



The effects of predation by planktivorous juvenile fish on the microbial food web

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Abstract

The feeding impact of planktivorous fish on microbial organisms is still poorly understood. We followed the seasonal dynamics of the food web in two natural fishponds for two years: one was stocked with planktivorous whitefish while the other had no planktivorous fish. The aim of the study was the simultaneous assessment of the feeding behaviours of planktivorous fish and of bacterivorous meta-/protozooplankters. We hypothesized that in the presence of planktivorous fish there would be fewer metazooplankton, more protozoans and decreased numbers of bacteria. Our results showed that the amount of metazooplankton eaten by the fish was indeed negatively correlated with metazooplankton biomass. The feeding impact of planktivorous fish in shaping the microbial loop was remarkable. The main grazers of bacteria in the fishpond were ciliates, whereas in the pond without fish these were heterotrophic nanoflagellates. In the fishless pond the role of the top predator shifted to the predaceous metazooplankter *Leptodora kindtii* which controlled the abundance of herbivorous metazooplankters. We found a negative relationship between the number of bacteria and flagellates in the fishless pond, while the number of bacterivorous ciliates was suppressed by predaceous ciliates. Therefore the bacteria-grazing activity was higher in the absence of planktivorous fish.

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Introduction

Zooplankton is the main food of fish larvae and fry in many aquatic systems (Cushing 1983; Mehner et al. 1996; Post and Kitchell 1997). Predation by adult planktivorous fish and the juveniles of all fish species is a very important factor determining the structure and abundance of the zooplankton community in lakes (Brooks and Dodson 1965; Hrbáček 1962). As a result of fish predation the density of large

cladocerans (e.g. *Daphnia galeata* Sars, *Leptodora kindtii* Focke) usually decreases while the proportion of smaller species (e.g. *Bosmina longirostris* O. Müller, *Ceriodaphnia* sp.) increases (Jeppesen et al. 2001; Ohtaka et al. 1996). The predation effects cascade through the food web and can be considered to be a major factor determining the dynamics of the planktonic community (Huston 1979). Usually predation by planktivorous fish mainly influences cladocerans, as the copepods are better adapted to avoid predation (Bergman 1990). Alterations in the metazooplankton (MZP) community structure can in turn influence the algal (Persson 1997) and protozooplankton (PZP) communities (Gilbert and Jack 1993; Jürgens and Jeppesen 2000; Wickham 1995). PZP

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abundance and species composition can directly influence bacterioplankton (Beaver and Crisman 1982; Gonzalez et al. 1990; Güde 1989; Hall et al. 1993) and the mediation of dissolved organic matter (DOM) to the higher food web levels. In addition to bacteria, heterotrophic nanoflagellates (HNF) are also able to consume DOM with a higher molecular mass (Sherr 1988). Direct ingestion of DOM by PZP is an alternative and efficient pathway for returning nutrients to higher trophic levels.

Despite the growing number of publications on the planktonic food web structure there is still a lack of studies that consider the cascading effect of planktivorous fish on the microbial loop. The role of fish is often neglected because of difficulties of assessing their abundance and feeding rate. Zingel et al. (2012) revealed that larval fish actively consume planktonic ciliates in a eutrophic lake. Riemann (1985) showed experimentally that increases in the number of planktivorous fish caused significant increases in HNF abundance. He attributed this increase to reduced predation from large cladoceran species. Subsequent enclosure experiments confirmed these early results (Christoffersen et al. 1993; Markošova and Ježek 1993). Fish treatments generally tend to increase the importance of small zooplankton species (Mazumder et al. 1988; Proulx et al. 1996; Vanni 1987). In comparing two lakes with contrasting food web structures, Vaque and Pace (1992) found that the lake dominated by planktivorous fish also contained the highest HNF abundance compared to the lake dominated by piscivorous fish. An enclosure experiment carried out in a small oligotrophic lake on the Canadian Shield (Tzaras et al. 1999) showed that fish alone had no significant effect on the abundance of bacteria and HNF. Müller-Solger et al. (1997) found in a mesocosm experiment conducted in a mesotrophic lake that in the presence of planktivorous fish the total ciliate biovolume increased. However, the impact on ciliates was species specific. Several studies have demonstrated that the addition of planktivorous fish increase rotifer abundance (e.g. Lazzaro et al. 1992; Mazumder et al. 1990).

We can conclude that there are numerous experiments on the food web effects of fish but much less attention has been paid to elucidating the direct and indirect consequences of fish feeding on microbial loop communities. Most data available have usually been obtained by short-term approaches. Without knowing the mechanisms driving the microbial loop community structure and functioning we cannot predict the possible response of the lake food web to changes in the environment. Our goal was therefore to simultaneously study planktivorous fish feeding on zooplankton and zooplankton feeding on bacteria, providing at the same time background data of the two-year seasonal dynamics of bacteria, protozoans, phytoplankton and MZP. We selected two large natural ponds where the actual food composition and abundance of planktivorous fish could be estimated. We hypothesized that in the pond in which planktivorous fish were present there would be less MZP, more PZP and consequently fewer bacteria than in the pond without planktivorous fish. We predicted

that the lowered MZP densities would have a positive effect on small bacterivorous ciliates since the MZP are known to prey on small ciliates (Agasild et al. 2012). Additionally, we assumed that in the absence of planktivorous fish the MZP and bacterial numbers would be much higher.

Material and Methods

To follow the impact of planktivorous fish on the planktonic food chain, we used two different model situations. We selected two large natural ponds (further described as F and nF) in the Härjanurme fish farm (Estonia). To the pond F the larvae of whitefish (*Coregonus lavaretus* Linnaeus) were introduced. The pond nF had no planktivorous fish at all. As the number of the ponds available for the study was limited we could not carry out any replication. Therefore we decided to repeat the study by extending it over a second year. The study was carried out from April 25 to September 29 in 2005 and from April 25 to September 28 in 2006. In the previous year (2004) both ponds were stocked with juvenile pikeperch (*Sander lucioperca* Linnaeus), which were removed at the end of the year. The plankton communities were checked in 2004 in both ponds and found to be generally similar.

The surface area of the ponds F and nF was 6 and 7.2 ha, respectively. The mean depth of both ponds was 1.6 m. Over the years studied, the average values of total phosphorus and nitrogen concentrations in July were $48 \mu\text{g L}^{-1}$, 0.9 mg L^{-1} and $47 \mu\text{g L}^{-1}$, 1.0 mg L^{-1} , respectively. The values of total phosphorus and total nitrogen in both ponds F and nF characterize them as eutrophic water bodies. The fish larvae were introduced to the pond F shortly after hatching (April 19–April 25) in both years. The ponds were emptied in late autumn and the fish were removed. The stocking density was approximately 6500 larvae per hectare. In both years the plankton sampling started on April 25. In 2005 the samples were collected every 10 days, while fish larvae were sampled every 20 days. In 2006 both plankton and fish larvae were sampled every 20 days. Water samples were collected using a Ruttner water sampler. All plankton analyses were made from pooled water samples collected at half-meter intervals (0, 0.5, 1 and 1.5 m). Each time, two subsamples were taken from the same places – one near the shore and one from the midpoint of the pond.

The total number of bacteria was determined by DAPI (4',6'-diamidino-2-phenylindole; Polysciences Inc.) direct count (Porter and Feig 1980). Formaldehyde-preserved subsamples were incubated with DAPI (final concentration $10 \mu\text{g mL}^{-1}$) for 5 min in the dark and filtered onto black $0.22\text{-}\mu\text{m}$ pore-size polycarbonate filters (Osmonics Inc.). The bacterial abundance was estimated by autofluorescence using an epifluorescence Zeiss Axiovert S100 microscope (Carl Zeiss MicroImaging GmbH, Jena, Germany). To count HNF taxa the samples were fixed with buffered formalin. Preserved samples were stained for 1–2 min with DAPI at a final concentration of $2 \mu\text{g mL}^{-1}$ and gently filtered through

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