

Zooplankton assemblage concordance patterns in Brazilian reservoirs

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Abstract The main goal of this study was to evaluate the assemblage concordance among three zooplankton groups (Rotifera, Cladocera and Copepoda) in 30 Brazilian reservoirs. According to Mantel tests and Procrustean analyses, there was a high level of assemblage concordance. Highest assemblage concordance was observed between cladocerans and copepods, while the lowest level of concordance was detected between copepods and rotifers. Based on environmental or biotic data, patterns of among-reservoir dissimilarities were fairly stable across the two seasonal periods analyzed in this study. Multiple Mantel tests were used to model the between-reservoir dissimilarities (Bray–Curtis distance) in zooplankton assemblage structure as a function of the limnological, geographical and morphological distances between pairs of reservoirs. The best predictor of faunistic dissimilarities was the matrix containing the limnological distances among the reservoirs. In general, these results are important for

monitoring purposes because they supported the use of surrogate taxa and indicate that community concordance analysis may be a powerful tool for enhancing the efficiency of monitoring programs, ensuring their long-term sustainability.

Keywords Concordance · Reservoir · Monitoring · Rotifera · Cladocera · Copepoda

Introduction

Quantifying the relationship between organisms and their environment is a paramount goal in aquatic ecology (Thornton et al., 1990). Particularly, this is a frequent issue in zooplankton ecology (Marzolf, 1990). However, there are few attempts to verify if different taxonomic groups (e.g. rotifers, cladocerans and copepods) show similar responses to environment gradients.

The degree to which patterns in assemblage structure in a set of sites are similar between two or more different taxonomic groups is defined as community concordance (Jackson & Harvey, 1993; Paszkowski & Tonn, 2000; Bini et al., 2007). These patterns can arise from several mechanisms, as biotic interactions (when a group is regulated by another by predation, competition or facilitation, for instance) and similar but independent responses to environmental gradients (Paavola et al., 2003).

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Studies dealing with community concordance are increasing rapidly. The interest on this issue is related with practical problems. Specifically, the validity of surrogate taxa, for conservation planning and monitoring purposes, depends strongly on community concordance (Paavola et al., 2006). For instance, Bilton et al. (2006) evaluated the performance of four taxonomic groups (Chironomidae, Coleoptera, Gastropoda and Trichoptera) as surrogates of community similarity between ponds. They found that the patterns of community similarity between ponds were satisfactorily predicted by Coleoptera and recommended this group as a surrogate taxon for the assessment of pond biodiversity. On the other hand, Heino et al. (2003), studying insects, reported low among-taxon concordance (as shown by Mantel tests) in streams across Finland and suggested that the use of single taxonomic groups as surrogates may be inadequate.

Indeed, a precondition for useful generalizations about human impacts on freshwater ecosystems, which are identified by a single taxonomic group, is that different taxonomic groups exhibit concordant patterns. Otherwise, environmental impacts cannot be generalized to all groups of interest (Paavola et al., 2003).

In this study, we examine broad scale patterns of concordance among zooplankton assemblages (rotifers, cladocerans and copepods) in 30 Brazilian reservoirs, in two seasonal periods. Specifically, our main questions may be stated as follows: (i) can assemblage patterns of one taxonomic group be used to predict patterns in other taxonomic groups? For example, can the reservoirs' scores derived from a given ordination technique and based on the rotifer assemblage be used as a surrogate for the pattern of reservoirs' ordination based on cladocerans? (ii) What set of environmental factors best predict the patterns of among-reservoir similarities derived from the taxonomic groups? (iii) Are the patterns of among-reservoir similarities stable between the seasonal periods?

Methods

Study area

The 30 reservoirs studied are located in the six hydrographical basins of the Paraná State (Piquiri,

Ivaí, Tibagi, Paranapanema, Iguaçu and Leste) (Fig. 1, Table 1). Reservoirs included in the analysis vary in surface area from 0.05 to 515 km² and in mean depth from 3.75 to 135 m. The oldest reservoir was created 85 year ago, while the most recent reservoir is only 4 years old (Table 1). The reservoirs are under the influence of distinct geologies. Water chemistry is varied throughout the study area. Conductivity ranged from 21 to 156 $\mu\text{S cm}^{-1}$ and pH from 5.8 to 8.8. Concentration of total phosphorous and total nitrogen varied from 0.18 to 1.75 $\mu\text{mol l}^{-1}$ and from 15.41 to 82.26 $\mu\text{mol l}^{-1}$, respectively. In addition, chlorophyll-*a* concentration (varying from values below the limit of detection to 77 $\mu\text{g l}^{-1}$) and water transparency (0.2–5.0 m) varied considerably (Table 1). In other words, the entire group of reservoirs represented a broad gradient from oligotrophic to eutrophic conditions. Although the reservoirs have multiple uses, most of them are regulated for hydroelectric power and some, situated in urban centers, are used for water supply.

Sampling and laboratory analysis

The zooplankton and water samples were gathered from 0.5 m depth in the pelagic zone of each reservoir. Sampling was conducted twice a year in 2001 during austral winter (July) and summer (November).

Zooplankton samples were collected with a motorized pump and filtered (600 l per sample) through a 68 μm plankton net. The samples were fixed immediately with 4% buffered formalin. Samples for physical and chemical analysis and chlorophyll-*a* measurements were collected using a Van Dorn sampler (5 l).

The following abiotic variables were determined: water column transparency (Secchi disc); turbidity (turbidimeter—Digimed); water temperature and dissolved oxygen (Horiba oxymeter); pH and conductivity (digital potentiometer—Digimed); alkalinity (Mackereth et al., 1978); nitrate (FIA—Zagatto et al., 1981); orthophosphate, total phosphorus and nitrogen, dissolved phosphorus (Mackereth et al., 1978); dissolved organic carbon (Carbon Analyser—Schimadzu TOC 5000). In order to analyze the chlorophyll-*a* concentrations (Golterman et al., 1978), samples were filtered in Whatman GF/C filters.

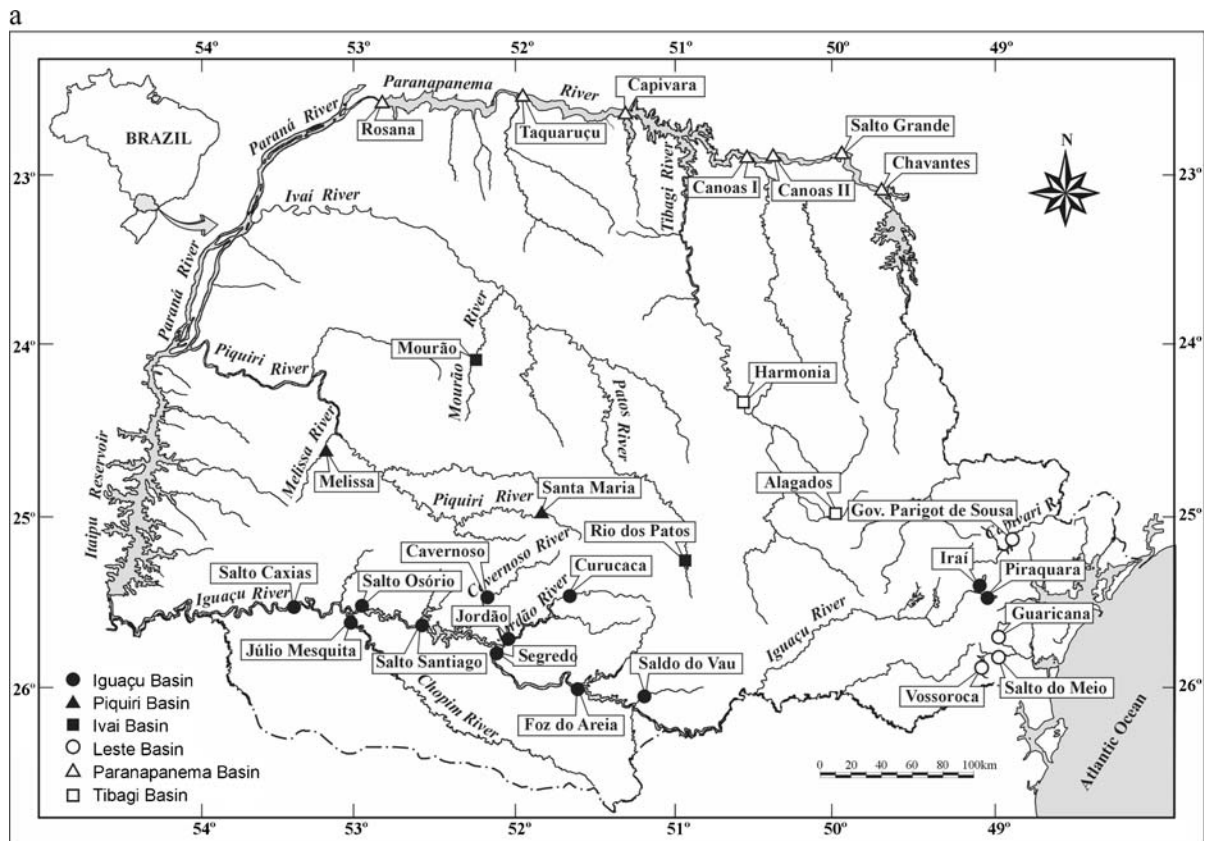


Fig. 1 The Paraná State map and the localization of the 30 reservoirs studied

Zooplankton counting was carried out using a Sedgwick-Rafter cell under optical microscope. A minimum of 100 individuals was counted in each three subsequent sub-samples (2.5 ml), obtained with a Hensel-Stempel pipette. Zooplankton density was expressed in individuals m^{-3} .

Data analyses

Patterns of assemblage concordance were assessed using two techniques. First, for each zooplankton group, dissimilarity in species composition between reservoirs was calculated by using the Bray–Curtis coefficient (Faith et al., 1987). Correlations among Bray–Curtis matrices were computed using the standardized Mantel statistic (Mantel, 1967; Legendre & Fortin, 1989; Diniz-Filho & Bini, 1996). Second, we compared axes derived from a principal coordinate analysis (Legendre & Legendre, 1998), carried out for each zooplankton group, using the

Procrustean approach (Jackson, 1995; Peres-Neto & Jackson, 2001). In this approach, ordination solutions (e.g. principal coordinate scores of reservoirs derived from cladocerans and copepods) are subjected to geometric transformations (standardization, mirror reflection, rotation and dilation) so that the sum of squared differences (the m^2 statistics) between ordination solutions is minimum.

We used the multiple Mantel test (Smouse et al., 1986; Manly, 1998) to examine the relationships between Bray–Curtis distance matrix Z (one for each taxonomic group) and the following explanatory matrices: water chemistry (standardized Euclidean distance: W), lake morphology (standardized Euclidean distance: M), geographical distance (Euclidean distance: G) and a connectivity matrix (Fortin & Gurevitch, 1993) indicating if the reservoirs are or not in the same river (C): pairs of reservoirs in the same river received a value of zero, whereas pairs of reservoirs in different rivers received a value of one. Thus, the following model: $z_{ij} = b_0 + b_1w_{ij} + b_2m_{ij}$

Table 1 Mean values (\pm standard deviation) of some environmental variables for the 30 reservoirs included in the multiple Mantel test

Reservoirs	River basin	pH	Conductivity ($\mu\text{S cm}^{-1}$)	Turbidity (NTU)	P-total ($\mu\text{mol l}^{-1}$)	N-total ($\mu\text{mol l}^{-1}$)	Chlorophyll- <i>a</i> ($\mu\text{g l}^{-1}$)	Depth (m)	Area (km^2)	Age (Year)
Cavernoso	Iguaçu	7.0 \pm 0.4	31.7 \pm 1.9	15.1 \pm 6.9	0.24 \pm 0.01	30.5 \pm 5.0	0.1 \pm 0.2	8.3	0.05	39
Curucaca	Iguaçu	6.5 \pm 0.5	28.7 \pm 5.2	12.1 \pm 1.2	0.22 \pm 0.09	32.0 \pm 1.6	0.7 \pm 0.5	10.5	0.8	22
Foz do Areia	Iguaçu	6.7 \pm 0.9	37.3 \pm 2.5	10.7 \pm 7.8	0.42 \pm 0.05	61.0 \pm 10.0	7.7 \pm 9.1	135	139	24
Irai	Iguaçu	6.9 \pm 0.1	50.0 \pm 0.2	20.3 \pm 15.0	1.75 \pm 0.04	82.2 \pm 33.4	77.1 \pm 8.3	8.5	14.4	5
JMF	Iguaçu	6.8 \pm 0.6	37.2 \pm 4.2	26.8 \pm 16.5	0.95 \pm 0.53	60.3 \pm 16.6	0.2 \pm 0.3	6	0.4	34
Jordão	Iguaçu	6.6 \pm 0.5	22.7 \pm 1.4	8.0 \pm 1.8	0.18 \pm 0.11	26.6 \pm 0.3	0.3 \pm 0.2	60	3.3	8
Passaúna	Iguaçu	8.8 \pm 0.0	125.6 \pm 0.0	2.3 \pm 0.0	0.48 \pm 0.02	41.3 \pm 8.8	5.5 \pm 0.3	14	8.3	?
Piraquara	Iguaçu	6.6 \pm 0.6	23.2 \pm 0.5	1.9 \pm 0.1	0.23 \pm 0.12	28.3 \pm 8.5	3.8 \pm 0.2	18	3.3	25
Salto Caxias	Iguaçu	6.6 \pm 0.9	36.5 \pm 4.3	2.7 \pm 0.3	0.33 \pm 0.08	49.0 \pm 8.1	3.6 \pm 3.5	53	141	6
Salto do Vau	Iguaçu	6.5 \pm 0.1	21.4 \pm 2.5	5.7 \pm 0.1	0.28 \pm 0.10	34.6 \pm 5.7	0.4 \pm 0.1	3.75	0.4	45
Salto Osório	Iguaçu	5.8 \pm 3.9	37.2 \pm 2.3	8.9 \pm 0.0	0.20 \pm 0.13	42.6 \pm 4.0	12.0 \pm 14.7	43	62.9	29
Salto Santiago	Iguaçu	7.7 \pm 2.1	37.7 \pm 2.5	4.7 \pm 3.6	0.37 \pm 0.07	48.1 \pm 9.4	11.2 \pm 14.8	78	208	24
Segredo	Iguaçu	6.5 \pm 0.6	37.4 \pm 4.2	10.5 \pm 5.8	0.31 \pm 0.15	50.7 \pm 9.4	3.3 \pm 1.7	101	80.4	12
Mourão	Ivaí	7.1 \pm 1.3	21.7 \pm 2.2	4.2 \pm 2.5	0.28 \pm 0.07	15.4 \pm 3.4	5.1 \pm 2.1	12.7	11.2	40
Rio dos Patos	Ivaí	6.6 \pm 0.3	40.3 \pm 8.0	31.3 \pm 14.3	0.86 \pm 0.57	47.7 \pm 1.5	0.2 \pm 0.2	5.75	1.3	55
Guaricana	Leste	6.6 \pm 1.1	26.3 \pm 2.2	3.5 \pm 0.6	0.54 \pm 0.20	24.9 \pm 7.7	8.2 \pm 3.1	17	0.8	47
Parigot de Souza	Leste	7.2 \pm 0.6	61.2 \pm 3.3	2.7 \pm 0.6	0.44 \pm 0.15	30.5 \pm 0.2	2.7 \pm 1.66	43	13	34
Salto do Meio	Leste	6.7 \pm 0.3	37.8 \pm 0.6	7.0 \pm 4.8	0.51 \pm 0.06	32.4 \pm 10.8	2.1 \pm 1.8	6.2	0.12	73
Voçoroca	Leste	6.7 \pm 0.9	40.2 \pm 0.6	5.3 \pm 3.8	0.54 \pm 0.24	30.9 \pm 13.8	2.9 \pm 1.6	12.5	5.1	55
Canoas I	Parapananema	7.2 \pm 0.2	61.1 \pm 3.1	3.4 \pm 0.2	0.33 \pm 0.02	23.9 \pm 2.0	2.8 \pm 1.1	26	30.8	5
Canoas II	Parapananema	7.3 \pm 0.5	61.6 \pm 0.6	8.2 \pm 4.3	0.34 \pm 0.08	25.5 \pm 1.8	4.4 \pm 4.1	16.5	22.5	4
Capivara	Parapananema	7.4 \pm 0.2	58.7 \pm 0.1	3.6 \pm 0.9	0.28 \pm 0.13	32.7 \pm 0.7	3.8 \pm 0.2	52.5	51.5	29
Chavantes	Parapananema	7.2 \pm 0.5	55.1 \pm 3.8	1.0 \pm 0.2	0.23 \pm 0.03	21.8 \pm 3.1	1.1 \pm 0.5	87	242	34
Rosana	Parapananema	7.7 \pm 0.1	59.0 \pm 1.2	5.2 \pm 1.9	0.34 \pm 0.02	34.0 \pm 4.3	4.2 \pm 1.1	26	220	18
Salto Grande	Parapananema	6.9 \pm 0.3	59.2 \pm 4.3	12.3 \pm 8.3	0.46 \pm 0.19	29.7 \pm 1.6	0.4 \pm 0.0	9.2	8.4	46
Taquaruçu	Parapananema	7.7 \pm 0.1	57.7 \pm 1.0	6.3 \pm 1.3	0.28 \pm 0.19	30.9 \pm 0.2	5.1 \pm 5.1	26.5	40.8	12
Melissa	Piquiri	6.3 \pm 0.6	32.3 \pm 2.3	93.9 \pm 70.8	1.20 \pm 1.24	58.1 \pm 7.6	0.0 \pm 0.0	5.3	0.05	42
Santa Maria	Piquiri	6.5 \pm 0.4	39.5 \pm 3.1	9.4 \pm 1.5	0.35 \pm 0.17	16.6 \pm 1.9	0.3 \pm 0.3	4.3	0.05	30
Alagados	Tibagi	7.2 \pm 0.5	39.8 \pm 2.6	7.7 \pm 2.6	0.55 \pm 0.13	30.5 \pm 4.5	7.65 \pm 6.0	9.25	7.3	85
Harmonia	Tibagi	7.2 \pm 1.5	28.8 \pm 3.1	3.5 \pm 0.2	0.37 \pm 0.13	21.9 \pm 1.8	23.2 \pm 11.9	12	0.6	62

+ $b_3g_{ij} + b_4c_{ij} + e_{ij}$ (with z_{ij} , w_{ij} , m_{ij} , g_{ij} and c_{ij} denoting the distance between reservoirs i and j in the matrices indicated above, respectively) was assumed, where b_1 measures the relationship between z_{ij} and w_{ij} , after allowing for any effects of the other elements (m_{ij} , g_{ij} and c_{ij}), b_2 measures the relationship between z_{ij} and m_{ij} after allowing for any of w_{ij} , g_{ij} and c_{ij} and, in this way, successively. Finally, e_{ij} is an independent error. We conducted a multiple Mantel test for each taxonomic group separately.

Furthermore, simple Mantel test was also used to test if among-reservoirs dissimilarities (as indicated by biotic and abiotic data) in the summer were correlated with the dissimilarities calculated in the winter. A significant and positive correlation indicates that the patterns of dissimilarities among reservoirs are stable or coherent.

In all cases, 10,000 random permutations of the data (Mantel and Procrustean tests) were used to test if the concordances between distance matrices and ordinations differed from the random relationships, and ensure the stability of the probability estimates (Jackson & Somers, 1989). Before analyses, all variables (excluding pH) were log-transformed to minimize the effects of outliers.

Principal coordinates analyses and Mantel tests were performed using the DISTPCOA (Legendre & Anderson, 1999; freely available on <http://www.bio.umontreal.ca/legendre/>) and the RT (Manly, 1998) programs, respectively. Procrustean randomization tests (PROTEST) were carried out with the program PROTEST, written by P. Peres-Neto (freely available on <http://uregina.ca/~peresnep/>)

Results

A total of 190 species was found in the zooplankton samples (132 species of Rotifera, 32 of Cladocera and 26 of Copepoda). Zooplankton density varied between 397 (Curucaca Reservoir) and 847,991 ind.m⁻³ (Iraí Reservoir) (Fig. 2). *Bosminopsis deitersi* Richard, *Bosmina hagmanni* Stingelin, *Gastropus hyptopus* (Ehrenberg), *Kellichotia bostoniensis* (Rousselet), *Ptygura* sp., *Synchaeta* sp. and *Ceriodaphnia cornuta* Sars, were the most abundant species. Naupliis and copepodits of calanoid and cyclopoid were also abundant in most reservoirs.

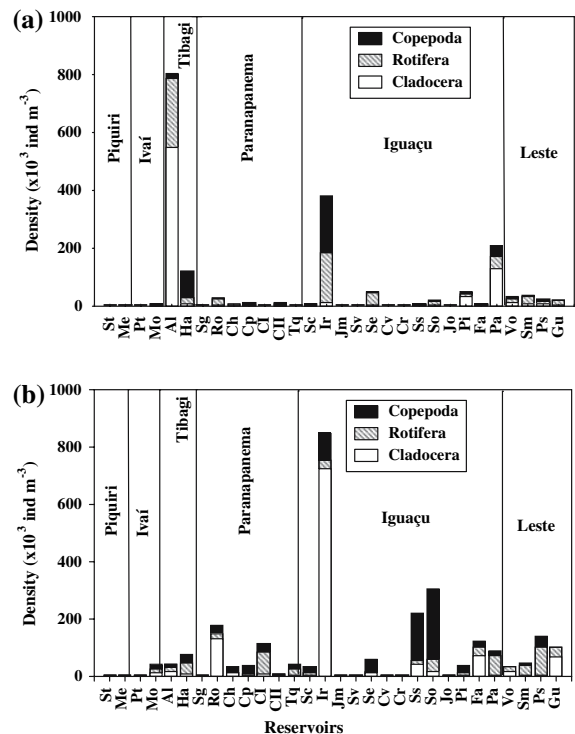


Fig. 2 Zooplankton group densities recorded in winter (July/2001) (a) and summer season (November/2001) (b), in the 30 reservoirs and their respective river basins

For cladocerans, copepods and rotifers, the first two principal coordinate axes explained, respectively, 54, 65 and 32% of the variation in the data matrices obtained in July 2001 (winter). In November 2001 (summer), these figures were equal to 63, 63 and 32%, respectively. Procrustean analyses on principal coordinate scores as well as Mantel tests showed significant concordance between all zooplankton groups (Table 2) and they also showed the highest concordance between cladocerans and copepods and a lowest level of concordance between copepods and rotifers (the lower the m^2 value the stronger the relationship indicated by a Mantel's test). The strong concordance between cladocerans and copepods ordinations can be also visualized in Fig. 3, as shown by the relationship between the first axes.

Simple Mantel tests pointed out that among-reservoir dissimilarities in assemblage composition of zooplankton groups and limnology were significantly concordant between the two seasons (Table 3).

In general, multiple Mantel test indicated that the limnological characteristics of reservoirs are the

Table 2 Statistics of concordance (m^2 statistic derived from the Procrustean approach and standardized Mantel's r) evaluating the relationships among the zooplankton groups

m^2		Cladocera	Copepoda	Rotifera	
July 2001 (winter)	Cladocera		0.0001	0.0001	
	Copepoda	0.52		0.0005	
	Rotifera	0.66	0.74		
November 2001 (summer)	Cladocera		0.0001	0.0001	
	Copepoda	0.48		0.0005	
	Rotifera	0.73	0.73		
r		Cladocera	Copepoda	Rotifera	
	July 2001 (winter)	Cladocera		0.0002	0.0002
		Copepoda	0.63		0.0004
Rotifera		0.42	0.36		
November 2001 (summer)	Cladocera		0.0002	0.0002	
	Copepoda	0.67		0.0007	
	Rotifera	0.39	0.39		

Probability levels are indicated in bold

unique significant predictors of among-reservoir patterns in assemblages of all zooplankton groups (Table 4). Thus, pairs of reservoirs with similar limnological characteristics tend to have similar zooplankton assemblages.

Discussion

Our results clearly show a significant level of assemblage concordance and parallels the results obtained by other studies encompassing aquatic communities in streams (Kilgour & Barton, 1999; Heino et al., 2003; Paavola et al., 2003, 2006) and in lakes (Jackson & Harvey, 1993; Allen et al., 1999; Paszkowski & Tonn, 2000; Bini et al., 2007).

The significant concordance among all groups (in both seasons) and, chiefly, the correlation found between these groups and abiotic data (water chemistry in particular) may indicate that few environmental gradients are structuring assemblages that are constituted by different taxonomic groups (Paavola et al., 2003). These results were not biased by spatial autocorrelation (Legendre, 1993) because geographical distances between reservoirs and their level of hydrological connectedness were ruled out by their inclusion in the multiple Mantel models.

The highest concordance between cladocerans and copepods and, concomitantly, the lowest concordance between rotifers and microcrustaceans could be explained by the fact that cladocerans and copepods

are more phylogenetically related to each other and, in this way, they possess similar environmental requirements. Also, rotifers and copepods present very distinct reproductive strategies and life cycles (shorter for rotifers) (Allan, 1976) and, consequently, they respond differently to underlying environmental gradients.

Usually, monitoring programs of freshwater ecosystems have used surrogate taxonomic groups, assuming that the results can be extrapolated to unstudied groups. Our results supported the use of surrogate taxa for monitoring purposes because patterns in assemblage structure between different taxonomic groups were concordant. In this manner, the use of cladocerans, for instance, as surrogate group, to predict the classification of these reservoirs by copepods assemblage can be a good alternative. At least for the set of reservoirs studied by us, the choice of a particular zooplankton group for monitoring purposes or for long-term ecological studies may be a valid one. The validity of a surrogate group was also indicated by the significant effect of a dominant and strong environment gradient. Otherwise, the potential of this approach to generate useful predictions on others taxonomic groups may be limited (Paavola et al., 2003). Also, among-reservoirs dissimilarities calculated in the summer were significantly correlated with among-reservoirs dissimilarities calculated in the winter. The temporal stability in the pattern of among-reservoirs dissimilarities is important for the optimization of any

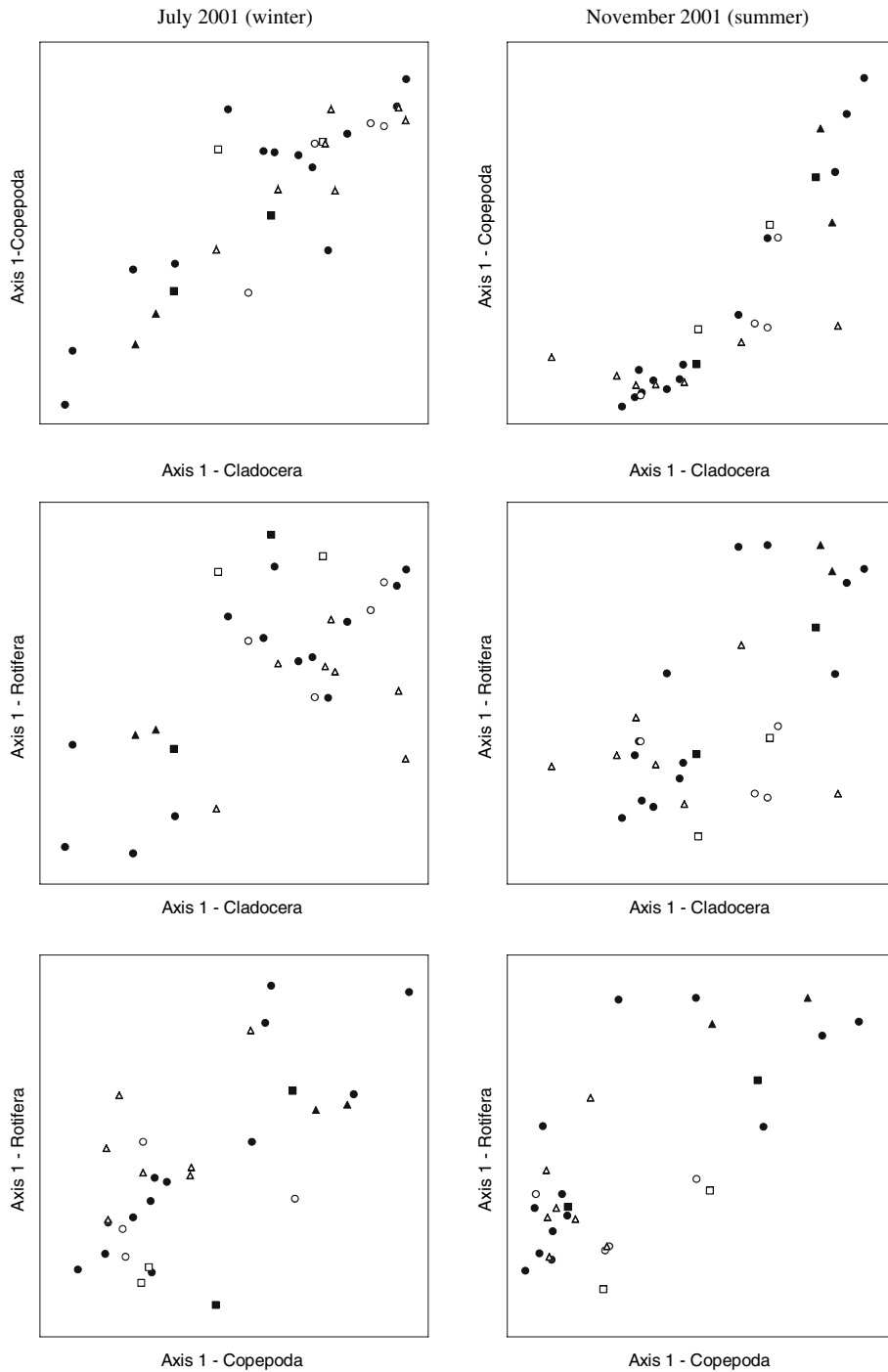


Fig. 3 Relationships between scores on the first axis of the cladocerans, copepods and rotifers principal coordinate analyses. Different symbols indicate reservoirs located in different

watersheds. Filled symbols: Iguagu (circles); Ivaí (squares); Piquiri (triangles); Empty symbols: Serra do Mar (circles); Tibagi (squares); Paranapanema (triangles)

monitoring program, considering the paucity of resources available to long-term studies. Specifically, if the main goal of a long-term study relies on

the comparison of reservoirs across time, our results indicate that sampling may occur in only one season of the year.

Table 3 Standardized Mantel statistics and associated probabilities levels evaluating the relationships between the two months studied

		November 2001			
		Cladocera	Copepoda	Rotifera	Limnology
July 2001	Cladocera	0.54 <i>P</i> = 0.0002			
	Copepoda		0.62 <i>P</i> = 0.0002		
	Rotifera			0.44 <i>P</i> = 0.0002	
	Limnology				0.66 <i>P</i> = 0.0002

Table 4 Partial coefficients and associated levels of significance (*P*) of each explanatory matrix included in the multiple Mantel model

	Limnology	Morphology	Geography	River basin
Cladocera	0.29	0.11	−0.20	0.08
<i>P</i>	0.0003	0.2387	0.5755	0.0953
Copepoda	0.26	0.05	−0.22	0.19
<i>P</i>	0.0009	0.9944	0.8793	0.3754
Rotifera	0.36	0.04	−0.11	0.13
<i>P</i>	0.0001	0.8092	0.6845	0.6982

The results obtained by Olden et al. (2006) supported the use of a single-year survey in cross-lake studies in freshwater community ecology. In our study, however, it should be stressed that, for applied issues (as stated above), we are assuming that the patterns of among-reservoir similarity in zooplankton community structure are stable across years. Unfortunately, there is a paucity of inter-annual data on zooplankton composition to test this assumption in the set of reservoirs studied by us.

Most probably, the significant degree of concordance among the groups (Table 2) was due to the large spatial extent of this study, which encompassed six major watersheds. At this broad geographic scale, the inclusion of reservoirs with different water chemistries is assured and the power to detect relationships between environmental factors and turnover in biological communities is increased. In short, the importance of the range considered for the environmental factors (which increases with the spatial extent of the study) should be taken into account in the interpretation of our results (see Jackson et al., 2001 for a review on the effect of scale on the ability to detect associations between environmental factors and community attributes). This was also the main conclusion reached by Paavola et al. (2006) in a study about the community

concordance among different taxonomic groups in boreal streams (Finland).

For broad-scale analyses, our results are promising due to the significant (and strong relationships between cladocerans and copepods) patterns of concordance that were detected. Taken as a whole, these results indicate that community concordance analysis may be a powerful tool for enhancing the efficiency of monitoring programs, ensuring their long-term sustainability.

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