

Effect of the connectivity on the diversity and abundance of cladoceran assemblages in lagoons of the upper Paraná river floodplain.

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ABSTRACT: Effect of the connectivity on the diversity and abundance of cladoceran assemblages in lagoons of the upper Paraná river floodplain. The objective of this study was to investigate the influence of the degree of connectivity and the flood pulse on the abundance and diversity patterns of planktonic Cladocera in lagoons of the Upper Paraná River floodplain. Samples were collected on the surface in the limnetic region of 9 lagoons, three having a high degree of connectivity, three with low degree of connectivity, and three no connected to the river, during the high and low water periods. Eighteen species of Cladocera were identified, and although not significant, there was a tendency for the lagoons with high connectivity to be more diverse during both sampling periods. This can be explained by the continuous fauna exchange between the river and the lagoons. The results of the diversity index suggest that the flood pulse exerts a homogenizing effect, which is most evident in the lagoons with a high degree of connectivity. With respect to abundance, the results also show a tendency for greater densities of Cladocera to occur in lagoons with a high degree of connectivity. However, when the abundance patterns of the dominant species are analyzed, it can be seen that these species answer in distinct ways to the degree of connectivity and the flood pulse.

Key-words: Cladocera, abundance, diversity, connectivity, floodplain.

RESUMO: Efeito da conectividade sobre a abundância e diversidade das assembléias de cladóceros no plâncton da planície de inundação do alto rio Paraná. Este estudo teve como objetivo investigar a influência do grau de conectividade e do pulso de inundação na determinação dos padrões de abundância e diversidade de cladóceros no plâncton da planície de inundação do alto rio Paraná. Amostragens de zooplâncton foram realizadas à superfície da região limnética, de 9 lagoas, sendo 3 com alto grau de conectividade com o rio, 3 com baixo grau e 3 sem comunicação com o rio principal, em dois períodos hidrológicos distintos (águas altas e águas baixas). Foram registradas 18 espécies de cladóceros e, embora não significativa, observou-se uma tendência de maior diversidade nas lagoas com alto grau de conectividade, em ambos períodos hidrológicos. Tal tendência pode ser explicada pelo contínuo intercâmbio da fauna entre o rio principal e as lagoas. Os resultados da diversidade sugerem um efeito homogeneizador do pulso de inundação o qual é mais evidente nas lagoas com elevado grau de conectividade com o rio principal. Em relação à abundância, os resultados também evidenciaram uma tendência de maiores densidades de cladóceros nas lagoas com alto grau de conectividade. No entanto, ao se analisar os padrões de abundância das espécies mais representativas, constata-se que estas espécies respondem de maneira distinta ao grau de conectividade e às flutuações do nível hidrológico.

Palavras-chave: Cladocera, abundância, diversidade, conectividade, planície de inundação.

Introduction

One of the most important objectives of aquatic ecology has been the study of spatial and temporal patterns in species richness and abundance of aquatic communities and the identification of the main physical, chemical and biological parameters responsible for these patterns.

In floodplain environments, physical and chemical parameters have been shown to be important in determining some patterns in the abundance and distribution of aquatic communities (Robertson & Hardy, 1984; Paggi & José de Paggi, 1990; Bonecker & Lansac-Tôha, 1996). However, other factors such as flood pulse, the morphology of rivers and lagoons, the presence or absence of aquatic macrophytes and more recently, the degree of connectivity of floodplain lakes to the main rivers have also gained attention as important parameters in structuring these aquatic communities (Lima et al., 1998; Tockner et al., 1998, 1999; Velho et al., 1999; Ward et al., 1999; Bini et al., 2003; Velho et al., 2003; Lansac-Tôha et al., 2004).

Within the zooplankton community, cladocerans participate actively in the energy flow and nutrient cycling of aquatic systems since they are predominantly filter feeders, filtering detritus, algae and bacteria (Payne, 1986), and also because they are important food items for a number of invertebrate and fish species. Several aspects of the structure and dynamics of cladoceran communities in lagoons of the Upper Paraná River floodplain have been studied by Lansac-Tôha et al. (1997, 2004), and Lima et al. (1998).

In this study we examine the effect of connectivity and flood pulse on the species richness and abundance patterns of Cladocera in nine lagoons of the Upper Paraná River floodplain.

Material and methods

Study area

The Paraná River is the main river in the Plata basin. It is also the fourth largest river in the world with respect to drainage basin and the tenth largest river in terms of discharge (Agostinho & Zalewski, 1996). The present study was undertaken in the Upper Paraná River floodplain, which is the last undammed stretch of the Paraná River in Brazil. In this braided floodplain, innumerable lagoons can be found connected directly or indirectly to the Paraná River itself or to its main tributaries in this area, the Baía and Ivinheima rivers (Fig. 1).

For the purpose of this study three categories of lagoons were selected: high connectivity lagoons, low connectivity lagoons and lagoons with no connectivity. High connectivity lagoons are considered to be those directly connected (by a wide opening) or by a short and wide channel to the rivers all year round. Low connectivity lagoons are those connected to the rivers by a long and narrow channel all year round, and lagoons with no connectivity are those lagoons with no direct connection to the rivers, except during exceptional floods. On each river-floodplain system (Paraná, Baía and Ivinheima) a set of the three categories of lagoons was sampled in a total of nine lagoons (Fig. 1 and Tab. 1).

Sampling

Sampling was undertaken during the high (February) and low water periods (August) of 2001. Fig. 2 shows the annual variation in the water level of the Upper Paraná River during the study period.

Zooplankton samples were collected in the pelagic regions of the lagoons with a motorized pump. The water collected at the surface (600 liters) was filtered through a 65 µm plankton net. The samples were immediately fixed with 4% buffered formalin.

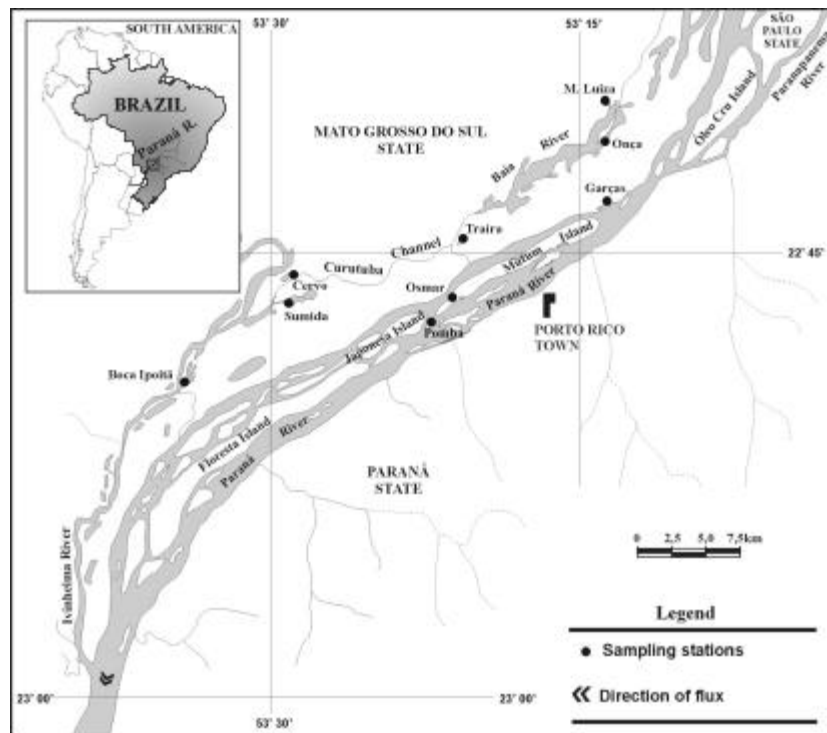


Figure 1: Study area and the sampling sites in the Upper Paraná River floodplain.

Table 1: List of the lagoons sampled, degree of connectivity and main river to which they are connected.

Lagoon	Connectivity degree	River
Pomba	high	Paraná
Garças	low	Paraná
Osmar	no	Paraná
Boca do Ipoitã	high	Ivinheima
Sumida	low	Ivinheima
Cervo	no	Ivinheima
Maria Luiza	high	Baía
Onça	low	Baía
Traira	no	Baía

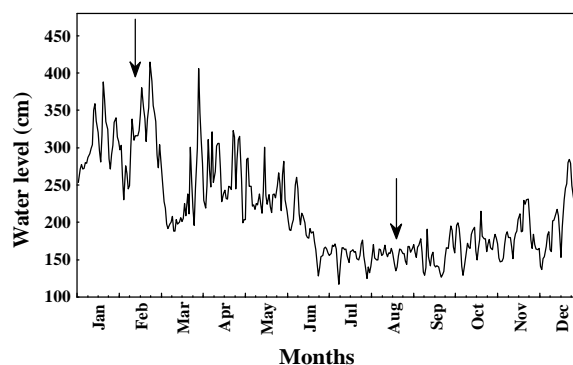


Figure 2: Annual variation of the water level of the Upper Paraná River from January to December 2001 (Arrows indicate the sampling dates).

Samples were counted in a Sedgwick-Rafter chamber and a optical microscope (magnification of 10x). A minimum of 50 individuals was counted in each one of the three sub samples taken with a Hensen-Stemple pipette. Abundance of cladocerans was expressed as ind./m³.

Data analysis

Two diversity indices were used: **a** and **b** diversity. The first is the number of species found in each sample, and the second, which quantifies the change in species composition in time or along an environmental gradient (Whittaker, 1960), was estimated by the coefficient **b-2** (Harrison et al., 1992; Blackburn & Gaston, 1996):

$$b-2 = ((R/a_{max})-1)/(n-1)$$

where **a_{max}** is the maximum value of species richness in the set of **n** samples (months or stations) and **R** is the total number of species in the **n** samples

The **b** diversity index was used to evaluate changes in space and in time. It was used to evaluate the change in the species composition in similar lagoons, among lagoons in the same connectivity category, and in each distinct hydrological period, high water and low water level. It was also used to evaluate the change in species composition in each category of lagoon between the hydrological periods.

An ANOVA was used to test the effect of type of lagoon and hydrological period on i) species richness; ii) abundance of cladocerans and iii) abundance of the dominant species (Sokal & Rohlf, 1991). Biotic data (abundance and species number) were log (x+1) transformed to approximate a normal distribution and to stabilize variance. These analyses were performed using the statistics package Statistica version 5.0.

Results and discussion

A total of 18 species of Cladocera were identified (Tab. II). The richest family in species was Chydoridae (8 species). Bosminidae and Daphniidae were represented by 3 species each, and the other families, Moinidae, Macrothricidae, Ilyocryptidae and Sididae were represented by one species. These families, genera and species have often been found as the most common in plankton samples from the Upper Paraná River floodplain (Lansac-Tôha et al., 1997, 2004; Lima et al., 1996, 1998; Serafim Jr. et al., 2003).

Table II: Cladocera species found in 9 lagoons in the Upper Paraná river floodplain in February and August 2001.

Chydoridae	Bosminidae
<i>Alona quadrangularis</i> (O.F. Müller, 1875)	<i>Bosmina tubicen</i> Brehm, 1953
<i>A. affinis</i> (Leydig, 1860)	<i>Bosmina hagmanni</i> Stingelin, 1904
<i>A. cf. verrucosa</i> Sars, 1901	<i>Bosminopsis deitersi</i> Richard, 1895
<i>A. poppei</i> Richard, 1897	
<i>Ephemeroporus hybridus</i> (Daday, 1905)	Daphniidae
<i>Euryalona occidentalis</i> Sars, 1901	<i>Ceriodaphnia cornuta</i> Sars, 1886
<i>Chydorus eurynotus</i> Sars, 1901	<i>Ceriodaphnia</i> sp.
<i>Disparalona dadayi</i> (Birge, 1910)	<i>Daphnia gessneri</i> Herbst, 1967
Macrothricidae	Moinidae
<i>Macrothrix spinosa</i> King, 1853	<i>Moina minuta</i> Hansen, 1899
Ilyocryptidae	Sididae
<i>Ilyocryptus spinifer</i> Herrick, 1882	<i>Diaphanosoma spinulosum</i> Herbst, 1967

Abundance and α and β diversity were analyzed with respect to the hydrological periods and the degree of connectivity of the lagoons. There was a tendency for higher α diversity values to occur in the lagoons with high connectivity during both high water and low water periods (Fig. 3). In floodplain systems, the connectivity between lagoons and rivers can be considered one of the main factors structuring aquatic communities and it is of fundamental importance in the maintenance of biodiversity in these systems, given that a greater connectivity between the environments allows for a greater exchange of the fauna assemblages from different areas (Ward et al., 1999).

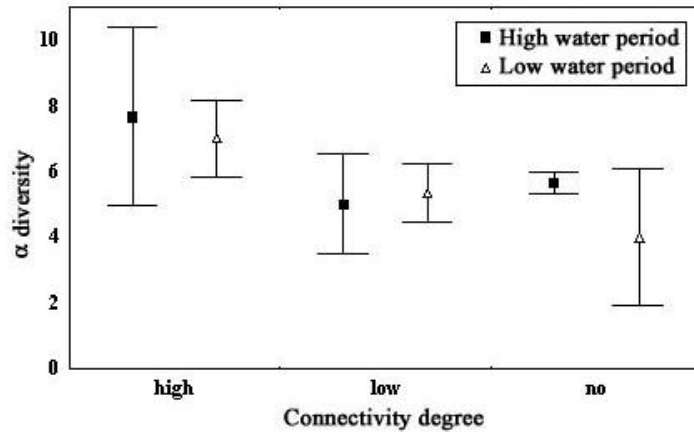


Figure 3: α diversity of Cladocera in lagoons with different degrees of connectivity during the high water and the low water period. (The dots represent the mean and the vertical bars, standard error).

Velho et al. (2004) investigated the distribution patterns in the species richness of testate amoebae in the Upper Paraná floodplain and observed high species richness in lotic environments. They suggested that the river functions as a collector of the fauna present in all of the floodplain. Therefore, as the interface between river and lagoons increases, the input of species from rivers to lagoons also increases. The spatial analysis of β diversity showed that greater values were observed during the low water period. Thus, in this period, all categories of lagoons are more distinct in relation to the cladoceran fauna composition than during the high water period (Fig. 4).

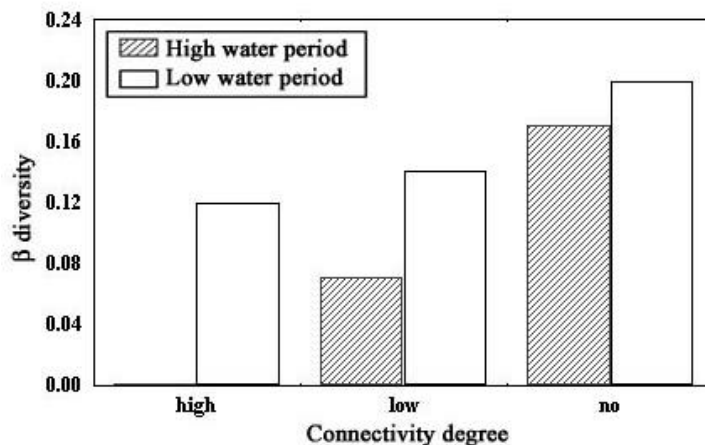


Figure 4: Spatial variation of β diversity during the high water and the low water periods.

Comparing different categories of lagoons, we observed that, in both periods, the β values increase with the decrease of the connectivity degree. In other words, a higher turnover in species composition was observed among lagoons with no connection and a lower turnover was recorded among lagoons with high connectivity (Fig. 4). In this way, these results suggest that a greater connectivity, mainly in the high water level period, determine a greater interchange of fauna among environments and, consequently, a greater similarity of cladocerans composition among lagoons with connectivity.

Since the lagoons tend to have a more similar Cladocera composition during the high water period supports, the flood has a homogenizing effect on the distribution of the fauna on the floodplain. This effect has been also observed for other zooplankton groups such as rotifers, copepods and testate amoebae (Bonecker et al., 2002; Lima et al., 1998; Velho et al., 2004). Moreover, the results also suggest that the effects of the flood pulse, in this study period, was most evident in lagoons with high connectivity and least evident in lagoons with low or no connectivity.

The results of the temporal β diversity, which evaluated the turnover of species composition of each lagoon between hydrological periods, showed higher values of β in lagoons with low connectivity degree (Fig. 5). The greatest change in species composition in these lagoons probably occurred due to the river influences only in the flood period.

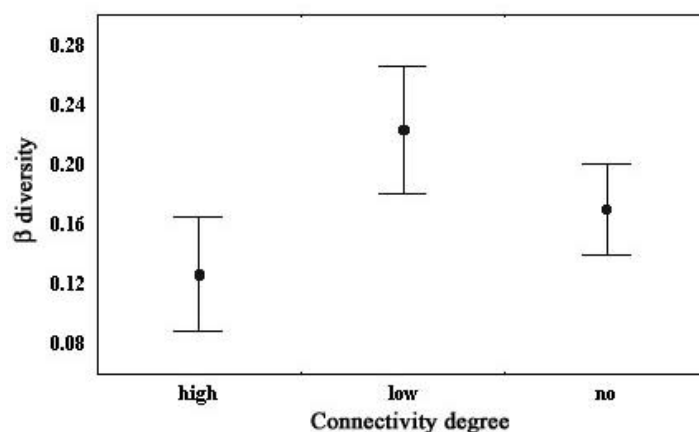


Figure 5: Temporal variation of β diversity for lagoons with different degrees of connectivity.

On the other hand, in the other categories of lagoons, the lower values of β diversity observed were probably due to the wide influence of the river on the lagoons with high connectivity, and due to the lack of river influence on the lagoons without connectivity, in both periods, determining a lower changes in cladoceran fauna composition between hydrological periods.

With respect to the total abundance of Cladocera, the most obvious differences among the different categories of lagoons were observed during the low water period (Fig. 6). Similarities in abundance observed during the high water period are a result of the homogenizing effect of the flood.

In the high water period, lagoons with high and low connectivities presented similar densities of Cladocera (Fig. 6). The rise in the river water level and the flood event, which increases the lagoon/river interface, probably acts in a similar way in all lagoons with some kind of connectivity. Lagoons with no connectivity had lower densities of Cladocera. These lagoons probably are less productive because they only are submitted to the nutrients input from the river during exceptional floods.

During the low water period, significant differences in the abundance of Cladocera were observed between lagoons with high connectivity and no connectivity. Lagoons with low connectivity presented intermediate values of abundance (Fig. 6).

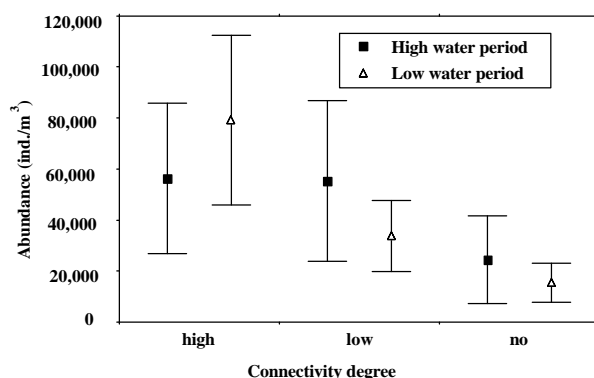


Figure 6: Abundance of Cladocera in lagoons with different degrees of connectivity during the high water and the low water periods. (The dots represent the mean and the vertical bars, standard error).

In relation to total abundance of cladocerans families, Daphniidae was the most abundant, followed by Moiniidae, Bosminidae and Sididae (Fig. 7). However, in relation to the connectivity degree, two distinct abundance patterns were observed. In relation to first pattern, a clear reduction of Daphniidae, Moinidae and Bosmiidae abundances with the redution of the connectivity degree was recorded, whereas to Sididae it was evidencied an increase in their densities with the redution of the connectivity (Fig. 7).

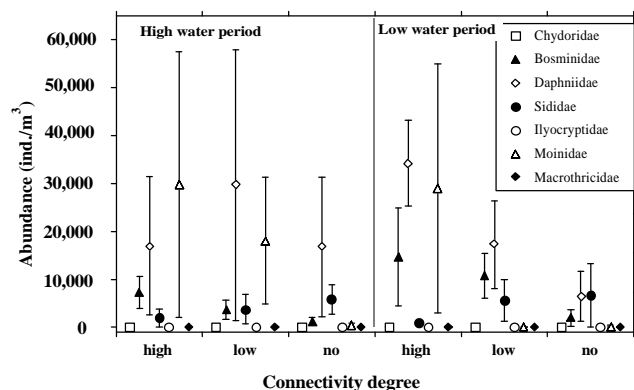


Figure 7: Abundance of Cladocera families in lagoons with different connectivity during the high and low water periods.

Considering that these patterns were evident for both hydrological periods, connectivity was a preponderant factor in determining families abundance. However, flood pulse must be also considered as a relevant factor, since that it affects the degree of connectivity. In this way, the water level influence is clear when we observed the patterns of families densities in the low connectivity lagoons, which showed a similar pattern to those observed for the high connectivity lagoons, at the high water level period, and similar to those observed at no connected lagoons at the low water period.

However, Lima et al. (1998) and Lansac-Tôha et al. (2004) in the same floodplain observed that only one family, Bosminidae, had greater densities during the low water period. Other planktonic species, and also the non-planktonic species, chydorids and macrothricids, presented greater densities during the high water period.

Although 18 species of Cladocera were identified in this study, the greatest mean abundances were observed in the typically planktonic species. *Ceriodaphnia cornuta* was the most abundant (14,200 ind./m³) followed by *Moina minuta* (12,925 ind./m³), *Daphnia gessneri* (5,888 ind./m³), *Bosmina hagmanni* (4,809 ind./m³), *Diaphanosoma spinulosum* (4,124 ind./m³) and *Bosminopsis deitersi* (1,799 ind./m³). These species have also been registered as abundant in the Middle Paraná River, Argentina (Paggi & José de Paggi, 1990), in the Amazon region (Robertson & Hardy, 1984) and in other lagoons of the Upper Paraná floodplain (Lansac-Tôha et al., 1993, 1997, 2004).

In lagoons with no connectivity, there was no difference between the densities of *B. hagmanni* and those species grouped as "other species" (mainly represented by Chydoridae and Macrothricidae families) between the hydrological periods. But, there was an expressive increase in the density of *D. gessneri* during the low water period (Fig. 8). In lagoons with connectivity, densities of *B. hagmanni*, "other species" and *D. gessneri*

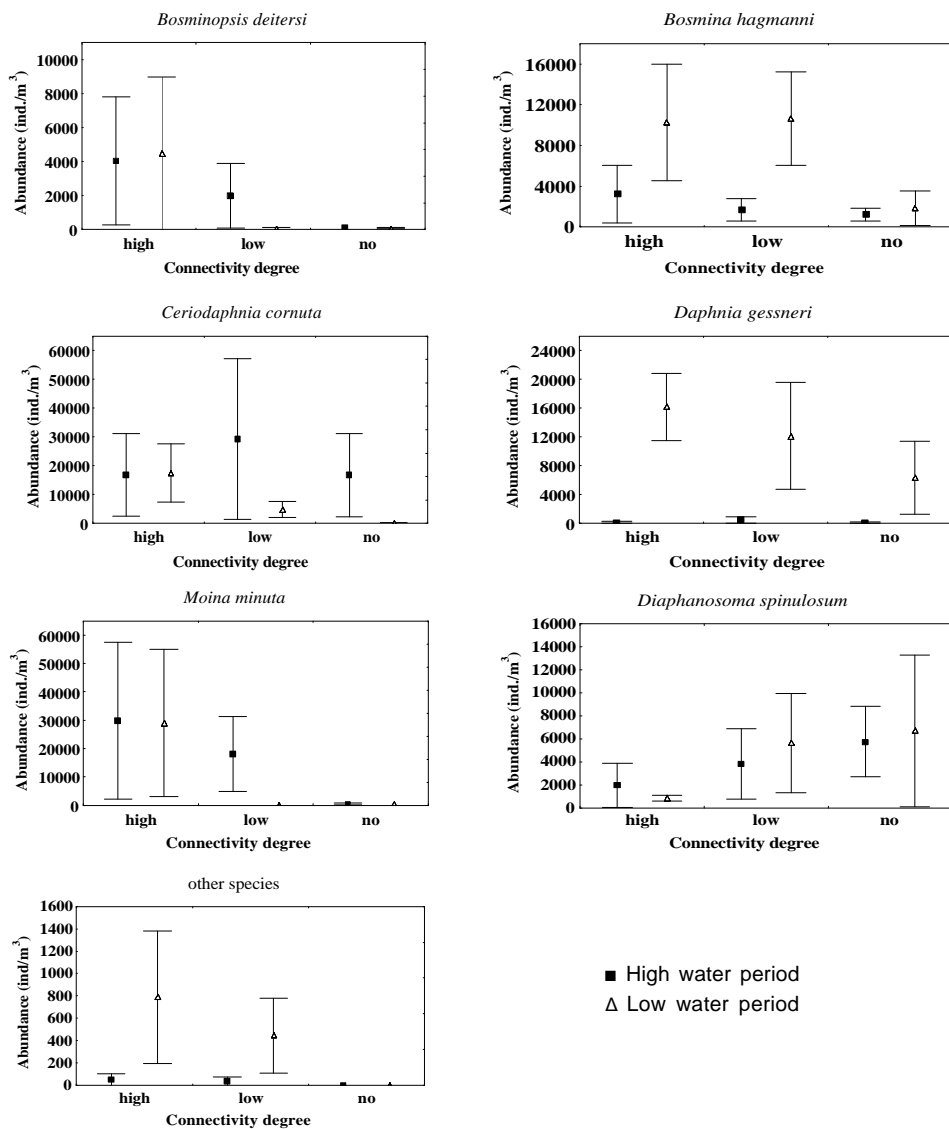


Figure 8: Density of Cladocera species in lagoons with different connectivity during the high water and the low water periods.

were higher during the low water period. The highest abundance of *B. hagmanni* in the low water period was probably related to the low values of pH observed in these environments in this period (Lima et al., 1998). Moreover, Maia-Barbosa (2000), studying cladocerans from Batata lake (AM), also observed high abundance values of this species in the same hydrological period, relating this fact with its capacity of feeding on filamentous algae, which were abundant in this period. In relation to *D. gessneri*, the lower abundance recorded in the high water period was probably related with predation by fishes larvae and juveniles, which are very abundant in the lagoons in this period.

In the lagoons with connectivity, *B. deitersi*, *C. cornuta* and *M. minuta* presented similar abundance patterns. In general, they were most abundant in the lagoons with high connectivity during both hydrological periods and in lagoons with low connectivity during the high water period. In lagoons with no connectivity, *B. deitersi* and *M. minuta* were scarce during both hydrological periods, but *C. cornuta* occurred with high densities during the high water period (Fig. 8). According to Wisniewski et al. (2000), *C. cornuta* has preference for high temperatures, that could justify its greater abundances at the high water period. On the other hand, the high densities observed to *M. minuta* in the same period, could be related to less eutrophic conditions at the flood period, since that this species have been found preferentially in oligo-mesotrophic conditions (Wisniewski et al., 2000; Panarelli, 2004). Considering the abundance distribution of *B. deitersi*, this species presented a distinct pattern of that expected for bosminids, with greater abundances at the high water period, at least for low connectivity lagoons. This species has been found mainly during the low water period in varzea lagoons from Paraná and Paranapanema river-floodplain systems (Lima et al., 1998; Lansac-Tôha et al., 2004; Panarelli, 2004).

In general, *D. spinulosum* presented an inverse pattern to that observed for the other species. Greatest densities were observed in lagoons with no connectivity and the lowest densities in lagoons with high connectivity (Fig. 8). *D. spinulosum* is a large Cladocera often preied upon by young fish. Fish eggs and larvae usually enter the floodplain lagoons during the flood period (Nakatani et al., 1997). However, during the studied period, river water levels were not exceptionally high and the flood did not reach the lagoons with no connectivity with the river. It is possible, then, that *D. spinulosum* populations developed in these lagoons because there was no input of young fish that year and, as a consequence, predation pressure was much reduced.

For the cladoceran species studied here, there seems to be at least three different abundance distribution patterns relative to water level and the degree of connectivity of lagoons on the floodplain. This suggests that different species are responding in different ways to variations of these factors.

Although the results presented above suggest that the flood pulse and the connectivity degree of the lagoons is important in determining the patterns of abundance and species richness in the Cladocera community, the ANOVA tests indicated that the values of species richness and total abundance of Cladocera were not significantly distinct between the different hydrological periods and between lagoons with different connectivity degree (Tab. III and IV). This analysis showed significant differences only for abundance of *D. gessneri*, between the hydrological periods, and for *M. minuta* abundance between the categories of lagoons. These results could have been influenced by several factors: i) sometimes the lagoons with low connectivity presented species richness and abundance values similar to those observed for lagoons with high connectivity and, at times, species richness and abundance values were similar to those of lagoons with no connectivity; ii) we observed distinct patterns between lagoons with connectivity and with no connectivity although a ANOVA cannot be used because the data set did not attend the variance homogeneity assumption; iii) species such as *C. cornuta* presented marked differences in density among the different categories of lagoons only during the low water period, but the ANOVA did not detect these differences as significant.

Table III: ANOVA results based on cladocerans species richness data (F.D. = degrees of freedom; * represents the interactions between effects).

Effects	F.D.>	F	p
Connectivity	2	0,293607	0,7512
Period	1	0,645165	0,4388
Conectivity * period	2	0,123086	0,8853

Table IV: Results of Analysis of Variance (ANOVA) from the total and species cladocerans abundance. P= period; C=connectivity; F.D. = Freedom Degree;* represents the interactions between effects; p values were considered significant (in bold) when $p > 0.05$.

Variables	Effect	F.D.	F	p
Total	P	1	0.00894	0.926529
	C	2	1.0.365	0.397339
	P * C	2	0.37557	0.696187
B. deitersi	P	1	0.48962	0.497438
	C	2	0.29752	0.747983
	P * C	2	0.45505	0.644628
C. comuta	P	1	1.76314	0.208938
	C	2	0.86895	0.444185
	P * C	2	1.12094	0.357835
D. gessneri	P	1	8.93066	0.011307
	C	2	0.38500	0.688561
	P * C	2	0.56992	0.580158
D. spinulosum	P	1	0.04678	0.832396
	C	2	0.54985	0.590905
	P * C	2	1.27159	0.315595
M. minuta	P	1	1.63769	0.224832
	C	2	4.02644	0.045923
	P * C	2	1.79976	0.207214

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