Challenges for the integration of process studies and modelling of marine zooplankton

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Ecosystem models are now both a fundamental tool of marine science and at the cutting edge of research. As sophisticated and as useful as these models are, concern is often raised regarding their representational fidelity, both for individual processes and for overall ecosystem function (Flynn, 2005; Anderson, 2005). Many constraints limit our ability to improve the match between our observation and understanding of marine biological processes and their numerical representation.

From 2-5 May a group of more than twenty-one scientists met to discuss the ties between ecological models and process studies (Fig. 1). The meeting was held at the French National Centre for Mathematics (CIRM) on the Luminy campus of the Université de la Méditerranée. The goal of the meeting was to discuss the relation between process studies of zooplankton in the ocean and the representation of these processes, and zooplankton in general, in numerical models. The meeting was jointly developed by GLOBEC Focus 2 (Process Studies) and Focus 3 (Predictive and Modelling Capabilities) Working Groups with the organisational lead taken by Francois Carlotti, David Mackas, Roger Harris, Jean-Christophe Poggiale and Brad deYoung.

We focused on marine zooplankton because they play a pivotal role in pelagic ecosystems both in trophic food chains and in biogeochemical fluxes (Banse, 1995). Our understanding of pelagic system dynamics is presently limited to basic trophic-level interactions in ecosystem models (e.g. N, P, Z models) and zooplankton processes and their mathematical representation present a major challenge because of the complexity of species life history and their interactions.

A previous meeting to discuss priorities in marine zooplankton research (Paffenhofer *et al.*, 2001) addressed three key issues: (i) significance of zooplankton hot spots (ii) information on individual species and (iii) zooplankton and biogeochemical cycles. Rather than review progress on these three issues, which remain of importance, we took a different approach with a focus on improving our understanding of key biological processes (i.e. trophic and metabolic rates, encounter rates, behaviour, mortality,…) that are central to marine zooplankton but for which progress is required to develop improved mathematical representation. Further advances will require new techniques (from molecular biology to new video microscopy), new observational tools and advances in computer technology and modelling techniques. Such developments should include new strategies for linking model concepts and data acquisition.

The interests of those who attended covered mathematical modelling, population modelling, spatially explicit modelling, process studies, field oceanography and evolution and ecology. The discussion was not limited to a single region or species but covered a broad range of zooplankton (including fish larvae) and ecosystems to enhance the impact and permit comparative ecological and oceanographic interpretation and analysis. The overarching goal and focus was to review our understanding of population structure and dynamics, and the behaviour and ecology of marine mesozooplankton. The groups discussed were copepods, euphausids, salps, appendicularians, chaetognathes, gelatinous zooplankton, pteropods, siphonophores and larval fish.

Figure 1. Attendees at the meeting included: Front row (left to right) Meng Zhou, Jose-Luis Acuna, Bas Kooijman, Dougie Speirs, Andrew Visser, Hiraki Siato. Second row (left to right) Lionel Eisenhauer, Jean-Christophe Poggiale, Tamara Benari, Hans-Jurgen Hirche, David Mackas, Albert Calbet, Roger Harris, Brad deYoung, Mike St. John, Harold Batchelder, Andrew Hirst, Xabier Irigoien, Roger Arditti, Oyvind Fiksen and Francois Carlotti. Missing from the photo are Delphine Thibault-Botha and Horst Malchow.

The three key characteristics that underlie population, behaviour and ecology of any species are development and growth, mortality and reproductive success. It can be argued that we know the least about mortality of marine organisms, not only what the mortality rate is but how to parameterise the process. While these three broad characteristics served as an overall framework for the meeting it was necessary to consider more specific processes to help to focus the discussions.

Our meeting was organised around five main topics: feeding, metabolism and growth, mortality, predator-prey interactions and habitat. Each of the attendees presented within one or more of these five organising topics. We allowed for discussion during the presentations but also had breakout discussions following the presentations. We framed a few general questions that we wanted to address as a group:

- When developing a zooplankton community, population or individual model, what processes are usually missing?
- What resolution of data is required for key variables, parameters or processes?
- Can we use theoretical approaches to guide our development of model design or the estimation of variables or parameters?
- How well integrated are experimental and modelling approaches?

We used the discussion to focus on ideas that would be useful for a review paper, to be published in the primary literature, suggesting stronger links between those designing and conducting observational programmes and modellers. We would also like to see more attention to the development of models as tools of exploration and perhaps to diminish the expectation that models are simply for simulating or predicting data. Models are also powerful tools for exploring process dynamics and patterns. There was a general view, however, that the tie between modellers and observationalists was not as strong as it should be. Observational programmes can benefit from considering modelling, both at the design and interpretation stages of the work, and clearly models require data from observational programmes, both for their setup and design, and for testing.

Our final discussion developed along somewhat different lines from those of the presentations. The five main areas of interest were:

- Model design and development
- Bridging spatial scales
- Individual based models
- Feeding studies
- New approaches to representing growth, metabolism and development

In designing models it is important that one carefully describes the problem, in essence the goals of the model so that they can be fit-to-purpose. We considered the balance between model payoff and complexity, noting that this relationship is typically dome-shaped, with payoff increasing with complexity up to some turning point. The coupling of data and ecosystem models is particularly important because such models are not built from a canonical set of equations and so the potential for error arising from poor model structure is significant.

We discussed the idea of "environmental grain", first suggested by Levins (1968), as a useful concept for explaining and raising new questions about zooplankton spatial pattern and habitat. This theory allows for the interpretation of differing approaches that organisms might take in response to environmental structure. If environmental variability is "fine-grained", an organism experiences environmental variability in approximately random order and in proportion to the probability density of each environmental "condition" within the environmental continuum. Levins' theory says that the best adaptive response by the organism is either to be a generalist, or to specialise on the "condition" or patch type that is most widespread (and therefore most frequently encountered) within the total environment. In contrast, if the environment is "coarse-grained" each individual can or must remain for prolonged periods of time in habitat that spans only part of the range of environmental conditions (in the extreme, an individual may spend its entire life within a single environmental patch). Over time it therefore integrates a selective subset of environmental conditions; its experience is very far from a non-selective overall average. According to the theory, the optimal exploitation strategy is for the individual to specialise on the conditions prevailing within the patch or (perhaps more commonly) to find and reside within a patch that matches its specialisations. For zooplankton, the difference between coarse and fine grained spatial structure is largely determined by how well the individual can control its location in the face of strong fluid advection and mixing (motility vs. passive drift). As this capability changes with life stage, improved understanding of zooplankton behaviour during its whole life is required. This includes behavioural studies and space and time scale resolutions which are still challenging for marine zooplankton research.

We reviewed the framework of individual based ecology (Grimm and Raisback, 2005) suggesting that individual based models, rich in mechanistic detail describing how individuals interact with each other and the environment, offer significant potential for integrating physical oceanography and behavioural ecology. The individual based model lies at the juncture between of three elements:

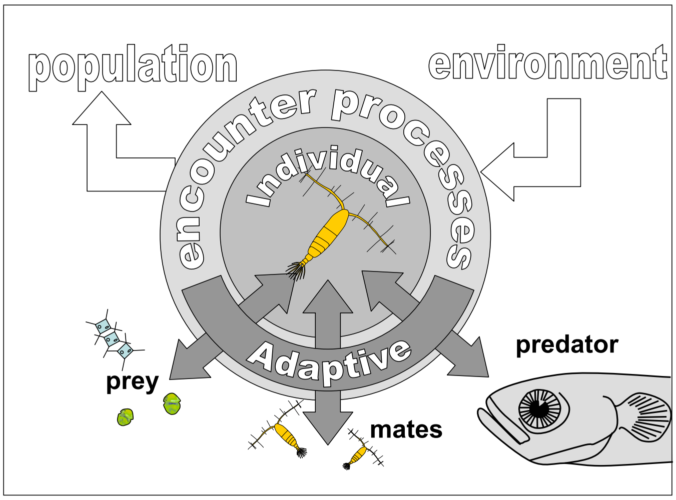

Figure 2 Conceptual framework of individual based ecology. An individual interacts with its environment (predators, prey and mates in particular) through encounter processes that are in part regulated by adaptive behaviours. Individual based zooplankton ecology seeks to find the fundamental rules by which zooplankton interact and optimise their behaviour and to predict population level patterns as emergent properties.

physical models of the environment, models of encounter rate and the representation of behaviour as an adaptive trait (Fig. 2).

We discussed relationships between theoretical and experimental research within a consistent framework such as Dynamics Energy Budget (DEB) theory (Kooijman, 2000), starting from the individual level, via the population to the ecosystem level. This framework imposes constraints, both on theoretical developments, and on experimental design. Mass and energy balances, stoichiometric constraints and surface area-volume interactions, play an important role here, and require a holistic approach to ecosystem structure and functioning. The step from individuals to population dynamics can be made within the framework of physiologically structured population dynamics, although the number of parameters and variables should be limited, such that the physical and biological interpretation of the parameters, and the link with the underlying processes, are preserved.

Improving our understanding of the dynamics of marine ecosystems can come about using various methodologies, from laboratory and field measurements to modelling and data syntheses, and the interactions between them. Each of these techniques has both strengths and weakness, and each can provide data or help resolve issues that the other techniques are unable to. With growing concerns about environmental change (change in climate, weather patterns, acidification, fishing pressure) there is an urgent need to be able to predict (model) the key processes in the marine environment under different change scenarios. For such models to be effective, we will need to develop an improved dialogue between modellers, experimentalists and data synthesizers as has been pointed out recently by Flynn (2005) in order to determine the scientific priorities and then undertake the key research needed. Modellers need to be clear about which measurements they lack, while those who have good insight into the organisms and systems they study experimentally must help shape how these are represented in models. Experimentalists should be open to testing the assumptions, results and hypotheses of models. Such dialogue between experimentalists and modellers is particularly needed if, for example, Plankton Functional Types are to be successfully incorporated into models (e.g. Anderson, 2005).

A draft paper has now been developed, following the meeting, which should be submitted for publication this fall. Anyone interested in obtaining a copy is encouraged to contact one of the five organisers (Carlotti, Mackas, Harris, Poggiale or deYoung).

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Human and Climate Forcing of Zooplankton Populations

4th International Zooplankton Production Symposium
28 May - 1 June 2007, Hiroshima, Japan

The 4th Zooplankton Production Symposium will be held 28 May - 1 June 2007 and will be co-sponsored by ICES, PICES and GLOBEC. This symposium is the first of the series to be held outside Europe and will focus on “Human and climate forcing of zooplankton populations”. As such, it represents a timely topic and will provide an important opportunity to further develop the truly international nature of zooplankton research.

Sessions and convenors:

Plenary
Michael Dagg, Roger Harris and Luis Valdes

s1: Global comparisons of zooplankton time series
David Mackas and Luis Valdes

s2: Importance of zooplankton in biogeochemical cycles
Hiroaki Saito and Deborah Steinberg

s3: The role of zooplankton in foodwebs: changes related to impacts of climate variability and human perturbation
Michael St. John

s4: Mortality impacts on the ontogeny and productivity of zooplankton
Mark Ohman and Serge Poulet

s5: Zooplankton functional groups in ecosystems
Sanae Chiba and Sun Song

s6: Microbial loop vs classical short food chains: implications for appraisal of foodwebs' efficiency and productivity
Ulf Bamstedt

s7: Environmental and other constraints on zooplankton behaviour, life histories and demography
Charles Miller and Atsushi Tsuda

s8: Zooplankton biochemistry and physiology: practical and potential biotechnology application
Adrianna Ianora and Kurt Tande

s9: Advance in image technologies and the application of image analysis to count and identify plankton
Cabell Davis and Xabier Irigoien

s10: Analysis and synthesis: modelling zooplankton in aquatic ecosystems
Daniel Grunbaum and Michio Kishi

Workshops

w1: Temporal and regional responses of zooplankton to global warming: phenology and poleward displacement
Wulf Greve

w2: Zooplankton research in Asian countries: current status and future prospects
Sanae Chiba, Young Shil Kang and Sun Song

w3: Krill research: current status and its future
So Kawaguchi and William Peterson

Registration

Registration is available from the symposium website.

Early registration fee: US $350 (prior to 16 December 2006)
Regular registration fee: US $450 (December 17 onwards)
Student registration fee: US $200

Financial support

Limited funds are available to assist younger scientists and scientists from countries with “economies in transition”. See the conference website for further details.

Abstracts

Scientific sessions will include invited and contributed papers. Contributed papers will be selected for oral or poster presentation. Abstracts must be submitted via the website by 16 December 2006.

Symposium website

For further details, registration and abstract submission see the symposium website at:

http://www.pices.int/meetings/international_symposia/2007_symposia/4th_Zooplankton/4th_Zoopl.aspx