Workshop on "*Individual-Based Models of Zooplankton*"

by Harold P. Batchelder, Douglas C. Speirs and Wendy C. Gentleman

Approximately 32 modelers, experimentalists and field scientists from 11 countries met to discuss zooplankton individual-based models (IBMs) at a workshop held on March 16, 2011, during the 5th International Zooplankton Production Symposium in Pucón, Chile. Here we briefly summarize the seven presentations (one invited) and subsequent discussions. The workshop focused on new methods and current challenges in the unification of individual-level and population modeling approaches. Several topics were identified that require additional consideration and should be emphasized in future research to improve the acceptance of the individual-based approach in zooplankton ecological investigations, and to better link IBMs with population-level modeling approaches.

IBMs explicitly represent individual organisms, or quasi-individuals representing homogeneous groups of individuals, as discrete elements of a computer simulation. Individuals have their own state characteristics, such as age, size, developmental stage, and physiological condition; population-level dynamics arise as emergent properties of the interactions among individuals and between individuals and their environment. This approach contrasts with population-level models (PLMs), or aggregated mathematical models, in which population processes are described by relationships between densities of individuals, all of whom have identical (mean-state) characteristics. One of the main appeals of IBMs is that they operate at the individual level at which adaptation and evolution occurs, and provide a simple approach to capturing population heterogeneity through inter-individual variability. Stochastic processes impacting individuals can readily be incorporated into simulations. A second advantage is the ease of introducing behavioral rules, especially those relating to movement, which can be difficult to represent in PLMs in a mathematically compact way.

Wendy Gentleman (Dalhousie University, Canada) provided an invited overview of how IBMs are appropriate for advancing fundamental understanding of key issues in zooplankton ecology such as the environmental control of development timing, optimal behaviors that increase fitness, influence of transport processes on distribution and demographic processes, and the importance of individual variability in individual rate processes and experienced history. A key point noted by Wendy, and many of the other speakers and participants, is that IBMs explicitly incorporate individual variability which is fundamental to survival, fitness and eventual change in phenology and genetic structure. As was pointed out a long time ago by Gary Sharp—"*the average fish is a dead fish*"—indicating that condition-dependent growth or mortality under conditions of high mortality mean that individuals that are of average condition are destined to perish. Thus, it is only the lucky or supremely well adapted (*e.g.*, having a set of characteristics that are extreme and favorable) individuals in a population that survive. This is true for any population, such as zooplankton, in which there is high production of young, and high mortality. IBMs are ideal tools for quantifying why some individuals survive while most do not. Equally important, Wendy concluded that IBMs are a good tool for many ecologically interesting questions, but they are not the only tool and may not be appropriate for examining zooplankton community production, trophic links among multiple species assemblages, and issues where density dependence is strong. For such questions PLM approaches may be the better tool.

Then followed a series of presentations on specific applications of IBMs to zooplankton. Gaël Dur (University of Shiga Prefecture, Japan) described an IBM development environment called MOBIDYC "Moby Dick" and its application to understanding the phenology of the egg-sac carrying copepod *Eurytemora affinis* in the Seine Estuary. MOBIDYC (**MO**delling **B**ased on **I**ndividual for **DY**namics **C**ommunities) was specifically used to investigate temperature sensitivity of reproduction and development, but included also non-specific (stage-based) mortality and predator-abundance correlated predation mortality.

Dougie Speirs (University of Strathclyde, Scotland) discussed several model approaches applied to *Calanus* *finmarchicus* in the Irminger Sea region of the North Atlantic. Mismatch of the model to the data was significant when a prior tuned *C. finmarchicus* model was used without alteration to the Irminger Sea. Five parameter estimation scenarios were examined using simulated annealing to tune between 16 and 22 model parameters simultaneously—most related to mortality, which is often the least well known rate process in population and individual models. These included parameters related to background mortality rates, temperature dependence of mortality, and prey-dependent mortality.

Matteo Sinerchia (London Imperial College, UK) presented a one-dimensional (vertical) multitrophic-level IBM of diatoms (producers), copepods (herbivores), two predators on copepods—squid paralarvae (the target species of particular interest) and a generalized other consumer—and a top predator that consumes squid paralarvae. The Lagrangian Ensemble Recruitment Model (LERM) is used to explore how environmental variability at a site in the Azores (Eastern North Atlantic) influenced the planktonic ecosystem and squid recruitment. The copepod IBM is based on the Carlotti and Wolf (1998; *Fisheries Oceanography*, 7, 191–204) model for *C. finmarchicus*, which includes staged growth, diel migration, ingestion based on gut volume and passage time, and dynamic allocation of ingested carbon into protein and lipids. The squid paralarvae IBM is based on the physiology, behavior and recruitment size of *Loligo*. Top predator dynamics are implemented using abundance, size, vertical distribution and trophic interactions based on ingestion equations of squid. The coupled equations achieve near stationarity after about 15 years. Simulation results suggest that squid mortality due to predation, especially on the smallest, least mobile squid paralarvae, is the most important factor controlling annual recruitment. Survival declined with increased egg production due to increased intra-population competition for prey. At highest egg production rates, predation was an additional source of mortality, indicating an interaction between density-dependent growth and predation determining density-dependent survival.

Jeff Dorman (University of California, Berkeley, USA) described the seasonal and interannual dynamics of *Euphausia pacifica* using an individual-based bioenergetics model coupled to NPZD-ROMS simulations of the central-northern California Current for the years 1991–2008. The bioenergetics model included temperature-dependent egg development, phytoplankton and temperature-dependent growth of feeding krill, and growth-dependent egg production by adult krill. Different simulations were initialized with either only eggs or only adult krill. The seasonal pattern of monthly mean larval growth and monthly mean adult growth was similar, with peak growth occurring when the

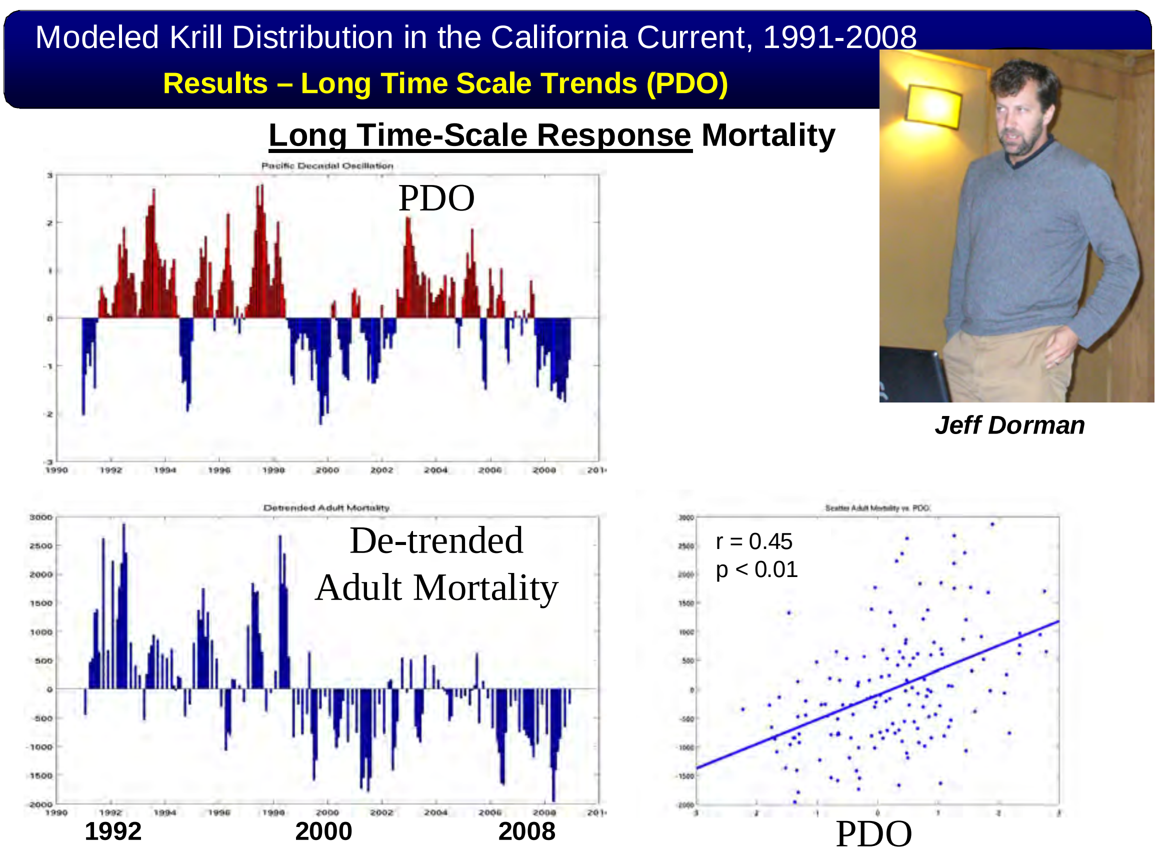


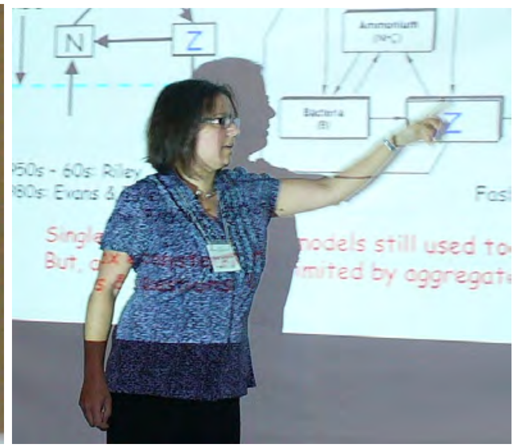
Fig. 1 Left panels show the time series of the Pacific Decadal Oscillation (PDO) and de-trended adult krill mortality from the krill IBM forced with fields from a coupled NPZD-ROMS. Lower right shows the scatter plot of adult mortality vs. PDO. Upper right is Jeff Dorman giving his talk.

population (eggs or adults) was initiated in spring (April–May; concurrent with peak phytoplankton concentration) and minimum growth in October–December (when phytoplankton is low). Conversely, monthly mean starvation was nearly uniform (but high, >60%) with start date for larvae, but variable with start date for adults, and lower (<30%), with highest mortality for adults that were initialized immediately following the spring phytoplankton bloom (*e.g*., June–July model starts) and which experienced high offshore temperatures. Interannual variability in growth, mortality and southward advection of adult krill were negatively, positively and not significantly correlated, respectively, with variability in the Pacific Decadal Oscillation for the years 1991–2008. Wintertime abundance of krill in the region of study was positively related to Cassin's Auklet reproductive success and Chinook salmon survival. Jeff Dorman was awarded a Best Presentation Award for his talk (Fig. 1).

Brie Lindsey (Oregon State University, USA) used an IBM (with egg production, temperature-dependent stage progression and temperature- and prey-dependent feeding and metabolism) coupled to the output of an NPZD-ROMS model to identify potential *Euphausia pacifica* egg production sites and advective pathways on the central Oregon continental shelf in 2002. Total egg production rate per adult female and observed larval growth rates from the coupled model were similar to published observations from the region. Comparison of pathways of eggs and larvae from the model to cross-shelf distributions in 2002 strongly suggested that egg-laying must occur in the near shelf region to yield larvae on the shelf. Reproduction is likely also occurring off the shelf break, but the probability of those progeny developing on the shelf is low.

The final talk by Hal Batchelder (Oregon State University, USA) described an implementation of a 5-stage model of *Euphausia pacifica* into the NEMURO concentration-based ecosystem model. NEMURO (**N**orth Pacific **E**cosystem **M**odel for **U**nderstanding **R**egional **O**ceanography) has large and small phytoplankton, three feeding types of zooplankton, and tracks both nitrogen and silica through the lower trophic food web. One of the more meaningful ecosystem forecasts from climate projection scenarios is





Dr. Harold (Hal) Batchelder (hbatchelder@coas.oregonstate.edu) is a Professor in the College of Oceanic and Atmospheric Sciences at Oregon State University, USA His research focuses on individual-based models that couple marine environments and marine populations, including studies on Calanus finmarchicus in the North Atlantic, and krill and juvenile salmon in the Northeast Pacific. In PICES, he served as Co-Chairman of the Climate Change and Carrying Capacity (CCCC) program and as a member on PICES Science Board from 2001–2009, and presently as a member of the FUTURE Advisory Panel on the Status, Outlooks, Forecasts and Engagement (SOFE-AP). He also leads the Marine Ecosystem Model Inter-comparison Project (MEMIP) of PICES. Hal served as Coordinator of the US GLOBEC National Program for 6 years, and as Executive Director of the US GLOBEC Northeast Pacific regional program for 12 years.

Dr. Douglas Speirs (d.c.speirs@strath.ac.uk) is a Lecturer in the Department of Mathematics and Statistics at the University of Strathclyde in Glasgow, Scotland. His research is diverse, spanning mathematics, including ecosystem models of marine systems and population dynamics models of Calanus finmarchicus and insects in stream communities. Doug has participated in a number of inte-disciplinary programs, including GLOBEC, and is currently active in the EU BASIN program and the UK Ocean Acidification Program. He is on the editorial board of the Journal of Biological Systems, and is a subject matter editor for the journal Ecology.

Dr. Wendy Gentleman (wendy.gentleman@dal.ca) is an Associate Professor in Engineering Mathematics with a cross-appointment in Oceanography at Dalhousie University, Canada. Her research uses models to understand how environmental variability affects zooplankton population dynamics, as well as trophic links between primary producers, zooplankton, and their predators. This work includes analyses of assumptions inherent in model equations, improving characterization of biological processes and physical–biological coupling, and investigation of the factors controlling observed variations in zooplankton density and production. Wendy collaborates with researchers across North America and Europe, and has documented the critical roles of the grazing functional response and mortality for copepod demography and ecosystem structure. She has been actively involved with several interdisciplinary research programs (e.g., GLOBEC, JGOFS).

information on the abundance and distribution of trophically important taxa such as krill. However, predictions of abundance (or biomass density) using the IBM approach are difficult (as described in the earlier talk by Wendy Gentleman). This talk explored the extent to which some of the advantages of the IBM approaches could be incorporated into concentration-based ecosystem models. One of these is explicit recognition that different stages of the life history of an organism feed on different prey, have different mortalities and different behaviors (such as diel vertical migration amplitudes), and different growth rates. Results from 0-D and 2-D models were used to illustrate how some of these "IBM features" were included in a concentration-based model. Specifically, a stage structured algorithm that eliminates numerical diffusion (*e.g.*, rapid growth through the life history) was implemented using the mean-age model (Hu *et al*., 2008, *MEPS*, 360, 179–187). The 0-D case study illustrated the strong interaction of development rate and stage dependent mortality on the total biomass of krill in the model, with strong consequences, acting through competition for food, for other consumers in NEMURO. The 2-D NEMURO model (a vertical section across the Oregon continental shelf) revealed that the mean-age model could be implemented in a way that allowed proper mixing and advection of biomass and mean age information for krill (or other plankters) using the standard ROMS codes. Important questions in plankton population dynamics are best answered by IBMs, but other questions are better examined by concentration, stage-structured or PLM-based methods. The appropriate modeling approach depends on the specific question.

During the last hour of the workshop, a general discussion of IBMs ensued, which included tradeoffs of super-individual *vs*. individual modeling, dealing with density dependence and feedback to forcing fields (especially prey depletion), examining methods for linking IBMs with other model approaches, such as ecosystem and structured models, and the need for modelers to work more closely with observational and experimental scientists to better constrain the biological, ecological and physiological information/parameterization of models. By working together, the cycle of testing models to data will suggest new experiments and observations and identify shortcomings in the models. Finally, there is a desire to better document individual-based models to enable independent evaluation of model results. A standard for Overview, Design Concepts and Details (ODD) has been proposed for the documentation of IBMs (Grimm *et al*., 2010; *Ecological Modelling*, 221, 2760–2768).

New Book Release on the 100th Anniversary of the T/S *Oshoro Maru*

It was my great pleasure to edit the book, "100th Anniversary of the T/S *Oshoro Maru*" together with many people who have worked with the *Oshoro Maru* over the years. The book includes photos and articles depicting the rich history of the *Oshoro Maru* training ships, from the first, which was built in 1909, to the most recent, fourth ship built in 1984. The *Oshoro Maru II* was commissioned in 1927 and was replaced in 1962 by the *Oshoro Maru III*. The annual summer cruises since 1955 have allowed long-term ecosystem observations, and have advanced cooperative research among PICES member countries. The data collected during T/S *Oshoro Maru* cruises are invaluable for addressing scientific problems of the North Pacific. More than 250 scientific papers have been published using these data. Recognition of the importance of the *Oshoro Maru* monitoring program led to the receipt of the first PICES Ocean Monitoring Service Award (POMA) at PICES-2008, in Dalian, China (www.pices.int/awards/POMA_award/POMA_award.aspx).

Copies of the book are available to PICES colleagues (contact me at ssaitoh@salmon.fish.hokudai.ac.jp), but the number is limited, and they will be distributed on a first come, first served basis. They will be sent by surface mail and priority will be given to library or public use.

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