Oceanography Committee **ICES CM 2002/C:09**

Report of the

Study Group on Modelling Physical/ Biological Interactions

Warnemünde, Germany
3–5 April 2002

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

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1 INTRODUCTION

This is the report of the second meeting of the ICES Study Group on Modelling Physical/Biological Interactions (SGPBI). The terms of reference for the meeting were:

The **Study Group on Modelling of Physical/Biological Interactions** [SGPBI] (Chair: C. Hannah, Canada) met in Warnemünde, Germany from 3–5 April 2002. The study group will:

a) review existing observational methodologies and new developments to support modelling and understanding of physical/biological interactions;
b) review the recent developments and results of 3-D physical/chemical/biological models;
c) continue the creation of a strategy for continued model development for understanding and forecasting of physical/biological/chemical interactions;
d) continue planning for the workshop on 'Future Directions for Modelling Physical Biological Interactions' in the summer/fall 2003.

The meeting was attended by 19 people, with only three returning from the first meeting. This major change in participants required that the group revisit many of the conclusions from the first meeting and to build a new consensus on the directions of the strategy for SGPBI.

The report is structured as follows. The recommendations are given in Section 2. Section 3 contains the conclusions derived from the discussions during the meeting. Section 4 is a chronological meeting summary that provides the background for the recommendations and conclusions, highlights the major items discussed at the meeting and provides context for the material presented in the Annex. The list of participants is given in Annex 1.

2 RECOMMENDATIONS

The Study Group on Modelling of Physical/Biological Interactions [SGPBI] (Chair: C. Hannah, Canada) will meet in March/April 2003 Chapel Hill N.C. USA from (March/April) 2003 to:

a) present and discuss new results related to developments in the modelling of physical/biological interactions;
b) review a paper prepared intersessionally which provides a derivation of model equations to form a basis for intercomparing model assumptions. The discussion will include the environmental from the atmosphere through the ocean to the benthos, chemical species to fish as well as a range of physical processes and parameters;
c) review existing modelling techniques for random walk in inhomogeneous turbulence for particles with active behaviour.
d) review the state of knowledge of zooplankton diapause and encystment and excystment of selected phytoplankton species.
e) review of the state of knowledge of light penetration into the water, the state-of-the-art models and the state of knowledge of how phytoplankton use light;
f) refine and revise the Group's strategy for continued model development for understanding and forecasting physical/biological/chemical interactions.

SGPBI will report by 15 May 2003 for the attention of the Oceanography Committee.

Supporting Information

Priority:

The SG should be given high priority since it is concerned with the evaluation and development of the tools, monitoring and modelling, used to increase the understanding of the interaction between the living resources in the sea and its ambient physical and abiotic environment. This understanding is essential to any development of modelling and prediction of biodiversity salient features.

Scientific Justification:

The goals of the Study Group are concerned with the evaluation and development of tools, methods, and models required to increase the understanding of the interaction between living resources in the sea and the physical environment. The report of the first meeting illustrates the enormous range of topics that this group must address. The discussions ranged from modelling the interactions of an individual planktonic organism with its environment to the need for comprehensive 3-d circulation models to provide the physical background for ecosystem models.

a) The study group decided that providing a forum for the presentation and discussion of new results was an important component of the group's activity.

b) There are a large number of models of physical/biological interactions. The diversity of notations and mathematical formulations makes it difficult to determine the essential similarities and differences between any two models and makes model intercomparison a difficult task. A subgroup consisting of Osborn (Chair), Fennel, Burchard and Stipa will provide a derivation of the basic equations that can form a basis for intercomparing model assumptions. The discussion will include the environmental from the atmosphere through the ocean to the benthos, chemical species to fish as well as a range of physical processes and parameters

c) The interaction of an individual with its turbulent environment is fundamental to modelling physical/biological interactions. The proper methods for modelling the random walk in inhomogeneous turbulence for a passive particle had been entered into the oceanographic literature. The next step is to understand the problems and modelling techniques for the random walk in inhomogeneous turbulence for particles with active behaviour. Thygesen will lead this item.

d) The transition of zooplankton into and out of diapause and the encystement and excystment of some phytoplankton species are key knowledge gaps. A review of the state of knowledge is timely and would help direct future research..

e) Light is a key physical parameter. There is large body of work on bio-optical models. A review of the state of knowledge of the light penetration into the water, the state-of-the-art models and the state of knowledge of how phytoplankton use light would be very useful to those involved in modelling lower trophic levels.

f) The inaugural terms of reference for SGPBI calls for a strategy for continued model development for understanding and forecasting of physical/biological/chemical interactions. The report of the 2002 meeting contains a draft strategy. This draft will be refined and revised.

3 CONCLUSIONS

1) The use of the coastal ocean is increasing. We need monitoring data, data assimilation techniques and models to help form enlightened decisions about the use and protection of the coastal ocean.
2) Oceanographic questions are inherently multidisciplinary and the interactions between the disciplines are fundamental to the solutions. As such, modelling physical/biological interactions is a key component to understanding how the ocean works.
3) The topic of physical/biological interactions is timely and there are a number of workshops and meetings (Annex 3) with sessions devoted to physical/biological interactions and we do not recommend holding an additional one. Therefore the SGPBI workshop on 'Future Directions for Modelling Physical Biological Interactions' (TOR d) has been put aside for now.
4) To encourage high quality reviews, arrangements should be made to publish the reviews in the GLOBEC or GEOHAB newsletters.
5) The ICES Oceanography Committee should encourage the ICES WGPE to complete its review of the problems related to extrapolating mesocosm experiments to the ocean.
6) SGPBI could make a contribution to the community as an information resource. Perhaps by creating and maintaining a website with information such as lists of good review papers and examples of best practice.

4 MEETING SUMMARY

Wednesday 3 April 2002

The meeting opened at 10 am Wednesday 3 April 2002 with a welcome from Bodo von Bodungen, the director of IOW. The rest of the morning and part of the afternoon was devoted for an open forum for the presentation of new results (the abstracts can be found in Annex 7**).** This forum served to introduce many of the new study group members and to introduce many of the ideas discussed later in the meeting.

There were many interesting questions raised during the presentations. The following two did not get answered or incorporated into other outputs of the meeting.

- Are second moment closure models useful for physical/biological modelling or do we need Large Eddy Simulation (LES) or Direct Numerical Simulation (DNS)?
- Can the mucus secreted by some plankton species have an observable affect on the local turbulence and mixing, i.e., can the plankton modify their physical environment?

The later part of Wednesday afternoon was devoted to the review of observational methodologies (TOR a). Tom Osborn presented two new instruments that have been developed at Johns Hopkins University. The first is an in *situ* Particle Image Velocimetry (PIV) system that allows measurements of the instantaneous distribution of two velocity components within a sample plane. This technique overcomes the inability to separate the unsteady flows associated with turbulence from those induced by surface waves in the coastal ocean, which adversely affects the data obtained using point measurement techniques. The second is a submersible system to record holograms of plankton in *situ* (developed by Edwin Malkiel and Joseph Katz). Each hologram provides a 3-dimensional snapshot of the particle field within a 732 ml volume. Within this volume they can resolve spherical particles as small 10–20 micron and linear characteristics (such as setae) with diameters as small as 3 micron.

Tapani Stipa presented a Finnish initiative, called Alg@line, that monitors the Baltic Sea surface layer with automated high-frequency sampling on board several merchant and passenger ships in the Baltic Sea.

Patrick Gentien's presentation in the open forum showed results from a profiling particle counter that he finds useful in his work on patches and thin layers of phytoplankton.

Patrick Gentien reported that there would be a major international workshop on 'Real-time coastal observing systems for ecosystem dynamics and harmful algal blooms' in Villefranche-sur-mer (France) on 11–21 June 2003. The purpose of the workshop is to review real-time and near real-time sensing systems applicable for observation, modelling and prediction of plankton dynamics in coastal waters, including HABs. There will be plenary lectures, contributed presentations, demonstrations and practical tutorials. The workshop will also provide a forum for viewing most of the commercially available observational technologies. The workshop is endorsed by GEOHAB and the Coastal Ocean Observing Panel (COOP) of the GOOS and is encouraged by ICES. People with an interest in observational technology are encouraged to attend.

Extended abstracts for the presentations by Osborn and Stipa are in Annex 4.

Thursday 4 April 2002

Thursday morning started with 2 presentations that spilled over from the open forum on Wednesday. The rest of the morning was devoted to the review of 3-d ecosystem models by Gentleman, Carlotti and Moll. The report was in three sections: transport models (where physical transport dominates), single species models, and 3-d ecosystem models of the North Sea. The presentations were thought provoking and provided the context for the discussions in the afternoon. The presentations could also be used to help introduce new scientists to the basic ideas and problem areas in the field. The reviews are presented in the next section.

The afternoon of April 4 was devoted to discussion. There were breakout groups on

1) Model equations/formulations that could form the basis for intercomparing models.
2) Modelling techniques for random walk in inhomogeneous turbulence for particles with active behaviour.
3) Life Histories

The discussions in each group were productive. The first group generated the new TOR b), the second group generated the new TOR c) and the third group generated the new TORs d) and e). A summary of the discussions on the 'Life Histories' group is provided in Annex 6.

The latter part of Thursday afternoon was a general discussion on the future of SGPBI. The two primary topics were 1) future activities of SGPBI and 2) the strategy for continued model development.

SGPBI could make a contribution to the community as an information resource. One possibility is a website with information such as:

- An annotated list of reviews on various aspects of modelling physical/biological interactions.
- An annotated list of published examples of best practice in modelling physical/biological interactions.
- Online copies of the review material that SGPBI will generate. The review presentations on 3-d ecosystem models provide good introductions to the field for students and professionals.

No decisions were reached about this activity.

The latter part of the Thursday afternoon was used to discuss the strategy for SGPBI (TOR c). Hannah presented the strategy document that was drafted intersessionally based on the conclusions of the first meeting. The discussion was lively and reflected the diversity of the group. The comments and questions were reflective of what one might expect when the strategy is presented to the community at large. The discussion revisited many of the conclusions from the first meeting and provided the basis for a new consensus on the directions of the strategy for SGPBI. The discussion also identified many areas that needed revision before being presented to the broader community. A subgroup revised the document on Friday and this draft is attached as Annex 2. This document will be revised intersessionally and reviewed at the next meeting (new TOR f).

Friday 5 April 2002

Friday morning was devoted to further discussion and to drafting the recommendations and conclusions. The Chair learned some lessons at the previous meeting and each TORs has someone responsible for accomplishing the item.

The meeting was adjourned at 11:30 Friday 5 April 2002.

The Chair thanked Wolfgang Fennel for the local arrangements (especially the lovely weather) and Morten Skogen for the rabbit jokes.

5 REVIEW OF THREE-DIMENSIONAL MODELLING OF PHYSICAL-BIOLOGICAL INTERACTIONS

The nature of the physical-biological coupling depends on both the specific scientific question being addressed and the specific system to which the models are applied. To quote Werner *et al.* (2001)

> The problem (in ecosystem modelling) is of such magnitude that we recognize that there is no single modelling approach, or even single model that can include all relevant processes (and scales). As such a hierarchy of models will need to be developed and maintained.

The objective of most applications of models coupling physics and (plankton) biology is to understand and predict spatial and temporal changes in production, distribution and structure of the populations in an ecosystem. As such, “physics” refers to current fields (i.e., u, v, w), mixing (i.e., both lateral and vertical, K_x, K_y, K_z), and temperature/salinity (T, S), which are all outputs of circulation models. “Physics” also means light, which is generally described by some kind of idealized parameterisation. “Population biology” refers to processes related to organism growth, development and mortality (including predation) and things related to organism behaviour (e.g., buoyancy regulation and/or motility).

Recent good reviews are:

1) GESAMP (Joint Group of Experts on the Scientific Aspects of Marine Pollution, 1991) for a discussion of the approaches to modelling transport processes in coastal areas for marine environmental management (the terms of reference were to evaluate the modelling, to determine generic or site specific parameters, and to recommend appropriate model types);
2) Evans and Fasham (1993) for coverage of all aspects of modelling ocean biogeochemical processes, especially for open ocean systems;
3) Olson and Hood (1994) for its elegant presentation of biogeographic models using simple physical and biological formulations when appropriate;
4) Hofmann and Lascara (1998) for an overview of interdisciplinary modelling for marine ecosystems;
5) Hofmann and Friedrichs (2002) for predictive modelling for marine ecosystems;
6) WGECO (ICES Working Group on Ecosystem Effects, 1999) for providing links to higher trophic level interactions within the environment.

Gentleman (2002) reviews the history of computer models used to study marine ecosystems. In this review we concentrate on the most recent 10 years. Model approaches can be broken into two general kinds 1) population dynamics and 2) biogeochemical/ecological dynamics. Traditionally models of population dynamics have concentrated on either physical transport with simplified biology or detailed biology with simplified transport. We found it useful to make the same distinction. This review has four components:

5.1 Transport models: based on the presentation by W. Gentleman;

5.2 Population models: based on the presentation by F. Carlotti;

5.3 Ecosystem models: based on the presentation by A. Moll;

5.4 Discussion.

The reviews and discussion below provide background information that SGPBI can draw upon in formulating its strategy (see the draft in Annex 2).

5.1 Transport Models

Advection and mixing processes affect plankton populations both directly through retention and dispersion of biota, and indirectly through their influence on the local environment (e.g., regulating nutrient, temperature, turbulence and light levels). The first part of the 3D model review focussed on models exploring the direct effects in order to address questions such as:

- What is the relative importance of advective loss compared to predation?
- How do maturation times compare to retention times?
- Where are potential upstream source populations or downstream recipients of production?
- How does circulation contribute to patchiness?
- Can we estimate export flux?
- How sensitive are the transport dynamics to changes in physical forcing?

Models investigating these issues can be formulated either in an Eulerian (concentration-based) or Lagrangian (particle-tracking) context, and require quantitative descriptions of both physical circulation and biological behaviour. The circulation component is comprised of three-dimensional velocity fields, which can vary in space and time. Transport with the mean fluid flow (u,v,w) is called advection, and transport with unresolved fluid motions, including turbulence and/or shear, is referred to as dispersion and typically represented by dispersion coefficients (K_x, K_y, K_z). The behavioural component most often includes regulated buoyancy, and diel or seasonal migrations (which occur in response to different physical and biological cues, e.g., light, temperatures, predators, prey, ontogeny) but they may also include mate-finding, foraging and predator escape. The scale of the biological motions depends upon the particular species, age/stage and environment under consideration. For example, the behavioural motions of *Calanus finmarchicus* range from eggs sinking at 0.1 mm/s to copepodite escape velocities of 350 mm/s. Biological velocities are comprised of both directed (i.e., advective) and random (i.e., dispersive) components, but advective and dispersive fluxes of individuals are not always the same as those of the population (see Flierl *et al.*, 1999).

We can normally neglect horizontal planktonic motions, because of the relative scales of physical and biological motions, and the fact that most biological cues are oriented vertically. However, we cannot usually neglect their vertical motions, and because of vertical shear in the currents, vertical positioning can indirectly affect lateral transport. It may be possible to simplify problems based on biological and physical Peclet numbers (non-dimensional number scaling advective to dispersive processes). Similarly, the dimensionality of the problem may also be reduced in specific cases (e.g., if organisms are always in the surface layer, the transport becomes a 2D problem).

Over the first 30 years of plankton modelling, most transport applications were limited to 1D or very simple 2D problems (Riley et al., 1946, Steele, 1974), but computational advances during the late 1970s and 80s allowed development of 2D models along both vertical and horizontal transects (Wroblewski, 1977, 1980, 1982; Davis, 1984). Continued technological advances, combined with increased scope and resolution of observations attained during the last decade, led to significant improvements in physical-biological transport models. Modern circulation fields are 3D and include more realistic representations of turbulence, which allows for more accurate modelling of transport (Franks, 1997b). Theoretical studies have highlighted how interaction of physical processes and biological behaviours can result in (i) residual transport of biota, even without any residual circulation (e.g., Hill, 1991a,b, Franks, 1992), (ii) patch forming mechanisms (Franks, 1997), and the (iii) critical influence of winds and fronts (Franks and Walstad, 1997). Theoretical studies have also investigated how individual behaviours are manifested as population level fluxes (Flierl *et al.,* 1999).

Applied models have demonstrated plausible source populations, explored hypotheses about controlling mechanisms, and demonstrated where observations are needed in order to improve our understanding (e.g., Hannah *et al.*, 1998; Lynch *et al.*, 1998; Miller *et al.*., 1998). Some studies have even identified circulation features that were previously unrecognised (e.g., Hood *et al*., 1999). More examples of modern applications are given in Annex 5.1 under the heading 'Physical-biological transport only in realistic flows: Modern applications.'

Most of these studies still use very simplified representations of behaviour (e.g., passive or sinking for phytoplankton, passive or surface seeking for zooplankton), akin to those used prior to the 1990s, and do not link the biological motions to any specific environmental variables. Furthermore, few applications conduct sensitivity analysis regarding their behavioural assumptions, despite the fact that those which do (e.g., Werner *et al.*, 1993; Hill, 1998) demonstrate that the results depend on the assumed behaviours. For example, export flux estimates depend on assumed sinking rates of phytoplankton, and both phytoplankton and zooplankton distributions depend on the assumed behaviour of zooplankton).

Based on the processes that past modelling efforts have recognized as important, we can identify several critical issues for future physical-biological transport modelling.

Physical circulation models will require realistic representation of (i) wind variability and Ekman dynamics, (ii) turbulence and mixed layer dynamics, and (iii) frontal regions (both resolution and dynamics). Additionally, circulation models may need to be forced with multiple tidal frequencies (e.g., S2 and K1) in order to study the net plankton transport arising from the resonance effect of diel migrations and similar tidal frequencies. Vertical grid resolution is also an issue, because there is usually a big mismatch between the grid used for the physical processes, and the scale at which the biological motions occur. We also need to put more focus on developing light (or radiation) models that quantify both light intensity and attenuation, since this is important for both phytoplankton growth and zooplankton behaviour. Physical modellers should consider ways to parameterise their 3D models to enable coupled physical-biological studies with reduced dimensionality.

Biological behavioural models need to account for the factors that ultimately determine the vertical distributions, including the effects of variable environmental conditions. For example, we need to quantitatively describe when and why organisms (i) exhibit diel migrations (e.g., related to predator density), (ii) initiate and terminate resting phases such as diapause or encystement, and (iii) change internal densities of eggs or phytoplankton when they are nutrient-limited. We recognize that this requires a vastly greater understanding of what mechanisms underlie different behaviours, and the influence of environmental variability. For the foreseeable future, we will have to continue to represent the biological motions with simple approximations. This means model investigations need to incorporate more sensitivity studies, to determine where the details of the behavioural assumptions are important for results. Specifically, ecosystem models should explore zooplankton behaviours, other than passive, and both ecosystem and population models may need to link behaviour to environmental cues. If results hinge on unknown biological responses, then the model has demonstrated where future field and laboratory experiments are critically required.

5.2 Population models

The purpose of population models is to describe and eventually predict the changes in abundance, distribution, and production of targeted species populations under forcing of the abiotic environment, food conditions and predation. The typical questions addressed are:

- What controls population dynamics of a species?
- How might environmental changes affect recruitment?

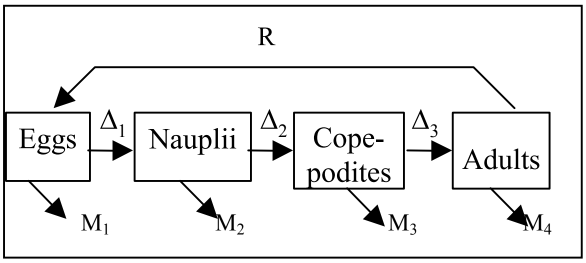
Two typical applications are to *Calanus marshallae* in the Oregon upwelling zone (Wroblewski 1982) and to *Gadus morua* (Atlantic cod) on Georges Bank (Werner *et al.* 1993, 1996).

When a single-species population model is coupled to a circulation model, then it can be thought of as a logical extension of the transport model. One starts with a transport model and adds more biological detail about stage structure and demographic processes. Here we focus on single-species population models for zooplankton. A complete review is provided by Carlotti *et al.* (2000).

A complete description of a population requires both individual and demographic information. Individual-based processes include growth rate, ingestion, excretion and respiration, and individual-based variables include body weight, reserves and gonads. The demographic processes include development rates, natural mortality and predation. The basic demographic variable is the number of individuals within a stage. A population model provides a link between individual processes and demographic processes.

An important characteristic of zooplanktonic organisms is that their life cycle involves development through various ontogenetic stages from egg to adult. The large size and weight change between egg and adult stages results in changes in swimming speed, prey size range and predator size range. Between egg and adult stages the size will increase by a factor of 20–100 and the weight will increase by a factor of 100–1000. The models need to account for these stage dependent characteristics.

Wroblewski (1982) provides an example of a stage-structured model including demographic processes. This is illustrated here.



R stands for reproduction, Δ_{stage} = (Stage duration)$^{-1}$,

and the stage duration is a of function temperature. The equation for the copedites (stage 3) can be written

$$\frac{dN_i}{dt} = \Delta_{i-1} N_{i-1} - \Delta_i N_i - M_i N_i + R\delta(i-1)$$

where N_i is the number of individuals in stage i, M_i is the mortality rate, R is the reproduction term (generation of eggs by the adults), and δ(i-1)=1 when i=1 and 0 otherwise. The generalization of this model is referred to as the McKendrick - von Foerster equation (see Annex 5.2).

There are 3 basic approaches to single species population modelling.

1) Single biomass entity (BM) model: use an NPZD model and interpret the Z variable as the zooplankton species of interest.
2) Structured population models (SPM) using an Eulerian approach (concentration based).
3) Lagrangian models (LM): the individual based model approach.

The simple Lagrangian approach using particles with simple biology such as specified birth and death rates has been widely used (see Annex 5.1). A more sophisticated approach with detailed biology and coupling with the physical and biological environment is becoming more common. The most advanced method, the Lagrangian ensemble (Woods 2002; Barkmann and Woods 1996; Carlotti and Wolf 1998), is still in the developmental stage.

A partial list of the strengths and weaknesses of the different approaches are listed here:

Model	**Strengths**	**Weakness**
BM	• One (or a few) variables • Validation against global proxies • Ease of coupling with 1D/2D/3D physical models • Useful for carbon flux quantification	• Meaningless for questions related to single populations • Parameter calibration • Mortality closure term
SPM	• Integration of specific stage and size dependent biological processes. • Coupling with 1D physical models.	• Validation: large number of state variables and biological parameters. • Representation of the trophic environment. • Mortality and predation processes • Behaviour • Lack of information on functional responses.
LM	• Integration of fine biological processes. • Individual variability of processes • Ease of coupling with 1D/2D/3D physical models • Large space and time range of processes.	• Validation: large number of biological parameters • Representation of the trophic environment. • Mortality and predation processes • Behaviour • Lack of information on functional responses. • Large space and time range of processes • Computer resources

5.3 Ecosystem models

Typically ecosystem models are used to address questions such as:

- What is the regional primary production?
- What is the succession of algae blooms?
- How do nutrients regenerate in the pelagic and benthic system?
- What is the role of the microbial loop in cycling of nutrients?
- What are the critical trophic relations in the ecosystem? (Mainly with reference to eutrophication issues.)

The absolute minimum requirements for ecosystem modelling are a description of how phytoplankton grows in response to light and nutrients. Depending on the question, ecosystem modelling will likely require some of the following:

(i) nutrient input fluxes from outside (as lateral boundary conditions, gas exchange at the surface, river flows, etc.)

(ii) physical transport descriptions for nutrients and all biota (e.g., lateral advection, vertical mixing, sinking),

(iii) descriptions of underwater light and suspended particulate matter for phytoplankton growth terms,

(iv) description of the chemical processes in the pelagic (e.g., nutrient uptake formulations),

(v) description of food webs interactions (i.e., relations between plants, relations between plants and animals, and relations between animals), and

(vi) description of the pelagic-benthic coupling with formulations for the benthic biological processes and the benthic sediment processes.

Food-webs are generally represented in the form of Nutrient-Phytoplankton-Zooplankton, or NPZ models, where N=nutrients (e.g., nitrate, ammonium, and other nutrients e.g.. silicate, phosphate), P=autotrophs (e.g., diatoms, dinoflagellates, and bacteria) and Z=heterotrophs (e.g., microzooplankton and mesozooplankton like copepods). Often these are expanded to have more than one N, P or Z state variable in order to explicitly include different size-classes. The models often include a detritus component (so called NPZD models).

Three-dimensional ecological modelling became feasible in the late 1980s when computer power reached the stage where the necessary trophic resolution could be combined with the desired spatial and temporal resolution. The development of these models has followed the availability of circulation models that could be used as forcing in ecological modelling. The bulk of the articles on this topic have appeared relatively recently.

About 1986 the development of three-dimensional ecological models started in Japan (Kishi and Ikeda, 1986) and in the USA (Walsh *et al.*., 1988). This work extended to the north Atlantic (Sarmiento *et al*., 1993; Wroblewski, 1989) and to the global scale (Maier-Reimer and Bacastow, 1990; Six and Maier-Reimer, 1996). These developments were all based on the modelling work done earlier using zero-, one- and two-dimensional ecological models.

The development of the global or basin-scale models and the shelf sea models has run in parallel with little exchange or model coupling, although many of the problems in modelling the biogoechemical cycles are the same. The large-scale ecological models have been mostly used to investigate problems connected to climate change, in particular natural carbon dioxide partial pressure (pCO_2) variations and anthropogenic carbon dioxide (CO_2) uptake in the oceans. The ecological models for the shelf seas have been mostly concerned with the investigation of the functioning of the ecosystem with regard to eutrophication problems, i.e., for the north-west European, see Zevenboom (1994).

For the coastal areas in the western North Atlantic, an ecosystem model was developed by Hofmann (1988); Hofmann and Ambler (1988); and Ishizaka and Hofmann (1988). McGillicuddy *et al.* (1995a), and McGillicuddy *et al.* (1995b) simulated the spring bloom of plankton in the North Atlantic using a three-dimensional meso-scale model. Franks and Chen (2001) presented a model for Georges Bank.

A lot of articles have appeared for the geographic region of the north-west European shelf (called greater North Sea). Several one-dimensional models were extended to three-dimensional models for the North Sea (Aksnes *et al*., 1995; Moll, 1995; Moll, 1998; Skogen *et al*., 1995). Articles on the greater North Sea area followed in the early 1990s (Skogen, 1993; NORWECOM), which first modelled the pelagic only (Skogen *et al*., 1995) and then included a simple bottom detritus compartment (Moll, 1995; ECOHAM). Another application treated the English Channel (Hoch and Garreau, 1998; ELISE). The Southern Bight of the North Sea was modelled by Luyten *et al.* (1999) in the EU project "Coupled Hydrodynamical Ecological model for Regional northwest-European Shelf seas (COHERENS)."

An example of model architecture for ecosystem modelling is provided by the extended box model in three dimensions by a group of scientists in the ERSEM (European Regional Seas Ecosystem Model) project. This complex ecosystem model was developed for the North Sea and used to investigate many aspects of this system. The results were published in two special issues: Baretta *et al.* (1995, Netherlands Journal of Sea Research and Baretta-Bekker and Baretta (1997, Journal of Sea Research). Blackford and Radford (1995) gave the rationale and model architecture for ERSEM. Allen *et al.*. (2001) introduced a full three-dimensional ERSEM application for the whole north-west European Shelf (POL3dERSEM).

Moll and Radach (2001) conducted a census and review of three-dimensional ecosystem models for the North Sea shelf system. "The overall aim of this report is to review the state-of-the-art in modelling related to marine ecosystem modelling of the greater North Sea. With this review we would like to provide an overview about three-dimensional models that describe and predict how the marine ecosystem of the North Sea functions and how concentrations and fluxes of biologically important elements (C,N,P,Si,O) vary is space and time, throughout the shelf over years, in response to physical forcing. Our objective is to illustrate the modelling approaches, modelling groups around the North Sea, their history and evolution and important results. Furthermore, we provide a framework for the development of subsequent marine ecosystem models to be used in the future for simulations to reproduce realistically a series of annual cycles and the observed interannual variability."

For the North Sea, Moll and Radach (2001) found eleven modelling systems published in sufficient detail to allow for review and seven were selected for detailed evaluation. They summarised the modelling of physical-biological interactions in a table (Table 1). The aggregation of different state variables and their associated basic processes into “key process complexes” was deemed necessary to assess whether the models could be used to build management tools for answering societal needs concerning issues like “eutrophication”. They also identified algal blooms (including spring blooms, annual phytoplankton cycles and species succession), nutrient regeneration, trophic relations in the food web, and pelagic-benthic coupling as key processes complexes.

Table 1: Implementation of “key process complexes” in the selected models. For each “key process complex” a short list of necessary criteria was defined, with SV=state variables, FU=functional units. The evaluation of the seven models is judged due to these criteria as: first line ‘Yes’= necessary state variables included; second line: explanation if necessary.

No	**Model Name**	**Algae Blooms**	**Nutrient Regeneration**	**Eutrophication**	**Tropic Relations**	**Pelagic-benthic coupling**
	Criteria	phytoplankton succession; nut. limitation	particulate and dissolved organic matter	nut: N/P ratio; phyto/zooplanktonbacteria/ oxygen	number of FU and SV; relations	Processes between pelagos and benthos
1	**NORWECOM**	Partly: only two groups	Partly: only POM	Partly: no microbial loop	No: only phy	Yes/restricted: no zoobenthos
2	**GHER**	Partly: only two groups	Yes: one DOM	No: only N cycle	Partly: phy/zoo/bac sum param.	Partly: Very crude parameterisation
3	**ECOHAM**	No: bulk formulation	Partly: only POM	No: only P cycle	No: only phy	Partly: Very crude parameterisation
4	**ERSEM**	Yes: four groups	Yes:	Yes/restricted: coarse resolution	Yes	Yes/restricted: large boxes
5	**ELISE**	Partly: only two groups	Partly: only POM	Partly: no microbial loop	No: only phy	Partly: only nutrients
6	**COHERENS**	No: bulk formulation	Partly: only POM	No: only N cycle	No: only phy	No: only SPM
7	**POL3d-ERSEM**	Yes: three groups	Yes: one DOM	Yes	Yes	Yes: Nutrients, POM zoobenthos

To understand and analyse “algae blooms”, the phytoplankton has to be separated into several distinct state variables with different parameterisations for nutrient limitation to cover the annual cycle and successions of different groups. For the simulation of “nutrient regeneration” it is necessary to differentiate between several particulate and dissolved organic compartments for the regeneration of the C, N, P, and Si matter cycles. The complex for “eutrophication” has by far the widest demands. It is necessary to simulate N:P nutrient ratios and to separate the microbial food web from the classical food chain for larger plankton particles. Oxygen demands have to be included. To study “trophic relations” the number of state variables has to be connected as a web. The “pelagic-benthic coupling” require a pelagic and benthic subsystem with appropriate physical forcing at the benthic boundary layer scale. “Recruitment” is a big issue for physical-biological interactions and it is necessary to simulate populations as structured size or age classes and take individual based species information into account. None of the models do this in the framework of an ecosystem approach.

5.4 Discussion

This subsection starts with a discussion of model testing and validation and continues with some discussion of several basic issues that need to be considered when developing more realistic and useful 3-d models. The subsection closes with a short list of review papers that can be used as an introduction to the state of the art in 3-d ecosystem. Many of the ideas presented here are also contained in the draft ‘Strategy Document’ (Annex 2), the report of the first meeting of the SGPBI, and the terms of reference for the next meeting (Section 2).

The review of North Sea ecosystem modelling by Moll and Radach (2001) was comprehensive and contains a list of 18 important tasks required in order to make progress in ecological modelling. The report is recommended reading for all students of 3-d ecosystem model. An important point is that they were unable to conclude that any one of the models was inherently better than the others because the publications do not contain the type of information required to make such a judgement. Tasks 15, 16 and 17 of Moll and Radach (2001) address the issue of validation and comparison. In summary:

- Quantitative local and global measures of goodness-of-fit should be applied for discriminating the validated, acceptable models from those, which need further validation.
- Well-defined, accepted methods for validation should be routinely used.
- Methods for stringent tests of model skills, sensitivity tests, standardised sets of validation exercises and techniques for inverse modelling and data assimilation should get more emphasis.
- The lack of data for testing three-dimensional models is a problem, and very rarely is a model tested with more than one data set.
- Model comparisons are needed between all types of models, e.g., more complex vs. less complex models, box models vs. three-dimensional models, among models with different spatial resolutions, and among different three-dimensional models.
- Model comparisons should be performed in which the models are driven by the same forcing functions.

These points are consistent with the conclusions from the first meeting of SGPBI (Hannah 2001).

Clearly, the community would benefit from a set of standard test data sets that could be used to evaluate regional three-dimensional ecosystem models. A data set must include bathymetry, initial conditions, lateral and surface boundary conditions for all state variables and interior data for comparison. This is required to separate the quality of the internal dynamics from the quality of the forcing. Such data sets have proven very useful in the development of mixed-layer models and one-dimensional turbulence closure models (e.g., www.gotm.net and Burchard *et al.* (1999)). The circulation modelling community has also started to use standard test cases to evaluate models (e.g., Haidvogel and Beckman 1998; Chassignet *et al.* 2000), although the test cases do not include observational data.

Standard goodness-of-fit metrics need to be defined, adopted and routinely used in publications. For comparing seasonal-means, Moll and Radach (2001) and references therein suggest the following. For a given quantity, first define the normalized deviation between model and data, $C_{x,t}$, for box x and season t as

$$C_{x,t} = \frac{M_{x,t} - D_{x,t}}{\sigma_{x,t}}$$

where $M_{x,t}$ is the mean value of the model results within box x and season t, $D_{x,t}$ is the mean value of the *in situ* data and $\sigma_{x,t}$ is the standard deviation of the *in situ* data within box x and season t. Overall scores can be computed by averaging over seasons, boxes and/or physical/chemical/ biological quantities (e.g., Moll 2000; Soiland and Skogen 2000).

During the meeting there were several presentations on modelling the Baltic. The model results were very encouraging. We hope that the Baltic modellers will take advantage of the goodness-of-fit metrics provided here and use them on a routine basis. Since the Baltic is a semi-enclosed sea and the open ocean boundary is relatively small, it may provide a better region for testing models than the North Sea.

Another approach to comparing models is to compare the different mathematical formulations of the various components of the biological equations. An example of applying this approach to models with multiple nutritional resources was given in the presentation by W. Gentleman in the open forum (Annex 5). The results showed that many of the formulations had strange and unexpected behaviours. Overall the reviews of Gentleman *et al.* (2002a, 2002b) provide a framework for comparing different formulations of the basic biological interactions in NPZD type models. This framework will be useful for evaluating ecosystem models.

Here we identify a number of basic issues that need to be considered when developing more realistic and useful 3-d models. The ideas are not mutually exclusive and should be pursued in parallel.

Developing an understanding of basic physical/biological processes and how to represent them in a model is closely linked to the problem of aggregation of state variables. A process defines a relationship between two (or more) state variables. Therefore changing a state variable, perhaps by splitting one highly aggregated phytoplankton state-variable into two or more, requires a change in the representation of the processes in the model. It also increases the number of model parameters, which is a serious issue when one tries to calibrate and/or validate the model.

There is a close relationship between modelling processes and the resolution in space and time. Important ecological processes occur at spatial scales below the oceanic meso-scale and so important causes of variability cannot be captured when the spatial and temporal scales are too coarse. The basic equations of fluid flow, the Navier-Stokes equations, also contain energy at all scales, but techniques have been developed so that modelling can proceed without modelling all the scales. The concept of the Reynolds stress provides a mechanism for linking the resolved and unresolved scales in the physical models. Theoretical work is necessary to create an analogue to the Reynolds stresses in biological modelling. This would allow model formulations in terms of mean and fluctuating states.

Many of the process descriptions used in models are derived from laboratory results that are transferred to space elements of much larger size without adaptation to the larger scales. In addition, many of the processes parameterisations are based on empirical relationships that express correlations between variables that can be measured (either in the lab or the field). Since the real ecological or physiological processes underlying the observed correlation are not explicit in these relationships they often do not survive changes in scale and/or environment. This was discussed at length at the first SGPBI meeting (Hannah 2001). One way forward is the concept of the Biological Primitive Equations (Woods 2002), whereby the biological models are sufficiently complete that the fundamental parameters are independent of scale and can be determined directly from laboratory experiments. Other ways forward will doubtless be proposed and pursued.

The “key process complexes” defined by Moll and Radach (2001) constitute important subsystems of the ecosystem. Several of them are common with the motivating applications discussed at the first SGPBI meeting (algal blooms, eutrophication, trophic relations and recruitment). Each complex links different sets of state variables and processes in a manner that is relevant to society; they deserve special attention and intensified research efforts.

There is recent work that links ecosystem modelling with bio-optical modelling (Bissett *et al.*, 1999a; Bissett *et al.*, 1999b) combining carbon and nitrogen cycling with four phytoplankton groups, bacteria, zooplankton and, labile and refractory dissolved organic matter. Two coloured dissolved organic carbon (CDOM) fractions and a spectrally resolved light field were used to couple the models. The basic assumption was that species composition must be modelled because each functional form of phytoplankton has a unique set of accessory pigments that utilize specific spectral windows.

We close with a short list of review papers that can be used as an introduction to the state of the art in 3-d ecosystem.

Carlotti, J., Giske, J., Werner, F. 2000. Modelling zooplankton dynamics. In*: ICES Zooplankton Methodology Manual*. Edited by R. Harris *et al.* Academic Press, London. 571–667 pp.

Crise, A., Allen, J. I., Baretta, J., Crispi, G., Mosetti, R., Solidoro, C. 1999. The Mediterranean pelagic ecosystem response to physical forcing. *Progress in Oceanography* 44:219–243.

Evans, G. T., Fasham, M. J. R. 1993. Towards a Model of Ocean Biogeochemical Processes. NATO ASI Series. Springer-Verlag. Berlin. 350 pages.

Franks, P.J.S. 2002. NPZ Models of Plankton Dynamics: Their Construction, Coupling to Physics, and Application *Journal of Oceanography,* 58: 379–387.

GESAMP Joint Group of Experts on the Scientific Aspects of Marine Pollution. 1991. Coastal Modelling. Reports and Studies GESAMP Volume 43. 187 pages.

Hofmann, E. E., and Friedrichs, M. A. M. 2002. Predictive Modelling for Marine Ecosystems. In: The Sea, Volume12. A. J. Robinson, J. J. McCarthy and B. Rothschild (Eds.). John Wiley, New York: 537–565.

Hofmann, E. E., Lascara, C. M. 1998. Overview of interdisciplinary modelling for marine ecosystems. In: *The Sea*, Volume 10. Edited by K.H. Brink and A.R. Robinson. John Wiley & Sons, Inc., New York. 507–540 pp.

ICES WGECO - Working Group on Ecosystem Effects, 1999. Report of the Working Group on Ecosystem Effects of Fishing Activities (WGECO) - Review of ecosystem models as basis for choosing metrics of ecosystem status and evaluating indirect effects of fishing. ICES, CM 2000(ACME:02): 93.

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.

Olson, D.B., and Hood, R.R., 1994. Modelling pelagic biogeography. *Progress in Oceanography*, 34: 161–205.

Robinson, A.R., and Lermusiaux, P.F.J. 2002. Data Assimilation for Modelling and Predicting Coupled Physical-Biological Interactions in the Sea, In: *The Sea*, Volume 12. Edited by Allan R. Robinson, James J. McCarthy and Brian J. Rothschild, John Wiley & Sons, Inc., New York.

Literature cited

Aksnes, D.L., Ulvestad, K.B., Balino, B.M., Berntsen, J., Egge, J.K., and Svendsen, E. 1995. Ecological modelling in coastal waters: towards predictive physical-chemical-biological simulation models. *Ophelia*, 41: 5–35.

Allen, J.I., Blackford, J., Holt, J.T., Proctor, R., Ashworth, M., and Siddorn, J. 2001. A highly spatially resolved ecosystem model for the North West European Continental Shelf. *Sarsia*, 86: 423–440.

Baretta, J.W., Ebenhöh, W., and Ruardij, P. 1995. The European Regional Seas Ecosystem Model (ERSEM), a complex marine ecosystem model. *Netherlands Journal of Sea Research*, 33(3/4): 233–246.

Baretta-Bekker, J.G., and Baretta, J.W. 1997. European Regional Seas Ecosystem Model (ERSEM) II. *Journal of Sea Research*, 38 (3–4).

Barkmann, W., and Woods, J. D. 1996. “On using a Lagrangian model to calibrate primary production determined from in vitro incubation measurements.” *Journal of Plankton Research* 18: 767–788.

Bissett, W.P., Carder, K.L., Walsh, J.J., and Dieterle, D.A. 1999a. Carbon cycling in the upper waters of the Sargasso Sea: II. Numerical simulation of apparent and inherent optical properties. *Deep-Sea Research* I, 46: 271–317.

Bissett, W.P., Walsh, J.J., Dieterle, D.A., and Carder, K.L. 1999b. Carbon cycling in the upper waters of the Sargasso Sea: I. Numerical simulation of differential carbon and nitrogen fluxes. *Deep-Sea Research* I, 46: 205–269.

Blackford, J.C., and Radford, P.J. 1995. A structure and methodology for marine ecosystem modelling. Netherlands Journal of Sea Research, 33(3/4): 247–260.

Burchard, H., Bolding, K., and Villareal, M.R. 1999. GOTM, a General Ocean Turbulence Model. Theory, implementation and test cases.

Carlotti, J., Giske, J., Werner, F. 2000. Modelling zooplankton dynamics. In: ICES Zooplankton Methodology Manual. Edited by R. Harris *et al*. Academic Press, London. 571–667 pp.

Carlotti, F., and U.Wolf. 1998. A Lagrangian Ensemble model of *Calanus finmarchicus* coupled with a 1-D ecosystem model. *Fisheries Oceanography* **7** 191–204.

Chassignet, E.P., Arango, H., Dietrich, D., Ezer, T., Ghil, M., Haidvogel, D.B., Ma, C.-C., Mehra, A., Paiva, A.M., and Sirkes, Z. 2000. DAMÉE-NAB: The base experiments. *Dyn. Atmos. Oceans*, 32, 155–184.

Davis, C. S. 1984. Interaction of a copepod population with the mean circulation on Georges Bank. Journal of Marine Research, 42: 573–590.

Evans, G.T. and Fasham, M.J.R. 1993. Towards a Model of Ocean Biogeochemical Processes. NATO ASI Series. Springer-Verlag, Berlin, 350 pp.

Franks, P. J. S. 1992. Sink or swim: accumulation of biomass at fronts. Marine Ecology Progress Series 82: 1–12.

Franks, P. J. S. 1997a. Spatial patterns in dense algal blooms. Limnology and Oceanography 42 (5 part 2): 1297–1305.

Franks, P.J.S. 1997b. New models for the exploration of biological processes at fronts. ICES Journal of Marine Science 54: 161–167.

Franks, P.J.S. and Chen, C. 2001. A 3-D prognostic model study of the Georges bank ecosystem. Part II: biological-physical model. *Deep-Sea Research* II, 48: 457–482.

Flierl, G., Grunbaum, D. Levin, S., and Olson, D. 1999. From individuals to aggregations: the interplay between behaviour and physics. Journal of Theoretical Biology 196(4): 397–454.

Franks, P.J.S., and Walstad, L.J. 1997. Phytoplankton patches at fronts: a model of formation and response to wind events. Journal of Marine Research 55: 1–29.

Gentleman, W.C. 2002. A chronology of plankton dynamics in silico: How computer models have been used to study marine ecosystems. *Hydrobiologia*. In Press.

Gentleman, W.C., Leising, A., Frost, B., Strom, S., Murray, J. 2002a. Ecosystem models with multiple nutritional resources: a critical review of the assumed biological dynamics. Part I: Zooplankton Intake. Submitted to *Deep Sea Research*.

Gentleman, W.C., Leising, A., Frost, B., Strom, S., Murray, J. 2002b. Ecosystem models with multiple nutritional resources: a critical review of the assumed biological dynamics. Part II: Phytoplankton Uptake (in prep).

GESAMP Joint Group of Experts on the Scientific Aspects of Marine Pollution, 1991. Coastal Modelling. Reports and Studies GESAMP, 43: 187.

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.

Hannah, C. G. (Ed.) 2001. Report of the First Meeting of the ICES Study Group on Modelling Physical/Biological Interactions (SGPBI). International Council for the Exploration of the Sea (ICES), Palaegade 2–4, DK-1261, Copenhagen K, Denmark. 32 pp.

Hannah, C. G., Naimie, C. E., C. E. Loder, C. E., and Werner, F. E. 1998. Upper-ocean transport mechanisms from the Gulf of Maine to Georges Bank, with implications for *Calanus* supply. Continental Shelf Research 17(15): 1887–1911.

Hill, A.E. 1991a. A mechanism for horizontal zooplankton transport by vertical migration in tidal currents. Marine Biology 111(3): 485–492.

Hill, A.E. 1991b. Vertical migration in tidal currents. Marine Ecology Progress Series 75: 39–54.

Hill, A.E. 1998. Diel vertical migration in stratified tidal flows: Implications for plankton dispersal. Journal of Marine Research 56: 1069–1096.

Hoch, T., and Garreau, P. 1998. Phytoplankton dynamics in the English Channel: a simplified three-dimensional approach. *Journal of Marine Systems*, 16: 133–150.

Hoch, T., and Menesguen, A. 1997. Modelling the biogeochemical cycles of elements limiting primary production in the English Channel: II. Sensitivity analyses*. Marine Ecology Progress Series*, 146: 189–205.

Hofmann, E.E. 1988. Plankton dynamics on the outer southeastern U.S. continental shelf. Part III. A coupled physical-biological model. *Journal of Marine Research*, 46(4): 919–956.

Hofmann, E.E., and Ambler, J.W. 1988. Plankton dynamics on the outer southeastern U.S. continental shelf. Part II. A time-dependent biological model. *Journal of Marine Research*, 46(4): 883–917.

Hofmann, E.E., and Friedrichs, M.A.M. 2002. Predictive modelling for marine ecosystems. *In*: A.R. Robinson, J.J. McCarthy and B.J. Rothschild (Editors), The Sea. The global coastal ocean. John Wiley & Sons, Inc., New York, pp. 537–565.

Hofmann, E.E., and Lascara, C.M. 1998. Overview of interdisciplinary modelling for marine ecosystems. In: K.H. Brink and A.R. Robinson (Editors), The Sea. The global coastal ocean. John Wiley & Sons, Inc., New York, pp. 507–540.

Hood, R. R., Wang, H. V., Purcell, J. E., Houde, E. D., and Harding Jr., L. W. 1999. Modelling particles and pelagic organisms in Chesapeake Bay: Convergent features control plankton distributions. Journal of Geophysical Research 1004(C1): 1223–1243.

ICES WGECO - Working Group on Ecosystem Effects, 1999. Report of the Working Group on Ecosystem Effects of Fishing Activities (WGECO) - Review of ecosystem models as basis for choosing metrics of ecosystem status and evaluating indirect effects of fishing. ICES, CM 2000(ACME:02): 93.

Ishizaka, J., and Hofmann, E.E. 1988. Plankton dynamics on the outer southeastern U.S. continental shelf. Part I. Lagrangian particle tracing experiments. *Journal of Marine Research*, 46(4): 853–882.

Kishi, M.J., and Ikeda, S. 1986. Population dynamics of "red tide" organisms in eutrophicated coastal waters - numerical experiment of phytoplankton bloom in the east Seto inland sea. *Ecological Modelling*, 31: 145–174.

Luyten, P.J., Jones, J.E., Proctor, R., Tabor, A., Tett, P., and Wild-Allen, K. 1999. COHERENS – A Coupled Hydrodynamical-Ecological Model for Regional and Shelf Seas: User Documentation. MUMM Report, Management Unit of the Mathematical Models of the North Sea, CD-ROM: 914.

Lynch, D. R., Gentleman, W. C., McGillicuddy Jr., D. J., and Davis, C. S. 1998. Biological/physical simulations of *Calanus finmarchicus* population dynamics in the Gulf of Maine. Marine Ecology Progress Series 169: 189–210.

Maier-Reimer, E., and Bacastow, R. 1990. Modelling of geochemical tracers in the ocean. In: M.E. Schlesinger (Editor), Climate-ocean interaction. Kluwer Academic Publishers, Niederlande, pp. 233–267.

McGillicuddy, D.J., McCarthy, J.J., and Robinson, A.R. 1995a. Coupled physical and biological modelling of the spring bloom in the North Atlantic (I): Model formulation and one dimensional bloom processes. *Deep-Sea Research*, 42(8): 1313–1357.

McGillicuddy, D.J., Robinson, A.R., and McCarthy, J.J. 1995b. Coupled physical and biological modelling of the spring bloom in the North Atlantic (II): Three dimensional bloom and post-bloom processes. *Deep-Sea Research*, 42(8): 1359–1398.

Menesguen, A., and Hoch, T. 1997. Modelling the biogeochemical cycles of elements limiting primary production in the English Channel: I. Role of thermohaline stratification. *Marine Ecology Progress Series*, 146: 173–188.

Miller, C. B., Lynch, D. R., Carlotti, F., Gentleman, W. C., and Lewis, C. V. W. 1998. Coupling of an individual-based population dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region. Fisheries Oceanography 7 (3/4): 219–234.

Moll, A. 1995. Regionale Differenzierung der Primärproduktion in der Nordsee: Untersuchungen mit einem drei-dimensionalen Modell. Berichte aus dem Zentrum für Meeres- und Klimaforschung; Reihe B: Ozeanographie, 19: 151.

Moll, A. 1998. Regional distribution of primary production in the North Sea simulated by a three-dimensional model. *Journal of Marine Systems*, 16: 151–170.

Moll, A. 2000. Assessment of three-dimensional physical-biological ECOHAM1 simulations by quantified validation for the North Sea with ICES and ERSEM data. *ICES Journal of Marine Science*, 57, 1060–1068.

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.

Olson, D.B. and Hood, R.R. 1994. Modelling pelagic biogeography. *Progress in Oceanography*, 34: 161–205.

Riley, G. A., H. Stommel, & D. F. Bumpus, 1949. Quantitative ecology of the plankton of the western North Atlantic. Bulletin of the Bingham Oceanography Collection 12(3): 1-169.

Sarmiento, J.L., Slater, R.D., Fasham, M.J.R., Ducklow, H.W., Toggweiler, J.R., and Evans, G.T. 1993. A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. *Global Biogeochemical Cycles*, 7(2): 417–450.

Six, K.D. and Maier-Reimer, E. 1996. Effects of plankton dynamics on seasonal carbon fluxes in an ocean general circulation model. *Global Biogeochemical Cycles*, 10(4): 559–583.

Skogen, M.D. 1993. A User's guide to NORWECOM: The NORWegian ECOlogical Model system. 6, Institute of Marine Research, Bergen-Nordnes.

Skogen, M.D., Svendsen, E., Berntsen, J., Aksnes, D.L., and Ulvestad, K.B. 1995. Modelling the primary production in the North Sea using a coupled three-dimensional physical-chemical-biological ocean model. *Estuarine, Coastal and Shelf Science*, 41: 545–565.

Soiland, H., and Skogen, M.D. 2000. Validation of a three-dimensional biophysical model using nutrient observations in the North Sea. ICES Journal of Marine Science, 57: 816–823.

Steele, J. H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge (UK), 128 pp.

Walsh, J.J., Dieterle, D.A., and Meyers, M.B. 1988. A simulation analysis of the fate of phytoplankton within the Mid-Atlantic Bight. *Continental Shelf Research*, 8: 757–787.

Werner, F. E., Page, F. H., Lynch, D. R., Loder, J. W., Lough, R. G., Perry, R. I., Greenberg, D. A., and Sinclair, M. M. 1993. Influences of mean advection and simple behaviour on the distribution of cod and haddock early life stages on Georges Bank. *Fisheries Oceanography* 2: 43–64.

Werner, F. E., Perry, R. I., Lough, R. G., and Naimie, C. E. 1996. Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep Sea Research* II 43(7–8): 1793–1822

Werner, C., Botsford, L., Brander, K., Carlotti, F., Fiksen, O., Heath, M., Kishi, M., Marrase, C., Moloney, C.L., Murphy, E., de Young, B., and Zhou, M. 2001. Report of the GLOBEC Focus 3 Working Group (F3WG).: 19.

Woods, J. 2002. Primitive Equation Modelling of Plankton Ecosystems. *In*: Ocean Forecasting, Conceptual Basis and Applications. N. Pinardi and J. Woods (Eds.). Springer Verlag. In Press.

Wroblewski, J. S. 1977. A model of phytoplankton plume formation during variable Oregon upwelling. Journal of Marine Research 35(2): 357–394.

Wroblewski, J. S. 1980. A simulation of the distribution of *Acartia clausi* during Oregon, USA, upwelling, Aug. 1973. Journal of Plankton Research 2 (1): 43–68.

Wrobleski, J. S. 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone - a simulation. Deep Sea Research 29 (6A): 665–686.

Wroblewski, J.S. 1989. A model of the spring bloom in the North Atlantic and its impact on ocean optics. *Limnology and Oceanography*, 34: 1565–1573.

Zevenboom, W. 1994. Assessment of Eutrophication and its effects in marine waters. Deutsche Hydrographische Zeitschrift, Supplement (1): 141–170.

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ANNEX 2: DRAFT OF STRATEGY DOCUMENT

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We recognize that the biology is so complex that we will have to approximate. The challenge is to determine the level of detail necessary to capture the essential features relevant to the problem being addressed. It is important to identify aspects of circulation and biological models requiring improvements in order to address our questions. This includes identification of areas where new approaches are needed. It is important to disseminate these ideas about the priorities to the community.

The proposed strategy for the future directions in modelling physical-biological interactions depends on the following:

1) Progress on understanding some of the processes of physical-biological interactions will require an individual based approach.
2) There are mechanisms by which species can adapt to changes in their environment: 1) genetic variability that provides the scope for adaptation and 2) phenotypic expression that includes for example physiological adaptation by individuals.
3) The factors affecting the individual and the population occur over a wide range of scales and we recognize that this is an important aspect of modelling PBI.

This provides the framework for the following elements of strategy for the future directions in modelling physical-biological interactions.

1) There must be increased effort towards formulating the physiology and behaviour of planktonic species in mathematical terms.
2) The basic description of a species should include quantified measures of:
    - the ability of organisms to adapt and exploit to the local environment;
    - the functional response to variation in resources and the environment;
    - the distribution of associated parameter values for that species;
    - phase transitions in the life cycle.

    The development of experiments to elucidate physical-biological interactions must include realistic variability in the environment. Experiments in stable conditions will not suffice.

3) Parameters derived in the laboratory are sometimes not helpful when scaled to the oceanic environment and the problems of extrapolation need to be better understood.
4) Current methods of model validation are primitive and we need to develop new and improved techniques for validation and intercomparison of PBI models. The validation metrics will be problem-dependent. We believe that available observational data sets are only able to reject badly flawed models. Therefore focussed experiments that result in high quality data sets are required.
5) Circulation models are required to provide 3D fields of velocity, temperature, dispersion and salinity as a background for quantifying the physical/chemical/biological interactions and to design field programs to provide the essential validation. Problems may require these models to incorporate higher frequency forcing and enhanced spatial resolution. Techniques for dealing with multiscale problems, such as adaptive and embedded grids, should be borrowed from other fields.
6) Priorities for R&D aimed at improving ecosystem models, which are designed to be useful in practical applications, depend on analysis and ranking of the sources of sensitivity and uncertainty in those models.
7) Methodologies are required for aggregating species into assemblages depending on the problem. These methods should account for the fact that changes in the biological and physical environment can shift the composition of the assemblage and thereby alter the associated functional responses and parameters.
8) Practical applications of biological models must be based on approximations consistent with individual dynamics. As computer power and the biological data required for IBMs increases the portion of the ecosystem represented by IBMs can increase.
9) We need to facilitate a community approach to modelling PBI. This could include community workshops and an internet mechanism for sharing tools (e.g., visualisation, test cases).

ANNEX 3: RELATED MEETINGS

In the next 14 months these meetings have sessions related to modelling physical/biological interactions:

- GLOBEC Open Science Meeting. Qingdao China (Beijing), 15–18 October 2002.
- ICES/PICES/GLOBEC Zooplankton Meeting May 2003 Gijon Spain.
- Theme sessions on ‘New Approaches to Zooplankton Modelling and ‘Physical Variability and Zooplankton Population Dynamics
- Workshop on ‘Real-time coastal observing systems for ecosystem dynamics and harmful algal blooms’ in Villefranche-sur-mer (France) on 11–21 June 2003. The workshop is endorsed by GEOHAB and the Coastal Ocean Observing Panel (COOP) of the GOOS and is encouraged by ICES.
- Gordon Conference on Coastal Modelling. New Hampshire June 2003.
  Session on modelling physical/biological interactions.

ANNEX 4: NEW TECHNOLOGY

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An *in situ* Particle Image Velocimetry (PIV) system has been developed at the Johns Hopkins University. It allows measurements of the instantaneous distribution of two velocity components within a sample plane. This technique overcomes the inability to separate the unsteady flows associated with turbulence from those induced by surface waves in the coastal ocean, which adversely affects the data obtained using point measurement techniques.

The submersible PIV system was deployed close to the LEO-15 site in 12–20m deep water. The system comprises two 2Kx2K pixels, 12 bits/pixel digital cameras operating simultaneously, each with a sample area of up to 0.5x0.5m. The sample areas are illuminated by a pair of flashlamp pumped-dye lasers located at the surface, which transmit pulses along optical fibres to submerged probes used for expanding the beams into light sheets. It records two exposures within each frame of the digital cameras. A hardware based `image shifter' creates a known fixed offset between exposures on the CCD array to remove directional ambiguity. Naturally occurring particles are used as tracers. Data analysis is based on calculating the auto-correlation function of the intensity distributions in subsections of the image. The components of the PIV system are mounted on a rigid sea bed platform, which enables it to align the sample areas with the direction of the mean current and to perform profiles from very close to the bottom up to 10m above the bed. Data were collected at different elevations and under different mean flow and wave conditions for periods in excess of 20min each, and at rates of up to 3.3Hz. The PIV data are augmented and compared to simultaneous measurements of turbulence using an airfoil probe and of surface waves using a pressure transducer. Ship-board CTD and ADCP are used for profiling the entire water column.

The results include vertical distributions of mean velocity, dissipation rate and shear stress under different mean current and wave conditions, including periods of zero mean flow. There is clear evidence that a log layer exists only when the amplitude of the wave induced motion is significantly smaller than the mean flow. Distributions of vorticity enable us to identify and follow the transport and development of large scale eddy structures within the sample areas. Conditional sampling enables us to correlate between the characteristics of the turbulence and the phase of the wave induced flows.

A submersible system to record holograms of plankton in *situ* has also been developed and deployed in the ocean by Johns Hopkins University scientists (Edwin Malkiel and Joseph Katz). Upon reconstruction, each hologram provides a 3-dimensional snapshot of the particle field within a 732 ml volume. Within this volume they can resolve spherical particles as small 10–20 micron and linear characteristics (such as setae) with diameters as small as 3 micron. Reconstructed volumes from holograms recorded during two deployments in the Strait of Georgia were scanned to collect focused images of particles, from which particle position, size, orientation and classification were obtained. Data from the first deployment show the variation of species distribution and diatom chain length with depth. Data from the second deployment, includes a set of holograms which were recorded during a 15 minute vertical transect of the top 30 m of the water column along with CTD, dissolved oxygen and transmissivity data. The CTD data showed this region to be characterized by 3 layers divided by two pycnoclines. The holographic data showed strong variations between class concentrations in the different layers. Concentration maxima of small dinoflagellates and diatoms were found at and below the lower pycnocline. There was also a predominant horizontal diatom orientation in this region. Below this pycnocline there is a substantial amount of fecal pellets remaining from what was apparently a previous zooplankton migration to the region. Individual holograms show clustering within different classes of plankton.

The submersible holographic system was attached to the Johnson Sea Link has recorded about 500 *in situ* holograms of marine particles and organisms in the open ocean (Gulf of Maine, Wilkinson Basin) as deep as 225 meters during horizontal transects and unpowered vertical ascents. The holograms were recorded across bioluminescent thin layers identified by measurements made prior to each dive with a HIDEX bathyphotometer and during each dive with intensified video camera recording of a transect screen.

Ship-of-opportunity measurements prove valuable for the study of physical and biological interactions in the Baltic Sea

Tapani Stipa, Anniina Kiiltomäki, Sari Pertola

Finnish Institute of Marine Research

Alg@line is a joint project of the Finnish Institute of Marine Research (FIMR), Finnish Environment Institute (FEI) and several Finnish regional environment centres as well as Estonian Marine Institute. Alg@line monitors the Baltic Sea surface layer with automated high-frequency sampling on board several merchant and passenger ships in the Baltic Sea. In this study, we have analysed nutrient measurements from the route of M/S Finnpartner between Helsinki and Travemünde. The ship completes four weekly transects over the Baltic Sea. On board an unattended flow-through equipment pumps constantly water from a fixed depth (about 5 m), and records *in vivo* chl-*a* fluorescence, temperature, salinity, position (latitude, longitude) and time. Spatial resolution of the recording is 100–200 m depending on the speed of the ship. In addition, the system collects weekly 24 water samples along one of the transects. Water samples are analysed at the Finnish Institute of Marine Research for chl-*a* and nutrient concentrations as well as relative abundance of phytoplankton species (Leppänen and Rantajärvi 1995). Chl-*a* analysis results are used for calibration when the *in vivo* fluorescence values are converted to chl-*a* values. A more detailed description of the unattended sampling method can be found in Leppänen *et al.* (1994).

A recently undertaken analysis of the annual course of nutrient concentrations in the Baltic Proper has found a large potential for the study of physical and biological interactions in the dense Alg@line data set. In particular, patterns of potential nutrient limitation are revealed, along with information on certain physiological characteristics of diatoms. Additionally, the data set will be utilised in model validation.

Leppänen J.-M., and Rantajärvi E. 1995. Unattended recording of phytoplankton and supplemental parameters on board merchant ships – an alternative to the conventional algal monitoring programmes in the Baltic Sea, In Harmful marine algal blooms. Edited by P. Lassus, G. Arzul, E. Erard-Le Denn, P. Gentien, and Marcaillore-Le Baut. (Lavoisier, Paris) pp.719–724.

Leppänen J.-M., Rantajärvi E., Maunumaa M., Larinmaa M., and Pajala J. 1994. Unattended algal monitoring system – a high resolution method of detection of phytoplankton blooms in the Baltic Sea, In OCEANS 94: Proceedings, Vol 1, 461–463.

ANNEX 5: PRESENTATIONS ON THE REVIEW OF 3D ECOSYSTEM MODELS

Annex 5.1 Transport Models

The overheads for this presentation were an excellent introduction to the topic of modelling physical/biological interactions using transport modelling. Unfortunately even when reduced to a small font they took up too many pages to justify including them here. An SGPBI web site would provide a place to distribute such presentations. We present here the list of references which provides a useful resource.

Example References

Historical Transport Models - 0D (Mixed Layer)

Riley and Bumpus, 1946. First plankton dynamics model to include mixing (as dilution).
Steele, 1974. Classic for NPZ modelling, with 2-layer sea for vertical transports.
Fasham *et al.*, 1990. Classic food web model with passive phytoplankton and behaviourally-dominated zooplankton

Historical Transport Models - 1D and 2D (Vertical and Horizontal)

Riley, 1951. Lateral transport of plankton.
Walsh and Dugdale, 1972. Lateral transport of phytoplankton and zooplankton.
Riley, 1976. Vertical migrations of zooplankton in tidal flows affect distributions.
Steele and Mullin, 1977. Effect on of different zooplankton behaves on phyto distributions.
Wroblewski, 1977. Influence of winds on primary production in upwelling zones.
Evans, 1978. Vertical migrations of zooplankton affect large scale patterns.
Wrobkewski, 1980. Influence of winds on passive copepods in upwelling zones.
Wroblewski, 1982. Copepods migrating in upwelling zones.
Davis, 1984. Horizontal transport of copepods with seasonal mean flows.
Ishizaka and Hofmann, 1988. Lagrangian study of passive particles in eddies and fronts.

Advances I: Biological Modelling

Hill 1991a,b. Theoretical models of plankton dispersal from migration and tides
Franks, 1992. Theoretical models of plankton patchiness from migrations and currents
Franks, 1997a. Theoretical models of plankton patchiness.
Franks and Walstad, 1997. Numerical flows for idealized system demonstrating importance of winds and frontal regions to transport and distribution of plankton
Flierl, 1999. Theoretical models of population fluxes based on individual behaviours.
Grunbaum, 1999.Theoretical models of population fluxes based on individual behaviours.

Advances II: Physical Modelling

Franks, 1997b. Demonstration that improved turbulence models yield more accurate representations of physical-biological interactions
Lynch *et al.*, 1996. Seasonal circulation fields with improved realism
(and LOTS of other circulation models, e.g., POM, ECOM)

Physical-biological transport only in realistic flows: Modern applications
Werner *et al.*, 1993. Ichthyoplankton with various behaviours in regional flows. various behaviours
Slagstad and Tande, 1996. Copepod ontogenic migration with regional circulation fields.
Page *et al.*, 1997. Ichthyplankton assumed to be homogeneous in vertical regional flows
Bryant *et al.*, 1998. Copepods in regional flow fields.
Hannah *et al.*, 1998. Copepods with various behaviours in regional flow fields.
Hill, 1998. Vertical migrations in stratified tidal flows.
Lynch *et al.*, 1998. Copepods in surface and water column in regional flow fields
Hood *et al.*, 1999. Pelagic plankton in estuaries
Incze and Naimie, 2000. Lobster larvae in regional circulation.
Shore *et al.*, 2000. Copepods in flows with wind variability
Gentleman, 2000. Copepods in regional flows with different behaviours.
Lewis *et al.*, 2001. Copepods in flows with wind variability

See also Table II in Hofmann and Friedrichs, 2002.

Transport in realistic flow fields with plankton dynamics: Modern applications

Sarmiento *et al*., 1993. Global biogeochemical model
Lewis *et al*., 1994. Ecosystem and population dynamics with winds on bank
Franks and Chen, 1996. Ecosystem with regional circulation
Hinkley *et al*., 1996. Early life history models of fish in regional circulation
Kawamiya *et al*., 1996. Ecosystem with regional circulation
Werner *et al.*, 1996. Early life history models of fish in regional circulation
Lynch *et al*., 1998. Copepod population dynamics with regional circulation
McGillicuddy *et al*., 1998. Copepod population dynamics with regional circulation.
Miller *et al*., 1998. Copepod population dynamics with regional circulation.
Gentleman, 2000. Copepods population dynamics with regional flows.
McGillicuddy *et al*., 2001. Coupled model used to assess sampling strategies.
See also Table II in Hofmann and Friedrichs, 2002

References

Bryant, A. D., Hainbucher, D., and Heath, M. 1998. Basin-scale advection and population persistence of Calanus finmarchicus. Fisheries Oceanography 7 (3/4): 235–244.

Davis, C. S. 1984. Interaction of a copepod population with the mean circulation on Georges Bank. Journal of Marine Research, 42: 573–590.

Evans, G. T. 1978. Biological effects of vertical-horizontal interactions. In J. H. Steele (ed.), Spatial pattern in plankton communities. Plenum, New York: 157–180.

Fasham, M. J. R., Ducklow, H. W., and McKelvie, S. M. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed-layer. Journal of Marine Research 48, 591–63.

Flierl, G., Grunbaum, D., Levin, S., and Olson, D. 1999. From individuals to aggregations: the interplay between behaviour and physics. Journal of Theoretical Biology 196(4): 397–454.

Franks, P. J. S. 1992. Sink or swim: accumulation of biomass at fronts. Marine Ecology Progress Series 82: 1–12.

Franks, P. J. S. 1997a. Spatial patterns in dense algal blooms. Limnology and Oceanography 42 (5 part 2): 1297–1305.

Franks, P. J. S. 1997b. New models for the exploration of biological processes at fronts. ICES Journal of Marine Science 54: 161–167.

Franks, P. J. S., and Chen, C. 1996. Plankton production in tidal fronts: a model of Georges Bank in summer. Journal of Marine Research 54: 631–651.

Franks, P. J. S., and Walstad, L. J. 1997. Phytoplankton patches at fronts: a model of formation and response to wind events. Journal of Marine Research 55: 1–29.

Gentleman, W. C. 2000. Factors controlling the abundance and distribution of *Calanus finmarchicus* in the Gulf of Maine/Georges Bank region. PhD. Thesis. Thayer School of Engineering Dartmouth College. 272 pp.

Grunbaum, D. 1999. Advection-diffusion equations for generalized tactic searching behaviours. Journal of Mathematical Biology 38(2): 169–194.

Hannah, C. G., Naimie, C. E., Loder, J. W., and Werner, F. E. 1998. Upper-ocean transport mechanisms from the Gulf of Maine to Georges Bank, with implications for *Calanus* supply. Continental Shelf Research 17(15): 1887–1911.

Hill, A. E. 1991a. A mechanism for horizontal zooplankton transport by vertical migration in tidal currents. Marine Biology 111(3): 485–492.

Hill, A. E. 1991b. Vertical migration in tidal currents. Marine Ecology Progress Series 75: 39–54.

Hill, A. E. 1998. Diel vertical migration in stratified tidal flows: Implications for plankton dispersal. Journal of Marine Research 56: 1069–1096.

Hinckley, S., Hermann, A. J., and Megrey, B. A. 1996. Development of a spatially explicit, individual-based model of marine fish early life history. Marine Ecology Progress Series 139:47–68.

Hofmann, E. E. and Friedrichs, M. A. M. 2002. Predictive Modelling for Marine Ecosystems. In The Sea 12. A. J. Robinson, J. J. McCarthy and B. Rothschild (Eds.). John Wiley, New York: 537–565.

Hood, R. R., Wang, H. V., Purcell, J. E., Houde, E. D., and Harding Jr., L. W. 1999. Modelling particles and pelagic organisms in Chesapeake Bay: Convergent features control plankton distributions. Journal of Geophysical Research 1004(C1): 1223–1243.

Incze, S. L., and Naimie, C. E. 2000. Modelling the transport of lobster (Homarus americanus) larvae and postlarvae in the Gulf of Maine. Fisheries Oceanography 9(1): 99–113.

Ishizaka, J., and Hofmann, E. E. 1988. Plankton dynamics on the outer southeastern U.S. continental shelf. Part 1. Lagrangian particle tracing experiments. Journal of Marine Research 46(4): 853–882.

Kawamiya, M., Kishi, M. J., Yamanaka, Y., and Suginohara, N. 1995. An ecological-physical coupled model applied to Station Papa. Journal of Oceanography 51: 635–664.

Lewis, C. V. W., Chen, C., and Davis, C. S. 2001. Effect of winter wind variability on plankton transport over Georges Bank. Deep Sea Research II 48: 137–158.

Lewis, C. V. W., Davis, C. S., and Gawarkiewicz, G. 1994. Wind forced biological-physical interactions on an isolated offshore bank. Deep Sea Research II 41(1) 51–73.

Lynch, D. R., Ip, J. T.C., Naimie, C. E., and Werner, F. E. Comprehensive circulation model with application to the Gulf of Maine. Continental Shelf Research, 16(7): 875–906, 1996.

Lynch, D. R., Gentleman, W. C., McGillicuddy Jr., D. J., and Davis, C. S. 1998. Biological/physical simulations of *Calanus finmarchicus* population dynamics in the Gulf of Maine. Marine Ecology Progress Series 169: 189–210.

McGillicuddy, D. J. Jr., Lynch, D. R., Moore, A. M., Gentleman, W. C., Davis, C. S. and Meise, C. J., 1998. An adjoint data assimilation approach to diagnosis of physical and biological controls on *Pseudocalanus* spp. in the Gulf of Maine-Georges Bank region. Fisheries Oceanography 7 (3/4): 205–218.

McGillicuddy, D. J. Jr., Lynch, D. R., Wiebe, P., Runge, J., Durbin, E. G., Gentleman, W. C., and Davis, C. S. Evaluating the synopticity of the U.S. GLOBEC Georges Bank broad-scale sampling pattern with observational system simulation experiments. Deep Sea Research II 48: 483–500.

Miller, C. B., Lynch, D. R., Carlotti, F., Gentleman, W. C., and Lewis, C. V. W. 1998. Coupling of an individual-based population dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region. Fisheries Oceanography 7 (3/4): 219–234.

Page, F. H., Sinclair, M., Naimie, C. E., Loder, J. W., Losier, R. J., Berrien, P., and Lough, R. G. Cod and haddock spawning on Georges Bank in relation to water residence times. Technical Report T:17, ICES, September 1997.

Riley, G. A. 1951. Oxygen, phosphate, and nitrate in the Atlantic Ocean. Bulletin of the Bingham Oceanographic Collection 13(1):1–126.

Riley, G. A. 1976. A model of plankton patchiness. Limnology and Oceanography 21(6): 873–880.

Riley, G. A., and Bumpus, D. F. 1946. Phytoplankton-zooplankton relationships on Georges Bank. Journal of Marine Research 6: 33–47.

Sarmiento, J. L., Slater, R. D., Fasham, M. J. R., Ducklow, H. W., Toggweiler, J. R., and Evans, G. T. 1993. A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. Global Biogeochemical Cycles 7: 417–450.

Shore, J. A., Hannah, C. G., and Loder, J. W. 2000. Drift pathways on the western Scotian Shelf and its environs. Canadian Journal of Fisheries and Aquatic Sciences 57(12): 2488–2505.

Slagstad, D. and Tande, K. S. 1996. The importance of seasonal vertical migration in across shelf transport of *Calanus finmarchicus*. Ophelia 44: 189–205.

Steele, J. H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge (UK), 128 pp.

Steele, J. H., and Mullin, M. M. 1977. Zooplankton Dynamics. In E. D. Goldberg, I. N. McCave, J. J. O'Brien and J. H. Steele (Eds.), The Sea, Vol 6. Wiley, New York: 857–890.

Walsh, J. J. and Dugdale, R. C. 1972. Nutrient submodels and simulation models of phytoplankton production in the sea. In H. E. Allen and J. R. Kramer (Eds.), Nutrients in Natural Waters, John Wilely & Sons, New York: 171–192.

Werner, F. E., Page, F. H., Lynch, D. R., Loder, J. W., Lough, R. G., Perry, R. I., Greenberg, D. A., and Sinclair, M. M. 1993. Influences of mean advection and simple behaviour on the distribution of cod and haddock early life stages on Georges Bank. Fisheries Oceanography 2: 43–64.

Werner, F. E., Perry, R. I., Lough, R. G., and Naimie, C. E. 1996. Trophodynamic and advective influences on Georges Bank larval cod and haddock. Deep Sea Research II 43(7–8): 1793–1822.

Wroblewski, J. S. 1977. A model of phytoplankton plume formation during variable Oregon upwelling. Journal of Marine Research 35(2): 357–394.

Wroblewski, J. S. 1980. A simulation of the distribution of *Acartia clausi* during Oregon, USA, upwelling, Aug. 1973. Journal of Plankton Research 2(1): 43–68.

Wrobleski, J. S. 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone - a simulation. Deep Sea Research 29(6A): 665–686.

Annex 5.2 Population models

General purpose of population models:

To describe and eventually predict the changes in abundance, distribution, and production of targeted species populations under forcing of the abiotic environment, food conditions and predation.

Two examples of population models

- with a copepod species: *Calanus marshallae* in Oregon upwelling zone (Wroblewski, 1982)

Purpose: To demonstrate how the interaction between the ontogenetic migration and the upwelling circulation maintains the population within the Oregon upwelling zone.

- with a fish species (planktonic larval stages): Gadus *morua* in Georges Bank gyre system (Werner *et al.*, 1993,1996).

Purpose: To explain the relative influences of biological processes (swimming behaviour, trophodynamics) and physical processes (advection) on cod larvae distribution in the Georges Bank.

In general, questions are:

⇒ What controls populations dynamics of species?
⇒ How might environment changes affect recruitment?

Recent scientific programs on targeted species

- TASC (Trans Atlantic Study of Calanus)
  - ➔ *Calanus finmarchicus*
- Various programs of fish larvae
  - Cod
  - Small pelagic fish

Characteristics of these zooplanktonic organisms

- Life duration (month to a few years)
- Development through various ontogenetic stages from egg to adult
- Large size/weight ranges between egg and adult stages

size: 1 → 20/100
weight: 1 → 100/1000

It induces changes in: - swimming speed
- prey size range
- predator size range

Description of a population

Individual-based processes
(unit: mass / time)

- Growth rate
/
- Ingestion
- Egestion
- Excretion /
Respiration

and variables (unit: mass)
- body weight
- structural weight
- reserves
- gonads

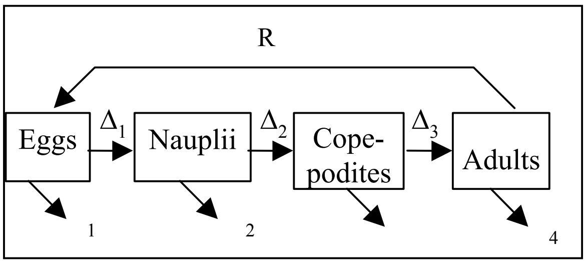
Demographic processes
(unit: numbers / time)

- Egg production
- Development rates
(Moulting rates)
- Mortality
- natural
- predation

and variables (unit: numbers)
- individual within stage

Example: Wroblewski (1982)'s model

Stage-structured model including demographic processes



Δ_{stage} = (Stage duration)$^{-1}$ and Stage duration = f(Temperature)
Belehradek equation

copepodids $\frac{dN_i}{dt} = D_{i-1}N_{i-1} - D_i N_i - M_i N_i$

The generalisation of this type of model is referred to as the McKendrick - von Foerster equation

$$\frac{\partial n(t,a,m)}{\partial t} + \frac{\partial n(t,a,m)}{\partial a} + \frac{\partial g(t,a,m)n(t,a,m)}{\partial m} = - \mu(t,a,m)\, n(t,a,m)$$

Most population models link individual-based processes and demographic processes.

Example: Carlotti and Sciandra's model

Present developments of population models deal with

- the coupling of demographic and trophodynamics processes with external physical and biological variables/processes, Example: Conceptual diagram for *Calanus finmarchicus*

- a better integration of internal processes within the population to represent the response capacity to external forcing.

Population models

- **Eulerian approach**

Structured Population models (McKendrick-von Foerster equation)

  - Age
  - Stage
  - Size / Weight

- **Lagrangian approach**

- Individual particles with simple biology (birth and death dates)
- Lagrangian Ensemble with detailed biology and coupling with the physical and biological environment
  (Woods and Barkmann, 1993, 1994, 1996, Carlotti and Wolf, 1998)

Spatial distributions of single populations

Dynamics of single populations in site-specific situations

Spatial plankton dynamics with advection - diffusion - reaction equations

$$\frac{\partial C}{\partial t} + \nabla \cdot (\nu_a C) - \nabla \cdot (K \nabla C) = \text{"}bio\log icalterms\text{"}$$

$\nu_a(u_a, v_a, w_a)$: advective fluid velocities in x,y,z directions;

K_x, K_y, K_z: diffusivities in x,y,z directions;

$\nabla = (\partial/\partial x, \partial/\partial y, \partial/\partial z)$ is the Laplacian operator.

Biological terms: sources and sinks of the biological variables in x, y, z

Biological variables: population described by equations of the McKendrick-von Foerster type.

Example: Wroblewski (1982)

Lagrangian models of planktonic organisms

$$\begin{tikzcd} & \text{Velocity vector} \arrow[d] & \text{Hydrodynamical model} \arrow[l] \\ d\,\mathbf{x} / dt = & \mathbf{v}(x,y,z,t) + v_{\text{biology}} & \end{tikzcd}$$

Example: Werner *et al.*. (1993)

Strong / weak points of zooplankton population models

- Single biomass entity (BM) model: use an NPZD model and interpret the Z variable as the zooplankton species of interest.

- Structured population models (SPM) using an Eulerian approach (concentration based).
- Lagragian models (LM): the individual based model approach.

Model	Strengths	Weakness
BM	• One (or a few) variables • Validation against global proxies • Ease of coupling with 1D/2D/3D physical models • Useful for carbon flux quantification	• Meaningless for questions related to single populations • Parameter calibration • Mortality closure term
SPM	• Integration of specific stage and size dependent biological processes. • Coupling with 1D physical models.	• Validation: large number of state variables and biological parameters. • Representation of the trophic environment. • Mortality and predation processes • Behaviour • Lack of information on functional responses.
LM	• Integration of fine biological processes. • Individual variability of processes • Ease of coupling with 1D/2D/3D physical models • Large space and time range of processes.	• Validation: large number of biological parameters • Representation of the trophic environment. • Mortality and predation processes • Behaviour • Lack of information on functional responses. • Large space and time range of processes • Computer resources

ANNEX 6: BREAKOUT GROUP ON LIFE HISTORY

Rapporteur: Wendy Gentleman.

We began our discussion by posing the question: What is needed for models to be able to address biological questions? We agreed that the answer depends upon the specific model application, however we quickly converged on the idea that understanding and representing life history events is critical. The life histories of both copepods and toxic phytoplankton include dormant phases wherein the organisms are not subject to advective transport in the surface waters, but are found in the deep water or sediment. Emergence from dormancy affects when and where subsequent "blooms" in plankton populations are found and thus the advective linkages between source and recipient regions. Similarly, the life history of fish dictates when and where eggs are released, and their subsequent transport pathways and the larvae's ambient environment. Hence, modelling Harmful Algal Blooms (HABs), copepods and/or larval fish (including the relevance of Marine Protected Areas) requires establishing the appropriate initial conditions based on the phase transitions of the organisms' life history (i.e., where and when are they “wake up” or are spawned)?

Our discussion identified areas where we need the help of the physicists/circulation modellers in order to tackle the biological questions. These included: (i) providing descriptions of the critical bottom stress for sediment transport models, (ii) accurate descriptions of deep flows for transport of copepods while they are in diapause, (iii) refined grids to increase resolution in the parts of the water column where the biology reside during different phases of their life history, and (iv) accurate descriptions of environmental cues thought to be related to changing phases (e.g., light and temperature)

We also identified areas where the biological models could be improved. These included: (i) explicit descriptions of each stage of life-history, (ii) exploration of new modelling approaches such as in Fisksen 2000, which uses genetic algorithms to study the optimal phenology for the timing of initiation and emergence from diapause, (iii) explicit inclusion of benthic/pelagic coupling.

Finally, we recognized that in order to model these things, we need to gain more biological knowledge about organismal life histories. This knowledge includes (i) understanding what triggers “waking up” from dormancy, and (ii) whether deep organisms are truly “passive”. There was also a suggestion that a theme session at an upcoming conference could be organized around such topics. Finally we also recognized that there is still a wealth of information needed with respect to the growing phase, not just transition to/from dormancy.

ANNEX 7: ABSTRACTS FROM THE OPEN FORUM

ERGOM – An Ecosystem Model of the Baltic Sea

Thomas Neumann – Baltic Sea Research Institute Warnemünde

A three dimensional circulation model (MOM) was coupled with a biogeochemical model and adjusted to the Baltic Sea. The biogeochemical model comprises nine state variables. Included are dissolved nutrients (nitrogen and phosphorus), three functional phytoplankton groups, zooplankton, detritus and oxygen. At the ocean floor a sediment module simulates the biogeochemical processes in sediments. The model is forced with river runoff and loads as well as meteorological data sets for the period 1980 until 1990. Interannual variations in the forcing field are reflected in corresponding variations of the model ecosystem. Thus the nitrogen fixation by cyano-bacteria was drop down in the middle of the 80s and recovered at the end of the decade.

Scenarios of river nutrient load reduction were used to investigate the reaction of the Baltic Sea ecosystem. The model displayed spatial and temporal patterns in the reduction efficiency. Coastal areas are more affected than the central basins. In the central part the reduction of biomass is very small. The reaction of the phytoplankton groups is quite different. Diatoms group is effectively reduced whereas cyano-bacteria abundance increases. Dissolved inorganic nitrogen is removed from the system due to reduced river loads much faster than phosphorus.

IBM Modelling of Baltic Cod Larval Drift and Survival

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Studies of recruitment process have often focussed on correlations among environmental factors, stock characteristics and recruitment levels, or alternatively, on single processes occurring at the level of individual organisms or single life stages, for example mortality or starvation. It is now more generally accepted that mechanisms operating on different temporal and spatial scales may be important, and that overall recruitment levels are unlikely to be controlled by only one factor, process, or life stage.

For Baltic cod, the potential exists for eggs and larvae of differing quality to be exposed to an environment varying due to a) temporally and spatially varying food environment, b) seasonal and inter-annual fluctuations in physical environmental conditions, c) varying transport potential, and d) variable predator/prey overlap. Resolving the importance of co-occurrence of larvae and the peak abundance of their prey requires the analysis of growth characteristics of larvae and juveniles over the range of potential prey abundance available to them during the season and in relation to survival success. Thus, an individual based modelling approach might be a useful tool in the analysis of the variability in feeding and growth characteristics of individual larvae.

We have developed a coupled hydrodynamic/trophodynamic individual based model (IBM) of drift and feeding designed to examine growth and survival of Baltic larval cod. The approach used in constructing an IBM of the feeding and growth of Baltic cod was to couple a trophodynamic model with an existing multi-level ocean model. This coupled model allows to examine the feeding, growth and starvation mortality of larval cod in the Baltic Sea in the context of their transports by utilizing trophodynamic relationships along their potential drift routes. The trophodynamic model calculated the encounter of food, foraging, growth and survival of individual cod larvae in the Baltic Sea. To simulate these processes, every cod larvae passed through a series of steps during each time interval (6 hours). Temperature influences metabolic processes and, besides prey availability, is the single most important factor that determines growth rates in fish. As obtained from rearing experiments with Norwegian coastal cod somatic growth in length and weight increased with increasing temperature. Specific length growth rates as well as larval stage durations have been determined by these relationships adjusted to observation of Baltic cod. After hatch but before reaching their length at which feeding is required for the first time (<4.5 mm) yolk sac larvae were only considered as passively drifting particles with growth exclusively determined by the environmental temperature conditions.

The primary aim of this study was to examine the influence of physical forcing variations on the potential larval and juvenile survival success of Baltic cod. Retention and dispersion from the main spawning area has been identified to be one of the key processes influencing recruitment success of the eastern Baltic cod stock. From the modelling results it turned out, that variations of the feeding conditions (temporal and spatial variations of food availability) had a strong impact on survival of first-feeding larval stages. The study also suggests, that food limitation for first-feeding larvae was caused by a pronounced decline of its main feeding component (copepod *P. elangatus*) during the last two decades. By the absence of this copepod, only larvae hatched at the outer edges of the Bornholm Basin at the end of the spawning period had higher probabilities to survive, because of their low drift distances towards the optimal feeding environments in more shallow coastal areas. In contrast, larvae hatched within the deep basin area of the Bornholm Basin required too much prey for survival along their drift routes in less favourable feeding conditions. Thus, enhanced larval survival success may either occur during periods of peak prey abundance or must be related to the occurrence of favourable environmental processes such as transport into optimal feeding environments, optimal turbulent conditions, or low ambient temperatures reducing the daily rations of food necessary for covering the standard metabolism.

Although, transport patterns of intermediate water layers where cod larvae mainly occur are relatively well known, validation of the results of our coupled physical/biological modelling approaches seems to be difficult due to several processes and factors partly unresolved and thus only parameterised in the model calculations. First, transport patterns of larvae are influenced by the initial spawning location, the vertical position in the water column and their behaviour, especially their diurnal vertical migration that varies with stage and size. Furthermore, transport rates of larvae are dependent on the peak egg abundance and timing of peak spawning of Baltic cod. Secondly, trophodynamics are the most difficult processes to implement in models of larval growth, because of the uncertainties in validating such models experimentally or by data obtained during field campaigns.

Statistical turbulence modelling with GOTM

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1) Introduction

GOTM stands for "General Ocean Turbulence Model" and means that the model simulates small-scale turbulence and vertical mixing as far as possible in a general manner and without calibration to specific applications. This general character is underlined by the fact that the model is applied to scenarios in various regions, specifications and scales, such that the model is frequently verified (and unfortunately sometimes falsified as well). The model is modular such that refinements or extensions especially for the turbulence models, but also for the mean flow modelling can easily be carried out. The aim of generality is very ambitious, and there are always situations for which turbulence closures on a higher level would be required. GOTM is a one-dimensional model for the water column, which means that all horizontal gradients have to be either prognostically prescribed, parameterised or neglected. The turbulence module inside GOTM is organised such that it can be integrated into three-dimensional ocean or atmosphere models for calculating the vertical exchange coefficients.

2) Mean currents and stratification

Standard transport equations for mean quantities are designed for horizontal velocity components, potential temperature, salinity and suspended matter. A general tracer algorithm is part of GOTM as well, allowing for easy implementation of biological models, if only the source and sink terms are known. Several terms, which contain horizontal gradients, need special treatment. The surface slopes, which represent the barotropic pressure gradients, can easily be determined by local observations or results from three-dimensional numerical models. It is also sufficient to prescribe a time series of near-bed velocity components for reconstructing the barotropic pressure gradient. The internal pressure gradient, which results from horizontal density gradients can be prescribed from observations or model results. Advective and horizontal diffusive terms are neglected in the velocity equations. Rotation and vertical mixing (assuming that an eddy viscosity is known) do not pose any problems. For the active tracer equations it is especially the advective terms which are not easy to handle. There are three options: neglect (especially in the open ocean), relaxation to observations or prescription of observed horizontal gradients. In cases where the vertical velocity is known from observations or theoretical considerations, it can be used for vertical advection. Standard relations are used as surface and bottom boundary conditions. At the sea surface, they have to be prescribed or calculated from meteorological observations with the aid of bulk formulae using the simulated or observed sea surface temperature. The suspended matter module is written so far for non-cohesive matter, but there are plans for refinements. The density is calculated by means of the UNESCO equation of state, either with the full version or linearisations of it. A somewhat exotic GOTM module simulates the interaction of sea grass canopies with turbulence and currents.

3) Turbulence

In GOTM, the modelling of turbulence is based on the Boussinesq eddy viscosity assumption, with which the turbulent fluxes are proportional to the gradients of the transported quantities. By doing so, phenomena such as counter gradient fluxes, which are relevant for convection scenarios, are however not reproducible. Another effect, which is not considered, is the direct effect of rotation on turbulent mixing, which is significant only for deep convection. The proportionality factors between the fluxes and the gradients are the vertical exchange coefficients, which are calculated according to the Kolmogorov-Prandtl relation as product of three factors: a dimensionless stability function, a turbulent velocity scale and a turbulent macro length scale. The stability functions, which are different for momentum and for tracers and which can depend on shear and stratification contain complex algebraic closures for the second moments. For the calculation of the velocity scale and the macro length scale, various zero-, one- and two-equation models are included into GOTM. The k-epsilon and the Mellor-Yamada models are the most well-known two-equation models inside GOTM. For these models some recent developments are considered.

4) Applications

The most well known GOTM application is the simulation of the mixed layer at OWS Papa in the Northern Pacific, for which data of temperature profiles and meteorological parameters for a period of about 20 years are available. Typical shelf sea applications which include surface as well as bottom processes, are located in the Irish Sea and the Northern North Sea, where FLEX (Fladenground-Experiment 1976) is the classical scenario. For the newer scenarios in Liverpool Bay, the Northern North Sea and in lake Lago Maggiore, observations of the turbulent dissipation rate have been made. Those could in principle be well reproduced by applying GOTM. GOTM also contains some idealised scenarios such as the penetration of a mixed layer into a stably stratified water column by means of wind (Kato-Phillips experiment) or cooling (Deardorff experiment).

Work on Modelling Multi-Annual Population of *Karenia Mikimotoi* in the Bay of Biscay

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These results were obtained in the context of recent Ph. D. work.

Karenia mikimotoi blooms occur regularly along the French Atlantic coast, with large inter annual variations in intensity and geographic extent. A species-specific model has been developed in an attempt to define the most important processes regulating *K. mikimotoi* population dynamics. This novel modelling approach does not necessarily imply a growth closure by inorganic nutrition. Formulation of the species dynamics is based on a detailed knowledge of the species biology. Growth rate depends on temperature and light. Formulation of light dependency takes into account the plasticity of the species regarding light regimes. An original formulation of the mortality rate related to shear has been included. Since this species has been shown in *situ* to rely solely on ammonium from remineralisation, it has been necessary to include this species model into a standard phytoplankton biomass model. These biological models are embedded into a 3D- hydrodynamical model of the whole continental shelf of the Bay of Biscay (5 n.m. mesh, 10 σ layers, 2.5 turbulence closure). Mortality rate parameterisation (tested in a 1-D vertical model under realistic forcing) reproduces confinement of the population in the pycnocline without any formulation of migration. 3-D simulation results without reseeding in winter, have been validated against observed time-series for the same period (1990–1995). Confinement in the pycnocline is adequately simulated as well as timing of the blooms. The model reproduces correctly 5 years out of 6 in terms of geographic extent and interannual variations in abundance. This species of interest model requires tuning of only 7 parameters and as a result, is probably more robust than a model which would take into account all the physiological processes observed, estimated or measured on this species.

Development of a Plankton Model for Physical-Biological Modelling in the NW Atlantic

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Monitoring of the NW Atlantic shelf since 1998 has documented strong interannual variability in physical conditions and in the timing, magnitude and spatial distribution of plankton production events (e.g., spring bloom). To better understand the processes responsible for this variability requires a physical-biological modelling system that can assimilate and interpret monitoring data. Our group at the Bedford Institute of Oceanography is currently developing a plankton model that would be suitable for such a system. Our modelling philosophy is that the research questions shape the structure, functional relationships and parameterisations of the plankton model. At this stage, we are searching for the plankton model with the minimum level of biological detail needed to reproduce the seasonal cycle of productivity in the shelf and open ocean realms of the NW Atlantic.

We focus initially on the Scotian Shelf off Halifax, Nova Scotia (43–44°N, 62–64°W). We use a mixed-layer model to force different versions of the plankton model and compare them against climatologies of chlorophyll and nutrients (Li and Harrison 2001; Petrie *et al.*. 1999). We begin with the simplest possible plankton model (two compartments: phytoplankton (P) and nitrogen (N)) and gradually add complexity until the match between model simulations and data cannot be improved. This "forward stepwise" process of model development deals both with model structure (How many compartments? What flows to include?) and with the functional relationships used to describe how the inter-compartmental flows are regulated. The parameters that describe how the rate of primary production changes with light and nutrients are obtained by fitting bio-optical models to the climatology of satellite-based primary production estimates (Longhurst *et al.* 1995). The remaining parameters that describe how primary production is processed by the food web are obtained by balancing the flows of nitrogen across the food web using inverse methods (Vezina and Savenkoff, 1999). At this point, we are using diagnostic 0-D (bulk) representations of the mixed-layer to force the plankton models because we found that 1-D prognostic mixed-layer models did not reproduce correctly the seasonal cycle of mixed layer depth on the Scotian shelf. This is probably related to the three-dimensional control of mixed-layer depth on the shelf.

The annual mixed-layer cycle is prescribed from climatologies of mixed-layer determinations from T and S profiles gathered on the Scotian shelf over the past 50 years. We run the plankton models with two scenarios of mixed-layer variability: climatological where the mixed-layer depth varies smoothly between monthly means and stochastic where the mixed layer changes daily within the variance prescribed by the mixed-layer climatology (Figure 1). This was done out of concern that a smooth climatological mixed-layer forcing might misrepresent the impact of high frequency mixed-layer variability on biological processes. In fact, we found a substantial impact of the forcing scenario on the plankton model simulation and on its degree of agreement with the chlorophyll and nutrient climatologies. Figure 2 illustrates the pattern found with all the versions of the plankton model that were tried so far. Simulations with both the climatological and stochastic forcing are in broad agreement with the data; however, only the simulation with stochastic forcing is able to match the timing of the spring bloom and reproduce the pattern of nutrient depletion during winter-spring. All model versions, whether they have only two compartments (P and N) or four compartments (zooplankton (Z) and detritus (D) added as prognostic variables), are able to get the timing of the spring bloom correctly with stochastic forcing. Conversely, none of the versions is able to get this timing right with climatological forcing. Therefore, if we limit our interest to the timing of the spring bloom, the biological details seem secondary to the physical forcing.

Looking at a broader range of diagnostics of the match between model and data gives a different picture but still illustrates the strong impact of the physical forcing scenario (Table 1). With climatological forcing, there are large differences in how different plankton model structures and parameterisations reproduce the data. These differences in model-data agreement are much reduced when the stochastic forcing is used. In fact, the only substantial impact on the diagnostics under stochastic forcing is the change from a 2- to 4-compartment structure. The 4-compartment (PZND) model gives not only better agreement with chlorophyll and nutrients but also a better representation of the annual primary production, the ratio of new to total production (f-ratio) and the peak intensity of the spring bloom. Herbivorous and omnivorous versions of the PZND model fit the data equally well and the choice of grazing function does not have an impact on model-data comparisons. These results are preliminary and subject to change pending the results of further sensitivity analyses. Nevertheless, they do illustrate that what plankton model is considered best depends to a large extent on the forcing used. Although a number of studies have shown the impact of short-term mixed-layer variability on plankton model results (e.g., Bissett *et al.* 1994), most plankton model development studies still use smooth climatological forcing (e.g., Spitz *et al.* 2001). Our results stress that the importance of the appropriate forcing should not be underestimated.

References

Bisset, W.P., Meyers, M.B., Walsh, J.J., and Muller-Karger, F.E. 1994. The effects of temporal variability of mixed layer depth on primary productivity around Bermuda. J. Geophys. Res. C: 99: 7539–7553.

Li, W.K.W., and Harrison, W.G. 2001. Chlorophyll, bacteria and picophytoplankton in ecological provinces of the North Atlantic. Deep-Sea Res. II 48: 2271–2293.

Longhurst, A., Satheyndranath, S., Platt, T., and Caverhill, C. 1995. An estimate of global primary production in the ocean from satellite radiometer data. J. Plank. Res. 17: 1245–1271.

Petrie, B., Drinkwater, K., Gregory, D., Pettipas, R., and Sandstrom, A. 1996. Temperature and salinity atlas for the Scotian Shelf and the Gulf of Maine. Can. Tech. Rep. Hydro. Oc. Sci. 171, v+398 pp.

Petrie, B., Yeats, P., and Strain, P. 1999. Nitrate, silicate and phosphate atlas for the Scotian shelf and the Gulf of Maine. Can. Tech. Rep. Hydro. Oc. Sci. 203, vii+96 pp.

Spitz, Y.H., Moisan, J. R., and Abbott, M. R. 2001. Configuring an ecosystem model using data from the Bermuda Atlantic Time Series (BATS). Deep-Sea Res. II, 48:1733–1768.

Vezina, A.F., and Savenkoff, C. 1999. Carbon and nitrogen flows in the surface layer of the NE Pacific. Deep-Sea Res. II, 46:2909–2939.

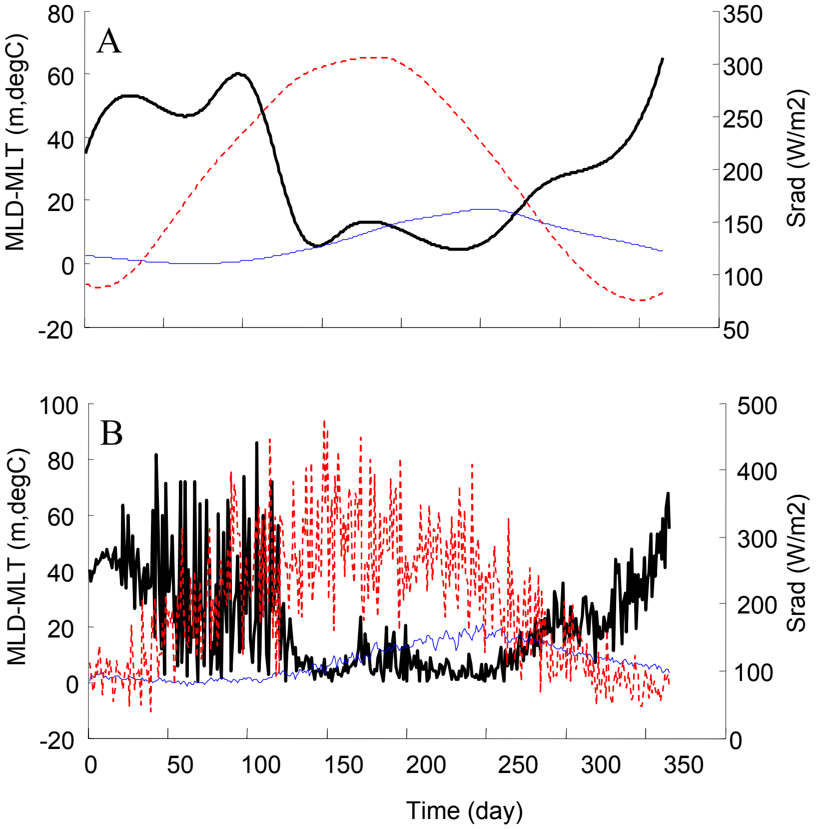

Figure 1. Forcing scenarios for 0-D plankton models of the Scotian shelf. Panel A- Climatological forcing where daily forcing variables are interpolated between their monthly means. Panel B- Stochastic forcing where daily forcing variables are drawn randomly from probability distributions determined from temperature, salinity and radiation climatologies. In both panels, the thick solid line is mixed-layer depth (MLD) in m; the thin solid line is mixed-layer temperature (MLT) in °C; and the dashed line is solar radiation (Srad) in W m^{-2}.

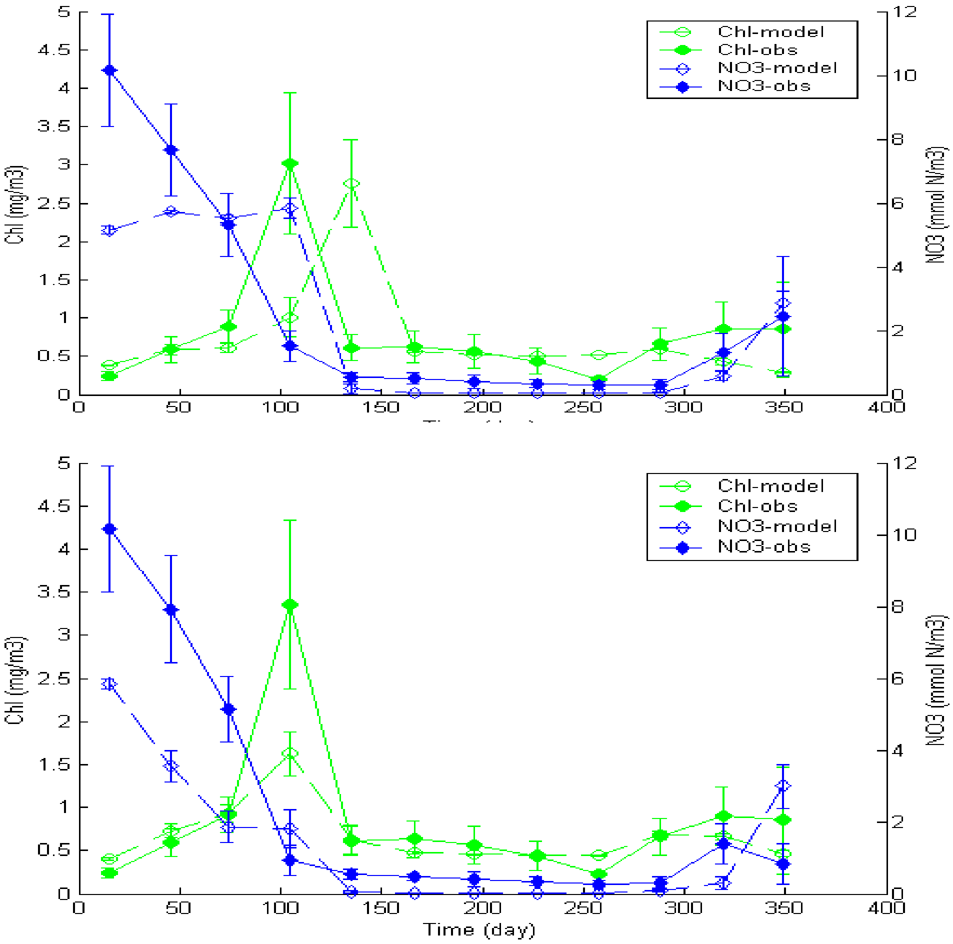

Figure 2. Comparison of model-simulated and observed (monthly climatologies) chlorophyll and nitrate for the Central Scotian Shelf. Top panel: PZND model with climatological forcing. Bottom panel: PZND model with stochastic forcing. Light (green) dots and lines represent chlorophyll; dark (blue) diamonds and dots are NO_3. Open symbols and dashed lines are simulated values; closed symbols and solid lines are observed values. Error bars for the observations represent the standard error of the monthly mean. Error bars for the simulation represent the standard error for the monthly mean of the simulated daily values.

Table 1. Diagnostics for model-data comparisons for different plankton model versions using climatological and stochastic forcing scenarios. The diagnostics include: the root mean square error (RMSE) between observed and simulated monthly means of chlorophyll (Chl) and nitrate (NO3); the annual mean primary production (PP) and the ratio of new to total production (f-ratio); and diagnostics of the timing and intensity of the spring bloom: month during which Chl rises above 1 mg m-3 (Onset), month during which the spring bloom reaches its maximum intensity (Maximum) and Chl level at the spring bloom maximum (Peak Chl). The first line of the table gives the diagnostics derived from the Chl, NO3 and PP climatologies for the Central Scotian Shelf (RMSE is 0 here). The other lines give the diagnostics from the simulations: PN, Phytoplankton-nutrient model; PZND-H, Phytoplankton-Nutrient-Zooplankton-Detritus model with grazing from Phytoplankton to Zooplankton; PZND-O, same as PZND-H except that Zooplankton graze on Detritus as well.

	RMSE		Annual mean		Spring bloom diagnostics		
	mg m^{-3}	mmol m^{-3}	mmol N m^{-2} yr^{-1}		months since Dec 31	months since Dec 31	mg m^{-3}
Source	Chl	NO_3	PP	f-ratio	Onset	Maximum	Peak Chl
Climatological obs.	0	0	2.03	0.3	4	4	3.2
CLIMATOLOGICAL FORCING							
PN	0.61	2.94	1.95	0.2	2	4	2.13
PZND-H	1.12	1.94	1.72	0.12	3	5	3.57
PZND-O	0.88	2.02	1.61	0.14	4	5	2.76
STOCHASTIC FORCING							
PN	0.62	2.31	1.45	0.63	4	4	1.43
PZND-H	0.52	2.13	1.54	0.39	4	4	1.64
PZND-O	0.53	2.16	1.51	0.47	4	4	1.70

Ecosystem Models with Multiple Nutritional Resources: A Critical Review of Assumed Biological Dynamics.

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Ecosystem models must quantify the intake of multiple nutritional resources (e.g., phytoplankton uptake of new and recycled nutrients, zooplankton consumption of different prey types) in order to partition fluxes, examine processes such as omnivory, estimate production and predict dynamics in nutrition-limited food webs. Implicit in the equations describing how such intake varies with resource densities are assumptions that are not often stated, let alone tested, despite the known sensitivity of models to the form of this functional response. I present a critical review of the assumed biological dynamics in multiple resource models found in the literature. Three classes of responses are defined, and seven diagnostics are used to evaluate example formulations for each class. These models are shown to make vastly different assumptions regarding resource preferences, implied single resource responses, changes in intake with changing resource densities, nutritional benefits of being a generalist and nutritional costs of selection. Some models are further shown to exhibit anomalous dynamics such as negative switching and sub-optimal foraging. I discuss the different ecological consequences, and how recognition of a model's assumptions helps constrain parameters, interpret behaviours, and identify limitations to a model's applicability. I further suggest strategies for assessing uncertainty and sensitivity, and how the model assumptions can help direct future experimental investigations.

An Operational Model System for the North Sea and the Baltic

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At the Federal Maritime and Hydrographic Agency (Bundesamt für Seeschifffahrt und Hydrographie, BSH) an operational model system has been in use for more than 15 years now. In daily routine runs, predictions for up to 84 hours are computed on the basis of meteorological and wave forecasts supplied by the German Weather Service (Deutscher Wetterdienst, DWD).

The main constituents of the model system are a hydrodynamic numerical model for the North Sea and the Baltic (circulation model), programmes to compute the drift and dispersion of substances (dispersion models), a surge model for the North Sea and local models for German estuaries

The circulation model predicts currents, water levels, water temperatures, salinity, and ice cover in the North Sea and Baltic Sea in nightly routine runs on two nested and interactively coupled grids. Grid spacing in the German Bight and western Baltic Sea is 1 nautical mile and 6 n.m. in the other North and Baltic Sea areas.

The model is three-dimensional and takes into account meteorological conditions in the North Sea and Baltic Sea area, tides and external surges entering the North Sea from the Atlantic as well as river runoff from the major rivers. The meteorological data are provided by an atmospheric model of the DWD. To compute the heat fluxes between air and water, the BSH model uses air temperature, cloud cover and specific humidity data above the sea. The circulation model simulates density driven (baroclinic) currents, which depend on the prevailing temperature and salinity distributions. As hydrodynamics is also influenced by ice conditions in the North Sea and Baltic, there is an ice model integrated to simulate formation, melting and drift of sea ice. The circulation model also simulates the falling dry and flooding of tidal flats.

The operational model results are used by different BSH services. Models are validated on a regular basis. As model forecasts are important tools in the BSH's water level prediction service their accuracy is checked daily by comparing measured and computed water levels. Another validation on a routine basis is carried out using data of the German Operational Coastal Monitoring Network (MARNET).

The BSH operates two types of dispersion models serving different purposes. Studies of the dispersion of water soluble substances and of the quality of North and Baltic Sea water are mostly performed using an Eulerian dispersion model while a Lagrangian Model is used primarily to support search and rescue operations and to assist the coast guard in cases of marine environmental pollution. Among its applications are drift forecasts for shipwrecked persons and floating objects (boats, lost cargo etc), as well as drift and dispersion computations for oil and water-soluble chemicals. The model is also used to trace back harmful substances and is thus a valuable tool in identifying environmental polluters.

In the future, efforts will have to be made in several fields of model development. In circulation models, turbulence schemes will have to be improved in order to obtain a better representation of fronts, eddies and stratification. Improving sea ice modelling will also be a subject of further research.

Also drift and dispersion models have to be further elaborated. Research is necessary to include additional chemicals. At the moment, BSH in co-operation with GKSS Research Centre is implementing an operational suspended matter transport model. This and other model improvements are important steps for the development of an operational ecological model for the North Sea and the Baltic.

Stage Resolving Models of Copepods

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An important step towards realistic models of the marine ecosystem is the coupling of biological and circulation models. While the modelling of the lower trophic levels has made progress in the last years the description of stage resolving zooplankton in a 3d ecosystem model is still in a preliminary state. The paper presents a zooplankton model which includes the lower trophic levels of the food web and which can be embedded in a circulation model in a consistent manner. The model has two sets of zooplankton state variables, the biomass and number of individuals of the stages. As the 'model-copepod' we choose (Pseudocalanus), but the model can be applied to other species in a straightforward way. The model is used to simulate rearing tank experiments under constant environmental conditions. A linkage to oceanic conditions was achieved by embedding the copepod component in an ecosystem model of the Baltic Sea. The temporal and spatial variations of various stages were presented.

The Vernal Bloom in the Heterogeneous Convection of the Baltic Sea

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The onset of the vernal phytoplankton bloom in heterogeneous convection at a temperature below the temperature of maximum density (θ_ρ) is studied by means of an idealized numerical model. The modelled setting resembles the well documented conditions in the Baltic Sea. The convection in this inland sea is initially driven by surface heating, in marked contrast to oceanic conditions, where cooling serves the purpose. The heterogeneity of the physical environment is enhanced by a lateral freshwater flux, which stratifies parts of the domain and allows the surface to warm above θ_ρ in the stratified areas. Consequently, the same surface heat flux may cause convection in some parts and stabilisation in other parts of the domain. The development of a layer of anomalously cold water with $\theta < \theta_\rho$ is demonstrated numerically.

The physical heterogeneity is strongly reflected in the development of the vernal bloom, with significant phytoplankton growth possible only in the stratified areas. The non-local turbulence in the mixing layer plays a dominant role in the development of the bloom.

Except in numerical and analytical models, the existence of a bloom in an unstratified water column is somewhat questionable. Turbulence in an unstratified fluid is known to be poorly described by local gradients. Instead, non-local effects (e.g., eddies occupying the whole water column, Langmuir cells, other boundary sources of turbulence) are known to be important for redistributing tracers in such layers. For state variables of seawater (salinity, temperature) the difference is not always obvious, because a stability-dependent parameterisation of vertical mixing (large Laplacian diffusion, convective adjustment) will under most conditions homogenise such tracers.

However, a reactive compound which is not a state variable of seawater, such as to a good approximation phytoplankton, may develop large vertical gradients if sufficiently weak Laplacian diffusion is used to describe the vertical mixing. Since the real physical mixing in the unstratified column under such conditions is largely determined by external fluxes, it is possible to create a model bloom in conditions where none would occur in Nature, due to the absence of a description of the non-local turbulence.

If a bloom is to occur under unstratified conditions in reality, as implied by the critical turbulence theory, this process is probably very sensitive to environmental conditions and therefore most likely to occur in sheltered environments where external disturbances, and hence also the non-local mixing, are minimized. The observational evidence for such blooms in open water bodies is scarce. On the other hand, Lagrangian evidence for a behaviour of the type shown in the present study is given e.g., in the results using neutrally buoyant Lagrangian drifters. In such observations, the stratifying effect of solar heating made the convection cease during daytime, to be continued at night, whereas in the present study the convection ceases for the rest of the season because of the stratifying effect of laterally spreading freshwater.

Environmental Status of the North Sea and Skagerrak 2000

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Introduction

NORWECOM (Skogen and Soiland, 1998), has been used to simulate the year 2000 in the North Sea and Skagerrak. The model outputs have been used to make an environmental status for that year. A nested model system has been used, with a coarse (20 km resolution) model for the North Sea and a fine scale (4 km) model for the Skagerrak. The North Sea model was spun up by running 1998 three times, and then 1998 through 2000 was run sequentially. The fine grid model was initialised with results from the coarse grid model 5 January 1999. The 4 km model was then run from 5 January 1999, through 2000 with boundary conditions from the 20 km model.

The models have been run with realistic forcing (wind, waves, light, heat fluxes, pressure, evaporation, precipitation and river runoffs). The main limitation in this context is the lack on data for the Baltic outflow, and the use of climatological values for a few rivers.

Results

The annual depth integrated primary production (gC/m^2/year) for the 20 km North Sea model is shown in Figure 1. For the North Sea the highest modelled production is along the southern North Sea continental coast with an annual production of more than 200 gC/m^2/year. This is more than 3 times the value in the central and northern North Sea. In the Skagerrak (except for the Danish coast), the coarse model gives production estimates between 100 and 150 gC/m^2/year, while the production outside the Norwegian west coast is around 100 gC/m^2/ye.

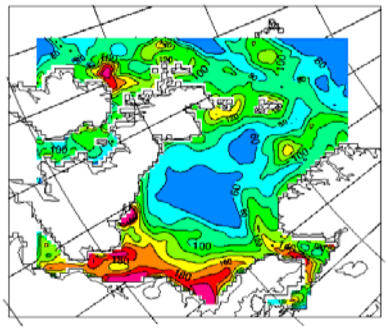

Figure 1. **Primary production.**

One of the main concerns related to eutrophication is oxygen depletion. High production can locally give rise to low oxygen values in stagnant water. In Figure 2 modelled oxygen in the lowermost model level (within 2.5 % above the sea bottom) for week 37 is shown. During summer, an oxygen minimum are developing south and east of the Dogger Bank, and two local oxygen minima (extending towards the Skagerrak) are seen in this area. They are both connected to a local minimum in the topography, where stagnant waters are appearing ant. At this time the modelled oxygen levels are just below 3 ml/l

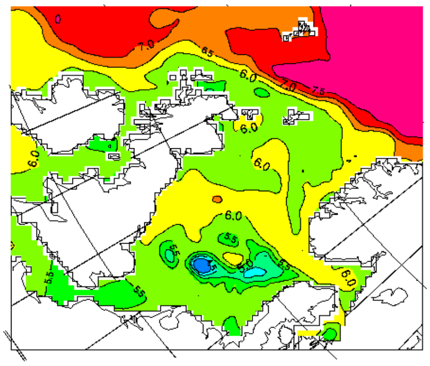

Figure 2. Oxygen week 37.

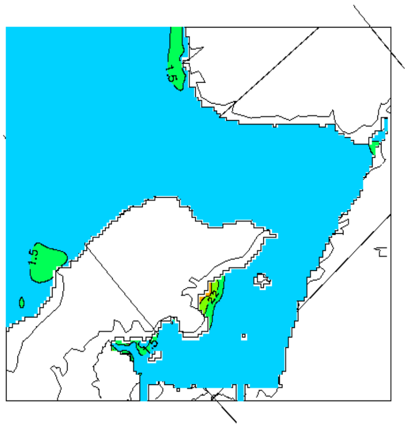

Figure 3. Chlorophyll eutrophication assessment.

The supply of nutrients and the possible eutrophication of the open sea and coastal waters (e.g., extensive algal blooms, oxygen depletion, extinction of bottom living species) can be studied with various types of measurements and observations. Accordingly, a number of parameters are needed as assessment criteria. The Swedish Environment Protection Agency has made such a set of assessment criteria (bottom oxygen, chlorophyll$_a$, winter nutrients) for Swedish and adjacent waters which can highlight the effect of eutrophication. In Figures 3 and 4, the assessment levels of chlorophyll$_a$ in August, and nitrate in January are shown. The results show some small areas on the Danish east and west coast with different levels of eutrophication.

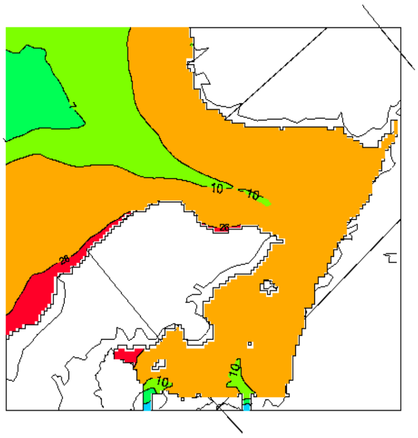

Figure 4. Winter nitrate eutrophication assessment.

References:

Skogen, M.D. and Soiland, H. 1998. A User's guide to NORWECOM v2.0. Tech. Report Fisken og Havet 18/98. Inst. of Marine Res., Bergen, Norway. 42pp.