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Ciliates and their picophytoplankton-feeding activity in a high-altitude warm-monomictic saline lake

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Abstract

The impact of feeding on autotrophic picoplankton (APP) on the ciliate composition of the assemblage was surveyed monthly along a depth gradient in the maar crater, athalassohaline, warm monomictic Lake Alchichica (Puebla, Mexico) from June 2003 to December 2005. Numbers of APP were evaluated from their autofluorescence. DAPI staining and the Fluorescently Labeled Bacteria technique were employed to count ciliates and estimate their feeding rates. A total of 38 taxa of ciliates have been identified using Quantitative Protargol Staining. Peritrichs followed by minute spirotrichs (particularly *Halteria grandinella*) often numerically dominated the ciliate assemblage and emerged as the most efficient APP feeders. A maximum of 54 ciliate cells ml⁻¹ was observed in the surface layer at the end of the mixing period, during the development of diatoms (*Cyclotella alchichicana*), the cyanobacterial bloom (*Nodularia* sp.) and its decay. Vorticellids (*Pelagovorticella natans*, *Vorticella* sp.) had the highest APP uptake (median 130 APP cil⁻¹ h⁻¹). Mixotrophic *Euplotes* cf. *daidaleos* were important APP grazers near the oxycline. Scuticociliates (*Cyclidium glaucoma*, *Uronema nigricans* and an anaerobic cf. *Isocyclidium globossum*), were numerically dominant within the hypolimnetic assemblages and did not ingest APP. Generally, APP were not an important food source for the majority of the ciliate assemblage, being positively selected by a few species during the APP decay in aerobic and microaerobic conditions.

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Introduction

Autotrophic picoplankton (APP) represent a potentially important carbon source for protists. According to

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various studies (e.g. James et al. 1996; Pernthaler et al. 1996; Šimek et al. 1995; Stabell, 1996), APP are positively selected from other picoplankton by fine-suspension feeding ciliates (*Halteria* spp., *Rimostrombidium brachykinetum*, *Cinetochilum margaritaceum*, etc.). Grazing has been identified as an important factor for the control of APP in many different water bodies (Callieri and Heinimaa, 1996; Callieri et al. 2002; Pernthaler, 2005; Pernthaler et al. 1996; Sherr and Sherr

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2002; Sherr et al. 1991; Šimek et al. 1995; Weisse 1993). Ciliates and heterotrophic nanoflagellates are also recognized as important consumers of APP in marine ecosystems (e.g., Christaki et al. 1999; Nakamura et al. 1995; Weisse 1993, 1996). However, other factors, such as light, temperature, nutrients and competition, can modulate the presence of APP in lakes [reviewed in (Stockner et al. 2000)]. There are very few studies that have considered the spatial and annual development of both ciliates and APP in oligotrophic, stratified water bodies in the tropics. APP, mostly picocyanobacteria, could form a very important part of the total picoplankton (TPP) biomass (Callieri and Bertoni 1999; Callieri and Stockner 2000; Padisak et al. 1997; Weisse 1993) especially in saline waters (Macek and Martínez Pérez 2002).

The use of fluorescently labeled particles (Sherr and Sherr 1993) has led to the discovery that free-living, microphagous plankton protozoa are ubiquitous components of pelagic food webs in freshwater and marine systems. Here they play an important role in the transfer of carbon from the picoplankton and nanoplankton to the metazoans (Callieri and Bertoni 1999; Pierce and Turner 1992; Sherr et al. 1991). The results were confirmed for APP by applying the dilution method to study the feeding budget (e.g., Dolan and Šimek 1999).

The importance of ciliates has been associated mainly with the microbial loop. There is increasing evidence that protists form a crucial step for phytoplankton control, consuming a wide spectrum of particles from bacteria-sized to large diatoms and dinoflagellates, as well as other ciliates. In the past few decades, much research effort has been devoted to finding factors that affect ciliate abundance, distribution and their trophic behavior in different environments. Among these factors, temperature and food availability, as well as predator density seem to be of paramount importance as bottom-up and top-down control factors, respectively (Levinsen et al. 2000; Verity 1985).

The aim of this study was to investigate the relationships between ciliate abundance, assemblage composition and one of their potential food sources – APP – along the depth, time, temperature and oxygen gradient. It is hypothesized that despite the physical and chemical changes in the water within the lake, other factors such as the availability and size class-distribution of food must also play an important role in the structure of ciliate assemblages.

Methods

Sampling site

We conducted the study in the large and deep maarcrater lake Alchichica (Puebla, Mexico) with extended

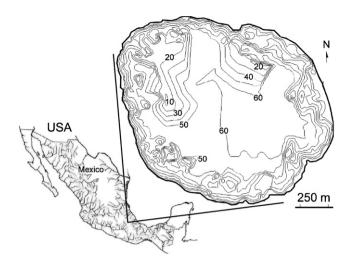


Fig. 1. Location and bathymetry of Lake Alchichica (according to Filonov et al. 2006), with depth contours in meters.

hypolimnetic anoxia. Lake Alchichica is situated at $19^{\circ}24'N$, $97^{\circ}24'W$ and $2340\,\mathrm{m}$ above sea level (Fig. 1). According to Lewis (1996) it is classified as tropical, warm and monomictic. Alchichica is deep (maximum depth $62\,\mathrm{m}$, mean depth $40.9\,\mathrm{m}$), with a surface area of $2.3\,\mathrm{km}^2$ and a volume of $9.4\times10^7\,\mathrm{m}^3$ (Filonov et al. 2006) of saline $(8.5\,\mathrm{g}\,\mathrm{l}^{-1})$ and alkaline (pH 9.5) water. Sodium and chloride dominate the ionic composition: $Na^+ > K^+ > Mg^{2+} > Ca^{2+}$ and $Cl^- > SO_4^{2-} > CO_3^{2-} > HCO_3^-$ (Vilaclara et al. 1993). Climate is dry and temperate, with a mean annual temperature of $12.9\,^{\circ}\mathrm{C}$, and mean annual precipitation of less than 400 mm (García 1980), concentrated in the rainy season (June–September). Due to the very small crater watershed, the lake level depends mainly on underground water inputs.

Due to the very steep walls of the crater, there is insignificant littoral vegetation. The lake phytoplankton biomass is dominated either by diatoms (*Cyclotella choctawhatcheeana*, *Cyclotella alchichicana*, *Chaetoceros elmorei*), chlorophytes (*Oocystis parva*, *O. submarina*) or filamentous cyanobacteria, *Nodularia* sp. (cf., Oliva et al. 2001, 2006). Among metazooplankton, rotifers and crustaceans are reduced to a few species: mostly the phytoplanktivorous calanoid copepod, *Leptodiaptomus novamericanus* (Lugo et al. 1999) and rotifers of the genera *Brachionus* and *Hexarthra*, which could feed upon ciliates. There are two endemic vertebrate species inhabiting the lake: the atherinid fish *Poblana alchichica alchichica* (Alvarez 1950) and the salamander *Ambystoma taylorii* (Brandon et al. 1981; Taylor 1943).

The sampling station was located above the maximum depth; three-bottle integrated samples (depth ± 1.5 m) were taken from the epilimnion, thermocline, maximum of chlorophyll a, the limit of anoxia or oxycline, and 1 m above the bottom, using a Niskin (USA) or IHE (Czech Republic) sampler. Subsamples of 500 ml from each layer were used for the experiments. Samples were taken

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