Oceanography Committee **ICES CM 2003/C:04**

Report of the

Study Group on Modelling of Physical/ Biological Interactions

Chapel Hill, USA
10–12 March 2003

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

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1 WELCOME AND OPENING OF THE MEETING

The meeting of the ICES Study Group on Modelling Physical-Biological Interactions (SGPBI) was held at the University of North Carolina, Chapel Hill, N.C. from 10–12 March 2003. The meeting opened at 10 am with a welcome from Cisco Werner, Chair of the Department of Marine Sciences, Chair of the International GLOBEC Scientific Steering Committee and our host.

The meeting was attended by 14 people (Annex A), of these nine had attended one of the two previous meetings and there were five new members.

The Study Group Chair, Charles Hannah (Canada), was unable to attend the meeting. Alain Vezina (Canada) acted as Chair for the meeting.

2 TERMS OF REFERENCE

The terms of reference for the meeting were as follows:

The **Study Group on Modelling of Physical/Biological Interactions** [SGPBI] (Chair: C. Hannah, Canada) will meet in Chapel Hill N.C. USA from 10–12 March 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.

The agenda for the meeting is given in Annex B. Beyond the stated terms of reference, the focus of this meeting was the future of SGPBI. This was the third meeting of the study group and a decision had to be made on how to proceed into the future.

3 CONCLUSIONS

1. The enormous increase in data that will result from GOOS will provide tremendous opportunities to explore new ideas and critically test existing hypotheses that have been intractable.
2. Trophic food web modelling is starting to incorporate turbulence as an environmental factor affecting different planktonic organisms and processes, e.g., nutrient fluxes towards osmotrophic cells and encounter rate kernels for zooplankton predators. The effects of turbulence on planktonic processes is an important factor within the framework of understanding ecosystem response to human activity and climate change.
3. The concept of state densities allow a consistent derivation of different types of models ranging from single individuals to many individuals, population and biomass models of different complexities. This approach, which may provide a way to bridge the gap between ecosystem models and fishery models, needs further elaboration.
4. The present state of the art for modelling the random walk in inhomogeneous turbulence in oceanography would benefit from adapting existing high performance algorithms for simulation of general stochastic processes. Extensions beyond a single passive tracer are available, but require careful model validation, because their foundation is more heuristic.
5. Diapause (a dormancy state) is an important component of the life cycle of a number of ecologically important zooplankton species. However, the factors responsible for the initiation and termination of diapause and the choice of overwintering depths are not sufficiently well known for the development of a generic model, even for the best

studied species, *Calanus finmarchicus*. Ongoing research, much of it associated with several GLOBEC programmes in the North Atlantic, should improve our understanding of this process.

6. SGPBI should be reconstituted as a Working Group (WGPBI) in order to continue with its work and a 5 year plan should be drafted before the next meeting.
7. WGPBI should work with other ICES Working Groups to identify emerging issues in physical-biological interactions.
8. SGPBI (and WGPBI) should make open, community modelling a central component of future efforts.

4 PRESENT AND DISCUSS NEW RESULTS (TOR A)

Eight presentations were given. The abstracts can be found in Annex C**.** This forum served to introduce the new study group members and to introduce many of the ideas discussed later in the meeting. The discussions were lively and wide ranging and are not reproduced here. Many of the presentations represented work that will be published in the open literature.

Wolfgang Fennel encouraged everyone to submit papers to the Special Session on Physical-Biological Interactions in Marginal and Shelf Seas at the ICES meeting in Tallinn, September 2003.

Cisco Werner (GLOBEC SSC) reported on two activities focusing on marine ecosystem modelling at basin-scales and in linking lower and higher trophic level models.

1) GLOBEC/IOC/SCOR workshop on “Extending Ecosystem Models to the Basin Scale”, Chaired by Brad de Young. A fundamental biological problem is how to resolve the mass-balance representation of production with the life-history developments that are important at higher trophic levels. Integrating detailed biological models with large-scale physical models begs fundamental scientific questions of model resolution and fidelity to key processes. This problem is at the forefront of marine science and while there have been some attempts at basin-scale, ecosystem models, there remain many fundamental issues to resolve. Many of the required components for the development of basin-scale ecosystem models now exist but uncertainty remains about how to put the pieces together. At these workshops a review of this problem would be undertaken with the following as the Terms of Reference:
    - To review and discuss approaches for the development of models that includes population structure and dynamics and how to integrate such models into basin-scale circulation models.
    - To review the necessary assumptions underlying the model architecture and consider different possible approaches for ensuring that the model is suitably designed for the basin-scale ecosystem problem.
    - To review and consider different numerical approaches, different possible trophic architectures and different possible population dynamics models. Integration across trophic levels, and fidelity to life history, will be key issues.
    - To review key work in the scientific literature on ecosystem modelling from four very different oceanographic regimes: the North Atlantic, the North Pacific, the Southern Ocean and the equatorial Pacific. Key species will differ between these basins as will the connections to higher and lower trophic levels.
    - The will be one workshop in May and one in the fall of 2003. The results will be targeted for publication in the primary scientific literature.
2) PICES activities on linking spatially-explicit higher and lower trophic level models. A workshop was held in Yokohama, Japan, the week of 3 March 2003. The objectives included:
    - Complete the 2-way dynamic linkage between the NEMURO Lower Trophic Level model (Kishi *et al.,* 2001) and the NEMURO.FISH Higher Trophic Level model (Megrey *et al.,* 2002);
    - Develop a plan to implement the 3-D spatially explicit version of NEMURO.FISH for the study of Pacific Saury (off the coast of Japan, in the area of the Kuroshio and Oyashio’s confluence) and Pacific Herring in areas including the Sea of Okhotsk, the Bering Sea and the Canadian and US west coasts; and
    - Begin to expand the scale of NEMURO to allow age-structured population dynamics in the NEMURO.FISH component.

    The workshop was successful in achieving several of these goals and publication of results is targeted for a special issue of Ecological Modelling - papers to be submitted in late 2003.

References

Kishi, M. J., Megrey, B. A., Eslinger, D., Rose, K. A., Ware, D. M., Werner, F. E. 2001. Report of the 2001 PICES MODEL Task Team workshop on strategies for coupling higher and lower trophic level marine ecosystem models: status of the LTL model. GLOBEC Newsletter 7(1): 3–6.

Megrey, B. A., Kishi, M. J., Hay, D., Ito, S., Klumb, R. A., Rose, K., and Werner, F. E. 2002 Report of the 2002 PICES MODEL/REX Task Team Workshop to Develop a Marine Ecosystem Model of the North Pacific Ocean Including Pelagic Fishes: NEMURO.FISH. GLOBEC Newsletter, 8(2):25–27.

5 REVIEW A PAPER WHICH PROVIDES A DERIVATION OF MODEL EQUATIONS TO FORM A BASIS FOR INTERCOMPARING MODEL ASSUMPTIONS (TOR B)

Wolfgang Fennel presented a paper on the ‘Derivation of Model Equations to Form a Basis for Intercomparing Model Assumptions’ by Fennel and Osborn (Annex D). The primary conclusions were that 1) the concept of state densities allows a consistent derivation of different types of models ranging from single individuals to many individuals, population and biomass model of different complexity; and 2) this approach, which may provide a way to bridge the gap between ecosystem models and fishery models, needs further elaboration. The work will be presented at the ICES ASC in Tallinn and a manuscript is in preparation for submission to a scientific journal.

The discussion of the paper focussed on the relationship between the state density concept and the super-individual approach in individual based models (IBM). This issue was not considered in the paper but the authors are confident that it can be resolved.

A second question was whether the state density approach could lead to a tool to provide guidance on whether an IBM model or a biomass model was appropriate for a particular problem. This question awaits further development of the state density approach.

6 REVIEW MODELLING TECHNIQUES FOR RANDOM WALK IN INHOMOGENEOUS TURBULENCE FOR PARTICLES WITH ACTIVE BEHAVIOUR (TOR C)

Uffe Thygesen gave a talk entitled ‘Lagrangian Random Flight Modeling of Turbulent Dispersal: A Brief Primer and Review.’ The full paper can be found in Annex G.

The talk provided a good presentation of the basic theory of how one combines particle tracking with in inhomogeneous turbulence. He defined a hierarchy of models:

1) Random walk where only the position is considered a Markov process. This is the diffusion limit.
2) Random flight where both the position and velocity are considered to be Markov processes. Compared with random walks, they offer greater accuracy at short scales - e.g., near a point source - because the random walk predicts infinite velocities and thus exaggerates initial dispersal.
3) Models where the acceleration is considered a Markov process.

Uffe explained that Random Walk (Random Displacement) and Random Flight models can be correctly applied in situations with inhomogeneous turbulence if they include a term that moves particle away from low diffusivity areas. He summarized the derivation of these ‘correction’ terms.

He also discussed issues related to the numerical discretisation of the stochastic differential equations and how one would move beyond passive tracers to active ones. Both of these areas are topics of future research and will be reported on at future meetings.

Important points from the talk and the discussion:

1) Most of the theory has been developed in the atmospheric literature and oceanographers and marine scientists take advantage of the developments in the atmospheric dispersion community.
2) Schemes must satisfy the ‘well mixed condition’
3) Can this work lead to guidelines for limits on the time step and vertical mesh size?

4) There need to be standard test cases for validation of numerical codes for the random walk (and flight) in inhomogeneous turbulence.

Much of the presentation covered similar material to the review of Brickman and Smith (2002). Publication of this work in the open literature will require a focus on the aspects that make it unique.

The area is a natural one for SGPBI to contribute to the dissemination of information on best practice.

7 REVIEW THE STATE OF KNOWLEDGE OF ZOOPLANKTON DIAPAUSE AND ENCYSTMENT AND EXCYSTMENT OF SELECTED PHYTOPLANKTON SPECIES (TOR D)

7.1 Zooplankton diapause

Annex E contains a report on ‘Overview of Dormancy (Diapause) in Copepods’ by Gentleman and Runge, which provides a review of what is known and not known about diapause with a focus on *Calanus finmarchicus*. The work is part of their research in the USGLOBEC Georges Bank programme. The report was presented by A. Vezina as W. Gentleman was unable to attend.

It is clear that diapause is an important component of the life cycle of zooplankton species such as *Calanus finmarchicus*. However, the factors responsible for the initiation and termination of diapause and the choice of overwintering depths are not sufficiently well known for the development of a generic model for the best studied species *C. finmarchicus*.

The discussions of the group indicated that diapause in *C. finmarchicus* was important and more basic biological research on the topic is required. The group expects that ongoing research in zooplankton ecology (for example work associated with WGZE and several GLOBEC programmes in the North Atlantic) will improve our understanding of this process.

7.2 Encystment and excystment of selected phytoplankton species

This topic was not dealt with as Patrick Gentien and Kaisa Kononen were unable to attend. This item will be reconsidered as part of the plan for the future activities of WGPBI.

8 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 (TOR E)

The Chair and the host were unable to get an outside expert to provide such a review for this meeting. This item will be reconsidered as part of the plan for the future activities of WGPBI.

9 REFINE AND REVISE THE GROUP’S STRATEGY FOR CONTINUED MODEL DEVELOPMENT FOR UNDERSTANDING AND FORECASTING PHYSICAL/BIOLOGICAL/CHEMICAL INTERACTIONS (TOR F)

This topic was broadened to include all discussions of the future of SGPBI. This was the third meeting of the study group and by ICES policy study group only exist for 2 or 3 meetings. A decision had to be made on how to proceed into the future. The document in Annex F was distributed before the meeting to stimulate discussion on this topic.

On Tuesday afternoon, there was a lively discussion of the progress that the group had made toward addressing the SGPBI’s original ToR. This discussion ranged broadly, but attention focused most on progress SGBPI has made toward defining “Best Practices” in modelling biological-physical interactions, and the challenges and opportunities that face researchers working at the interface of biology and physics as global ocean observing systems become operational.

Attendees concluded that the study group had made progress in defining “Best Practices” in modelling biological-physical interactions. The review of prey selection by W. Gentleman (Canada; last year’s report), the theoretical foundation of individual-based model and aggregated cohort models currently being developed by W. Fennel (Germany) and T. Osborn (USA) and the review of the incorporation of small-scale turbulence in particle tracking algorithms by U. Thygesen (Denmark) were viewed as representative of these efforts. Some attendees expressed concern that the resolution and scales of models of biological-physical interactions considered to date has been narrower than is desirable. Peters (Spain) urged the group to consider how physical interactions can best be represented in ecosystem level questions that would intractable if dealt with at an individual-level basis. Concern was also expressed that the SG had not clearly defined links to management problems and concerns that could be addressed with models of biological-physical interactions. Attendees suggested that only within such a context could "best practices" be adequately defined. Svendsen (Norway) suggested that identification of the scale and scope of the process to be predicted is required to determine the level of resolution required in the model. He urged more consideration be given to this issue to determine whether SGBPI could provide suitable guidance.

Werner (USA) brought to the Study Group's attention the opportunities and challenges arising from international efforts to institute global ocean observing systems (GOOS) that lay ahead in modelling biological-physical interactions. Werner recommended that the SGPBI consider the opportunities that the tremendous increase in data that will result from GOOS will provide over the next decade. Osborn (USA) concurred, indicating that this represents an opportunity to explore new ideas and critically test existing hypotheses that have been intractable up until now. Fennel (Germany) noted the benefits of open, community modelling and encouraged the SG to make such openness a central component of future efforts. Thygesen (Denmark) suggested that the role of benchmark data sets to which models could be compared would be beneficial also. The use of the Bermuda, and Hawaiian time series in climate modelling were cited as examples.

Following this broad ranging discussion, the group began to develop new ToR that seek to define and promulgate best model practices but also look to future opportunities and challenges.

Wednesday morning was devoted to writing the resolution for the conversion of the Study Group to a Working Group. The results of most of the discussion are reflected in the resolution and are not repeated here.

In discussions before the meeting, C. Hannah (Chair) had suggested that an important item for the new WG was a 5 year plan to help focus the efforts of the WG. Participants suggested that a draft of a 5-year plan should be circulated before the next meeting. This would facilitate discussion at the meeting.

The following items should be considered in the development of such a plan:

- C. Werner urged the group to think about WG deliverables and specific actions. Participants discussed hosting theme sessions at ASC, inviting other WG members to our meetings, holding special symposiums, and being ex-officio members on other committees.
- C. Werner suggested that the important review and synthesis work of SG members should be available to as wide an audience as possible. He reported that the GLOBEC modelling group is conducting a review of the state of the art in basin scale ecosystem modelling with the goal of producing a position paper in *Science* or *Nature*. Instead of just communicating results in SG reports, he encouraged U. Thygesen and W. Fennel to publish their presentations, and suggested that these types of publications be one of the proposed WG goals and deliverables for the 5-year plan.
- Linking large global models with regional models.
- Model validation issues.
- Review numerical experimental simulation of nutrient load reduction. What kind of products could come out from this type of modelling? (Neumann, Einar, Stipa)
- How do we introduce turbulence into basin scale models? Tim Peddley's group in Cambridge is working on it (Ashley Metcall).
- F. Peters and A. Gallego suggested that future meetings of the potential WGPBI could be organized around specific themes like diapause or laboratory techniques to simulate turbulence. The WG could invite experts to present their research and summarize the state of the art in their field during the first two days of the meeting. WG members could hold the regular procedural meeting on the third day. Although this type of 'theme meeting' may not be appropriate for the next meeting when we discuss the 5 year plan, it could provide a useful model for future meetings. Its success would depend upon the interest of, and funds available to, the invited experts. Drawbacks might include a drop in attendance of WG members if the meeting theme was too narrowly focused, as well as the difficulty of 'un-inviting' the experts to the WG meeting on the third day.
- Plans to promote the use of physical-biological model results through improved dissemination of hindcasts, nowcasts and forecasts for management concerns that are relevant to ICES.
- Enhance existing physical-biological modelling by identifying areas of lack of knowledge or lack of skill that constrain progress, by providing reviews of best modelling practices, including model calibration and validation, and by promoting exchanges of latest technologies/ideas on model development.

- Provide guidance for future developments in physical-biological modelling needed to incorporate new data from observing systems, to take advantage of new observational technologies, to integrate with regional and global models, and to incorporate new insights into coastal oceanography, e.g., thin layers.
- Over the short term the plan should include special sessions at ICES ASCs devoted to the topic of physical-biological interactions. On the short and medium term there needs to be constant liaising with other relevant Working Groups. On the medium term (5 years) there should be a major a symposium on advances in MPBI.

Participants agreed that the WG should continue to establish links with other working groups, like the Zooplankton and Recruitment Processes Work Group, before and during the meeting next year. The group asked that the Chair work with other ICES WG to identify emergent physical-biological interaction issues. We could:

- Invite experts and members from other WG to the proposed WG meetings.
- Hold an informal meeting in Tallinn, invite experts and members of other WG, and ask meeting participants to identify priority areas for modelling physical-biological interactions.
- Send a survey to Working Groups, talk to other WG members at ASC and prepare a review of WG needs for discussion at the next meeting.
- Establish ex-officio members of other WG.

Attendees agreed that it was important to be responsive to the needs of other WG, but not become driven by them. A balance should be struck between service and leading.

The Chair had asked for a discussion of the draft strategy document that was included with the 2002 report. There were mixed feeling about the strategy document and its usefulness was questioned. Some participants thought it was too biased toward the IBM approach. Others found it generally acceptable. Most agreed that none of the major issues were problematic, just that the document was a bit biased. Due to the lack of time, participants suggested that C. Hannah and A. Vezina re-work the document and send another draft to SG members. Participants made the following suggestions:

- The idea that the IDM approach is the unique solution to every problem should be downplayed (esp. point 8).
- Change the order of the topics in the second paragraph, placing topic 3 first and topic 1 last.
- The strategy document should incorporate ideas that we discussed at this meeting (improve utilization, enhance present understanding, provide a vision for the future) so that the strategy document is consistent with discussions at this meeting as well as with those at previous meetings.

Participants discussed delivery of the strategy document and suggested that C. Hannah give a brief presentation at the PBI Theme session at the ASC in September. Members agreed to send him pictures and animations if he would like to use them.

10 CONCLUDING BUSINESS

The final two issues were the location of the next meeting and a nomination of the Chair for the new working group.

- F. Peters agreed to host the next meeting in Barcelona, Spain, in March.
- Members agreed that C. Hannah should continue as Chair of the proposed WG.

A. Vezina closed the meeting at 12 noon Wednesday March 12, 2003, declaring it a success.

11 ACTIONS, RECOMMENDATIONS AND DRAFT RESOLUTIONS

Action 1: C. Hannah will prepare a paper for the Special Session on Physical-Biological Interactions in Marginal and Shelf Seas at the ICES ASC in September.

Action 2: C. Hannah and others will prepare a draft 5 year plan to WGPBI for consideration at the next meeting.

Recommendation I:

The **Study Group on Modelling Physical/Biological Interactions** [SGPBI] will be re-established as the **Working Group on Modelling of Physical/Biological Interactions** [WGPBI] (Chair: C. Hannah, Canada) and will meet on 10–11 March 2004 in Barcelona to:

a) Present and discuss new results related to developments and validation in the modelling of physical/biological interactions;
b) Review experimental simulations on nutrient load reduction;
c) Review the findings of the Workshop on Future Directions in Modelling Physical-Biological Interactions [WKFDPBI]
d) Identify emergent physical-biological interaction issues relevant to other ICES Working Groups;
e) Review the strategic plan prepared intersessionally that will provide the framework for the future activities of the WG;
f) Cooperate with the ICES/BSRP SG to explore Baltic ecosystem models.

WGPBI will report by 15 May 2004 for the attention of the Oceanography Committee.

Supporting Information

Priority:

The WG should be given high priority since it is concerned with the evaluation and development of the modelling tools 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 the successful development of predictive capability of the state and evolution of the ecosystem for issues such as harmful algal booms, eutrophication, marine protected areas, fish recruitment, and global change. This contributes directly to fulfilling the vision of ICES, “to improve the scientific capacity to give advice on the human impact on, and impacted by, marine ecosystems.”

Scientific Justification:

The field of physical-biological interactions (PBI) is growing rapidly and is central to understanding zooplankton dynamics and predicting HABs, fish recruitment, and the response of the marine ecosystem to human activities and the influences of climate change. Physical-biological interactions are a core element of international programs such as GLOBEC, GEOHAB and the new IGBP/SCOR program in ocean chemistry and ecosystem analysis. The complexity and highly variable dynamics of the ocean anticipates that significantly improved quantitative and qualitative ecological understanding and predictability can only be achieved by extensive use of mathematical models in close integration with regular observations and basic knowledge of the functioning of the marine ecosystem. Therefore modelling physical-biological interactions is required in order to extrapolate beyond the range of observational experience and to explore scenarios to assist in management decisions.

In three years SGPBI has grown to include 29 members and has established strong linkages with modelling groups in GLOBEC and GEOHAB. One of the goals of SGPBI was to provide a venue for communication between ICES scientists involved in modelling physical/biological interactions and the broader international community. We have been successful and the proposed WG will carry on with this activity.

Improvements in observational and computational capabilities mean that new questions will continue to arise and lead to new solutions. Over the next 5–10 years, observing systems will provide vastly improved physical and biological fields in real time for the initialization and validation of physical-biological models. This will shift the emphasis in modelling from hindcasting past conditions towards nowcasting and forecasting physical and biological conditions. A working group is required now to work towards modelling tools that successfully meet the challenge of nowcasting and forecasting in support of ecosystem-based research and management.

A WG is needed to exchange ideas among the diverse fields that utilize modelling of PBI, to review and summarize progress and to communicate these advances to the scientific and management community. The working group format will allow the group to take a longer perspective and to develop a plan for activities on projects that require more than 2 or 3 meetings.

Terms of Reference:

a) Providing a forum for the presentation and discussion of new results is an important component of the group's mandate.

b) The issue of how an ecosystem will respond to nutrient load reductions is of wide interest. Members of WGPBI will conduct a joint review of their experimental simulations of nutrient load reduction in the Baltic and the North Sea/Skagerrak.

c) The WG has proposed a workshop on 'Workshop on Future Directions in Modelling Physical-Biological Interactions [WKFDPBI] immediately before the WG meeting. The purpose of the workshop is to identify key areas where existing techniques for modelling physical-biological interactions need to be improved. These findings will be reviewed and considered for incorporation into the strategic plan for the WG.

d) WGPBI will work with other ICES Working Groups to identify emerging issues in physical-biological interactions so that the work of WGPBI remains relevant to ICES.

e) The plan will describe the goals of the WG and include specific workshops and manuscripts. The plan will likely include items on best modelling practices, including model calibration and validation, modelling the interaction of turbulence and plankton, and the promotion of the use of physical-biological model results through improved dissemination of hindcasts, nowcasts and forecasts for management concerns that are relevant to ICES, and over the medium term (5 years) a symposium on advances in modelling PBI (likely joint with GLOBEC, PICES, and GEOHAB).

f) The Baltic Sea Regional Project is supported by the World Bank and aims at improvement of infrastructure for science driven monitoring. The data are needed for assessment and modelling. To support future generations of models of the Baltic Sea the requirements for data set need to be defined in order to make best use of the invested funds. Ecosystem models of the Baltic covering the food web from nutrients to zooplankton. The top down control is truncated and parameterized in terms of mortality while fishery models ignore widely the bottom up effects. Future generation of Baltic Sea models can be envisaged which link bottom up and top down controls.

Relation to Strategic Plan:

All proposed activities are essentially directed towards scientific objectives 1a, 2a and 2b and contribute directly to fulfilling the vision of ICES, "to improve the scientific capacity to give advice on the human impact on, and impacted by, marine ecosystems."

Resource Requirements:

No specific resource requirements beyond the need for members to prepare for and participate in the meeting.

Participants:

The working group benefits from the participation of those outside of the modelling community. Observational and experimental scientists with an interest in physical-biological interactions are encouraged to attend.

Secretariat Facilities: None

Financial: None

Linkages to Advisory Committees:

Relevant to the work of the ACFM, ACE

Linkages to other Committees or Groups: ICES-IOC Working Group on Harmful Algal Bloom Dynamics, WGZE, WGRP

Linkages to other Organisations: GEOHAB (IOC/SCOR), GLOBEC (IOC/SCOR), PICES

Recommendation II:

A workshop on **Future Directions in Modelling Physical-Biological Interactions** [WKFDPBI] (Co-Chairs: F. Peters, Spain, and C. Hannah, Canada) will be held in Barcelona Spain from 8–9 March 2004 to:

a) Review the current state of the art in several fields that require modelling physical-biological interactions and are relevant to ICES: e.g., fisheries recruitment, harmful algal blooms, eutrophication.
b) Identify the key areas where model improvements are required.

The workshop will report by 15 May 2004 for the attention of the Oceanography Committee.

Supporting Information

Priority:

This workshop is an important information gathering activity for WGPBI as it develops its strategic plan.

Scientific Justification:

The Study Group on Modelling Physical-Biological Interactions (SGPBI) has been active for 3 years and has proposed conversion to a Working Group (WGPBI). As part of this conversion a strategic plan is being developed. This workshop will provide a forum for the discussion of the current generation of models and their strengths and weaknesses. The results of the workshop will be used to ensure that the WGPBI work plan is consistent with the needs of the community. The workshop will also enable WGPBI to establish lines of communication with modelling communities throughout ICES member countries. The four proposed themes of the workshop are: Fish stock recruitment, Harmful algal blooms/Eutrophication; Modelling approaches; and Ecosystem integration and questions of scale.

Relation to Strategic Plan:

The workshop will help WGPBI develop its plan for future activities. The goals of WGPBI are directed towards scientific objectives 1a, 2a and 2b and contribute directly to fulfilling the vision of ICES, "to improve the scientific capacity to give advice on the human impact on, and impacted by, marine ecosystems."

Resource Requirements:

No specific resource requirements.

Participants:

Participants: This Workshop should attract 25–40 participants. This is expected to include some scientists from outside the regular ICES scientific community. We will invite participation from ICES Working Groups (and other ICES groups) with an interest in Physical/Biological Interactions (e.g., WGPE, WGZE, WGHABD, WGCCC, WKHABWATCH, PGNSP, SGGOOS) and from groups such as GLOBEC and PICES.

Secretariat Facilities: None

Financial: None

Linkages to Advisory Committees:

Relevant to the work of the ACFM, ACE

Linkages to other Committees or Groups:

ICES-IOC Working Group on Harmful Algal Bloom Dynamics, WGZE, WGRP

Linkages to other Organisations:

GEOHAB (IOC/SCOR), GLOBEC (IOC/SCOR), PICES

ANNEX A: LIST OF PARTICIPANTS

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ANNEX B: DRAFT AGENDA

ICES Study Group on Modelling Physical/Biological Interactions

3nd meeting, Chapel Hill, North Carolina, USA, from 10–12 March 2003

Monday 10 March

09:00	Pick up at the hotel (Cisco Werner)
10:00	Opening, Introduction and Logistics (Alain Vezina and Cisco Werner)
11:00	Presentations #1 (4 talks)
12:30	Lunch
2:00	Presentations #2 (5 talks)
4:00	Model Equations (Wolfgang Fennel plus others)
6:00	Done for the day

Tuesday 11 March

9:00	Modelling techniques for the random walk (Uffe Thygesen)
10:30	Break
11:00	Plankton reviews (Alain Vezina)
12:00	Review Agenda
12:30	Lunch
2:00	Future plans for SGPBI
4:00	Strategy Document
5:30	Discuss location and time for next meeting
6:00	Done for the day

Wednesday 12 March

9:00	Write key resolutions
11:00	Chose location and time for next meeting
12:00	Adjourn

ANNEX C: ABSTRACTS FROM THE OPEN FORUM

A model of the effects of stock structure and spatio-temporal factors on cod and haddock recruitment

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This work describes a bio-physical model developed during the course of the EU-funded STEREO project (FAIR-CT98–4122). The model itself was mostly developed by scientists at FRS Marine Laboratory and the University of Aberdeen but it is based on the collaborative work of colleagues from the Danish Institute for Fisheries and Marine Research, the Institute of Marine Research (Bergen, Norway), the Institute fur Meereskunde (Hamburg University, Germany), the Marine Research Institute (Iceland) and the University of Strathclyde (Glasgow, Scotland). The overall objective of the project was to develop dynamic stock-recruitment relationships for cod and haddock which take account the effect of both the environment and the internal structure of the spawning stock.

The model can be conceptually divided into three modules:

- an egg production model
- an early life history transport, growth and survival module; and
- a settlement module

The egg production model

The rationale behind the egg production model is that the structure of the spawning stock (relative abundance of age classes, spawning history, condition, etc.) has the potential to influence the timing and duration of spawning, its geographical location and the characteristics of the eggs produced. The inputs into this model are stock assessment data (VPA) on numbers at age, disaggregated by means of statistical tools developed from the analysis of historic survey data. Estimates of fishing and natural mortality (in the case of the former, spatially and temporally resolved) were applied to account for the effect of the spawning stock mortality on the quantitative spatio-temporal patterns of egg production. The model was constructed and parameterised using field (samples from survey and commercial sources) and experimental data. The output of the egg production model was the number of eggs (of given characteristics) at the nodes of a regular grid covering the model domain produced daily over the duration of the spawning season. These data were the main input into the early life history transport, growth and survival module.

The early life history transport, growth and survival module

This model is based on particle tracking methodology. Particles representing the daily egg production at each egg production model grid node (or a proportion of the egg production, if multiple particles per start location were seeded, as in the case of runs where horizontal diffusion was implemented) were tracked within the model domain at hourly intervals for a period of several months (generally until the end of August). The particles were advected horizontally by flowfields produced by a statistical version (SNAC) of the HAMSOM hydrodynamic model (plus tidal and horizontal diffusion velocities), and vertical movements were prescribed semi-stochastically by an ontogenetic relationship developed from the analysis of published data. The duration of the egg stage was a function of the temperature history of the particles representing eggs.

The eggs hatched into pelagic larvae of a size which was a function of egg diameter. From then on, pelagic larval growth in length was estimated purely as a function of temperature exposure. A version to model growth in weight as a function of prey concentration has not yet been implemented. Mortality during the egg stage was size (diameter) dependent (derived from published data). Larval mortality was also size (weight) dependent. The parameters of the larval size dependent function were fitted to match a daily mortality rate compatible with that derived from the re-analysis natural mortality rates used by ICES North Sea stock assessment working groups, while at the same time produce a realistic survivorship from egg to the end of the simulation period, compared to stock assessment results. Mortality was implemented at each time step by reducing the weighting of each particle, i.e., the number of identical larvae from the same origin (in time and space) represented by each particle.

The settlement module

Once the larvae reached a given length, they were allowed to settle if the conditions were right. A grid of carrying capacity was superimposed onto the model domain, on the basis of suitable seabed area (area within a given depth range, at present) and the historic maximum observed density of demersal juveniles. The carrying capacity can also be qualified by the presence of 1-group juveniles. Two settlement scenarios were tested. The "competitive exclusion" scenario only allowed settlement in a cell while there was free space in that cell. The larvae that were unable to settle would remain pelagic (subject to increased mortality levels) until they found a suitable free settlement area or died. Demersal growth (and consequently mortality) could be either density dependent or independent. In the "all settle" scenario, all larvae were allowed to settle, as long as there was any suitable area in a given cell, regardless of the number of juveniles already present in that cell. Demersal mortality was density dependent, and demersal growth could be either density dependent or independent. In a version of the "all settle" scenario, the strength of density dependent mortality (and growth, if relevant) could ease as a result of the declining number of demersal juveniles as the season progresses. In another version, however, the density dependent effect was not allowed to ease and would increase as numbers of settlers increased, regardless of how many died.

The model is proving to be a very useful tool to investigate the effects on recruitment of the environment, spawning population structure, distribution of the spawning stock in time and space, and a wide range of many other factors. It can be used to identify areas and periods with the greatest contribution to recruitment, and to assess the likely effect of exploitation patterns and conservation measures on year-class strength. The exploitation of the full potential of this tool is only just starting.

Modeling physical and biological processes in an estuarine turbidity maximum: the challenges of sinking particles and inhomogeneous turbulence

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Estuarine turbidity maxima (ETMs) are characterized by elevated turbidity and suspended sediment concentrations compared to those up- and down-estuary. ETMs are found in coastal plain estuaries throughout the world, including the Tamar, Gironde, Elbe, Weser, St. Lawrence, Fraser, San Francisco Bay/Delta, Columbia, York, Hudson, and Chesapeake Bay estuaries. ETMs are often zones where increased retention and high zooplankton biomass form important larval fish nursery areas. In Chesapeake Bay, the ETM provides nursery habitat for commercially important anadromous fish like striped bass (*Morone saxatilis*).

Episodic discharge, wind events and annual differences in river flow could influence the retention of striped bass early-life stages and their copepod prey in the ETM region. We are evaluating this hypothesis with a coupled biological-physical model of a theoretical estuary. This research is part of the BITMAX program (Bio-Physical Interactions in the Turbidity Maximum, www.BITMAX.org). BITMAX is a multiple-investigator, interdisciplinary program sponsored by the National Science Foundation that applies both field and modelling techniques to answer the question: How do estuarine turbidity maxima entrap particles, retain zooplankton, and promote fish recruitment?

To address this question in a theoretical framework, the BITMAX modelling group adapted the Princeton Ocean Model (POM), a three-dimensional hydrodynamic model, to a straight-channel estuary that was loosely scaled to match upper Chesapeake Bay characteristics. Our enhancements to POM include sediment settling, erosion, deposition and burial components. In addition to Eulerian sediment modelling, we constructed a Lagrangian particle tracking model within the numerical circulation model to simulate the transport of individual particles in the 3-D flow field.

The hydrodynamic model does not simulate sub-grid scale turbulence, an important physical process that influences the distribution of planktonic organisms. We added two sub-grid scale turbulence generators to the particle tracking model: 1) a random walk model with a Markovian process (Dutkiewicz *et al.* 1993, Hood *et al.* 1999) and 2) a random displacement model (RDM) (Visser 1997). Comparison of these models' simulation of neutrally buoyant particle behaviour reveals the challenges of modelling turbulent processes in highly stratified conditions with inhomogeneous turbulence. In the random walk model with a Markovian process, particles artificially accumulated in areas of low diffusivity. Although particle behaviour in the RDM was improved, transient accumulations of particles appeared in areas of sharp gradients in vertical diffusivity. In addition, the RDM was sensitive to the spacing used to calculate the vertical gradient in diffusivity. {Discussions with SGPBI participants U. Thygesen and T. Stipa indicate that using a higher-order interpolation scheme for parameterizing vertical diffusivity in the RDM may correct these problems.}

To evaluate the effects of episodic wind and river flow on transport and retention of striped bass eggs, particles with the sinking speed of striped bass eggs were released up-estuary of the salt front in steady-state, river pulse and wind event scenarios. Striped bass egg sinking speeds (m s^{-1}) were calculated with constant egg density (specific gravity) and egg diameter (2.5 mm), and variable water density and viscosity. Water density and viscosity at the particle location were passed to the particle tracking model from the hydrodynamic model. Because Reynolds numbers for striped bass eggs are between 3 and 4, we used a series of equations that described the sinking speed of spherical particles at Reynolds numbers < 800 (Raudkivi 1990). Results of scenarios using this iterative technique were compared to scenarios using Stokes law alone to examine the impact of sinking speed parameterizations. In addition, scenarios were conducted with and without sub-grid scale turbulence to examine the sensitivity of results to the inclusion of sub-grid scale turbulence.

Results of the 2-day model scenarios indicate that the number of egg-like particles within the optimum ETM retention area varied and depended upon egg density and release location. Both a sudden increase in freshwater flow and a down-estuary wind event reduced the total number of egg-like particles transported to the optimum ETM nursery area compared to steady-state conditions. These results were sensitive to the parameterization of sinking speed as well as the inclusion of sub-grid scale turbulence.

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A modelling approach to marine ecosystem research and management: An ecosystem approach to fisheries management

by Einar Svendsen

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What do we mean with ecosystem research and management and in particular an ecosystem approach to fisheries management? Why should we do it? How shall we do it and what does it take to do it?

From my point of view an ecosystem approach is simply “to consider the most important driving forces on, and the processes within the ecosystem”. In this respect the driving forces are simply:

- Climate-physics
- Fisherman-fisheries management
- Pollution?

A question-mark is put on the pollution as a major driving force, since so far it has to our knowledge not been proven that pollution so far has a significant effect on large scale ecosystem functioning and stocks (in north Atlantic waters).

A major issue is how food webs are controlled or regulated by their environment and human interference. This obviously has important implications for the management of marine resources, whether the agenda is harvesting of marine resources or protection of species. Globally, second and third-level carnivorous fish such as cod are over-fished, forcing fisheries in many parts of world to harvest at lower trophic levels. Data for cod show that our northern waters make no exception.

Moreover, the extreme variation in physical factors in northern waters, especially light, temperature, and ice cover, that occur over seasonal, inter-annual and longer time-scales, cause major fluctuations at all trophic levels of the food web.

Thus there is no such thing as an “ecological balance” on these time-scales. Knowledge of the ecosystem dynamics is required to make proper evaluation and prediction of the impact of fishing on a marine food web, and a fundamental challenge in this context is distinguishing the impact of man from large natural variation. Due to the complexity of this challenge, this can only be solved by an extensive use of mathematical models. Norway has therefore put forward the ideas for a major 10 year research and development plan called AMOEBE (A Model based and data driven Operational Ecological Biomass Estimator), very much in line with the new vision of ICES to: improve the scientific capacity to give advice on the human impact on, and impacted by, marine ecosystems. Several model results of the lower trophic levels in the North Sea were presented.In addition to the relatively new science of coupled (physics, chemistry, biology) ecosystem modelling, Norway has followed two lines of research that are particularly relevant for AMOEBE. One is the fishery investigation tradition, which has given Norway a high capability of studying and quantifying fish from a stock assessment perspective. In AMOEBE, this capability will be put in a wider ecological context, putting fish as a quantitative and dynamic food-web component. The second tradition is the running of broad marine ecological research programmes. Especially the programmes Pro Mare (Barents Sea ecology; 1984–1989) and Mare Cognitum (Nordic Seas ecology; 1993–2002) did provide holistic ecosystem knowledge that AMOEBE will be built on.

Advances in modelling the effects of small-scale turbulence on plankton

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Small-scale turbulence is here understood *sensu lato* to refer to the flow at scales close to the Kolmogorov microscales (L_K) and below. The body of experimental data on effects of turbulence on plankton organisms and processes has grown in recent years (Peters and Marrasé 2000). Turbulence has been shown to affect planktonic organisms from fish larvae and copepods to small microbes. Most effects seem to be related to an increased mixing of solutes and particles, which give higher uptake, ingestion and growth rates. For zooplankton and dinoflagellates there are direct effects on behavioural responses as well. Strong turbulence seems to interfere with a series of processes, after particles have been encountered, that result in lower zooplankton ingestion rates and give a dome-shaped response of ingestion versus turbulence. In the case of dinoflagellates, there is general trend towards lower growth rates under turbulence, although there are exceptions and there seems to be a large species-specificity. Swimming patterns have been shown to be affected by turbulence (Karp-Boss *et al*., 2000).

Trophic food web modelling is starting to incorporate turbulence as an environmental factor affecting different planktonic organisms and processes. The increased nutrient fluxes towards osmotrophic cells can be parameterized using Sherwood numbers (Karp-Boss *et al*., 1996), and there is a framework to calculate bulk encounter rate kernels for zooplankton predators under turbulence (Kiørboe and Saiz 1995). Further theoretical developments may be more appropriate for the latter case (Lewis and Pedley 2000). Within the NTAP project we have improved a 0-dimensional food web model (Thingstad *et al.* 1999) to incorporate effects of turbulence (Metcalfe *et al.* in prep). The model depends quite strongly on effects of turbulence on the top predator (copepods) and on the growth of diatoms. The authors are now in the process of fine-tuning the model and validating results with experimental data from mesocosms and microcosms. Albeit effects of turbulence on small microbes are not included in the model based on theoretical considerations, experiments are showing that bacterial concentrations can be affected through indirect food web trophic cascade processes (Peters *et al.* 1998, Peters *et al.* 2002).

System level processes and parameters, which can serve as system indicators, have been shown to vary with turbulence. Under a low nutrient load, turbulence seems to favour the production of organic matter and especially the heterotrophic components, while the interaction of turbulence and nutrient loads produces a shift towards autotrophic biomass and affects the stoichiometry of organic matter shifting it towards a higher than Redfield ratio carbon content. There are some concerns about experimental data results, especially in understanding how turbulence should be affecting settling of particles, and how effects on planktonic population dynamics should be corrected for it.

Some of the challenges in the field of turbulence and plankton interactions include:

1) to abstract population information from detailed modelling studies of flow around individual zooplankters (e.g., Jiang *et al.* 2002a, b);

2) to include turbulence as an environmental variable into food web modelling and 3-D flow models;

3) to determine at which point it is necessary to model a certain trophic level by tracking individual particles (individual-based models, IBM);

4) to asses turbulence effects by using realistic turbulence time series.

In all cases, it is extremely important to have adequate observational or experimental data (which is currently very scarce), from the individual to the system level, to validate and improve models.

It is expected that effects of turbulence on planktonic organisms and processes will be of increasing importance and concern within the framework of global changes. On the one hand, nutrient loads to the coastal zone keep increasing and turbulence may significantly increase phytoplankton growth and eutrophication. On the other hand, climate change scenarios predict a growing intensity and frequency of storms further adding to the same phytoplankton enhancement. Other global change parameters, such as coastal line development and stabilization, may increase the surface of confined areas along the very coast line which reduces turbulence and produces favourite growing conditions for harmful algal blooms. We need to address modelling the effects of turbulence on planktonic organisms and processes and coastal ecosystems with these societal problems in mind.

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A new project on modelling transport and survival of early life stages of commercial fishes in the bay of Biscay

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Variability in the size populations of fish commercial species is a crucial issue in stock assessment. Fishing pressure exerts a great influence on stock sizes. Nevertheless, there are considerable studies which demonstrate that environment may also play an important role (Anderson, 1998, Borja *et al*., 1998). The influence of environment on fish populations is especially strong during the initial phases of development (Pepin, 1991). During these early life stages, small variations in available food, predators pressure, or advection to sites of different suitability for survival and development may cause great changes in growth and survival rates, which finally will reflect in the number of young fish which join to the adult population.

Traditionally, the study of the impact of environment conditions on fish recruitment has been carried out through observational field ecology and correlation techniques. Nevertheless, observational data sets are limited and inevitably biased to “normal conditions”, while occasional extreme events are more likely to generate insight into causative processes (Bartsch and Coombs, 2001). More recently, mathematical modelling have allowed the simulation of physical and biological oceanographic processes, providing unlimited different scenarios.

This may be the case of anchovy, *Engraulis encrasicolus*, in the Bay of Biscay. Anchovy is one of the most important fish species in the Bay of Biscay. In the 60s about 60000 tonnes per year were caught, but in last 10 years only 15000 tones in average have been fished. Anchovy spawning takes place in late spring in the Bay of Biscay and it is mainly associated with river plumes, oceanic gyres and shelf break fronts. In recent years several studies demonstrated the strong relationship among anchovy recruitment during last three decades and, upwelling and turbulence during the development of egg and larval stages. Nevertheless in last years the obtained recruitment index has not supplied correct estimations of anchovy recruitment. For this reason a new project to model dispersion and survival of early life stages of anchovy and other commercial species, such as mackerel and hake, is going to be initiated in order to better understand processes affecting recruitment.

The project will develop a physical model which simulates transport of anchovy eggs and larvae in the Bay of Biscay. On the other hand, growth of anchovy larvae will be parameterised as a function of temperature and/or food availability. The final objective of the project will be to estimate mortalities, but the first module to be develop will be growth. For fishes, during larval and post-larval stages, growth and mortality are close and inversely related, since faster growing larvae remain the more vulnerable sizes for less time than slower growing larvae and experience higher survival rates. Biological model will be finally incorporated to the general transport model to simulate transport and survival of early stages of anchovy.

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A modeling project on the circulation and hydrography and implications for biology and fisheries over the Newfoundland Shelf

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Ocean circulation and hydrography over the Newfoundland Shelf and Slope are highly variable because of intense interactions with large-scale ocean circulation (the colder and fresher equatorward Labrador Current and the warmer and saltier poleward North Atlantic Current), atmosphere and ice. In addition to variations of the Labrador Current strength and pathway, meanders and frontal eddies pinched from the North Atlantic Current can generate prominent temporal and spatial variability in regional hydrography and circulation, resulting in intensive shelf/deep-ocean interactions.

During the past decade, significant variations in physical environments were observed off Atlantic Canada, e.g., south-north shift of the Gulf Stream position in relation to the North Atlantic Oscillation, and interannual variability of the Labrador Current transport. The biological productivity and fish stocks also experienced dramatic changes, e.g., the drastic collapse of the northern cod in the early 1990s. Efforts have been put to understand these profound changes from various perspectives, e.g., the Atlantic Zone Monitoring Program. One of critical gaps for the Newfoundland Shelf is a modelling component with an emphasis on physical environments and its interactions with biological and fisheries processes. The present project aims to fill this gap. Our objectives are to study climatological seasonal–mean circulation and hydrography, to investigate effects of climatic variability on the seasonal circulation and dynamics in the 1990s, and to assess potential implications for the biological and fisheries issues.

We have chosen to use the Dartmouth College finite element circulation models. Linear diagnostic frequency-domain models were implemented for the Newfoundland and Labrador Shelf to investigate barotropic tidal currents and seasonal wind- and density-driven circulation. Solutions for leading tidal constituents are forced by tidal elevations specified at the open boundary and by tide-generating potential. Monthly-mean wind-driven circulation was computed with wind stresses from the NCEP-NCAR reanalysis data prescribed at the sea surface and large-scale remote forcing specified at the open boundary determined from a North Atlantic model. Density-driven circulation was also simulated with prescribed density gradients from a regional temperature and salinity climatology. Model results reveal significant seasonal and interannual variations in wind- and density-driven circulation fields. These seasonal and interannual variations are being examined for relative importance of local to remote forcing.

We are working on prognostic refinement of the diagnostic circulation fields. The refinement will be carried out within a fully nonlinear primitive circulation model with an advanced turbulence scheme under joint forcing of wind, density and tides. The results will be verified against and discussed together with *in situ* observations, for major current features, seasonal and interannual variations, and underlying dynamics.

A 3-D particle-tracking package specifically designed for the finite element model will be applied to obtain pathways of numerical particles. The prognostically refined model circulation fields and turbulence fields will be used to examine trajectory paths of the particles released at selected locations and depths under different forcing scenarios. The effects of baroclinic circulation, tidal currents, wind-driven circulation, and turbulent mixing will be investigated. The results will be used to discuss transport mechanisms and implications for biological and fisheries issues.

Our longer-term plan is to include intra-seasonal processes in circulation models and to implement more complex biological models, toward improved representation of both physical and biological dynamics and their interactions. We look forward to working closely with group members to tackle outstanding issues of importance in modelling physical and biological interactions.

ANNEX D: DERIVATION OF MODEL EQUATIONS TO FORM A BASIS FOR INTERCOMPARING MODEL ASSUMPTIONS

Derivation of Model Equations to Form a Basis for Intercomparing Model Assumptions

by

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1. Introduction

Modelling marine ecosystems involves models of individuals, populations, biomass, and combinations thereof linked to physical models. Requirement for any consistent type of model: Dynamical variables (individual properties, state variables and process rates) must be observable and reproducible quantities

Marine ecosystems consist of individuals (cells, copepods, fish), which form populations, have biomass and are controlled by physical processes.

Different cuts through the natural system may give models which look specifically at one or several of these aspects.

Different models have the same theoretical roots but can be formulated by isolating certain aspects or parts of the food web dynamics and ignoring or simplifying links to other parts of the web.

2. Individual Based Models (IBM's)

Individuals possess a dynamical signature, genetic code, phenotypic aspects (react to environmental conditions within a certain range).

Biological component:

Dynamical equations for the development of characteristic features or properties (e.g., mass).

Physical component:

Movement through advection, turbulence and active motion, (integration of velocity field to estimate trajectories).

Links to other parts of the food web:

Moving individuals (bioenergetics) may sense environmental state (T, S, nutrient, food items or prey, etc., may avoid predation etc.), required information prescribed by data from observation or models.

Modelled individuals

Are from all levels of the marine food web, i.e., cells, copepods, fish

Mathematical representation

Define state density, where an individual is characterized by a point in the state space *(x,y,z,m),* the point moves around with time:

$$\rho(\vec{r},t) = \delta(\vec{r} - \vec{r}_{ind}(t))\,\delta(m - m_{ind}(t))$$

$$\vec{r}_{ind}(t) = \int_{t_0}^{t} dt'\,(v(\vec{r}_{ind},t') + \vec{\xi}), \quad m_{ind}(t) = \int_{t_0}^{t} dt'\,\frac{dm_{ind}(t')}{dt'}$$

The trajectory, $\vec{r}_{ind}(t)$, follows from integration of the velocity (currents and individual motion and a noise, $\vec{\xi}$, due to turbulence. The mass development is given by the growth equation, $\frac{d}{dt}m = (g - l)m^{p}$.

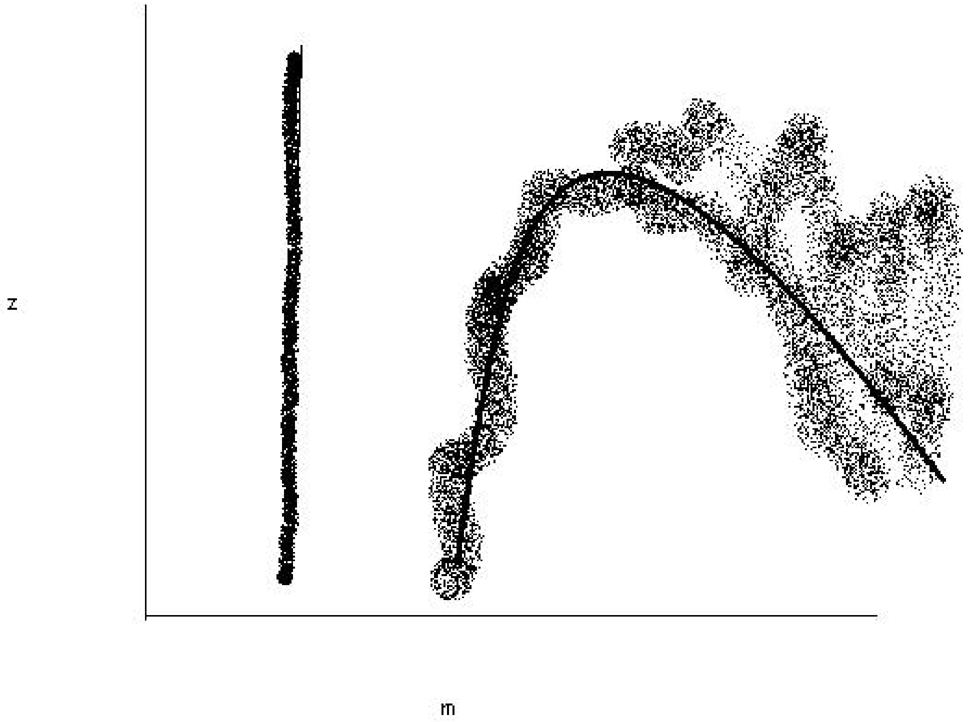

Figure 1. Schematic of the representation of individuals with a narrow mass interval e.g., phytoplankton cells, and broad mass interval, e.g., copepods, in the state space (z,m).

For a single individual an IBM is the natural choice, (e.g., trajectory and life cycle of a whale).

Note that mortality and reproduction are not well defined in for a model of a single individual, if it dies the modelling is finished if it lay eggs we have to add new individuals. If we look at many individuals, then the number must be manageable otherwise population models may be more appropriate.

3. Population Models

Populations: Consist of many individuals of a species with a certain degree of genetic variability, (usually the number is too high to follow the properties of each individual) If the number is not too high we can look at many individuals and take averages over the individuals, if the number is high, then we use functions describing the distributions, i.e., abundance as functions of space and time, $n(\vec{r},t)$. Note that the number of individuals per unit volume has to be high enough that the abundance can be treated as analytical function of *(x,y,z,t)*.

3.1 Average over many IBM's

Biological component:

Similar as IBM's but with prescription of mortality (e.g., random numbers generator) and birth.

Physical component:

Lagrangian trajectories of many individuals.

Links to other parts of the food web:

Moving individuals (bioenergetics) may sense environmental conditions (T, S, nutrient, food items or prey, etc., may avoid predation etc.), required information prescribed by data from observation or models.

3.2 Abundance Model

Biological component; Dynamical change of abundance driven by birth and death rates, prescribed as certain fraction of the abundance.

Physical component:

Advection diffusion equations links to biological dynamics.

Alternatively, quasi Lagrangian trajectories of water parcels.

Links to other parts of the food web

The rates depend on environmental conditions (T, S nutrient, food items or prey, etc., may avoid predation etc.), required information prescribed by data from observation or models

Mathematical representation

State density of many individuals → 'points in the state space *(x,y,z,m)*

$$\rho(\vec{r},t) = \sum_i \delta(\vec{r} - \vec{r}_i(t))\, \delta(m - m_i(t))$$

$$\vec{r}_i(t) = \int_{t_0}^{t} dt'\, v(\vec{r}_i,t')\,, \quad m_i(t) = \int_{t_0}^{t} dt'\, \frac{dm_i(t')}{dt'}$$

For very many individuals (no. → ∞), we can define abundance $n(\vec{r},t)$ as state variable

$$\frac{\partial}{\partial t} n(\vec{r},t) + \nabla \cdot \vec{v} n(\vec{r},t) = -\mu\, n(\vec{r},t) + r_{birth} n(\vec{r},t).$$

Incorporation of life cycles requires structured population models, see ‘theoretical considerations’ below

4. Biomass Models

Looks at the biomass per unit volume of the species considered. For individuals, which occupy only narrow mass interval during their life cycle, the biomass is closely related to the population models.

Biological component:

Dynamical change of biomass driven by nutrient uptake and loss rates such as respiration and mortality, prescribing a percentages of biomass

Physical component:

Advection diffusion equations links to biological dynamics.

Links to other parts of the food web:

Rates are usually prescribed functions of other state variables and environmental conditions (e.g., T, nutrients) and require information prescribed by models or other data.

Advantage: the model equations are constrained by the conservation of mass

Mathematical representation

Small mass intervals

Biomass, $B = m \cdot n$, multiply population model by mean mass *m*

$$\frac{\partial}{\partial t} m\, n(\vec{r},t) + \nabla \cdot \vec{v} m\, n(\vec{r},t) = -\mu\, m\, n(\vec{r},t) + r_{birth} m\, n(\vec{r},t).$$

$$\frac{\partial}{\partial t} B + \nabla \cdot \vec{v} B = (g - l - \mu) B.$$

The model can be expanded to a NPZD model by adding equations for nutrients, zooplankton and detritus. Advantage: the law of conservation of mass can be applied to constrain the model. For incorporation of life cycles see ‘theoretical considerations’ below.

5. Model of a Community (this discussion is restricted to biomass models)

Several interacting populations, expressed in state variables abundance or biomass or both. Involve interaction of populations, i.e., competition for nutrients, advantages of certain species at certain environmental conditions, etc.

Biological component:

Several state variable for different functional groups, Dynamical change of biomass driven by nutrient uptake and loss rates such as respiration and mortality, prescribing a percentages of biomass.

Physical component:

Advection diffusion equations for the state variables.

Links to other parts of the food web:

Rates are usually prescribed functions of other state variables and environmental conditions (e.g., T, nutrients) and require information prescribed by models or other data.

Mathematical representation

Equations for biomass of the different species or functional groups*, i,:*

$$\frac{\partial}{\partial t}B_i + \nabla \cdot \vec{v}B_i = (g_i - l_i - \mu_i)B_i .$$

Such models can be expanded to complex NPZD models for several functional groups by adding equations for nutrients, zooplankton and detritus. Advantage: that the law of conservation of mass can be applied to constrain the model.

For incorporation of life cycles see "theoretical considerations".

6. Theoretical considerations

There are no principles, which directly provide the chemical biological equations for the marine ecosystem models (as for example in the geophysical fluid dynamics, where the model equations are the mathematical formulation of basic laws). The formulation of process rates, used in chemical-biological models to describe reason-cause relationships, are taken from experiments and transformed into mathematical expressions.

We address the question, whether there is a ***unifying theoretical concept***, which can be used as a basis for the derivation of the different model types. In the following we try to sketch an approach.

We start with 'state density' of N individuals (of the same species), which represents each individual as a point in the 'state space' *(x,y,z,m),* and which is defined by:

$$\rho(\vec{r},t) = \sum_{i=1}^{N} \delta(\vec{r} - \vec{r}_i(t))\, \delta(m - m_i(t))$$

For different times the 'points' move around in the state space, where the motion is controlled by the currents, $v(\vec{r}_i,t)$, and the development of the mass:

$$\vec{r}_i(t) = \int_{t_0}^{t} dt' (\, v(\vec{r}_i,t') + \vec{\xi}(t')) , \quad m_i(t) = \int_{t_0}^{t} dt' \, \frac{dm_i(t')}{dt'}$$

where the individuals obey a growth equation of the type $\frac{d}{dt}m = (g-l)m^p$, or in case of phytoplankton cells, where the individual mass is almost constant, $\frac{d}{dt}m \approx 0,$ cell division increases the number of individuals. The integral over space and mass gives the total number:

$$N(t) = \int_V d\vec{r} \int dm \rho(m,\vec{r},t)$$

In general, N is not conserved due to (i) cell division (primary production if we look at phytoplankton) or reproduction (egg laying for copepods), and (ii) mortality (natural death or predation).

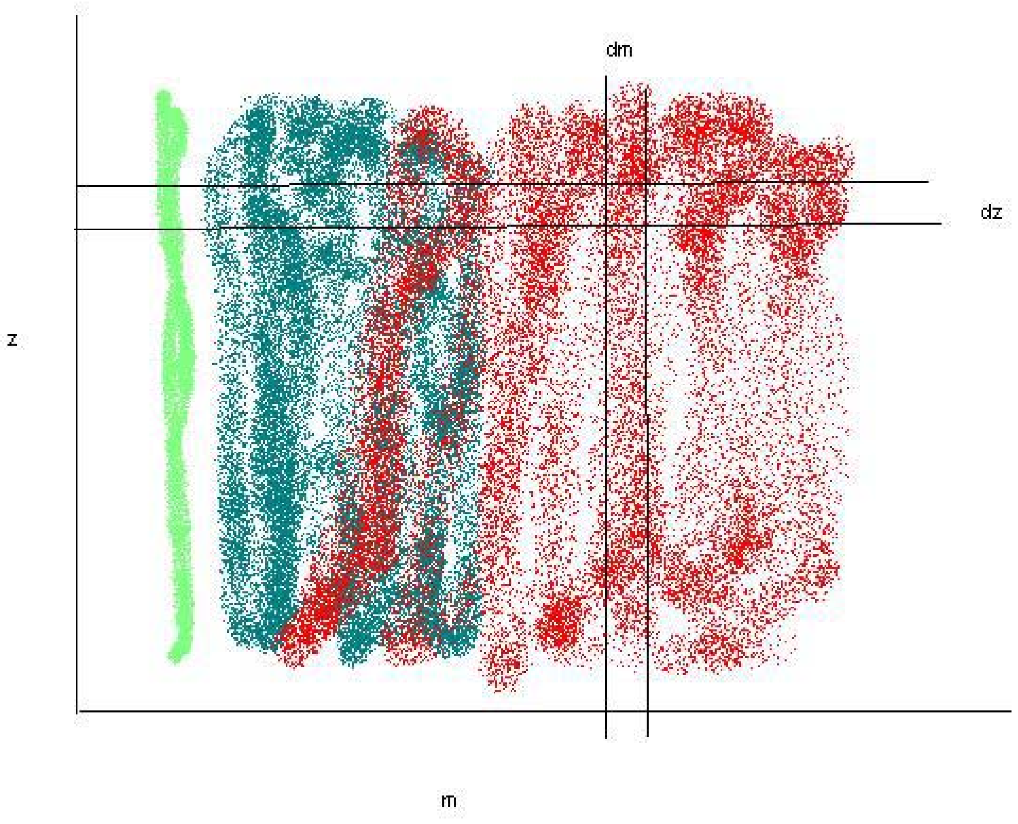

Figure 2. Example for state densities for several groups of individuals with different ranges of mass development.

How can a 'many individuals' approach developed?

For a community of interaction population we have several 'state densities':

$$\rho = \rho^p + \rho^\alpha + \rho^\beta + \rho^\chi + ...$$

For phytoplankton, ρ^P, the primary production can be expressed by the repeated application of an ‘creation-operator’, Π, which applied onto ρ^P increases the number of cells,

$$\Pi\rho^P(\vec{r},t)=\Pi\sum_{i=1}^{N^P}\ \delta(\vec{r}-\vec{r}_i^{\,P}(t))\,\delta(m-m_i^P(t))=\sum_{i=1}^{N^P(1+\Delta)}\delta(\vec{r}-\vec{r}_i^{\,P}(t))\,\delta(m-m_i^P(t))$$

where $\Delta\leq 1$, but such that $N^P(1+\Delta)$ is an integer. For $\Delta=1$, each cell divides. The process depends on external parameters such as nutrients light etc. which must be prescribed as continues function of space and time. After many repeated application of the operator Π, e.g., once per day, the nutrients are depleted and Δ tends to zero.

Let α, β, γ, indicate grazers, e.g., stages of copepods of increasing size, e.g.,

$$\rho^\alpha=\sum_{i=1}^{N^\alpha}\ \delta(\vec{r}-\vec{r}_i^{\,\alpha}(t))\,\delta(m-m_i^\alpha(t))$$

then the grazing can occur if:

$$|\,\vec{r}_i^{\,P}-\vec{r}_j^{\,\alpha}\,|\leq\varepsilon$$

(encounter of prey items). Grazing reduces the number of cells but fuels the growth of the copepods. Similar mortality can be introduced as an ‘annihilation-operator’ which decreases the numbers of individuals, e.g., by a random number generator applied to the individuals (e.g., Batchelder, Williams 1995). Obviously this type of approach becomes very complex. A reasonable practical application is only feasible for a certain, not too large, number of individuals with simplified interaction terms. If various species and very many individuals are considered then the introduction of continuously distributions, abundance or concentrations, is appropriate.

State variable approach (abundance and concentration)

With the help of the state density we can define the state variables needed in the different types of models.

The population density is related to state density as:

$$\sigma(\vec{r},t)=\frac{1}{\Delta V}\int_{\Delta V}d\vec{r}\,\rho(\vec{r},t)$$

By definition $\sigma\,dm$ is the number of individual (per unit volume, *ΔV*) in the interval *(m,m+dm).* Abundance follows from the population density as:

$$n(\vec{r},t)=\int_{m_{\min}}^{m_{\max}}dm\,\sigma(m,\vec{r},t)$$

and the biomass as:

$$B(\vec{r},t)=\int_{m_{\min}}^{m_{\max}}dm\,m\,\sigma(m,\vec{r},t)$$

For populations where the mass of individuals change only in a narrow interval, e.g., for phytoplankton cells, the dynamics, apart from advection and turbulent mixing, is governed by birth rate and mortality:

$$\frac{\partial}{\partial t}\sigma = -\mu\sigma + r_{birth}\sigma, \quad (*)$$

The dynamical equation for $n(\vec{r},t)$ follows from integration of (*)

$$\frac{\partial}{\partial t}n(\vec{r},t) = -\mu\, n(\vec{r},t) + r_{birth}n(\vec{r},t).$$

If we take the spatial dimension into account we find

$$\frac{\partial}{\partial t}\sigma + \nabla\cdot\vec{v}\sigma = -\mu\sigma + r_{birth}\sigma,$$

and

$$\frac{\partial}{\partial t}n(\vec{r},t) + \nabla\cdot\vec{v}n(\vec{r},t) = -\mu\, n(\vec{r},t) + r_{birth}n(\vec{r},t).$$

To obtain an equation for the biomass we multiply this equation by *m*

$$\frac{\partial}{\partial t}B + \nabla\cdot\vec{v}B = (g - l - \mu)B$$

where growth minus loss *(g-l)* corresponds to the birth rate.

Life cycles

For a population of a species with a life cycle where the mass increases over orders of magnitudes the population density propagates along the 'm-axis' and obeys a von Foerster equation. This situation corresponds to an equation of continuity regarding the mass variable. Let us for a moment ignore the transport in the physical space. The number of individuals, which enter a certain interval of mass and propagates through it, must be the same, which leaves the interval minus those, which died (and plus newborns if the reproduction occurs in that interval), i.e.

$$\frac{\partial}{\partial t}\sigma + \frac{\partial}{\partial m}\left(\frac{dm}{dt}\sigma\right) = -\mu\sigma + r_{birth}\sigma, \qquad (**)$$

where μ is the mortality rate, r_{birth}, the birth rate.

$$\frac{d}{dt}m = (g - l)\, m^{p}, \qquad (+)$$

is the growth equation for the individual and *p* is an allometric exponent. Note the allometric scaling can be achieved either by $p<1$ and constant g and *l*, or by $p=1$ and stage dependent *g* and *l*. We chose the latter option.

To resolve different stages we may introduce stage dependent population densities, σ_i 's, which are defined for the mass interval X_{i-1} to X_i, e.g., molting mass for copepods.

Then integration of (**) over the mass interval of one stage gives:

$$\frac{\partial}{\partial t}\int_{X_i}^{X_{i+1}} dm\,\sigma_i = -\frac{dm}{dt}\sigma_i\,|_{m=X_i} + \frac{dm}{dt}\sigma_i\,|_{m=X_{i-1}} - \mu_i \int_{X_{i-1}}^{X_1} dm\,\sigma_i$$

or equivalently

$$\frac{\partial}{\partial t}\sigma_i(m) = -\mu_i\sigma_i - \frac{dm}{dt}\sigma_i\delta(m - X_i) + \frac{dm}{dt}\sigma_i\delta(m - X_{i-1}), \qquad (++)$$

Transfer between stages (e.g., molting):

$$T_{i,i+1} \sim \frac{dm}{dt}\sigma_i(X_i,t) \approx \frac{\Delta m}{\Delta t}\sigma_i(X_i,t)$$

$\Delta m\sigma_i(X_i)$ is by definition the number of individuals of mass around X_i which are going to enter the next stage *i+1* in the time interval *Δt*. Parameterization of these terms, e.g., with stage duration time, D_i, (Gupta *et al.* 1994, Lynch 1998), gives after integration of (++):

$$\frac{\partial}{\partial t}n_i + \nabla\cdot\vec{v}n_i = \frac{1}{D_{i-1}}n_{i-1} - \mu_i B_i - \frac{1}{D_i}n_i,$$

Other parameterizations of the transfer rates were proposed by Carlotti Sciandra (1989), which relate the transfer to individual grow (applies to coherent cohorts), and Fennel (2001), where the transfer is related to the mean development, described by a mean individual mass. Development of biomass in a stage is given by:

$$B_i(\vec{r},t) = \int_{X_{i-1}}^{X_i} dm\,m\,\sigma_i(m,\vec{r},t)$$

Multiply (+) by σ_i and (++) by m and add the result:

$$\frac{\partial}{\partial t}m\sigma_i = (g_i - l_i)m\sigma_i - \mu_i m\sigma_i - m\frac{dm}{dt}\sigma_i\delta(m - X_i) + m\frac{dm}{dt}\sigma_i\delta(m - X_{i-1}),$$

Then integration over the mass interval gives:

$$\frac{\partial}{\partial t}B_i + \nabla\cdot\vec{v}B_i = T_{i-1,i}B_{i-1} + (g - l - \mu)B_i - T_{i,i+1}B_i$$

For elaborated prescription of the transfer terms are functions of the mean individual mass in a stage:

$$\overline{m}_i = \frac{B_i}{n_i}, \quad T_{i,i+1} = T_{i,i+1}(\overline{m}_i, X_i).$$

If the mass of the mean individual approaches the molting mass, then the transfer terms are switched on. Two sets of equations, for n_i and B_i are required to link aspects of population biomass models including individual aspects.

7. Concluding Remarks

The concept of state densities allow a consistent derivation of different types of models ranging from single individuals to many individuals, population and biomass model of different complexities.

This approach, which may provide a way to bridge the gap between ecosystem models and fishery models, needs further elaboration. A more detailed description will be provided in a manuscript, which is going to be submitted to a scientific journal.

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ANNEX E: OVERVIEW OF DORMANCY (DIAPAUSE) IN COPEPODS

OVERVIEW OF DORMANCY (DIAPAUSE) IN COPEPODS

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INTRODUCTION

Copepod life history strategies are complex, and the factors controlling their dormancy are largely unknown. Such ignorance has serious implications for our ability to understand and predict copepod dynamics, production and distribution. This document summarizes the current knowledge, areas of ignorance, and potential modelling investigations that would improve our understanding.

WHAT WE KNOW

The life history of many organisms involves a prolonged period of dormancy, ranging from a slowed metabolism (quiescence) to arrested development (diapause), which is thought to help them survive unfavourable abiotic and/or biotic environmental conditions. Free-living freshwater and marine copepods in three taxa, *Harpacticoida*, *Cyclopoida* and *Calanoida*, exhibit dormancy as resting eggs, nauplii or copepodite stages, with the timing of initiation, duration and termination varying by geographic region and climate (Dahms, 1995; Norrbin, 1996; Ohman, 1998; Mauchline, 1998; Heath *et al*., 2000).

Calanus finmarchicus is the copepod species for which the life history and role of dormancy has probably been best characterized (Marshall and Orr, 1955; Miller *et al*., 1991; Conover, 1988; Gaard, 1996; Hirche, 1996; Mauchline, 1998). Their emergence from diapause occurs sometime between late-fall and early-spring, and varies latitudinally (e.g., Nov-Jan in the Gulf of Maine: Durbin *et al*., 1997 vs. Feb on Scotian Shelf: Sameoto and Herman 1990), such that their growing period is generally coincident with peaks in primary production (Falkenhaug *et al*., 1997). After 1–2 generations (typically), the late-stage copepodites of *C. finmarchicus* migrate to deep waters, initiate diapause, and spend the summer-fall period "overwintering" at depth. The most common resting stage for *C. finmarchicus* is C5, but C4s and females have also been found (Hirche, 1996). Both descent and emergence occur in under 2 months (estimated from Miller *et al*., 1991; Huntley *et al*., 1994), and the depths at which they diapause vary geographically (e.g., 1000–1500m in the Greenland Sea: Hirche, 1996; 400–500m in the New England Slope Water: Miller *et al*., 1991; and 150–200m along the basins along the continental shelf: Sameoto and Herman, 1990; Osgood, 1997).

Presently, determination that a population is in diapause is made through a combination of indices, including digestive enzyme patterns, reduced feeding rates, reduced metabolic rates, reduced RNA content, arrested or delayed development or molting, increased lipid storage, and vertical distribution of the population (Miller *et al*., 1991; Ohman *et al*., 1998; Wagner *et al*., 1998).

WHAT WE DON'T KNOW

There are many large gaps in our knowledge about the details of diapause, due in a large part to the fact that it is difficult to produce and sustain in a laboratory setting, and that field observations are limited by winter sea conditions and deep depths of diapausing organisms. Furthermore, none of the existing methods of detection are useful at individual level, which probably will require as yet undeveloped techniques involving gene expression. Problems are compounded for resting eggs, because of the long time-scales (decades) for which are involved.

Neither the factors responsible for initiation nor termination of dormancy are well understood (see reviews in Miller *et al*., 1991 and Hirche, 1996). Regulation by photoperiod is known to trigger diapause in insects, and is generally the principal cue thought to affect copepods. However, modelling studies suggest photoperiod is not a prerequisite (Hind *et al*., 2000), and temperature, densities of prey, population and predators, and/or "biological clocks" have also been suggested as factors contributing to the induction of dormancy in copepods (Dahms, 1995; Kaartvedt, 1996; Hind, 2000). Termination of diapause occurs when copepods are agitated or experience a change in light levels (Miller *et al*., 1991). It is also commonly hypothesized that diapause is terminated when lipid reserves are exhausted (Fiksen, 2000), however this is contrary to observations that the earliest animals to emerge are large ones with a disproportionate potential for lipid storage (Miller *et al*., 2000). Temperature, salinity, oxygen, phytoplankton concentration or population density may also play a role (Dahms, 1995), although direct evidence is weak. Improved evolutionary fitness in the face of environmental variability is suggested as a motivation for a portion of each generation to enter dormancy while others remains active, however, we do not know these fractions, nor how such bet-hedging is determined.

We do not fully understand why certain areas are “chosen” as overwintering locales, or the extent to which different candidate overwintering populations contribute to active copepod populations emerging in spring. Advective transport is sure to play a role. The interaction of ontogenic vertical migration coupled with physical advection has been proposed as the mechanism for the accumulation of calanoid copepods in shelf basins (Herman *et al*., 1991, Osgood, 1997), their movement onto coastal shelves from deep overwintering sites (Slagstad and Tande, 1996), and their persistence in coastal upwelling and recirculation regions (Peterson, 1998; Bryant *et al*., 1998). However, we don’t know what cues determine the depth of their migration, we therefore don’t know which currents are responsible for transport. As well, it is likely that dormant vs. active copepods experience different mortality rates, given their different habitat and behaviour (Bagoien, 1999; Dale *et al*., 1999), and this idea is supported by simulations (Gentleman, 2000), but the relative predation risks are generally poorly known.

POTENTIAL MODEL INVESTIGATIONS

There are a wealth of different modelling simulations that could serve to improve our understanding, any one of which could (and should) be conducted for populations in different regions. Some examples are:

1) Optimization methods used to explore long-term fitness of different diapausing strategies in response to varying environmental cues (akin to Fiksen, 2000).
2) Simulations of deep-water transport to study dispersal of dormant phases to determine where animals entering diapause end up (e.g., are populations in monsoon regions of Arabian sea connected to those in Africa?)
3) Studies examining whether parameterizations derived from data for one population/year can explain data for another (e.g., Hind *et al*., 2000 suggest can correlate with time one, but this may not be sufficient to explain observations in the Northwest Atlantic).
4) Others??? (open for discussion).

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ANNEX F: POTENTIAL IDEAS FOR NEXT FEW YEARS

The following was distributed by C. Hannah and A. Vezina before the meeting to stimulate discussion on the future directions for SGPBI.

A potential big idea is to work towards providing information on 'Best Practices' in modelling physical-biological interactions. This would require understanding the differences between the large number of different models and being able to describe how these differences affect the results of the models in different applications. Members of SGPBI are doing work in this direction.

Specific ideas:

1. Provide a framework for understanding and describing the differences between different NPZ type models. This would be the natural follow on to the work that will be presented by Wolfgang Fennel and others this year and to Wendy Gentleman's presentation last year (Ecosystem Models with Multiple Nutritional Resources: A Critical Review of Assumed Biological Dynamics).

2. Chaotic behaviour is seen in some plankton ecosystem model. Is this chaotic behaviour a fundamental response of the ecosystem or is it a result of the particular equations used? Focus on NPZ type dynamics:

    - Is it a function of the continuous equations?
    - Is it a function of the discretization used?
    - Are Lagragian methods the only way out?
    - Why do some people find chaotic behaviour and other don't.

John Woods (Imperial College) and John Brindley (University of Leeds) are writing a short paper on the predictability of plankton ecosystems, as simulated by (1) field equation (population-based) models, and (2) individual-based models. The aim is to compare and contrast.

This would provide the technical background to a paper aimed at a broader audience. The aim would be to establish (to borrow John's words) 'a clearer paradigm regarding the inherent predictability of the natural ecosystem, as against the predictability of particular modelling techniques, at NPZD or higher levels.' We would discuss whether the chaos is real, whether it matters, and what the implications are for different applications. Has this been done or is it an open field?

3. Modelling the effects of small-scale turbulence on plankton. This would build on the work of Uffe Thygesen and probably the work of Francesc Peters (talk title: Advances in modelling the effects of small-scale turbulence on plankton) and Elizabeth North (talk title: Modeling physical and biological processes in an estuarine turbidity maximum: the challenges of heavy particles and inhomogeneous turbulence). This is technical work and it is important for the long term health of individual based models.

4. Where should physical model development go in order to provide the greatest benefit to the modelling of physical-biological interactions? We make some general statements about this is the strategy document. What are the specifics? Patrick Gentien has proposed that the biologists pose some questions to the physicists. This might point to required improvements in the physical models.

5. Many believe that the next generation of models will evolve in response to rigorous evaluation against observations. So long term questions might be:

    - Do we have the tools/concepts to make these rigorous evaluations (can we falsify these models)?
    - Do we have the observations needed or are the right kind of observations being planned to do these evaluations (even if we have the tools/concepts)?

6. The next generation of models will have to incorporate biology that adapts to changing circumstances. For phytoplankton, we already have photo adaptation as a near routine feature of models. Future models will need to incorporate more parameterizations of physiological adaptation. An even more complex issue is how do communities/trophic levels (the basic units of PZND-type models) change as the mix of species changes in response to physical change? What can we contribute here?

ANNEX G: LAGRANGIAN RANDOM FLIGHT MODELING OF TURBULENT DISPERSAL: A BRIEF PRIMER AND REVIEW

Please see following pages.

Lagrangian Random Flight Modeling of Turbulent Dispersal: A Brief Primer and Review

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Abstract

This summary note reviews the use of Lagrangian stochastic simulation models for analysis of turbulent dispersal. Numerical particle tracking with random flight models builds on the classic statistical theory of turbulence. Thus, the models are developed for intermediate time scales, i.e. in the inertial subrange, but are often found to be applicable also for larger time-scales. In anisotropic conditions the difficulty arises that common flow statistics are insufficient to specify the model uniquely. In heterogeneous turbulence the model must be amended with a corrective acceleration term in order to avoid unphysical accumulation of particles in regions of low turbulence. Extensions beyond passive tracers exist (e.g., pairs of tracers, heavy particles, and individuals with active behavior) but are less well founded on first principles. The discretisation and implementation of the models has been subject of some investigation, but high-performance algorithms have not yet been developed or adapted from the more general literature. As a result the computations can be quite demanding, in particular under very heterogeneous conditions, and when the flow statistics are known only at grid points.

1 Introduction

Turbulence is one of the important processes in the coupling between the physics and the biology of the ocean. One the large scale, turbulence determines the dispersal of nutrients and planktonic individuals (Hermann et al., 2001; Werner et al., 2001), primarily because vertical mixing distributes them over the water column and thus into layers of different horizontal velocities. On smaller scales, turbulent mixing affects the rate with which individuals are brought into contact with dissolved nutrients, prey, and mates.

This review focuses on dispersal, where Lagrangian stochastic simulation (i.e., particle tracking) is one common approach to analysis. The advantage of Lagrangian simulation is that there is no need to resolve the turbulent fluctuations, *except* at positions where a tracer happens to be found. This offers great reduction in computational complexity compared to for instance a direct numerical simulation.

Much of the theory for Lagrangian modeling of turbulence was done in an atmospheric context, e.g. (Thomson, 1987). As was emphasized in in (Brickman and Smith, 2002), a fruitful endeavour would be to adapt the results to oceanic applications. Thus, this review of random flights model aims to cover

1. the foundation in the statistical theory of turbulence,
2. the progress of the 1980's and the 1990's concerning random flights in heterogenous and anisotropic athmospheric turbulence, and
3. issues concerning discretisation and numerics where common practice in Lagrangian modeling does not take into account the state of the art in general stochastic processes.

2 The order of a Lagrangian model

Lagrangian simulations may be ordered after the number of variables used to describe the state of the individual. The simplest *Random Walk* models arise when only the position itself is considered a Markov process; these are termed *Random Displacement* models by e.g. (Brickman and Smith, 2002) and correspond to a diffusion approximation to the turbulent dispersal.

Next level in the hierarchy is occupied by *Random Flight* models where the position and velocity together constitute a Markov process. Compared with random walks, they offer greater accuracy at short scales - e.g., near a point source - because the random walk predicts infinite velocities and thus exaggerates initial dispersal. The discourse is entirely analogous to that of molecular diffusion in kinetic gas theory, where the *Langevin* or *Ornstein-Uhlenbeck* random flight model is preferred from Einstein's Brownian motion at length scales comparable to the mean free path, (Gardiner, 1985).

Further levels in the hierarchy appear as the acceleration is included in the Markov state (Reynolds, 1999a). When considering biological individuals rather than passive tracers, additional state variables could include age, size, or energy reserves. However, there appears to be no studies that couple internal dynamics of the individual with the turbulent dispersal.

3 Random flights in ideal environments

The starting point for the development of a Lagrangian stochastic model of turbulent dispersal is the Lagrangian time spectrum $\chi_{ij}(\omega)$, which decomposes the turbulent kinetic energy of a passive tracer into contributions from cycles of different frequencies (Tennekes and Lumley, 1987; Monin and Yaglom, 1975). Such a spectrum is seen in figure 1.

Below Kolmogorov scales a reasonable model of the spectrum is

$$\chi_{ij}(\omega) = \delta_{ij}\frac{\beta}{3}\epsilon\frac{1}{\omega^2+\omega_0^2} \tag{1}$$

and with this model we can establish a constraint between the turbulence statics

$$3u^2 = \langle u_i(t)\ u_i(t) \rangle = \int_{-\infty}^{+\infty} \chi_{ii}(\omega) d\omega = \pi\beta \frac{\epsilon}{\omega_0} \tag{2}$$

in 3 dimensions. Here u is the r.m.s. speed along each coordinate-ordinate, ϵ is the energy dissipation rate, and $\omega_0 = 1/T_L$ where T_L is the Lagrangian time scale, in this case equal to the decorrelation time of the velocity.

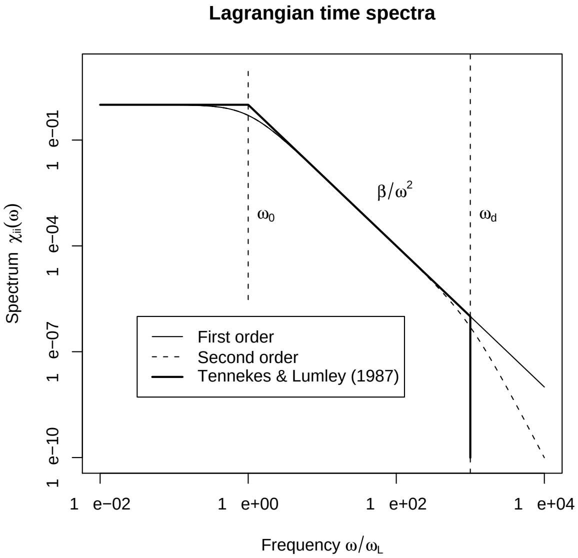

Figure 1: Lagrangian time spectrum of velocity in stationary homogeneous isotropic turbulence. The form in the inertial subrange, between ω_0 and ω_d, is universal and derived from similarity theory. Below ω_0 the form is flow dependent; to make progress in general theory one chooses the simplest possible form. Above ω_d viscosity becomes important and the roll-off becomes steeper; if one wishes to include the effect it may be done with a second-order model.

The Lagrangian time spectrum χ coincides with that of an Ornstein-Uhlenbeck process v_t governed by the Langevin stochastic differential equation (Gardiner, 1985; Øksendal, 1995; Kloeden and Platen, 1995)

$$dx_i = v_i\ dt \quad , \qquad dv_i = -\omega_0 v_i\ dt + \sqrt{C_0 \epsilon}\ dB_i \tag{3}$$

where B_i is Brownian motion, i.e. a continuous Markov process with independent increments, the variance of which are equal to the time increment. Here, $C_0 = 2\pi\beta/3$ so that $2\omega_0 u^2 = C_0\epsilon$. (Du, 1997) argues that C_0 is universal and near 3; see also (Reynolds, 1998a; Du, 1998).

We have now obtained a stochastic Markov process v_t the spectrum of which co-incides with the Lagrangian time spectrum at frequencies smaller than $\omega_d \approx 0.74(\epsilon/\nu)^{1/2}$. The high-frequency cut-off near Kolmogorov scale in figure 1 is typically ignored; an exception is (Reynolds, 1999a). Thus, *a priori* we would expect the model to be valid in the inertial subrange, but it has been shown to be fairly accurate also at larger scales in some flows, e.g. (Mordant et al., 2001).

3.1 Random walk models: The diffusion limit

If our time scale of interest is much larger than $T_L = 1/\omega_0$, the velocity process will effectively appear δ-correlated - i.e., as white noise. Thus the position process $x_i(t)$ approaches integrated white noise or Brownian motion:

$$\langle \Delta x_i(T) \cdot \Delta x_j(T) \rangle \sim 2D_{ij} \cdot T \tag{4}$$

where

$$\Delta x(T) = x(T) - x(0) \quad \text{and} \quad D_{ij} = \pi \chi_{ij}(0) = \delta_{ij} \frac{C_0 \epsilon}{2\omega_0^2} = \delta_{ij} u^2 T_L \quad . \tag{5}$$

This corresponds to a Fickian diffusion equation governing the concentration $\rho(x,t)$ of tracers:

$$\frac{\partial \rho}{\partial t}(x,t) = D \nabla^2 \rho(x,t) \quad \text{with isotropic diffusivity } D = u^2 T_L \quad . \tag{6}$$

Although this diffusion limit of the random flight model (3) is unambiguous from a mathematical point of view (Gardiner, 1985), its physical relevance is less clear (Monin and Yaglom, 1975, p. 528) because it relies on the form of the spectrum χ below the Lagrangian cut-off frequency ω_0, which is not universal. Nevertheless, it provides the standard way of approximating a random flight model with a random walk model.

4 Non-uniqueness in anisotropic turbulence

We have seen that in isotropic situations, the r.m.s. turbulent velocity u along each coordinate, and the energy dissipation rate ϵ, together specify the Lagrangian time scale $T_L = 1/\omega_0$ and thus the random flight model. This is convenient because the known statistics of the flow often are exactly u and ϵ (or equivalent information), for instance obtained from circulation models with one-point turbulence closure. In anisotropic conditions, this sufficiency no longer holds. For instance the following two random flight models in 2D have the same (isotropic) inertial subrange and the same steady state velocity distribution:

$$dx_t = v_t \; dt \quad , \quad dv_t = A v_t \; dt + dB_t \quad : \quad A_1 = \begin{bmatrix} -1 & 0 \\ 0 & -1 \end{bmatrix} , \quad A_2 = \begin{bmatrix} -1 & -\frac{1}{2} \\ \frac{1}{2} & -1 \end{bmatrix} \tag{7}$$

Thus, to determine a unique random flight model, more information is required beyond the energy dissipation and the steady-state distribution of turbulent velocity fluctuations. This information could be related to cross-spectral densities between the velocity components, or to mean direction of turning (Reynolds, 1999b).

In lack of such knowledge, it is tempting to assume *zero spin* (Thomson, 1987; Reynolds, 1999b) - in the example above this corresponds to A_1. It is interesting to notice that this - at least for the simple 2D example above, but most likely in greater generality - leads to the greatest possible equivalent diffusivity. The issue remains somewhat unclear, although it is generally believed that the difficulty does not seriously limit the validity of dispersal models. It should be noted that the problem is not associated with the Lagrangian approach *per se*, but rather that the energy dissipation and the steady-state velocity distribution are not sufficient statistics of the turbulence with respect to dispersal. The difficulty would also exist in an Eulerian approach.

The problem is also relevant in the common situation where turbulence is 3D and anisotropic, but the model only concerns the vertical component. Ignoring the issue, as is often done, amounts to assuming local independence between vertical and horizontal motion.

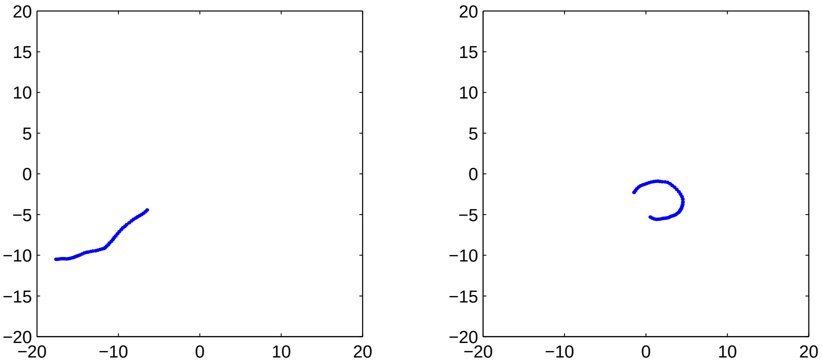

Figure 2: Trajectories of a particle simulated with the model (7). Left panel: $A = A_1$. Right panel: $A = A_2$. With A_2 the trajectories have a tendency to turn counter-clockwise; with A_1 turns are rarer and have no preferred direction.

5 Corrective acceleration in heterogeneous turbulence

In heterogeneous turbulence a first thought could be to maintain the random flight model (3) (or its anisotropic generalization), but let the parameters ω_0, ϵ vary in space. However, such a model would lead to accumulation in regions where the turbulence has low intensity.

This situation is analogous to random walk models of diffusion, where an unbiased random walk with spatially varying intensity causes particles to accumulate where the intensity is low. The remedy in this case is to introduce a drift term in the direction of increasing intensity (Visser, 1997). The exact form of the corrective drift term may be obtained from the Fokker-Planck equation (Gardiner, 1985), the steady-state of which must be uniform. This constraint effectively determines the corrective drift term uniquely.

In random flight models, the remedy is similar as is the way it is determined (Thomson, 1987): Inspecting the Fokker-Planck equation for the *joint* density of position and velocity, we require a steady-state solution with uniform concentration in space and specified local (i.e., conditional) velocity distribution. This effectively specifies a corrective acceleration term in the random flight model, although the ambiguity from anisotropy remains as in the homogeneous case. In one dimension the resulting random flight model is (Thomson, 1987, eq. 30):

$$dx_t = v_t \; dt \quad , \qquad dv_t = a(x_t, v_t) \; dt + \sqrt{C_0 \epsilon(x_t)} \; dB_t$$

with mean acceleration

$$a(x,v) = -\frac{1}{2}\frac{C_0\epsilon}{u^2} v + u\frac{\partial u}{\partial x} + \frac{v^2}{u}\frac{\partial u}{\partial x} \quad .$$

The first term, linear in v, is expected from the homogeneous random flight (3). The subsequent two terms are corrective accelerations, both accelerating in direction of more intense turbulence, i.e. higher r.m.s. velocity u. A version of this model which also accounts for instationarity and a mean flow field is given in (Thomson, 1987; Brickman and Smith, 2002).

We have thus obtained a model which possesses the right steady-state distribution in phase space, and the right inertial subrange. These two criteria are equivalent to the *Well-Mixed Condition* (Thomson, 1987) that if a number of tracers are sampled uniformly from the fluid, they will remain uniformly distributed in the fluid. It is demonstrated in (Thomson, 1987) that the Well-Mixed Condition is equivalent to, or stronger than, a number of other reasonable requirements. Once a well-mixed model has been obtained we can therefore consider the modeling task completed (up to the ambiguity relating to anisotropy).

6 Particle pairs

A random flight model as described in the previous can generate one realization of the trajectory of a passive tracer. By replication, this enables us to compute ensemble average concentrations resulting from, say, a point source of pollution or larvae. However, in many applications these ensemble averages are insufficient: We may also be interested in ensemble variations in the concentration at a fixed point, in the probability that the concentration exceeds a given threshold, or in the concentration as perceived by a typical tracer. In order to assess such properties and other higher-order statistics of the point pattern (Stoyan, Kendall, and Mecke, 1996), a reasonable first step is to model the simultaneous dispersal of *two* particles embedded in the flow (Thomson, 1990).

In isotropic, stationary and homogeneous turbulence, (Richardson, 1926) found a scaling law for the separation distance $R(t)$ of a particle pair

$$\langle R^2(t)\rangle = G_\Delta \epsilon t^3 \tag{8}$$

valid at intermediate times t; see also (Monin and Yaglom, 1975, p. 545). The constant G_Δ is approximately 0.1 (Fung et al., 1992). The empiric scaling of Richardson has later been supported by arguments from statistical fluid mechanics (Monin and Yaglom, 1975) and by kinematic simulations (Bofetta et al., 1999).

The mean-square separation distance $\langle R^2(t)\rangle$ is related to the variance of a plume resulting from a point source, i.e. the mean-square distance from a typical particle in the cloud to the center of mass. The *expected* such variance is $\langle R^2(t)\rangle/2$; the similar expression holds for the covariance matrix in anisotropic conditions.

The scaling law (8) is largely consistent with a diffusion model of the separation distance where the diffusivity $D = D(r)$ varies with separation distance r:

$$\frac{\partial\rho}{\partial t}(r,t) = \frac{1}{r^2}\frac{\partial}{\partial r}\left(r^2\ D(r)\ \frac{\partial\rho}{\partial r}(r,t)\right) \qquad \text{with} \quad D(r) = \frac{1}{2}(G_\Delta\epsilon)^{1/3}r^{4/3} \tag{9}$$

Here $\rho(r,t)$ is the concentration of neighboring particles a distance r from a typical particle, at time t. In fact this model predicts that $\langle R^{2/3}(t)\rangle$ grows linearly with time, as may be shown with Itô's lemma, the chain rule of diffusions (Øksendal, 1995). The difference between this and the scaling (8) appears to be relatively unimportant.

The diffusion model (9) allows a random-walk type simulation of the distance between two particles, using the method for heterogeneous diffusion in (Visser, 1997), or one of the general-purpose schemes in (Kloeden and Platen, 1995).

The above reasoning applies to ideal turbulence. A number of random-flight models have been proposed for more general turbulence, see (Thomson, 1990; Reynolds, 1998b; Du, 2001; Crone et al., 1999; Pozorski and Minier, 1998). Differing in complexity and degree of realism, and all suffering from at least minor theoretical flaws, they have been fairly successful in specific applications.

7 Beyond passive tracers

The previous has all concerned passive tracers. When tracers differ from the embedding fluid, the modeling is more heuristic. The first generalization is that of spherical particles with a different density than the fluid. If we let the density of the tracer approach infinity the Lagrangian time spectrum of the tracer should approach the Eulerian time spectrum of the fluid. This implies that random flight models such as (3) will not do, because the spectrum of any such model has a roll-off in the high frequency range governed by a power law with a negative even integer exponent. To overcome this, (Shao, 1995) builds a model based on the fractional Langevin equation; i.e. the Brownian motion in (3) is replaced by fractional Brownian motion (Metzler and Klafter, 2000). However, in oceanographic applications the density of the relevant tracers often differs only slightly from the ambient water. Then it is appealing to avoid the theoretical difficulties associated with the fractional dynamics approach, and rather maintain the structure (3), simply adjusting the parameters. This approach is pursued in (Sawford and Guest, 1991); (Coppen, Manno, and Rogers, 2001) discuss aggregation and other statistics in a simulation model based on direct numerical simulation of the flow.

Ultimately, we would like to address situation where the behavior of the individuals interferes with the large-scale turbulent dispersal. It appears that this interference has not been pursued in the literature. For bacteria it is also relevant to study the small-scale dispersal; in particular the ability to locate small "hot spots" with elevated concentrations of nutrients using chemotaxis. At these scales turbulence effectively appears as shear; the effect is studied in (Luchsinger, Bergersen, and Mitchell, 1999) by means of simulation and in (Bearon and Pedley, 2000) by means of advection-diffusion approximations.

8 Discretisation and numerical issues

In general terms, the simplest approach to discretisation of a stochastic differential equation is the *explicit Euler scheme*, which for the random flight in 1D is

$$x_{t+h} = x_t + v_t\ h \quad , \qquad v_{t+h} = v_t - \frac{h}{T_L(x_t)} v_t + \sqrt{C_0 \epsilon(x_t)} \cdot (B_{t+h} - B_t) \quad . \tag{10}$$

Here $B_{t+h} - B_t$, the increment of Brownian motion, is sampled at time t independently from a Gaussian distribution with mean 0 and variance h.

It is well known that the explicit Euler scheme has poor performance: Stability requires $h < 2T_L$, and acceptable accuracy requires $h \ll T_L$ since the scheme, in general, has strong order 1/2 and weak order 1 (Kloeden and Platen, 1995).

To avoid part of these problems, it is standard in the literature to replace the explicit Euler stepping of velocity with the *exact* solution for the homogeneous case:

$$x_{t+h} = x_t + v_t \; h \quad , \qquad v_{t+h} = v_t \exp\left(-\frac{h}{T_L(x_t)}\right) + \sqrt{C_0 \epsilon(x_t)}(\tilde{B}_{t+h} - \tilde{B}_t) \tag{11}$$

This avoids unbounded velocities even for large time steps. However, the explicit Euler stepping of position leads to exaggerated dispersal even in homogeneous turbulence, because the instantaneous velocity v_t is more erratic than the average velocity over the time interval $[v_t, v_{t+h}]$.

For reference, the exact solution in the case of homogeneous turbulence can be found using general techniques (Øksendal, 1995). It is:

$$\begin{pmatrix} x_{t+h} \\ v_{t+h} \end{pmatrix} \sim N\left(\begin{pmatrix} x_t + T_L(1 - e^{-h/T_L})v_t \\ e^{-h/T_L} v_t \end{pmatrix}, \begin{bmatrix} \Sigma_{xx} & \Sigma_{xv} \\ \Sigma_{vx} & \Sigma_{vv} \end{bmatrix} \right) \tag{12}$$

Here, $N(\mu, \Sigma)$ denote the multivariate normal distribution with mean μ and dispersion (covariance) matrix Σ, and the distribution is conditional on (x_t, v_t). The elements in Σ are

$$\begin{aligned} \Sigma_{xx} &= u^2 T_L \left(2h - T_L e^{-2h/T_L} + 4T_L e^{-h/T_L} - 3T_L\right) && (13) \\ \Sigma_{xv} &= u^2 T_L (1 + e^{-2h/T_L} - 2e^{-h/T_L}) && (14) \\ \Sigma_{vv} &= u^2 (1 - e^{-2h/T_L}) && (15) \end{aligned}$$

It may be advantageous to use this "exact" solution with frozen turbulence parameters in situations with weak heterogeneity, because the largest acceptable time step is then only limited by heterogeneity. This issue, including implementation, will be pursued elsewhere.

To deal with heterogeneity it would probably be worthwhile to consider the higher-order schemes developed in (Kloeden and Platen, 1995), or the Heuhn predictor-corrector scheme quoted in (Gard, 1988) for the Stratonovich formulation. It would also be useful to make more use of the general methods in (Kloeden and Platen, 1995) for assessing the accuracy of an implementation, in order to determine if the chosen time step is small enough for the given purpose.

The standard approach for determining the time step is to ensure that it is much smaller than the time constants of the system, (Wilson and Flesch, 1993; Thomson, 1987). For the random walk model for pure stationary diffusion, these time constants are L^2/D, $D/(D')^2$, and $1/|D''|$; the first being the diffuse time scale and the two last being related to the expected relative change of diffusivity over a time step. A particular consequence of the time constant $1/|D''|$ is that the discretisation scheme should deal explicitly with points where D'' does not exist, i.e. corners, or an exceedingly small time step is required. Hence, if the local diffusivity is computed by interpolation between grid points in a look-up table, one should use a higher-order interpolation scheme, e.g. global polynomial fitting (Brickman and Smith, 2002) or splines.

In situations with strong heterogeneity it is tempting to use a variable step size, adapted to local time constants, since this can reduce computational efforts significantly. This is warned against in (Wilson and Flesch, 1993) where it is demonstrated that one such adaptation scheme can lead to bias; see also (Brickman and Smith, 2002). A worthwhile effort would be to single out the mechanisms that cause the bias and construct remedies.

Apart from numerical issues concerning discretisation, individual-based simulation also raises statistical questions related to the confidence in the obtained results, as in any other Monte Carlo technique. Indeed, (Graham and Moyeed, 2002) emphasize that practitioners of Lagrangian stochastic modeling should consider themselves experimentalists, rather than analysts. For instance, the experimental design should include replicates to assess the accuracy of the results (Brickman and Smith, 2002).

In some applications we would wish to have increased resolution in sample space near critical events: For instance we may track a batch of larvae from hatching to a nursey ground; in this case we would require accurate statistics mainly for the small fraction which actually arrive and do so while still alive. A technique for obtained such increased resolution is *particle splitting*, developed in (Thomson, 1990) for the case of simultaneous dispersal of two particles. The technique effectively "zooms in" on the realizations of interest, in this case pairs of particles that are close to each other.

9 Conclusions

Lagrangian stochastic modeling is an efficient approach to turbulent dispersal in the ocean, in particular when ensemble average concentrations are required for the purpose at hand, and when the particles being tracked behave as passive fluid elements.

Standard statistics (u, ϵ) are insufficient to determine the remaining statistics of the flow, such as the spin and the equivalent diffusivity. The issue relates to both anisotropy, and non-universality in the energy subrange. Although there appears to be consensus that the problem is not very critical, the ultimate validation of e.g. the zero-spin model is comparison between synthetical drifters and physical drifters. A convincing case could be made if the Kalman predictor (Ljung, 1999) based on the random flight model generates white noise residuals when fed with real observations. In principle this must be done for a wide range of different flows, since universality does not apply.

Despite the immediate applicability of existing modeling techniques for tracking of single particles, the state of the art may be advanced by adapting existing high-performance algorithms for simulation of general stochastic processes. Techniques with particular promise are probably predictor-corrector schemes to allow increased step sizes, and variable step sizes based on local time constants. The task would be worthwhile, since experience shows that existing algorithms require substantial computational ressources.

Extensions beyond the single passive tracers are available, but require more careful model validation, because their founding is more heuristic. A point which could deserve special attention is the inclusion of density-dependent processes, e.g. growth and mortality. Inspiration can be obtained from two-particle models, which are being used for chemically active flows and for assessment of variations in concentrations. Nevertheless many different approaches can be envisioned, and it is yet to be clarified which are more fruitful.

In summary, Lagrangian models serve as a useful tool even with the current state of the art, and yet they remain a fertile research area in themselves.

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