupled Physical-Chemical-Biological Prognostic Models

3-D models which today include realistic atmospheric forcing and physical/biological interactions, are on the biological side limited to primary production with one or a few species and with some including secondary production with varying complexity. Some models also include individual based models of fish larvae, and a few deal with plankton-feeding adult fish migration. In general there is a great lack of validation or 'quality assurance' of these models, mainly due to lack of relevant validation data and large uncertainties, especially in the mortality rates due to species and interactions that are not modelled.

Most of these models are being used for research, but in some cases they are also used operationally and/or for management purposes. Examples of this are:

- simulations of the potential effects of reduced inputs of anthropogenic nutrients into the North Sea (used within the OSPAR system);

- predictions of fisheries recruitment from modelling the interannually varying transports of water masses and/or primary production (used by fisheries management in Norway);

- operational modelling of the development and decay of observed harmful algal blooms such as the *chatonella* blooms in the eastern North Sea in 1998 and 2000 (used by the harmful algae warning system in Norway);

- nowcasting of the distribution of fish larvae and frontal structures used in relation to field surveys and accidental contaminant spills.

In addition, long-term simulations (several decades) are increasingly being used to produce new time-series as input to statistical investigations of the variability within the fisheries, for example. Even if modelled parameters (often not measured or nor measurable) do not have a sufficient absolute accuracy or no uncertainty estimates at all, the relative variability due to naturally varying physical forcing/climate may give valuable insight into the biological fluctuations on different space and time scales.

The consensus of the group was that the present generation of 3-D coupled physical-chemical-biological prognostic models, or ecosystem models, are extremely useful. They are powerful research tools and in some cases the model results have been judged useful by management. However, the group believes that these models have not yet been pushed to their full potential. There is a growing need for comprehensive data sets that can be used to test the models and improved methods for error analysis. The continued development, application, and testing of 3-d ecosystem models is encouraged.

Moll and Radach (2001) provide a comprehensive review of 3-d ecosystem models applied to the North Sea and make recommendations for future work. We obtained a copy of this review after the meeting, so it was not discussed at the meeting.

4.8 Individual Based Models (IBMs)

There are two basic formalisms for modelling: concentration based and individual based:

- In the concentration-based model, one assumes that the species of interest can be represented as a continuous field (e.g., the concentration of *Calanus finmarchicus*). The equations are derived by analogy with the equations for physical properties such as temperature. The resulting equations are demographic or population equations and the interactions with the environment are described in terms of the local concentration of the population. The idea of the life history trajectory of an individual organism is lost.

- In the individual based model (IBM) approach the equations governing the interaction of an individual with its environment are integrated along the trajectories of individual organism. The properties of the population are then computed by summing over all the individuals.

The concentration-based model is the most common approach. However the IBM approach is becoming more common. The presentation of the Lagrangian Ensemble Method and the demonstration of the Virtual Plankton Workbench by John Woods provided examples of population-ecology products from an individual based modelling system (Woods 2001).

Detailed arguments in favour of IBMs in ecology are made in the book edited by DeAngelis and Gross (1992). The primary advantage of IBMs is that they obey one of the fundamental tenets of biology that 'biological individuals are unique, differing from each other physiologically and behaviourally, depending on their specific genetic and environmental influences' (the preface to DeAngelis and Gross 1992). The concentration-based models violate this

tenet by making the assumption that individuals can be aggregated into a population and then modelled using demographic type equations.

Here we briefly review some of the advantages and disadvantages of the IBM approach:

Advantages:

The details of many of the physical/biological interactions are the result of the interaction of an individual organism with its environment. Thus is makes sense to integrate along the trajectory of an individual organism and the models are often easier to formulate in this frame of reference.

The IBM approach avoids the bias associated with $\overline{A \times B} \neq \overline{A} \times \overline{B}$

The focus on the individual provides a natural framework for studying how a population and/or community might evolve in response to changes in the physical environment or to the introduction of new species. Population based models do not naturally allow for intra-species variability and natural selection of individuals which is the basis of evolution.

Disadvantages:

A large number of particles are generally required to achieve statistically reliable results, especially for 3-d problems. As a result IBMs are computationally intensive and require substantial computer resources.

In the coastal ocean there are large vertical gradients in the intensity of vertical mixing. This causes severe problems for the present generation of models of the interaction between particles and turbulence. In addition the present theories assume that the particles are neutrally buoyant, which is not generally true for zooplankton and larval fish. In these cases, the basic assumptions of the Markov chain process start to break down. These issues are discussed in Brickman and Smith (2000).

A mixed approach, where the species of interest is modelled using IBMs and the rest of the biological community modelled using concentration based models, may prove useful.

5 MOTIVATING APPLICATIONS AND LIMITATIONS

To explore the limitations of the present generation of models and identify areas for progress, the group considered five motivating applications. The goal was to identify where the interaction between the physics and biology was the limiting factor and identify the key modelling technologies required to address these interactions. The five areas were:

1) Harmful Algal Blooms
2) Fish Recruitment
3) Eutrophication and Water Quality
4) Biological Influences on Climate Change
5) Ecosystem Structure and Dynamics

5.1 Harmful Algal Blooms

Most of the field of Harmful Algal Blooms (HAB) is an exercise in physical/biological interactions. Physical models are needed to provide horizontal advection at all scales, dispersion, thermocline structure, the details of thin layers in the thermocline, and sediment resuspension. Reasonable 3-d advective fields can be obtained using existing technology. There are the usual requirements for computer power and the models require coupling to large-scale models. In some cases, the HAB problems require a coupled model of the bottom boundary layer dynamics because some toxic algae spend part of their life cycle as cysts in the sediment.

Light levels are an important factor. As cells move into shallow and turbid water, one needs to model the amount of light received by the cell as it is mixed up and down in water column. The turbidity model needs to include inputs from both the physical and biological environment.

There are basic biological questions that need to be answered about many of the species involved in harmful algal blooms:

- What controls transformation into cysts and out of cysts?

- How well are basic growth rates known?

- What controls mortality?

The harmful algal bloom problem involves patches in the horizontal and thin layers in the vertical. Some general questions are:

- Do we need adaptive grids to track evolution of patches?

- Do we need to model small-scale horizontal structure?

- Can we develop methods for modelling small-scale horizontal and vertical structures in the region following a patch?

- Are the thin layers observed in the Bay of Biscay, the Kattegat, and some U.S. estuaries a general phenomenon?

- Are the thin layers a function of vertical mixing profiles? Are the organisms modifying the vertical mixing parameters?

The effect of turbulence on encounter rates should play a role in both the feeding and growth of the algae and the effectiveness of grazing on the algae by predators. Both effects should play a role in the population dynamics and the magnitude of a particular bloom. Detailed models of grazing will require more detailed models of turbulence. A good questions is 'How sensitive are feeding, growth and grazing to mixing and other physical processes?'

There are general questions about what spatial and temporal scales need to be modelled and when sub-grid scale averaging will suffice.

Often ignored when discussing modelling is the initial condition problem. A crucial question for predictive modelling is 'Is the seed stock localized?' To resolve this question, new methodologies are required which allow measurement of cell densities at the level of 1 cell per litre or less.

5.2   Fisheries Recruitment

Physical/biological interactions play a large role in the fisheries recruitment problem. Circulation models are required to describe the temperature field, advection at the shelf scale and the bank scale, and to describe meso-scale motions and local (and possibly transient) retention mechanisms. As well the physical environment has a large influence on the location and timing of the food for fish larvae.

Reasonable representation of the 3-D temperature and advective fields can be obtained by existing technology. There are limitations with respect to resolutions and small-scale baroclinic motions, especially related to mesoscale turbulence (vortex dynamics) and non-hydrostatic motions.

At intermediate scales, mesoscale turbulence may spread out the time scale over which the food from the spring bloom is available at a fixed point in space (compared with 1-D model). At the very small scales, turbulence is believed to influence the encounter rate of fish larvae with food and predators. But this has not been demonstrated conclusively.

Vertical resolution not as important as for harmful algal blooms.

One of the limiting areas are models for larval growth. Do larval trophodynamics models such as Werner *et al.* (1996) and Lynch *et al.* (2000) make sense? Do they agree with empirical growth-temperature relations from the field? This is an area that has been moving towards a set of biological primitive equations, but there is still much work to do.

Better modelling of laboratory experiments should lead to improved models of basic biological models and interactions with turbulence.

For species for which the spawning and nursery areas are known, a zero-order model for fisheries recruitment can be based on advection and simplified biology (e.g., temperature dependent growth). This could form the basis of a null hypothesis for testing more complex recruitment models. Such a scheme would require observations of timing and location of spawning.

Important questions:

- How accurately can we predict fish recruitment without considering food?

- Can we separate temporal and spatial variability in predator fields?

Fisheries recruitment is a field where there is room for mixture of dynamical and empirical models.

5.3 Eutrophication and Water Quality

The setting for studies of eutrophication, the addition of nutrients to an ecosystem, is generally the near-shore zone, especially bays and estuaries. As is the previous applications, the physical processes set the background against which the biological and chemical processes act. The physical processes determine the circulation and the mixing levels, which play a large role the retention, and flushing time scales.

The eutrophication problem requires much more attention to the chemistry and the interaction with the sediment than is usual in shelf studies. For example, modelling oxygen depletion, a primary concern for the long-term health of an ecosystem, requires understanding the physical/chemical/biological processes that go on in the sediment. This requires good vertical resolution for both the biology and chemistry, especially in the sediments. It also requires modelling biological and physical sedimentation and bioturbation.

Given the complexity of the system and the requirement for accurate models, eutrophication studies are a natural place to:

- study and test reduced models;

- study whether our best ecosystem models can predict change in ecosystem composition.

In water quality and pollution studies, one of the key quantities that need to be estimated is exposure time. This requires knowledge of the sources of the material of interest, models for physical transport, and good models of the interaction of the material with its biological and chemical environment. We note that the transport pathways and the biological availability of the material of interest will depend on whether it exists as a dissolved substance or is bound up with other substances.

5.4 Biological Influences on Climate Change

Three biological feedbacks on global climate and climate change were identified:

1. The carbon cycle: where increased radiation, reduces the winter mixed layer depth, reducing the entrainment of nutrients, reducing the spring bloom, reducing the amount of carbon fixed by the ocean, thereby reducing the amount of carbon dioxide removed from the atmosphere.

2. The sulphur cycle: It has been postulated that, among the biosphere-geosphere interactions that contribute to stabilise climate, the feedback link between oceanic microbiota and solar irradiance through the emission of dimethyl sulphide (DMS) and its effects on aerosol and cloud albedo over the oceans plays a major role. Advances in our understanding and quantification of this coupled ocean-atmosphere system require gains in predictive capability. This is a considerable modelling challenge, as the marine biogeochemical DMS cycle is complex and sensitive to both ecological (food-web structure and dynamics) and physical (vertical mixing, SST, radiation) changes in the upper ocean.

3. There is a small sensitivity of summer SST to the magnitude of spring bloom. In the open ocean it amounts to a few 0.1 C.

There is a growing interest in biological feedbacks on global climate and it seems likely that more feedback mechanisms will be identified. For example, in April 2001 there was a meeting at the Scripps Institution of Oceanography on 'Climate Forcing of Oceanic Ecosystems: Are Significant Biological Feedbacks Possible on Interdecadal Timescales?'

Modelling the carbon cycle involves many of the aspects of modelling physical/biological interactions discussed above. There is a need for biological primitive equations since one needs confidence that the model will function correctly as the environment changes. There is also a need to create sensible functional groups of phytoplankton in order to create models that are both tractable and useful. For example, the carbon flux in the Antarctic is heavily dependent on the type of phytoplankton cells produced: there can be order of magnitude differences depending on whether dense diatoms are produced. As well grazing parameterisations are important since this determines how much phytoplankton (carbon) sinks out of surface layer.

5.5 Ecosystem Structure and Dynamics

Ecosystem structure and dynamics is an underlying theme in all of the discussions; it is the framework for all the applications. There is a growing demand by regulatory agencies for the prediction of changes in ecosystem structure due to human activities in the near-shore zone. The clients include regulatory agencies, coastal managers, developers, local and national governments, impact assessment agencies, and wildlife protection agencies. As well, many of the questions related to the potential impacts of climate change are questions about how a particular ecosystem will respond to a modified climate. Thus the community needs to be able to model the structure and dynamics of complex ecosystems.

Many of the physical/biological interactions at the small scales involve bacteria and small organisms and one important question is 'How does turbulence affect the organisms and their interactions?' This will require detailed modelling of the microcosm (or mesocosm) in order to develop and test models of the detailed interactions.

6 RELATED PROGRAMMES AND WORKING GROUPS

There are numerous national and international programmes with at least some interest in modelling physical and biological interaction. Several members of this Study Group are participants in GLOBEC and/or GEOHAB. For example, Francois Carlotti is a member the International GLOBEC Scientific Steering Committee and of the GLOBEC Focus 3 Working Group (F3WG); and Patrick Gentien is the chairman of the GEOHAB Scientific Steering Committee.

The recent GLOBEC workshop on the 'Assimilation of Biological Data in Coupled Physical/Ecosystem Models' (Robinson and Lermusiaux, 2000) and the 2000 meeting report of the GLOBEC F3WG on Modelling and Predictive Capabilities (GLOBEC Focus 3 Working Group, 2000) contain discussions and information that is closely related to the goals of SGPBI. The SGPBI would benefit from a close working relationship with GLOBEC and the F3WG in particular.

The work of the climate modelling community is also of interest to the SGPBI. Studies of the carbon cycle and biogeochemical processes contain important elements of physical/biological interactions. There is growing interest in the possible biological feedbacks on the global climate (see Section 5.4).

The development of the next generation of models and modelling technologies for application in the coastal zone would benefit from collaboration with the climate modelling community.

7 FINAL COMMENTS

This report summarizes the discussions of the first meeting of the ICES Study Group on Modelling Physical/Biological Interactions. This meeting is the first step in the process of meeting the goals of the group as specified in the introduction. Here we consider how the meeting addressed the terms of reference:

a) This issue of the suitability of existing coastal models as a basis for modelling physical/biological interactions is addressed in Conclusions 5 and 6 and Section 4.1. There are many suitable models. The important point is that progress requires that the physical simulations be as comprehensive as possible.

b) The discussions touch on many of the issues that need to be addressed in a strategy for 'continued model development for the understanding and forecasting of physical/biological/chemical interactions.' The conclusions reached are very similar to the requirements for future modelling developments identified by Moll and Radach (2001) in their review of three dimensional ecological modelling related to the North Sea.

c) This meeting did not review existing observational methodologies.

We close this report with a list of general themes from the discussions that have not been elevated to conclusions:

• Many of the problems involve multiple scales in space and/or time. For example the harmful algal bloom problem in the Bay of Biscay requires simulation of thin vertical layers, meso-scale circulation features and the full shelf-scale circulation.

• Benthic/pelagic coupling is important in the near-shore and of growing importance on the shelf. It relates to some aspects of harmful algal blooms, food for suspension feeders and resuspension of carbon and nutrients. This will require the routine addition of wave models and sediment models to the simulations.

• A good model representation of the physical environment is necessary for good modelling of physical-biological interactions. The requirements for a 'good model representation of the physical environment' are not well defined

and are certainly problem dependent. Clearly, the models need to provide the correct large-scale physical environment. Embedded in the large-scale circulation are small and/or transient features such as upwelling over small-scale topography, meso-scale eddies, and narrow jets which probably have important impacts at the population level. We note that many physical processes which are presently sub-grid scale processes in physical models are likely important to the planktonic organisms.

- A complete physical simulation needs to resolve the internal Rossby radius (order of 5 km on the shelf) in order to model the baroclinic instability processes which given rise to many of the small-scale features observed in the ocean. This is not commonly done in shelf-scale simulations.

- Continued effort will be required to model turbulence at a scale appropriate to the physical/ biological interactions of interest.

- Success in modelling physical/biological interactions requires a clear question and good knowledge of the organism being studied.

7.1   Acknowledgements

8   REFERENCES

Brickman, D., and Smith, P. C. 2000. Lagrangian stochastic modelling in coastal oceanography. Submitted to J. Atmospheric and Oceanic Technology.

Ghanem, R., and Knio, O. 2001. "A probabilistic framework for the validation and certification of computer simulations" Unpublished manuscript, Department of Mechanical Engineering, Johns Hopkins University.

GLOBEC Focus 3 Working Group: Modelling and Predictive Capabilities (9–12 July 2000, Chapel Hill, N.C. USA). Available from the GLOBEC International Project Office, CCMS Plymouth Marine Laboratory, Prospect Place, Plymouth, PL1 3DH, U.K. Also available from www.globec.org under Publications.

Greatbatch, R. J., and Mellor, G. L. 1999. An overview of coastal ocean models. In: Coastal Ocean Prediction. Coastal and Estuarine Studies 56, C.N.K. Mooers (ed). American Geophysical Union. Pages 31–57.

Griffies, S. M., Boning, C., Bryan, F. O., Chassignet, E. P., Gerges, R., Hasumi, H., Hirst, A., Treguier, A.-M., and Webb, D. 2000. Developments in ocean climate modelling. Ocean Modelling. 2: 123–192.

Haidvogel, D. B., and Bechmann, A. 1998. Numerical models of the coastal ocean. In: The Global Coastal Ocean: Processes and Methods. The Sea 10. K.H. Brink and A.R. Robinson (eds.). John Wiley and Sons. Pages 457–482.

Liu, C.-C., and Woods, J. D. 2001. "Retrieving information from patchy observations of ocean colour for validating a plankton ecosystem model" *J.Geophysical Research* (submitted).

Moll, A., and Radach, G. 2001. Synthesis and new conception of North Sea Research (SYCON) - Working Group 6: Review of three-dimensional ecological modelling related to the North Sea shelf. Ber. Zent. Meeres- Klimaforsch. Univ. Hamb. (Z Interdiszipl. Zentrumsber.) Report number 8. 229pp.

Robinson, A. R., and Lermusiaux, P. F. J. (eds.), 2000. Workshop on the Assimilation of Biological Data in Coupled Physical/Ecosystem Models. GLOBEC Special Contribution 3, 152 pp. Available from the GLOBEC International Project Office, CCMS Plymouth Marine Laboratory, Prospect Place, Plymouth, PL1 3DH, U.K.

Woods, J. 2001. Primitive Equation Modelling of Plankton Ecosystems. *In*: Ocean Forecasting, Conceptual Basis and Applications. N. Pinardi and J. Woods (eds.). Springer Verlag. (Submitted).

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Physical-Biological Interactions: The Case of Anchovy (*Engraulis encrasicolus*) in the Bay of Biscay

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The relationship between anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay and environmental variables during the planktonic phase (March to July) was both investigated with an eulerian approach at mesoscale and a lagrangian approach at finescale.

First, we used a 3D hydrodynamic model to characterise three major physical mesoscale processes affecting vertical structure in southeast Biscay spawning grounds: stratification, upwelling and river plume extent. Indices were estimated from the model outputs to characterise and quantify the space/time evolution of these structures during the period March to July. A multiple linear regression analysis was then used to analyse hierarchy in the explanatory power of the physical indices. Coastal upwelling and shelf stratification breakdown indices were the most significant explanatory variables, with positive and negative effect on recruitment, respectively. A model with these two indices explains 75% of the recruitment variability of anchovy observed in the period 1987–1996 (Allain *et al*. 2001). These two physical processes are related to two exclusive meteorological regimes in spring and summer: moderate northerly to northeasterly winds (anticyclonic regime) and westerly gale winds (cyclonic regime), respectively.

The physical-biological interactions at the scale of the larvae remain hypothetical (indirect positive effect of weak upwelling, direct negative effect of extreme turbulence) and retention mechanisms are still unknown. Therefore, we used the same hydrodynamic model with a lagrangian approach to investigate the relationships between the individual growth history of larvae and the physical history of associated water masses (Allain *et al*. 2000).

The coupling of individual larval growth *in situ* and environment in order to better understand fish recruitment processes has been performed both directly, by repeated sampling of a patch of larvae and simultaneous environmental measurements (Gallego *et al*. 1996, Gallego *et al*. 1999) and indirectly, using an individually based growth model along particles tracked in a hydrodynamic model (Heath *et al*. 1997).

An intermediate approach is presented here. It consists in associating sampled larvae with water masses tracked in a hydrodynamic model and potentially representative of the trajectory and environment experienced the larvae. The growth history of the larvae determined by otolith microstructure analysis can then be related to the physical history of the coupled water masses.

Daily increments in the otoliths of anchovy larvae sampled in 1998 were used to determine individual growth curves and hatch dates. Virtual buoys were released in the hydrodynamic model on these hatch dates in order to track water masses until the sampling dates. Then the buoys trajectories ending in the sampling area on the sampling dates were considered as potentially representative of the trajectory and environment experienced by the larvae. Along the buoys trajectories, means of physical variables were calculated over the upper 30 m layer, considered as representative of the habitat of anchovy larvae (Palomera 1991, Garcia & Palomera 1996). The first observations show that temporary drops the otolith growth rate of several larvae is associated with drops in stratification and temperature with a lag of one to a few days. On the contrary, continuously increasing growth rates are generally associated with more stable stratification and temperature conditions linked to lenses of plume water.

Our objective is to define the good/bad conditions for larval growth and survival by coupling such physical and biological histories and integrate this individual-based stochastic model to the population scale to derive a more comprehensive recruitment index.

References:

Allain, G., Petitgas, P., Lazure, P., and Grellier, P. 2000. Coupling the otolith growth history of anchovy larvae with the physical history of water masses tracked in a hydrodynamic model. ICES CM 2000/N:10.

Allain, G., Petitgas, P., and Lazure, P. 2001. The influence of mesoscale ocean processes on anchovy (Engraulis encrasicolus) recruitment in the Bay of Biscay estimated with a 3D hydrodynamic model. Fish. Oceanogr. 10:1 (in press).

Gallego, A., Heath, M. R., Basford, D. J., and Mackenzie, B. R. 1999. Variability in growth rates of larval haddock in the northern North Sea. Fish. Oceanogr. 8(2): 77–92.

Gallego, A., Heath, M. R., Mackenzie, E., and Cargill, L. H. 1996. Environmentally induced short-term variability in the growth rates of larval herring. Mar. Ecol. Prog. Ser. 137: 11–23.

Garcia, A., and Palomera, I. 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Sci. Mar. 60 (supl. 2): 155–166.

Heath, M., and Gallego, A. 1997. From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. J. Fish Biol. 51 (Suppl. A): 1–29.

Palomera, I. 1991. Vertical distribution of eggs and larvae of *Engraulis encrasicolus* in stratified waters of the western Mediterranean. Mar. Biol. Vol.111, n°1: 37–44.

The « Species-of-Interest » Approach in Understanding Harmful Algal Blooms: Implications in Modelling Population Growth of *Gymnodinium mikimotoi*

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Gymnodinium mikimotoi is an ubiquitous ichtyotoxic dinoflagellate species causing harm in North Sea, Atlantic, Japan, South America, South Africa. Its blooms have deleterious effects on marine aquaculture stocks (fish and shellfish), on species recruitment (shellfish and probably fish) and possibly on marine flora and ecosystems.

Toxicity of this species is due to a labile exotoxin (20 min. half-life time). Synthesis of this exotoxin has allowed to determine the mechanism of action of this toxin: it inhibits in a non-specific way membranes ATPases. These enzymes are the energy source for ions exchanges at membranes. Biological targets are, therefore, incapacitated in their osmotic pressure regulation. The effects of these exotoxins have been studied in terms of economic losses, but never in terms of the effects on the ecology and the development of a bloom. The spatial scale of action in relation to degradation is of the order of few centimetres. Since individual cells have been observed to aggregate during the growth phase of the population, it is very likely that the population creates its own specific environment.

In order to define the specifics of this environment in terms of population dynamics, the effect of the toxins on different control factors have been examined.

Oxygen radicals produced by decay of the toxin can only optimise the organic matter uptake. Allelopathic properties of the toxin have been demonstrated and reduce competition for substrate. Toxins and the mucus produced by the dinoflagellate population lowers the grazing pressure. On the other hand, though less sensitive than their competitors, *G. mikimotoi* cells are sensitive to their own toxins. Cells have developed an anti-collision system, effective in still environments, which is proven not to act above a certain threshold of turbulence. Based on the hierchization of the processes, a simple formulation of population growth has been used to simulate hindcast time-series in the Bay of Biscay (France) according to the following formulation:

$$\frac{dC}{dt} = \mu(T, h\nu)C - \alpha\chi C^2$$

with growth rate, hν: light intensity and shear.

The inclusion in this equation of the mortality rate controlled by agitation allows to reproduce the confinement of the population in the pycnocline. This formulation of a new control process allows a better understanding of the role of biological behaviour in a stratified environment. It allows to reduce the model complexity: a purely biological model requires a specific formulation and optimisation of 7 parameters, some of which are not easily accessible by experimentation

A 3D Hydrodynamical Model of the Continental Shelf of the Bay of Biscay

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A 3-D model of the Atlantic shelf has been developed and applied to assess shelf dynamics and evolution and hydrology at time scale from the hour to several years. The grid size is 5 km and 10 vertical sigma levels are considered. The model takes the main physical processes: tides, wind induced circulation, river discharges, and surface heat flux.

Tidal currents are weak over most of the shelf, except on the northern part of the Bay around Ushant and Sein Island where strong mixing induces tidal fronts. The calculated Eulerian tidal residual currents are very weak over a large part of the shelf (<1cm/s), except in coastal areas such as western Brittany. Therefore, at depths greater than 30 m, the subtidal transport will depend on winds or the density gradient.

The monthly average winds are from SW during autumn and winter and rotate to NW during spring and summer. However, a strong inter annual variability is observed. The SW winds induce northward circulation whereas NW winds induce an offshore transport in the surface Ekman layer and upwelling along the coasts. Thus, the Landes and Vendée coasts and, to a lesser degree, the southern part of Brittany are the most sensitive areas. Upwellings are not generated under the same wind directions on either side of Loire estuary because of the coastline orientations: northwesterly to northerly winds in the south of Loire, westerly winds along the Brittany coast.

The continental shelf of the Bay of Biscay is characterised by strong freshwater inputs. The Loire and Gironde are the two main rivers along the Bay of Biscay coast. Their annual mean freshwater outflow is about 900 m^3/s each, with peak runoffs in winter or spring often exceeding 3000 m^3/s. River discharges may induce strong density currents during the runoff period. Near the estuary mouth, low salinity water flowing out forms a surface-layer plume with characteristic current directions, i.e., downstream at the surface and upstream at the bottom. Model simulations have highlighted several features of river plumes (Lazure and Jegou 1998): In early winter and periods of high river runoff, plumes usually spread northwards and along shore due to earth rotation and wind effects. During winter, vertical stratification is weak on the shelf. When river discharges decrease and when prevailing winds are from the northwest, the northward spreading of plumes may be stopped. In that case, plumes may be driven offshore or southwards. This path change usually occurs in spring. Salinity gradients become weaker under mixing and spreading effects. The low-salinity strip along the shore seldom builds up again, and the shelf circulation of water masses becomes mainly wind-driven.

Realistic simulations need time series of meteorological parameters (winds, cloud cover, air temperature, relative humidity) and river discharges. The last 15 years have been simulated and some validations have been performed by comparison between hydrological past surveys and model results.

Different applications of the 3D model have been made. A biological model has been added to the hydrodynamical model to reproduce evolution of phytoplanckon, nutrient transport and primary productivity (Loyer *et al.* 2001). All states variables are transported by advection and diffusion.

The model has been used to assess the effect of meteorological conditions in spring on the extent of a gymnodinium cf. *nagasakiense* bloom (Gentien *et al.* 1998). It has been shown that inoculation areas may exist over the shelf and that dynamics of HAB may be strongly influenced by retention structures.

Some applications to anchovy recruitment have been recently performed. The hydrodynamical model has been used to construct environmental variables. It has been shown that 2 physical variables (upwelling and destratification events) explain 80% of the recruitment variability (Allain *et al.* 2001).

Conclusion

A 3-D hydrodynamical model of the continental shelf of the Bay of Biscay has been elaborated and it is used for biological applications. Even if the model is not completely validated, it has provided the necessary physical background to the understanding of some biological parameter and their interannual evolution. Works are ongoing to improve the coupling with large-scale circulation and meteorological model, to permit vertical refinement and to decrease horizontal grid size.

Bibliography

Allain, G., Petitgas P., Lazure, P. 2000. The influence of meso-scale oocean process on anchovy recruitment in the Bay of Biscay using a 3D hydrodynamical model. Fisheries Oceanography. (in press).

Gentien, P., Lazure, P., Raffin, B. 1998. Effect of meteorological conditions in Spring on the extension of a Gymnodinium cf Nagasakiense bloom. ICES/HAB, Vigo (Spain).pp200–204.

Lazure, P., Jegou, A. M., 3D 1998. Modelling of seasonal evolution of Loire and Gironde plumes in the Bay of Biscay continental shelf, Oceanologica Acta, 21, 2: 165–177.

Loyer, S., Lazure, P., Ménesguen, A., Lampert, L., Druon, J. N. sous presse. Primary production model of the Bay of Biscay. Actes du VII ColloqueInternational d'Océanographie du Golfe de Gascogne, Biarritz 4–6 avril 2000.

Bioturbation Effects of Various Abundances of the Gastropod *Hydrobia ulvae* on Sediment Erodability: Results From Flume Experiments and Modelling Approach Using the Sam-1dv Model

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Short Title: Modelling *Hydrobia ulvae* bioresuspension influence

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The resuspension of a mudflat top sediment layers is known to enhance both water turbidity and planktonic biomass of microbiota (bacteria and benthic diatoms). This process is primarily dependent on hydro sedimentary factors but is also controlled by biological activities, namely bioturbation. Benthic macrofauna bioturbation is a complex phenomenon by which organisms living on or within sediments may modify features of their habitat throughout their feeding and burrowing activities. The aim of this study is to describe the bioturbation activities of various densities of the mud snail *Hydrobia ulvae* (the most abundant species on mudflats in the Marennes-Oléron Bay, France, with reported local abundances of 20000 ind.m^{-2}) and to quantify the consequences of their actions in terms of particulate fluxes across the sediment-water interface under flowing conditions. *Hydrobia ulvae* belongs to «biodiffusor species» and they crawl above the water-sediment interface. In local zone of these tracks, this gastropod alters bulk sediment properties and especially erodability by producing mucus, faecal pellets and by reworking superficial layers. It finally forms a biogenic matrix that is easily resuspended in comparison to the sediment bed itself.

Two sets of experiments were lead in a hydraulic benthic flume in order to quantify the influence of various snail densities on the resuspension fluxes on sedimentary structures that were classically met on the mudflats of Marennes-Oléron Bay and which differs by their water content vertical profile. Five fixed *Hydrobia ulvae* densities (0, 1000, 5000, 10000 and 50000 ind.m^{-2}) were used for each experiment and the snails were lain on the bed for 5 hours of bioturbation. In the absence of macrofauna, recorded turbidity increases with a shear stress up to 0.2 Pa and the addition of the animals lead to enhance levels of resuspension for all velocities up to these values. The amount of resuspended mud clearly depends on *Hydrobia* population densities and on mud water content.

The model (SAM-1DV, IFREMER) is used to describe the magnitude of turbidity enhancement under each shear stress condition and parameters of classical erosion law (duboy kind). In this model, erosion fluxes depends on the excess free-stream near-bed velocity above a critical threshold velocity. It concerns the mass erosion of the sediment bed itself (which does not occur during these experiments as the resuspension results concern the erosion of the biogenic matrix formed on the sediment bed).

This mathematical model is here modified in order to integrate these bioturbation processes. Comparison of turbidity results from bioturbation experiments to simulated turbidity results allows us to test several mathematical formulations reflecting the biological influence. Finally, biological deterministic processes have been integrated in this model by applying a new specific erosion law adapted to the precocious resuspension of this biogenic matrix. In this erosion law, the "tracks weight" parameter appears and it is the one which varies as a function of snail densities and water content. The parameterisation of this "track weight" was lead by regarding tracks formation processes. It was realised more precisely with the help of experimental results concerning the evolution in time of a sedimentary surface covered by tracks during a low tide period. The parameters of the equation describing these bioturbation kinetics (« Von bertalanffy » asymptotic law) are crawling speed and tracks width. Once the whole sediment surface is bioturbated (all covered by tracks), the amount of sediment available for resuspension remains constant. With such assumptions, the bioturbation time, snails densities and water content interact to modify the amount of easily resuspended sediment.

So, without changing the direct influence of the shear stress on the mass erosion of the sediment bed itself (which is considered with classical erosion law), the erosion of the biogenic matrix is also simultaneously integrate in the same model. Due to the choice of deterministic biological equations in the numerical model SAM1DV, it is now possible to examine both single influences and their interactions between benthic biological effects and physical forcing in terms of

cohesive sediment resuspension under varying conditions (with different emersion and bioturbation time, different *Hydrobia ulvae* abundance, different dry density profile) in order to evaluate the real contribution of benthic organisms in hydrosedimentary dynamics in this ecosystem. This processes will also be integrated in spatial models describing water masses transport on Marennes-Oléron Bay used to study hydrosedimentary dynamics. This local model is also a good basis to quantify the benthic algal biomass that is exported in water column via bioturbation activities.

Physical-Biological Interactions: Effects of Small-Scale Turbulence on Plankton

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There is an incipient body of experimental data on turbulence-plankton interactions, which, nevertheless, has started to grow exponentially (Figure 1). Experiments range from organisms as small as bacteria to copepods and fish larvae. One of the biggest challenges is to derive generalities from these data, which have been gathered across varying experimental and physiological conditions and parameters of interest, different turbulence set-ups, and across a range of biological taxa.

We here define small-scale turbulence 'sensu lato' to refer to the flow at scales close to the Kolmogorov microscales (L_K) and below. In the ocean the main energy inputs for this turbulence are wind stress on the surface and the breaking of waves. Even though many planktonic organisms are smaller than L_K and would not be affected by inertial motions, we use the term turbulence to keep a common thread. However, the Kolmogorov microscale is theoretical and is statistically based and it is not clear when microorganisms are no longer sensing inertial motions. Additionally, any remaining laminar motion below L_K is fuelled by the small-scale turbulence and the intensity of the shear rate can be calculated from it. For all these reasons we refer to small-scale turbulence 'sensu lato' and estimate the intensity in terms of turbulent kinetic energy dissipation rate (ε).
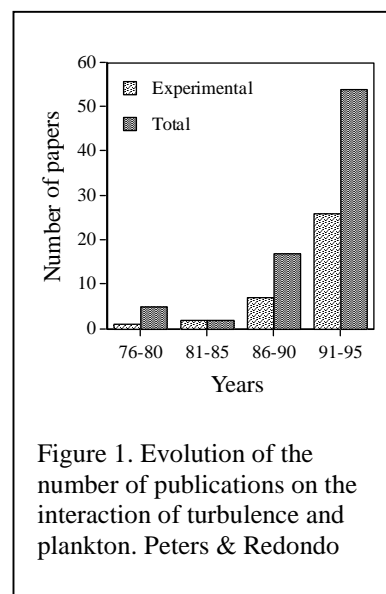
We have seen effects of turbulence down to the micrometer scale of bacteria (Peters *et al.* 1998). There seems to be a grazing pressure release on the bacteria under turbulence when protozoa can feed on somewhat larger picoplankton as alternative prey. One trophic link seems to be sufficient for this indirect effect (mediated through a trophic cascade) of turbulence on bacteria. At the largest level, the system will be driven towards hetrotrophy or autotrophy depending on the interaction of turbulence with the nutrient load (Peters *et al.* submitted).

Figure 1. Evolution of the number of publications on the interaction of turbulence and plankton. Peters & Redondo
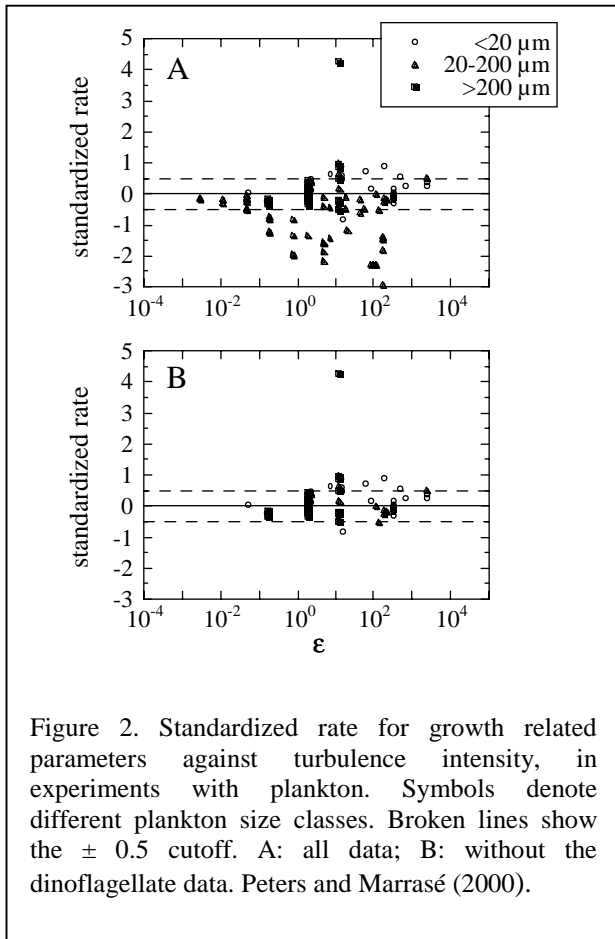
In order to compare the effects of turbulence on biological rates across experimental set-ups, taxa, and parameters of interest, a standardisation can be achieved by using

$$rate_x = \frac{rate_{tur} - rate_{control}}{\left| rate_{control} \right|}$$
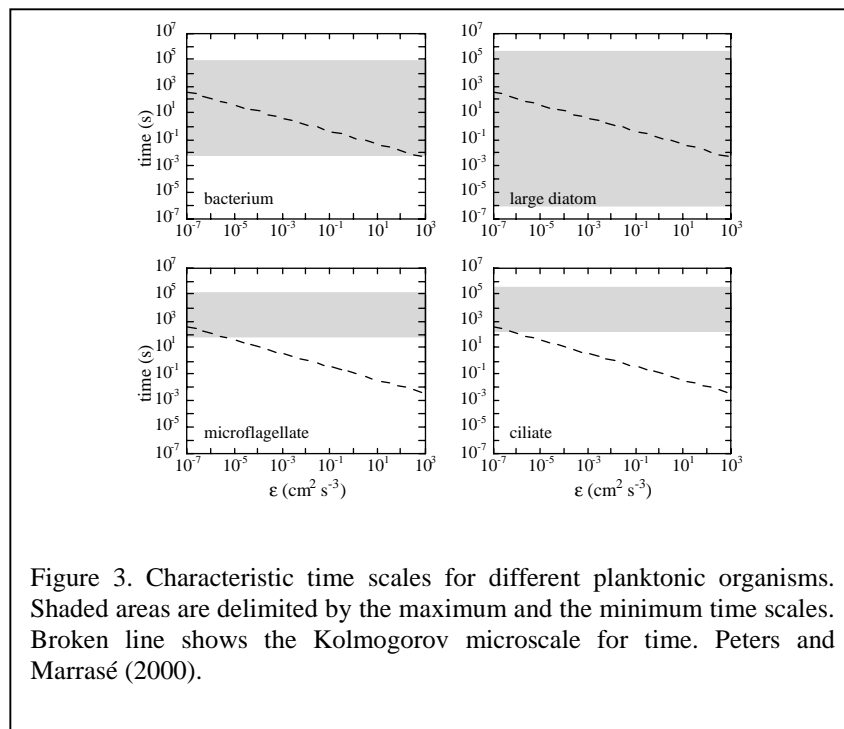
where $rate_{tur}$ and $rate_{control}$ are the rates measured under turbulent and still water conditions respectiveley. Data analysis of an extensive literature survey (Peters & Marrasé 2000) shows that growth rates of micro organisms are, in general, not affected by turbulence. The exception is the dinoflagellates, which show a clear growth inhibition when subjected to turbulence (Figure 2). Phagotrophic micro organisms (i.e., those that feed on particles) show a trend towards increased ingestion rates under turbulence. There is an urgent need to broaden our experimental database with a wider range of planktonic organisms, since much information refers to only a few species. For a group of organisms, namely the dinoflagellates, we are starting to have information about the variability of the responses to small-scale turbulence (Berdalet *et al.* submitted).

Characteristic time scales of planktonic organisms and processes with respect to the time scales of water velocity fluctuations is an avenue largely unexplored with experiments. Even laminar flow below the Kolmogorov microscale is not constant in space and time. For organisms that are smaller than L_K, it may be crucial to know whether velocity or scalar fluctuations can be experienced over the life time or other characteristic times of the organisms (Figure 3).

Figure 2. Standardized rate for growth related parameters against turbulence intensity, in experiments with plankton. Symbols denote different plankton size classes. Broken lines show the ± 0.5 cutoff. A: all data; B: without the dinoflagellate data. Peters and Marrasé (2000).

Clearly, there is a need for more and better measurements of ε in the ocean especially in coastal areas, shallow waters and near the surface. These are the locations where turbulence has the largest potential to influence plankton population and system functioning. Measurements under stormy conditions are also needed. Turbulence generation and measurement in the laboratory also have to keep improving for better experimental assessment on biological organisms and processes. Gliding over these issues is a lack of understanding of the physics at the dissipation scales. Let us illustrate our uncertainty with an example. The coefficient for the Kolmogorov length microscale has been suggested ranging from 2π to $1/6$, that is a 38 fold range. In terms of ε this means a $2 \cdot 10^6$ fold difference! The errors of the measurements of ε, even with all the biasing and averaging problems, are well within the order 10^6. Thus, it is imperative to know what happens below the inertial subrange. In the meantime assessments of small-scale turbulence on organisms and processes need to progress. We have to improve the number and quality of measurements and make an effort to have experiments that are comparable if we are to draw meaningful comparisons and generalities from the data. While waiting to have a more complete physical frame, biologists have to approach the effects of turbulence more like engineers, and try to give parameterisations to modellers and answers to society problems in general, even without a complete understanding of the fundamental mechanisms underlying small-scale turbulence.

Figure 3. Characteristic time scales for different planktonic organisms. Shaded areas are delimited by the maximum and the minimum time scales. Broken line shows the Kolmogorov microscale for time. Peters and Marrasé (2000).

References

Berdalet, E., Koumandou, L., Roldán, C., Peters, F., Estrada, M. Comparative study of the response to turbulence by three dinoflagellate species: *Gymnodinium* sp., *Alexandrium minutum* and *Prorocentrum triestinum*. Submitted.

Peters, F., Marrasé, C., Gasol, J. M., Sala, M. M., Arin, L. 1998. Effects of turbulence on bacterial growth mediated through food web interactions. Mar Ecol Prog Ser 172:293–303.

Peters, F., Marrasé, C., Havskum, H., Rassoulzadegan, F., Dolan, J., Alcaraz, M., Gasol, J. M. Turbulence and the microbial food web: effects on bacterial losses to predation and on community structure. Submitted.

Peters, F., Redondo, J. M. 1997. Turbulence generation and measurement: Application to studies on plankton. Sci Mar 61(Supl 1):205–228.

Peters F., Marrasé, C. 2000. Effects of turbulence on plankton: an overview of experimental evidence and some theoretical considerations. Mar. Ecol. Prog. Ser. 205: 291–306.

Modelling within MARE – Marine Research on Eutrophication.

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MARE (Marine Research on Eutrophication) is a Swedish contribution to a more effective international environmental management framework in the Baltic Sea Area. MARE is a multidisciplinary research programme involving about 40 scientists from different fields of research. MARE is funded by MISTRA, the Swedish Foundation for Strategic Environmental Research.

The overall goal of the MARE research programme is to develop, and get general acceptance for, an open user-friendly decision-support system. A system that can be used as a tool to develop and test cost-effective strategies to reduce eutrophication and effects thereof, in the Baltic Sea. The MARE system will build on a series of models linking information about ecosystem properties, biogeochemical processes, physical transports, nutrient inputs, and costs for nutrient abatements.

A coupled physical-biogeochemical model of the Baltic is a central kernel of the model system. MARE has initially chosen a model system based on coupled 1D models. The rationale behind this was that this was the only available model system that, at time of the decision, manages to simulate the evolution of the Baltic on time scale of several decades. With this choice, the models developed will describe basin-wide properties of the major sub-basins of the entire Baltic and the transports between them (Kattegat, Baltic proper, Gulf of Riga and Bothnian Sea and Bay).

The Baltic can in many respects be compared to a fjord with shallow sills restraining the ventilation of deeper layers and a freshwater surplus driving an estuarine circulation. The salinity stratification is rather permanent and the turnover time in the deep water is long, 10 years or more. This is of major importance for the overall nutrient conditions, which to a large extent are governed by the redox conditions. The latter can be considered to be a result of a sensitive balance, between the supply of oxygen through advection and mixing, and the supply of organic matter from the surface layer. A prerequisite for successful modelling of the nutrient dynamics is therefore a physical model, which correctly can account for the ventilation of the halocline as well of the layers below.
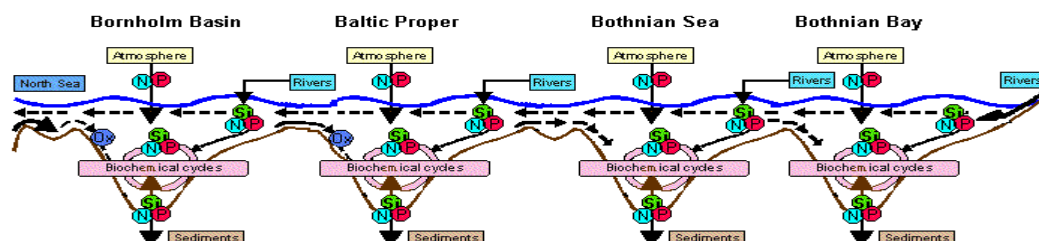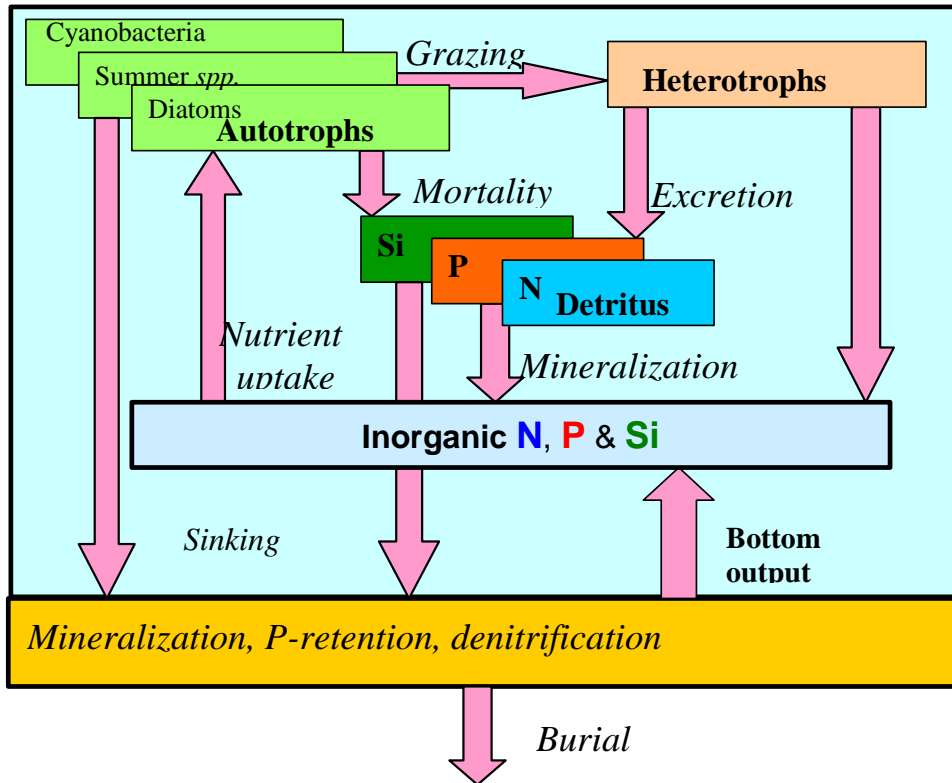
The Hydrodynamic Model

The physical model is a process based time dependent multi-basin 1D layer model with high vertical resolution. Important processes such, as dense bottom currents, diapycnical mixing are resolved using supplementary models. The Baltic is divided into 10 sub-basins. The borders between sub-basins are chosen as the narrowest cross-sections. The stratification within each sub-basin is assumed to be horizontally homogeneous while the vertical stratification is resolved by a variable number of layers.

The Biogeochemical Model

Within each sub-basin a biogeochemical model including pelagic and sediment systems describe the internal nutrient dynamics. The model contains twelve pelagic state variables and 3 in the sediment. The biomasses of autotrophs and heterotrophs are expressed in nitrogen units. The food consumption by heterotrophs is modelled with the " water clearance" concept. Limiting effects of nutrient concentrations are described by Michaelis-Menten expressions.

Model Implementation

The model has been calibrated for the time period 1971–1990 using observed meteorological and river runoff data. The model is initialised using observed hydrographic fields. At the open boundary to the Skagerrak the deep water characteristics are also described by observations.
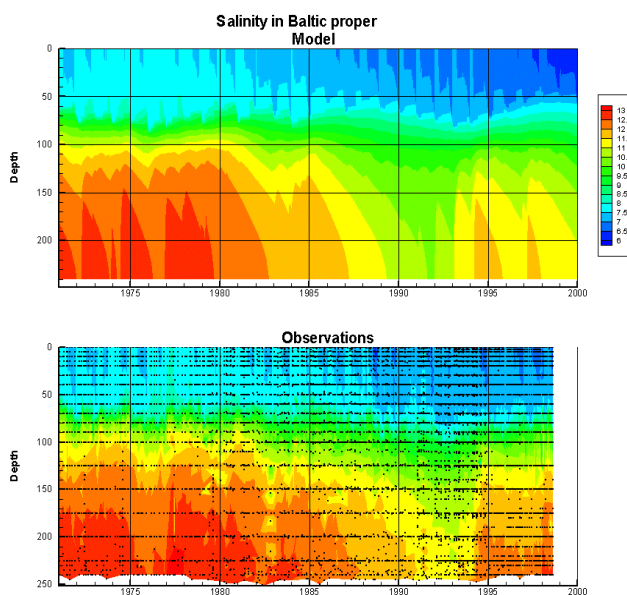
Model verification and Results

A comparison between observed and calculated salinity fields in the Baltic proper indicates realistic model behaviour. The timing and strength of saline inflows seems to be accurately described and the model also seems to be able to describe the general characteristics of the halocline.

The model is quite successful in describing the long term characteristics of oxygen concentrations and can reproduce the strong coupling between nutrient dynamics and redox conditions as well. However, a closer study reveals that the model

- Do not resolve major inflows with enough precision. Small errors in the calculated timing and intensity of major inflows result in deficits in the nutrient dynamics e.g., excessive accumulation of nitrate in deeper layers and an increased retention of phosphorous in sediment.
- Allow for too much mixing resulting in too much erosion of the chemocline.
- Overestimate the temperature of the inflowing water resulting in an intensified mineralization in the sediments.
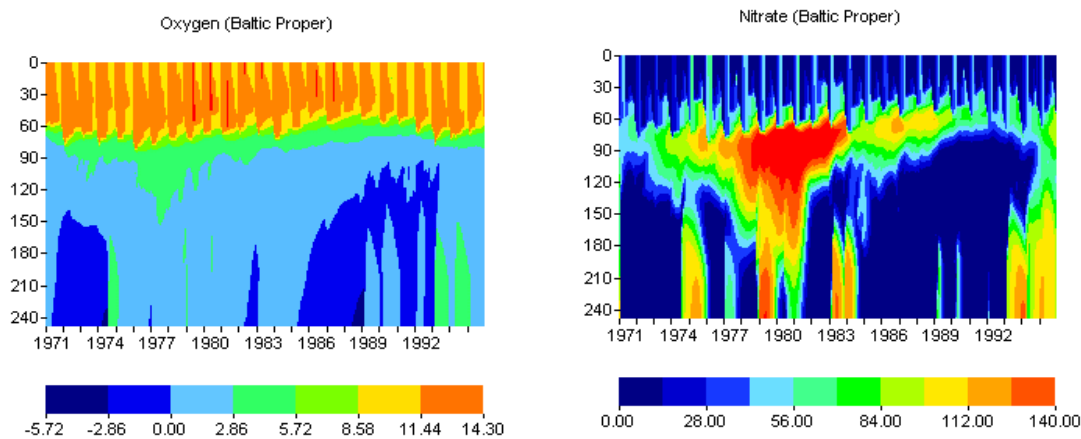
References

Gustafsson, B. 1999. Simulation of the long-term circulation of the Baltic Sea. Extended abstract in Proceedings of the Third BASYS Annual Science Conference (Warnemuende, Germany, 20–22 September, 1999), 153pp.

Gustafsson, B. G., 2000b. Time-dependent modelling of the Baltic Entrance Area. 2. Water and salt exchange of the Baltic Sea. Estuaries, 23(2), 253–266.

Savchuk, O., 1999. Simulation of the Baltic Sea Eutrophication. Extended abstract in Proceedings of the Third BASYS Annual Science Conference (Warnemuende, Germany, 20–22 September, 1999), 153pp.

Stigebrandt, A., and Wulff, F. 1987. A model for the dynamics of nutrients and oxygen in the Baltic Proper. J. Mar. Res, 45, 729–759.