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Bridging the gap between marine biogeochemical and fisheries sciences; configuring the zooplankton link

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ABSTRACT

Exploring climate and anthropogenic impacts on marine ecosystems requires an understanding of how trophic components interact. However, integrative end-to-end ecosystem studies (experimental and/or modelling) are rare. Experimental investigations often concentrate on a particular group or individual species within a trophic level, while tropho-dynamic field studies typically employ either a bottom-up approach concentrating on the phytoplankton community or a top-down approach concentrating on the fish community. Likewise the emphasis within modelling studies is usually placed upon phytoplankton-dominated biogeochemistry or on aspects of fisheries regulation. In consequence the roles of zooplankton communities (protists and metazoans) linking phytoplankton and fish communities are typically under-represented if not (especially in fisheries models) ignored. Where represented in ecosystem models, zooplankton are usually incorporated in an extremely simplistic fashion, using empirical descriptions merging various interacting physiological functions governing zooplankton growth and development, and thence ignoring physiological feedback mechanisms. Here we demonstrate, within a modelled plankton food-web system, how trophic dynamics are sensitive to small changes in parameter values describing zooplankton vital rates and thus the importance of using appropriate zooplankton descriptors. Through a comprehensive review, we reveal the mismatch between empirical understanding and modelling activities identifying important issues that warrant further experimental and modelling investigation. These include: food selectivity, kinetics of prey consumption and interactions with assimilation and growth, form of voided material, mortality rates at different age-stages relative to prior nutrient history. In particular there is a need for dynamic data series in which predator and prey of known nutrient history are studied interacting under varied pH and temperature regimes.

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Changing perspectives of zooplankton in marine ecosystems

Prior to the 1980s, the structure of the ecosystem in the pelagic marine waters was typically described through what is now

termed the “classical” food web (Steele, 1974; Cushing, 1975). Within this structure, primary production is attributed to photoautotrophic phytoplankton. These phytoplankton are then consumed by the “herbivorous” zooplankton (i.e., primary consumers) which are in turn ingested by carnivorous zooplankton and pelagic fish, which then serve as food for larger fish. Despite some earlier suggestions to modify this classic food web structure (e.g., Pomeroy,

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1974), it was not until the early 1980s that the importance of microbial production gained recognition (Williams, 1981; Fenchel, 1982), and the planktonic food web concept was broadened towards a more integrated view (the microbial food web). In this new defined structure phytoplankton as well as bacteria are consumed by protozoan grazers (Sherr and Sherr, 1994; Calbet, 2008), thus providing an additional food source for copepods and higher trophic levels. Following such studies, Azam et al. (1983) proposed the “microbial loop” as an addition to the food web, within which dissolved organic carbon (DOC) is reincorporated into the food web, mediated by microbial activity.

The recognition of the importance of the microbial loop led to the “link-sink” debate (Gifford, 1991), questioning whether the activity of the protozoan grazers served as a “link” between the microbial loop and the classical food chain (Sanders and Porter, 1987), or as a “sink” for carbon (Ducklow et al., 1986). Various field studies, experimental results and modelling efforts have subsequently shown microzooplankton to be a link between the classical and microbial food webs in marine as well as fresh water bodies thus acting as conduits of energy and nutrients between the microbial level and higher trophic levels (Suttle et al., 1986; Frost, 1987; Cushing, 1995; Calbet and Saiz, 2005). Additionally, based on stoichiometric and biochemical grounds, microzooplankton, rather than phytoplankton, could be expected to be better prey for mesozooplankton (Klein Breteler et al., 1999; Broglio et al., 2003; Mitra and Flynn, 2005). The latest twist to this is the concept that much of the plankton community currently split between either phototrophic phytoplankton or heterotrophic microzooplankton should be recognised as mixotrophic (Flynn et al., 2013; Mitra et al., 2014).

Today, the construction, testing and deployment of mathematical descriptions of plankton dynamics are central planks in marine ecology and climate change research. Many of these studies are based on the classic ecosystem model of Fasham et al. (1990), or variations on that theme. However, while over the last half century our understanding of aquatic ecology has undergone a substantial change, models portraying these systems have not developed in line with field and laboratory observations. Model structure and complexity has not typically changed in ecosystem models to reflect improvements in our understanding of biological complexity with its attendant feedback mechanisms (Mitra and Davis, 2010; Rose et al., 2010). The dramatic increase in model complexity over this period has been almost wholly focussed on the phytoplankton–nutrient link, with regard to variables, processes and parameters. Very little, by comparison, has been done with the Z component, quite often employing only 2 classes (e.g., 78 P boxes vs. 2 Z boxes in Follows et al., 2007). Despite the plethora of mechanistic zooplankton models which have been developed over the past two decades (e.g., Carlotti and Hirche, 1997; Carlotti and Wolf, 1998; Mitra, 2006; Mitra and Flynn, 2007; Flynn and Irigoien, 2009), the Z-boxes within ecosystem models are still biologically extremely simplistic with little or no differences in the physiological descriptions between the different Z-boxes. This is despite the manifest difference in the ecophysiology of the protist microzooplankton and the metazoan zooplankton. Increased complexity has usually been in numerical rather than detailed structural complexity; for example, 1-box representing the entire zooplankton (Z) community vs. 3-boxes representing different zooplankton functional types (e.g., Franks, 2002 vs. Blackford et al., 2004).

The zooplankton community has thus been typically side-lined within ecosystem studies, not receiving the same level of importance as the phytoplankton and fish communities. Within biogeochemical models, zooplankton represent the top trophic level acting as a closure function, while within many fisheries models, zooplankton form the bottom level (see reviews by Plagányi (2007), Carlotti and Poggiale (2010), Fulton (2010)). However, there is a growing recognition of the need to bring together these

two strands of research (biogeochemical and fisheries) through development of end-to-end ecosystem models combining physico-chemical oceanographic descriptors with the biology of all trophic levels from microbes to higher-trophic-level, including humans, in a single modelling framework (Mitra and Davis, 2010; Rose et al., 2010). Fig. 1 presents a conceptual model of such an end-to-end food web ecosystem. The zooplankton community (Z) acts as the conduit for the transfer of energy and material from the primary producers to the higher trophic levels and has a pivotal role in recycling and export of nutrients. Thus the zooplankton community is the critical link between biogeochemistry and fisheries (Carlotti and Poggiale, 2010; Mitra and Davis, 2010).

Here, we demonstrate the need to ensure that the description of this Z-link is appropriate for the task at hand, identifying the mismatch between our biological understanding and mathematical descriptions and thence proposing a guide for future experimental (laboratory and field) as well as modelling efforts. As an additional justification for such work, we point to the need to find out how various environmental and climatic factors may impact on ecosystem services important to humans (e.g., fisheries). Key amongst those factors are the rather well studied affects of temperature and the far less well understood implications of ocean acidification (OA; Royal Society London, 2005). All of this requires a good understanding of the processes governing the functioning of the ecosystems. This can be best achieved through an iterative process involving observations, experimentation and modelling, in which enhancements in understanding in any one component prompts renewed emphasis in others.

We commence by investigating the influence different vital rates and physiological functions have on zooplankton dynamics. We then examine the experimental (field and laboratory) and modelling approaches which underpin zooplankton research (especially related to the Z-vital rates) with an aim to determine the level of mismatch in the two approaches. Using this information we provide a roadmap of how the gaps between these two research strands may be narrowed such that the Z-link in end-to-end studies can be configured more realistically. The findings from this work will act as a basis for the development of the next generation ecosystem models which will aid understanding of the ocean ecosystem dynamics under changing anthropogenic and climate events and thence inform various ocean management and policy formulations through, for example, the EURO-BASIN project.

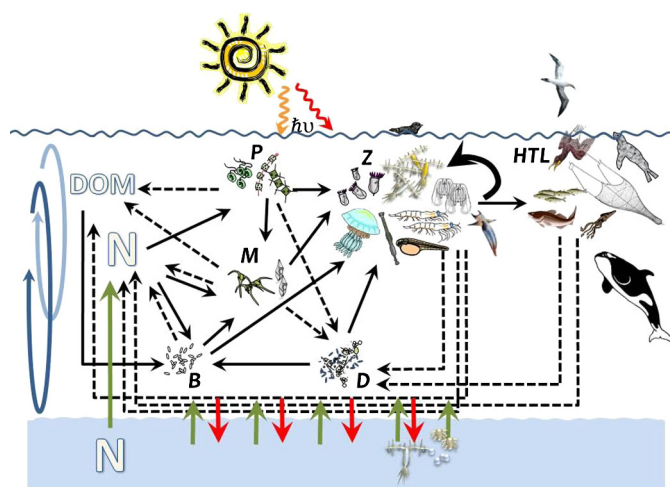


Fig. 1. Conceptual model of marine food web. P, phytoplankton, Z, zooplankton, N, nutrients, M, mixotroph, B, bacteria, D, detritus, HTL, higher trophic levels; solid arrows, inputs; dashed arrows, outputs; blue arrows, mixing; red and green arrows, exchange between the mixed surface layer and lower water. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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