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Bottom-up versus top-down effects on ciliate community composition in four eutrophic lakes (China)

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Abstract

Previous studies have shown that ciliate plankton is generally controlled by food resources (e.g., algae) and predators (e.g., metazooplankton). Among lakes with similar trophic levels but different distributions of phyto- and metazooplankton, the main forces acting on ciliate assemblages may be different. We investigated the relationship between ciliate communities and bottom-up versus top-down variables based on a survey of four subtropical eutrophic lakes (China). Two of the lakes (Chaohu, Taihu) are located on the Mid-lower Yangtze Plain near sea level, and the other two (Dianchi, Xingyunhu) on the Yunnan-Kweichow Plateau at 1700 m above sea level. Blooms of cyanobacteria developed during summer in Lakes Chaohu and Taihu and throughout the year in Lakes Dianchi and Xingyunhu. Ciliate functional feeding groups differed significantly between lakes. The results of canonical correspondence analysis (CCA) and variation partitioning showed that cyanobacteria significantly influence ciliate species, whereas 'edible' algae (cryptophytes, diatoms) and cladocerans were the important variables in explaining the ciliate community structure of Lakes Dianchi and Xingyunhu compared with Lakes Taihu and Chaohu. Our results highlight the importance of consistent cyanobacterial blooms in shaping the ciliate community in subtropical eutrophic shallow lakes by interacting with top-down and bottom-up factors.

Keywords: Bottom-up effects; Ciliates; Cyanobacterial blooms; Heterotrophic nanoflagellates; Metazooplankton; Top-down control

Introduction

Ciliates, which are a large group of unicellular heterokaryotic organisms, play an important role in both lacustrine freshwater and marine environments (Beaver and Crisman 1989; Montagnes et al. 2010; Porter et al. 1985; Sherr et al. 1986; Weisse 2003). Due to their powerful consumption of auto- and heterotrophic pico- and nanoplankton (Burian et al. 2013) and their role as food for metazooplankton groups, ciliates are indispensable linkages in transferring primary production to high trophic levels (Agasild et al. 2012; Kamjunke et al. 2012; Rollwagen-Bollens et al. 2013; Sherr et al. 1986).

The food resources of ciliates, notably small bacteria (Hahn and Höfle 2001), algae (Burian et al. 2013; Zingel et al. 2007), other picoplankton and debris (Kalinowska et al. 2013), are important factors influencing ciliate community dynamics ('bottom-up-control'). First, food limitations suppressing ciliate numbers exist in some oligotrophic and mesotrophic lakes (Galbraith and Burns 2010; Sommaruga

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and Psenner 1993). Further, food quality directly influences ciliate growth and species composition (Andrushchyshyn et al. 2006; Combes et al. 2013). According to Combes et al. (2013), some ciliate species were able to consume toxic cyanobacteria, but they displayed slower growth rates than did ciliates feeding on non-toxic cyanobacteria strains. Andrushchyshyn et al. (2006) attributed ciliate species composition differences in two ponds in Canada to the differing food availability.

The suppressive impact on ciliates by zooplankton groups (‘top-down control’) has been observed both in laboratory study (Dhanker et al. 2013; Weisse and Frahm 2002) and in in situ experiments (Agasild et al. 2013; Ventelä et al. 2002). One of the most important planktonic grazers in freshwater lake systems is the *Daphnia* group (Gilbert 1989; Jack and Gilbert 1994; Jürgens 1994; Pace and Funke 1991; Zöllner et al. 2003). *Daphnia* has well-known strong predation effects on microbial components ranging from bacteria to organisms as large as 50 μm (Gaedke and Straile 1998; Ventelä et al. 2002; Zöllner et al. 2003). Due to their variable cell size, ciliates and nanoflagellates can meet the size-selected food needs of *Daphnia* species (Zöllner et al. 2003). However, in a mesotrophic lake (Lake Mahinerangi, New Zealand), the suppression effect on ciliate abundance has only been observed when *Daphnia* was present at more than 330 $\mu g\,L^{-1}$ (Burns and Schallenberg 1996). Small-bodied cladocerans, specifically *Bosmina* (Agasild et al. 2012) and *Chydorus* (Ventelä et al. 2002), have also produced detectable suppression effects on ciliates in eutrophic lakes. Several studies have documented that copepods sharply suppress ciliate abundance in marine systems (Berk et al. 1977; Dhanker et al. 2013). The copepods–ciliates link in freshwater food webs has also been examined, and copepod predation has been identified as an important controlling factor for the ciliate community (Sanders and Wickham 1993; Jürgens and Jeppesen 2000; Zingel et al. 2016).

Predators and food antagonistically influence ciliate assemblages. Generally, increasing ciliate abundance has been associated with an increase in available food supply, whereas a decreasing ciliate number is associated with increased predators. Previous research on the regulation mechanisms of planktonic ciliates and other protists in freshwater lake systems suggests that the bottom-up effect (food supply) is strong and the top-down effect is weak in oligotrophic waters (Conty et al. 2007; Galbraith and Burns 2010), whereas with an increasing trophic level, top-down control by metazooplankton is strengthened (Sanders and Wickham 1993); in eutrophic waters, top-down control is more important than bottom-up effects (Jürgens et al. 1999). Blooms of cyanobacteria are common in eutrophic lakes worldwide; however, less knowledge exists concerning the role of cyanobacterial blooms and their interactions with top-down and bottom-up forces on ciliates.

In this study, we performed a survey in four shallow, eutrophic lakes that are currently in a turbid stable state (China), where submerged macrophytes were absent and intensive blooms of cyanobacteria (mainly *Microcystis*) occurred. The ciliate community in each lake was monitored at three time points between July 2009 and April 2010 by quantitative protargol staining (QPS). Physicochemical and biotic parameters were also analyzed. The aims were (1) to clarify the variations in ciliate functional feeding groups (e.g., algivores, bacterivores, mixotrophs) and (2) to test the relative importance of top-down (predators) and bottom-up (food) factors. In particular, the potential effect of cyanobacteria was emphasized.

Material and Methods

Study site and sampling

Lakes Taihu (TH, 30°55′40″–31°32′58″N, 119°52′32″–120°36′10″E), Chaohu (CH, 31°25′–31°43′N, 117°16′–117°5′E), Dianchi (DC, 24°40′–25°2′N, 102°36′–102°47′E), and Xingyunhu (XYH, 24°17′–24°23′N, 102°45′–102°48′E) are four subtropical eutrophic shallow lakes in China. CH and TH develop blooms of cyanobacteria (mainly *Microcystis*) in summer, while DC and XYH experience persistent blooms throughout the year (Chen et al. 2003; Deng et al. 2007).

Four fixed locations (pelagic zone) were sampled in each lake in July and December 2009 and in April 2010. Considering the vertical distribution of cyanobacteria, six water samples for each lake at each sampling occasion were collected separately: samples from the surface layer of all sites and an additional sample at a 2-m depth at two of the four locations. For each water sample, 20 L of water was mixed before subsampling using an improved Patalas sampler (50 cm length, volume 5 L). A subsample of 1 L was fixed with Bouin’s solution for the analysis of ciliates (5% final concentration). A subsample of 30 mL was fixed with formalin solution (2% final concentration) to analyze bacterioplankton and heterotrophic nanoflagellates (HNFs). For the analysis of phytoplankton and rotifers, a subsample of 1 L was fixed with Lugol’s solution (1% final concentration). A subsample of 10 L was filtered through a 63-μm mesh size filter, concentrated to 50 mL, and preserved in 4% (v/v) formalin solution for the analysis of crustaceans. For quantification of the other parameters (nitrogen, phosphorus, and chlorophyll *a*), an untreated 2 L subsample was transported as soon as possible to the laboratory in a cooler box. The water temperature, pH, turbidity, and conductivity were then measured in situ using a YSI multiparameter probe (YSI 6600).

Sample Analyses

Chemical analyses

The chlorophyll *a* (chl *a*) concentration was measured by filtering 50–200 mL of lake water on a Whatman GF/F filter (equivalent 0.7 μm glass fiber filter). The filters were then placed in 90% acetone solution for 24 h for chl *a* extraction,