Hydrobiologia **345:** 185–196, 1997.

Macroinvertebrates on *Eichhornia crassipes* roots in two lakes of the Paraná River floodplain

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Received 9 July 1996; in revised form 18 February 1997; accepted 26 February 1997

Key words: floodplain lakes, phytophilous macroinvertebrates, *Eichhornia crassipes*, hydrological regime

Abstract

Changes in the abundance, biomass and in the relative proportions of functional feeding groups of macroinvertebrates were studied for 17 months during low and high water periods in two floodplain lakes with indirect connections to the Paraná River.

At low water, *Eichhornia crassipes* root clusters were colonized by comparatively low densities of macroinvertebrates, especially in the lake more distant to the river. Collector-gatherers and predators were the most abundant functional feeding groups, but different taxa of these groups dominated in the two lakes during low water.

At high water, macroinvertebrates densities increased as a result of increased flow through the roots. In this period, collector-filterers dominated at both lakes and constituted over 34% of the macroinvertebrates. Four independent variables (conductivity, hydrological periods, dissolved oxygen and site) explain 87% of the variability in macroinvertebrates density expressed as the number of individuals per m^2. No significant relationship were found between macroinvertebrate biomass and any of the independent variables.

Introduction

Downstream from its confluence with the Paraguay River, the Paraná River is bordered by a complex alluvial floodplain from 6 to 40 km width with islands, sand bars, levees, secondary channels, lakes and swamps.

In these lakes and oxbow lakes, the water hyacinth (*Eichhornia crassipes*) is the most abundant macrophyte in terms of coverage and biomass. It normally forms cohesive floating meadows which may cover 20–100% of the available surface, with biomass ranges from 8.6 to 24 t ha^{-1} (Neiff & Poi de Neiff, 1984).

Compared to the Amazon and the Orinoco, the Paraná River has an irregular hydrological regime. Floods may occur 1–3 times per year for periods of two week to three month, and the water level fluctuations are relatively small (2–6 m). During normal floods (water level at Puerto Corrientes: 6.5 m) turbid river water does not penetrate very far into the floodplain, even if most of 10 km wide floodplain becomes flooded. During extreme floods, when the Paraná River water level exceeds 8 m, the entire floodplain may become submerged for several months.

Physical disturbances, such as flooding, have a great influence on the biota of the floodplain lake systems (Reice, 1985; Junk et al., 1989; Neiff, 1990). However, most studies have focused on the dynamic of fish assemblages.

There have been few studies to examine the effect of the hydrological regime upon invertebrates communities on the floodplains of rivers despite of the importance of the flood pulse (Junk et al., 1989; Junk & Welcomme, 1990).

Hamilton et al. (1990) observed that at rising waters, zooplankton density is greatly reduced during passage through a large bed of *Paspalum repens* mats.

The aims of this paper are (1) to describe the changes affecting macroinvertebrates density and biomass during the low and high water periods (2) to learn the effects of the hydrological dynamics of the river on the relative abundance of functional feeding groups.

Site description

The study was conducted in lakes San Nicolás (Site A, 27°27′S; 58°51′W) and Esperanza (Site B, 27°30′S; 58°51′W).

Site A is located in the right margin of the Paraná River, farther (2 km) from the river channel (Figure 1). The lake is small and shallow and connected to the river three or more times per year when the water level is above 5.5 m mark at Puerto Corrientes. The water hyacinth *Eichhornia crassipes* forms meadows that may cover 100% of the surface of the lake.

Site B is located on the Barranqueras Islands in the main course of the Paraná River. The lake is bounded by alluvial levées occupied by a gallery forest (Figure 1). The river communicates with the lake by a narrow channel when the water level is above 4 m mark at Puerto Corrientes. The coverage of the lake by *E. crassipes* is less than 40%.

The floating roots of *E. crassipes* accumulate deposits of river-borne sediment as well as particulate organic matter produced in the floodplain. The amount of all particulate matter retained was estimated by Poi de Neiff et al. (1994) at 925 g m^{-2} in the lake located near the main channel and 511 g m^{-2} in the lake located farther from the river.

The physical and chemical characteristics recorded in each of the sites are shown in the Table 1. At Site A, the dissolved oxygen concentration was lower than at Site B, attributable to intense heterotrophic activity among the roots. Vertical profiles taken at Site A showed depletion of dissolved oxygen to 0 mg l^{-1} at a depth of 1 m during the warm period (Poi de Neiff et al., 1994). Further information on the nutrients in these floodplain lakes can be found in Carignan & Neiff (1992).

Material and methods

Macroinvertebrates were sampled in the two lakes during the low and high water periods. Between November 1988 and March 1990, three replicate root samples were taken on 15 occasions (Figure 2).

Macroinvertebrates were collected by enclosing 962 cm^2 of *E. crassipes* stands with a 225 μm mesh net. The samples were placed into plastic bags and preserved in 5% formalin.

In the laboratory, the root clusters were thoroughly washed to detach the macroinvertebrates and the detritus. The suspensions obtained were filtered through a 1 mm and 500 μm sieve. The cleaned roots were dried at 105 oC for 96 hours.

Macroinvertebrates were preserved in 80% ethanol separated into taxonomic groups. After identification macroinvertebrates were dried at 60 oC. Each taxon was allocated to a functional feeding group according to their trophic category as assigned by Merritt & Cummins (1978). However, feeding groups of some larvae, for example Neotrichia (Trichoptera) are still unclassified. For these taxa morphological information of its mouthparts was supplemented by observation of live material in the laboratory. Taxa, such as *Ablabesmyia* larvae were categorised functionally as predators or collectors, depending on the instar (Merrit y Cummins, 1978).

Relationships between the abundance and biomass of invertebrates, sampling date, water level, sampling site, temperature, oxygen concentration and conductivity, were quantified using ANOVA and forward stepwise multiple regression analysis of normalized ($\log x$) data.

Two additional independent binary variables were used in the regression analyses to test the effects of site (lake A = 1, lake B = 2) and hydrological period (low water = 1, high water = 2) on invertebrate abundance and biomass. The hydrological period was defined as low or high when the river stage was lower or higher than the level required for hydrological contact between the lake and the river (5.5 m for Site A, and 4.0 for Site B).

The relative abundance of functional groups were transformed using the arcsine square root procedure (Zar, 1984) to normalize the distributions and compared statistically with ANOVA.

Similarity of the macroinvertebrates communities in the two lakes on each hydrological period was estimated by mean of the Dice-Sorensen index:

$$\mathrm{DS} = \frac{2.Q}{N_A + N_B},$$

where: N_A = number of taxa at Site A; N_B = number of taxa at Site B; Q = number of species in common between A and B. The index ranges from 0 (minimum similarity) to 1 (maximum similarity).

Figure 1. Location of the sampling sites on the right bank of the Paraná River downstream from the confluence with Paraguay River. A. San Nicolás lake; B. Esperanza lake

Table 1. Physico-chemical and biological features of the lakes during November 1989-March 1990.

	Site A – San Nicolás 27°27′S 58°55′W	Site B – Esperanza 27°30′S 58°55′W
Area of the lake	200 × 2000 m	25 ha
Depth (m)	0.40–2	0.60–2.5
pH	6–7	6–7
Secchi Disk (m)	0.20–0.40	0.20–0.78
Cover of *E. crassipes* (%)	100	40
Particulate matter retention by roots ($g.m^{-2}$) (average for the period)	511	925
Water temperature (°C)	17–28	17–28
Dissolved oxygen ($mg.l^{-1}$)	0.5–1.9	1.9–3.9
Conductivity ($\mu S.cm^{-1}$)	140–240	122–198

Results

The water level of the Paraná River at Puerto Corrientes fluctuated between 1.66 and 7.92 m during the sampling period (Figure 2). The hydrological regime was characterized by floods in February–March 1989, in September 1989 and in January 1990. During these floods, the water of the Paraná River flowed across Sites A and B through the gallery forest, marginal wetlands and secondary channels. Low water phases occurred from October 1988 through March 1989,

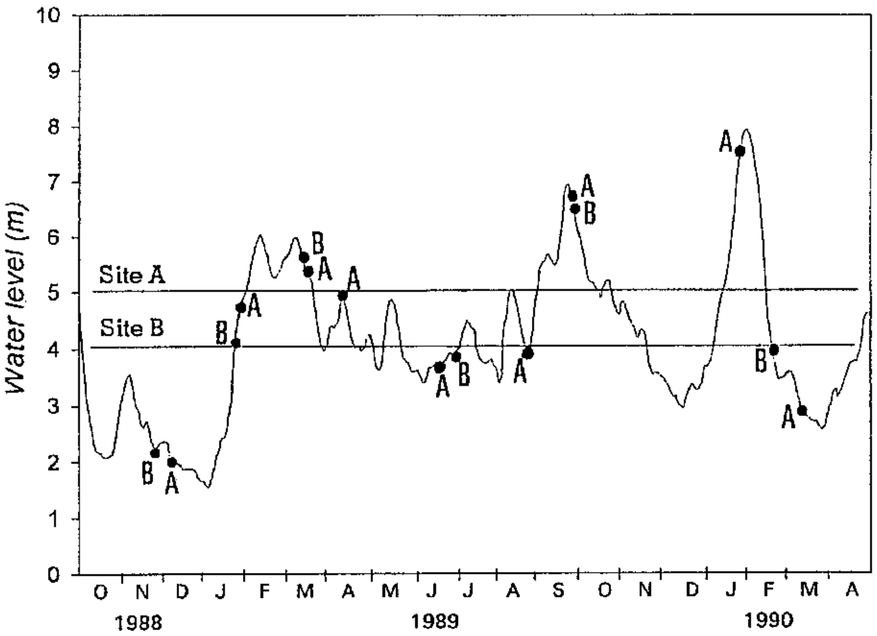

Figure 2. Water level of the Paraná River at Puerto Corrientes between 1988 and 1990. No more Paraná water enters the Site A and B below the level indicated by the horizontal lines. The closed circles indicated the dates of samples in the two lakes.

Table 2. Eichhornia crassipes root dry weight and associated macroinvertebrates (abundance and biomass) at Site A.

	Root dry weight (g.m^{-2})	Macroinvertebrate abundance		Macroinvertebrate biomass		Hydrological period
		ind.m^{-2}	ind per 100 g root dry weight	g.m^{-2}	g per 100 g root dry weight	
December 1988	287.3	6902	2251	4.2	1.4	LW
	± 23.1	± 1462	± 546	± 1.7	± 0.7	
February 1989	320.9	5395	1727	3.3	1.0	LW
	± 42.8	± 695	± 557	± 1.2	± 0.4	
March 1989	240.5	24116	10043	6.4	2.8	HW
	± 56	± 2140	± 1215	± 1.2	± 0.6	
April 1989	223.4	14995	6693	6.2	2.8	HW
	± 12.5	± 2153	± 433	± 0.7	± 0.1	
June 1989	281.0	7583	2738	2.5	0.7	LW
	± 43	± 161	± 360	± 0.24	± 0.0	
August 1989	217.4	13142	7454	3.0	1.2	LW
	± 83.8	± 494	± 3783	± 1.3	± 0.7	
September 1989	217.9	18815	8702	6.9	2.6	HW
	± 23.4	± 2020	± 2640	± 1.0	± 0.6	
January 1990	364.0	19023	5228	5.9	2.3	HW
	± 34	± 1840	± 970	± 2.0	± 0.4	
March 1990	194.9	8077	4492	2.3	0.9	LW
	21.4	± 1018	± 1010	± 0.6	± 0.1	

Table 3. E. crassipes root dry weight and associated macroinvertebrates (abundance and biomass) at Site B.

	Root dry weight (g.m^{-2})	Macroinvertebrate abundance		Macroinvertebrate biomass		Hydrological period
		ind.m^{-2}	ind per 100 g root dry weight	g.m^{-2}	g per 100 g root dry weight	
November 1988	115.8 ± 6.1	11777 ± 405	10180 ± 189	8.7 ± 1.1	7.5 ± 1.3	LW
February 1989	213.2 ± 30	12645 ± 2115	5912 ± 156	4.1 ± 0.3	1.9 ± 0.1	LW
March 1989	242.3 ± 26	20369 ± 3903	8680 ± 2545	2.4 ± 0.2	1.0 ± 0.0	HW
June 1989	240.1 ± 46	14210 ± 1950	5917 ± 243	5.7 ± 0.7	2.6 ± 0.2	LW
September 1989	245.6 ± 32.1	23193 ± 4610	9047 ± 2740	2.9 ± 0.5	0.6 ± 0.0	HW
February 1990	158.4 ± 42	11902 ± 2240	7246 ± 2100	1.9 ± 0.3	0.9 ± 0.1	HW

Reference: LW = low water; HW = high water

Table 4. ANOVA comparisons between low and high water periods. No sig = not significant.

	P value	Site A	Site B
Total abundance (ind.m^{-2})	P<0.01	F = 67.3	F = 21.8
Total abundance (ind per 100 g dry weight)	P<0.01	F = 33.53	No sig
Total biomass (g.m^{-2})	P<0.01	F = 9.19	No sig.
Collectors - Filterers (relative abundance)	P<0.01	F = 44.8	F = 43.07
Collectors - Gatherers	P<0.01	No sig.	F = 16.21
Predators	P<0.01	F = 18.78	No sig.
Scrapers	P<0.01	F = 10.49	No sig.

from April through August 1989 and from October 1989 to January 1990.

The average weight of the *Eichhornia crassipes* root clusters was lower at Site B than at Site A (Tables 2 and 3). There were significantly more roots per m^2 in the nitrogen-limited lake (Carignan & Neiff, 1992) situated farther from the main channel than in the lake situated near the river (ANOVA, P <0.01), which is exposed more frequently to high NO_3^- loads from the river.

Nine major groups of macroinvertebrates were found associated with *E. crassipes* roots in the flood-plain lakes studied, encompassing 40 families and 78 species (Table 6). The macroinvertebrates communities at both sites included similar number of the major taxonomic groups. At Site A there were 50 to 58 macroinvertebrates; at Site B 62 to 64 taxa, were identified.

The Dice-Sorensen similarity index indicates that the macroinvertebrate communities of the two lakes were more similar at high water (DS = 0.85) than at low water (DS = 0.75).

The average abundance of macroinvertebrates per m^2 was 13 116 and 15 516 at Site A and B respectively (Tables 2 and 3). The average biomass of the macroinvertebrates in the lakes was 4.28 and 4.55 g m^{-2} at Site A and B, respectively.

No significant differences (P <0.01) were found when ANOVA was used to compared macroinvertebrates abundance and biomass at both sites. However, there were more invertebrates per m^2 at Site B than Site A (P >0.05).

The effect of hydrological periods, was tested using ANOVA (P <0.01) (Table 4). During the high water period, there were more invertebrates per m^2 than during low water period in the two lakes. Comparison

Table 5. Results of fitting a multiple linear regression model to describe the relationship between macroinvertebrates density and six independent variables: temperature, sampling date, hydrological period, conductivity, oxygen concentration and site.

Total abundance at both lakes

Dependent variable: density per m^2

Parameter	Estimate	Standard error	Cumulative r^2
Constant	4.3725	0.1568	0.00
Conductivity	−0.0029	0.00049	0.55
Hydrological period	0.2046	0.0306	0.81
Oxygen	0.0848	0.0510	0.85
Site	−0.1444	0.0199	0.87

Total abundance at both lakes

Dependent variable: density per 100 g of roots

Parameter	Estimate	Standard error	Cumulative r^2
Constant	4.7910	0.2062	0.00
Conductivity	−0.005	0.0007	0.55
Oxygen	0.1711	0.0361	0.69
Site	−0.3279	0.0849	0.72

Total abundance at lake A alone

Dependent variable: density per m^2

Parameter	Estimate	Standard error	Cumulative r^2
Constant	4.1177	0.1891	0.00
Conductivity	−0.0028	0.0007	0.71
Hydrological period	0.2546	0.0339	0.89
Oxygen	0.0999	0.0338	0.92

Total abundance at lake B alone

Dependent variable: density per m^2

Parameter	Estimate	Standard error	Cumulative r^2
Constant	3.8641	0.0499	0.00
Hydrological period	0.2331	0.0353	0.73

between hydrological period on the number of invertebrates per 100 g of root dry weight and biomass revelealed only significant differences at Site A.

Multiple regression reveals that four variables (conductivity, hydrological period, dissolved oxygen and site) explain 87% of the variability in macroinvertebrates density when expressed as the number of individuals per m^2 (Table 5). When the macroinvertebrates density is expressed as the number of individuals per 100 g (dry weight) of roots, three variables (conductivity, site and dissolved oxygen) explain 72% of the variability. At Site A alone, 93% of the variability in macroinvertebrates density (individuals per m^2) is explained by conductivity, hydrological period and dissolved oxygen, whereas at Site B alone, hydrological period explains 73% of the variability. On the other hand, no significant relationship were found between macroinvertebrates biomass and any of the independent variables.

The absence of clear relationships with biomass was probably due to the large biomass variability caused by species with high density in one sampling date such as *Hyalella curvispina* at Site B in November 1988 or the sporadic presence of species with high individual dry weight such as *Trichodactylus borellianus*, *Miathyria marcella*, *Aeschna* sp. and *Ampullaria canaliculata*.

Figure 3 shows the trophic structure of the macroinvertebrates living on the roots at Sites A and B. During high water, collector-filterers dominate at both sites, and constitute over 34% of the macroinvertebrates. Significant differences were found in their relative abundances during different hydrological periods (Table 4).

The main taxa in this group are *Cyclestheria hislopii* and *Cytheridella ilosvayi*. The dynamics of the collector-filterers were similar at both sites. Their density increased significantly during the high water period (Figures 4 and 5).

At low water, there were proportionally more collector-gatherers at Site B and predators at Site A. (Figure 3, Table 4). Different taxa of collector-gatherers dominated in the two lakes: *Hyalella curvispina* was the most abundant at Site B, while *Dero* spp. and other invertebrates were more abundant at site A. The strikingly high density of *H. curvispina* population during November 1988 at Site B (Figure 5) produced an increase of the biomass to 8.7 g m^{-2}. There was a great richness of predator species, numbering about 30, the majority present at low population. Seasonal variation of the most abundant predator (*Ablabesmyia* spp.) can be seen in Figures 4 and 5. At low water, collector-filterers decreased in both sites and *Cyclestheria hislopii* was not found at Site A (the farthest from the river).

Scrapers were represented by six species, but only *Drepanotrema lucidum* and *D. anatinum* (Figures 4 and 5) were numerically predominant. These two species constituted a significant fraction of the biomass. During floods Scrapers were most abundant at Site A. The relation between the abundance of this functional feeding group and the water level was not clear at Site B

Table 6. Occurrence of macroinvertebrates in the floodplain lakes at high and low waters periods.

Functional feeding groups	Macroinvertebrates	Site A low water	Site A high water	Site B low water	Site B high water
	OLIGOCHAETA				
	Naididae				
Cg	*Slavina evelinae* (Marcus)	–	+	+	+
Cg	*Dero (Dero) cooperi* Stephenson	+	+	+	+
Cg	*Dero (Dero) multibranquiata* Stieren	+	+	-	–
Cg	*Dero (Aulophorus)* sp.	+	+	+	+
Cg	*Dero (Aulophorus) pectinatus* Stephen.	+	+	+	+
Cg	*Pristina leidyi* Smith	–	+	+	+
Cg	*Pristina macrochaeta* Stephen.	–	+	+	+
Cg	Lumbricomorpha	+	–	+	+
	OSTRACODA				
	Cytherideidae				
Cf	*Cytheridella ilosvayi* Daday	+	+	+	+
	Candonidae				
Cf	*Candonopsis brasiliensis* Sars	+	+	+	+
	CONCHOSTRACA				
	Leptestheridae				
Cf	*Cyclestheria hislopii* (Baird)	–	+	+	+
	AMPHIPODA				
	Talitridae				
Cg	*Hyalella curvispina* Shoemaker	+	+	+	+
	DECAPODA				
	Trichodactylidae				
Om	*Trichodactylus borellianus* Nobili	–	–	+	–
	INSECTA				
	Pleidae				
Pr	*Neoplea maculosa* Berg	+	+	+	+
	Naucoridae				
Pr	*Pelocoris nigriculus* Berg	+	+	+	+
	Notonectidae				
Pr	*Buenoa* sp.	+	–	+	–
	Hebridae				
	Lipogomphus lacunifera Berg	–	–	+	–
	Corixidae				
Cg	*Tenagobia selecta tarahui* Bachmann	–	–	–	+
	Coenagnonidae				
Pr	*Telebasis* sp.	+	+	+	+
	Libellulidae				
Pr	*Miathyria marcella* Selys	+	+	+	+
Pr	*Perithemis* sp.	–	+	+	+
	Aeschnidae				
Pr	*Aeschna* sp.	+	–	+	+
	Caenidae				
Cg	*Caenis* sp.	–	+	+	+

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Table 6. Continued.

Functional feeding groups	Macroinvertebrates	Site A low water	Site A high water	Site B low water	Site B high water
	Baetidae				
Cg	*Callibaetis* sp.	–	+	–	+
	Veliidae				
Pr	*Microvelia* sp.	–	+	+	+
	Belostomatidae				
Pr	*Belostoma elegans* (Mayr)	–	–	+	–
Pr	*Belostoma micantulum* Stal	+	+	–	–
	Chironomidae				
Pr	*Procladius* sp.	–	–	–	+
Pr	*Labrundinea* sp.	–	+	+	+
Pr	*Ablabesmyia* sp.	+	+	+	+
Pr	*Monopelopia* sp.	+	+	–	–
Cg	*Chironomus* sp.	+	+	+	+
Cg?	*Tribelos* sp.	–	+	+	+
Sh	*Polypedilum* sp.	–	+	+	+
Cg	*Goeldichironomus* sp.	–	+	–	+
Cg	*Stenochironomus* sp.	–	–	–	+
Cf, Cg	*Microtendipes* sp.	–	–	–	+
Cf	Tanytarsini no det.	+	+	+	–
	Tabanidae				
Pr	*Lepiselaga crassipes* Fabricius	+	–	+	–
	Syrphidae				
Cg	*Eristalis* sp.	+	–	–	–
	Ephydridae				
Sh	*Hydrellia* sp.	–	–	+	+
Cg	*Brachydeutera* sp.	+	–	–	–
	Culicidae				
Cg	*Mansonia* sp.	+	+	+	+
Cf	*Anopheles* sp.	–	–	–	+
	Ceratopogonidae				
Pr	*Bezzia* sp.	+	+	+	+
Cg	*Dasyhelea* sp.	+	+	+	+
Cg	*Forcipomyia* sp.	+	–	–	–
	Polycentropodidae				
Cg	*Cyrnellus* sp.	–	+	+	+
	Hydroptilidae				
Cg	*Neotrichia* sp.	–	+	–	+
Cg	*Oxyethira* sp.	–	+	–	+
	Curculionidae				
Sh	*Neochetina brucchi* Hustache	+	+	+	+
Sh	*Neochetina eichhorniae* Warner	+	+	+	+
	Dytiscidae				
Pr	*Desmopachria* sp.	+	+	+	+
Pr	*Laccophilus* sp.	+	+	+	+
Pr	*Pachidrus globosus* (Aubé)	+	+	+	+
	Noteridae				
Pr	*Hydrocanthus* sp.	+	+	+	+
Pr	*Suphis cimicoides* Aubé	+	+	+	+
Pr	*Suphisellus grossus* Sharp	+	+	+	+

Continued on p. 193

Table 6. Continued.

Functional feeding groups	Macroinvertebrates	Site A low water	Site A high water	Site B low water	Site B high water
	Hydrophilidae				
Pr	Larvae	+	+	+	+
Cg?	*Derallus rudis* Sharp	+	+	+	–
Cg	*Enochrus* sp.	+	+	+	+
Cg?	*Helochares* sp	+	+	+	+
Sh	*Hydrochus richteri* Bruch	+	–	+	–
Cg	*Tropisternus lateralis* Brulle	+	+	+	+
Cg	*Berosus patruelis* Berg	+	+	+	+
Sc	*Berosus* Larvae	+	+	+	+
Cg	*Paracymus* sp.	–	–	+	+
	Helodidae				
Cg	*Scirtes* sp.	+	+	+	+
	MOLLUSCA				
	Planorbidae				
Sc	*Drepanotrema anatinum* (D'Orb.)	+	+	+	+
Sc	*Drepanotrema lucidum* (Pfeiffer)	+	+	+	+
	Ampullaridae				
Sc	*Ampullaria canaliculata* Lamark	+	+	+	+
	Ancylidae				
Sc	*Uncancylus concentricus* (D'Orb.)	+	+	–	+
	Hydrobiidae				
Sc	*Littoridina guaranitica* (Doering)	–	+	+	+
	Sphaeridae				
Cf	*Eupera platensis* Doello–Jurado	–	–	+	+
	HIRUDINEA				
Pr	*Helobdella* sp.	+	+	+	+
Pr	HIDRACARINA				
	sp. 1	+	+	+	+
	sp. 2	+	+	+	+
	sp 3	+	+	+	+
	sp. 4	+	+	+	+
	sp. 5	–	+	+	+
	Total number of species	50	58	62	64

References: Cg = collector-gatherers Cf= collector-filterers Pr = predators Sc = scrapers Sh = shredders Om = omnivorous

(Table 4). Shredders were fewer in number during both hydrological periods.

Discussion

Multiple regression analysis shows that the abundance of macroinvertebrates associated with the roots of *E. crassipes* are closely related to three or four recurring variables: conductivity, hydrological period, dissolved oxygen and site. Seasonality (sampling date) and water temperature does not influence macroinvertebrates abundance in the floodplain lakes studied.

Site effects

Roots of *E. crassipes* growing near the river (Site B) support more invertebrates than those growing in the lake more distant of the main channel (Site A). Site B

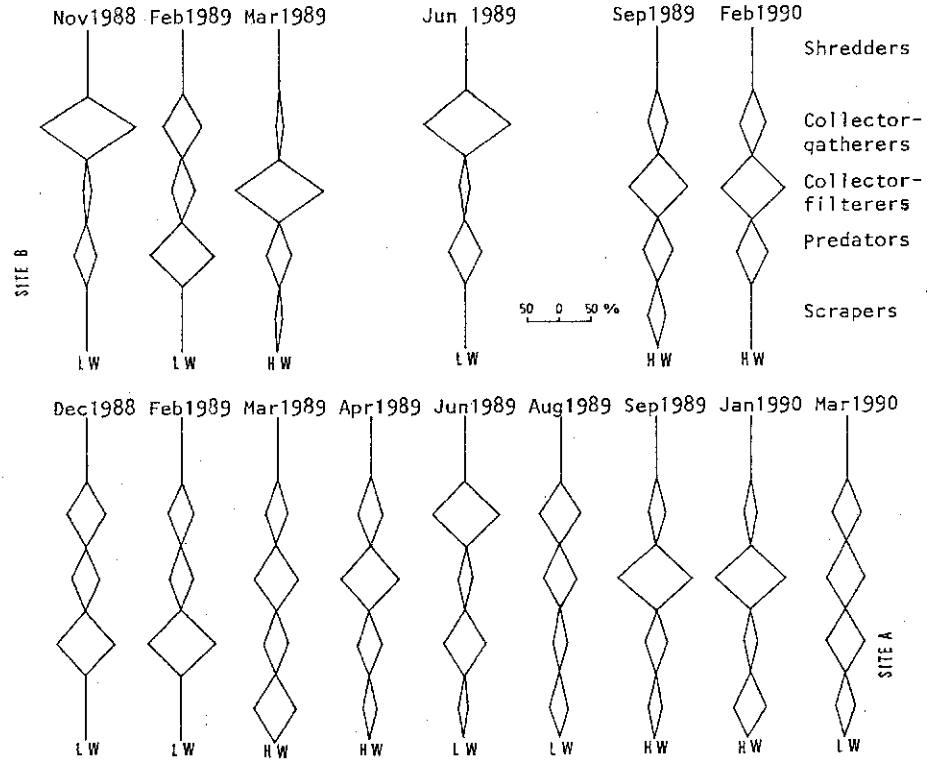

Figure 3. Percentage composition of invertebrates functional feeding groups at Site A and Site B.

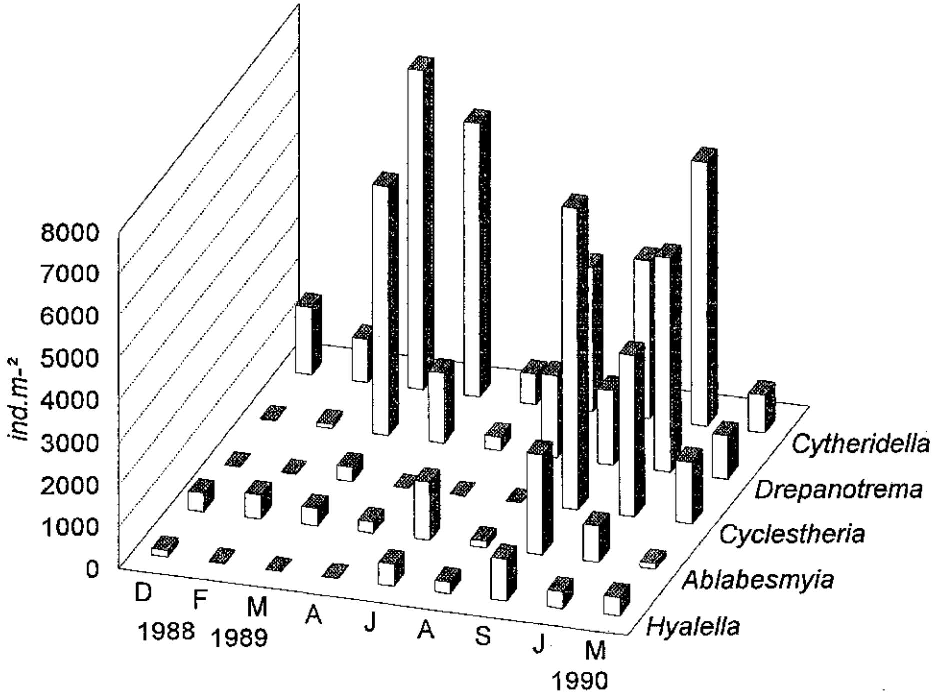

Figure 4. Density of main representative populations at Site A.

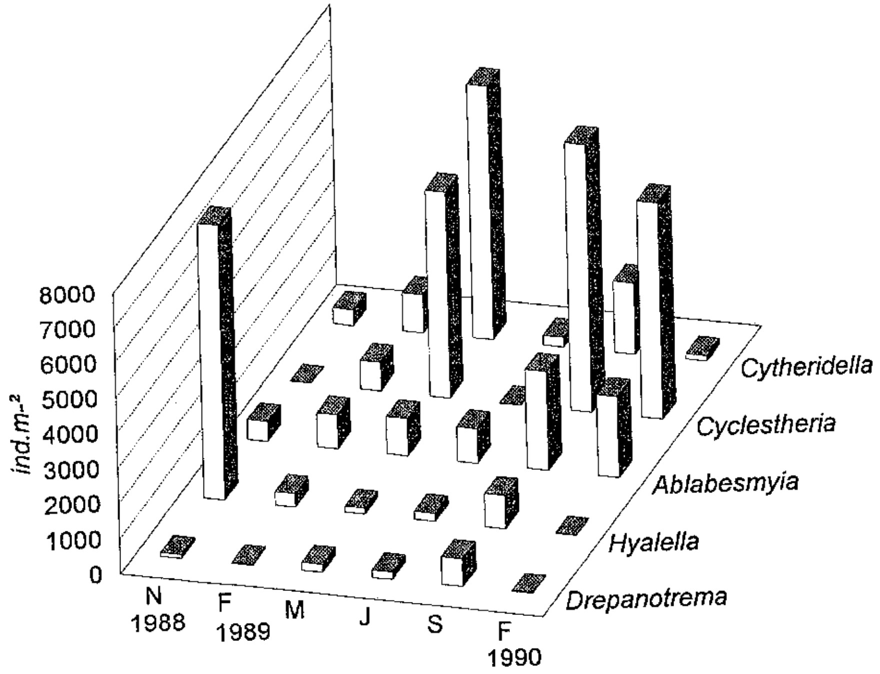

Figure 5. Density of main representative populations at Site B.

has more frequent and more prolonged contacts with the river, and therefore receives higher nutrient loads. Thus, at Site B the root clusters are considerably smaller, whereas they reach a length of 80 cm at Site A. Such morphological differences between roots of floating macrophytes growing near the river compared with isolated water have been reported by others and have been attributed to differences in nutrient supply (Junk, 1970). According to Carignan & Neiff (1992), *E. crassipes* growth is limited by nitrogen during summertime low water period at Site A. In this site, the decrease of invertebrates density is more pronounced than at Site B.

Dissolved oxygen effects

Plant cover and root density influence oxygen concentration in the root zone. When *E. crassipes* forms cohesive mats, a considerable biochemical oxygen demand is created by both trapping organic matter and by the decay of their own vegetative parts. Re-aeration of the water is prevented by reduced wind and wave action on the surface of the water. This results in dwindling oxygen concentration during the warm season. According to Irmler (1975), a stress factor for aquatic invertebrates on the Amazon floodplain is oxygen deficiency. This condition causes a decrease in total abundance of invertebrates and an increase in the number of species adapted to survive hypoxic conditions such as: *Lepiselaga, Eristalis* sp., *Scirtes* and *Forcipomyia.*

The degree of deoxygenation below the floating mat depends on water movements, for in strong currents the oxygen gradient beneath the mat may be eliminated (Welcomme, 1985). As floodwaters invade the floodplain of the Paraná River there is an initial rise in dissolved oxygen concentrations in the open water and under floating vegetation.

Conductivity effects

Conductivity has a negative effect on macroinvertebrate densities (Table 5). This effect is probably indirect and can be explained by the fact that during low water period, nutrients are depleted (Carignan & Neiff, 1992) and conductivity increases in the lakes.

Hydrological period effects

During rising water, the roots of *E. crassipes* act like filters and trap riverborne particulate matter as well as particulate organic matter produced in the floodplain (Poi de Neiff et al., 1994).

Since connection of the lakes with the main channel of the Paraná River is indirect, river water passes through flooded forest and wetland before reaching the lakes and their floating meadows. When macrophyte mats occur at the inflow of the lakes, as in the case of lakes San Nicolás and Esperanza, they tend to retain coarse debris and drifting invertebrates. According to Poi de Neiff y Bruquetas (1983, 1989) the main invertebrate taxon retained by the roots are: *Cyclestheria hislopii*, *Cytheridella ilosvayi*, larvae and pupa of Chironomidae and *Oxyethira*, nymphs of *Caenis* and *Callibaetis*, *Drepanotrema* and species of Hidracarina.

During high water, retention of inorganic sediments by the roots is very high especially in the lake located near the river channel (Poi de Neiff et al., 1994). Yet, collector filterers such as *Cyclestheria hislopii* reach a maximum density during high water. This suggests that increases in macroinvertebrate densities are not due to a higher production, but rather to the retention effect by the roots of the floating meadows. These populations do not persist after floods. Retention of invertebrates by aquatic plants affects trophic relations by increasing the invertebrate available as food to other communities such as fish or birds.

Floods have similar effects on the function and on the community structure of invertebrates associated with the root system of *E. crassipes* in the Orinoco floodplain lakes (Blanco et al., 1995).

Changes in the hydrological regime also influence benthic communities of the Paraná River floodplain lakes. Bechara & Andreani (1989) stressed comparatively low species diversity and scarce abundance of benthos macroinvertebrates during falling water, in contrast to their highly diverse fauna and high density during floods. Only the extreme floods cause a decrease of the benthic fauna.

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