



## The influence of zooplankton enrichment on the microbial loop in a shallow, eutrophic lake

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### Abstract

With increasing primary productivity, ciliates may become the most important members of the microbial loop and form a central linkage in the transformation of microbial production to upper trophic levels. How metazooplankton, especially copepods, regulate ciliate community structure in shallow eutrophic waters is not completely clear. We carried out mesocosm experiments with different cyclopoid copepod enrichments in a shallow eutrophic lake to examine the responses of ciliate community structure and abundance to changes in cyclopoid copepod biomass and to detect any cascading effects on bacterioplankton and edible phytoplankton. Our results indicate that an increase in copepod zooplankton biomass favours the development of small-sized bacterivorous ciliates. This effect is unleashed by the decline of predaceous ciliate abundance, which would otherwise graze effectively on the small-sized ciliates. The inverse relationship between crustacean zooplankton and large predaceous ciliates is an important feature adjusting not only the structure of the ciliate community but also the energy transfer between meta- and protozooplankton. Still we could not detect any cascading effects on bacterio- or phytoplankton that would be caused by the structural changes in the ciliate community.

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### Introduction

Zooplankton plays an important role in the food web of freshwater lakes, serving as a link between lower (phyto-, protozooplankton) and higher (fish) trophic levels. Selective feeding pressure by different planktivorous fish larvae is one of the most important factors shaping zooplankton

communities, affecting the structure, abundance and biomass of different organism groups (Jeppesen et al. 1992; Mills and Forney 1983). Alterations in metazooplankton community structure can in turn influence algal and protozoan communities (Gilbert and Jack 1993; Jürgens and Jeppesen 2000; Wickham 1995a). Thus the ability of zooplankton to prey on phytoplankton and/or different protist groups and the suitability of zooplankton as food for fish determines the efficiency of matter and energy transformation through the food web. Depending on zooplankton food source the energy is transported to upper trophic levels via two different

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pathways—through the classical grazing food chain and the microbial loop, which are connected to each other in many indirect and direct ways (Riemann and Christoffersen 1993). When phytoplankton cannot be grazed by metazoans, they enter the less efficient microbial loop that is mediated by bacteria and protists. As a result, planktonic protists are currently the subject of greater scrutiny in aquatic food web studies.

The microbial loop is widely studied in lakes of contrasting trophic status and different geographical areas (Amblard et al. 1995; Gobler et al. 2008; Kisand et al. 1998; Peštova et al. 2008; Zingel 2005; Zingel et al. 2006). With increasing primary productivity, ciliates may become the most important members of the microbial loop (Sherr and Sherr 2002). They can be a significant food source for metazooplankters (Adrian and Schneider-Olt 1999; Hansen 2000; Wiackowski et al. 1994) and in turn major bacterivores, the most important early spring algivores and the main consumers of heterotrophic protozoans (Šimek et al. 1990; Weisse et al. 1990; Zingel and Nöges 2008), thus forming a central linkage in the transformation of microbial production to upper trophic levels.

The cascading effect of copepod and cladoceran dominated zooplankton community on microbial assemblages has been studied quite extensively in freshwater systems (Jürgens et al. 1994; Jürgens and Jeppesen 2000; Wickham 1998; Zöllner et al. 2003). In particular, cyclopoid and calanoid copepods are known to be efficient selective grazers of planktonic ciliates (Burns and Gilbert 1993; Wiackowski et al. 1994; Wickham 1995b), while relatively unselective filter-feeding cladocerans (e.g. *Daphnia* spp.) have strong top-down impacts on protozoans as well as phytoplankton and large sized bacterial communities (Jürgens 1994; Porter et al. 1988). Still, there are few studies (Jürgens et al. 1994; Jürgens and Jeppesen 2000; Zöllner et al. 2003, 2009) that have examined if the predatory effect of zooplankton on protists cascade down to heterotrophic bacterial communities. In most studies the protozoan communities were usually strongly controlled by metazoan predation but changes in the amount of ciliates did not significantly alter the abundance and biomass of bacterial communities (Sipura et al. 2003; Ventelä et al. 2002; Wickham 1998). In contrast, strong direct effects on bacterial abundances were found when zooplankton community was represented by unselective filter-feeding cladoceran *Daphnia* spp. in lakes (Jürgens 1994; Pace et al. 1999). Still, most of the experiments indicate that changes in grazer community might cause alterations in cell morphology and community composition rather than change the abundance and biomass (Jürgens et al. 1999, 1994; Zöllner et al. 2003).

Our recent works have shown the importance of planktonic ciliates in the food web of the shallow eutrophic Lake Võrtsjärv (Southern Estonia, Northern Europe) because of their high abundances (reaching values up to 191 cells ml<sup>-1</sup>) and biomass values (constituting more than half of the total zooplankton biomass (Zingel and Nöges 2010)). The positive correlation between the biomass of ciliates and metazooplankters implies that the small-sized protozooplankters are

regulated by bottom-up (food availability) rather than top-down factors (Zingel and Haberman 2008; Zingel 1999). Live labeling experiments conducted in Võrtsjärv (Agasild et al. 2012) have shown that microciliates (15–40 µm) were consumed by all dominant cladoceran and copepod species (mainly by *Chydorus sphaericus* and cyclopoid copepods) but their predation effect on ciliates was relatively weak. Our further enclosure studies (Agasild et al. 2013) in Võrtsjärv revealed that the removal of a large fraction of crustaceans also initiated a decrease in the total abundance of ciliates. At the community level, we observed a substantial increase in large-sized predaceous ciliates (>100 µm) and a simultaneous decrease in the abundance of smaller ciliates, which however did not cascade down to the level of bacteria and edible phytoplankton. It was suggested that an important trophic link exists between cyclopoid copepods and the large-sized predatory ciliates that triggered the trophic cascade in the planktonic ciliate assemblage.

In the present study, mesocosm experiments with different cyclopoid copepod enrichments were conducted to (i) examine the responses of ciliate community structure and abundance to changes in cyclopoid copepod biomass; (ii) detect cascading effects on bacterioplankton and on edible phytoplankton. Our hypothesis was that in a shallow eutrophic lake, the ciliate community structure is controlled by copepods. Copepods can suppress predaceous ciliates, leading to an increase in small-sized ciliate abundance.

## Material and Methods

### Study site

Võrtsjärv, the second largest lake in Estonia, is situated in the South-Estonian pre-glacial basin, centred at 58°15'7" N and 26°1'47" E (Fig. 1). The lake has an elongated shape, with a surface area of 270 km<sup>2</sup>, length of 34.8 km and width of 14.8 km. Despite the large surface area, the lake is shallow with a mean depth of 2.8 m and a maximum depth of 6 m. Lake water is well mixed and turbid due to surface waves and currents. During the growing season Secchi depth usually does not exceed 1 m in the central parts of the lake (Nöges et al. 1998). The average concentrations of total phosphorus (0.05 mg P L<sup>-1</sup>) and nitrogen (2 mg N L<sup>-1</sup>) characterise the lake mostly as a eutrophic to hypertrophic water body (Tuvikene et al. 2004).

The shallowness of the lake together with wave-induced resuspension of bottom sediments is responsible for algal blooms and contributes to the formation of high seston concentrations and high turbidity during summer. The phytoplankton community is mainly dominated by two groups, the narrow filamentous cyanobacteria and the diatoms. Among the cyanobacteria, four filamentous species *Planktolyngbya limnetica* [(Lemm.) Kom.-Legn.], *Limnothrix planktonica* [(Wolosz.) Meffert], *Limnothrix redekei* [(van Goor) Meffert] and *Aphanizomenon skujae* (Kom.-Legn. et Cronb.) are the

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