

Crustacean zooplankton in lakes and reservoirs of temperate and tropical regions: variation with trophic status

Ricardo Pinto-Coelho, Bernadette Pinel-Alloul, Ginette Méthot, and Karl E. Havens

Abstract: The influence of trophic status on the crustacean zooplankton community was investigated in lakes and reservoirs in temperate and subtropical–tropical regions. We tested if there is a consistent relationship between crustacean species richness, assemblages, and abundance and trophic indices such as total phosphorus and chlorophyll *a*. We also examined if these patterns differ between regions. Cumulative species richness and assemblages varied among regions. The greatest number of crustacean species was found in the temperate oligotrophic region with the largest number of lakes sampled. However, cumulative species richness was similar in temperate and subtropical–tropical regions when comparing subsets with a similar number of lakes and reservoirs. The relationships between species richness and latitude or trophic status were difficult to assess owing to imbalance among regions in number of lakes and reservoirs sampled and to biogeography and fish predation potential influences. Trophic status was associated with changes in abundance of all major crustacean zooplankton groups. Eutrophic ecosystems supported greater crustacean abundances at all latitudes. However, cladocerans and cyclopoids were more abundant in eutrophic lakes and reservoirs, whereas calanoids were more abundant in temperate oligotrophic lakes. Total phosphorus was found to be a better predictor of the biomass of major crustacean groups than chlorophyll *a* in all regions.

Résumé : L'influence du statut trophique sur la communauté de crustacés planctoniques a été évaluée dans des lacs et réservoirs des régions tempérée, subtropicale et tropicale. Nous avons analysé les relations existant entre la richesse en espèces, les assemblages et l'abondance des crustacés et les indices trophiques comme le phosphore total et la chlorophylle *a*. Nous avons testé si ces relations différaient entre les régions. La richesse cumulée en espèces et les assemblages de crustacés variaient entre les régions. Le plus grand nombre d'espèces a été trouvé dans les lacs oligotrophes de la région tempérée, les plus nombreux. Toutefois, la richesse en espèces dans chaque des régions était semblable lorsque l'on comparait des sous-ensembles ayant le même nombre de lacs ou de réservoirs. Les relations entre la richesse en espèces et la latitude ou le statut trophique étaient difficiles à évaluer à cause du déséquilibre dans le nombre de lacs et de réservoirs étudiés dans chaque région et de l'influence potentielle de la biogéographie et de la prédation par les poissons. L'abondance des groupes de crustacés variait avec le statut trophique. Les milieux eutrophes supportaient des populations de crustacés plus abondantes à toutes les latitudes. Toutefois, les cladocères et les copépodes cyclopoïdes étaient plus abondants dans les lacs et réservoirs eutrophes, tandis que les copépodes calanoïdes étaient plus nombreux dans les lacs oligotrophes tempérés. Dans toutes les régions, le phosphore total avait un meilleur pouvoir de prédiction de la biomasse de la majorité des groupes de crustacés que la chlorophylle *a*.

Introduction

The empirical relationships between aquatic communities and lake trophic status have been studied extensively. Consistent models relating phytoplankton biomass to nutrients or water transparency have been developed for both temperate

and tropical lakes (Vollenweider 1976; Salas and Martino 1991). Despite some criticism and alternative proposals, the positive relationship between total phosphorus (TP) and phytoplankton chlorophyll *a* (Chl *a*) is one of the most robust global patterns in freshwater ecology. Recent efforts emphasize a more holistic approach, analyzing phytoplank-

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R. Pinto-Coelho. Depto. Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, 31270-901 Belo Horizonte, Brazil.

B. Pinel-Alloul¹ and G. Méthot. Groupe de Recherche Interuniversitaire en Limnologie (GRIL), Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succ. Centre-ville, Montréal, QC H3C 3J7, Canada.

K.E. Havens.² South Florida Management District, West Palm Beach, FL 33416, USA.

¹Corresponding author (e-mail: bernadette.pinel-alloul@umontreal.ca).

²Present address: Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL 32653-3071, USA.

ton responses to lake trophy over large geographic scales or under different food web and morphometry conditions (Mazumder and Havens 1998).

Zooplankton have long been used as an indicator of lake trophy (Gannon and Stemberger 1978; Bays and Crisman 1982; Pejler 1983). Nonetheless, variable responses of zooplankton to trophic status are common (Ravera 1996), perhaps in part because zooplankton also respond to other environmental factors, such as lake water chemistry, shoreline disturbances, and watershed land use (Pinel-Alloul et al. 1990; Stemberger and Lazorchak 1994; Patoine et al. 2000) as well as levels of vertebrate and invertebrate predation (Hulot et al. 2000). Moreover, most studies dealing with zooplankton communities have focused on lakes with similar features located in restricted latitude ranges.

The main goal of this study is to test if there are consistent relationships between crustacean zooplankton community characteristics and trophic indices across a large geographic scale covering a variety of lakes and reservoirs in temperate and subtropical–tropical areas. The specific objectives are to (i) identify and compare the patterns of responses of species richness and abundance of major groups of crustacean zooplankton to increasing trophy in temperate and subtropical–tropical regions, (ii) test which indicator (e.g., TP and Chl *a*) of trophic status is the best predictor of the variability in crustacean zooplankton biomass, and (iii) test if the relationships between these trophic indicators and the biomass of crustacean zooplankton in lakes and reservoirs differ among regions.

Methods

Study regions

In carrying out a comparison of lakes in different geographic regions using preexisting survey data, it is an optimal strategy to establish if the lakes selected for study are unbiased representatives of the regions under consideration. In reality, however, the availability of similar data makes it difficult to reach this goal, especially when data from tropical regions are compared. In this study, we attempted to use the most representative data available in temperate and subtropical–tropical areas.

In the temperate zone, we used data from Canadian lakes covering a wide range of trophic states. The Coldwater region in northwestern Ontario (Fig. 1) is represented by five small, dimictic lakes (Table 1). They have mean depths less than 12 m and areas up to 57 ha and are oligotrophic, with low concentrations of Chl *a* (1–3 $\mu\text{g}\cdot\text{L}^{-1}$) and TP (4–8 $\mu\text{g}\cdot\text{L}^{-1}$). The Boreal Shield Sustainable Forest Management (SFM) region is represented by 38 headwater lakes in Quebec (Fig. 1; Table 1). Mean depth and area in these lakes range between 2 and 10 m and between 14 and 81 ha, respectively. They are oligomesotrophic with maximum Chl *a* and TP reaching 3 and 11 $\mu\text{g}\cdot\text{L}^{-1}$, respectively. The Terrestrial Riparian Organisms of Lakes and Streams (TROLS) region is represented by 12 small, shallow eutrophic lakes on the Alberta Boreal Plain (Fig. 1; Table 1), with higher levels of Chl *a* (6–33 $\mu\text{g}\cdot\text{L}^{-1}$) and TP (26–123 $\mu\text{g}\cdot\text{L}^{-1}$).

In subtropical Florida, data are available for five lakes (one lake including two basins) encompassing a wide range of trophic state (Fig. 1; Table 1). The lakes are located in the

headwaters of the Kissimmee River, a major inflow to Lake Okeechobee. They have large surface areas (27–144 km^2) but very shallow depths (2–4 m maximum depth) and are eutrophic with Chl *a* concentrations being generally above 20 $\mu\text{g}\cdot\text{L}^{-1}$, except for two lakes below 6 $\mu\text{g}\cdot\text{L}^{-1}$. TP concentrations vary from 31 to 84 $\mu\text{g}\cdot\text{L}^{-1}$.

The tropical South America region was represented by reservoirs because natural lakes are scarce in that geographic region (Tundisi et al. 1981). Additionally, as most natural lakes in this area are very small and strongly influenced by flooding from their adjacent large river systems, they were not included in the comparison. The four Brazilian reservoirs differ widely in their trophic state. The Volta Grande reservoir (age 24 years, former land cover *cerrado* vegetation) is located in the lower Rio Grande, one of the rivers forming the Paraná River. It is an oligomesotrophic reservoir with an area of 205 km^2 and a volume of $2.3 \times 10^9 \text{ m}^3$ (Table 1). Chl *a* concentrations were lower than 4 $\mu\text{g}\cdot\text{L}^{-1}$. Mean TP concentration was 14.3 $\mu\text{g}\cdot\text{L}^{-1}$ and ranged from 7 to 30 $\mu\text{g}\cdot\text{L}^{-1}$. Furnas Reservoir, located in the upper Rio Grande (Fig. 1), is one of the largest reservoirs of South America (age 41 years, former land cover *cerrado* vegetation). It has a flooded area of 1459 km^2 , a volume of $2.3 \times 10^{10} \text{ m}^3$, a maximum depth of 90 m, and a mean depth of 15.7 m. Trophic state varies within the reservoir, and TP concentrations are low (6–7 $\mu\text{g}\cdot\text{L}^{-1}$) in the central zone but reach higher values (35 $\mu\text{g}\cdot\text{L}^{-1}$) in the most eutrophic zones (Sapucaí River). Chl *a* ranges from 1–2 $\mu\text{g}\cdot\text{L}^{-1}$ in the central zone to 7–11 $\mu\text{g}\cdot\text{L}^{-1}$ in the eutrophic zones (Table 1). Pampulha and Ibitiré reservoirs are urban, shallow, and eutrophic and are located in the northern part of Belo Horizonte City, Brazil. The former land cover of both reservoirs consisted of transitional vegetation between *cerrado* and tropical rain forest. Both reservoirs have a small surface area (2.1–2.7 km^2) and mean depth (3.4–4.8 m) (Table 1). In Pampulha reservoir (age 64 years), Chl *a* concentrations range from 12 to 59 $\mu\text{g}\cdot\text{L}^{-1}$ and TP concentrations reach 269 $\mu\text{g}\cdot\text{L}^{-1}$. In Ibitiré reservoir (age 27 years), Chl *a* reaches a maximum of 50 $\mu\text{g}\cdot\text{L}^{-1}$ and TP ranges from 35 to 45 $\mu\text{g}\cdot\text{L}^{-1}$.

Further details about the limnological characteristics of the different ecosystems were previously presented in Carignan et al. (2000), Steedman (2000), and Prepas et al. (2001) for Canadian lakes, Havens et al. (2000a) for Florida lakes, and Pinto-Coelho (1998) for Brazilian reservoirs.

Sampling and analysis of zooplankton

The database included seasonal or annual means of crustacean zooplankton abundance (density and biomass). In the temperate region (Northern Hemisphere), samples were collected during the ice-free season (May–October). In Brazilian reservoirs, we took annual means excluding only data from periods of heavy rains. In Florida, the averages were based on bimonthly sampling over a 21-month period. The objective was to exclude periods with extreme conditions (ice-cover during winter in temperate regions and high flushing in the tropics) and thereby increase the possibility of detecting differences that could be attributed to trophic state.

In a large comparison of zooplankton from different regions, it is optimal if sampling methods do not vary in a manner that might bias the results and conclusions. In this study, most of the zooplankton were collected in the whole

Fig. 1. Locations of the study lakes and reservoirs in North and South America.

water column with vertical net tows of small mesh size nets (53–150 μm) that retain most adult crustaceans (Table 2). The fixation and counting procedures were quite similar and the biomass estimations (milligrams dry weight per cubic metre) were done using length–biomass allometric equations.

The Coldwater lakes were sampled seven times during the ice-free season (May–October) from 1991 to 1995 summing 175 samples (Table 2). In the Boreal Quebec SFM lakes, sampling was carried out in 38 lakes in June, August, and September 1996 (114 samples). In the TROLS lakes, the data set includes 48 seasonal integrated samples obtained for

each lake during the years 1995–1998. These composite year samples integrate 7–11 samples taken in each lake during the ice-free season. In Florida, sampling was conducted in the five lakes (at six collecting sites because the largest lake had two distinct segments) between April 1997 and January 1999 (98 samples). In Volta Grande reservoir, the sampling was done at a central site from November 1997 to January 1999 (14 composite samples). In Furnas reservoir, the data set includes 11 sites distributed in four regions in the reservoir along a trophic gradient from oligotrophic to eutrophic sites, and the sampling was done every 3 months between

Table 1. Localization, morphometric characteristics, and trophic features of the selected ecosystems.

Region	Latitude	Longitude	No. of lakes (sites)	Area (km ²) (min.–max.)	Volume (m ³) (min.–max.)	Z _{max} (m) (min.–max.)	Z _m (m) (min.–max.)	TP (µg·L ⁻¹) (min.–max.)	Chl <i>a</i> (µg·L ⁻¹) (min.–max.)
Ontario Coldwater lakes	49°07'N	92°12'W	5	0.28–0.57	1.7 × 10 ⁵ – 6.2 × 10 ⁵	13.5–37	6.4–11.8	4–8	1–3
SFM lakes	48°50'N	75°00'W	38	0.14–0.81	4.5 × 10 ⁶ – 8.5 × 10 ⁶	5–34	2.0–10.0	7–11	2–3
TROLS lakes	55.1°–55.4°N	111.7°–113.8°W	12	0.14–1.57	3.7 × 10 ⁶ – 7.4 × 10 ⁶	2.1–9.4	0.6–4.7	26–123	6–33
Florida lakes	27–28°N	81°W	5 (6)	27–144	—	2–4	—	31–84	3–31
Volta Grande reservoir	19°–20°S	47°–48°W	1	205	2.3 × 10 ⁹	19–22	8.2–11.2	7–30	1–4
Furnas reservoir	20°–21°S	45°–46°W	1 (11)	1459	2.3 × 10 ¹⁰	85–90	10.7–15.7	6–35	1–11
Ibirité reservoir	19°S	43°W	1 (2)	2.7	1.0 × 10 ⁶	11–13	3.4–3.7	35–45	8–50
Pampulha reservoir	19°S	43°W	1 (9)	2.1–2.4	1.1 × 10 ⁷ – 1.2 × 10 ⁷	16–17	4.8–5.2	25–269	12–59

Note: Data are ranges of seasonal means in epilimnion waters. Seasonal averages (May–October) were considered for temperate lakes. Annual averages were considered for Florida lakes and tropical reservoirs (excluding rainy period for the latter). Z_{max}, maximum depth; Z_m, mean depth; TP, total phosphorus; Chl *a*, chlorophyll *a*; SFM, Quebec Sustainable Forest Management; TROLS, Alberta Terrestrial Riparian Organisms of Lakes and Streams.

August 1999 and July 2000 (total of 48 samples). For Ibirité reservoir, the data set includes samples collected at two different sites every 2 weeks between August 1996 and January 1997 (12 samples). The data for Pampulha reservoir includes two sampling periods: October 1984 to November 1985 and February 1993 to November 1998. Samples were collected at three different stations in 1984–1985 and in a single station located in the central part of the reservoir during 6 years from 1993 to 1998 (total of 150 samples).

In the Coldwater, Quebec, and Alberta lakes, the zooplankton were sampled at the deepest point in each lake using a conical net or a cantilevering net with a 53-µm mesh size (Table 2). Vertical tows were made upwards through the water column from 1.0 m above the sediment to the surface. Filtered water volume varied from 80 to 1200 L. The biomass was estimated using length–weight equations (Malley et al. 1989). In Florida lakes, macrozooplankton were collected with two vertical tows of conical plankton net (30 cm in diameter, 150-µm mesh size). Tows were made from near the lake bottom to the water surface. Duplicate samples were pooled and preserved with 10% formaldehyde. In Volta Grande, Furnas, and Ibirité reservoirs, zooplankton were collected by means of vertical net hauls (65 cm in diameter, 90-µm mesh size) from 1.0 m from the lake bottom to the surface. In Pampulha reservoir, for the 1984–1985 period, zooplankton also were sampled using a conical 45-cm-diameter net with a 90-µm mesh size gauze, while a 5.13-L Schindler–Patalas trap with a 70-µm mesh size was used for the other periods. For subtropical and tropical regions, species biomass was estimated using length–weight equations provided by McCauley (1984).

Statistical analysis

To visualize and compare the effects of trophic status and latitude on crustacean zooplankton species assemblages, we used linear and nonlinear canonical correspondence analyses (CCAs) (ter Braak 1994; Legendre and Legendre 1998; Makarenkov and Legendre 2002). The annual maximum biomass of Cladocera, Cyclopoida, and Calanoida were considered as dependent variables. The independent variables were latitude, TP, and Chl *a*. All data were log transformed prior to analysis to better approximate normal distributions.

To assess and separate the possible effects of latitude and trophic status on each crustacean zooplankton group, we performed two-sample *t* tests. Following this, regressions between each zooplankton group and Chl *a* and TP were done. ANCOVA was used to evaluate and compare the regressions after first testing homogeneity of slopes. All analyses were performed using SYSTAT version 8.0 (SYSTAT Software Inc., Point Richmond, California).

Results

Species richness and crustacean community structure

Total cumulative species richness including all three groups of crustacean zooplankton (Cyclopoida, Calanoida, and Cladocera) was much higher in temperate oligotrophic lakes of Canada (region 1: 52 species) than in the other geographic regions or trophic categories (Table 3). Eutrophic lakes and reservoirs had lower cumulative species richness in both temperate (region 2: 26 species) and subtropical–

Table 2. Zooplankton sampling devices, net mesh sizes, sampling depths, study periods, and total sampling effort and samples in each lake region and reservoir.

Region	Sampling device	Net mesh size (μm)	Sampling depth	Study period	Sampling effort per season and total samples
Ontario Coldwater lakes	Conical net	53	Total column	1991–1995: May–October	7 samplings per year, 5 lakes, 175 samples
SFM lakes	Cantilevering net	53	Total column	1996: June, August, September	3 samplings per year, 38 lakes, 114 samples
TROLS lakes	Conical net	53	Total column	1995–1998: May–October, composite samples	12 lakes, 4 years, 48 samples
Florida lakes	Conical net	150	Total column	1997–1999: 21-month survey	5 lakes, 6 sites, 98 samples
Volta Grande reservoir	Conical net	90	Total column	1997–1999: composite samples	1 site, 14 samples
Furnas reservoir	Conical net	90	Total column	1999–2000: 1-year survey	11 sites, 48 samples
Ibirité reservoir	Conical net	90	Total column	1996–1997: 6-month survey	2 sites, 12 samples
Pampulha reservoir	Conical net	90	Total column	1984–1985	3 sites
	Schindler–Patalas trap			1993–1998	1 site, 6 years, 150 samples

Note: SFM, Quebec Sustainable Forest Management; TROLS, Alberta Terrestrial Riparian Organisms of Lakes and Streams.

tropical regions (region 3: 21 species; region 5: 15 species). Oligotrophic tropical reservoirs also presented lower total species richness (region 4: 25 species).

Sixteen species of cyclopoids were found in the oligotrophic lakes in Canada (region 1 in Table 3), including the following genera: *Acanthocyclops*, *Cyclops*, *Diacyclops*, *Eucyclops*, *Mesocyclops*, *Orthocyclops*, *Paracyclops*, and *Tropocyclops*. In the eutrophic lakes in Canada (region 2), seven cyclopoid species were present. In Florida lakes (region 3), only three cyclopoid species were found (*Acanthocyclops vernalis*, *Mesocyclops edax*, and *Tropocyclops prasinus*); all of them also occurred in Canadian lakes. In the tropical reservoirs (regions 4 and 5), six cyclopoid species were recorded, at both eutrophic and oligotrophic sites. These species are endemic to tropical areas and were not found in the temperate or subtropical lakes (Table 3).

Calanoid species are more diversified in oligotrophic than in eutrophic systems, and they form a regional fauna, since no calanoid species co-occurred in the three regions studied (Canada, Florida, and Brazil). In the oligotrophic lakes in eastern Canada (region 1 in Table 3), nine calanoid species were recorded: *Aglaodiaptomus spatulocrenatus*, *Aglaodiaptomus* sp., *Epischura lacustris*, *Leptodiaptomus ashandi*, *Leptodiaptomus minutus*, *Leptodiaptomus sicilioides*, *Leptodiaptomus sicilis*, *Leptodiaptomus* sp., and *Skistodiaptomus oregonensis*. In the eutrophic lakes in western Canada (region 2), only three species of calanoids were present: *Acanthodiaptomus denticornis*, *E. lacustris*, and *S. oregonensis*. In Florida lakes, just two diaptomids were found: *Diaptomus dorsalis* and *Diaptomus floridanus*. Calanoids were relatively diverse in oligotrophic tropical reservoirs, where up to six different species (*Argyrodiaptomus furcatus*, *Notodiaptomus iheringi*, *Notodiaptomus* cf. *nordestinus*, *Notodiaptomus cearensis*, *Notodiaptomus henseni*, and *Scolodiaptomus corderoi*) were found, whereas only one species (*S. corderoi*) was recorded in the eutrophic tropical reservoirs.

One typical feature of cladoceran assemblages in the temperate region is higher species richness, especially for the genus *Daphnia* (Table 3). Fourteen species of *Daphnia* were

found in the oligotrophic lakes in Canada (region 1). In the eutrophic lakes in Canada (region 2), the richness in *Daphnia* was lower but not less than eight different species were found. In contrast, 14 cladoceran species and only two *Daphnia* species (*Daphnia laevis* and *Daphnia gessneri*) were found in the Brazilian oligotrophic and eutrophic reservoirs (regions 4 and 5). The cladoceran community in Florida lakes (region 3) was relatively rich, with 16 species being reported, but it contained just two daphnids (*Daphnia ambigua* and *Daphnia lumholtzi*), one of which is an introduced exotic (Table 3). The predacious *Leptodora kindtii*, a common predator zooplankton in the Coldwater lakes, as well as the gelatinous *Holopedium gibberum* (Coldwater and SFM lakes) are missing in the Brazilian reservoirs. However, Florida lakes have some cladoceran species in common with Canadian lakes such as *H. gibberum*, *D. ambigua*, *Diaphanosoma brachyurum*, *Sida crystallina*, *Chydorus sphaericus*, and *Alona guttata*. Florida lakes also contain *L. kindtii* (K.E. Havens, personal observations), although none were contained in the samples evaluated here. Other species such as *Bosminopsis deitersi* and *Ceriodaphnia rigaudi*, common in Florida lakes, are recorded in the tropical reservoirs as well. In Florida lakes, a number of noneuplanktonic cladoceran species like *Ilyocryptus spinifer*, *Macrothrix rosea*, or *A. guttata* also appear, probably associated with the high biomass of floating aquatic vegetation that develops during summer in these ecosystems.

The structure of zooplankton communities at different latitudes was further explored by CCA ordination of crustacean species assemblages (Fig. 2). The statistics associated with this analysis indicate that the variables describing trophic state (TP and Chl *a*) as well as latitude explained a high and significant proportion of the total variability in crustacean zooplankton community structure, expressed in terms of biomass of zooplankton groups. The mean coefficient of determination (R^2) was 0.70. The percentage of total variance explained by the first two axes was 69% and the sum of the two first canonical eigenvalues was 0.30 (first = 0.23, second = 0.07). Both linear and nonlinear models have statistical sig-

Table 3. Crustacean species in the selected lakes and reservoirs of each region.

Species	Region				
	1	2	3	4	5
Cyclopoida					
<i>Acanthocyclops carolinus</i>		×			
<i>Acanthocyclops vernalis</i>	×	×	×		
<i>Cyclops scutifer</i>	×				
<i>Diacyclops bicuspidatus thomasi</i>	×	×			
<i>Diacyclops nanus</i>	×	×			
<i>Daicyclops navus</i>	×				
<i>Eucyclops serrulatus</i>	×				
<i>Eucyclops speratus</i>	×				
<i>Mesocyclops brasilianus</i>					×
<i>Mesocyclops edax</i>	×	×	×		
<i>Mesocyclops leuckarti</i>	×	×			
<i>Mesocyclops longisetus</i>				×	×
<i>Mesocyclops meridianus</i>				×	×
<i>Mesocyclops ogunnus</i>			×		
<i>Mesocyclops</i> sp.	×			×	
<i>Metacyclops mendocinus</i>			×	×	
<i>Orthocyclops modestus</i>	×				
<i>Paracyclops affinis</i>	×				
<i>Paracyclops poppei</i>	×				
<i>Thermocyclops decipiens</i>				×	×
<i>Thermocyclops minutus</i>				×	
<i>Tropocyclops prasinus</i>	×	×	×		
<i>Tropocyclops prasinus mexicanus</i>	×				
<i>Tropocyclops</i> sp.	×				
Total	16	7	3	6	6
Calanoida					
<i>Acanthodiaptomus denticornis</i>		×			
<i>Aglaodiaptomus</i> sp.	×				
<i>Aglaodiaptomus spatulocrenatus</i>	×				
<i>Argyrodiaptomus furcatus</i>				×	
<i>Epischura lacustris</i>	×	×			
<i>Diaptomus dorsalis</i>			×		
<i>Diaptomus floridanus</i>			×		
<i>Leptodiaptomus ashlandi</i>	×				
<i>Leptodiaptomus minutus</i>	×				
<i>Leptodiaptomus siciloides</i>	×				
<i>Leptodiaptomus sicilis</i>	×				
<i>Leptodiaptomus</i> sp.	×				
<i>Notodiaptomus iheringi</i>				×	
<i>Notodiaptomus</i> cf. <i>nordestinus</i>				×	
<i>Notodiaptomus cearensis</i>				×	
<i>Notodiaptomus henseni</i>				×	
<i>Scolodiaptomus corderoi</i>				×	×
<i>Skistodiaptomus oregonensis</i>	×	×			
Total	9	3	2	6	1
Cladocera					
<i>Acroperus harpae</i>			×		
<i>Alona guttata</i>		×	×		
<i>Alonella nana</i>	×				
<i>Alonella excisa</i>		×			
<i>Bosmina hagmanii</i>				×	×
<i>Bosmina longirostris</i>	×			×	×

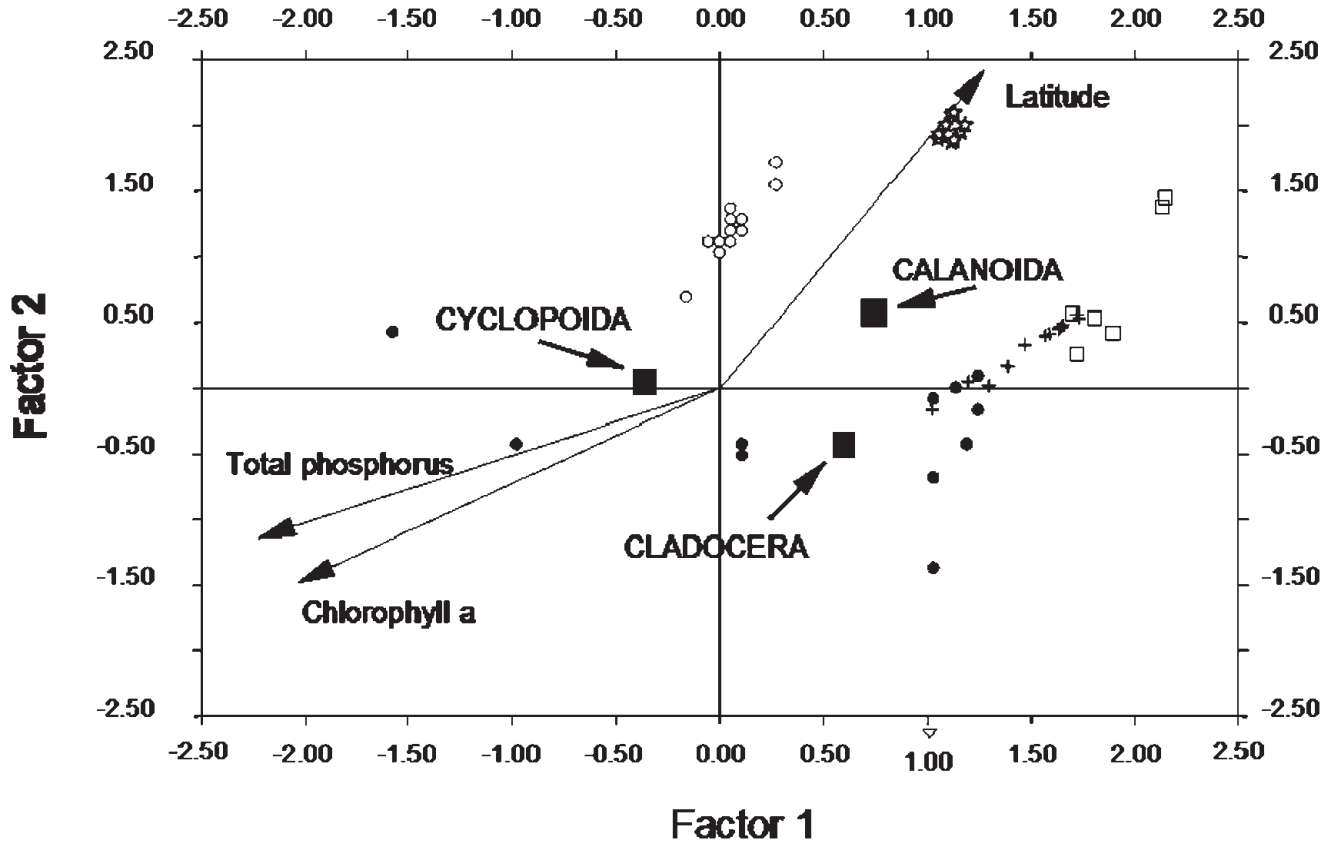
Table 3 (concluded).

Species	Region				
	1	2	3	4	5
<i>Bosminopsis deitersi</i>			×	×	
<i>Camptocercus rectirostris</i>			×		
<i>Ceriodaphnia cornuta</i>				×	×
<i>Ceriodaphnia c. righaudi</i>			×	×	×
<i>Ceriodaphnia lacustris</i>	×	×			
<i>Ceriodaphnia megops</i>		×			
<i>Ceriodaphnia pulchella</i>	×				
<i>Ceriodaphnia</i> sp.	×			×	
<i>Chydorus sphaericus</i>		×	×		
<i>Chydorus piger</i>	×	×			
<i>Daphnia ambigua</i>	×		×		
<i>Daphnia catawba</i>	×	×			
<i>Daphnia dubia</i>	×				
<i>Daphnia galeata</i>	×	×			
<i>Daphnia gessneri</i>				×	×
<i>Daphnia laevis</i>	×				×
<i>Daphnia longiremis</i>	×	×			
<i>Daphnia longispina</i>	×				
<i>Daphnia lumholtzi</i>			×		
<i>Daphnia mendotae</i>	×	×			
<i>Daphnia middendorffiana</i>	×				
<i>Daphnia parvula</i>	×	×			
<i>Daphnia pulex</i>	×	×			
<i>Daphnia retrocurva</i>	×				
<i>Daphnia rosea</i>	×	×			
<i>Daphnia</i> sp.	×	×			
<i>Diaphanosoma birgei</i>				×	×
<i>Diaphanosoma brachyurum</i>	×	×	×		
<i>Diaphanosoma brevireme</i>				×	
<i>Diaphanosma fluviatile</i>				×	
<i>Diaphanosoma spinulosum</i>				×	
<i>Diaphanosoma</i> sp.	×	×			
<i>Echinisca rosea</i>			×		
<i>Eubosmina longispina</i>	×				
<i>Eubosmina tubicen</i>			×		
<i>Holopedium gibberum</i>	×		×		
<i>Ilyocryptus spinifer</i>			×		
<i>Leptodora kindtii</i>	×				
<i>Macrothrix rosea</i>			×		
<i>Moina micrura</i>				×	×
<i>Moina minuta</i>				×	
<i>Ophryoxus gracilis canadiensis</i>	×				
<i>Pleuroxus striatus</i>			×		
<i>Sida crystallina</i>	×		×		
Total	27	16	16	13	8

Note: Region 1, oligotrophic lakes in Canada (Ontario Coldwater and Quebec Sustainable Forest Management lakes); region 2, eutrophic lakes in Canada (Alberta Terrestrial Riparian Organisms of Lakes and Streams lakes); region 3; Florida lakes; region 4, oligotrophic reservoirs in Brazil (Volta Grande and Furnas); region 5, eutrophic reservoirs in Brazil (Pampulha and Ibirité).

nificance ($P = 0.001$, 999 permutations), and the probability of a significant difference between the models was not significant ($P = 0.338$). Thus, we used the simpler (linear) com-

Fig. 2. Biplot diagram of canonical correspondence analysis (CCA). Zooplankton data used: maximum values of biomass of crustacean groups. Scaling of rows and columns: centering the biotic variables in relation to the site variables. Environmental variables: total phosphorus, chlorophyll *a*, latitude vectors (arrows). Biotic variables: Cyclopoida, Cladocera, and Calanoida (solid squares). Sites: region 1, temperate oligotrophic lakes (stars); region 2, temperate eutrophic lakes (open circles); region 3, subtropical Florida lakes (open squares); region 4, tropical oligotrophic reservoirs (crosses); region 5, tropical eutrophic reservoirs (solid circles). All data were log transformed.



bination of environmental and zooplankton variables in the CCA ordination (Fig. 2).

The two-dimension graph of CCA results (Fig. 2) clearly displays three main clusters of crustacean zooplankton associated with oligotrophic Coldwater-SFM lakes, eutrophic TROLS lakes, oligotrophic and eutrophic Brazilian reservoirs, and some of the Florida lakes. A fourth cluster contains two of the most oligotrophic Florida lakes (Fig. 2, upper right) and two sites from the Pampulha reservoir were spread in opposite direction (Fig. 2, lower left). The scaling procedure centered the scores (coordinates) of the biomass of the three crustacean groups in relation to the site scores. Cyclopoids and cladocerans were associated with the more eutrophic lakes and reservoirs. Cladocerans were positioned more closely to eutrophic tropical reservoirs, whereas cyclopoids appeared to be associated with the TROLS lakes and the hypertrophic Pampulha reservoir. Calanoids occupied a distinct position, in association with more oligotrophic ecosystems in both latitudinal regions.

The vectors of environmental variables were positioned in different regions of the CCA ordination (Fig. 2). In the negative region of axes 1 and 2, the variables were associated with trophic indices (TP and Chl *a*). The latitude vector appeared in the positive region of axes 1 and 2. This suggests

the existence of different effects of latitude and trophic state on crustacean zooplankton structure.

Crustacean density and biomass

The comparison between annual means and annual maximum values of crustacean biomass and density revealed clear differences between tropical and temperate areas. The highest values of mean density and biomass were always observed in small eutrophic tropical systems for the cladocerans and cyclopoids, but no difference was found for the calanoids (Table 4).

The range of variability in the data was considerably greater in the small eutrophic tropical systems. The cyclopoids exhibited a large range of variation in abundance (density and biomass) across the trophic state gradients in temperate and tropical regions (Table 4). In temperate systems, cyclopoid mean density ranged from 14.2 individuals·L⁻¹ (biomass = 7.5 mg dry weight·m⁻³) in the Coldwater lakes to 45.2 individuals·L⁻¹ (biomass = 13.6 mg dry weight·m⁻³) in the TROLS lakes. The abundance of cyclopoids was low in the Florida lakes as well as in the large oligotrophic tropical reservoirs (density = 0.7–2.6 individuals·L⁻¹, biomass = 1.2–2.0 mg dry weight·m⁻³). In the small eutrophic tropical reservoirs, cyclopoid abundance was much higher (density = 88.2 individuals·L⁻¹, biomass = 79.1 mg dry weight·m⁻³).

Table 4. Mean and maximum abundance (density and biomass) of major crustacean zooplankton groups in the selected temperate and tropical ecosystems.

Lake regions	Cyclopoida				Calanoida				Cladocera			
	Density (individuals·L ⁻¹)		Biomass (mg dry weight·m ⁻³)		Density (individuals·L ⁻¹)		Biomass (mg dry weight·m ⁻³)		Density (individuals·L ⁻¹)		Biomass (mg dry weight·m ⁻³)	
	Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.
Temperate regions												
SFM lakes	19.2	60.1	10.1	30.3	12.2	88.8	9.6	26.9	1.4	28.0	22.7	375.5
Ontario Coldwater lakes	14.2	62.4	7.5	68.7	7.7	43.9	10.6	59.9	3.8	19.0	2.8	18.3
TROLS lakes	45.2	266.2	13.6	116.3	18.5	98.8	10.3	56.9	10.5	63.2	14.8	133.8
Tropical regions												
Florida lakes	0.7	7.0	1.2	51.7	1.7	31.9	10.2	158.2	3.6	52.4	4.4	74.0
Large oligotrophic tropical reservoirs	2.6	9.8	2.0	14.4	1.7	7.5	2.1	11.9	7.3	66.1	8.2	92.4
Small eutrophic tropical reservoirs	88.2	2148.1	79.1	1829.7	9.1	175.4	7.6	102.7	34.8	286.5	169.9	4263.0

Note: In temperate regions, averages were based on ice-free months (May–October or June–September). In tropical regions, the averages refer to the annual cycle excluding the periods of heavy rains (months with more than 100 mm rainfall). SFM, Quebec Sustainable Forest Management; TROLS, Alberta Terrestrial Riparian Organisms of Lakes and Streams.

The mean density of calanoids in temperate regions ranged from 7.7 to 18.5 individuals·L⁻¹ (Table 4). The biomass values of this group of crustaceans in Canadian lakes varied in a narrow range of values (9.6–10.6 mg dry weight·m⁻³). In the tropical regions, calanoids always exhibited lower values of density (up to 9.1 individuals·L⁻¹) or biomass (up to 10.2 mg dry weight·m⁻³).

As was the case for cyclopoids, cladoceran abundance increased along trophic gradients in temperate and tropical regions (Table 4). Their mean density increased from 1.4 individuals·L⁻¹ in the oligotrophic Quebec lakes to 10.5 individuals·L⁻¹ in the eutrophic TROLS lakes. It ranged from 7.3 individuals·L⁻¹ in oligotrophic tropical reservoirs to 34.8 individuals·L⁻¹ in eutrophic tropical reservoirs. Cladoceran mean biomass increased from 8.2 to 169.9 mg dry weight·m⁻³ along the trophic gradient in those reservoirs. In contrast, mean cladoceran biomass in the temperate region was lower in the more eutrophic TROLS lakes (14.8 mg dry weight·m⁻³) than in oligotrophic Quebec lakes (22.7 mg dry weight·m⁻³).

The CCA (Fig. 2) suggests the existence of some latitudinal and trophic influence on the structure of crustacean zooplankton. We tested if these effects can be isolated from each other and if they are significant (Table 5). The two-sample *t* test revealed that latitude has a significant relationship with mean density and biomass of calanoids, whereas trophic has no significant relationship with this zooplankton group. In contrast, the lake trophic gradient displayed significant differences in mean and maximum densities of cyclopoids, while latitude had no relationship with this group. The cladocerans were most strongly associated with these explicative variables, since both latitude and lake trophic are significantly related to variation in their mean and maximum density as well as trophic with mean biomass.

Relationship of crustacean zooplankton to trophic state indicators

Since the CCA retained both Chl *a* and TP as explanatory variables, we investigated the relative power of these vari-

Table 5. Probability of accepting the null hypothesis (no difference between means) in the two-sample *t* test with crustacean zooplankton abundance (density and biomass) in response to the following treatments: latitude and trophic gradients.

	Density		Biomass	
	Latitude	Trophy	Latitude	Trophy
Cyclopoida				
Mean	0.925	0.029	0.223	0.066
Max.	0.229	0.035	0.173	0.112
Calanoida				
Mean	0.002	0.109	0.027	0.307
Max.	0.213	0.470	0.509	0.082
Cladocera				
Mean	0.015	0.000	0.054	0.026
Max.	0.006	0.000	0.116	0.102

ables in explaining the responses of crustacean zooplankton across latitudinal gradients. A series of linear regressions using these independent variables and biomass of each major group of crustacean zooplankton as dependent variables was performed. Concentration of TP was the best predictor (Fig. 3) for total crustacean zooplankton, cyclopoids, and especially cladocerans. Previous results have demonstrated that calanoids prefer oligotrophic systems but their biomass values were not significantly correlated with TP or Chl *a* (Fig. 3). The assumption of parallel slopes could be accepted for the regression models of two major crustacean groups (Cyclopoida and Cladocera). This allowed us to perform the ANCOVA (Table 6) to test for differences in zooplankton – trophic state relationships across latitudinal regions. We found significant differences in the parameters of regression models for cyclopoids and cladocerans with TP (i.e., these regressions have significantly different slopes), suggesting different responses to TP in temperate and tropical regions. The analysis of TP–biomass relationships suggests that these

Fig. 3. Scatterplots and linear regressions between mean biomass (log transformed) of total crustacean zooplankton, groups (Cladocera, Calanoida, and Cyclopoida), and trophic indices (log total phosphorus (TP), log chlorophyll *a* (Chl *a*)) in temperate and tropical ecosystems. Linear regressions parameters are presented in the legend when significant ($P \leq 0.05$).

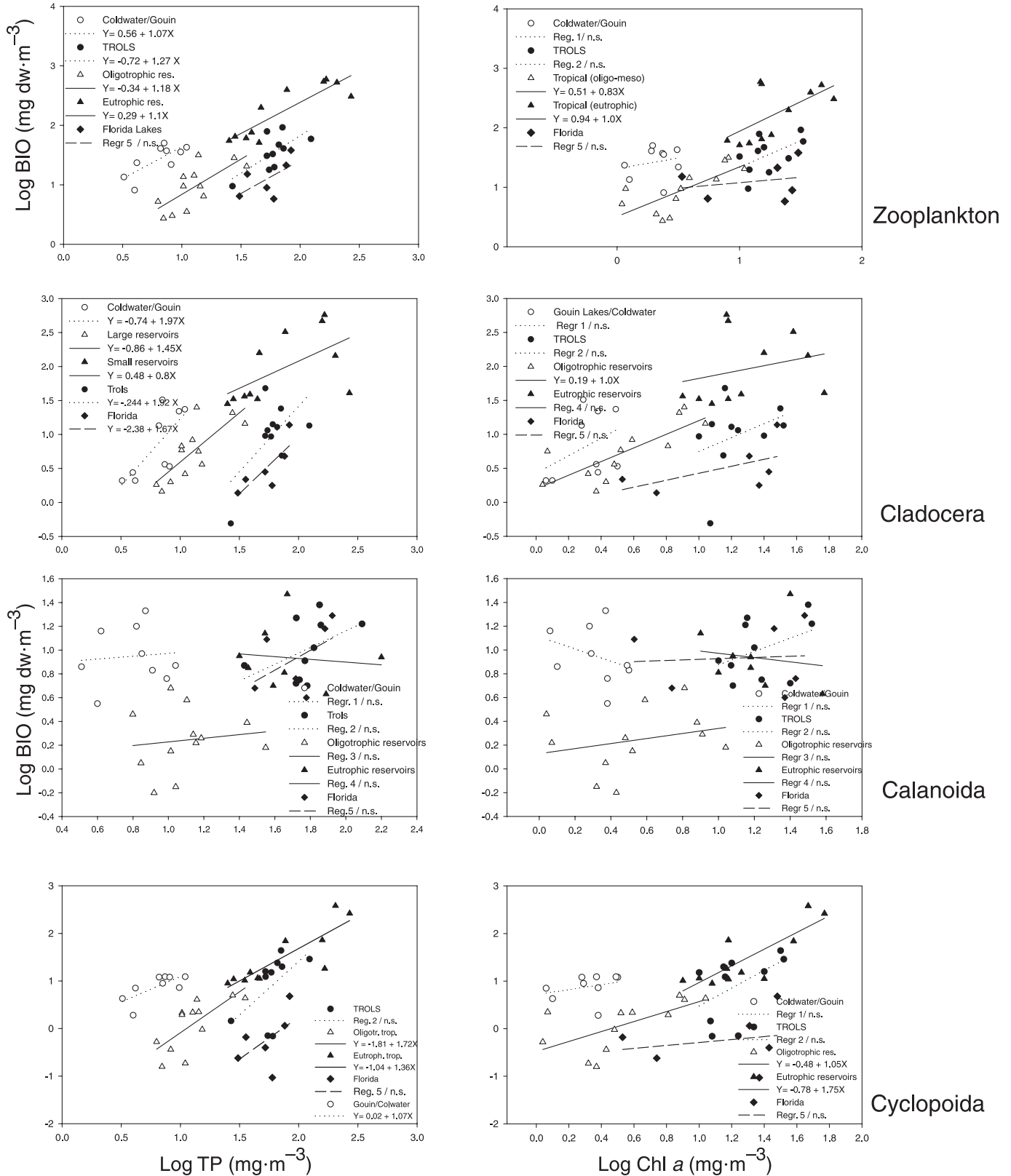


Table 6. ANCOVA of biomass of zooplankton groups in response to eutrophication measured as total phosphorus (TP) and chlorophyll *a* (Chl *a*) and temperate and subtropical–tropical regions as treatments.

	Source	SS	df	MS	<i>F</i>	<i>P</i>
TP						
Cyclopoida	Treatment	17.931	4	4.483	23.228	<0.001
	Total phosphorus	6.364	1	6.364	32.975	<0.001
	Error	8.492	44	0.193		
Calanoida	Treatment	3.526	4	0.881	8.278	<0.001
	Total phosphorus	0.053	1	0.053	0.502	0.483
	Error	4.366	41	0.106		
Cladocera	Treatment	9.490	4	2.373	16.730	<0.001
	Total phosphorus	3.447	1	3.447	24.305	<0.001
	Error	6.240	44	0.142		
Chl <i>a</i>						
Cyclopoida	Treatment	15.786	4	3.946	16.220	<0.001
	Chl <i>a</i>	4.150	1	4.150	17.058	<0.001
	Error	10.706	44	0.243		
Calanoida	Treatment	3.458	4	0.865	8.048	<0.001
	Chl <i>a</i>	0.015	1	0.015	0.139	0.711
	Error	4.404	41	0.107		
Cladocera	Treatment	8.731	4	2.183	11.852	<0.001
	Chl <i>a</i>	1.584	1	1.584	8.601	0.005
	Error	8.103	44	0.184		

Note: Region 1, temperate oligotrophic (Quebec Sustainable Forest Management and Ontario Coldwater lakes); region 2, temperate eutrophic (Alberta Terrestrial Riparian Organisms of Lakes and Streams lakes); region 3, subtropical lakes (Florida); region 4, tropical large oligomesotrophic reservoirs; region 5, tropical hypereutrophic reservoirs. The homogeneity of slopes tests were positive for all groups but not for the total crustacean zooplankton.

responses are more intense in the tropical regions. A similar but weaker result was obtained using Chl *a* as the independent variable.

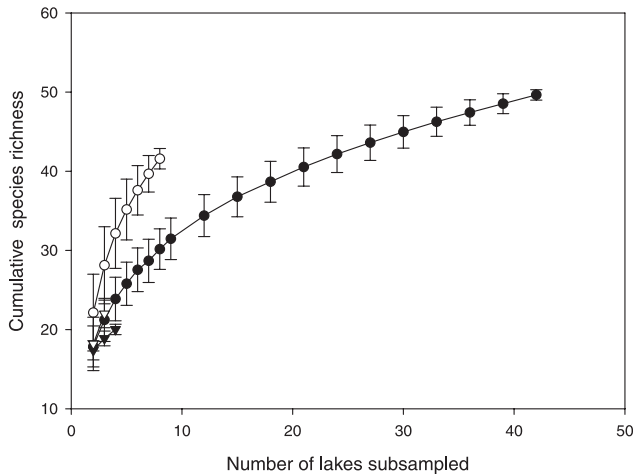
Discussion

Crustacean zooplankton taxonomic structure

In our study, we have used multiple-year sampling to estimate cumulative species richness at regional scale instead of single-year sampling, as suggested by Arnott et al. (1998). We found that oligotrophic lakes of the temperate region (SFM lakes in Quebec, Coldwater lakes in Ontario: region 1) host the richest zooplankton community, reaching a cumulative richness of 52 crustacean species. Other geographic regions have lower cumulative species richness, ranging from 15 to 26, the lowest species richness occurring in the eutrophic tropical reservoirs. The greatest number of crustacean species was found in the region with the largest number of lakes sampled. So despite having similar and large numbers of samples for both temperate (337 samples) and tropical regions (332 samples), one might argue that the observed spatial variation in species richness among temperate and subtropical–tropical regions is just a function of lake number and area (Dodson 1991; Arnott et al. 1998). To evaluate this possibility in our data sets, we estimated the average cumulative species richness that one would find if the number of lakes in the temperate oligotrophic regions would be equal to the number of lakes and reservoirs in the subtropical–tropical regions. We compared the average cumulative species richness for equal number of lakes in the temperate oligotrophic region (region 1) and lakes and reservoirs in the

subtropical–tropical regions (regions 3–5). To conduct this assessment, we performed 1000 subsamples without replacement for each subset of increasing number of lakes (2–42) in temperate oligotrophic lakes (region 1: subsets of 2–42 lakes) and lakes and reservoirs in the subtropical–tropical regions, either when pooling Florida lakes with Brazilian reservoirs (regions 3–5: subsets of two to eight lakes and reservoirs) or when using separately the five subtropical Florida lakes (region 3: subsets of two to five lakes) and the Brazilian reservoirs (regions 4 and 5: subset of two and three reservoirs). Based on these subsamples, we calculated the average cumulative species richness for each subset of increasing number of lakes and reservoirs in each region (Fig. 4). We found that the average cumulative crustacean species richness in the temperate oligotrophic lakes (region 1) was lower than the values obtained in subtropical lakes and tropical reservoirs for subsets of lakes and reservoirs varying from two to eight (Fig. 4). However, high cumulative species richness in subtropical–tropical systems (regions 3–5) may be due to the great dissimilarity in species assemblages between Brazilian reservoirs and Florida lakes, the latter having more species in common with temperate regions than with tropical reservoirs. When separating Florida lakes (region 3) from Brazilian reservoirs (regions 4 and 5), the cumulative species richness for same subsets of lakes and reservoirs was slightly lower in subtropical lakes (around 20 species for five Florida lakes compared with 24 species in temperate oligotrophic lakes), and similar in the Brazilian reservoirs (21 species in average in subsets of three temperate oligotrophic lakes compared with 22 species in subsets of three tropical reservoirs). Thus, owing to unbalance among

Fig. 4. Cumulative species richness (mean and error type) in subsets of increasing number of lakes and reservoirs in temperate oligotrophic lakes (region 1, solid circles) compared with subtropical–tropical regions: Brazilian reservoirs and Florida lakes pooled (regions 3–5, open circles), only Florida lakes (region 3, solid inverted triangles), and only Brazilian reservoirs (regions 4 and 5, open inverted triangles).



regions in the number of ecosystems studied, our study does not allow us to relate change in species richness between regions to latitude or lake trophy.

Finally, as deeper lakes often tend to be more oligotrophic, our results might also have been confounded by lake depth and size. To test this additional factor, we performed a simple linear regression between maximum and mean depth, area, and zooplankton species number on natural lakes, and we did not find any association between these variables.

Nevertheless, despite bias owing to difference in the number of lakes in the temperate and subtropical–tropical regions, the cumulative species richness estimated in each region was similar to other regional estimates. In temperate lakes in North America, Patalas (1975) found a total of 33 species in a survey of 14 large lakes. In northern Ontario, total crustacean species pool ranged from 21 to 40 species in lakes of similar morphometry and trophy to our temperate oligotrophic set of lakes (Keller and Pitblado 1989; Arnott et al. 1998). In Florida lakes, the cumulative species richness of 21 is quite similar to what has been previously reported for other lakes in the region (Crisman et al. 1995; Beaver and Havens 1996; Tugend and Allen 2000). Low diversity of crustaceans is a common feature of lakes in Brazil (Matsumura-Tundisi 1989; Bozelli 1992; Rocha et al. 1995). In a recent study, Sendacz and Junior (2003) reports only 16 species of mesozooplankton in a series of seven lakes of Paraná River in São Paulo State, Brazil, a similar value found in the selected reservoirs of the present study. One of the largest and deepest natural and oligotrophic lakes in eastern Brazil, Bispo Lake hosts only nine species of crustacean zooplankton (Matsumura-Tundisi 1997). Thus, we believe that our multiple-year survey and large sampling effort in both temperate and tropical regions give good estimates of crustacean species richness at the regional scale. In the Environmental Monitoring and Assessment Program – Surface Waters pilot survey of zooplankton richness in lakes of the

northeastern United States, Stemberger et al. (1996) indicate that local species richness can be effectively extrapolated to the regional scale.

Among zooplankton groups, calanoid species richness is lower in eutrophic ecosystems than in oligotrophic ones in both temperate and tropical regions, as previously reported in temperate regions (Pace 1986). Calanoids seem to be sensitive to lake eutrophication and other lake watershed disturbances such as clearcut logging (Patoine et al. 2000). In the tropics, large calanoids like *E. lacustris* are absent, and calanoids often disappear from eutrophic lakes and reservoirs (Dussart et al. 1984; Matsumura-Tundisi 1986). Cyclopoid copepods also have lower diversity in the eutrophic systems in temperate lakes, whereas cladoceran species richness decreases in eutrophic systems within both tropical reservoirs and temperate lakes. In particular, the low diversity of *Daphnia* seems to be an outstanding feature of cladoceran assemblages in tropical systems, either oligotrophic or eutrophic. Matsumura-Tundisi (1984, 1989) found only 10 species of crustaceans and just one *Daphnia* species in the pristine Bispo (D. Helvécio) Lake and reported only three species of *Daphnia* for all fresh water systems in Brazil, where *Diaphanosoma* spp., *Moina* spp., and *Bosmina* spp. are the dominant species.

The low diversity of crustacean zooplankton found in the subtropical lakes of Florida and the tropical reservoirs of Brazil might also be a result of biogeography and fish predation. Peculiar geomorphology and geography of South America might also be important. Soto and Zuñiga (1991) observed that temperate lakes in Chile also have a much lower species diversity of crustacean zooplankton when compared with similar systems in North America. They explained these differences as a result of geographical isolation and species colonization history. The more diverse cladoceran fauna of Florida lakes also is probably a result of biogeography and peculiar ecological and morphometric conditions. These lakes occur relatively near to temperate areas of North America, in a very different biogeographic context, as compared with its counterpart systems in South America. These different geographic conditions could explain the differences between the available pool of species in tropical waters of Florida and South America. However, there are other studies suggesting that tropical waters usually have a lower diversity of zooplankton, especially for *Daphnia* species (Fernando et al. 1987). In a recent study, Aka et al. (2000) found no *Daphnia* species in a set of 49 reservoirs in the tropical Ivory Coast (Africa). In tropical lakes and reservoirs, fish predation is known to be a key factor structuring zooplankton communities, and the strong dominance of small copepods and cladocerans in tropical lakes (for instance, *D. dorsalis* in Florida lakes and *Moina* spp. in Brazilian reservoirs) and the disappearance of large cladocerans (*Daphnia* spp.) may be due to the high densities of zooplanktivorous fish (threadfin shad in Florida lakes and introduced African *Tilapia* in the Pampulha and Ibirite reservoirs) (Beaver and Havens 1996; Pinto-Coelho et al. 2000). The higher number of noneuplanktonic cladocerans in the Florida lakes may be associated with the presence of large stands of the submersed macrophyte *Hydrilla* that offer refuge against fish predation. The Florida lakes also have been colonized by exotic species, including *D. lumholtzi*, which is

native to southeastern Asia, Australia, and eastern Africa (Havel and Hebert 1993; Havens et al. 2000a).

Crustacean density and biomass relationships

In our study, both the lowest and the highest densities (and biomass) of crustacean zooplankton were consistently found in the tropics, i.e., this region displayed the greatest interlake variability. This was particularly evident for the cyclopoids and cladocerans. High densities of total zooplankton (over 10^3 individuals·L⁻¹) are common in tropical waters. Crustacean zooplankton, especially small cladocerans and cyclopoids, can often reach such densities in hyper-eutrophic lakes, reservoirs, and fertilized ponds of hatchery stations (Branco and Senna 1996). Even the small calanoid *Scolodiaptomus corderoi* can occur and even form large populations in the most eutrophic reservoirs of Brazil (Reid et al. 1988).

The higher abundance of cladocerans found in tropical eutrophic waters might be a result of several interacting factors. Cladocerans typically have shorter development times compared with copepods and thus are able to exploit unstable and changing environments such as tropical reservoirs suffering from eutrophication. These systems often experience blooms of cyanobacteria and floating macrophytes. The increase in macrophyte beds creates a variety of new habitats favorable for zooplankton. Basu et al. (2000) observed a ninefold increase in biomass of zooplankton within dense macrophyte beds in fluvial lakes of the St. Lawrence River. The existence of long-lasting blooms of algae, such as cyanobacteria or filamentous diatoms like *Aulacoseira*, also creates favorable conditions for some smaller cladocerans such as *Bosmina longirostris* or *Bosmina hagmanii* (Branco and Senna 1996) or *Ceriodaphnia* (Ferrão-Filho et al. 2000). As stated before, the presence of efficient plankton feeders in Florida lakes (Beaver and Havens 1996) and Brazilian reservoirs (Pinto-Coelho et al. 2000) may favor the dominance of small copepods and cladocerans.

Responses of zooplankton to trophic gradients

Our study confirmed that more nutrient-enriched lakes or reservoirs support greater crustacean zooplankton density and biomass. This is valid for both temperate and tropical regions. The regression models relating biomass of total crustacean zooplankton to TP were significant for most regions (excepting only Florida lakes) with R^2 varying between 0.45 and 0.77. The predictive power of our large-scale regression models is similar to that of other studies ($R^2 = 0.63$ – 0.86) done either at large geographic scales including 44 lakes mostly from temperate regions of North America and Europe (Hanson and Peters 1984) or at small regional scales in 16 nutrient-poor lakes in southcentral Ontario (Yan 1986) and 12 mesoeutrophic lakes in southern Quebec (Pace 1986). Patalas (1972) also found a significant regression ($R^2 = 0.92$) between crustacean abundance and phosphorus loading in the Great Lakes.

Considering previous studies and our results, it seems that there is a trend for crustacean zooplankton biomass to covary strongly with TP (Hanson and Peters 1984; Pace 1984; Yan 1986) and less with Chl *a*. A possible initial explanation could be the higher seasonal variability found for Chl *a* when compared with TP (Hanson and Peters 1984).

However, there is an alternative explanation supporting this trend in tropical regions. The better power of TP for explaining the variability of crustacean zooplankton was also recently confirmed for tropical regions, such as the Pampulha Reservoir (Pinto-Coelho 1998). In this system, there is an imbalance between algae production and the biomass of zooplankton in reservoirs, since the assimilation rate of these consumers is not covered by phytoplankton production alone (Araújo and Pinto-Coelho 1998). In this kind of situation, where the detrital food chain is important, Chl *a* from algae cells certainly is not the best variable to be considered. Detritus food chains have also been found to be a major resource for zooplankton in a wide range of temperate lakes, and thus, TP has a better chance to reflect the total edible material than Chl *a* (Yan 1986). Likewise, Havens et al. (2000b) documented that phytoplankton-based food chains have low ecological transfer efficiency in a Florida lake and that much of the carbon and energy transfer to macrozooplankton must come from bacteria-based chains in the “microbial loop”. Havens (2002) presented a simple conceptual model, based on zooplankton research in south Florida, indicating that while phytoplankton biomass is controlled by nutrients, zooplankton biomass is primarily controlled by productivity of bacteria. In systems of this type, it might be optimal to predict macrozooplankton biomass based on the combined biomass of phytoplankton and bacterioplankton. However, if effective predictions can be made based on TP, this would be the preferred approach owing to the much lower cost and effort.

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