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Trophic interactions of the pelagic ciliate *Stentor* spp. in North Patagonian lakes

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Abstract

The zooplankton of oligotrophic lakes in North Patagonia is often dominated by mixotrophic ciliates, particularly *Stentor amethystinus* and *Stentor araucanus*. Therefore, we tested whether *Stentor* spp. (i) is an important food for juvenile endemic (*Cheirodon australe*, *Galaxias maculatus*, *Odontesthes mauleanum*, *Percichthys trucha*) and introduced (*Oncorhynchus mykiss*) fish species, and (ii) represents a remarkable grazer of bacteria. Ingestion rates of fish estimated by disappearance of *Stentor* in feeding experiments ranged between 8 (*G. maculatus*) and 53 (*C. australe*) ciliates per fish and day, and assimilation rates measured by using radioactively labelled *Stentor* ranged between 3 (*P. trucha*) and 52 (*C. australe*) ciliates per fish and day. However, although we detected the consumption of *Stentor* by fish, the daily consumption amounted to at most 0.2% of the fish biomass which can not cover the energy requirement of the fish. Furthermore, the daily consumption was equivalent to a maximum of 1.6% of the *Stentor* standing stock so that fish predation does not seem to be an important mortality factor for the ciliates. The clearance rate of *Stentor* sp. on natural bacteria was on average $3.8\,\mu l\,cil^{-1}\,h^{-1}$. The daily ingestion (mean $3.9\,ng\,C\,cil^{-1}\,d^{-1}$) was about 3.5% of the individual biomass of *Stentor* sp. Therefore, bacteria ingestion might explain a ciliate growth rate of appr. $1\%\,d^{-1}$, which was about 17% of the photosynthesis of endosymbiotic algae. The maximum density of *Stentor* sp. in the lake could ingest about $1\,\mu g\,C\,L^{-1}\,d^{-1}$ bacteria which is only 3% of average bacterial production. Thus, grazing by *Stentor* sp. does not seem to be a main loss factor for the bacteria.

Keywords: Mixotrophic ciliates; *Stentor*; Fish predation; Bacteria; North Patagonian lakes

Introduction

The plankton composition of lakes of the Southern hemisphere shows some specific characteristics compared to lakes of the Northern hemisphere. For instance, important invertebrate predators from the northern lakes, such as *Chaoborus*, *Leptodora* and *Bytothrephes*, are completely absent in the North Patagonian lakes, and water mites (e.g. *Limnesia patagonica*) and cyclopoid copepods play only a minor role (Soto and Zuniga, 1991). Calanoid copepods dominate the mesozooplankton and are more important than cyclopoid copepods and cladocerans (Soto and Zuniga, 1991; Villalobos, 1994). The phytoplankton is dominated by mixotrophic chrysophyceae and large diatoms (Soto and Stockner, 1996).

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One particular characteristic is the occurrence of mixotrophic ciliates (*Ophrydium*, *Stentor*) with endosymbiontic algae in high abundances (Modenutti et al., 1998; Woelfl, 2007). These organisms are an important component of the pelagic part of marine and freshwater food webs at times (Dolan, 1992; Laybourn-Parry et al., 1997), especially in comparison with the total ciliate biomass and total zooplankton biomass (Laybourn-Parry et al., 1997; Woelfl and Geller, 2002; Woelfl, 2007). In the southern hemisphere, the mixotrophic ciliate of the genus *Stentor* is one of the most important zooplankton groups in lakes in Australia, New Zealand and North Patagonia (James et al., 1995; Laybourn-Parry et al., 1997; Modenutti et al., 1998; Woelfl and Geller, 2002). Two species of *Stentor* (*S. amethystinus* and *S. araucanus*) always containing symbiotic green algae of the genus *Chlorella* formed a significant component of the zooplankton biomass in four out of 13 examined deep North Patagonian lakes (Woelfl, 2007). Mixotrophic ciliates contributed 14–76% (annual average 47%) to total zooplankton biomass in temperate, oligotrophic Lake Pirehueico in North Patagonia (Woelfl and Geller, 2002). In Lake Caburga, they comprised $69 \pm 28\%$ (annual mean $\pm$ SD) of the total zooplankton biomass (Woelfl, 2007). *Stentor* co-inhabited lakes with calanoid copepods (*Boeckella*, *Tumeodiaptomus*) and small cladocerans (*Eubosmina*, *Ceriodaphnia*) and was negatively correlated with cyclopoid copepods and large cladocerans (Woelfl, 2007).

However, little is known about trophic interactions regarding mixotrophic ciliates so far. *Stentor* is hardly ingested by calanoid copepods and small cladocerans so that the trophic link from ciliates via large zooplankton to fish seems to be developed rather weakly. One open question is their importance as potential food for small fish. While, tintinnid ciliates and naked ciliates have been found in the gut of field-collected marine fish larvae (e.g. Fukami et al., 1999; Nagano et al., 2001), few studies have been based on laboratory experiments (Stepien, 1976; Nagano et al., 2000) or investigations in freshwater ecosystems (Korniyenko, 1971; Lair et al., 1994). Heterotrophic ciliates are used for breeding of tropical aquarium fish and in aquaculture but there is little field evidence that fish larvae feed on naked ciliates because of their small size, the lack of hard structures and the quick decomposition by gastric juices (Kentouri and Divanach, 1986). On the other hand, the high abundance of *Stentor* in some North Patagonian lakes, the large size (up to 300 μm), and the remarkable colouring/visibility of *Stentor* due to their endosymbiontic algae make them potentially interesting for fish. However, up to now there have been no studies about the effect of predation by fish on *Stentor* in North Patagonia. Therefore, in the first part of the present study, we investigated a possible predation by fish on the pelagic ciliate *Stentor* sp. in North Patagonian lakes. We tested whether different endemic and introduced fish species do indeed ingest *Stentor*, and performed ingestion and assimilation experiments.

Furthermore, the mixotrophic ciliates might influence lower trophic levels of the food web. Because of their endosymbionts, *Stentor* contributes significantly to the primary production: during the spring and autumn peak phases, the depth-integrated photosynthesis of *Stentor* amounted to $3–5\,\mathrm{mg\,C\,m^{-2}\,h^{-1}}$ or 20–25% of total primary production, respectively (Woelfl and Geller, 2002). Besides that contribution to primary production, they potentially ingest bacteria. Ciliates represent a significant trophic link between the microbial food web and metazoans and some are important grazers of bacteria (Porter et al., 1985; Sherr and Sherr, 1987). The protozooplankton of the Patagonian lakes is dominated by large ciliates which even can be more abundant than small ciliates (Woelfl and Geller, 2002), and also flagellates are found in low densities (Woelfl, 1995). Again, little is known about bacteria ingestion of *Stentor* in North Patagonian lakes. In a recent study, Modenutti et al. (2008) did not detect an ingestion of bacteria by *S. araucanus*. Thus, in the second part of the present study, we measured ingestion rates of bacteria by *Stentor* and compared them with bacterial production.

Material and methods

Organisms

Two mixotrophic ciliates of the genus *Stentor*, *S. amethystinus* and *S. araucanus*, were used. Most of the ciliates were *S. amethystinus* and their length ranged between 200 and 300 μm. The ciliates were collected from the epilimnion of the oligotrophic lakes, Lago Caburgua (39°07′S/71°45′W, Chile; surface area: 51.9 km^2, maximum depth: 327 m) and Lago Pirehueico (39°57′S/71°48′W, Chile; surface area: 30.5 km^2, maximum depth: 145 m), using a 55 μm plankton net. Ciliates were cultured in plastic pails (volume: 3.5 L) placed in flow-through basins (250 L). The water used in these basins came directly from the epilimnion of Lago Panguipulli and had a temperature between 12 and 20 °C. Four endemic fish species were investigated: *Cheirodon australe* (Characiformes; <6 cm long), *Galaxias maculates* (Osmeriformes; <16 cm long) whose juveniles feed on plankton (Cervellini et al., 1993), *Odontesthes mauleanum* (Atheriniformes; <30 cm long) feeding on plankton and chironomid larvae as juveniles (Klink and Eckmann, 1985), and *Percichthys trucha* (Perciformes; <50 cm long) mainly ingesting benthic insect larvae (Ruzzante et al., 1998). Juvenile fishes were collected at Lago Panguipulli (39°43′S/72°13′W,