



The role of microzooplankton trophic interactions in modelling a suite of mesocosm ecosystems



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ABSTRACT

The zooplankton components in biogeochemical models drive top-down control of primary production and remineralisation, and thereby exert a strong impact on model performance. Who eats whom in oceanic plankton ecosystem models is often largely determined by body size. However, zooplankton of similar size can have different prey-size spectra. Thus, models with solely size-structured trophic interactions may not capture the full diversity of feeding interactions and miss important parts of zooplankton behavior.

We apply an optimality-based plankton ecosystem model to analyse trophic interactions in a suite of mesocosm experiments in the Peruvian upwelling region. Sensitivity analyses reveal a dominant role of trophic structure for model performance, which cannot be compensated by parameter optimisation. The single most important aspect governing model performance is the trophic linking between dinoflagellates and ciliates. Only with a bidirectional link, i.e., both groups can prey on each other, is the model able to reproduce the differential development of the microzooplankton communities in the mesocosms. Thus, we conclude that a solely size-based trophic structure may not be appropriate to represent the most important trophic interactions in plankton ecosystems. The diversity of feeding interactions needs to be adequately represented to capture community dynamics.

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1. Introduction

Biogeochemical models usually incorporate plankton communities by means of NPZD-type formulations to represent major functional groups of plankton ecosystems, e.g., inorganic Nutrients, Phytoplankton, micro- and mesoZooplankton, and Detritus (Prowe et al., 2012a; Aumont et al., 2015; Le Quéré et al., 2016). While zooplankton and related parameters clearly exert a strong impact on model performance (e.g., Fulton et al., 2003a; Pahlow et al., 2008), finding and constraining the most appropriate representation of zooplankton dynamics remains a major challenge (Håkanson, 1995; Fulton et al., 2003b). Mesocosm experiments can help address this kind of questions as they allow frequent sampling of enclosed ecosystems, providing more coherent observations than is possible with field surveys and allowing for more natural conditions than laboratory studies.

In the present study, we examine the trophic roles of microzooplankton communities using data from two shipboard mesocosm experiments conducted in the coastal upwelling region off Peru

(PU1, PU2, Hauss et al., 2012; Franz et al., 2012a,b). In this region, surface waters are characterised by high nutrient concentrations with low N:P ratios (compared to the Redfield N:P ratio of 16, Redfield, 1934) due to denitrification and anaerobic ammonium oxidation (anammox) in the underlying Oxygen Minimum Zone (OMZ, Deutsch et al., 2007; Kalvelage et al., 2013; Su et al., 2015). In order to investigate the influence of low N:P ratios on the growth and community composition of plankton, the mesocosms have been initialised with various DIN:DIP ratios. Distinctly different zooplankton communities developed in the PU1 and PU2 mesocosm experiments, with PU1 dominated by dinoflagellates and PU2 by ciliates, possibly related to the different nutritional quality of the phytoplankton communities (Franz et al., 2012b; Hauss et al., 2012).

Marine dinoflagellates can be autotrophic, heterotrophic or mixotrophic (Stoecker et al., 2017). Heterotrophic and mixotrophic species feed on a wide range of prey, including bacteria, phytoplankton, dinoflagellates and ciliates, using a variety of feeding strategies (Strom, 1991; Hansen, 1991; Jeong et al., 2010; Hansen et al., 2016). Several *Dinophysis* species feed on ciliates often larger than themselves (Hansen, 1991; Nishitani et al., 2008; Park et al., 2010). *Dinophysis caudata* accounted for up to 42% of the dinoflagellate community biomass in the PU1 and PU2 mesocosm

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experiments (Hauss et al., 2012). Planktonic ciliates are another important component of the microzooplankton community in the ocean. They serve as food for larger organisms, e.g., copepods and fish larvae. Ciliates can consume a wide spectrum of food types and sizes (Yasindi and Taylor, 2006). Similarly to dinoflagellates, ciliates can also prey on bacteria, phytoplankton, dinoflagellates and ciliates (Sherr and Sherr, 1987; Dolan and Coats, 1991; Jakobsen et al., 1997; Jeong et al., 2013). Tintinnid ciliates are heterotrophic and feed primarily on photosynthetic algae and bacteria (Stoecker, 2012; Montagnes, 2013), whereas many oligotrich ciliates are mixotrophic (Dolan, 1992).

In plankton ecosystem modelling, trophic relations among zooplankton compartments are often based on body size (Hansen et al., 1994), which is generally considered a master trait for trophic interactions in plankton (Banas, 2011; Andersen et al., 2016). However, traits shaping feeding interactions are diverse and size relations between predators and prey can also result from foraging types and morphologies (Wirtz, 2012). Size ratios between predators and their prey are about 0.4–7 for dinoflagellates and 2.5–30 for ciliates (Hansen et al., 1994). Hence, dinoflagellates can prey on particles larger than their own size, whereas ciliates can only eat smaller prey (Jakobsen et al., 1997).

For analysing above mesocosm experiments, Marki and Pahlow (2016) developed an optimality-based model, which also forms the foundation for our present study. Optimality-based models rest on the assumption that evolution favours organisms with more efficient strategies in the continual competition for resources. In our present model, phytoplankton, dinoflagellates and ciliates are represented by optimality-based formulations (Pahlow and Prowe, 2010; Pahlow et al., 2013). These are mechanistically founded on trade-offs among energy and resource requirements of plankton organisms and can describe the observed behaviour of a wide range of phyto- and zooplankton species in laboratory experiments. A major advantage of these models is the low number of parameters required to describe fairly complex behaviour. For example, only six tuneable parameters need be calibrated for simulating four variables (C, N, P, Chl) with the phytoplankton model of Pahlow et al. (2013). Given the difficulties usually associated with constraining model parameters with (limited) observations (Schartau et al., 2017), keeping the number of parameters low greatly facilitates not only model calibration but also the disentangling of parameter and structural uncertainties.

Marki and Pahlow (2016) use their model to explore how microzooplankton respond to the different food quality of phytoplankton in terms of elemental composition, caused by the different nutrient enrichments in the mesocosms. Variations in phytoplankton C:N:P composition in response to ambient nutrient (DIN, DIP) stoichiometry in the Peruvian upwelling region alone, as described by the model of Pahlow et al. (2013), could not explain the differential development of the mesocosm plankton communities. Marki and

Pahlow (2016) highlight the importance of intraguild predation and find that some of the differences among the mesocosms might be explained by variations in the zooplankton stoichiometry, pointing towards the importance of zooplankton flexible stoichiometry in marine ecological models. Marki and Pahlow (2016) also examine a more complex model configuration with two separate compartments for dinoflagellates and ciliates, with the larger (ciliates) feeding on the smaller (dinoflagellates) zooplankton, but this (size-based) modification did not improve model performance.

For the present study, we relax two restrictions applied by Marki and Pahlow (2016). (1) Instead of using pre-defined parameter sets for microzooplankton, we identify and optimise sensitive model parameters in order to separate parameter and structural model uncertainty. (2) We examine the effect of the size-based restriction that ciliates feed on dinoflagellates but not vice versa by introducing a new model configuration with a bidirectional link, i.e., dinoflagellates and ciliates can prey on each other. We base our analysis on the configuration with separate microzooplankton compartments for dinoflagellates and ciliates. This avoids a solely size-based trophic structure, and allows for a potentially greater diversity of trophic interactions. We then compare the predictive skill of the configurations with and without the bidirectional link in order to assess the importance of microzooplankton trophic interactions for plankton ecosystem modelling.

2. Methods

2.1. Data

We use data from two mesocosm experiments (PU1 and PU2, Table 1) in the upwelling region of the eastern tropical South Pacific off Peru (Hauss et al., 2012; Franz et al., 2012a,b). The influence of the stoichiometry of inorganic nutrient supply on growth and composition of plankton communities was investigated by monitoring mesocosms initialised with different nitrate and phosphate concentrations and ratios (Table 1). Each of PU1 and PU2 consisted of 12 mesocosms, with four replicates of three treatments (N:P ratios) in PU1 and three replicates of four treatments in PU2. Light intensity was reduced by 70% using shading nets, intending to mimic conditions at a depth of 10 m. All mesocosms were restocked with 5 μm -filtered ambient surface seawater on days 3 and 5 of the experiments, due to the large amounts of water required for sampling. Trace metal and silicate compounds were added to avoid trace metal and silicate limitation at the start of each experiment, and also on day 5 in PU2 only.

Samples were taken daily for measuring dissolved inorganic nutrients (DIN, DIP and SiO_3^{2-}), chlorophyll (Chl), particulate organic nitrogen (PON), particulate organic phosphorus (POP), and community composition (Hauss et al., 2012; Franz et al., 2012a,b). To measure dissolved inorganic nutrient concentrations, samples

Table 1
Summary of the mesocosm experiments PU1 and PU2 off Peru.

	PU1			PU2			
Latitude (S)	12°2.05'			16°0.01'			
Longitude (W)	77°47.33'			74°37.04'			
PAR ($\text{E m}^{-2} \text{d}^{-1}$)	43.2			60.48			
Duration (days)	6			7			
Treatment N:P (mol mol^{-1})	20	3.4 (ambient)	2.8	16	8	5 (ambient)	2.5
DIN ($\mu\text{mol L}^{-1}$)	32	5.5	5.5	16.0	16.0	5.0	5.0
DIP ($\mu\text{mol L}^{-1}$)	1.6	1.6	2	1.0	2.0	1.0	2.0
Zooplankton community	Dinoflagellates dominant ^a			Ciliates dominant ^a			

^a Hauss et al. (2012).

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