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## Plankton functional group models – An assessment

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### Abstract:

This Discussant's Report provides a summary of the discussions that followed presentation of the approaches and ideas described in Thingstad et al. (this volume). The discussions, which addressed aspects of conceptual understanding and parameterization that are relevant to development of ecosystem models capable of emergent behavior at a range of scales, the benefits of functional group modeling, and some of the limitations of this approach, provide insights that are relevant to setting directions for future research efforts. One important point emerging from the discussions was that reconciling the requirements of simplicity versus complexity with the desire to obtain predictive capability is an important area where biogeochemical and ecosystem models can be improved.

## 1. Introduction

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The pioneering models of Gordon Riley (1946; 1947) showed that quantitative mathematical frameworks could be used to understand seasonal changes in planktonic biomass and to estimate the magnitudes of the rates and processes responsible for these changes. Since that time, mathematical modeling has become an accepted and important tool in biological oceanography for exploring controls and linkages in the lower trophic levels of the food web and for development of new ideas and understanding of energy and material cycling. Advances in conceptual understanding, modeling techniques, and data availability have made predictive models for marine ecosystems a feasible goal (e.g. Friedrichs et al. 2007). However, much remains to be done in development of modeling structures and parameterizations so that full use can be made of new conceptual understanding of marine ecosystems and of data sets acquired with new and existing technologies.

Part of the focus of the Symposium on *Parameterization of Trophic Interactions in Ecosystem Modelling* was to "...identify weaknesses in our approaches to parameterization of modeling tools, gaps in understanding and aid in the development of best practices for their future development". The paper by Thingstad et al. (this volume) addresses aspects of conceptual understanding and parameterization that are relevant to development of ecosystem models capable of emergent behavior at a range of scales (e.g. Wiggert et al. 2005, 2008; Follows et al. 2007). Complex models developed for small scale systems allow study of interactions of competition, predation and environmental conditions at a detail not possible for larger scale systems. However, as shown by Thingstad et al. (this volume), even small scale systems exhibit marked increases in model complexity for seemingly small changes in dynamical connections. Understanding of these interactions is a necessary prerequisite for development of parameterizations that retain the desired dynamics when incorporated into larger scale models.

Thingstad et al. (this volume) examined food web linkages and responses using plankton functional (types) groups (see Flynn 2005; Hood et al. 2006) as a modeling framework. This structure affords the ability to include dynamics associated with species-specific or functional-group behaviors. The increased realism potentially allows emergence of complex interactions from the model dynamics beyond what is obtained from marine ecosystem models that are based on aggregate plankton populations, e.g. a single phytoplankton component with characteristics representative of a mean population, which may be sub-divided, usually based on size (e.g. Fasham et al., 1990). However, the use of functional groups as a modeling framework has limitations and drawbacks which may limit its application for some systems. The Thingstad et al. (this volume) paper outlines some of the benefits of functional group modeling as well as bringing attention to some of the limitations. Although their study is focused on microbial systems, many of the conceptual issues may apply to higher trophic level models if it can be shown that the need for complexity at smaller scales is transferred to larger scales that are more influenced by environmental processes.

The discussions that followed presentation of the approaches and ideas described in Thingstad et al. (this volume) highlighted some important issues associated with development of complex models (even for simple systems) and models that are based on functional groups. Although few definitive answers were forthcoming from the discussions, important issues were highlighted which provide directions for future

research efforts. The following sections attempt to capture these issues and accompanying discussion.

## 2. Functional Groups

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The discussion of functional groups as modeling structures pointed out that most functional group models are in practice based on data sets collected for a single or, at best, a few plankton species. In this regard, functional group models could be viewed as simply an aggregate model with dynamics determined by a particular set of data or organisms for which the most data are available. Hood et al. (2006) defined functional groups as groups of organisms that mediate specific chemical reactions in the ocean. Thus, functional groups are composed of many different species with a common biogeochemical function, such as nitrogen fixation.

The above definition places constraints on what constitutes a functional group and provides guidance as to the types of data needed to parameterize the processes unique to the group. Thingstad et al. (this volume) introduced a functional group definition that is based on selectivity properties of different loss functions. This is the basis for the “kill the winner” concept in which selective loss of the best competitor for a limiting resource prevents consumption of the resource thereby allowing an inferior competitor the possibility of survival. Thingstad et al. (this volume) note that this approach to defining functional groups allows for different food web pathways for the same substrate which increases resiliency in the ecosystem. The different behaviors obtained using different functional group definitions highlights fundamental questions for marine ecosystem modeling: what constitutes a functional group and how are these incorporated into marine ecosystem models?

The different food web pathways that result simply from the functional group definition (Fig. 1, Thingstad et al. this volume) have important implications for understanding (and predicting) ecosystem shifts due to climate change, for example. The basic structure used for marine ecosystem models is a controversial topic with no obvious resolution (e.g. Flynn 2005; Anderson 2005; Thingstad et al. this volume). What was clear from the discussions at the Symposium was the desire for model structures that allow functional groups to emerge as part of the model properties rather than being a fixed feature that is specified *a priori*.

The biological and/or environmental factors that underlie diversity within and among functional groups may provide the basis for shifts in ecosystems, such as the flagellate-ciliate to copepod-diatom succession described in Thingstad et al. (Fig. 3, this volume), which has important implications for material cycling and trophic transfers. Understanding and describing these dynamics were identified as important and deserving of further experimental as well as modeling efforts. As noted by Thingstad et al. (this volume), translation of conceptual frameworks, such as that given in Figure 3 of their paper, to actual simulation models does not always yield expected results. Although functional groups may inherently advance the realism of marine biogeochemical models, only limited progress has been made in incorporation of these groups into the models and many important functional groups have yet to be included in models. This is in large measure an experimental data limitation, but the modeling structures may not be adequate to fully use such data sets even if they were available (Thingstad et al. this volume).

A further complication is the potential for some microbial organisms to change size through carbon storage without an accompanying increase in demand for mineral nutrients. As a result, an organism increases its competitive advantage for nutrients while also reducing its vulnerability to predation. This particular strategy, if it occurs, makes construction of functional groups problematic and complex (Thingstad et al. this volume). Representation of biogeochemical and food web linkages is a daunting task for models that attempt to represent end-to-end ecosystem processes.

### **3. Higher Trophic Levels**

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The importance of higher trophic level processes in determining expression of different functional groups is essentially unknown and as a result not adequately incorporated into marine biogeochemical and food web models. Grazing by zooplankton, for example, can determine which phytoplankton or microbial group dominates the plankton species assemblage, thus altering nutrient and carbon cycling and export production. The different model structures reviewed in Thingstad et al. (this volume) illustrate that small changes in linkages between autotrophic and heterotrophic components of the food web result in large changes in system persistence, resiliency, and material cycling. How grazer functional groups are defined in relation to functional groups of lower trophic levels is poorly understood, but it is clear that grazing and predation processes deserve more attention than the simple closure terms that are now used in many models. Even a simple closure term can have unexpected consequences for model behavior (e.g. Franks et al. 1986; Steele and Henderson 1992; Fussmann and Blasius 2005). Approaches for defining closure terms for food web/biogeochemical models are needed but equally important are studies of how these approaches influence model outcomes.

The degree to which higher trophic levels influence lower trophic levels is a matter of debate (Hood et al. 2006) and represents a philosophical division in terms of regulation of marine ecosystems by top down (e.g. Verity and Smetacek 1996) versus bottom up (Cullen et al. 2002) controls. Thingstad et al. (this volume) suggest that the differences in defense (resource limited) versus competition (predation controlled) specialists underlies differences in biodiversity and ecosystem function in oligotrophic (competition specialist dominated) and eutrophic (resource specialist dominated) environments. Whether this is as simple as suggested is a matter of debate. However, structuring a model along the lines suggested by Thingstad et al. (this volume) may provide an approach for furthering conceptual understanding of ecosystem properties and function. There is a need for the marine modeling community to engage in discussions and testing of approaches, including development of basic ecosystem theory, for incorporation of higher trophic level functional groups into marine biogeochemical and food web models. The examples given in Thingstad et al. (this volume) suggest that this is fundamental issue.

### **4. Parameterization and Interactions**

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Parameterization of model dynamics determines the robustness and realism of the model solutions. Thus, it is surprising that the approaches for describing dynamics of marine ecosystem processes are so empirically-based and diverse. For example,

much of the effort in development of marine ecosystem models has focused on formulation of approaches for representing primary production because this is of such fundamental importance to correct simulation of material and energy cycling. These formulations are largely empirical (e.g. Jassby and Platt, 1976; Behrenfeld and Falkowski 1997), have different levels of acceptance (e.g. Brush et al. 2002), and are based on poorly constrained parameters (e.g. Friedrichs et al. 2007). The question is then, are there basic principles that allow parameterization of trophic interactions? Addressing this question requires interactions between modelers and experimentalists because the limitations of the models as well as those of the measurements must be understood. (see discussion in Hofmann et al. 2008) An integral part of parameterization is estimation of parameter values. The nature of parameterization of biological processes and trophic linkages typically results in empirical relationships with numerous parameters that are difficult to measure with current approaches. Thus, data assimilation techniques, such as variational adjoint methods, provide approaches for estimating parameter values and associated uncertainties in an objective manner (Hofmann and Friedrichs 2001, Friedrichs et al. 2006). The Symposium discussions did not resolve these issues but did highlight this as an area where incremental progress can result in large advances in marine ecosystem modeling. Thus, this is an important area for future research.

Thingstad et al. (this volume) discuss the importance of resolving dynamics internal to a specific functional group, which has not been done in existing functional group models. Their example of viral lysis selectively increasing predation loss within a particular microbial group highlights the importance of within functional group diversity and the potential of this to alter apportionment of material and energy to other food web components. Thingstad et al. (this volume) suggest a possible modeling structure that accounts for diversity within and among functional groups (Fig. 4). Within functional group diversity is a manifestation of genetic diversity of the organisms making up the group. Dynamic simulation of this diversity and its consequences for population structure, energy flow and food web function ultimately will require models that couple physiology, population processes, and genetic structure. The emerging field of genomics will perhaps provide the conceptual understanding and experimental basis for such models (Doney et al. 2004). However, functional groups provide a useful structure for investigating climate change effects on marine systems (Boyd and Doney 2002) and approaches for incorporation of these effects remain to be developed.

Most functional group models (and ecosystem models) are constructed for a particular type of biogeochemical cycling, e.g. carbon. The expansion of modeling frameworks to allow for interactions between different cycles, such as nitrogen, silica, phosphorus, iron and calcification, provided much discussion. Functional group models that allow more than one nutrient cycle are feasible (e.g., Bissett et al. 1999; Vichi et al. 2003, Blackford et al. 2004, Salihoglu and Hofmann, 2007), but are limited by data availability, conceptual understanding, and scale of application.

## **5. Paleo-oceanographic Inputs**

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The paleo-oceanographic record provides a means for studying factors that influence functional group composition and diversity over time. Thingstad et al. (this volume) point to the importance of evolutionary factors in defining microbial interactions, hence functional group interactions, which in turn define higher trophic level interactions.

Also environmental processes act on these biological interactions, providing another set of possible outcomes. Environmental changes may be subtle, such as relatively minor changes in stratification which alter nutrient supply rates, but result in large-scale modification of functional groups. How these various changes are offset or mitigated by other environmental and biological factors is unknown, but the range of possible outcomes can be investigated via models. The message from Thingstad et al. (this volume) and the Symposium discussions is that the biological mechanisms that develop in response to evolutionary forces are diverse and the large range of possibilities are only now beginning to be understood. Models that include evolutionary considerations are not necessarily needed to address consequences of climate change, which occurs at shorter space and time scales. However, the scales at which interactions between climate change and evolutionary forces interact are unknown and models provide a means to investigate these.

## **6. Modeling Approaches**

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The degree to which current modeling approaches and tools are adequate for complex functional group models is a matter of debate. Functional group models have been developed for site-specific one-dimensional applications (e.g. Bissett et al. 1999, Salihoglu and Hofmann 2007) and have been generalized to basin-scale applications (e.g. Boyd and Doney 2002, Le Quéré et al. 2005, Follows et al. 2007). Attention is now being directed at coastal, continental shelf, and estuarine systems, which are the focus for many of the important issues facing marine ecosystems and resources (e.g. Baretta et al. 1995, Lacroix et al. 2007). These systems are characterized by considerable temporal and spatial variability, which produces variability in biological production and food web structure. Thus, these systems present special challenges for models based on functional groups. Issues such as succession, changes in biogeochemical and/or species diversity, especially for applications that span oligotrophic and eutrophic environments, need to be resolved and functional group models may allow evaluation of possible scenarios and outcomes of increasing eutrophication, changed freshwater inputs, and carbon cycling on these systems (e.g. Lancelot et al. 2007). However coastal systems often have more extensive and complete data sets that are available for open ocean systems and therefore may be better regions for testing development of functional group models. The outcomes of the “kill the winner” structure (Thingstad et al. this volume) clearly show the importance of functional group choices and parameterization in allowing particular behaviors and responses to emerge from the model.

It is appealing to propose development of more complex models for marine ecosystems. However, there is no guarantee that increased complexity will lead to increased understanding or predictive capability (e.g. Friedrichs et al. 2007). In fact, Thingstad et al. (this volume) suggest that alternate approaches that do not require detailed representation of underlying biological detail are needed to model emergent system-level behavior; added complexity obscures what is desired from the model.

The previous statement suggests that simplicity may be more compatible with predictive requirements. Some support for this is provided by a comparative study of the skill of 12 lower trophic level models (Friedrichs et al. 2007). Increased complexity did not result in better comparison between simulated and observed distributions, but increased complexity did allow for portability of the models (Friedrichs et al. 2007). Perhaps the most intriguing result of these model comparisons was that different models

provided similar model-data mis-fits, but these were produced via different flow pathways. There is still much to be done in defining linkages, dynamics and structures for marine biogeochemical and ecosystem models. The small set of functional groups used currently in models is limited by the availability of data to objectively constrain them, which limits the conclusions drawn from the simulations. Thus, collection of sufficient data, including rates as well as biomass standing stock, to allow development of robust models with believable skill is integral to advancing functional group models. Reconciling the requirements of simplicity versus complexity with the desire to obtain predictive capability is clearly an important area of research for improving marine biogeochemical and ecosystem models. Thingstad et al. (this volume) suggest that this issue can be rephrased in terms of how much detail can be removed from a model without losing the predictive skill of the model. Climate scale predictions may require only simple model structures which capture the dominant functional groups. Seasonal and interannual predictions may require complex biogeochemical and food web interactions. Modeling for prediction is still relatively new for marine biogeochemical and ecosystem applications. Much still remains to be done in developing appropriate modeling frameworks and in collection of data sets that support predictive modeling for marine ecosystems.

## Acknowledgments

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EH would like to thank the IGBP programs IMBER and GLOBEC as well as the Network of Excellence EUR-OCEANS of the European Union's 6th Framework Program for funding the symposium on "Parameterization of Trophic Interactions in Ecosystem Modelling", Cadiz, March 2007, and the meeting conveners for the invitation to participate. The conveners are also thanked for their patience with the writing of this discussant report. Comments from two reviewers were helpful in clarifying various points raised in this discussant report. Partial travel support for attending the workshop and support for preparation of this discussant report were provided by NASA grant number NNG04GL68G and the National Science Foundation, Office of Polar Programs grant number ANT-0523172.

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