



Potential effects of warming on the trophic structure of shallow lakes in South America: a comparative analysis of subtropical and tropical systems

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Abstract To investigate the potential long-term consequences of environmental warming in subtropical systems, we compare the trophic structure of shallow lakes in tropical and subtropical regions. In total, 25 meso-eutrophic lakes with piscivorous fish were sampled during summer along a latitudinal gradient in South America. The fish catch per unit of effort and the omnivorous fish to zooplankton biomass ratios were significantly lower in the tropical lakes.

Despite the lower fish biomass, no significant difference was found in zooplankton or phytoplankton communities or in the zooplankton to phytoplankton biomass ratio between the two sets of lakes. Nevertheless, regression models based on the combined dataset show higher cyanobacteria and total phytoplankton biomass at lower zooplankton to phytoplankton biomass ratio and higher omnivorous fish to zooplankton biomass ratio. Cyanobacteria biomass was dominated by non bloom-forming taxa and was inversely related to the biomass of calanoid copepods suggesting that these herbivores may play an important role in controlling edible cyanobacteria in warm shallow lakes. Overall, our results, however, suggest that warming will have relatively minor impacts on the pelagic trophic structure of shallow subtropical lakes supporting the idea of weaker trophic cascades in

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warm (sub)tropical lakes in comparison to temperate ones.

Keywords Climate change · Trophic interactions · Trophic cascade · Food webs · Cyanobacteria

Introduction

Shallow lake ecosystems are highly sensitive to climate change. Several previous studies have investigated the potential effects of global warming on the structure and functioning of such ecosystems, often using different theoretical frameworks for setting hypotheses and predictions (Meerhoff et al., 2012; Jeppesen et al., 2014). There is evidence for an increase in total phytoplankton biomass and strong evidence for an increase in phytoplankton dominance by cyanobacteria with warming (Kosten et al., 2012; Meerhoff et al., 2012; Jeppesen et al., 2014). In addition, there are indications for a decrease in zooplankton size and grazing capacity, as well as a decrease in fish size and an increase in fish omnivory with warming (Iglesias et al., 2011; Meerhoff et al., 2012; Jeppesen et al., 2014; González-Bergonzoni et al., 2016).

Environmental warming may affect trophic interactions through several mechanisms, including increasing consumption rates and the variety of prey consumed (Arim et al., 2010). It may also enhance omnivory at different levels of biological organization (González-Bergonzoni et al., 2016), including an increase in species richness of omnivores within fish communities (González-Bergonzoni et al., 2012), and a decrease in fish species trophic position and community food chain length (Arim et al., 2007; Iglesias et al., 2017; Dantas et al., 2019; Lacerot et al., 2021). Indications of changes in the strength of trophic interactions can be obtained from biomass ratios of adjacent trophic levels, i.e., piscivorous to planktivorous fish, planktivorous fish to zooplankton, and zooplankton to phytoplankton. Evidence from such biomass ratios between trophic levels reported in previous studies suggests a reduction in the strength of piscivorous-planktivorous fish and zooplankton-phytoplankton interactions but an increase in the strength of omnivorous/planktivorous fish-zooplankton interactions with raising temperatures in shallow lakes (e.g. Meerhoff et al., 2007a, b; Brucet et al., 2010; Jeppesen et al., 2010, 2012, 2020; Meerhoff et al., 2012).

Comparisons of systems that are similar in key limnological features (such as area, depth, trophic state, etc.) but are located in different climates have

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been widely used to elucidate the potential long-term consequences of climate changes. Several studies address latitudinal gradients (Moss et al., 2004; Stephen et al., 2004; Gyllström et al., 2005; Declerck et al., 2005; Kosten et al., 2012) whereas others focus on cross-comparisons (Meerhoff et al., 2007a, b; Teixeira-de-Mello et al., 2009; Brucet et al., 2010; Jeppesen et al., 2020). This space-for-time substitution approach has provided one of the most plausible empirical ways to find patterns and test the theoretical predictions of long-term effects of global warming on the community structure of shallow lakes (Meerhoff et al., 2012; Jeppesen et al., 2014). However, the approach has limitations as there are potential confounding effects of, among others, geology, geomorphology, land use and biogeography (Woodward et al., 2010; Meerhoff et al., 2012; Jeppesen et al., 2014).

Previous studies using this approach focused on comparisons between polar and temperate lakes or between temperate and subtropical or Mediterranean lakes (summarized in Meerhoff et al., 2012; Jeppesen et al., 2014). Therefore, the potential effects of warming on already warm (sub)tropical lakes have received little attention. The bias towards temperate systems likely reflects the longer limnology history in Europe and North America, but hampers to make predictions about climate change effects at lower latitudes because subtropical and tropical systems may respond to climate change in a different way, and previous studies focusing on comparisons with lower latitude lakes have mainly dealt with subtropical lakes (e.g. Iglesias et al., 2011; Jeppesen et al. 2007, 2010; Meerhoff et al., 2007a, b; Teixeira-de-Mello et al., 2009).

The aim of this study is to compare the trophic structure of shallow lowland lakes in tropical and subtropical regions of South America to evaluate similarities and differences in key structural properties. Moreover, this comparative analysis could help elucidate the potential long-term consequences of environmental warming in subtropical shallow lakes. Based on empirical patterns reported by previous studies on the effects of warming on shallow lakes (Meerhoff et al., 2012; Jeppesen et al., 2010, 2014), we hypothesize that the ratio between omnivorous fish and zooplankton biomass (a proxy of fish predation pressure on zooplankton) are higher, while the ratio between zooplankton and phytoplankton biomass (a proxy of zooplankton grazing on phytoplankton) are

lower in tropical than in subtropical lakes. Moreover, we expect higher phytoplankton biomass and cyanobacteria dominance in the warmer tropical lakes.

Material and methods

Selected lakes

We selected a subset of 25 from the 83 shallow lakes sampled during summer in 2004 (subtropical) and 2005 (tropical) along a latitudinal gradient in South America for the South America Lake Gradient Analysis (SALGA) project (see Kosten et al., 2009 for more details and sampling protocol). All lakes selected for this study are natural coastal lowland lakes, with elevation ranging from 1 to 36 m above sea level, and belong to the South Atlantic tectono-sedimentary domain mainly created by fluvial sediment budgets and quaternary fluvial-coastal-oceanic processes and tectonics (Petry et al., 2016). The selected lakes have a similar trophic state (i.e., with total phosphorus concentrations ranging between 50 and 150 $\mu\text{g l}^{-1}$) and the presence of piscivorous fish in the fish catch. These criteria were used to ensure comparability of lakes regarding trophic state and food web length, given their relevance for shallow lake functioning and trophic cascade effects. All lakes were shallow (mean depth < 4.5 m and > 1.3 m) with a surface area ranging from 16 to 242 ha. The selected lakes were divided into two groups following the Köppen climatic system: 14 subtropical and 11 tropical lakes (Fig. 1) with a mean (\pm 1SD) annual air temperature of 18.3 (\pm 1.0) and 24.1 (\pm 1.1) °C, and annual precipitation of 1,400 (\pm 177) and 1,149 (\pm 143) mm, respectively. These climate variables differed significantly between the two climatic regions ($P < 0.001$, Mann–Whitney–Wilcoxon test). Data for these climatic variables were obtained for the 1970–2000 period from *WorldClim* (Fick & Hijmans, 2017).

Catchment area and land use/cover

The catchment areas were obtained using the Nested Watershed in South America shapefile from Petry and Sotomayor (2009). Images of all lakes were downloaded from Google Earth Pro Historical Imagery at its maximum resolution (4800 \times 2623) and then georeferenced. Using the following formula: Map Scale =

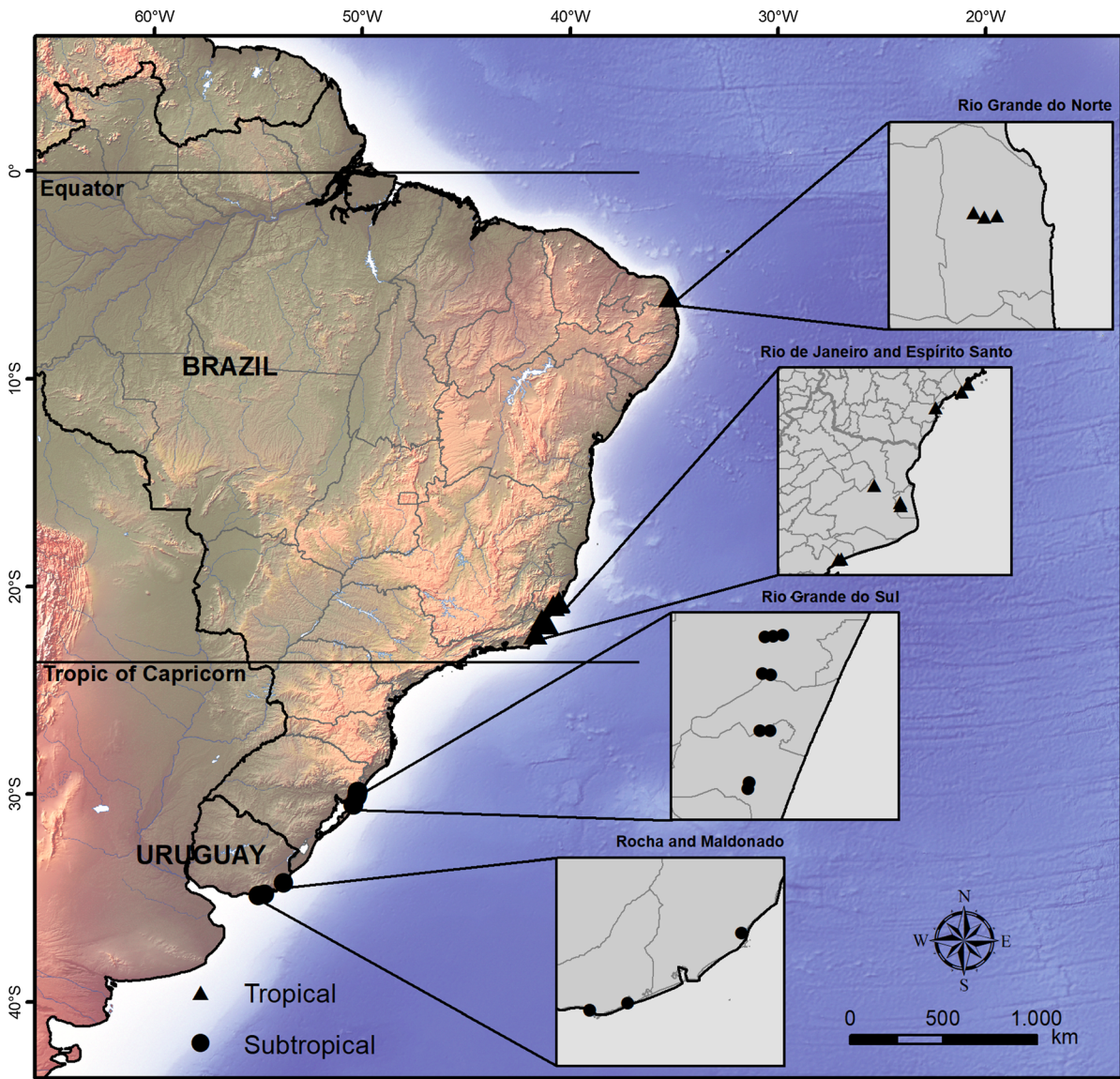


Fig. 1 Map of South America highlighting the lakes sampled in tropical and subtropical regions; enlarged view of the points shows the location of the lakes in Brazil (Rio Grande do Norte,

Rio de Janeiro, Espírito Santo, and Rio Grande do Sul) and Uruguay (Rocha and Maldonado)

Raster resolution (in meters) $\times 2 \times 1000$ (Tobler, 1987), the maps were produced at an average scale of 1/2500. Image dates were selected to be as close as possible to the sampling dates. We drew polygon vectors around each lake and created a 500 m wide buffer around these polygons. Next, we assigned the land use classes to the pixels within the cluster using classified rasters created with a supervised classification where class signatures were manually collected and used by the maximum likelihood classifier. The

classified rasters were converted to polygons, and after vector manual corrections, areas of each class areas (ha) were computed for each buffer.

Six major land-use and land cover (LULC) classes were identified in the 500 m- wide buffer zone: (1) Woodland, natural lands that include tall trees higher than 2 m; (2) Shrubland, vegetation characterized by a predominantly shrubby stratum, shrubs sparsely distributed over a grassy stratum; (3) Grassland, cultivated pastures or natural grasslands for grazing of

cattle and other animals, both with high anthropic interference such grass planting, weed elimination, land clearing, preparation for temporary or semi-perennial crops, including set-aside and wetlands; (4) Bare soil, including areas without vegetation, such as rocky outcrops, terrains with active erosion processes, dirt or gravel roads, beaches and dunes; (5) Artificial surfaces, areas where non-agricultural man-made surfaces predominate such as buildings and road systems, urban areas, industrial and commercial complexes and other infrastructures; (6) Surface water, represented by small reservoirs, coastal water bodies, streams, canals and other linear water bodies.

Sampling

We sampled the entire water column with a 2-m PVC tube with a one-way valve at the bottom at 20 points randomly selected within the lake polygon and included pelagic and macrophyte-covered areas. When the water column was deeper than 2-m we first sampled the lower 2 m using a rope attached to the PVC tube and then the remaining upper part of the water column. All random points were integrated into a single sample from which subsamples were taken for total alkalinity, concentrations of suspended solids, total nitrogen (TN), total phosphorus (TP), and chlorophyll *a*, and phytoplankton analyzes. For zooplankton analysis, two liters from each of the 20 random points were pooled into a bulk sample (final volume = 40 l), filtered through a 50- μm mesh size sieve, and preserved in a 4% formaldehyde solution.

The fish community of each lake was sampled using a stratified random approach with multi-mesh benthic gillnets (Appelberg et al., 2000). Each net was 30- m long and 1.5- m deep and included 12 different mesh sizes ranging from 5 to 55 mm (knot to knot), randomly distributed in 2.5 m sections. The number of nets placed in each lake varied between 3 and 5, depending on the lake surface area. The nets were randomly distributed between pelagic and littoral areas and were placed at dusk and removed at dawn.

Coverage of macrophytes was estimated from observations of coverage estimations at 13–47 points (depending on the lake size, average 22; with an approximate area of 3 m² each) that were equally distributed along three to eight parallel transects. In addition we used macrophyte presence/absence data from the 20 random points in the lake where we took

water samples to make an estimate of the entire lake coverage. The number of transects varied with the shape and size of the lake. A grapnel was used if water transparency was too low to see the lake bottom.

Water turbidity, electric conductivity, oxygen, and pH were measured using a multi-parameter analyzer U-22 HORIBA (Kyoto, Japan). Water transparency was measured with a Secchi disk. The coefficient of light attenuation (K_d) was estimated using the Lambert–Beer law and irradiation data. Alkalinity was derived by titrating the sample with HCl. Suspended solids were determined on pre-weighed GF/F Whatman filters after drying at 105°C for one night. TP and TN were analyzed using a continuous flow analyzer (Skalar Analytical BV, Breda, The Netherlands) following NNI protocols (NNI, 1986, 1990), except UV/Persulfate destruction, which was not executed beforehand but integrated into the system. Chlorophyll *a* was extracted from filters (GF/C S&S) with 96% ethanol, and absorbance was measured at 665 and 750 nm (Nusch, 1980).

Lake communities

Phytoplankton was quantified according to Utermöhl (1958) using an inverted microscope. The individuals (cells, colonies, and filaments) were enumerated in random fields (Uehlinger, 1964), with an error $\leq 20\%$ and a confidence interval of 95% (Lund et al., 1958). The organisms were identified using the main morphological and morphometrical characteristics of the vegetative and reproductive phases. To estimate the phytoplankton biovolume ($\text{mm}^3 \text{ l}^{-1}$), here used as an expression of biomass, at least 25 individuals of each species were measured, using similar geometric solids (Hillebrand et al., 1999).

Zooplankton was counted in 1–5 mL aliquots depending on sample concentration. Counting was stopped when reaching 100 specimens of the most abundant species of each taxonomic group (rotifers, copepods, cladocerans). If necessary, the whole sample was counted. For each lake, we measured at least 20 individuals of each rotifer species found and calculated their biovolume (μm^3) using geometric formulas (Ruttner-Kolisko, 1977). The dry weight ($\mu\text{g DW l}^{-1}$) was calculated as a percentage of the biovolume (Pauli, 1989). For rare rotifer species and those undergoing marked changes in morphology due to formaldehyde, biomass data were taken from the

literature (Dumont et al., 1975; Bottrell et al., 1976; Pauli, 1989). This procedure was also used to estimate copepod nauplii biomass. For copepods and cladocerans, we measured 50 specimens of each species and calculated their biomass using length/weight regressions available in the literature (Bottrell et al., 1976; McCauley, 1984; Culver et al., 1985).

All fish caught were counted and measured (full length). Catch per unit of effort (CPUE) was expressed as the number of fish individuals caught per unit of gillnet area per the total number of hours with the nets displayed ($\text{kg m}^{-2} \text{12 h}^{-1}$). Fish were classified as piscivores if they fed on other fish at some stage of their life (in addition to other prey) or as omnivores, otherwise. This classification was made following an exhaustive review of the bibliography for each species and considering fish stage-structured trophic interactions and ontogenetic niche shifts. In this study, we used the broader definition of omnivory as feeding on more than one trophic level instead of the definition of omnivory as feeding on animal and plant or detritus material. This is because we were interested in the potential top-down cascading effects on plankton communities by piscivorous fish and the proportion of piscivorous to non-piscivorous (i.e., omnivorous) fish in our catches was the most relevant metric of fish trophic structure (Lazzaro et al. 2003). We assumed that all omnivorous fish in our catch could feed on zooplankton and were potential prey for the piscivorous fish, at least in some stage of their life.

To elucidate differences in the potential predation pressure by piscivorous fish (PISC) on omnivorous fish (OMN), and by OMN on total zooplankton (TZOO), between the two groups of lakes, we used the ratios PISC:OMN and OMN:TZOO, respectively. Likewise, to elucidate differences in the potential grazing pressure by TZOO on total phytoplankton (TPHY) between the two groups of lakes, we used the biomass (dry weight) ratio TZOO:TPHY. For this ratio, total phytoplankton biomass (dry weight) was roughly estimated as 66 times the chlorophyll *a* concentration to allow comparisons with earlier studies (Jeppesen et al., 2007; Havens et al., 2009; Havens & Beaver, 2013). Finally, to investigate the relative importance of cyanobacteria (CYA) for the total phytoplankton biomass in the studied lakes, we used the CYA:TPHYTO ratio. Likewise, to investigate the relative importance of cladocerans (CLA) and calanoids copepods (CAL) for the total zooplankton

biomass, we used the CLA:TZOO and CAL:TZOO ratios, respectively.

Total phytoplankton biomass was quantified in our study in two different ways and is expressed hereby with two different acronyms: TPHY ($\mu\text{g DW l}^{-1}$) and TPHYTO ($\text{mm}^3 \text{l}^{-1}$). This was done for two reasons: (1) to have two independent measures of phytoplankton biomass in the predictor (TZOO:TPHY) and response (TPHYTO, CYANO:TPHYTO) variables to reduce autocorrelation in our statistical analyzes and (2) to compare our zooplankton to phytoplankton biomass ratio (TZOO:TPHY) with those from other studies that have estimated this variable in the same way (Jeppesen et al., 2007; Havens et al., 2009; Havens & Beaver, 2013). We performed a regression between TPHY and TPHYTO and found these variables were significantly ($P < 0.01$) but not strongly related (adjusted $R^2 = 0.47$). Moreover, changing the estimates for phytoplankton biomass in the variable zooplankton to phytoplankton biomass ratio did not change our results.

Statistical analysis

A Mann–Whitney–Wilcoxon test was used to compare the abiotic and biotic variables between the two groups of lakes ($\alpha = 0.05$). The function *wilcox.test* from the R *stats* package (R Core Team, 2020) was used to perform the Mann–Whitney–Wilcoxon test. To analyze whether total phytoplankton, cyanobacteria, and CYA:TPHYTO were influenced by climate (subtropical and tropical) and trophic structure (i.e., TZOO:TPHY, CLA:TZOO, CAL:TZOO, and OMN:TZOO), and to analyze whether cladocerans, calanoids, CLA:TZOO, and CAL:TZOO were influenced by climate and trophic structure (i.e., CYA:TPHYTO and OMN:TZOO), we ran analyzes of covariance (ANCOVA) using climate and the above covariates (indicators of trophic structure) as predictors with the *lm* function from the R statistical package *stats* (R Core Team, 2020). To validate ANCOVA models assumptions (i.e. normality, homogeneity of variance and linearity) the function *gvlma* from the *gvlma* R package was used (Pena & Slate, 2019). All observations were independent from each other and all models were tested for homogeneity of regression slopes (i.e. slopes are equal between tropical and subtropical regions). Data were log- or square root-transformed to improve normality whenever necessary. To assess

whether climate (categorical variable) affected the relationship between continuous variables, we individually fitted the models assuming different slopes and intercepts. We then simplified them by removing non-significant terms until we were left with the minimal adequate model, in which all the parameters were significantly different from zero. For instance, if there was no indication of any difference in the slope of the relationship between climate types, we deleted the non-significant term from the model before testing for equal slopes in the ANCOVA models. The function *update* was used for manual model simplification from the R *stats* package (R Core Team, 2020). Finally, to assess whether or not climate had a significant effect on response variables, we compared the full models with equal slopes with their corresponding reduced model by analyzes of variance (Crawley, 2013). All graphics were made with the package *ggplot2* in the software R version 4.0.2 (Wickham, 2009; R Core Team, 2020).

Results

The catchment area (CA), lake area (LA), and the CA:LA ratio did not differ significantly between the tropical and subtropical regions (Table 1). Overall, the proportion of the area around the lakes covered by the six land-use classes did not differ between regions, except for the higher percentage of shrubland in tropical than in subtropical regions (Table 1). As

expected from their latitudinal difference, surface water temperature in summer was higher in the tropical than in the subtropical lakes (Table 2; Fig. 2B), but the water temperature at the bottom and the dissolved oxygen concentrations at the lake surface and bottom were similar (Table 2). Mean depth, electric conductivity, TN concentration, and TN:TP ratio were also higher in the tropical than in the subtropical lakes, while the reverse pattern was observed for TP concentration (Table 2; Fig. 2). Water pH, alkalinity, Secchi depth, coefficient of light attenuation, suspended solids and chlorophyll *a* (CHL) concentrations, as well as the CHL:TP and CHL:TN ratios, were similar in both sets of lakes (Table 2). The coverage of emergent macrophytes was higher in the subtropical than in the tropical lakes, while no significant difference was observed for submerged macrophyte coverage (Table 2).

Total fish CPUE, the CPUE of piscivorous (PISC) and omnivorous (OMN) fish, as well as the ratio between omnivorous fish CPUE and total zooplankton biomass (OMN:TZOO), were significantly higher in the subtropical than in the tropical lakes (Table 3; Fig. 3). Despite the higher fish biomass in the subtropical lakes, no significant difference was found in the PISC:OMN and TZOO:TPHY ratios between the two sets of lakes (Table 3). Total zooplankton biomass and total phytoplankton biomass were similar in the two groups of lakes (Table 3). We found no significant differences in the biomass of the taxonomic groups of zooplankton and the biomass of the

Table 1 Catchment area (km²), lake area (km²), catchment to lake area ratio (CA:LA), and percentage coverage of land-use types in a zone of 500 m around the subtropical and tropical lakes

	Subtropical		Tropical		W	P
	Mean	SD	Mean	SD		
Catchment area (CA)	524.2	112.3	655.9	674.5	95	0.318
Lake area (LA)	0.7	0.6	0.7	0.3	70	0.727
CA:LA	1298.6	1155.8	901.5	577.8	85	0.686
Woodland	13.2	8.6	11.9	12.3	83	0.739
Shrubland	9.8	6.4	16.6	8.5	41	0.048*
Grassland	56.2	14.1	46.3	27.8	97	0.273
Artificial surfaces	1.6	2.5	2.7	3.9	61	0.395
Bare soil	7.7	13.0	9.3	11.5	70	0.701

Mann–Whitney–Wilcoxon test for differences in these variables between the two groups of lakes

Significant results are highlighted in bold

*Values considered significant assuming $\alpha = 0.050$

Table 2 Mann–Whitney–Wilcoxon test for differences in some limnological variables between the subtropical and tropical lakes

	Subtropical		Tropical		W	P
	Mean	SD	Mean	SD		
Surface temperature (°C)	24.8	1.5	26.3	1.6	37.0	0.029*
Bottom temperature (°C)	23.9	1.3	24.5	2.3	70.5	0.722
Surface dissolved oxygen (mg l ⁻¹)	7.6	0.5	7.3	1.8	89.5	0.493
Bottom dissolved oxygen (mg l ⁻¹)	7.5	0.7	5.7	2.7	97.5	0.261
Mean depth (m)	1.7	0.5	2.8	1.0	27.5	0.007*
Secchi depth (m)	1.0	0.5	1.6	1.5	72.5	0.805
Light attenuation coefficient (m ⁻¹)	2.7	1.7	2.8	2.4	98.5	0.238
Suspended solids (mg l ⁻¹)	10.3	9.8	8.7	10.9	108.0	0.090
pH	6.9	0.6	6.7	1.1	101.0	0.189
Alkalinity (meq l ⁻¹)	0.48	0.5	0.9	1.5	53.0	0.315
Conductivity (µS cm ⁻¹)	125.4	98.3	355.2	339.8	33.0	0.015*
Chlorophyll <i>a</i> (CHLA, µg l ⁻¹)	3.5	1.2	7.3	9.8	75.0	0.913
Total phosphorus (TP, µg l ⁻¹)	117.1	25.3	77.7	15.2	137.5	0.001*
Total nitrogen (TN, µg l ⁻¹)	219.2	100.8	520.3	319.6	31.5	0.013*
TN:TP	1.84	0.74	6.76	4.02	8.00	< 0.001*
CHLA:TP	0.03	0.01	0.09	0.12	68.0	0.648
CHLA:TN	0.02	0.01	0.01	0.02	104.0	0.149
% Submerged macrophytes	9.7	24.0	25.6	34.7	48.0	0.105
% Emergent macrophytes	27.4	18.7	9.9	7.7	129.5	0.003*

Significant results are highlighted in bold

*Values considered significant assuming $\alpha = 0.050$

taxonomic groups of phytoplankton between the subtropical and tropical lakes (Table 3). Zooplankton was mainly composed of cladocerans (CLA), constituting on average 60% and 36% of the total zooplankton biomass (CLA:TZOO) in the subtropical and the tropical lakes, respectively (Table 3). Calanoid copepods (CAL) comprised on average 16% and 21% of the total zooplankton biomass (CAL:TZOO) in the subtropical and tropical lakes, respectively (Table 3). On the other hand, phytoplankton was composed mainly of cyanobacteria (CYA), constituting on average 42% and 31% of the total phytoplankton biovolume (CYA:TPHYTO) in the subtropical and the tropical lakes, respectively (Table 3). Among cyanobacteria, higher contribution of life-forms was from small colonies (< 20 µm), followed by small single cells, while filamentous and bigger colonial cyanobacteria showed lower contributions (Table 4). In subtropical lakes, the prominent representatives of Cyanobacteria were the colonial Chroococales with tiny cells (e.g., *Aphanocapsa delicatissima*, *A.*

incerta, *Cyanodictyon imperfectum*) followed by filamentous Oscillatoriales (*Planktolyngbya limnetica*, *Pseudanabaena recta*). In tropical lakes, Chroococales were also the groups with higher biovolume. Still, colonies shared them with tiny (*Aphanocapsa delicatissima*, *Epigloeosphaera brasiliica*, *Lemmermaniella pallida*) and large cells (*Microcystis protocystis*, *M. ichtiobabel*, *M. wesenbergii*).

The regression analyzes performed on the pooled dataset (both regions together) showed that the lower the TZOO:TPHY and CAL:TZOO ratios and the higher the OMN:TZOO ratio, the higher were the biomass of cyanobacteria (CYA), total phytoplankton (TPHYTO), and CYA:TPHYTO ratio (Fig. 4). On the other hand, the higher the CYA:TPHY and OMN:TZOO ratios, the lower were the biomass of calanoids (CAL) and the CAL:TZOO ratios (Fig. 5). Unlike calanoids, the biomass of cladocerans was not related either to the CYA:TPHY or OMN:TZOO ratios (Fig. S1). The analysis of covariance showed that including the geographical region as a categorical

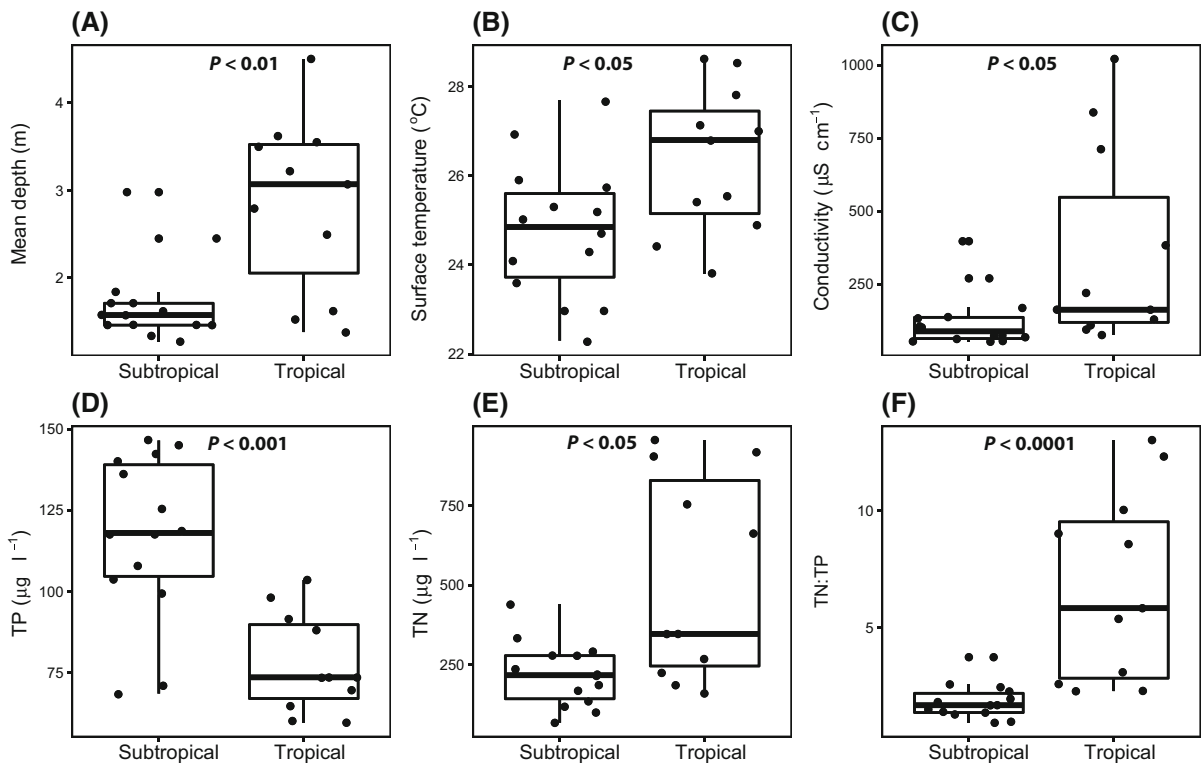


Fig. 2 Mann–Whitney–Wilcoxon test for differences in (A) mean depth, B surface temperature, C electric conductivity, D total phosphorus (TP), E total nitrogen (TN), and F TN:TP ratio between tropical and subtropical lakes. Boxplots (25–75%,

boxes; 10–90%, lines; median, horizontal line into the boxes). The black dots are irregularly distributed along the boxplots to avoid overlapping. Only significant results are shown in the figure

variable in the models, led to an improvement of the explanatory power for the following models: CYA:T-PHYTO vs. TZOO:TPHY and CAL vs. OMN:TZOO (Table 5). In both models, the intercepts for the tropical lakes were lower than for the subtropical lakes. This implies a lower proportion of cyanobacteria in the total phytoplankton biomass under a similar zooplankton grazing pressure (TZOO:PHY) and a lower calanoid biomass under a similar fish predation pressure on zooplankton (OMN:TZOO) in the tropical than in the subtropical lakes.

Discussion

This study aimed at comparing the trophic structure and other limnological properties of shallow lakes in tropical and subtropical regions of South America, as a way to approach the potential consequences of climate warming for subtropical systems. Our results did not show significant differences in the trophic structure

and most limnological features between the two sets of lakes. Contrary to what we expected from empirical patterns reported by previous comparative studies in latitudinal gradients (see reviews in Meerhoff et al., 2012; Jeppesen et al., 2014), we found higher fish CPUE and higher potential for fish predation pressure on zooplankton (OMN:TZOO) in subtropical than in the warmer, tropical lakes. Although the differences in zooplankton biomass were not large enough to be significant, the tropical lakes seemed to host less zooplankton despite having a lower fish biomass and lower OMN:TZOO ratio. Tropical lakes also seemed to contain higher phytoplankton biomass, particularly cyanobacteria, at higher TN and lower TP concentrations, suggesting a lower efficiency in N use and a higher efficiency in P use by tropical phytoplankton. However, just as the differences in zooplankton above, the differences in phytoplankton biomass between the two sets of lakes were not significant.

In addition, based on previous empirical work, we expected a decrease in the grazing pressure (expressed

Table 3 Mann–Whitney–Wilcoxon test for differences in the fish catch per unit of effort (CPUE), zooplankton biomass and phytoplankton biovolume between the subtropical and tropical lakes

	Subtropical		Tropical		W	P
	Mean	SD	Mean	SD		
<i>Fish CPUE (kg m⁻² 12 h⁻¹)</i>						
Total fish	203.75	190.41	48.17	58.04	133.00	0.002*
Piscivores (PISC)	17.73	28.74	2.05	1.87	133.50	0.002*
Omnivores (OMN)	183.53	183.80	45.95	57.20	122.00	0.014*
PISC:OMN	1.79	6.37	0.58	1.14	71.0	0.742
OMN:TZOO	5.24	4.27	1.14	1.61	117	0.008
<i>Zooplankton biomass (μg DW l⁻¹)</i>						
Total zooplankton (TZOO)	77.51	85.51	52.47	29.85	66.00	0.750
Rotifera	1.76	2.10	5.16	10.69	87.00	0.369
Cladocera (CLA)	39.36	46.09	21.56	33.26	99.00	0.111
Calanoida (CAL)	23.29	36.17	11.28	17.42	55.50	0.354
CLA:TZOO	0.60	0.24	0.36	0.38	97.00	0.139
CAL:TZOO	0.16	0.21	0.25	0.34	54.50	0.323
TZOO:TPHY**	0.47	0.62	0.32	0.30	74.00	0.884
<i>Phytoplankton biovolume (mm³ l⁻¹)</i>						
Total phytoplankton (TPHYTO)	2.54	2.43	5.16	7.29	80.00	0.870
Bacillariophyceae	0.33	0.68	0.48	1.45	101.00	0.187
Chlorophyceae	0.23	0.19	0.33	0.41	80.00	0.870
Chrysophyceae	0.15	0.26	0.04	0.04	110.00	0.071
Cryptophyceae	0.10	0.12	0.15	0.20	84.00	0.702
Cyanobacteria (CYA)	1.45	1.71	3.76	7.20	78.00	0.956
Euglenophyceae	0.04	0.05	0.05	0.11	71.00	0.734
Dinophyceae	0.04	0.05	0.04	0.10	103.00	0.141
Zygnemaphyceae	0.01	0.02	0.13	0.32	51.50	0.153
CYA:TPHYTO	0.42	0.30	0.31	0.35	91.5	0.427

Significant results are highlighted in bold

*Values considered significant assuming $\alpha = 0.050$

**TPHY is the total phytoplankton biomass estimated as 66 times the chlorophyll *a* concentrations

as the TZOO:TPHY ratio) with an increase in temperature (Gyllström et al., 2005; Meerhoff et al., 2012). However, the differences in TZOO:TPHY were not significant, despite the significantly lower (instead of higher as expected) OMN:TZOO ratio in the warmer tropical lakes. Overall, the results above suggest that the lower fish biomass observed in the tropical lakes did not result in higher zooplankton biomass and lower phytoplankton biomass. This finding suggests that the pelagic trophic cascade seems even weaker in tropical than in subtropical regions. This finding is in line with a previous study showing that the introduction of the piscivorous peacock bass in tropical lakes had marked effects on the fish community structure, but only modest cascading effects on zooplankton and phytoplankton (Menezes et al., 2012). It also support the idea that the classic trophic cascading effects from piscivorous fish

to phytoplankton usually found in temperate lakes are more unlikely to occur in warm (sub)tropical lakes (Lazzaro, 1997; Jeppesen et al., 2007, 2010; Gelos et al., 2010; Lacerot et al., 2013). However, our regression analysis on the combined dataset showed a significant decrease in the total phytoplankton and cyanobacteria biomass (and the proportion of cyanobacteria to the total phytoplankton biomass) with an increase in the total zooplankton potential grazing pressure (for which we used the TZOO:TPHY ratio as a proxy). Phytoplankton biomass and cyanobacteria biomass also decreased with an increase in the ratio of calanoids to the total zooplankton biomass (CAL:TZOO), while it correlated positively to the omnivorous fish potential predation pressure on zooplankton (OMN:TZOO), indicating some recognizable cascading effects from the omnivorous fish on the phytoplankton communities of the studied lakes.

Fig. 3 Mann–Whitney–Wilcoxon test for differences in the catch per unit of effort (CPUE) of **A** total fish, **B** omnivores (OMN), and **C** piscivores (PISC) as well as **D** the ratio between OMN and total zooplankton biomass (OMN:TZOO) between tropical and subtropical lakes. Boxplots (25–75%, boxes; 10–90%, lines; median, horizontal line into the boxes). The black dots are irregularly distributed along the boxplots to avoid overlap. Only significant results are shown in the figure

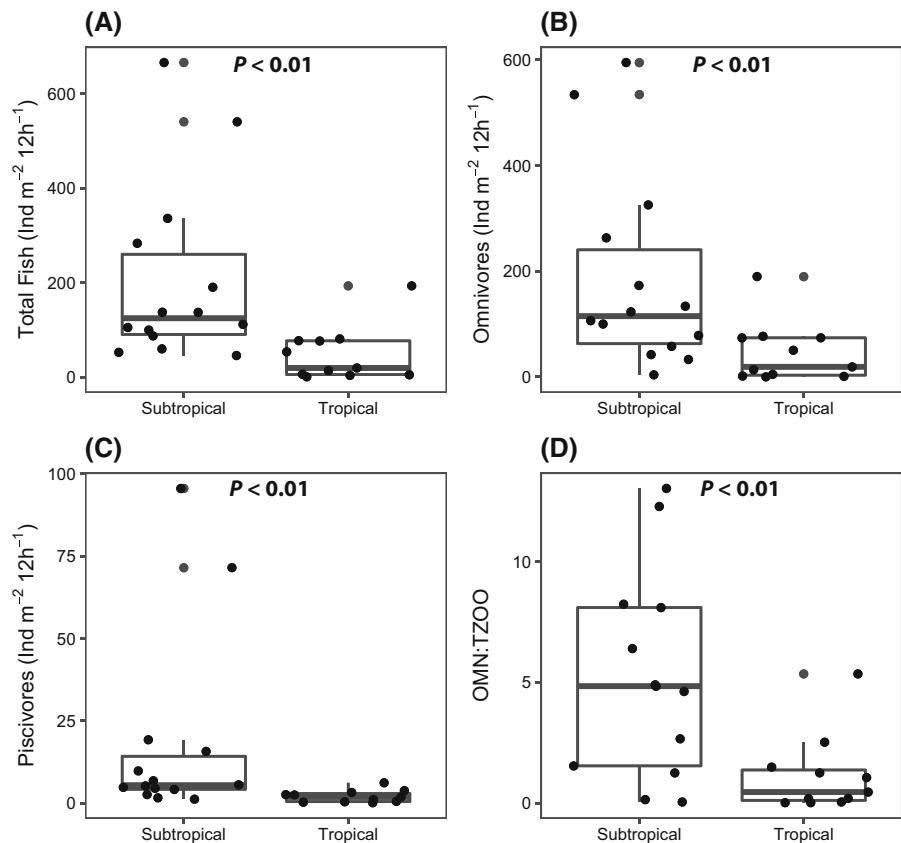


Table 4 Phytoplankton biovolume for cyanobacteria orders in subtropical and tropical lakes

Biovolume (mm ³ l ⁻¹)	Subtropical		Tropical	
	Mean	SD	Mean	SD
Chroococcales (tiny unicells)	0.155	0.222	0.138	0.079
Chroococcales (colonies; tiny cells)	1.108	1.444	1.957	4.412
Chroococcales (colonies; large cells)	0.061	0.153	1.426	5.046
Nostocales (filamentous; N-fixing)	0.002	0.007	0.116	0.393
Oscillatoriales (filamentous; non-N-fixing)	0.317	1.044	0.163	0.186

Results from the regression analyzes also showed a significant reduction in the biomass of calanoid copepods (and their proportion in the total zooplankton biomass) with an increase in the fish potential predation pressure on zooplankton (OMN:TZOO) and the proportion of cyanobacteria in total phytoplankton biomass (CYA:TPHYTO). This was not observed for cladoceran biomass. These results might indicate that calanoid copepods may have played an important role in controlling cyanobacterial biomass in these warm (sub)tropical lakes, although the negative relationship could also indicate that the cyanobacteria reduced the

fitness of these herbivores (Ger & Panosso, 2014; Ger et al., 2016a, b). Bloom-forming cyanobacteria are considered inedible or poor quality prey for zooplankton, and are increasingly becoming the dominant primary producers in lakes and reservoirs globally due to eutrophication and climate warming (Paerl & Huisman, 2008; Moss et al., 2011; Paerl & Paul, 2012). However, the dominant cyanobacteria in the studied lakes were not those forming blooms, but consisted mostly of small colonies and tiny unicells which can be edible to calanoid copepods and other zooplankters. Moreover, it may be expected that some

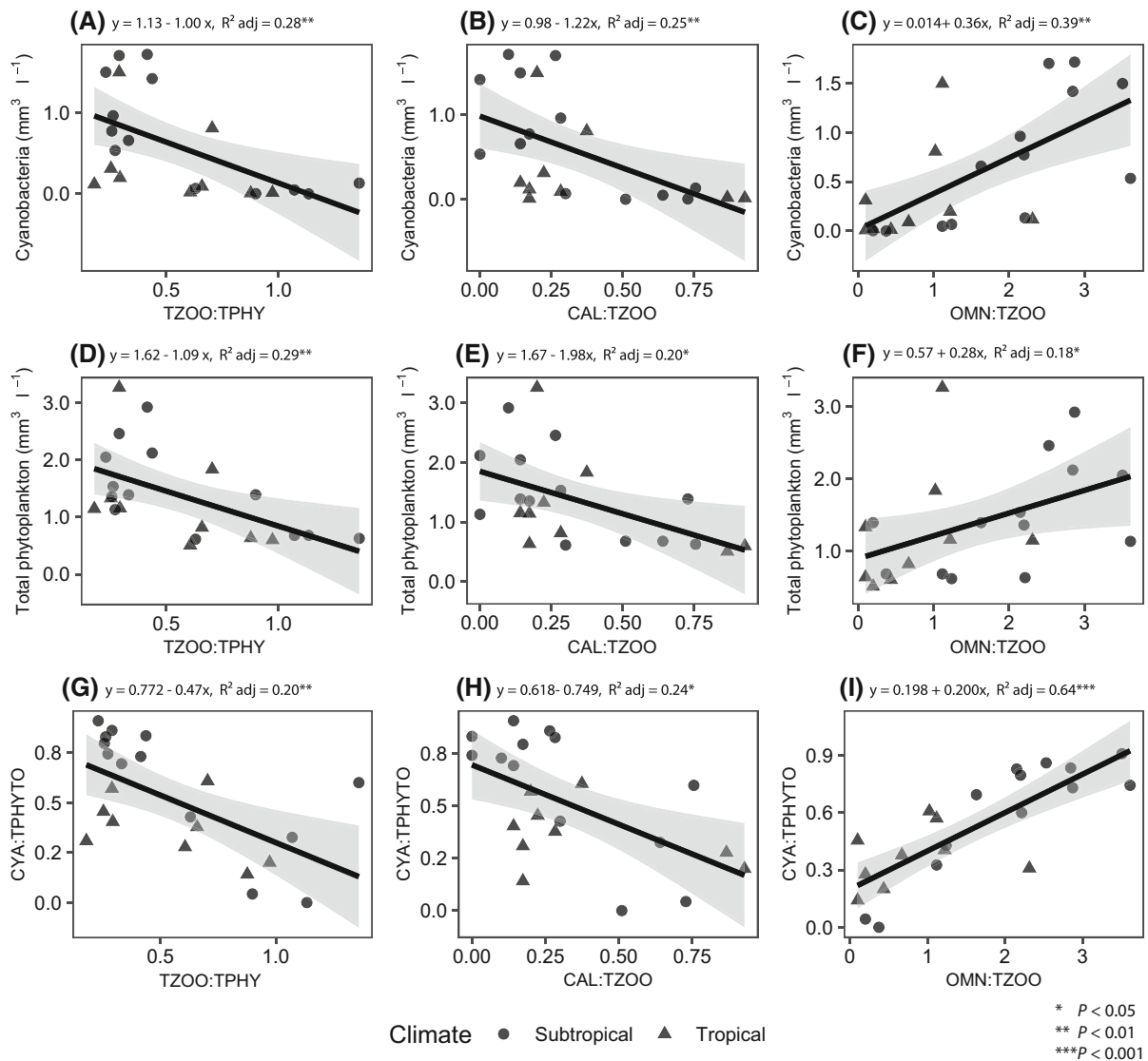


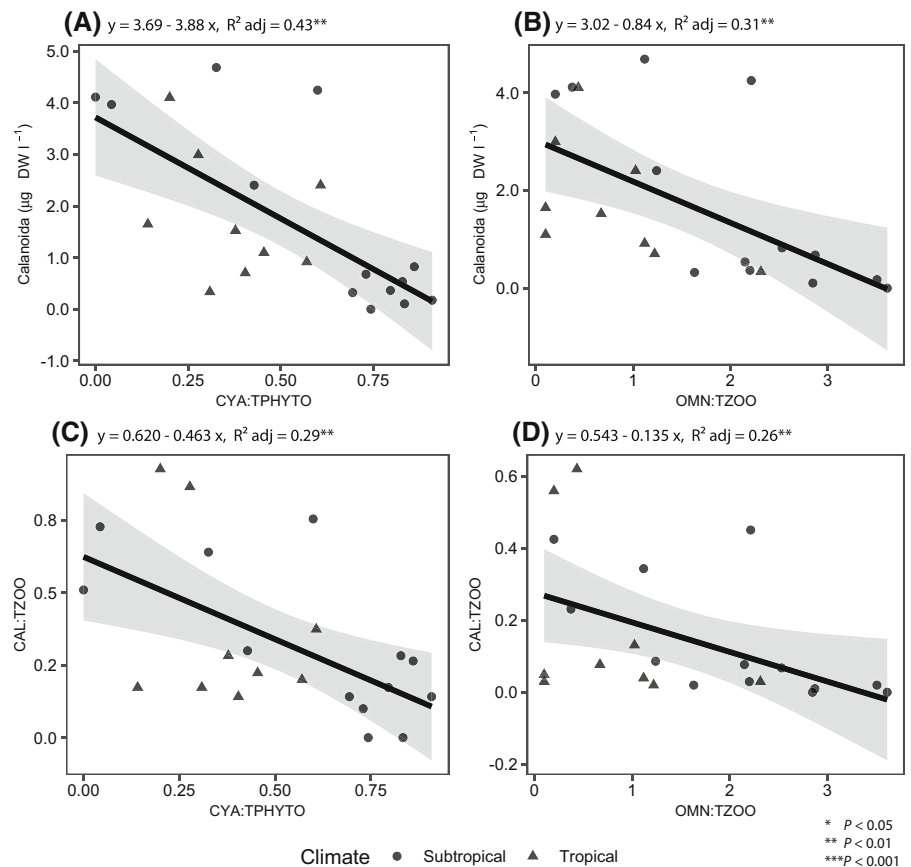
Fig. 4 Simple linear regressions using cyanobacteria (CYA), total phytoplankton (TPHYTO), and cyanobacteria to total phytoplankton ratio (CYA:TPHYTO) as the response variables, and total zooplankton to total phytoplankton (TZOO:TPHY),

calanoids to total zooplankton (TCAL:TZOO), and omnivorous fish to total zooplankton (OMN:TZOO) as the predictor variables in subtropical and tropical lakes. The shaded areas on the regression lines denote a 95% confidence interval

zooplankton have already evolved tolerance to cyanotoxins produced and may feed on cyanobacteria in environments where cyanobacterial blooms are historically common and persistent as in many warm (sub)tropical lakes. For instance, it has been demonstrated that grazing by neotropical calanoid copepods from the genus *Notodiatomus* can reduce the growth and biomass of the filamentous cyanobacteria *Raphidopsis raciborskii* (Leitão et al., 2020). All the seven species of calanoid copepods found in our studied

lakes belong to the *Notodiatomus* genus. This genus was the most abundant copepod taxa in our studied lakes, when compared to other genus of cyclopoid copepods. *Notodiatomus* can co-exist with and even graze down blooms of cyanobacteria and often dominate zooplankton biomass during long-lasting blooms (Panosso et al., 2003; Ger et al., 2016a, b). They may also promote cyanobacterial dominance by selectively grazing on their eukaryotic competitors (Ger et al., 2019; Leitão et al., 2018), but the strength

Fig. 5 Simple linear regressions using calanoids (CAL) and calanoids to total zooplankton ratio (CAL:TZOO) as the response variables, and cyanobacteria to total phytoplankton (CYA:TPHYTO) and omnivorous fish to total zooplankton (OMN:TZOO) ratios as the predictor variables in subtropical and tropical lakes. The shaded areas on the regression lines denote a 95% confidence interval



and duration of this copepod-enhanced cyanobacterial dominance is likely to depend on the traits of cyanobacteria in addition to the grazers (Ger et al., 2016a, b). Although the interpretation of causality in regression models from empirical data is problematic, our results support the idea that calanoid copepods from the genus *Notodiaptomus* can play an important role as keystone herbivores in warm (sub)tropical lakes dominated by non bloom-forming cyanobacteria.

Previous studies show that the combination of anthropogenic nutrient loading, rising temperatures, and enhanced vertical stratification favor cyanobacterial dominance in a wide range of aquatic ecosystems (reviewed by Paerl & Paul, 2012). For instance, Kosten et al. (2012) found that cyanobacteria biomass and the percentage of total phytoplankton biomass attributable to cyanobacteria increased markedly with temperature and total nitrogen concentrations in the water. Our results show that the warmer tropical lakes had higher TN but lower TP concentrations and higher

biomass of cyanobacteria than the subtropical lakes. The TN:TP ratio was also significantly higher in the tropical lakes, but in both sets of lakes, this ratio was low and below 16:1 (molar based), indicating potential nitrogen limitation of phytoplankton growth, which can favor nitrogen-fixing cyanobacteria. The low TN:TP ratio may reflect high temperature in the sediment, leading to intense bacterial activity, increased phosphorus release from sediments to the water column (Jensen and Andersen, 1992) and reduced nitrogen concentrations due to enhanced denitrification (Lewis Jr., 2000; Veraart et al., 2011; Moss et al., 2013). However, TN and TP concentrations in lake water are primarily a function of nutrient loads, which are strongly affected by hydrology and watershed characteristics such as soil type, land cover, and land use (Downing et al., 1999). We found no significant differences in land cover and land use patterns in the catchment of the studied lakes, but the higher TN and lower TP concentrations in the tropical lakes may result from differences in soil types.

Table 5 Analyses of covariance with a significant effect of the categorical variable climate (subtropical and tropical) on the explanatory power of the models

Models and response variables	Estimates	CI	<i>P</i> value	<i>R</i> ² adjusted	Model <i>P</i> value
(A) CYA:TPHYTO					
<i>Full model</i>					
Intercept	0.89	0.71–1.07	< 0.001	0.521	0.0004
TZOO:TPHY	– 0.50	– 0.75 to – 0.25	0.001		
Climate	– 0.25	– 0.42 to – 0.08	0.007		
<i>Reduced model</i>					
Intercept	0.77	0.58–0.97	< 0.001	0.327	0.003
TZOO:TPHYTO	– 0.47	– 0.77 to – 0.18	0.003		
<i>ANOVA</i>					
					0.007
(B) CAL (μg DW l⁻¹)					
<i>Full model</i>					
Intercept	4.2	2.83–5.56	< 0.001	0.450	0.001
OMN:TZOO	– 1.21	– 1.79 to – 0.63	< 0.001		
Climate	– 1.48	– 2.77 to – 0.19	0.027		
<i>Reduced model</i>					
Intercept	3.02	2.02–4.03	< 0.001	0.319	0.004
OMN:TZOO	– 0.84	– 1.38 to – 0.31	0.004		
<i>ANOVA</i>					
					0.027

(A) cyanobacteria to total phytoplankton ratio (CYA:TPHYTO) as a function of total zooplankton to total phytoplankton ratio (TZOO:TPHY) and climate, (B) calanoid biomass (CAL) as a function of omnivorous fish to total zooplankton ratio (OMN:TZOO) and climate. Significant *P* values (*P* < 0.05) are shown in bold. *N* = 22 lakes in all models; ANOVA test for differences between the explanatory power of the full and reduced models

CI confidence interval

In our study we controlled for many factors that could confound our analysis, such as sampling effort and methods, lake size and trophic state, and food web length (i.e., grossly approximated by piscivorous fish in the catch). However, we were not able to control for biogeography and biodiversity. In eastern South America, coastal lakes and lagoons have lower fish species richness in the tropical than in the subtropical regions (Petry et al., 2016). This pattern of fish species richness was also observed in our study and is congruent with the freshwater ecoregions of the world (Abell et al., 2008). Historical and biogeographical factors most likely caused the pattern of fish species richness we found. Fish species diversity is often positively correlated with fish biomass and productivity (Worm et al., 2006; Duffy et al., 2016). Besides, many factors, other than this biodiversity-ecosystem functioning relationship, may help explain the higher fish biomass observed in the richer subtropical lakes

when compared to the tropical ones, including metabolic restrictions at higher temperatures, different histories of fisheries or other unknown anthropic or natural variations.

Species interactions can profoundly alter species' responses to climate change (Gilman et al., 2010). The precise consequences for a given group of organisms or a given species depend, among other factors, on the direct effects of climate change on the species, the direct effects on interacting species, and the strength and climatic sensitivity of the interactions. Our results suggest that linear trophic cascade effects in lake communities do not occur with the same strength in warm (sub)tropical lakes compared to temperate ones. It is relevant to highlight, however, that several key components of shallow lake communities were not included in our study (e.g., benthic and littoral macroinvertebrates, and periphyton). Benthic macroinvertebrates can largely subsidise fish, leading

to different outcomes for other prey communities such as zooplankton, as found in lakes in different climatic zones (e.g., Vander Zanden & Vadeboncoeur, 2002). Periphyton can also subsidise fish where omnivory is extensive, as in warm regions (González-Bergonzoni et al., 2012, 2016). Other factors than direct effects of temperature may also affect the different lake communities and the interactions among them, producing unpredicted patterns in our focal groups. Changes in the precipitation regime might be more important than warming itself for the structure and functioning of subtropical and tropical shallow lakes, as suggested in a previous study comparing tropical semi-arid and humid lakes (Menezes et al., 2019).

Clearly, more studies on the effects of global warming on shallow lakes and other aquatic ecosystems at lower latitudes are needed as we cannot assume that already warm (sub)tropical systems will respond to warming in the same way as colder systems at higher latitudes. Such ecosystems may respond non-linearly to warming along a latitudinal gradient generating patterns at lower latitudes different from what is expected at higher latitudes.

Conclusions

Our results suggest that climate warming may have relatively minor impacts on the trophic structure and potentially also on the dynamics of shallow subtropical lakes; a suggestion that needs to be validated by other complementary approaches. South American tropical and subtropical coastal shallow lakes, despite having different fish biomass, did not show equally significant differences in the structure of plankton communities (as indicated by several variables and proxies). This suggests that linear trophic cascade effects on open water communities do not occur with the same strength in warm (sub)tropical lakes compared to temperate ones.

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Author contributions NM, SK, GL, and EJ contributed to the conceptual and methodological development of the ‘South

American Lake Gradient Analysis’ (SALGA) project. GL and SK co-coordinated the fieldwork. GL, SK, EJ, NM, VH, CWCB, DMM, JLA, and RFM conducted the fieldwork. VH and CK analyzed the phytoplankton samples, GL and CWCB analyzed the zooplankton samples, FTM, JHCG, JLA, NM, and GL analyzed the fish samples. This particular study was conceived by JLA, who wrote the first draft of the manuscript. RFM ran the statistical analyzes and made the tables and most figures. CCCM made Fig. 1 and the analyzes of land use/cover. MM contributed with a theoretical background and valuable suggestions to improve the manuscript. All authors discussed the results, commented on previous versions of the manuscript, and approved this final version.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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