

A Component of the U.S. Global Change Research Program

**Secondary Production Modeling
Workshop Report**

U.S. Global Ocean Ecosystems Dynamics

Report Number 13

June 1995

U.S. GLOBEC

Global Ocean Ecosystems Dynamics

A Component of the U.S. Global Change Research Program

Secondary Production Modeling Workshop Report

Report Number 13

June 1995

This is a report of the U.S. GLOBEC Workshop on Secondary Production Modeling held in Savannah, Georgia, USA, at the Skidaway Institute of Oceanography on 23–25 February 1993, E. E. Hofmann and G.–A. Paffenhöfer, conveners. The Skidaway Institute of Oceanography provided facilities for our workshop. The National Science Foundation, Division of Ocean Sciences, Biological Oceanography, through the U.S. GLOBEC Coordination Office, provided travel funds for some of the participants.

Produced by

U.S. GLOBEC
Scientific Steering Committee Coordinating Office
Department of Integrative Biology
University of California
Berkeley, CA 94720-3140

Phone: 510-643-0877
FAX: 510-643-6264
E-mail: kaygold@uclink2.berkeley.edu

Additional copies of this report may be obtained from the above address

Table of Contents

Executive Summary	1
Introduction	2
Workshop Organization	2
Opening Plenary Session	2
Summary of Questionnaire Responses	4
Working Group Reports	5
Behavior	5
Integration Across Scales and Linking of Scales	6
Structural Aspects of Secondary Production Models	7
References	9
Appendix A. Questionnaire.....	10
Appendix B. Questionnaire Responses	11
Appendix C. Participants	15

Executive Summary

From 23-25 February 1993, twenty-one scientists from the physical and biological community with expertise in modeling and empirical observations, met in Savannah, GA for a U.S. GLOBEC sponsored workshop on secondary production modeling. The goal of the workshop was to assess the present state of secondary production modeling in the sea and to provide recommendations for future research directions. Of particular importance, the workshop identified several scientific areas that are, perhaps, presently limiting advancement in the modeling of zooplankton population dynamics and production.

Following nine overview presentations, the participants formed working groups to discuss issues related to three of these scientific areas: 1) animal behavior; 2) integration across scales and the linking of information at different scales; and, 3) structural aspects of secondary production models. The primary recommendations that resulted from these working group discussions are to:

Develop models that include our understanding of the mechanics underlying animal behaviors, including proximal and ultimate environmental factors controlling behavior.

Develop nested models that encompass biological processes from the level of the individual to the level of the population. Such models must bridge a wide range of temporal and spatial scales, i.e., from the local to the regional in space, and from the hourly to the annual in time.

Develop detailed mechanistic models for a few key zooplankton species that allow for the inclusion of inter-individual variability, including genetics. These models need to consider more complex structural aspects of the system that impact the key species, such as the dynamics of primary producers and microzooplankton grazers, which represent much of the prey resources for the larger zooplankton.

Besides these specific recommendations of the working groups, two recurrent themes emerged from the plenary and working group discussions. First, **there was a consensus for the development of stronger ties between empiricists and modelers at all scales.** Scale considerations include temporal, spatial, and ecological (individuals-to-populations-to-ecosystems). Moreover, cooperation between empiricists and modelers will become more important as biological models move toward the development of fully data assimilative models. Two way interactions are needed: empiricists need to consider the, potentially unique, data requirements of the modelers-e.g., the types of data, and their spatial and temporal frequency; modelers, on the other hand, need to consider the observationalist's ability to collect suitable data, and the empiricist's need for parameter estimation. Second, **it is desirable to make biological models, especially models of zooplankton population dynamics, accessible to a broader segment of the biological oceanographic community.** This is especially true for those models that couple the biological dynamics of populations to the physics of the environment, particularly when more than one dimension is included. U.S. GLOBEC should support the development of a biological oceanography community model(s), similar to those available for physical oceanography.

Introduction

The objective of the U.S. GLOBEC program is to understand how changes in the global environment, especially climate, affect the abundances, variation of abundance, and production of animals in the sea. Modeling is one of the approaches identified as a means of realizing this objective. In particular, the U.S. GLOBEC initial science plan states that this understanding "*...must necessarily involve coupled physical-biological models, linking performance of individual organisms to local and mesoscale physical processes and linking both the biology and local and regional physics to basin scale changes in global climate.*" Thus, from its inception, the U.S. GLOBEC program has emphasized and supported modeling studies. The U.S. GLOBEC Long Range Science Plan recently stated, "*A long-term goal of U.S. GLOBEC is to bring predictive models for a limited set of ecosystem properties to an operational stage in the next decade.*"

To further its modeling goals, U.S. GLOBEC supported a workshop at the Skidaway Institute of Oceanography in Savannah, Georgia on 23-25 February 1993. The workshop brought together twenty-one scientists (Appendix C) with expertise in measuring and/or modeling zooplankton population dynamics and secondary production. The workshop provided a forum for the exchange of ideas between empiricists and modelers.

Workshop Organization

The workshop began with overview presentations that were intended to introduce some of the issues that might need to be considered to advance the development of biological and coupled biological-physical models in ocean ecosystems. Participants then broke into working groups to discuss: 1) animal behavior, specifically why and how it should be incorporated into models; 2) issues related to integration of models across scales; and, 3) structural aspects of models. Early in the workshop, the participants completed a questionnaire that was designed to stimulate and focus the discussion of secondary production modeling.

Opening Plenary Session

The plenary talks (Table 1) addressed several issues: aspects of animal behavior (Werner, Paffenhöfer, Yen), scaling (Squires, Strickler, Klinck, Hofmann), model structure and biological complexity (Verity, Hofmann), and interactions (coupling) between physics and biology (Werner, Strickler, Hofmann, Taylor).

The first presentation focused on a three-dimensional model of the circulation on Georges Bank that was used to track the transport of cod and haddock larvae. The primary focus of this particular modeling study is to determine to what extent the retention of the larval stages of these fish on the bank is physically determined. The simulations indicated that surface waters (the upper 15 m) on the southwestern part of Georges Bank are advected offshore relatively rapidly; conversely, most of the water at greater depths (near 30 m) is recirculated and remains within the 100 m isobath on the Bank. This implies that passively transported larvae have a better chance of remaining on the Bank, and surviving to recruit if they remain in the deeper portions of the water column. Simulation experiments indicated that interaction of vertical migration behavior and advective transport could be important in determining the fate of individual larvae in this ecosystem.

Interactions between the physical environment and organisms at very small scales were addressed by two presentations. The first included a model of turbulence, which described three-dimensional turbulent fields and provided an indication of the spatial (length) and temporal (persistence) scales of turbulence. A second presentation considered the effects of turbulence on the feeding currents of copepods. Turbulent intensity can markedly affect feeding success and feeding behavior. For example, in experiments different levels of turbulence led to different allocations of time among various feeding behaviors (e.g., slow swimming, fast swimming, etc.). More studies are needed to better document the effects of variable turbulence on feeding and animal behavior more generally. Scaling the results of single individual turbulence experiments (which document cm scale interactions) to populations of organisms operating on much larger spatial scale and longer temporal scales is a major difficulty that needs to be addressed. Parameterizing the effects of animal-turbulence interactions may be a way to incorporate their effects into larger-scale models.

Three presentations focused on biological aspects of secondary production measurement and modeling. The first related to the relatively recent recognition that protozooplankton are a major grazer in most ocean ecosystems. Clearly, if much of the primary production is being consumed by this group, this will have an impact on the overall energy available to the mesozooplankton, including larval fish. Protozooplankton are also consumers of smaller producers (nannophytoplankton and bacteria) that are directly unavailable to mesozooplankton. Thus, the protozooplankton may be an important trophic link between small producers and larger consumers. For example, models that ignore the grazing impact of protozooplankton will underestimate food available for metazooplankton and overestimate mortality of young fish larvae. The second presentation highlighted the importance of including inter-individual variability in making estimates of and modelling production. Examples from the literature on copepod weights, gut contents and feeding rates were used to illustrate the extreme variability that could exist between individuals subjected to presumably similar environmental conditions. Also emphasized was the behavioral flexibility that permits individual organisms to react to environmental change. The third presentation described a fluid mechanics model of the filtering current of a large calanoid copepod.

The scales of the biological and physical processes that are presently modeled are mismatched. For example, existing circulation models cover a large range of space and time. They tend to be developed for advective processes that occur over long (month to year) time scales and large (regional to basin) spatial scales. Spatial resolution of a typical ocean circulation model might be 30 km in the horizontal and 25 to 250 m in the vertical dimension. Biological processes, such as trophic interactions, vertical distributions and vertical migrations, typically occur at much finer spatial and shorter time scales in the ocean. Examples are the <1 day doubling times of phytoplankton and the strongly heterogeneous vertical distributions, on scales of cm to m, of both phytoplankton and zooplankton. This mismatch in time-space domains of the two disciplines (biological and physical) creates difficulties in developing coupled bio-physical models. One strategy, albeit an expensive one, to couple biological and physical processes in models is to increase the spatial resolution and decrease the time step of circulation models to match more closely the biological requirements. An alternative approach is to understand the biological interactions at the smaller scales, but parameterize their effects, treating them as subgrid scale processes, for inclusion in physical circulation models.

Some of the issues involved in coupling a biological-biooptical model to a physical circulation model were discussed in the specific context of a coupled circulation-biooptical model of the California Current Transition Zone. Biological features represented in the model included nutrient concentrations, nutrient uptake and growth of two size classes of phytoplankton, and the dynamics, including growth and reproduction, of three classes of zooplankton. The model simulations indicated the importance of including the microbial loop and the stage (or size) dynamics of the zooplankton in the model structure. Examples of how to model zooplankton by including information on their size or stage were presented and the advantages and disadvantages of the various approaches discussed. Three questions were then posed for general discussion. If models like the ones discussed were made generally available to the oceanographic community, would they have wide applicability and would they be used? What level of support or documentation would be needed to make such models generally useful? What basic model structures (e.g., size-structured or stage-structured herbivores; number and complexity of the trophic web; single-species vs. multispecies) are the most useful for producing model estimates of zooplankton secondary production?

The final presentation described a 25-year data set on phytoplankton and zooplankton abundance in the North Atlantic obtained from the Continuous Plankton Recorder survey program. A correlation was observed between annual increases in zooplankton abundance west of the British Isles and northward displacements of the Gulf Stream off the U.S. The absence of a time lag between the physical evidence off the U.S. and the plankton data off the United Kingdom suggests that the forcing for both may be due to large-scale atmospheric events.

Table 1. Speakers and topics of plenary presentations.

<u>Speaker</u>	<u>Topic</u>
Francisco Werner	Circulation modeling, including animal behavior
Kyle Squires	Turbulent motion at small scales
Rudy Strickler	Turbulence and copepod behavior
Peter Verity	Protozooplankton
Gustav Paffenhöfer	Variability in zooplankton
Jeannette Yen	A model of a copepod feeding current
John Klinck	Large-scale physical processes and scales
Eileen Hofmann	Coupled biological-physical modeling
Arnold Taylor	Interannual variability of phyto- and zooplankton abundance

Summary of Questionnaire Responses

Appendix A lists the questions provided to the workshop participants. Written responses to the questionnaire are summarized here. Although most of the questions were directed towards modeling, many of the responses were much broader in scope, and included comments on empirical observations and what is needed both from an observational-empirical and modelling perspective to improve our understanding of secondary production in the ocean.

Not surprisingly, responses on the ultimate goal were diverse, ranging from specifics on modeling goals and approaches to a very broad view of understanding how marine ecosystems are structured and how they function. Time-dependent, three-dimensional models that couple physics and biology were consistently emphasized. Useful models should consider in situ growth and reproduction, spatial gradients in target species abundances, abundances of potential prey and predators and their interactions with the target species, and realistic animal behavior. They should include the detail necessary to provide 1) an understanding of the processes and mechanisms which affect the vital rates (birth, growth, reproduction) of zooplankton, 2) accurate hindcasts of the distribution and abundance of the targeted species, with special emphasis on hindcasting interannual variability, and 3) a framework for evaluating the impact of potential climate change on the structure and dynamics of zooplankton populations in different marine ecosystems.

Other emergent themes resulted from the responses to the questionnaire. First, there is a need for a unifying conceptual framework in marine secondary production ecology. There are many models of zooplankton population dynamics and secondary production—including complex models, simple models, single species models, multiple species models, individual-based models (IBMs), metapopulation models, models that include no, some or extensive physics, and time-dependent and equilibrium models. One feature universal to most, if not all, of the models, however, is that they are untested and therefore of little general value. Validation and testing of models, which involves the cooperation of empiricists and modelers, is critical to improving our understanding of zooplankton production.

Responses indicated an interest in understanding the linkages (coupling) between major components; for example, how variability in fish stocks and recruitment is related to physical forcing; how short-term, but perhaps extreme, environmental or physical events influence secondary production and population structure.

More detailed responses to the questionnaire are presented in Appendix B.

Working Group Reports

Behavior. Strickler (Chair), Batchelder, Jonsson, Kiørboe, Yen

Animal behavior includes a wide range of activities—swimming, feeding activity, migration, mating, reproduction and escape behaviors—that can greatly influence survival, growth, and reproduction. Few of these behaviors have been investigated adequately to permit their inclusion in mechanistic models of secondary production. The working group identified three aspects of animal behavior where intensified research could lead to improved mechanistic models of secondary production.

First, **investigation of the mechanisms underlying individual behavior** is needed. Individual behavior is influenced by a milieu of environmental factors—hydrography (temperature and salinity), light intensity, food resources (quantity and quality), predator distributions—and factors intrinsic to the individual—general physiological condition, including size (stage or age), hunger, reproductive condition. As an example, it is clear from numerous studies that the timing of diel vertical migration in many species is closely tied to light intensity. In some cases, the depth of daytime residence is adequately explained solely by light intensity, in others it is also dependent upon swimming speed (Buskey et al., 1989). The cues that regulate night-time depth are less clear.

Temperature and food concentration and quality have vertical gradients and often large discontinuities at scales of tens of centimeters to meters that may be important (Cowles et al. 1993; Harris, 1988). Vertical migration amplitudes in copepods can be modified by food availability (Daro, 1985). The uneven distribution of food in all three dimensions, its varying quality and composition, and its generally low abundance require a wide behavioral repertoire on the part of consumers to acquire sufficient amounts of food, especially in the presence of predators. Numerical models are useful for exploring the effect of different animal behaviors interacting with the patterns and dynamics of patchy prey and predator aggregations in respect to obtaining resources, growing, reproducing and surviving. For instance, fecundity in the copepod *Labidocera* is dependent upon the interaction of photoperiod and food patchiness, e.g., the time of the day when food is available (Marcus, 1988).

Second, **interactions among individuals need to be examined.** These include conspecific interactions such as finding mates (Yen, 1988), cannibalism of younger by older stages, and schooling behavior; and interspecific interactions such as foraging, and avoiding and escaping predators.

Third, **behaviors which result in the retention of individuals, patches and populations in favorable environments need investigation.** This is perhaps the topic of most immediate relevance to U.S. GLOBEC, in that the interaction of zooplankton behavior and advection can have direct and strong impacts on the survival and productivity of zooplankton. These include behaviors at various temporal and spatial scales. Behavior can maintain individuals in favorable food environments (Price, 1989) and can involve the recognition of and reaction to changing conditions. Well-documented examples whereby zooplankton have behavioral adaptations to maintain themselves in favorable locales include regions of vertically sheared (often reversed) flow like the Oregon upwelling zone (Wroblewski, 1980; 1982), and tidally dominated regions.

Integration Across Scales and Linking of Scales. Botsford (chair), Klinck, Paffenhöfer, Prestidge, Smith

The working group focused on the many and often wide ranging scales that are involved in measuring and modeling secondary production. The overarching theme that emerged was a concern for how to measure secondary production processes so that observed distributions of secondary production could be understood and modeled. The measurement of secondary production was felt to be straightforward, but understanding the underlying processes responsible for the temporal and spatial patterns is difficult. It is the latter part of the problem that is most relevant to the goals and objectives of U.S. GLOBEC.

Secondary production in marine environments is usually measured on groups of similar (patches or aggregations) or dissimilar (communities, ecosystems) organisms. However, processes that occur at the scale of the individual organism may determine secondary production patterns observed at the larger scales. In order to understand secondary production at larger scales, processes at the scale of the individual need to be understood. Thus, for example, efforts might be directed toward obtaining a better understanding of the full range of ingestion responses by the individual. The working group recommended that **modeling over a range from individuals to populations to metapopulations to communities might be done with nested models**, each of which considers processes

over a limited range of space and time scales. Also, this may be an area in which Individual Based Models (IBMs) might be an appropriate modelling framework as opposed to the more traditional stage, size and age structured models.

Development of models that treat a wide range of spatial and temporal scales will require concurrent development of techniques to transfer information between scales. The working group recommends **the development of approaches (i.e., parameterizations) for transferring information from smaller to larger scales (scale-up)**. Additionally, it was recognized that models constructed for one scale (e.g., turbulent, regional) must be able to include forcing (e.g., climate) from larger scales (scale-down) and consider larger-scale boundary conditions. For modelers to successfully address this "scale-transfer" issue will require coordination with experimental and empirical scientists. Moreover, it is necessary for those doing the experimental studies to work at scale interfaces as well as at particular scales, which will require coordination among empiricists who work at different scales.

The complexity of integrated processes in models of secondary production should not be beyond what can be justified by experimental data. Not all the complexity at one particular level has to be transferred to the next higher level. Modeling can occur on different levels simultaneously. **Empirical information presently available at two or more scales provide starting points for initiating cross-scale modeling efforts.** This collaboration is encouraged.

Structural Aspects of Secondary Production Models. Hofmann (chair), Durbin, Landry, Moloney, Nival, Taylor

The working group identified four issues related to the structural aspects of models that should be part of U.S. GLOBEC modeling activities.

Realistic Model of a Key Species—The development of a detailed model that realistically parameterizes and describes processes for a single zooplankton species should be undertaken. Such a model will require approaches for partitioning the organism into basic biochemical components (e.g., lipids), which would allow differentiation of energy within the animal (e.g., separate reproductive and somatic tissue). Parameterization of an animal in this manner will require improved information on the biochemistry (especially of growth and lipid storage) of marine zooplankton and its effect on behavioral and physiological ecology. Also, measurements that will allow parameterization of environmental control on animal metabolism, through temperature variability for example, are needed. Thus, development of this type of individual based model will require considerable effort from experimentalists as well as modelers. Specific recommendations are to: 1) use common units for measurements so that they can be easily incorporated into models; 2) refine temperature relationships for organism metabolic responses for modeling and experimental studies; and, 3) to allow the model for a specific organism to have a mechanistic basis that incorporates variability within the species.

Population Dynamics Model—The existence of population models would allow comparisons between different species, processes underlying co-existence of species, investigation of trade-offs and balances that different species make, and the role of nonlinear processes in the control of population dynamics. Initially these models should focus on a small set of species and the models should be structured to track animal

growth. It is also important for population models to include natural population variability that arises through genetic variations. This introduces stochastic variations into population models, which has not traditionally been done, but may be important.

Type of Model—Lagrangian and Eulerian models provide frameworks for investigating questions relating to the growth and development of marine zooplankton populations. Each approach has strengths that can be exploited to provide insight as to the role of circulation and biological factors in regulating zooplankton population structure and secondary production. At present, most of the models for secondary production provide simulations of secondary production or animal concentration on a fixed grid (i.e., an Eulerian approach). However, circulation models are becoming more generally available and these can be used in a Lagrangian mode to consider basic questions relating to animal distribution and dispersion. This is a promising approach for combining circulation and individual based models.

The use of stochastic modeling, in which a range of outcomes is allowed, e.g., encounter models, should be encouraged. This will allow for uncertainty in model solutions and in sensitivity studies performed on the model parameters. This is in contrast to what can be obtained with deterministic models, which give a single solution for a set of parameters. Additionally, for some applications, it may be possible to recast a detailed model in a simpler form by using stochastic input functions. This will give a range of possible outcomes that may more accurately reflect the possibilities in nature than the single outcome from the deterministic model.

Importance of Lower Trophic Levels—The characteristics of the lower trophic levels (the prey field) are important inputs to models of secondary (animal) production. The structure of the food source (e.g., phytoplankton community composition), the quality of the food (carbon to nitrogen ratios) and the quantity of the food all regulate secondary production. Moreover, microzooplankton may be as important as phytoplankton as prey for mesozooplankton. This has implications for trophic efficiency of the planktonic system, and for response (turnover) times to environmental perturbations. Generally, the lower trophic levels may respond faster to environmental perturbations, thereby providing a filter through which these variations are transferred to predators. However, the longer time response of marine mesozooplankton can make it difficult to include detailed models of primary production (or microzooplankton) in a model of secondary production. Therefore, modeling effort should be directed at developing parameterizations of feeding responses that can incorporate many of these effects and account for flexibility in feeding environments. Moreover, microbial processes, seasonal changes in phytoplankton community composition and changes in environmental conditions all contribute to regulation of the food resources that are available to marine zooplankton. Hence, it is important to distinguish what would be needed to construct true ecosystem-level models as opposed to models in which a food supply is simply specified.

References

- Buskey, E. J., K. S. Baker, R. C. Smith, and E. Swift. 1989. Photosensitivity of the oceanic copepods *Pleuromamma gracilis* and *Pleuromamma xiphias* and its relationship to light penetration and daytime depth distribution. *Mar. Ecol.-Prog. Ser.*, 55, 207-216.
- Cowles, T. J., R. A. Desiderio, and S. Neuer. 1993. In situ characterization of phytoplankton from vertical profiles of fluorescence emission spectra. *Mar. Biol.*, 115, 217-222.
- Daro, M. H. 1985. Feeding rhythms and vertical distribution of marine copepods. *Bull. Mar. Sci.*, 37, 487-497.
- Harris, R. P. 1988. Interactions between diel vertical migratory behavior of marine zooplankton and the subsurface chlorophyll maximum. *Bull. Mar. Sci.*, 43, 663-674.
- Kils U. 1990. On the micro-structure of micro-layers: results of an in situ zooplankton-counter. *EOS*, 71, 94.
- Marcus, N. H. 1988. Photoperiodic conditions, food patchiness and fecundity. *Bull. Mar. Sci.*, 43, 641-649.
- Price, H. J. 1989. Swarming behavior of krill in response to algal patches: a mesocosm study. *Limnol. Oceanogr.*, 34, 649-659.
- Wroblewski, J. S., 1980: A simulation of the distribution of *Acartia clausi* during Oregon upwelling, August 1973. *J. Plankton Res.*, 2, 43-68.
- Wroblewski, J. S., 1982: Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone--a simulation. *Deep-Sea Res.*, 29, 665-686.
- Yen, J. 1988. Directionality and swimming speeds in predator-prey and male-female interactions of *Euchaeta rimana*, a subtropical marine copepod. *Bull. Mar. Sci.*, 43, 395-403.

Appendix A. Questionnaire

- Question 1. What is (are) our ultimate goal(s)?
- Question 2. Where are we positioned now?—Present status of recruitment modeling.
- Question 3. What would be the next successive steps?
- Question 4. Which are the variables causing most of the recruitment variability?
- Question 5. Which are the variables mainly responsible for mortality?
- Question 6. What detail on small scales is needed to determine and model recruitment?
- Question 7. What happens to zooplankton in optimal vs. suboptimal conditions?
- Question 8. Recruitment (secondary production) modeling: What degree of differentiation is envisioned concerning:
I. regions?
II. taxonomic groups?

Appendix B. Questionnaire Responses

For several questions, the responses covered a wide range and some gave considerable detail. Other questions resulted in low variability of answers. Most of the workshop participants usually did not limit themselves to direct comments on modeling but viewed the secondary production modeling issue in a wider frame, i.e., what is needed to enhance our understanding of production in the ocean. This in turn led to comments on needed empirical observations.

Question 1—Comments on the ultimate goal ranged from specifics on modeling to an overall view of understanding how ecosystems are structured and how they function. Overall, three-dimensional models coupling physics and biology over time are needed. They should consider in situ growth and reproduction, spatial gradients and realistic animal behavior. They should have the potential to 1) understand the processes and mechanisms that affect rates of zooplankton, 2) provide an accurate hindcast of distribution and abundance of zooplankton species, of interannual variability, and 3) eventually result in an understanding of the effects of global environmental changes on zooplankton structure and dynamics. One respondent provided a time-line for his perception of the future: after 2 years we should have initial results on coupling physical transport models with biological models; after 5 years one should use these first generation models during U.S. GLOBEC field studies and begin to reformulate the models; and after 10 years we should be able to use second generation models, i.e., reformulated first generation models that have been tested against field observations.

Many of the comments were aimed at eventually obtaining an understanding of processes, rates and structures. These included coupling of major components; how (and if) variability in fish stocks and recruitment are related to physical forcing via the zooplankton (serving as food); how short-term, intense events vs. time-averaged processes affect species abundance; and how a long-term perturbation will affect an ecosystem. A better integration of observations and modeling was requested. Models should also be sufficiently mechanistic to allow testing, including concepts. However, development of elaborate, detailed models may not be useful, if the models cannot be understood or verified. Development of models that are simple and with few parameters should be encouraged. To come to grips with recruitment models, and observational efforts, we need to focus on mortality, immigration and emigration. Eventually one would like to predict recruitment, at least its potential, from few observational variables.

Question 2—Answers concerning the present status of recruitment (secondary production) modeling were rather diffuse. However, the general theme in the answers was that no present model is satisfactory for making realistic secondary production estimates. One respondent summarized the current state of secondary production modeling as a few models with no unifying theme. However, others indicated that current conceptual models of the processes controlling secondary production appear to be correct, but translation of these poorly constrained concepts into mathematical models often gives unsatisfactory results. It was felt that this arises because the resources (prey fields) of the zooplankton are correctly simulated but ad hoc approaches are used to represent processes at the upper end of the food web, such as mortality and predation.

It was also felt that current models of secondary production are complex and that this complexity obscures the understanding that could be gained from the models. Several respondents recommended that secondary production models be reduced to basic

elements to give simple models with few parameters. An issue that arose was how simple do the models need to be to address questions about the basic processes that underlie secondary production.

Several comments were made about processes not presently (or inadequately) included in existing secondary production models. These include: descriptions of the predator and prey fields, realistic predation mortality, the effects of prey spectrum on prey-specific removal, and treatment of spatial heterogeneity in the predator and prey fields. One respondent pointed out that existing secondary production models have not undergone rigorous testing to determine how well they work and evaluate their more general use. For this to happen, modeling approaches need to be available to the community so that observations can be more readily input to models. Also, several respondents indicated the need for models that can include fast and slow processes (e.g., multiple scales). There is also a need to study the structure of secondary production models to understand under what conditions the models are stable and to understand the effect of forcing functions.

Question 3—Concerning next successive steps to be taken, the comments, as in question 1, ranged from needed modeling efforts to needed empirical observations, and interactions of both. Several participants recommended that physics and biology needed to be closely coupled not only in modeling but also in field observations, and that modeling and field observations be coupled by design. One participant suggested "to hold empiricists' feet to the modeling fire"! One approach for facilitating this interaction is to develop generic models that can be used widely and have the flexibility to incorporate knowledge and measurements from different locales and regions.

An understanding of detailed mechanisms (of recruitment dynamics) is needed. Appropriate models must be formulated and their implications assessed. Several steps, however, need to be taken to obtain such an understanding. They include small-scale animal behavior (0.1 to 100 m vertically) and its coupling to physics and food distribution; data on effects of behavior on growth and predation mortality; data on in situ growth rates of different stages (no more black box approaches, such as using biomass) of target species; and eventually a small-scale feeding model should be constructed to integrate feeding behavior, turbulence and small-scale patchiness. In addition, a thorough ecosystem monitoring was recommended to capture event-scale phenomena (=continuous in situ observations). For example, continuous assessment of the spatial and temporal structure of water column variables would allow us to parametrize heterogeneity.

Above all, there appears to be a need for a unifying conceptual basis. To foster this development, a rigorous review of what has been done should be undertaken. This review would be two-fold. The first part would focus on what has been done in marine secondary production as well as what has been done in other related fields, such as evolutionary biology. The second part would focus on models that have done a satisfactory (or not) job of handling secondary production. Sponsorship of such reviews was thought to be within the stated objectives of U.S. GLOBEC.

Question 4—As to variables causing variability of recruitment, there was good agreement among the workshop participants. These responses are summarized in the table given below.

<u>Biological Variables</u>	<u>Physical Variables</u>
Predation vulnerability	Temperature
Resource availability	Horizontal advection, including squirts, jets
Genetics	Catastrophic events (e.g., volcanoes)
Parasites	Turbulence
Catastrophic episodes of predation (e.g., fish schools)	Vertical distribution of variables at various time scales
Biochemical composition abundance and size distribution of food particles	Meteorological events over days to years
Competition from other zooplankton (e.g., Thaliacea affect copepods)	

Question 5—Variables which are responsible for mortality were largely included in the response given in question 4. These include predation, advection, parasites, starvation, temperature, event-scale processes, but also longer term changes such as variations in temperature.

Question 6—The importance of small scales (mm to m) to recruitment processes received much and quite uniform attention by the workshop participants. For most secondary producers, i.e., zooplankton, coupling with biology and physics occurs at the scales of their ambit, which can range from <1 mm to >100 m in the vertical. They perceive food and predators in the mm range, and can move several cm to m in a minute. Major processes of predation occur at scales of mm to cm. For example, Kils (1991) showed how a school of juvenile herring found a 10 cm thick layer of the ciliate *Stenosomella*, and consumed it within 20 min. There was general agreement that our community lacks information on rate processes and their variability on these spatial and also on short temporal scales.

Specifically, observations on behavioral characteristics of various stages and species of zooplankton and fish larvae are needed, including daily ambits (range of operation) of respective species and vertical distributions of zooplankton, their food and their predators over time. Variability of these should be investigated in conjunction with physical variables such as temperature; this would include species- and stage-specific aggregation dynamics.

To develop models, functional relationships for zooplankton behavior, shear and turbulence have to be obtained; and real-world small structure and small-scale processes have to be adequately addressed in such models. It is at these scales that the interactions between the various components of the plankton occur. It is also these scales about which our knowledge is severely limited. An understanding of mechanisms governing animal's existence at small scales, as mentioned earlier, is essential to comprehend processes on much larger scales.

Question 7—The answers as to what zooplankton do in optimal and suboptimal conditions varied little among the participants, like high survival and fast growth in

optimal, and the opposite in suboptimal conditions. One respondent suggested conceptual consideration of the effects of optimal versus suboptimal effects on zooplankton. Some interesting questions were posed which should receive some attention:

How could optimal and suboptimal conditions be defined for different species or guilds?

At what time of life of a zooplankton species are suboptimal conditions likely to occur?

Question 8—The last question was addressed by only a few participants. Concerning secondary production modeling the initial focus should be on regions about which we possess fairly comprehensive empirical information such as the North Atlantic, Subarctic Pacific, the California Current, and some shelf regions. One might then focus on regions with less data such as the Antarctic, the Arctic and the equatorial Pacific. As to taxonomic groups, emphasis should be placed on species or orders that are characteristic of each region. In general they should include protozoa, calanoid and cyclopoid copepods, euphausiids, pelagic tunicates, and respective fish target species.

Appendix C. Participants

H. P. Batchelder
Department of Integrative Biology
University of California
Berkeley, CA 94720-3140

Phone: 510-642-7452
Fax: 510-643-6264
halbach@violet.berkeley.edu

L. W. Botsford
Dept. of Wildlife and Fish Biology
214 Briggs Hall
University of California
Davis, CA 95616

Phone: 916/752-6169
FAX: 916/752-4154
lwbotsford@ucdavis.edu

A. G. Durbin
Graduate School of Oceanography
University of Rhode Island
Narragansett, RI 02882

Phone: 401/792-6695
adurbin@gsosun1.gso.uri.edu

B. W. Frost
Department of Oceanography WB-10
University of Washington
Seattle, WA 98195

Phone: 206/543-7186
frost@ocean.washington.edu

E. E. Hofmann
Center for Coastal Physical Oceanography
Crittenton Hall
Old Dominion University
Norfolk, VA 23529-0276

Phone: 804/683-5334
FAX: 804/683-5550
hofmann@ccpo.odu.edu

P. Jonsson
Tjärnö Marine Biological Laboratory
PL-2781
S-45296 Stromstad
SWEDEN

Phone: Int. + 46526 25200
FAX: Int. + 46526 25387

uzipj@gd.gu.se

T. Kiørboe
Danish Institute for Fishies & Marine Research
Charlottenlund Castle
DK-2920 Charlottenlund
DENMARK

Phone: Int. + 453396 3401
FAX: Int. + 453396 3434

J. M. Klinck
Center for Coastal Physical Oceanography
Old Dominion University
Norfolk, VA 23529-0276

Phone: 804/683-6005
FAX: 804/683-5550

klinck@kuroshio.ccpo.odu.edu

M. R. Landry
Department of Oceanography
University of Hawaii at Manoa
1000 Pope Road
Honolulu, HI 96822

Phone: 808/956-7776
FAX: 808/956-9516
landry@iniki.soest.hawaii.edu

C. L. Moloney
Zoology Department
University of Cape Town
Rondebosch 7700
South Africa

Phone: 27-21-650-3300
FAX: 27-21-650-3726
cmoloney@ucthpx.uct.ac.za

P. Nival
Station Zoologique
F-06230 Villefranche-sur-Mer
FRANCE

Phone: Int. + 33 93 76 38
FAX: Int. + 33 93 76 38 34
pn@ccr.jussieu.fr

G.-A. Paffenhöfer
Skidaway Institute of Oceanography
10 Ocean Science Circle
Savannah, GA 31411

Phone: 912/598-2489
FAX: 912/598-2310
cmp@peachnet.skio.edu

T. M. Powell
Department of Integrative Biology
University of California
Berkeley, CA 94720-3140

Phone: 510-642-7455
Fax: 510-643-6264
zackp@violet.berkeley.edu

M. Prestidge
Plymouth Marine Laboratory
Plymouth PL1 3DH
UNITED KINGDOM

Phone: Int. + 44 752 222 772
FAX: Int. + 44 752 670 637

S. L. Smith
Rosenstiel School of Marine & Atmospheric
Sciences
University of Miami
Miami, FL 33149-1098

Phone: Int. + 44 752 222 772
FAX: Int. + 44 752 670 637
ssmith@rsmas.miami.edu

K. D. Squires
Dept. of Mechanical Engineering
University of Vermont
Votey Building
Burlington, VT 05405

Phone: 802/656-1940
FAX: 802/656-1929
squires@emba.uvm.edu

J. R. Strickler
Center for Great Lakes Studies
University of Wisconsin
600 East Greenfield Avenue
Milwaukee, WI 53204

Phone: 414/382-1700
FAX: 414/382-1705

A. H. Taylor
Plymouth Marine Laboratory
Plymouth PL1 3DH
UNITED KINGDOM

Phone: Int. + 44 752 222 772
FAX: Int. + 44 752 670 637

P. G. Verity
Skidaway Institute of Oceanography
10 Ocean Science Circle
Savannah, GA 31411

Phone: 912/598-2489
FAX: 912/598-2310

F. E. Werner
University of North Carolina at Chapel Hill
CB# 3300, 12-5 Venable Hall
Chapel Hill, NC 27599-3300

Phone: 919/962-0269
FAX: 919/962-1254
cisco@snapper.chem.unc.edu

J. Yen
Marine Science Research Center
State University of New York
Stony Brook, NY 11794-5000

Phone: 516/632-6913
FAX: 516/632-8820
jyen@ccmail.sunysb.edu