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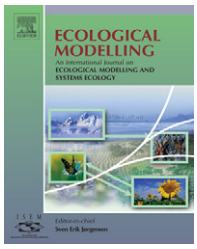

Plankton community patterns across a trophic gradient: The role of zooplankton functional groups

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ABSTRACT

We use a complex aquatic biogeochemical model to examine competition patterns and structural shifts in plankton communities under nutrient enrichment conditions. Our model simulates multiple elemental cycles (organic C, N, P, Si, O), multiple functional phytoplankton (diatoms, green algae and cyanobacteria) and zooplankton (copepods and cladocerans) groups. The model provided a realistic platform to examine the functional properties (e.g., grazing strategies, food quality, predation rates, stoichiometry, basal metabolism, and temperature requirements) and the abiotic conditions (temperature, nutrient loading) under which the different plankton groups can dominate or can be competitively excluded in oligo-, meso- and eutrophic environments. Our analysis shows that the group-specific maximum grazing rates, the predation rates from planktivorous fish, along with the temperature requirements to attain optimal growth can be particularly influential on the structure of plankton communities. The model also takes into account recent advances in stoichiometric nutrient recycling theory, which allowed examining the effects of the cyanobacteria food quality, the critical threshold for mineral P limitation, and the half saturation constant for assimilation efficiency on the zooplankton functional group biomass across a range of nutrient loading conditions. Our study highlights the adverse effects that the cyanobacteria food quality can have on the two functional zooplankton groups in productive systems, despite the differences in their feeding selectivity strategies, i.e., cladocerans are filter-feeders with equal preference among the different types of food, whereas copepods are assumed to be capable of selecting on the basis of food quality. Finally, we conclude that the articulate representation of the producer–grazer interactions using stoichiometrically/biochemically realistic terms will offer insights into the patterns of nutrient and energy flow transferred to the higher trophic levels.

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1. Introduction

The central role of herbivory in shaping the structure of plankton communities (i.e., competitive exclusion or species coexistence mediated by herbivores, evolution of the phytoplankton growth strategies induced by grazing selectivity) and in linking the standing biomass of algae with fish populations has been extensively highlighted in aquatic ecology (Lampert and Sommer, 1997; Grover, 1997). Despite the tremendous effort and a wide variety of approaches devoted to studying this topic, the drivers of the variability at the phytoplankton–zooplankton interface remain controversial and arguably only partially understood (Lehman, 1988; Brett and Goldman, 1997; Polis et al., 2000). A recent meta-analysis

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of 153 aquatic biogeochemical modelling studies provided evidence that zooplankton dynamics is the most poorly predicted component of planktonic systems (Arhonditsis and Brett, 2004). Specifically, the median relative error from approximately thirty zooplankton simulations was 70%, and more than a quarter of the studies reported error higher than 100% (see Fig. 3 and Table 1 in Arhonditsis and Brett, 2004). Although these results can partly be explained by the paucity of zooplankton data and the error associated with converting the collected information (in units of individuals per volume) to the modelled units (usually carbon or nitrogen mass per volume), the considerable model misfit mainly stems from our inability to mathematically depict the behavioural complexities, the idiosyncrasies of metabolic regulation, and the diverse patterns of somatic growth and reproduction of zooplankton communities (Fennel and Neumann, 2001; Franks, 2002).

A typical thorny issue in food web modelling is the optimal aggregation level of the zooplankton community, where the existing strategies span a very wide range of complexity. Early aquatic biogeochemical models typically regarded zooplankton as an aggregated biotic entity and parameterized bulk properties such as grazing rates, assimilation efficiency, metabolic strategies, and consumer-driven nutrient recycling (McGillicuddy et al., 1995; Doney et al., 1996; Arhonditsis et al., 2000; Franks and Chen, 2001). These studies mainly aimed to quantify the transfer of mass and energy among trophic levels, to address local management issues (e.g., eutrophication control), and to understand the interplay between hydrodynamic patterns and mesoscale nutrient and plankton distributions in oceanic systems. On the other hand, there are ecological questions that require more sophisticated formulations and higher resolution of the zooplankton compartment (Broekhuizen et al., 1995; Fennel and Neumann, 2001; Arhonditsis and Brett, 2005a). For example, the explicit consideration of smaller and larger size zooplankton classes allows to more realistically assess the connections between the ocean's carbon cycle and global climatic variability (i.e., the "biological pump"), and insights into the plankton succession patterns in epilimnetic environments can only be gained by distinguishing among different functional groups (e.g., copepods, cladocerans). Other authors have also pointed out that the only effective way to predict zooplankton dynamics is to fully simulate zooplankton life histories, e.g., the copepod-submodel suggested by Fennel (2001) that included eggs, nauplii, copepodites and adults as state variables.

Another topic that has received considerable attention is the mathematical representation of the biochemical heterogeneity at the primary producer–grazer interface to illuminate the patterns of nutrient and energy flow transferred through the food web (Andersen, 1997; Loladze et al., 2000; Arhonditsis and Brett, 2005a; Mulder and Bowden, 2007). The aquatic ecology literature suggests that the algal taxonomic differences in food quality due to differences in their highly unsaturated fatty acid (HUFA), protein, amino acid content, and/or digestibility determine the strength of the trophic coupling in aquatic pelagic food webs, e.g., HUFA bottom–up hypothesis (Brett and Muller-Navarra, 1997; Muller-Navarra et al., 2004). Other studies underscore the importance of the constraints imposed from the mass balance of multiple chemical elements (C, N, P) on ecological interactions pinpointing the critical role of the discrepancy between the prey and predator elemental somatic ratios on food web structure and pelagic ecosystem functioning (Elser and Urabe, 1999). In this regard, our theoretical understanding has advanced from a series of stoichiometric models that account for the effects of P-deficient food on the rate of P zooplankton recycling by explicitly considering animal demands (e.g., respiration, biomass production) for both C and P (e.g., Hessen and Andersen, 1992; Andersen, 1997). The Loladze et al. (2000) and Mulder and Bowden (2007) modelling studies are two characteristic examples with particularly intriguing findings that need to be tested in real world conditions. Loladze et al. (2000) modified the Rosenzweig-MacArthur variation of the Lotka-Volterra equations and demonstrated that the chemical heterogeneity in the first two trophic levels can result in interesting dynamic behaviour under nutrient limiting conditions; in particular, the two biotic compartments (prey and predator) can be transformed into competitors for phosphorus and their interactions shift from the typical (+, −) class to the paradoxical (−, −) type. Mulder and Bowden (2007) relaxed the assumption of strict homeostasis of the grazer and showed that variable zooplankton stoichiometry allows overcoming poor food quality limitations in high-energy, low-nutrient environments.

In this study, we use a complex aquatic biogeochemical model to examine competition patterns and structural shifts in the plankton community across a trophic gradient. Our model simulates multiple elemental cycles (organic C, N, P, Si, O), multiple functional phytoplankton (diatoms, green algae and cyanobacteria) and zooplankton (copepods and cladocerans) groups. The model provides a realistic platform to examine the functional properties (e.g., grazing strategies, food quality, predation rates, stoichiometry, basal metabolism, and temperature requirements) and the abiotic conditions (temperature, nutrient loading) under which the different plankton groups can dominate or can be competitively excluded in oligo-, meso- and eutrophic environments. Finally, our study attempts to elucidate aspects of the zooplankton feeding and growth efficiency modelling strategies by assessing the effects of the cyanobacteria food quality, the critical threshold for mineral P limitation, and the half saturation constant for growth efficiency on the zooplankton functional group biomass across a wide range of nutrient loading conditions.

2. Methods

2.1. *Aquatic biogeochemical model*

2.1.1. *Model description*

The spatial structure of the model is composed of two compartments representing the epilimnion (upper layer) and hypolimnion (lower layer) of a lake. The model simulates five biogeochemical cycles, i.e., organic carbon, nitrogen, phosphorus, silica and dissolved oxygen. The particulate phase of the elements is represented from the state variables particulate organic carbon, particulate organic nitrogen, particulate organic phosphorus, and particulate silica. The dissolved

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