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ORIGINAL ARTICLE

The trophic role and impact of plankton ciliates in the microbial web structure of a tropical polymictic lake dominated by filamentous cyanobacteria

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ABSTRACT

*The recent interest in the plankton structures and dynamics in tropical and subtropical lakes has revealed important trends that set these lakes apart from temperate lakes, and one of the main differences is the enhanced importance of the microbial food web with respect to net plankton. Ciliates are a key component of subtropical and tropical microbial webs because of their role as dominant picoplankton grazers and their ability to channel picoplankton production to the uppermost trophic levels. Plankton ciliates have been found to play a crucial role in the survival of fish larvae in lakes that share several features with Lake Catemaco, a eutrophic tropical Mexican lake. Therefore, the plankton ciliate composition, abundance, and biomass of Lake Catemaco were studied to assess their role in the microbial food web. The data were obtained from surface and bottom water samples collected at eleven points during three surveys in 2011 and an additional survey in 2013, with the surveys covering the local climatic seasons. The most abundant components of the plankton ciliate assemblages were small prostomatids (*Urotricha *spp.), choreotrichs (*Rimostrombidium *spp.), cyclotrichs (*Mesodinium *and* Askenasia*), and scuticociliates (*Cyclidium*,* Cinetochilum*,* Pleuronema*, and* Uronema*). Other important ciliates in terms of abundance and/or biomass were haptorids (*Actinobolina*,* Belonophrya*,* Monodinium*,* Paradileptus*, and* Laginophrya*),* Halteria*, *oligotrichs (*Limnostrombidium* and *Pelagostrombidium*),* Linostomella*,* Bursaridium*,* Cyrtolophosis*, and* Litonotus*. The ciliate abundance averaged 57 cells mL^{-1} and ranged from 14 to 113 cells mL^{-1}. The mean ciliate biomass was 71 μg C L^{-1} and ranged from 10 to 202 μg C L^{-1}. Differences were not detected in ciliate abundance or biomass between the sampling points or sampling depths (surface to bottom); however, significant differences were observed between seasons for both variables. Nano-sized filamentous cyanobacteria were the most abundant component of the plankton, and their abundance was assessed through epifluorescence microscopy counts. The autotrophic and heterotrophic picoplankton abundance was measured through epifluorescence, and their abundance and biomass were higher at the study site relative to other shallow freshwater ecosystems. The total ciliate biomass distribution patterns were similar to those of filamentous cyanobacteria and autotrophic or heterotrophic picoplankton, although the nanociliate biomasses peaked when the picoplankton and filamentous cyanobacteria were least abundant. The consequences of this increased importance of ciliates on the structure of the plankton at Lake Catemaco will be discussed along with the probable causes.*

Key words: Cylindrospermopsis*; eutrophic; microbial food web; nanociliates; picoplankton.*

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INTRODUCTION

Recently, microbial communities in shallow tropical lakes have received increasing attention (Sarmento, 2012), and their key importance to the structure and function of temperate lake ecosystems has been acknowledged. The microbe-related changes occurring in these lakes are relevant because of their impact on water quality and their likely increase through climate change in particular (Kosten *et al.,* 2012). Ciliates have the potential to play a pivotal role in these processes because of their ability to control harmful algal blooms (Davis *et al.,* 2012) and act as an interface between picoplankton and mesozooplankton (Sherr and Sherr, 2002).

Lake Catemaco is a eutrophic tropical lake that has suffered from the impacts of human activities, particularly over the last forty years. The limnological records on the conditions of the lake prior to 1980 are scarce as to determine whether the current plankton communities are the product of environmental degradation or normal ontogenetic stages. Catemaco is an important lake in the country based on its fisheries and biological productivity (Torres-Orozco and Pérez-Rojas, 1995) as well as the presence of endemic fish species (Miller and Van Conner, 1997). The local social and economic welfare largely depend on the lake's health; thus, it is important to monitor its condition. The microbial food web components in this lake have not been previously investigated. The only well-described feature is the domination of the microbial web and the entire pelagic environment at Catemaco by filamentous cyanobacteria (Komárková and Tavera, 1996). The relative importance of ciliates appears to be higher in polymictic lakes where these cyanobacteria are abundant than in other temperate lakes (Zingel *et al.*, 2007). Moreover, the ciliate importance to the food web increases with higher primary productivity (Sherr and Sherr, 2002), although it remains to be shown if this relationship holds true for tropical lakes, such as Catemaco.

The nature of lacustrine trophic microbial web components and their interactions have been studied for temperate lakes with different trophic statuses (Straškrabová *et al.*, 1999; Pfister *et al.*, 2002; Auer *et al.*, 2004; Chróst *et al.*, 2009; Agasild *et al.*, 2013; Van Wichelen *et al.*, 2013), including eutrophic temperate lakes affected by cyanobacterial blooms (Moustaka-Gouni *et al.*, 2006; Zingel *et al.*, 2007; Zingel and Nõges, 2010), shallow soda lakes of Africa (Burian *et al.*, 2013), relatively shallow eutrophic lakes, deep oligotrophic tropical lakes of Eastern Africa (Yasindi and Taylor, 2003), deep athalassohaline lakes of North America (Macek *et al.*, 2008; Peštová *et al.*, 2008), and shallow subtropical lakes with differing trophic statuses (Beaver and Crisman, 1989; Beaver and Crisman, 1990; Gomes and Godinho, 2003; Machado-Velho *et al.*, 2005; Havens *et al.*, 2007; Bagatini *et al.*, 2013; Machado-Velho *et al.*, 2013). These studies have demonstrated that microbial food webs, particularly the composition, abundance, biomass and diversity of ciliates, present specific responses to the geographic, climatic and ecological features of different lakes and reservoirs. A meta-analysis has shown that the trends observed in temperate lakes cannot be extrapolated to tropical lakes. Small forms of plankton dominate tropical lake communities, and their presence corresponds to a diminished efficiency in biomass transfer to the uppermost trophic levels (Sarmento, 2012). Microbial webs are more important in tropical lakes and filamentous cyanobacteria-dominated lakes (Davis *et al.*, 2012), a condition that has obvious impacts on fisheries. Torres-Orozco and Zanatta (1998) reported low densities of net zooplankton for Catemaco that are dominated by rotifers, including genera reported as potential competitors or predators of small ciliates (Sanders *et al.*, 1994; Weisse and Frahm, 2002). Catemaco's depauperated net zooplankton and profuse filamentous cyanobacteria growth may affect the prey-predator interactions among microbial web components. The prevailing conditions at Catemaco indicate the enhanced importance of microbial webs, particularly of the plankton ciliate assemblages. Plankton ciliates drive biomass from autotrophic and heterotrophic picoplankton to upper trophic levels; therefore, the abundance of autotrophic and heterotrophic picoplankton abundance was simultaneously recorded. Based on their size and other features, plankton ciliates are the most likely food source for first-feeding larvae of fish species that support local fisheries, and because this stage is considered critical in fish life cycles, the maintenance of fish stocks depends on ciliates (Zingel *et al.,* 2012). The selective filter-feeding activity of these fish species is believed to be at least partially responsible for Catemaco's plankton composition (Kormákova and Tavera, 2003). Therefore, the composition, abundance, and biomass of plankton ciliates were studied to assess their trophic role in the microbial food web of Lake Catemaco and determine how the ciliate assemblages respond to tropical, eutrophic, and polymictic environments that are dominated by filamentous cyanobacteria and impacted by human activities.

METHODS

Study site

Lake Catemaco is delimited by the coordinates 18°17' to 18°21' N and 95°01' to 95°07' W (Fig. 1), and it is located next to Los Tuxtlas, the last stand of what was once an extensive tropical forest, which is 20 km from the Gulf of Mexico at an altitude of 332 m a.s.l. Catemaco is a eutrophic lake, volcanic in origin and has a main length of 12.32 km and a maximum width of 10.25 km, with an area of 72.5 km^2 (Pérez-Rojas and Torres-Orozco, 1992). The mean depth is 7.6 m, and the volume is 5.23×10^8 m^3. The profile of the lake resembles that of a pan with a relative depth of z_r=0.23%, which results in water column instability and frequent mixing by the winds blowing through this region. Brief stratification events generally occur in October (Torres-Orozco *et al.*, 1996).

Three seasons occur in this region: a rainy season from July to October, a north winds season from November to March, and a dry season from April to June. The average rainfall is at least 2000 mm per year, and it primarily occurs from July to October, although the north winds are occasionally associated with rain. Catemaco's only drain is through the Rio Grande de San Andrés at its northwestern shore. Tavera (1996) estimated an average water retention time of 0.875 years for Lake Catemaco during the period from 1991-1994. The catchment basin surrounding this eutrophic lake was originally covered by tropical forest; however, with the exception of stands at its eastern shore, the area has been cleared for agricultural, livestock husbandry or urban purposes. Although raw sewage from the town of Catemaco is not discharged into the lake, heavy rainfall results in overflow from the sewer system into the lake (Esquivel *et al.*, 2009).

Sample collection

For sample collection, ten points were set at the lake's periphery and a further point was located at the lake's center. Water samples were collected with a 2 litre van Dorn sampler in March (north winds season), May (dry season) and October (rainy season) 2011 and May 2013 (dry season) at 0.3 m from the surface and 0.3 m above the bottom. One hundred millilitre aliquots were drawn, with one aliquot fixed with 0.2-µm-filtered formalin to a final concentration of 2% for epifluorescence (Kepner and Pratt, 1993; Straškrabová *et al.*, 1999) and another fixed with 2% acid Lugol's iodine solution for plankton counting under an inverted microscope. The samples for the quantitative protargol stain (QPS) were fixed with Bouin's fixative at a final concentration of 7% (Montagnes and Lynn, 1987).

Light measurements were not performed, but the Poole and Atkins equation (Idso and Gilbert, 1974) was employed to calculate the average extinction coefficient for water from the Secchi disk depth (Idso and Gilbert, 1974). This value was then used to determine the depth at which 1% of the incident light would occur.

The physical, chemical and biological variables were measured, including the temperature, conductivity, Secchi disk depth, pH, dissolved oxygen (Winkler's method; APHA *et al.*, 1992), nitrate-N, nitrite-N, ammonia-N, soluble reactive phosphorus (SRP) were spectrophotometri-

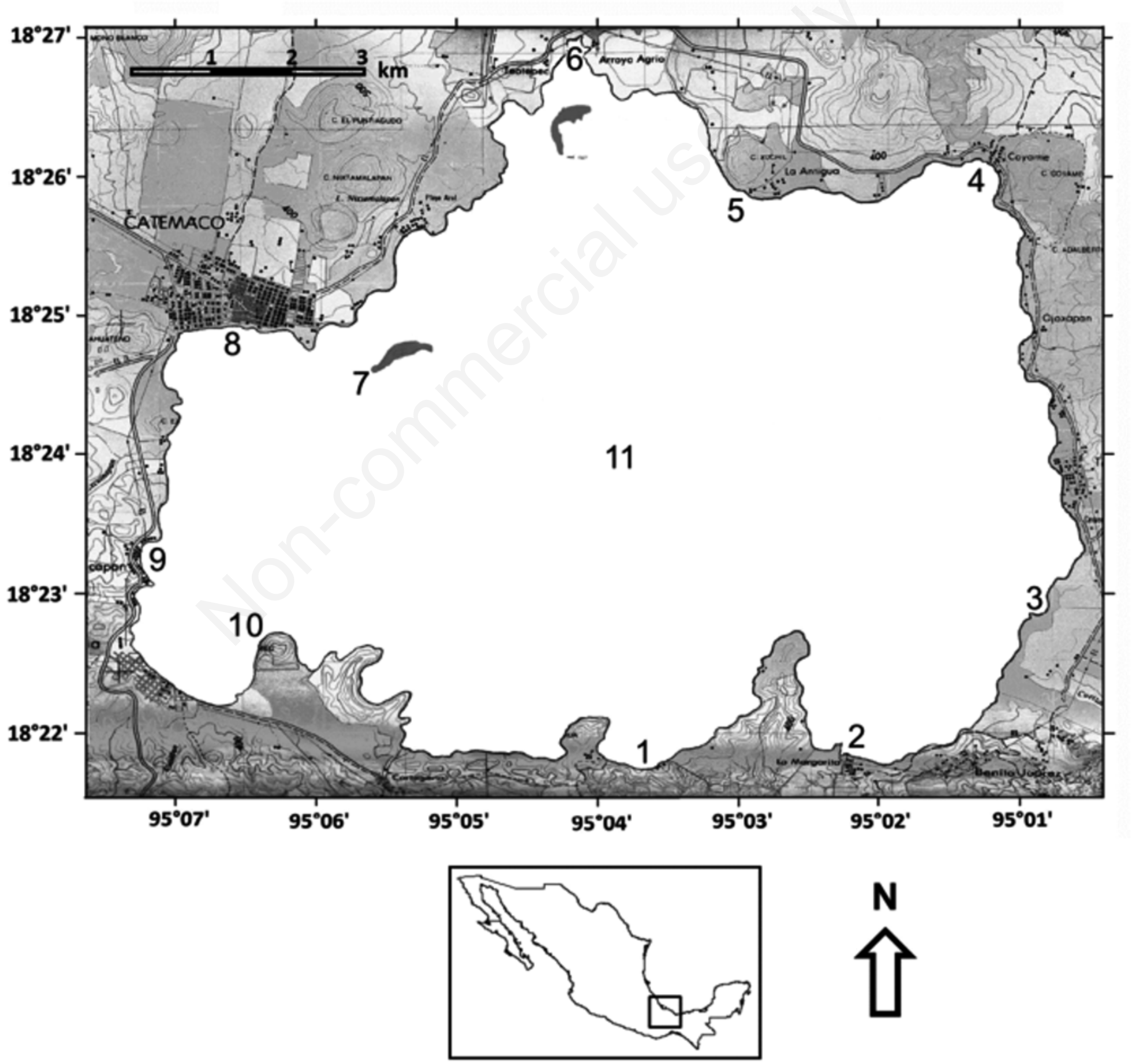

Fig. 1. Lake Catemaco. Location and sampling points.

cally measured (APHA *et al.*, 1992), and total P, which was measured after a sodium persulphate digestion. The soluble inorganic N:P ratios were calculated from these measurements, and chlorophyll *a* was assessed spectrophotometrically using the trichromatic method described by Jeffrey and Humphrey (1975).

Prokaryote enumeration

Sample processing was performed according to the Kepner and Pratt (1993) method through filtering on 0.22 µm black polycarbonate membranes and staining with DAPI (4',6-diamidino-2-phenylindole) (Porter and Feig, 1980). Prokaryotes, including filamentous cyanobacteria, were enumerated from counts of at least 400 cells from a minimum of 20 fields (Straškrabová *et al.*, 1999) under an Olympus BX53 epifluorescence microscope using a DAPI filter set (emission 420 nm, excitation 330-385 nm, and dichroic mirror 400 nm) for heterotrophic picoplankters and a chlorophyll filter set (emission 510 nm, excitation 460-495 nm, dichroic mirror 505 nm).

Ciliate identification, abundance and biovolume

Ciliates were identified to the least possible taxonomic level from QPS slides based on the methodology of Dragesco *et al.* (1986), Foissner and Berger (1996), and Foissner *et al.* (1999) and arranged according to the system of Lynn (2008). Other relevant information, such as the feeding habits, food source preferences, habitat and distribution, was determined from these sources.

Samples fixed with Bouin's fixative were passed through 3-µm mixed cellulose-ester filters and then QPS stained (Montagnes and Lynn, 1993; Skibbe, 1994). These slides were completely scanned to identify, count and measure the ciliates; however, the ciliate counts and biovolumes are reported for the samples fixed in Lugol's iodine because the counts and morphotype number were smaller in the QPS-stained samples. The Lugol's iodine-fixed samples were homogenized and placed into 10-mL Utermöhl's sedimentation chambers and allowed to settle for 24 h (Hasle, 1978). They were then analyzed with a Zeiss Axiovert 25 CFL inverted microscope at 400× magnification. One-half of the chamber bottom was observed for ciliate enumeration. At least 30 organisms were measured for each morphotype to calculate their biovolumes by comparing their forms to those of standard geometrical bodies (Hillebrand *et al.*, 1999). The factor 190 fg C μm^{-3} for the Lugol's iodine-fixed samples (Putt and Stoecker, 1989) was employed to calculate the biomass from the biovolume because this factor considers the ciliate shrinkage of the fixed samples (Gifford and Caron, 2000). The ciliate biomasses were further divided into total ciliates and nanociliates.

Statistical analysis

A non-parametric Kruskal-Wallis analysis of variance (ANOVA) was employed to detect the significant differences in the abundance and biomass associated with factors such as the season, sampling points, and sampling depth because the conditions for a parametric ANOVA, including a normal data distribution and homoscedasticity (Sokal and Rohlf, 2012), were not met. A pairwise Tukey's HSD test was employed as a *post-hoc* test to determine the cases with significant differences. These tests were performed with the software Statistica 7 (StatSoft, Tulsa, OK, USA).

RESULTS

Physico-chemical and ecological background

Windy conditions occurred during the surveys except for those in the dry season of 2013. The water temperature was ≥22°C and ≤30°C for the survey period. The average Secchi disk depth was 0.77 m; thus, the euphotic zone consisted of a depth to z_{eu}=2.2 m. Therefore, because the lake's mean depth is 7.6 m, a sizable fraction of the lake's water would receive less than 1% of the surface light.

The total ammonia content ranged from non-detectable values up to 5.21 µM, to 2.86 µM for nitrite, and to 1.60 µM for nitrate. The SRP concentrations varied from 0.26 µM to 63.63 µM, significant differences in SRP, detected through Kruskal-Wallis ANOVA occurred among surveys (H=49.25, P<0.0001) but not among sampling depths (H=0.87, P=0.352). The N:P ratios were ≤2.40 for the three 2011 surveys and up to 8.53 were attained for the dry season of 2013, although the values for 2013 were also likely indicative of N limitations. Significant differences for N:P ratios between the surveys were detected through the Kruskal-Wallis ANOVA (H=54.48, P<0.0001), whereas no differences were detected between sampling depths (H=0.87, P=0.35). The increased N:P ratio during the dry season of 2013 was caused by a decrease in the SRP rather than the higher concentrations of DIN species (Tab. 1).

The chlorophyll *a* concentrations ranged from 2 to 154 µg L^{-1} (Tab. 1). The Kruskal-Wallis ANOVA detected significant differences among surveys (H=23.00, P<0.0001), but not significant among sampling depths (H=0.45, P=0.504). The lowest values occurred during the rainy season of 2011, and the highest values of 154 µg L^{-1} and 130 µg L^{-1} occurred at the bottom in the south region of the lake and at the surface center during the dry season of 2011, respectively. In addition to the ever-dominant *Cylindrospermopsis* (Seenayya and Subbaraju, 1972), the most abundant phytoplankton organisms were the chain-forming diatom *Aulacoseira granulata* (Ehrenberg) (Simonsen, 1979) and the filamentous cyanobacteria *Planktolyngbya regularis* (Kormákova and Tavera, 1996). The small pennate diatoms *Cymbella minuta* (Hilse, 1862), *Navicula exigua* (Patrick, 1945) and *Gomphonema* spp. (Ehrenberg, 1832) were also abundant. The most abundant metazoan plankton included rotifers of the genera *Brachionus* (Pallas, 1776), *Keratella* (Bory De St. Vincent, 1822), *Trichocerca* (Lamarck, 1801), and *Hexarthra* (Schmarda, 1854).

Prokaryote abundances

The bacterial abundances were 2.37×10^5 cells mL^{-1} to 5.47×10^6 cells mL^{-1}, and definite distribution patterns were not observed for the surveys (Kruskal-Wallis test H=3.44, P=0.97 for the sampling points). However, the abundance significantly differed between the survey seasons (H=62.61, P<0.0001) and had higher values during the north wind season of 2011 and the dry season of 2013, a trend that was also observed for the picocyanobacteria and filamentous cyanobacteria. For both the surface and bottom samples, the lowest bacterial densities were found throughout the lake during the rainy season of 2011, whereas higher densities occurred during the north wind season of 2011 and the dry season of 2013; the same pattern occurred for picocyanobacteria and filamentous cyanobacteria (Fig. 2).

The bacterial densities did not differ between the surface and bottom samples (H=0.42, P=0.51), and this was also observed for the remaining microbial web components. The picocyanobacteria abundance ranged from 1.27×10^4 mL^{-1} to 8.05×10^5 mL^{-1} and presented the same trend as that of the filamentous cyanobacteria (see below), which had abundances that were noticeably lower in the dry and rainy season (in particular) of 2011 compared with that of the north wind season of 2011 and the dry season of 2013 (H=66.04, P<0.0001). Spatially, definite patterns were not observed except for the lower abundances at the northernmost sampling point (6) and occasionally at the lake center (11) (H=2.01, P=0.996 for sampling points; H=0.32, P=0.57 for sampling depths) (Fig. 2). The filamentous cyanobacteria abundance ranged from 3.64×10^3 to 7.08×10^5 trichomes mL^{-1} and density varied by approximately 100 fold from the dry and rainy seasons of 2011 to the bloom conditions in the north wind season of 2011 and the dry season of 2013 (H=62.23, P<0.0001). These filamentous cyanobacteria are N-fixing nanoplanktic filamentous cyanobacteria, mostly from the *Cylindrospermopsis* genus. The most abundant was *Cylindrospermopsis catemaco*, which presents 2 to 4 cells per trichome (Komárková and Tavera, 1996). Differences were not detected between sampling points (H=6.33, P=0.79) or sampling depths (H=0.07, P=0.80) (Fig. 2).

Tab. 1. Physical, chemical and biological data for each survey and sampling depth.

	North winds 2011 Surface	North winds 2011 Bottom	Dry 2011 Surface	Dry 2011 Bottom	Rainy 2011 Surface	Rainy 2011 Bottom	Dry 2013 Surface	Dry 2013 Bottom
Temperature (°C)	23.9 23.0-25.0	24.0 22.0-29.0	28.1 25.1-30.0	28.3 25.8-29.7	25.2 24.7-26.0	25.0 24.5-25.5	25.2 24.0-26.0	25.2 24.0-27.0
Secchi disk depth (m)	0.82 0.67-1.20		0.66 0.55-0.73		0.82 0.50-1.34		0.80 0.53-1.13	
z_{eu} (m)	2.3 1.9-3.3		1.9 1.6-2.0		2.3 1.4-3.6		2.2 1.5-3.1	
pH	8.15 7.2-9.0	7.75 7.2-8.3	7.59 6.6-8.3	7.45 6.3-8.4	6.83 6.6-7.2	6.90 6.4-7.5	7.36 6.9-8.0	7.42 7.0-7.9
Dissolved oxygen (mg L^{-1})	5.9 2.2-8.0	5.4 3.9-9.3	4.1 3.0-6.7	3.7 2.6-4.8	7.2 5.1-8.6	6.8 3.3-8.2	4.5 2.4-7.1	3.6 0.0-6.4
NH_3-N (µM)	1.40 0.00-2.16	1.39 0.21-2.86	1.61 0.04-5.21	2.21 0.47-3.74	0.35 0.16-0.57	0.52 0.19-0.96	0.69 0.09-1.57	0.60 0.00-1.65
$^{-}NO_2$-N (µM)	0.23 0.00-0.85	0.21 0.00-0.84	0.38 0.02-1.03	0.37 0.00-1.02	0.28 0.03-0.82	0.30 0.01-0.80	1.09 0.00-2.38	0.41 0.11-1.02
$^{-}NO_3$-N (µM)	0.06 0.00-0.17	0.06 0.00-0.15	0.03 0.00-0.09	0.06 0.00-0.18	0.54 0.16-1.07	0.52 0.17-1.60	0.01 0.00-0.03	0.01 0.00-0.05
SRP (µM)	3.19 1.28-10.26	9.00 1.33-44.18	3.62 1.38-11.68	2.28 0.63-4.16	27.29 0.97-63.63	14.02 1.10-61.63	0.32 0.27-0.38	0.32 0.26-0.40
N:P	0.75 0.04-2.00	0.52 0.10-1.34	0.68 0.09-1.10	1.23 0.73-1.71	0.40 0.01-1.31	0.66 0.02-2.40	5.46 3.32-7.36	5.67 2.62-8.58
Chlorophyll *a* (µg L^{-1})	62 20-100	62 17-101	97 25-130	99 13-154	60 22-97	60 2-101	70 10-97	82 45-109

The data include the mean, minimum and maximum for each variable.

Ciliate identification

Twenty-eight morphotypes were identified to the genus level, and they belonged to 18 orders (Tab. 2). Small choreotrichs, cyclotrichs, prostomatids, and scuticociliates were the most abundant forms in the assemblage containing algivorous heterotrichs, such as *Linostomella*, predaceous forms, such as *Paradileptus* and *Litonotus*, and organisms with other feeding strategies. The individual sizes ranged from 13 µm to over 150 µm in length.

Ciliate abundance

The ciliate abundance ranged from 14 cells mL^{-1} to 113 cells mL^{-1}, and the average for the entire survey period was 57 cells mL^{-1}. Differences were not detected between sampling points (H=10.70, P=0.38) or sampling depths (H=0.10, P=0.75), although highly significant differences were observed between survey seasons (H=46.92, P<0.0001). The ciliate abundances were higher during the rainy season of 2011 and particularly high during the dry season of 2013. The average abundance for the first two surveys was 40 cells mL^{-1}, whereas the abundance for the last two surveys was 74 cells mL^{-1}. This pattern is inconsistent with what was found for prokaryotes because the rainy season survey of 2011 presented low abundances and the north wind season survey of 2011 presented high abundances.

Ciliate biomass

The total ciliate biomass varied from 10 µg C L^{-1} to 202 µg C L^{-1}. The Kruskal-Wallis ANOVA indicated significant differences between sampling points (H=19.00, P=0.04), whereas Tukey's pairwise HSD test resulted in marginal differences (P=0.07 and Pp=0.06 for sampling points 1 and 2 and to point 10, respectively). The biomasses increased in October 2011 and especially in May 2013 (H=20.27, P<0.0001); however, significant differences were not observed for the sampling depth (H=1.25, P=0.26) (Fig. 3).

Tab. 2. Ciliate genera, arranged according to Lynn (2008).

Order Heterotrichida Stein, 1859	*Linostomella* Aescht in Foissner, Berger & Schaumberg, 1999
Order Euplotida Small & Lynn, 1985	*Euplotes* Ehrenberg in Hemprich & Ehrenberg, 1831
Order Choreotrichida Small & Lynn, 1985	*Rimostrombidium* Jankowski, 1978
Order Stichotrichida	*Hypotrichidium* Ilowaisky, 1921
Order Sporadotrichida Fauré-Fremiet, 1961	*Halteria* Dujardin, 1841
Order Strombidiida Petz & Foissner, 1992	*Limnostrombidium* Krainer, 1995 *Pelagostrombidium* Krainer, 1991
Order Haptorida Corliss, 1974	*Actinobolina* Strand, 1928 *Belonophrya* André, 1914 *Monodinium* Fabre-Domergue, 1888 *Paradileptus* Wenrich, 1929 *Lagynophrya* Kahl, 1927
Order Pleurostomatida Schewiakoff, 1896	*Litonotus* Wrzesniowski, 1870
Order Cyclotrichiida Jankowski, 1980	*Askenasia* Blochmann, 1895 *Mesodinium* Stein, 1863
Order Dysteriida	*Trochilia* Dujardin, 1841
Order Bursariomorphida Fernández-Galiano, 1978	*Bursaridium* Lauterborn, 1894
Order Colpodida de Puytorac *et al.*, 1974	*Colpoda* O.F.Müller, 1773
Order Cyrtolophosidida Foissner, 1978	*Cyrtolophosis* Stokes, 1885
Order Prorodontida Corliss, 1974	*Balanion* Wulff, 1919 *Pelagothrix* Foissner, Berger & Schaumberg, 1999 *Urotricha* Claparède & Lachmann, 1859
Order Peniculida Fauré-Fremiet in Corliss, 1956	*Frontonia* Ehrenberg, 1838
Order Philasterida Small, 1967	*Cinetochilum* Perty, 1849 *Uronema* Dujardin, 1841
Order Pleuronematidae Fauré-Fremiet in Corliss, 1956	*Cyclidium* O.F. Müller, 1773 *Pleuronema* Dujardin, 1841
Order Sessilida Kahl, 1933	*Pelagovorticella* Jankowski, 1980

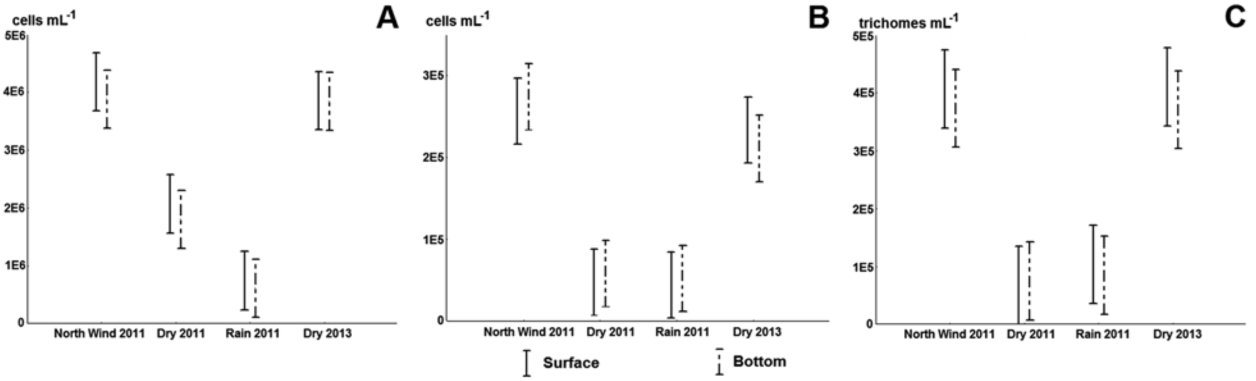

Fig. 2. Confidence intervals (0.95) of the mean for heterotrophic and autotrophic picoplankton (cells mL^{-1}) and filamentous cyanobacteria (trichomes mL^{-1}) per survey and sampling depth. A) Bacteria. B) Picocyanobacteria. C) Filamentous cyanobacteria.

Nanociliates were defined as those with a maximum length ≤20 µm. The nanociliate biomass ranged from 1.9 µg C L^{-1} to 28.2 µg C L^{-1}, which was approximately 10% of the total ciliate biomass. Differences were not observed between sampling points ($H=9.40$, $P=0.49$) nor sampling depths ($H=2.54$, $P=0.11$); however, the differences between surveys were highly significant ($F=18.94$, $P<0.0001$). Based on Tukey's HSD, significant pairwise differences were found between the bottom samples from the dry season of 2013 and the surface and bottom samples from the north wind season of 2011 ($P=0.013$ and $P<0.0001$, respectively) as well for the bottom samples from the rainy season of 2011 ($P=0.001$) (Fig. 3). In addition to the general trends, ciliate biomass can also be described in more specific terms. The ciliate size was more important than the abundance for determining the total biomass per sample, which was demonstrated by the proportion of nanociliate biomass to the total ciliate biomass.

The morphotype biomass was pooled by group to provide a synoptic representation of the biomass (Fig. 4). Regardless of whether differences occurred between sampling points or sampling depths for the total and nanociliate biomass, the more detailed representation showed the differences between all of these factors. Despite their abundance, scuticociliates and small prostomatids provided a low contribution to the total ciliate biomass because of their small size. Scuticociliates were less abundant in the surface and bottom samples from the north wind season and reached their peak values of approximately 10 µg C L^{-1} at a point northeast of the lake during the rainy season (Fig. 4). The prostomatids were least abundant at the surface and bottom during the dry season of 2011 and reached their peak values of approximately 20 µg C L^{-1} in a bottom sample from the north wind season in a southwest region of the lake (Fig. 4).Choreotrichs were more abundant when picoplankton densities were high, *i.e.* the north wind season 2011 and the dry season 2013, and were particularly rare in the dry season 2011 (Fig. 4). In the north wind season, choreotrichs and oligotrichs presented higher biomass (close to 10 µg C L^{-1}) in the surface samples, whereas in the dry season of 2013, the highest values occurred in the bottom samples, particularly at a point west of the lake for oligotrichs, which reached 15 µg C L^{-1} (Fig. 4). Low cyclotrich biomass was observed in the surface samples from the north wind season, and the peak biomass of 40 µg C L^{-1} was observed at a point south of the lake, and the lowest biomass in the bottom samples occurred during the dry and rainy seasons of 2011, whereas the maximum biomass of 30 µg C L^{-1} occurred at a point in the northeast region of the lake (Fig. 4).

Haptorids were present at all of the sampling points and primarily represented by the small and ubiquitous *Actinobolina* and *Belonophrya* and the larger and frequent *Lagynophrya*; however, the peak values of >50 µg C L^{-1} were observed in a surface sample southeast of the town of Catemaco during the north wind season, and other high biomass values were observed in the surface and bottom samples of the dry season of 2011, which was caused by the presence of the more sparsely distributed *Monodinium* and the large *Paradileptus*, in particular (Fig. 4).

Linostomella was scarce in the surface and bottom samples from the rainy season and abundant in the surface and bottom samples from the dry season of 2011; how-

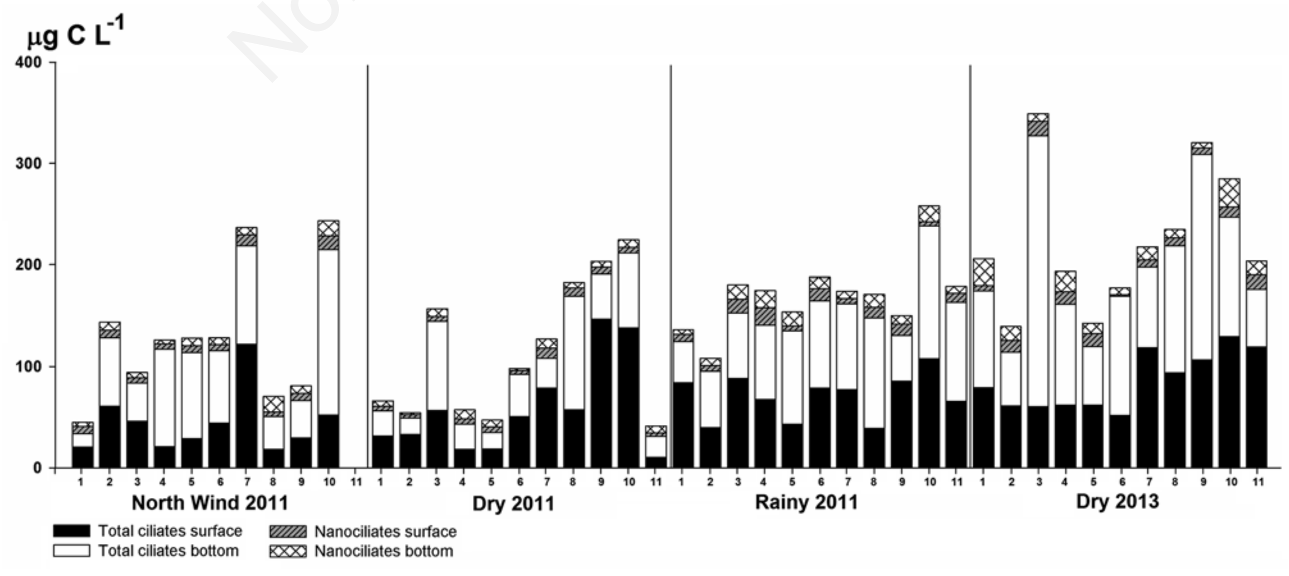

Fig. 3. Total ciliate and nanociliate biomass per sample (µg C L^{-1}) for surface and bottom samples.

ever, these organisms were particularly abundant in the bottom samples from the north wind season and presented values of 50 µg C L^{-1} in a region north of the lake. *Litonotus* was not observed in the dry season of 2011 and presented relatively low biomass except for a peak value close to 30 µg C L^{-1} at a point southwest of the lake during the north wind season.

DISCUSSION

Environmental background for ciliates

Lake Catemaco is a eutrophic lake characterized by the profuse growth of N-fixing filamentous cyanobacteria, and it is thoroughly mixed by wind. The data also indicate that this lake is light- and N-limited (Tab. 1), conditions that favour N-fixing cyanobacteria over other algal groups (Reynolds *et al.*, 2002), and imply that N is trapped in the organic matter of these cyanobacteria and only available to other organisms through grazing or when a bloom decays and bacterial growth occurs (Engström-Öst *et al.*, 2013). Therefore, bacterial growth can be limited when N limitation occurs, even if organic C is available (Mills *et al.*, 2008). This point is emphasized because sizable ciliate grazing activity on filamentous cyanobacteria was not observed; thus, the alternative prey species, especially for nanociliates, would have been bacteria and picocyanobac-

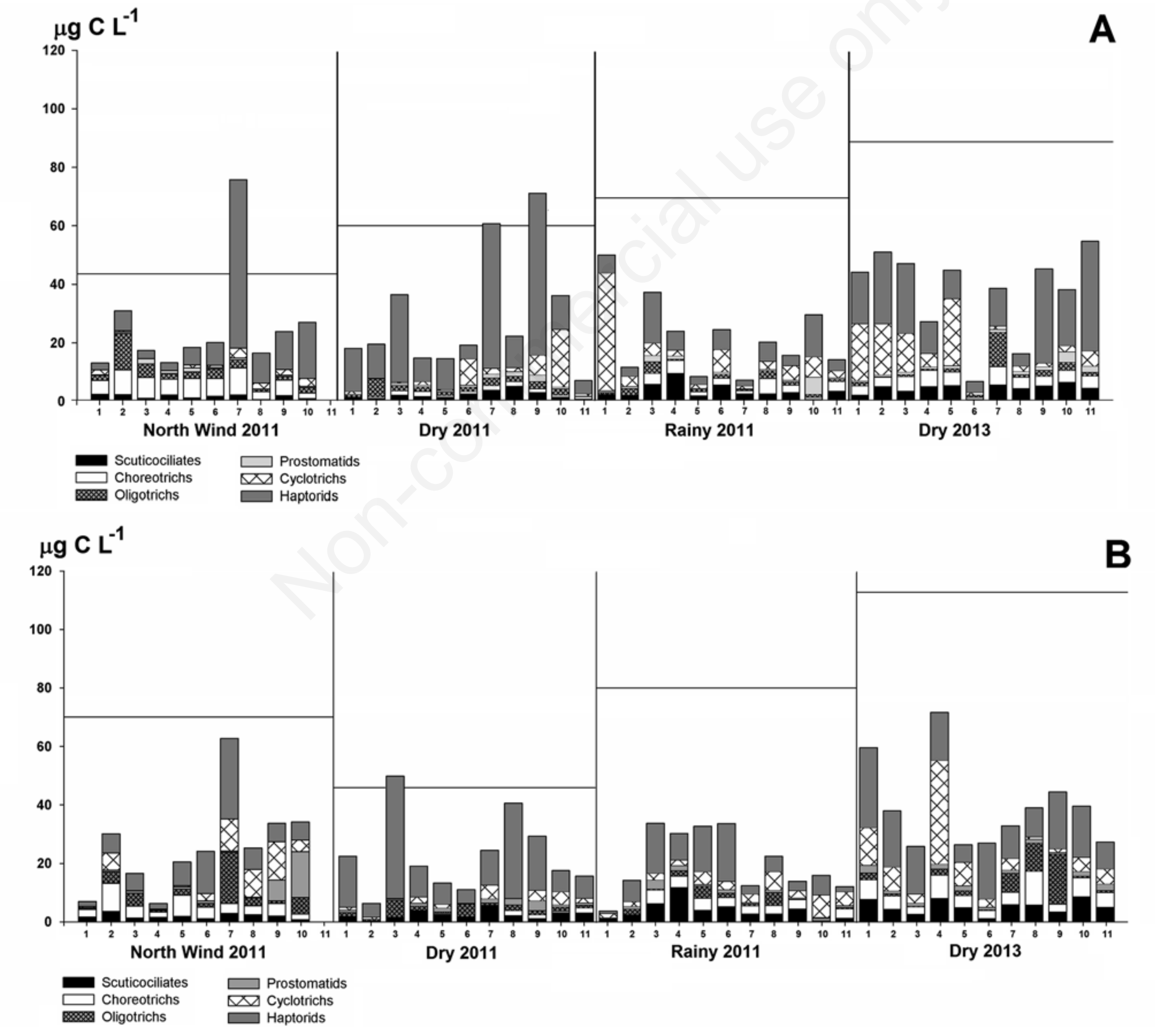

Fig. 4. Biomass per sample (µg C L^{-1}) for certain ciliate orders. Full lines are the average biomasses per survey and depth. A) Surface. B) Bottom water.

teria (Sherr and Sherr, 2002). The highest bacterial density was 5×10^6 cells mL^{-1} during the period reported here, and this value is within the range for temperate mesotrophic-eutrophic lakes (Wetzel, 2001). The bacterial cell morphologies were diverse at certain sampling points, and they were commonly dominated by micrococci along with filiform bacilli and certain bacterial aggregates, all of which are considered morphological responses to prevent their predation (Jürgens *et al.*, 1997; Jürgens and Jeppesen, 2000; Pernthaler, 2005; Salcher, 2014). These changes are indicative of the pressure exerted by bacterivores.

The picocyanobacterial density was as high as 5×10^5 cells mL^{-1} for the epifluorescence microscopy counts, which is considered a high value (Sarmento *et al*., 2008), although their biomass was low with respect to the filamentous cyanobacteria, a common trend for systems with increasing trophic status (Callieri and Stockner, 2002). Nevertheless, because evidence of ciliate grazing on filamentous cyanobacteria was not observed, picoplankters appeared to represent the preferred food source, which would indicate that the abundances observed here are capable of sustaining sizable phagotrophic nanoprotist populations when associated with rapid turnover rates. An important fraction of 1 µm to 2 µm cells were observed under the microscope, and this size allows the organisms to be grazed by phagotrophic nanoplankters (Jürgens *et al.*, 1999a).

The most noticeable feature of the plankton in Catemaco was the dominance by N_2-fixing filamentous cyanobacteria, which occurred to such an extent that Komárková and Tavera (2003) described *Cylindrospermopsis* as forming a background for the rest of the plankton because of its overwhelming abundance. This condition appeared to be promoted by low N:P ratios that favour the growth of these organisms. N limitation has been described for systems where P inputs surpass N inputs, a condition that cannot always be overcome by biological N fixation (Mischler *et al.*, 2014). Reynolds *et al.* (2002) related this state to a more complex interplay of conditions, including wind-induced mixing, relatively prolonged residence times for water (Tavera, 1996), and diminished light penetration of water, although Havens *et al.* (2003) found that low N:P ratios and diminished light penetration favoured non-N_2-fixing filamentous cyanobacteria at a tropical lake. All of these conditions occur at Catemaco.

Regarding other plankton components, chain-forming and small pennate diatoms and chlorophytes were abundant, even if they occurred in lower numbers compared with the filamentous cyanobacteria. Moreover, evidence of chain-forming and small pennate diatom consumption by the ciliate *Linostomella* was recorded. However, a number of rotifers, including *Brachionu*s and *Keratella* species, have been found to compete with or even prey on small ciliates in laboratory experiments and in field conditions (Ventela *et al.*, 2002; Weisse and Frahm, 2002), although they can also be preyed upon by large raptorial ciliates, such as *Paradileptus* (Foissner *et al.*, 1999). Other predators of plankton ciliates are fish larvae, and a population of threadfin shad *Dorosoma petenense* at Catemaco supports a fishery. Because this shad is a clupeiform fish, its first-feeding larvae are dependent on 35-45 µm prey, such as dinoflagellates or ciliates (Hunter, 1981). Ciliate are adequate as food sources for first-feeding fish larvae because feeding success is related to non-armoured prey, whereas feeding failure occurs with armoured dinoflagellates because these organisms may pass unaltered through the larval gut (Scura and Jerde, 1977; Lasker, 1981). Ciliates have been found to sustain the survival and growth of first-feeding larvae at other eutrophic shallow lakes (Zingel, 2012), and at Catemaco, they similarly sustain the threadfin shad fishery.

Ciliate assemblage composition

The ciliate composition to the genus level at Catemaco resembles the composition found at other shallow tropical freshwater ecosystems, such as those reported by Bagatini *et al.* (2013) for 13 Brazilian lakes or Beaver and Crisman (1982, 1989, 1990) for eutrophic lakes in Florida. These findings may generalize to an almost cosmopolitan distribution throughout these aquatic systems (Pfister *et al.*, 2002). Several of the observed morphotypes, such *Uronema, Cyclidium, Rimostrombidium* (Šimek *et al.*, 1995; Zingel *et al.*, 2007), *Mesodinium, Colpoda* (Foissner *et al.*, 1999; Zingel and Nõges, 2010), and *Halteria* (Šimek *et al.*, 1995), graze on picoplankton, these may include nanociliates which play an important role in energy and matter transfer through the microbial web because of the high metabolic rates associated with their small size.

For subtropical eutrophic lakes, Beaver and Crisman (1982) reported that small-bodied forms (20-30 µm) replace larger ciliates as the trophic level increases. Because these authors considered that the smaller forms were essentially bacterivorous, they related this trend to a higher bacterial availability in eutrophic systems. Thus, the ciliate assemblage of the eutrophic Lake Catemaco is consistent with the size distribution proposed by Beaver and Crisman (1982) for subtropical lakes.

The ciliate assemblages also contained *Actinobolina, Belonophrya, Mesodinium, Monodinium,* and *Lagynophrya*, which prey on smaller protists, including ciliates (Foissner *et al.*, 1999; Jürgens *et al.*, 1999b; Zingel and Nõges, 2010). Several of the genera mentioned thus far have also been reported to graze on microalgae, such as *Halteria, Mesodinium, Rimostrombidium, Limnostrombidium* and *Pelagostrombidium* (Foissner *et al.*, 1999; Zingel and Nõges, 2010), as well as certain larger ciliates, such as *Bursaridium,* and *Linostomella,* the latter of which is a particularly voracious grazer upon the chain-forming *A. granulata* and small pennate diatoms. Predatory forms, such as *Paradileptus* and *Litonotus*, were also found.

Ciliate abundance and biomass

The microbial web components, including ciliates, have been found to increase in abundance and biomass along with the trophic level of freshwater ecosystems (Auer *et al.*, 2004). As a eutrophic lake, Catemaco is consistent this trend because the ciliate abundance and biomass were both high compared with that of other temperate subtropical and tropical freshwater lakes of differing trophic statuses (Tab. 3).

The total ciliate and nanociliate biomass were lower during the north winds and dry seasons of 2011 and increased during the rainy season of 2011 and dry season of 2013 (Fig. 3). Therefore, the nanociliate abundance increased during the rainy season (third survey) when the bacteria, picocyanobacteria and filamentous cyanobacteria were least abundant. This apparent lack of correlation is inconsistent with what occurs in bottom-up-regulated ecosystems (by resources) (Auer *et al.*, 2004; Zingel and Nõges, 2010), where significant correlations are found among ciliates and chlorophyll *a* or picoplankton densities. However, a careful follow-up of the nanociliate and picoplankton densities for several days would be necessary to determine if top-down control actually prevails or if the observed pattern observed was a result of picoplankton depletion by nanociliates. The ciliate biomass did not appear to be affected by the filamentous cyanobacteria density, which is inconsistent with what was found for a lake with toxic cyanobacterial blooms, where *Cylindrospermopsis raciborskii* (but not *Microcystis aeruginosa*) blooms depressed both the nanoflagellate and nanociliate assemblages (Moustaka-Gouni *et al.*, 2006).The biomass distribution by morphotype differed between the surface and bottom samples despite the mixed character of the water column, and this result may be indicative of a patchy distribution (Fig. 4).

Predation, filamentous cyanobacteria, and ciliate assemblage regulation

Jürgens *et al.* (1999b) found abundant small ciliates at a temperate hypertrophic lake and determined that their

Tab. 3. Ciliate abundance and biomass at different freshwater lakes.

Water body	Trophic status	Ciliate abundance cells (mL^{-1})	Ciliate biomass (µg C L^{-1})	Reference
Lake Oglethorpe, USA	Eutrophic	110 (max)		(Pace and Orcutt, 1981)
Lake Lanao, Philippines	Deep Subtropical, eutrophic	28 (avg)		(Lewis, 1985)
Lake Valencia, Venezuela	Eutrophic	218 (avg)		(Lewis, 1985)
Rio Grande Reservoir, Brazil	Eutrophic	17		(Maluf-Barbieri and Godinho-Orlandi, 1989)
Lake Kingsley, USA	Oligotrophic	45 (max)		(Beaver and Crisman, 1990)
East Lake, USA	Mesotrophic	86 (max)		(Beaver and Crisman, 1990)
Lake Scott, USA	Eutrophic	356 (avg)		(Beaver and Crisman, 1990)
Lake Houhu, China	Mesotrophic	35.5 (avg)		(Song, 2000)
Lake Nani Tal, India	Eutrophic	55-116 (min-max)		(Shukla and Gupta, 2001)
Lake Victoria, Tanzania Lake Malawi, Tanzania	Relatively shallow, eutrophic deep, oligotrophic	20.1 (avg) 1.5 (avg)	36 (24.2-61.8) 1.8 (0.03-7.82)	(Yasindi and Taylor, 2003)
Lake Monte Alegre, Brazil	Eutrophic	389 (surf.) 97 (bot.)		(Gomes and Godinho, 2003)
55 lakes in North Germany	Different trophic statuses		19 (13-28) mesotrophic 30 (22-40) slightly eutrophic 99 (70-140) very eutrophic 132 (88-198) hypertrophic	(Auer *et al.*, 2004)
Irai Reservoir, Brazil	Eutrophic	7.2-47.1 (min-max)		(Machado-Velho *et al.*, 2005)
Six lakes in the Masurian Lake District Poland	Mesotrophic, eutrophic, polyhumic	5.2-27.8 (min-max avg values)	14.9-90.0 mesotrophic-polyhumic	(Chróst *et al.*, 2009)
Lake Araras, Brazil		51.91 (max)		(Bagatini *et al.*, 2013)
13 water bodies in Brazil		14.89 (2.03-61.10)		(Bagatini *et al.*, 2013)
Lake Võrtsjärv	Shallow eutrophic	68 (basal condition) 35 (excluding mesozooplankton)	88 (basal condition) 94 (excluding mesozooplankton)	(Agasild *et al.*, 2013)
Urban lake, Brazil	Shallow eutrophic subtropical	3.50 (surf.) 17.99 (bot.)	2.02 (surf.) 18.27 (bot.)	(Machado-Velho *et al.*, 2013)
Monjolinho Reservoir, Brazil	Shallow eutrophic subtropical	3.7-16.0		(Hisatugo *et al.*, 2014)
Lake Catemaco	Shallow mesotrophic-eutrophic	57 (14-113)	71.1 (10.4-202.2)	This work

populations were regulated by predators (top-down) instead of by food availability (bottom-up). This result may indicate a trend whereby top-down control becomes more important for higher trophic states of subtropical lakes (Havens *et al.*, 2007), and the authors stated that fish predation must exert a stronger top-down control on the pelagic food web in subtropical lakes than in temperate lakes of similar trophic status. Catemaco's plankton assemblage is the result of selective predation pressure by planktivorous fish, which prey on the larger zooplankton, including the large non-selective daphnids that graze on cyanobacterial trichomes and consume the more edible phytoplankton species, thus leaving behind trichome-enriched water (Komárková and Tavera, 2003). Physical interference by trichomes has been proposed as a mechanism that reduces ciliate predation, and it is an important process because top-down control by predatory fish likely has a strong effect on the microbial web of tropical lakes (Havens *et al.*, 2007). Zingel *et al.* (2007) determined that ciliates are the dominant microbial grazers at a temperate lake that is also dominated by filamentous cyanobacteria because top-down control by fish predators did not occur under these conditions.

The dominant cyanobacteria at Catemaco produce toxins (Berry and Lind, 2010) that have unknown effects on other components of the microbial web, and the effect of these toxins on the ciliate assemblages is also unknown. The ingestion of *Cylindrospermopsis* by ciliates cannot be excluded because there is experimental evidence that toxin-producing filamentous cyanobacteria can sustain ciliate growth and survival (Fabbro *et al.*, 2001; Combes *et al*., 2013). Fabbro *et al.* (2001) indicated that toxin-rich *Cylindrospermopsis* present straight trichomes, whereas the less toxic forms present coiled trichomes, and this prevents their attack by ciliates that ingest them *end first*. The dominant morphology at Catemaco during the surveys was coiled, such as a key ring. Large daphnids are regarded as natural control agents against filamentous cyanobacteria proliferation; however, at least one report has indicated that their filtering efficiency is negatively correlated with trichome density (Davis *et al.*, 2012). Therefore, whether large cladocera would be able to control the *Cylindrospermopsis* densities found in Catemaco remains unclear. Further experimental evidence is required to determine whether large cladocera have been excluded for this reason or if their absence is because of the selective activity of planktophagus fish, including the native threadfin shad *Dorosoma petenense* (Günther, 1867), the endemic *Bramocharax caballeroi* (Contreras-Balderas and Rivera-Tiellery, 1985), or the exotic and more efficient tilapia *Oreochromis niloticus* (Linnaeus, 1758; Miller and Van Conner, 1997). The absence of these cladocera, which are non-selective filter-feeders that also prey on micro- and nanociliates, as well as on competing or predating rotifers, may cause cascading trophic effects (Sommer *et al.*, 2003). Fish predation on zooplankton is believed to prevent microcrustaceans from preying on ciliates, and this results in a lower HNF biomass because of higher predation by ciliates (Ozen *et al.*, 2014), which would also explain the low HNF abundances (results not shown) at Catemaco.

CONCLUSIONS

Plankton ciliate assemblages, particularly nanociliates, play an enhanced role in the microbial food web at Catemaco. The abundance and biomass of plankton ciliates are high at the study site compared with that of other shallow freshwater ecosystems, and they are likely the main picoplankton grazers at Catemaco because phagotrophic nanoflagellates are not abundant. This condition appears to be the result of large cladocera exclusion, either by selective fish predation or decreased filtering efficiency because of high filamentous cyanobacteria densities. The size class composition of these ciliates also suggests that they are the most probable prey for the first-feeding fish larvae of the species that sustain the local fisheries; thus, plankton ciliates may be a critical factor for appropriate recruitment.

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