

Macroinvertebrates living on *Eichhornia azurea* Kunth in the Paraguay River.

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ABSTRACT: Macroinvertebrates living on *Eichhornia azurea* Kunth in the Paraguay River. Ten sites along the Paraguay River fringing floodplain, from Porto Cáceres to the confluence with the Paraná River, were sampled during high (June-July 1995) and low (December 1995) water periods in order to explain the abundance and proportion of functional feeding groups of macroinvertebrates living on *Eichhornia azurea*. The mean abundance of macroinvertebrates varied between 3,565 ind.m⁻² and 25,145 ind.m⁻². Depending on the sampling sites insects larvae (Chironomidae and Hydroptilidae) or crustaceans (Lepthesteridae) were the main representative taxa. Similarity between the morpho species of invertebrates was quite high for sites located in the Upper (from the headwater to the Appa River) and the Lower Paraguay. During high water, filtering collectors (FC) dominated and constituted over 40% of total abundance. The ratio FC/GC varied between 2.1 and 6.2 and the ratio SC/SH+Total Collectors between 0.06 and 0.2. At low water there were proportionally more collector-gatherers (GC) predators or scrapers (SC). In comparison with the high water period, the ratio FC/GC decreased and the ratio SC/SH+Col increased. Shredders (SH) were fewer in number during both hydrological periods. Although no significant relationship was found between total abundance of macroinvertebrates and hydrological periods, functional group analysis is sensitive to changes in the importance of the food resource (detritus, periphyton, macrophytes or prey) during low and high water periods.

Key-words: Paraguay river, phytophilous macroinvertebrates, functional feeding groups, *Eichhornia azurea*.

RESUMO: Macroinvertebrados vivendo em *Eichhornia azurea* Kunth no rio Paraguay. Dez locais da planície de inundação lateral do Rio Paraguay, de Porto Cáceres à confluência com o Rio Paraná, foram amostrados durante os períodos de cheia (Junho-Julho de 1995) e estiagem (Dezembro de 1995) da água com finalidade de verificar a abundância e a proporção de grupos funcionais alimentares vivendo em *Eichhornia azurea*. A abundância média de macroinvertebrados variou entre 3.565 ind.m⁻² e 25.145 ind.m⁻². Dependendo dos locais de amostragem, as larvas de insetos (Chironomidae e Hydroptilidae) ou crustáceos (Lepthesteridae) foram as principais taxas representativas. A similaridade entre as morfo espécies de invertebrados foi bastante alta para locais situados no Alto (da cabeceira ao Rio Appa) e Baixo Paraguay. Durante o período de cheia, os coletores filtradores (CF) dominaram e constituíram acima de 40% da abundância total. A razão CF/CC variou entre 2.1 e 6.2 e a razão CR/FR + total de coletores entre 0.06 e 0.2. Na estiagem houve proporcionalmente mais predadores-catadores-coletores (CC) ou raspadores (RS). Em comparação com o período de cheia, a razão CF/CC diminuiu e a razão CR/FR + coletores aumentou. Os fragmentares (SH) foram pouco numerosos em ambos os períodos hidrológicos. Embora nenhuma relação significativa foi encontrada entre abundância total de macroinvertebrados e períodos hidrológicos, a análise de grupo funcional é sensível a mudanças na importância do recurso alimentar (detrito, perifiton, macrófitas ou presa) durante os períodos de cheia e estiagem de água.

Palavras-chave: rio Paraguay, macroinvertebrados fitófilos, grupos funcionais alimentares, *Eichhornia azurea*.

Introduction

The Paraguay River is the Paraná River's largest tributary. It drains the Pantanal, a 138,000 km² water-logged wetland (Neiff, 2001) located on the Brazilian Shield. Flooding in the region is distinctly seasonal, although the high water phase may be delayed 4 to 6 months after the summer rains due to the slow passage of floodwater through the Pantanal. Vegetated water, dominated by *Eichhornia azurea*, *E. crassipes*, *Scirpus cubensis* and *Salvinia auriculata*, is by far the most extensive aquatic environment of the Paraguay River floodplain. The plasticity in structure and morphology of *Eichhornia azurea* in relation to changes in water level allows its growth in periods of drought and flood. Moreover, growth occurs on sandy, acid clayey or alkaline soils (Pott & Pott, 2000). Periphyton that grows on *E. azurea* meadows in the Pantanal of Mato Grosso is also important for their production (De Paula et al., 1996).

Macroinvertebrates (approximately > 0.5 mm in size) stand as the link among algae, macrophytes and micro-organisms, which serve as their primary food resources, and the fish (and other vertebrates), which prey on them (Petts & Callow, 1996). Their role in the trophic webs of the littoral zone is very important because of the shortage of benthos biomass in the main channel of large rivers (Welcome, 1992). Invertebrates living on aquatic macrophytes have received much less attention than benthic and plankton communities in spite of their importance in tropical rivers (Por & Rocha, 1998). In particular, few studies (specially on microcrustaceans, e.g. Heckman, 1994; Rocha & Por, 1998) were conducted in the Pantanal.

This study provides the first estimate of abundance of macroinvertebrates living on *Eichhornia azurea* meadows along the Paraguay River from its headwaters to the mouth. The proportion of functional groups during low and high water periods were compared in order to determine the importance of the food resource (detritus, periphyton, macrophytes or prey) in the fringing floodplain.

Site description

Although the Paraguay River is a tropical system, there is seasonal variation in the flowing water temperature. In the Upper section (from the headwaters to the Apa River, Sites 1 to 5), temperature ranged between 29-31°C (December) and 23.8-25°C (June-July), but there was major variation (10°C seasonally) near the confluence with the Paraná River (Tab. I). pH of the Paraguay River's water tended from slightly acid

Table I: Physico chemical characteristics of the vegetated waters of the Paraguay River fringing floodplain during low and high water periods

Sites	1	2	3	4	5	6	7	8	9	10	
Temperature (°C)	30.9 ± 1.9	29 ± 0.9	-	30.4 ± 0.2	31 ± 0.2	-	31	-	29	28	LW
	23.8 ± 2.1	24.9 ± 0.7	25 ± 0	-	24.6 ± 0.5	23.9 ± 0.07	23.7 ± 0.42	20 ± 0	18	-	HW
Dissolved O ₂ (mg.l ⁻¹)	5 ± 0.2	1.8 ± 0.7	-	5.1 ± 0.2	2.9 ± 0.14	-	6.6	-	6.7	6.6	LW
	6.8 ± 0.8	6.5 ± 0.7	7.6 ± 1.1	-	4.0 ± 0	2.1 ± 0.6	4.4 ± 0.4	5.7 ± 0.2	7.2	-	HW
pH	6.2 ± 0.14	5.7 ± 0.6	-	6.1 ± 0.14	6.3 ± 0.2	-	7.7	-	7.8	7.8	LW
	6.3 ± 0.05	6.7 ± 0.07	7.05 ± 0.07	-	6.6 ± 0.2	6.7 ± 0.07	6.4 ± 0	6.4 ± 0.1	6.9	-	HW
Conductance (mS.cm ⁻¹)	52.5 ± 3.5	67 ± 17	-	55.5 ± 0.7	50 ± 0	-	92	-	160	70	LW
	33.3 ± 4.9	40.7 ± 0.3	46 ± 7	-	68.5 ± 4.2	51 ± 1.4	90	76.5 ± 2.1	100	-	HW
Secchi disk (cm)	26 ± 1.4	51 ± 26	-	22.5 ± 35	17 ± 1.4	-	38	-	11	28	LW
	35 ± 5	41 ± 1.4	80 ± 0	-	100.5 ± 0.7	102.5 ± 10.6	67	87 ± 4.9	26	-	HW
Flow (m.s ⁻¹)	VF	NVF	-	VF	NVF	-	NVF	-	NVF	NVF	LW
	0.40	0.15	NVF	-	0.30	0.50	VF	NVF	VF	-	HW

1 = Cáceres; 2 = Taiaimá; 3 = Novo Horizonte; 4 = Km 1811; 5 = Corumbá; 6 = Murtinho;
7 = Concepción; 8 = Dalmacia; 9 = Downstream Bermejo River; 10 = Confluence
VF = Visible flow; NVF = No visible flow- No sample
LW = Low water (December)
HW = High water (June-July)

to neutral, in the range of 5.7-7.8. The Upper section was relatively poor in inorganic content, with a conductance of 33-68 $\text{mS}\cdot\text{cm}^{-1}$. In the Lower section, conductance increased up to 160 $\text{mS}\cdot\text{cm}^{-1}$ (Tab. I) during summer. The high suspended load of the Bermejo River, originated from erosion of the Andes, strongly influences the physico-chemical composition of the Paraguay River (Carignan & Vaithyanathan, 1999).

At the studied sites, the concentration of dissolved oxygen ranged from 1.8 to 7.6 $\text{mg}\cdot\text{l}^{-1}$ (Tab. I). According to Soldano (1947), the water level of the Paraguay River fluctuates between mean values of 2.5 m (Cáceres, in low water) and 8.70 m (Confluencia, in high water). Vegetated waters, which had lateral water movements from the river towards the floodplain and vice versa, were the shallowest environments. In these areas, the flow varied between 0.15 $\text{m}\cdot\text{s}^{-1}$ (Tiamá) and 0.5 $\text{m}\cdot\text{s}^{-1}$ (Porto Murtinho) during high water (HW). At low water (LW), the flow was imperceptible at most sampling sites (Tab. I).

Methods

Samples were collected during high (June-July 1995) and low (December 1995) water periods from 10 sites along the Paraguay River fringing floodplain (Fig. 1): 1- Porto Cáceres (km. 2200, 16°04'57"S-57°42'33"W), 2- Tiamá (km.2002, 16°55'15"S-57°27'17"W), 3- Porto Novo Horizonte (km. 1855, 17°31'52"S-57°27'17"W), 4- Bela Vista (km. 1811, 17°43'53"S-57°39'52"W), 5- Corumbá (km. 1522, 19°15'43"S-57°14'17"W), 6- Pto. Murtinho (km. 1100, 21°43'03"S-57°54'47"W), 7- Concepción (km. 710, 23°26'57"S-57°26'22"W), 8- Dalmacia (km. 270, 25°39'10"S-57°44'25"W), 9- Downstream from the Bermejo River (km.64, 26°51'37"S-58°23'08"W) and 10- Confluence with the Paraná River (km. 0, 27°31'S, 58°54'W).

At each site, the stems of *E. azurea* inside a 0.30 m^2 circular plot were cut off at about 50-70 cm below the water surface and collected with a 225 μm mesh net. Samples extracted in triplicate were placed in plastic bags and preserved in 4% formaldehyde. At the laboratory, the stems were washed to detach macroinvertebrates, and suspensions obtained were filtered through 1 mm and 500 μm sieves. The largest fraction was processed, and then invertebrates were manually separated from plant and detritus rests. An aliquot of the smallest size fraction was counted under the microscope.

Each taxa was allocated to a functional feeding group (Merritt & Cummins, 1996), based on four basic nutritional resource categories: *detritus* (coarse or fine particulate organic matter), *periphyton*, live *macrophytes* and *prey*. Morphological information of invertebrate mouthparts was supplemented by observation of live material at the laboratory. In this study, filtering collectors or suspension feeders were separated from gathering collectors or deposit feeders. Scrapers (SC) included invertebrates that, although pierce algal cells, such as *Neotrichia* larvae (Angrisano, 1992), also use ephyphytes associated with *E. azurea*. The trophic category of *Berosus* and *Corynoneura* larvae was based on complementary bibliography (Kesler, 1981; Poi de Neiff, 1990).

The ratio of shredders to total collectors (SH/Col, Petts & Calow, 1996) is an index of the degree of the Coarse Particulate Organic Matter influence as a food source. The ratio of scrapers to shredders+total collectors, SC/(SH+Col), can serve as an index of the participation of the periphytic algae in invertebrate feeding. The balance between the depositional component and the transport component of total Fine Particulate Organic Matter (FPOM) can be reflected in the ratio of filtering collectors to gathering collectors (FC/GC, Petts & Calow, 1996). ANOVA was used to determine significant differences on normalized data (logarithmic transformation or arcsine square root procedure). Spearman's rank correlation coefficient (Steel & Torrie, 1980) was used in order to relate invertebrate abundance with different independent variables (flow, temperature, dissolved oxygen, pH and Secchi disk).

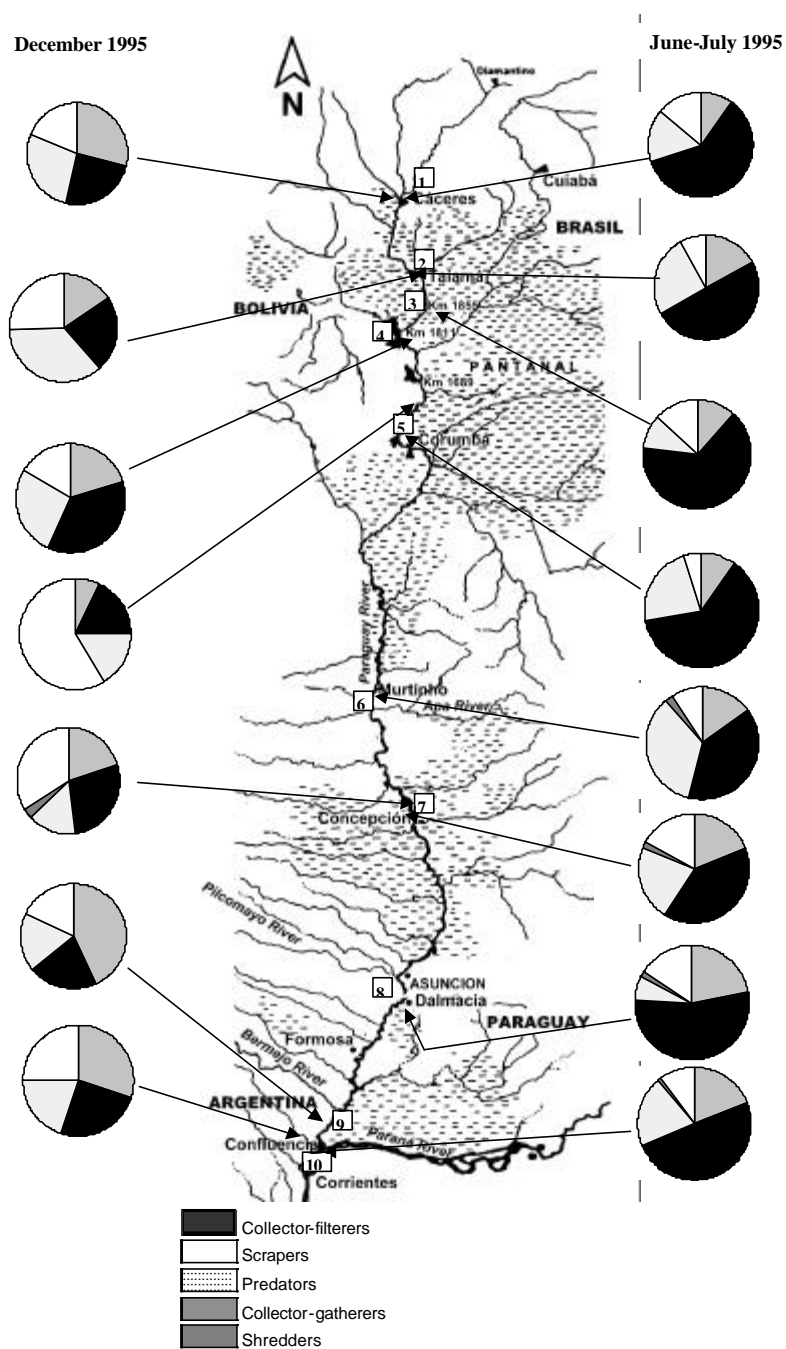


Figure 1: Percentage composition of invertebrates functional feeding groups at study sites.

Results

The mean number of macroinvertebrates (Tab. II) varied between 3,565 ind.m⁻² (Porto Murtinho) and 25,145 ind.m⁻² (Dalmacia). No significant differences ($F=0.35$, $P<0.01$) were found when ANOVA was used to compare abundance between low and high phases of the hydrological pulse. This also implies the absence of significant seasonal differences. In the littoral areas of the river course (near the floodplain) local

variations in water velocity were observed due to the lateral movements from or towards the river course. During the low water phase there was a perceptible flow at sites 1 and 4, whereas at high water the flow velocity was not visible when sampling at sites 3 and 8 (Tab. I). The correlation (Spearman's rank coefficient) between invertebrate abundance and flow at the sampling sites was -0.77. No significant correlations were found between macroinvertebrate abundance and any independent variable. The macroinvertebrate fauna was dominated by insects (larvae of Chironomidae and Hydroptilidae), crustaceans (Leptesteridae and Cytherideidae) and Oligochaeta (Tab. II). Ephemeroptera and Odonata nymphs were another groups of importance. Some taxa were found irregularly in several sites (e.g., Planorbiidae) and some were present only in the low water period (e.g., Elmidae in Tab. II)

Table II: Comparison of total invertebrates abundance (ind.m⁻²), density of main representative taxa (ind.m⁻²) and functional feeding group ratios for the Paraguay River at low and high water periods.

Sites	1	2	3	4	5	6	7	8	9	10		
Oligochaeta	62	597	-	322	468	-	1842	-	851	4439	LW	
Naididae	124	208	374	-	270	62	239	467	301	-	HW	
Ostracoda	228	1415	-	291	996	-	156	-	467	129	LW	
Cytherideidae	0	125	343	-	1042	0	52	0	10	-	HW	
Conchostraca	155	52	-	10	0	-	0	-	0	0	LW	
Leptesteridae	104	1091	8295	-	252	499	1871	6216	228	-	HW	
Mollusca	350	10	-	0	135	-	613	-	176	77	LW	
Planorbiidae	0	62	374	-	239	21	0	10	0	-	HW	
Diptera	707	5915	-	928	1580	-	5100	-	8164	4994	LW	
Chironomidae	2942	3035	5104	-	1029	1829	1019	8607	2952	-	HW	
Ephemeroptera	436	561	-	72	93	-	52	-	145	31	LW	
Caenidae	143	51	21	-	0	10	0	176	530	-	HW	
Baetidae	345	395	-	166	31	-	10	-	384	36	LW	
	239	145	135	-	10	166	488	676	135	-	HW	
Trichoptera	83	3145	-	259	7003	-	3528	-	1020	4254	LW	
Hydroptilidae	592	187	2079	-	209	145	1372	3532	301	-	HW	
Odonata	125	10	-	62	550	-	156	-	0	103	LW	
Libellulidae	10	20	31	-	41	114	124	176	0	-	HW	
Coleoptera	0	1206	-	73	0	-	155	-	353	0	LW	
Elmidae	0	0	0	-	0	0	0	0	0	-	HW	
Total abundance of macroinvertebrates	3638 ±220 4667	15728 ±2010 6855 ±1080	- 20333 ±1730	2900 ±243	12505 ±1994 6975 ±440	- 3565 ±365	14168 ±1640 6018 ±1212	- 25145 4312	13607 ±1950 5031 ±603	18497 ±2115	-	LW HW
SC/(SH + COL)	0.3 0.2	0.7 0.1	- 0.2	0.3 0.1	2.4 -	- 0.2	0.7 0.3	- 0.2	0.3 0.1	0.4 -	-	LW HW
FC/GC	0.9 6	1.4 2.9	- 5.4	1.8 6.2	2.5 -	- 2.6	1.4 2.1	- 2.4	0.5 2.6	0.8 -	-	LW HW

1 = Cáceres; 2 = Talamá; 3 = Novo Horizonte; 4 = Km 1811; 5 = Corumbá; 6 = Murtinho;

7 = Concepción; 8 = Dalmacia; 9 = Downstream Bermejo River; 10 = Confluence

- No sample

LW = Low water (December)

HW = High water (June-July)

Seventy-seven morpho-species were registered (Tab. III). The Dice-Sorensen similarity was quite high, about 0.70 (LW) and 0.80 (HW) for sites located in the Upper and Lower Paraguay. The comparison between these sections showed that only two species (*Hyalella curvispina* and *Trichoctylus borellianus*) were not registered in the Upper Paraguay. The first one was collected below Dalmacia and the second one was collected below Porto Murtinho.

Figure 1 shows the percentage composition of functional feeding groups of macroinvertebrates living on *E. azurea* at studied sites. Significant differences were found in the relative abundance of collector filterers (F=41.3, P<0.01) and scrapers (F=11.8, P<0.01) during different hydrological periods.

At high water (June-July), filtering collectors dominated and constituted over 40% of total abundance. The main taxa in this group were *Cyclestera hislopii* (Conchostraca), *Cytheridella ilosvayi* (Ostracoda) and *Rheotanytarsus* sp., (Diptera,

Chironomidae). The ratio FC/GC varied between 2.1 and 6.2. The ratio SC/(SH+Col) fluctuated between 0.06 and 0.2 (Tab. II).

During low water (December), Chironomidae larvae (*Tribelos* sp., *Harnischia* sp., *Ablabesmyia* sp.), Hydroptilidae larvae (*Neotrichia* sp.) and Ephemeroptera nymphs were dominant. Depending on the sampling sites there were proportionally more collectors, predators or scrapers (Fig. 1). At some sites (e.g., Porto Cáceres), the main taxa of scrapers were mollusks (Planorbidae), while at others (e.g., Taiamá) the larvae of *Neotrichia* sp., *Corynoneura* sp. and Elmidae were the most abundant. In comparison with the high water period, the ratio FC/GC decreased and the ratio SC/(SH+Col) increased (Tab. II).

In both hydrological periods, the ratio SH/Col was 0 or near 0, e.g. in Concepción (0.06, LW and 0.03, HW), Murtinho (0.03, HW), Dalmacia (0.01, HW) and Confluencia (0.01, HW). Herbivore populations were abundant, reaching up to 50 ind.m⁻² (*Neochetina* spp.) and 400 lepidopteran larvae m², but their proportion was low regarding the total abundance of macroinvertebrates.

Table III: Functional feeding groups according to their trophic category

Predators	Collectors gatherers
<i>Neoplea maculosa</i>	<i>Slavina evelinae</i>
<i>Pelocoris nigriculus</i>	<i>Dero(Dero) cooperi</i>
<i>Lipogomphus lacunifera</i>	<i>Dero(Dero) multibranchiata</i>
<i>Belostoma micantulum</i>	<i>Dero (Aulophorus) sp.</i>
<i>Telebasis</i> sp. (nymphs)	<i>Dero (Aulophorus) pectinatus</i>
<i>Miathyria marcella</i> (nymphs)	<i>Pristina leidyi</i>
<i>Perithemis</i> sp. (nymphs)	<i>Pristina macrochaeta.</i>
Saldidae	<i>Hyalella curvispina</i>
<i>Mesovelia</i> sp.	<i>Tenagobia</i> sp.
<i>Ablabesmyia</i> sp.(larvae)	<i>Caenis</i> sp. (nymphs)
<i>Labrundinia</i> sp. (larvae)	<i>Callibaetis</i> sp.(nymphs)
<i>Monopelopia</i> sp. (larvae)	<i>Chironomus</i> sp. (larvae)
<i>Bezzia</i> sp. (larvae)	<i>Micropsectra</i> sp. (larvae)
Polycentropodidae (larvae)	<i>Stenochironomus</i> sp.(larvae)
<i>Copelatus</i> sp.	<i>Dicrotendipes</i> sp. (larvae)
<i>Desmopachria</i> sp.	<i>Zavreliella</i> sp. (larvae)
<i>Laccophilus</i> sp.	<i>Harnischia</i> sp.(larvae)
<i>Hydrocanthus</i> sp.	<i>Tribelos</i> sp. (larvae)
<i>Suphis cimicoides</i>	<i>Parachironomus</i> sp. (larvae)
Hydrophilidae (larvae)	<i>Mansonia</i> sp. (larvae)
Lampyridae (larvae)	<i>Oxyethira</i> sp. (larvae)
Staphylinidae	<i>Scirtes</i> sp. (larvae)
<i>Helobdella</i> sp.	<i>Enochrus</i> sp.
Hidracarina	<i>Helochaeres</i> sp
sp. 1	<i>Paracymus</i> sp.
sp. 2	<i>Tropisternus lateralis</i>
	<i>Derallus</i> sp.
Scrapers	Collectors filterers
<i>Corynoneura</i> sp.(larvae)	<i>Cytheridella ilosvayi</i>
<i>Neotrichia</i> sp. (larvae)	<i>Cypricercus</i> sp.
Elmidae (larvae)	<i>Strandesia</i> sp.
Berosus (larvae)	<i>Cyclestheria hislopji</i>
Dryopidae	<i>Rheotanytarsus</i> sp.(larvae)
<i>Drepanotrema anatinum</i>	<i>Smicridia</i> sp. (larvae)
<i>Drepanotrema lucidum</i>	<i>Eupera platensis</i>
<i>Uncancylus</i> sp.	<i>Asthenopus curtus</i> (nymphs)
<i>Littoridina guaranitica</i>	
<i>Ampullaria canaliculata</i>	
Shredders (Herbivores)	Omnivorous
<i>Cricotopus</i> sp.(larvae)	<i>Trichodactylus borellianus</i>
<i>Polypedilum</i> sp. (larvae)	<i>Macrobrachium</i> spp.
<i>Neochetina brucchi</i>	
<i>Neochetina eichhorniae</i>	
<i>Hydrochus richteri</i>	
Lepidoptera (larvae)	

Discussion

In the fringing floodplain of the Paraguay River, *Eichhornia azurea* meadows are inhabited by a rich invertebrate fauna which shows a similar taxonomic composition when different sites of the floodplain along the river course are compared. Although this similarity is real, its magnitude is accentuated by the large numbers of immature forms that could not be identified to species level. The high similarity in taxonomic composition observed in this study is frequently mentioned for pleuston (Por & Rocha, 1998). The composition of microcrustaceans of vegetated water of the southern Pantanal is similar both in the rainy season and the dry season (Rocha & Por, 1998). When stands of free floating meadows of the same species (*Pistia stratiotes*) growing at very distant latitudes (Florida, USA, and Chaco, Argentina) were compared, the conspicuous species of invertebrates in both areas were also the same ones (Escher & Lounibos, 1993). The absence of some species, such as *Hyalella curvispina*, in the floating meadows of the Upper Paraguay is coincident with what was pointed out by Por & Rocha (1998).

The total macroinvertebrates abundance is similar than that found in *E. crassipes* floating meadows growing in the Paraná River floodplain lakes (Poi de Neiff & Carignan 1997). In these lakes the abundance is closely related to hydrological periods and the oxygen depletion, which causes a decrease in total abundance of invertebrates, is found at low water. This pattern is not so clear for the Paraguay River because of the influence of variations in flux velocity at different sites. Although the degree of deoxygenation below the macrophytes depends on water movements (Welcome 1992), in the Upper Paraguay anoxic event was observed at high water during the first contacts of the rising water with the previously dry floodplain (Hamilton et al., 1997). This observation is interesting because anoxic water has rarely been reported for large rivers which typically display maximum oxygen concentration at high water. In this study, low concentration of dissolved oxygen was registered at high and low water depending on sampling sites, but the oxygen depletion is less pronounced than that registered in sites located far from the river course, such as the anoxic vegetated waters mentioned by Hamilton et al. (1995) for the Pantanal.

Invertebrate functional group analysis is sensitive to hydrological and seasonal changes that occur along river systems from the headwaters to the mouth. The reduced ratio shredders:collectors reflects the scarce proportion of herbivores (chewers and miners) on live macrophytes. These results agree with what was pointed out for the Paraná River floodplain in floating meadows of *Eichhornia crassipes* (Poi de Neiff & Carignan, 1997) and in that of the Orinoco River (Blanco Belmonte et al., 1998).

The sampling procedure used may have overlooked fauna which drops off the plant during its removal from the stand or other animals, such as boring insects which fail to emerge from internal plant tissues. In spite of this possible underestimation, herbivores are generally assumed to be rare on aquatic macrophytes (Newman, 1991). The scarce proportion of herbivores does not indicate that they are not important. Populations of *Neochetina* spp. with only 120 ind.m⁻² produce accumulative damages that contribute to the annual decadence of *Eichhornia crassipes* in the northeast of Argentina (Casco & Poi de Neiff, 1998). There is little doubt that senescent macrophytes and macrophyte detritus are important in food webs.

The increase of filtering collectors in high water coincides with what was found in vegetated areas of the Paraná River floodplain, where the ratio FC/GC reaches 6 (sites located far from the river) or 15 (sites located near the main channel) during extraordinary floods (calculated from the data mentioned by Poi de Neiff & Carignan, 1997). This ratio reflects the prevalence of dissolved and fine organic matter transported by the river in high water that would represent an important food resource for filtering collectors. However, vegetated areas play a double role as inorganic sediment traps and invertebrate retention (Poi de Neiff et al., 1994) during high water. Por & Rocha (1998) mention seasonal differences in the abundance of *Cyclotheria*

hislopii (filter feeder), which is extremely frequent during the dry season in the Pantanal and rare in the flood season. Because the Paraguay River drains the Pantanal, the hypothesis of material (sediments and invertebrates) retention by plants from transported load during the floods seems more logical than the increment of *C. hislopii* populations from a greater offer of FPOM.

The ratio SC/(SH+Col) indicates a low use of the periphytic algae as food resource in June-July during high water of the Paraguay River and the importance of this trophic resource in December during the low water period. Results obtained in the Pantanal show variations observed in the periphyton of *E. azurea* at different times of the year and in different parts of the same plant (De Paula et al., 1996). Heckman (1994) found that in the drought period the environmental conditions are more favorable for the development of dense populations of epiphytic algae, especially Oedogoniaceae and Diatomaceae. The low scraper proportion registered in the Paraná River floodplain (Poi de Neiff & Carignan, 1997) would be related to the low epiphytic growth (Planas & Neiff, 1998) on the submerged parts of *Eichhornia crassipes*. According to these authors, this fact is due to the low light transmission through the canopy of this plant.

On the functional level, invertebrates living on aquatic plants in the Orinoco floodplain lakes showed a similar structure but scrapers were an important fraction (Blanco Belmonte et al., 1998).

This study demonstrated that littoral areas populated by *E. azurea* provide shelter habitat from predators and substrate for growth of epiphytic algae, but also for invertebrates that still use the particulate organic matter. When extensive samplings are carried out, the proportion of different trophic groups between hydrological periods and among sites is variable. Results obtained in the Orinoco River using stable carbon and nitrogen isotope (Hamilton et al., 1992) would indicate that microalgae (including both phytoplankton and epiphytic forms) are the predominant energy source for aquatic animals in vegetated waters. Additional studies, including macroinvertebrate dominant groups which use the fine particulate organic matter (collectors), as well as living macrophytes (herbivores), would be needed to have more clear evidences about energy sources in these areas.

Aknowledgment

The study would not have been possible without the help of Juan José Neiff who made the sampling programme. Carlos A. Patiño and Casimiro T. Roberto help in a field work. Manuscript was improved by the comments of two anonymous reviewers.

Research was possible through the economical support of the Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (grant numbers: 0815; 4242 and 4244).

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Received: 09 September 2002

Accepted: 19 November 2002