
Defining the “to” in end-to-end models

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Abstract:

Robust models relating climate change to fish production require an adequate description of planktonic intermediaries between phytoplankton and fish in end-to-end models. In turn this requires and justifies a proper testing of zooplankton models. Fundamental issues regarding inclusion of zooplankton in these end-to-end models are discussed. It is argued that the complexity of the zooplankton component requires careful consideration and should not be simplified arbitrarily relative to higher and lower trophic levels. Future modelling studies are needed to rigorously examine the effects of increasing complexity within the zooplankton component on ecosystem dynamics. Acquisition of data from targeted field and laboratory studies, including mesocosms, is needed for testing mechanistic end-to-end models and optimizing the balance between fidelity and simplicity in the zooplankton component.

1. Preamble

Carlotti and Poggiale (this volume) consider the design and implementation of zooplankton models for placement within end-to-end models. Here we raise some fundamental questions concerning this topic.

2. How do we define the “to” in end-to-end models?

A main objective of ecosystem end-to-end models is to assess the impacts of climate change and fishing on ecosystem dynamics (Travers et al., 2007). At the base of these models are the primary producers (i.e. phytoplankton), which through carbon fixation impact on planetary biogeochemical cycling and CO₂ sequestration, while at the top are the different fish communities. The question then arises how best to define the zooplankton component within end-to-end models? While it is possible to empirically relate phytoplankton and fish production, without explicitly describing zooplankton, a mechanistic understanding of ecosystem dynamics obviously requires inclusion of a zooplankton component.

The fate of phytoplanktonic primary production is a cornerstone process in marine ecology. Most aquatic primary production is directly or indirectly channelled through zooplankton to higher trophic levels impacting on fish production. The body size of zooplankton ranges over six orders of magnitude (from 2µm to >2m), including the vast majority of animal species (e.g., heterotrophic protists, crustaceans, molluscs, jellyfishes) and biomass throughout the world ocean and freshwater systems (Harris et al., 2000). They are consumers of phytoplankton, bacteria, other zooplankton and in turn are consumed by invertebrate predators and fish. Thus, zooplankton form the lynch-pin between primary production and fish production – the “to” in end-to-end models.

To properly formulate the “to” in end-to-end models, an important consideration is the feeding behaviour of zooplankton in response to different food types. Zooplankton display diverse interactions between prey (food) selection, ingestion and digestion depending on the quantity and quality of available food (Davis and Alatalo, 1992; Jones and Flynn, 2005; Menden-Deuer and Grünbaum, 2006; Mitra and Flynn, 2007; Carlotti and Poggiale, this volume). In nature often good quality food is at a premium (low availability), or poor quality food is in relative abundance. This scarcity of good food is accentuated through intra-specific as well as inter-specific competition. When confronted with food of disadvantageous composition, a consumer may compensate for (ingest or assimilate more) or exacerbate (typically by prey rejection) the impacts of dietary deficiency (Mitra and Flynn, 2005). Consumption of different prey species and/or gut evacuation rates vary in order to maintain a high growth rate (Liu et al., 2006; Mitra and Flynn, 2007) with prey consumption varying in linear or non-linear relationship with prey availability (Hansen et al., 1990). Such feeding behaviours impact nutrient and energy flow across trophic levels. Trophic dynamics and biogeochemical cycling thus vary greatly between feeding on low-quantity/high-quality versus high-quantity/low-quality food. In nature these extremes can be represented by pre- versus peak-algal bloom conditions, resulting in variations in zooplankton feeding activity affecting the fate of algal biomass, secondary production and nutrient regeneration leading to promotion of algal blooms (such as harmful algal blooms or red tides; Mitra and Flynn, 2006a) and other trophic cascade events (Daskalov et al., 2007). We can conclude that zooplankton feeding activity cannot be easily predicted. Nor can it be readily simplified; a situation that contrasts sharply with the effort typically expended in configurations of zooplankton component in ecosystem models (Carlotti and Poggiale, this volume).

In view of the abundance and importance of zooplankton, in order to describe the transfer between phytoplankton and fish production it is essential to get the explicit description of zooplankton within ecosystem models correct. A failure to adequately describe the zooplanktonic component in ecosystem models may have widespread ramifications resulting in a loss of fidelity in our understanding and modelling trophic cascades (Davis, 1987). The complexity of the activities of zooplankton in nature appears to be so great that there could be a serious danger of misinterpretation, or, indeed erroneous predictions through lumping zooplanktonic activities into very few (typically one) groups. We are thus in danger of not so much describing zooplankton through a rhomboid approach, but more like literarily the converse with the emphasis on the top

and the bottom trophic levels and minimal emphasis on the middle. As a result we may fail to recognize the importance of the contribution of the individual zooplankton species to the zooplankton component.

Critically, the behaviour and population dynamics of individual zooplankton species that represent cornerstone species for certain fish, and which are subjected to climatic shifts, may be missed (Richardson and Schoeman, 2004); this is rather akin to not separating diatoms and non-diatoms in phytoplankton models. The Black Sea ecosystem is an example of one in which the activities of the zooplankton community, enhanced by anthropogenic activities (such as over-fishing removing the top predator), have resulted in various trophic cascades leading to a regime shift (Daskalov et al., 2007). Historically, the ecosystem of the Black Sea was dominated by fish as the top predator. In the absence of grazing pressure applied by the original top predator (i.e. fish), the gelatinous zooplankton community (*Mnemiopsis leidyi*) was free to propagate. The resultant large growths of “jellys” further adversely affected the already depleted fish stocks stabilising the regime shift. A decade later, the *M. leidyi* population was in turn subjected to grazing by another invader - *Beroe ovata* resulting in a decrease in their population (Kideys et al., 2004). Understanding such processes requires an end-to-end approach. The zooplankton community, as the lynch-pin between primary producers and fish production, requires an explicit well-conceived modelling effort.

3. What is the principle challenge for zooplankton models?

Phytoplankton models are traditionally biomass based, often tuned using field estimates measured in terms of chlorophyll (e.g., Moloney and Gibbons, 1996). Such models describe primary production at the population biomass level rather than of individuals. Models of fish production, on the other hand, are based on biomass as well as numeric abundance (Shin and Cury, 2001; Travers. et al., 2007). The objective of fish community models is to enable effective fisheries management (establish the yield of different fish species, species-specific mortality etc.), utilizing such information to determine a sustainable fishing budget. Ultimately fisheries management requires information at the individual species level with details of size, weight, age, and geographical location, and how these variables change through the life cycle of the fish species (Fulton et al., 2005). Traditional models of fish production do not include planktonic interactions in any detail (if at all); models that include planktivorous fish may make reference to the planktonic food web in an implicit fashion using a carrying capacity parameter for their description (Travers et al., 2007). The challenge for the zooplankton component in end-to-end models is to provide a sensible bridge between the diverse modelling strategies used in descriptions of the lower and higher trophic levels (see conclusion section in Carlotti and Poggiale, this volume). This challenge can be divided into two components; one relates to the basis of the zooplankton description required, the second relates to the number of zooplankton functional types. Both of these challenges are wrapped up with the level of detail necessary for compatibility with upper and lower trophic level formulations and to the complexity elsewhere in the ecosystem model.

4. Should the detail in the description of the zooplankton component match the detail of the descriptors of primary production?

Models of phytoplankton have undergone significant development since the early 1990s. There have been two recent advances in modelling primary production within ecosystem models; (i) description of the nutrient status (biochemical composition) of the phytoplankton (Anderson and Mitra, 2006; Flynn, 2008b), and, (ii) description of phytoplankton functional types (pPFT; quasi-taxonomic composition; Anderson, 2005).

The movement to construct multinutrient variable stoichiometric models is being driven by the appreciation that fixed Redfield ratios do not give adequate descriptions of reality (Anderson and Mitra, 2008; Flynn, 2008b). In order to realistically simulate the interactions between nutrients and primary production, detailed models of phytoplankton capable of simulating growth in response to

light and variable nutrients (such as nitrogen (N), phosphorus (P), silica (Si), iron (Fe)) have been generated (e.g., Tett and Droop, 1990; Flynn, 2003, 2008a). These models not only simulate the growth of the phytoplankton in response to variable nutrient supply, they also simulate the removal of the non- or lesser-limiting nutrients. This latter point is important because the removal of these nutrients affects biogeochemical cycling and hence trophic dynamics (Flynn 2008b).

Phytoplankton are subjected to bottom-up and top-down control. While the driver for the development of pPFT models is often based upon an implicit belief that bottom-up control is most important, the chemical and taxonomic quality, as well as the outright biomass, of phytoplankton exerts critical leverage on zooplankton growth. It is logical, therefore, to also enhance the capabilities of the zooplankton component in order to match, and take advantage of, improvements in the phytoplankton model components. Thus in a multinutrient food web model there is a requirement for multinutrient zooplankton models, with appropriate prey selection and handling descriptors (e.g., describing variable assimilation efficiency; Mitra et al., 2007; Carlotti and Poggiale, this volume; Flynn, 2008b). This aspect is particularly important, since zooplankton (and bacterioplankton) regenerate N, P and Fe in forms usable by phytoplankton. As C:N:P(:Si) varies in phytoplankton so regeneration of N, P (,Si) will vary on consumption of these organisms by zooplankton.

Incorporation of detailed submodels (functional types) of each of the components of the food web has been expected to provide an improved understanding of the system. Ecosystem models including a planktonic component typically categorize phytoplankton into at least two functional types, diatoms and non-diatoms (e.g., Hannon et al. 2001) in recognition of the important differences between these groups. The numbers of pPFTs employed within ecosystem models have gradually increased (Anderson, 2005) with the increase in the knowledge of importance of particular groups of phytoplankton within particular regions. In contrast, as indicated by Carlotti and Poggiale (this volume), literature studies reveal little evidence of the existence of ecosystem models incorporating the different types of zooplankton in detail, making reference to only cell numbers or to a single nutrient type (e.g., nitrogen). Planktonic ecosystem models often include a single generic compartment representing all zooplankton, the “Z box”, without a differentiation even between microbial and metazoan zooplankton, and no consideration of inter- and intra-specific zooplankton predation (Evans and Garçon, 1997). Indeed, while the numbers of pPFTs implemented in ecosystem models are on the rise varying from 3 to as many as 78 (Chifflet et al., 2001; Follows et al., 2007), the zooplankton communities remain lumped into one or two “boxes” (Carlotti and Poggiale, this volume). Furthermore, other than a difference in values of constants describing maximum growth rates and assimilation efficiency etc., those depictions of zooplankton functional types (zPFT) that do find themselves in models are invariably very simplistic (e.g., Blackford et al., 2004). Such an approach is driven by the perceived need to maintain model simplicity and due to difficulties in parameterising the models. Anderson (2005) discusses the problems of using different pPFTs without adequate parameterisation; such problems are not unique for phytoplankton but are equally applicable to functional groupings of the different ecosystem components. Zooplankton clearly require a much greater emphasis than currently given.

5. What is the best basis of the zooplankton component?

A successful linkage between the mechanistic multinutrient phytoplankton models and models of fish communities may require that the zooplankton models are not only biomass based (to match the description of pPFTs, which are invariably biomass) but also include numeric components defining the species, size, lifecycle, geographical location of the zooplankton community (to match the models of fish communities). This thus requires implementation of an individual based model (IBM) type approach (i.e. Lagrangian system; e.g., Carlotti and Wolf, 1998; Gentleman et al., 2008) in association with a biomass-based approach (i.e. Eulerian system; e.g., Runge et al., 2004; Mitra, 2006; Hu et al., 2008), or a whole-system Lagrangian system, with pPFTs being described as cell-based entities. For descriptions of zPFTs one may question whether it is really necessary to model mechanistically various intricate microscale biological-physical interactions such as the relation between water turbulence and copepods for example. However, laboratory, field, and modelling

studies have found that such interactions are critically important for zooplankton feeding, growth, and mortality (e.g., Marrase et al., 1990; Davis et al., 1991, 1992; Visser et al., 2009). Further experiments which provide data over whole life cycles (such as Davis and Alatalo, 1987; Jones and Flynn, 2006; Koski et al., 2006) of the different species are necessary. Many of the studies on copepods, for example, focus on short-term experiments with egg-producing females thus ignoring not only the male population but also the naupliar and juvenile stages. Further, often experiments on various zooplankton communities focus on either the quantity of available food (e.g., Liu et al., 2006) or the quality (typically defined by taxonomic differences; e.g., Jones and Flynn, 2006) of food. However, in nature, changes in quality and quantity synergistically affect community dynamics, in some instances resulting in mass extinction events (fish kills caused by harmful algal bloom events; Kempton et al., 2002). Thus in order to determine the descriptors of the zooplankton models, further experiments providing data on the impacts of food quantity and quality on consumer dynamics are required (e.g., Cowles et al., 1988). Modelling studies also can be used to explore potential impacts of food quality and quantity on zooplankton and ecosystem dynamics.

6. How many zooplankton functional types (zPFTs)?

Given the increasing number of functional types in the lower trophic level models of planktonic production (Follows et al., 2007) and the higher trophic level models of fish production (Shin and Cury, 2001; Fulton et al., 2005), an important issue is the number of zPFTs necessary. At the lowest level one may argue for two zPFTs, representing (i) the single celled protist community, and, (ii) the multicelled metazoan community. Ecosystem models which employ zPFTs often resort to such a division (Evans and Garçon, 1997; Blackford et al., 2004). In reality, however, the multicelled component will include zooplankton which are smaller than phytoplankton on one hand (e.g., juvenile copepods at <100µm versus large diatoms at >200µm) and those which are larger than fish on the other (e.g., jellyfish at 10s of cm. versus larval fish at less than 1cm). Additionally, larval fish are planktonic and thus fall within the multi-celled zooplankton component.

An alternative strategy may be to model only key zooplankton species, such as *Calanus* and *Pseudocalanus* (Davis, 1987; Carlotti and Poggiale, this volume). However, we then are confronted with the problem of how to group the remaining species that are not explicitly modelled and how to handle their closure. This issue becomes even more complicated for species which are part of different food chains during their life cycle. Insights can be gained through theoretical model constructs and acquisition and analysis of data from future laboratory and field studies. Certainly an order of magnitude difference in zPFTs compared to pPFTs is a gross simplification of the importance of zooplankton both in top-down regulation of phytoplankton and as bottom-up moderators of fish production.

7. The way forward

Mechanistic models describing zooplankton dynamics as required for implementation in end-to-end models already exist. In most instances the most sophisticated of these models operate in a rhomboidal fashion with detail of bottom-up and top-down processes minimized (GLOBEC, 1992; de Young et al., 2004). As Carlotti and Poggiale (this volume) say, “this (rhomboidal) approach can be error-prone due to error propagation of knowledge beyond the scales on which it was acquired”. The rhomboidal approach, however, allows focus on individual trophic levels and species, providing insights into appropriate parameterizations and simplifications of adjacent trophic levels. At the end of the day, one could ask whether we need to employ the complexity of mechanistic models in our studies of ecosystem dynamics, fish production and climate change; is the complexity in such models too great? With our present knowledge (lack of) we cannot readily determine whether this is so. However, unless we can rigorously demonstrate that an explicit description of zooplankton activity is never justified within end-to-end models then we must not assume that we can ignore or grossly simplify their contribution.

A way forward is to critically examine and quantify the effects of model simplification (e.g., Davis, 1987) using theoretical approaches as well as through acquisition of data from targeted field and

laboratory studies. The latter approach could include data from closed mesocosms comprising the entire food web (phytoplankton through to fish), with respect to taxonomic, numeric and biochemical composition, so that we can meticulously test alternate modelling strategies. This sort of combination of theoretical and rigorous empirical testing of model complexity is required in order to determine the validity of model simplifications.

In contrast to the drive for simplicity, we may actually have to consider the inclusion of additional detail, which will inevitably raise model complexity, but also will lead to better parameterizations. One of the biggest challenges for modellers is the description of behavioural plasticity, the way in which behavioural traits vary under different conditions. For example, changes in prey selectivity with food quality and quantity require a much more elaborate description than is typically used to describe zooplankton prey preference (Cowles et al., 1988; Mitra and Flynn, 2006b). It is important to develop methods for describing such behaviour because these can be the key in defining emergent properties of ecosystem models (Mitra and Flynn, 2006a).

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