Composition and seasonality of planktonic rotifers in limnetic and littoral regions of a floodplain lake (Paraná river system)

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Abstract

El Tigre is a shallow lake ringed by macrophytes. It is connected with the Correntoso river, during the flood of the Paraná river. The rotifer communities of limnetic and littoral zones (with different macrophyte species) were compared in an annual cycle. Significant differences between both areas are given at species level. The limnetic assemblage was characterized by the predominance of the genera Keratella, Filinia *and* Polyarthra *and lower species richness. In the littoral community, the genera* Lecane, Lepadella, Trichocerca *and* Testudinella *predominated, and species richness was highest. The seasonal patterns of richness, diversity and abundance of rotifers were similar in both areas, but the seasonal changes were more attenuated in the littoral stations. Although hydrologic factors are a major cause of seasonal patterns, other factors may also be involved.*

Key words : Rotifers — Littoral microfauna — Limnetic plankton — Macrophytes — Calanoids — Cyclopoids — Floodplain lakes — Flood Paraná river — South America.

Résumé

Composition et variations saisonnières des rotifères planctoniques d'un lac de la plaine d'inondation du Paraná

El Tigre est un lac peu profond entouré de macrophytes. En période des eaux hautes du Paraná, il est relié à la Rivière Correntoso.

La structure du peuplement en rotifères a été analysée au cours d'une année dans la zone centrale du lac, et dans les diverses espèces de macrophytes littoraux. Les différences entre zones sont décrites. La zone centrale était caractérisée par la prédominance des genres Keratella, Filinia *et* Polyarthra, *et par une faible richesse spécifique. Dans les peuplements littoraux, la richesse spécifique était plus élevée, avec dominance des genres* Lecane, Lepadella, Trichocerca *et* Testudinella. *Les variations saisonnières de la richesse, de la diversité et des abondances sont semblables pour les deux zones, avec une amplitude moins prononcée dans la zone littorale. Les facteurs hydrologiques sont la principale cause des variations saisonnières, mais d'autres facteurs peuvent aussi intervenir.*

Mots clés : Rotifères — Microfaune littorale — Plancton — Macrophytes — Calanoides — Cyclopoides — Lac de plaine d'inondation — Amérique du Sud.

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Resumen

Composición y estacionalidad de rotíferos planctónicos en las áreas limnética y litoral de una laguna de planicie de inundación (Río Paraná)

El Tigre es una laguna de conexión indirecta con el río Correntoso, un cauce secundario del Paraná. Posee un litoral somero con macrófitas arraigadas y flotantes, y su nivel de agua y volumen varían en relación al régimen hidrológico del río. Se analizaron comparativamente los rotíferos de las zonas litoral y limnética, a lo largo de un año. Las diferencias más importantes se dieron en la composición específica. El taxoceno limnético se caracterizó por el predominio de los géneros Keratella, Filinia y Polyarthra y una menor riqueza específica. El littoral, en cambio, por la dominancia de los géneros Lecane, Lepadella, Trichocerca y Testudinella y mayor riqueza. El patrón de variación estacional de riqueza, diversidad y abundancia fue similar para ambas áreas. Sin embargo, los cambios fueron más atenuados en las estaciones litorales. Si bien los factores hidrológicos fueron las causas principales de la estacionalidad, también otros factores estarían involucrados.

Palabras claves : Rotíferos — Plancton — Litoral — Macrófitas — Calanoideos — Cyclopoideos — Lagunas de valles aluviales — America del Sur.

INTRODUCTION

The littoral microfauna has received some attention on a global level, particularly the crustaceans (Wetzel, 1983), but very little attention has been paid to the microfauna of shallow floodplain lakes of the large South American rivers. Floodplain waters of the Amazon and Orinoco basins were studied by Green (1972), Rodriguez Hardy (1980), Rey and Vasquez (1986). Faunistic studies of littoral rotifer assemblages were provided by Koste (1972, 1974, 1986, 1988). For the Paraná River, Dioni (1975) reported on the rotifers of plant roots and free living among macrophytes in a shallow lake covered with floating meadows, where limnetic and littoral areas are not well defined.

Most lentic waters on the broad floodplain of the Paraná River are shallow lakes ("lagunas"), with a littoral weedy area. The macrophytes contribute significantly to the productivity of the system, and also increase the environmental heterogeneity. Seasonal patterns of general limnological variables in these waterbodies are strongly regulated by hydrologic regimes, as in Amazon and Orinoco floodplain lakes (Junk *et al.* 1989, Hamilton *et al.* 1990).

The aim of this study was to determine the differences in species composition, numerical abundance and seasonality of the rotifer community of limnetic and littoral weedy areas in the same lake, and to analyse the parameters influencing community structure.

STUDY SITE

El Tigre, a typical shallow floodplain lake, is located at 31°41'S / 60°40'W in a region of transition between tropical and temperate climates. It is an obstruction lake (Fig. 1) indirectly connected with the Correntoso River, an anabranch of the Paraná River. The lake is circular, with a 33,500 m² area in the isolation period, and 3.4 m maximum depth. It can be classified thermally as continuous warm polymictic (Drago, pers. commun.).

Water level fluctuations during the study period (Fig. 2) reflected the Correntoso River flows. During low flows the lake was completely separated from the river, but at high discharge it was inundated. The range of such changes was 2.5 m. Four hydrological phases were distinguished :

a) filling phase, when water from the river entered indirectly by seepage and through a swamp located to the south ;

b) inundation phase, when the river connected directly with the lake ;

c) drainage phase ;

d) isolation phase when the lake was not connected to the river (Fig. 2).

During the period of study the volume of the lake varied approximately seven fold.

Floating and attached vegetation permanently ringed the lake during the study period, with *Eichhornia crassipes*, *Paspalum repens*, and *Typha* sp. dominant.

MATERIAL AND METHODS

During Feb. 1987-April 1988 the lake was sampled at 15-day intervals. Although this frequency does not allow to detect the succession of species precisely, it is adequate to indicate the general trends and basic pattern of variations of the "standing crop"

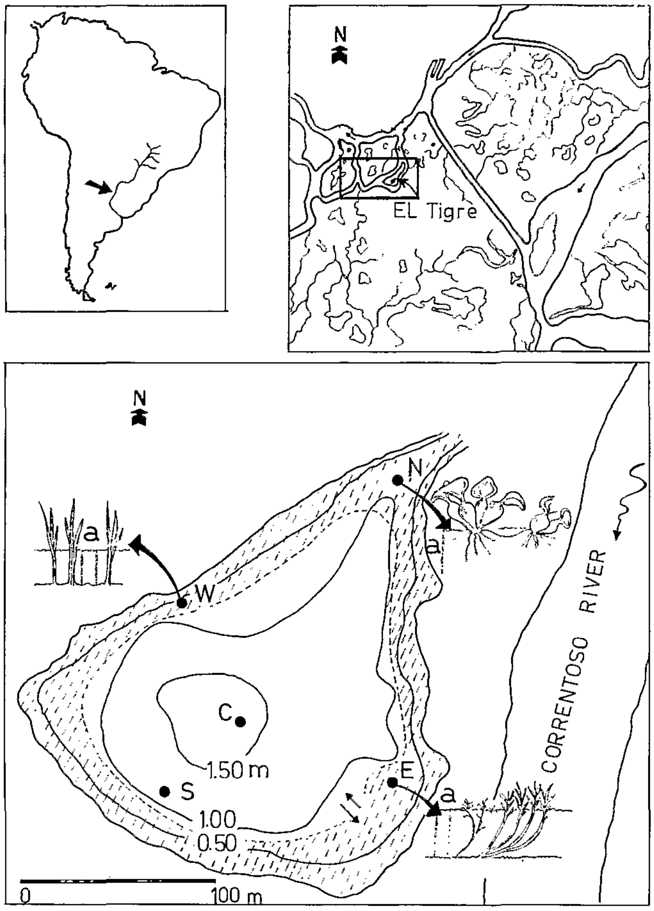

Fig. 1. — Map of El Tigre lake.
C : limnetic station, W, E, N : littoral stations, S : transition area station ; a : sampling site among plants. Shaded area indicates the littoral weedy area.
Situation du lac El Tigre et stations de prélèvement.
C : station centrale, W, E, N stations littorales, S station de transition. a indique le site d'échantillonnage dans les zones à macrophytes figurées en hachuré.

(Hillbricht-Ilkowska 1965, Berner-Fankhauser 1987).

Samples were taken at five stations (Fig. 1) : one in the open water (C), one in a transition zone, close to the littoral area (S), and three in the free water among macrophytes of the littoral : N with prevailing *Eichhornia crassipes*, W with *Paspalum repens* and E with dominance of *Typha* sp.

Data measured on site were : depth, temperature, transparency (Secchi disk), pH, conductivity and dissolved oxygen (Table I). Plankton samples in the limnetic area were collected using a Schindler-Patalas plankton trap. In the littoral areas, owing to the

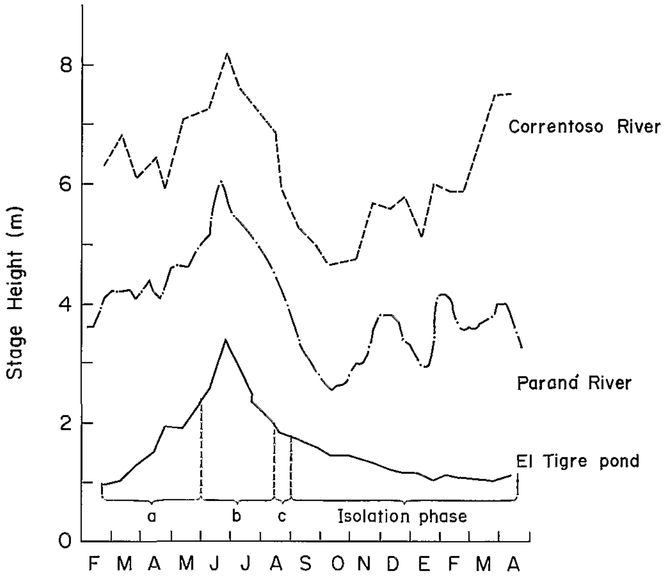

Fig. 2. — Seasonal variations of the stage height of Correntoso River (in front of El Tigre), Paraná River and El Tigre lake.
Variations du niveau de l'eau dans le Correntoso, le R. Paraná et dans El Tigre.

Table I

Mean values of environmental factors in the different stations, and hydrological phases
Valeurs moyennes des variables d'environnement dans les différentes stations au cours des différentes phases hydrologiques

Stations	Parameters	Hydrological phases a	b	c	d
C	Transparency (m)	0.4	0.8	1.2	0.4
	Temperature (°C)	21.3	12.5	15.6	24.8
	Conductivity (µS/cm)	274.5	141.0	159.0	187.4
	pH	7.3	6.9	6.9	6.8
	Oxygen (mg/l)	6.7	7.8	9.2	5.8
S	Transparency	0.6	0.9	1.2	0.4
	Temperature	21.5	12.5	14.3	25.5
	Conductivity	273.5	145.8	161.0	190.5
	Oxygen	6.9	8.2	10.9	4.8
E	Transparency	0.5	0.8	1.0	0.3
	Temperature	21.7	13.2	16.6	26.0
	Conductivity	273.0	138.0	160.3	193.1
	Oxygen	6.2	7.6	7.6	3.8
W	Transparency	0.7	0.8	1.2	0.4
	Temperature	20.1	12.6	15.5	25.2
	Conductivity	248.2	143.8	159.3	187.8
	pH	7.2	6.9	6.9	6.9
	Oxygen	6.4	7.9	9.1	5.3
N	Transparency	0.6	0.8	1.0	0.4
	Temperature	21.5	12.7	16.2	25.6
	Conductivity	277.0	145.3	159.0	190.4
	Oxygen	6.0	8.3	9.3	5.2

a = filling ; b = inundation ; c = drainage ; d = isolation
a = remplissage ; b = inondation ; c = vidange ; d = isolement

TABLE II

List of rotifers from El Tigre
Liste des espèces de rotifères du lac El Tigre

Anuraeopsis fissa (Gosse)	*L. hamata* (Stokes)
A. sp.	*L. lunaris* (Ehrb.)
Beauchampiella eudactylota (Gosse)	*L. monostyla* (Daday)
Brachionus angularis (Gosse)	*L. pyriformis* (Daday)
B. bidentata Anderson	*L. quadridenta* (Ehrb.)
B. budapestinensis Daday	*L. stenroosi* (Meissner)
B. calyciflorus Pallas	*L.* (s. str) *curvicornis* (Murray)
B. caudatus Barroia & Daday	*L. elsa* (Hauer)
B. cf. *austrogenitus* Ahlstrom	*Lecane doryssa* Harring
B. cf.*personatus* Ahlstrom	*L. elegans* Harring
B. cf. *insuetus* Ahlstrom	*L. flexilis* (Gosse)
B. chelonis Ahlstrom	*L. hastata* (Murray)
B. dolabratus Harring	*L. leontina* (Turner)
B. falcatus Zacharias	*L. ludwigi* (Eckstein)
B. havanensis Rousselet	*L. luna* (O. F. M.)
B. mirabilis Daday	*L. nana* (Murray)
B. mirus Daday	*L. papuana* (Murray)
B. patulus O. F. M.	*L. signifera* (Jennings)
B. quadridentatus Hermann	*L. tenuiseta* Harring
B. sessilis Varga	*L. ungulata* (Gosse)
B. urceolaris (O. F. M.)	*L.* sp.
B. u. *bennini* (Leissling)	*Lepadella acuminata* (Ehrb.)
Cephalodella catellina (O. F. M.)	*L. latusina* (Hilgendorf)
C. gibba (Ehrb.)	*L. rhomboide* (Gosse)
C sp.	*L. ovalis* O. F. M.
Colurella adriatica Ehrb.	*L. patella* O. F. M.
C. cf. *obtusa* (Gosse)	*L.* sp.
C. sp.	*Monommata longiseta* (O. F. M.)
Collotheca sp.	*Mytilina* cf. *bisulcata* (Lucks)
Conochilus ceonobasis Scoricoff	*M. unguipes* (Lucks)
C. unicornis (Rousselet)	*M. ventralis* (Ehrb)
Dicranophorus sp.	*M.* sp.
Dipleuchlanis propatula (Gosse)	*Platyias quadricornis* (Ehrb.)
Epiphanes clavulata (Ehrb.)	*Ploesoma truncatum* (Levander)
E. macrourus (Barrois & Daday)	*Polyarthra dolichoptera* Idelson
Euchlanis dilatata (Ehrb.)	*P. vulgaris* Carlin
E sp.	*P.* sp.
E. cf. *meneta* Myers	*Pompholyx complanata* Gosse
Filinia longiseta Ehrb.	*Ptygura* sp.
F. opoliensis (Zacharias)	*Rotaria* sp.
F. pejleri Hutchinson	*Scaridium longicaudum* (O. F. M.)
F. terminalis (Plate)	*Squatinella* sp.
Hexarthra intermedia Wisniewski	*Synchaeta stylata* Wierzejski
H. i. braziliensis (Hauer)	*S.* sp.
H. sp.	*Testudinella ahlstromi* Hauer
Horaella sp.	*T. patina* (Hermann)
Keratella americana Carlin	*T.* cf. *trilobata* Anderson & Shephard
K. cochleris (Gosse)	*Trichocerca brachyura* (Gosse)
K. cf. *tecta* (Lauterborn)	*T. cylindrica* (Imhof)
K. lenzi Hauer	*T. rattus* (O. F. M.)
K. tropica (Apstein)	*T. similis* (Wierzejski)
Lecane (Monostyla) *bulla* (Gosse)	*T.* sp.
L. closterocerca (Schmarda)	*Trichotria tetractis* (Ehrb)
L. cornuta (O. F. M.)	*Trochosphaera* sp.
L. decipiens (Daday)	

shallow depth and bearing in mind the advisability of this methodology to obtain samples of a "true" littoral community (PENNAK 1966), a Van Dorn bottle was used. Integrated samples of the water column were filtered through a 40 μm net.

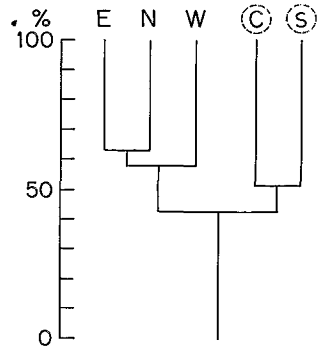

FIG. 3. — Faunistic affinity (Jaccard coefficient) between littoral stations (W, E, N), limnetic station (C) and transition area station (S.).
Affinités faunistiques (indice de Jaccard) entre stations.

Identification of rotifers was based primarily on RUTTNER-KOLISKO (1974) and KOSTE (1978). Counts were made under a binocular microscope according to conventional techniques (PREPAS 1984). Statistical treatments applied were : specific diversity according to the Shannon-Weaver index (H'), faunistic affinity by Jaccard coefficient (Sj) and IBD index (KOCH 1957). This index involves the total faunistic similarity among many sub-areas within the same area of lake, e.g. IBD = 0 % means that each of the species in the biota of the lake is restricted to one of its sub-areas. Conversely, IBD = 100 % means that all species in the biota of the lake are represented in each of the lake sub-areas. Comparison between means was made by Student t-test, or Kruskal-Wallis non-parametric test when the homocedasticity requirement was not fulfilled (SOKAL and ROHLF, 1979).

RESULTS

Species composition and richness

A number of 111 rotifer species was recorded, representing 32 genera (Table II). *Lecane* (25 taxa) and *Brachionus* (19 taxa) had the greatest species richness. The total numbers of species differed between stations. The limnetic site (C) had 44 taxa, the littoral sites (N,E, and W), 62, 66 and 69 respectively. The station located in the transition area (S) had 60 taxa. The greatest faunistic similarity was observed between the littoral stations (Sj 60 %), although the limnetic assemblage also was similar to that of station S (Fig. 3). Notably, the limnetic and littoral areas were separated faunistically because of a group of uncommon taxa. The greatest differences

TABLE III

Station's H (Shannon Weaver) compared with t test
Comparaison des indices de Shannon-Weaver par test de t

Stations	t	S
C-S	2.11	ns
C-W	3.62	**
C-E	3.54	**
C-N	3.80	**
W-E	1.17	ns
W-S	8.68	**
W-N	9.95	**
S-E	1.58	ns
S-N	1.38	ns
E-N	3.00	**

S = level of signification **$p < 0.01$, nS = non significant
*S = niveau de probabilité ** = P < 0,01 et NS = non significatif*

among them was shown by the richness of the genus *Lecane* in the littoral stations.

Diversity indices (mean H' for each station) are compared in Table III. Those of the limnetic and the transition zone were not significantly different, but station C had a different Shannon index with respect to each of the littoral stations. Species richness showed similar fluctuations at all stations. The lowest values were observed in winter, June-July, with only 2 species in the limnetic station C, 6 in the transition zone, and up to 11 in littoral stations. Also, there was a trend to progressive increase during spring-summer (Fig. 4). The faunistic similarity between stations was very low, and minimal during the inundation phase when the river inundated the lake (Fig. 5).

Species richness was higher throughout the study in the littoral area, particularly in station W, with *Paspalum repens*. Predominant genera in the littoral rotifer community were *Lecane*, *Lepadella*, *Trichocerca* and *Testudinella*, with several co-occurring congeners (2 species of *Testudinella*, up to 3 of *Trichocerca* and up to 7 of *Lecane*). Relatively high densities of some lecanids were noted (e.g. *L. bulla* was found with up to 151 ind.L^{-1}).

In contrast, the limnetic community was characterized by the predominance of the genera *Keratella*, *Filinia* and *Polyarthra*, and by a somewhat lower species richness, particularly at station C. Coexisting congeners were less frequent (2 species of *Brachionus* and 2 of *Keratella*).

Three groups of species were detected according to the frequency of occurrence in the different environments of the lake (see Table IV). The first group included *Anuraeopsis fissa, Brachionus budapestinensis, B. dolabratus, B. falcatus, Conochilus coenobasis, Filinia longiseta, Keratella americana, K. tropica, Synchaeta* sp.. These species presented their highest frequency in limnetic waters. A second group, inclu-

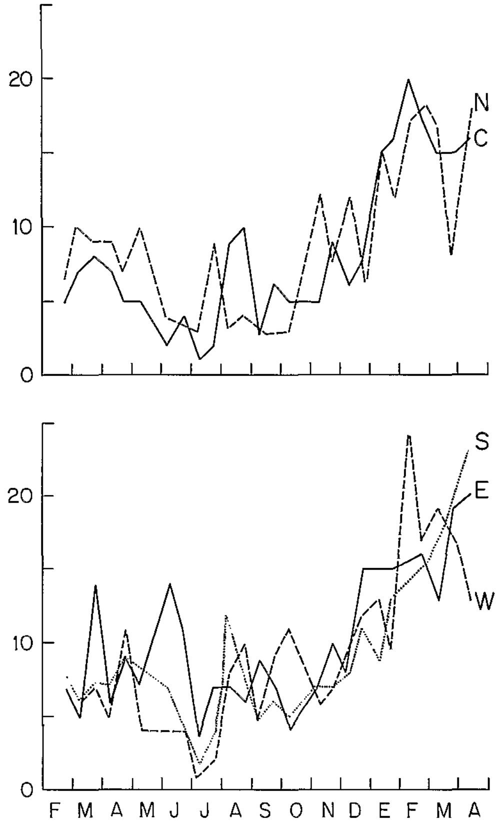

FIG. 4. — Variations in the species number at the different stations.
Variations du nombre d'espèces en fonction du temps pour les différentes stations.

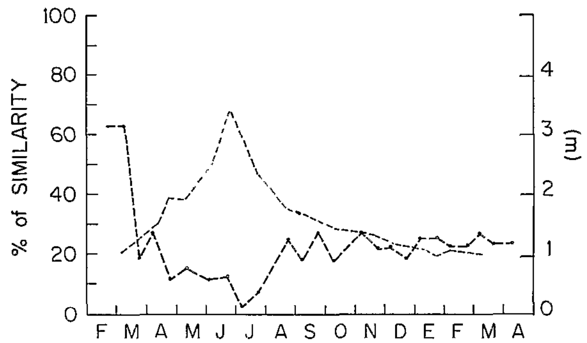

FIG. 5. — Seasonal variation of faunistic similarity (Koch index) among stations and seasonal variation of stage height.
Variations saisonnières de l'indice de similarité de Koch entre stations (échelle de droite, tireté épais) et du niveau de l'eau (échelle de gauche, tireté fin).

TABLE IV

Frequency of occurrence of rotifer species in the lake at the different stations

Fréquence d'occurrence des espèces de rotifères dans les différentes stations

	C	S	N	E	W
Anuraeopsis fissa	23	15	4	3	11
Brachionus angularis	26	5	37	32	23
B. bidentata	0	0	12	20	19
B. budapestinensis	23	26	4	0	0
B. calyciflorus	0	3	4	0	3
B. dolabratus	46	34	8	4	11
B. falcatus	30	23	8	8	3
B. quadridentatus	0	0	29	28	46
Conochilus coenobasis	30	38	16	12	11
Filinia longiseta	61	57	16	16	20
Keratella americana	34	7	4	12	19
K. cochlearis	50	65	20	24	38
Lecane (M) *bulla*	3	19	29	32	30
L. closterocerca	0	0	12	12	0
L. cornuta	0	0	20	16	11
L. hamata	0	0	16	28	15
L. pyriformis	0	0	8	16	11
L. quadridentata	0	0	0	12	11
L. (s.str.) *curvicornis*	11	11	12	12	7
L. leontina	0	0	16	28	6
L. papuana	11	3	8	8	7
L. ungulata	3	0	0	12	3
Lepadella ovalis	7	15	16	28	23
Polyartha vulgaris	73	65	50	60	65
Synchaeta sp.	26	15	12	8	7
Testudinella patina	7	15	29	44	26

TABLE V

Mean abundance of rotifers (ind./L) in the stations at different hydrological phases

Abondance moyenne des rotifères (ind./L) dans les cinq stations en fonction de la phase du cycle hydrologique

Stations	Hydrological phases			
	a	b	c	d
C	546	6	798	854
S	363	9	376	266
W	467	55	478	643
E	596	241	267	601
N	199	91	214	370

Symbols as in table I

Mêmes symboles que dans le tableau I

ded *B. quadridentatus*, *Lecane bulla*, *L. closterocerca*, *L. cornuta*, *L. quadridentata* and *Lepadella ovalis*, which had the highest frequency or were only present in the littoral stations. The third group of species : *B. angularis*, *L. curvicornis*, *L. papuana* and *Polyartha vulgaris*, had a similar frequency in limnetic, littoral and transition zone.

Abundance

Significant differences were observed in the rotifer density at each of the five stations (Kruskal-Wallis test, H = 11.30 ; X2 05(4) = 9.48). The limnetic station, C and the littoral zones with *P repens* and *Typha* sp. dominance, showed the highest abundance. Station S and station N (with *E. crassipes*) had the lowest values (Fig. 6, table V).

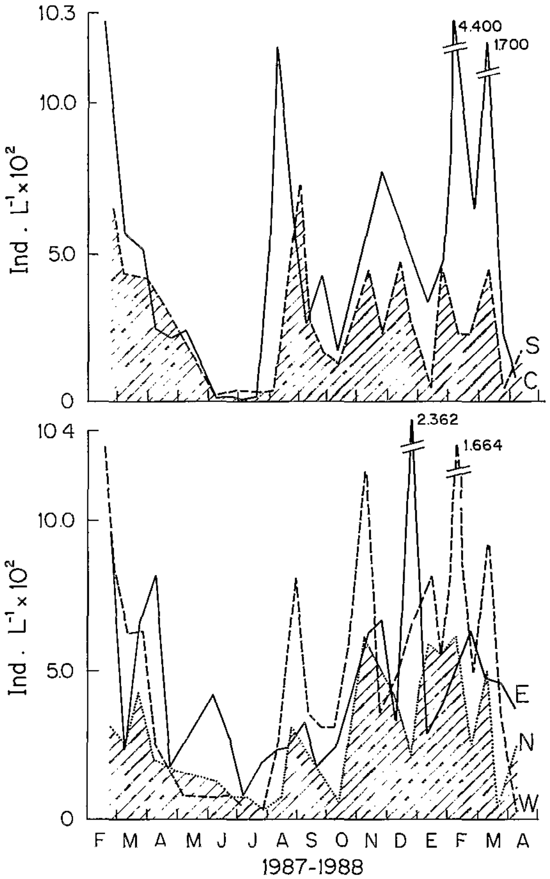

FIG. 6. — Seasonal variations in rotifer abundance.

Variations de l'abondance des rotifères en fonction du temps pour les différentes stations.

The dominant species in the limnetic area were *B. falcatus*, *F. longiseta*, *K. americana*, *K. cochlearis*, and *P. vulgaris*. In the littoral area *B. patulus*, *L. bulla*, *L. curvicornis* and *Testudinella patina* were predominant. *B. falcatus* and *P.vulgaris* were dominant on occasions in both areas. Although some of the above taxa were more or less similarly abundant at different stations, others were more abundant in open waters (e.g. *C. coenobasis*) or in the littoral region (e g. *B. bidentatus*).

Marked fluctuations were observed in rotifer densities during the year, but abundance patterns were similar at all stations (Fig. 6, table V). Lowest values were recorded in winter, during the inundation

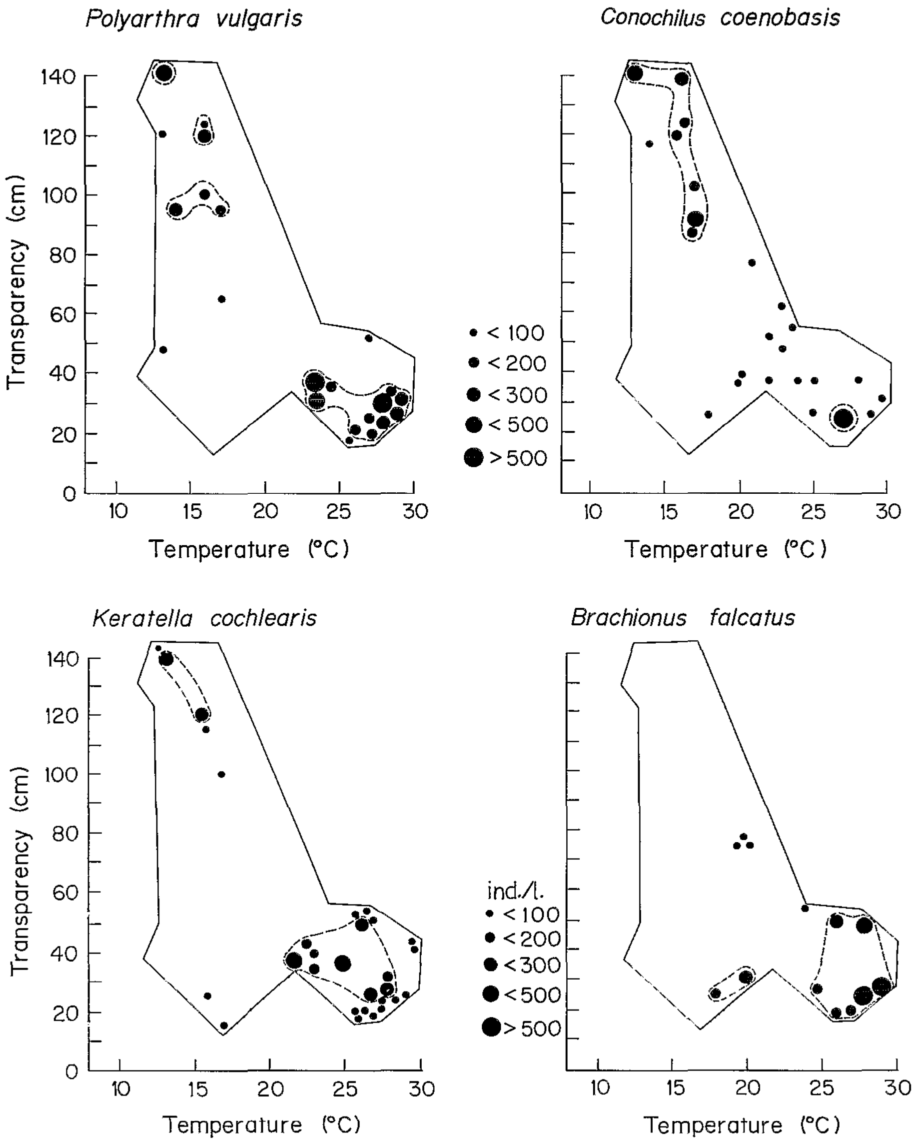

FIG. 7. — Occurence and abundance (ind/L) in relation to temperature and transparency.
The continuous line includes all the combinations of temperature and transparency occurring in the lake during the present study. The broken line indicates the range in which numbers were highest (after diagramms by ELLIOT 1977).
Occurrence et abondance des rotifères en fonction de la température et de la transparence.
La ligne continue inclut toutes les combinaisons t°-transparence observées. La ligne en tireté indique le domaine où ont été observés les plus forts effectifs.

phase. However, while the limnetic station C had only 10 ind.L^{-1}, the littoral stations had 81, 100 and 271 ind.L^{-1} respectively. During spring and summer, the isolation phase of the lake, the rotifer abundance progressively increased, reaching 4 300 ind.L^{-1}, at limnetic station C, and 2,362 ind.L^{-1} at littoral station E.

Environmental factors and seasonality

Distribution and abundance of some species were analysed in relation to temperature and transparency (Fig. 7); temperature because of its direct relation to the reproductive processes of rotifers, and transparency as a factor associated with the particulate organic matter and the biomass of phytoplankton in the lake. *K. cochlearis*, although it is a eurythermal species, was more abundant at high temperatures and low transparency, unlike *B. dolabratus*, *B. falcatus* and *C. coenobasis* which were more abundant at 12-19 °C and high transparency. Correlation of rotifer density with temperature was statistically significant (Table VI).

A negative relationship was observed between abundance, richness and water level. When flooding occurred, there was entry of river water into the lake through the N and S stations. It produced mainly a dilution, with a decrease in conductivity and turbidity. Under these conditions, in July, the rotifer densities were at their minimum values. There was no evidence that the river water contributed rotifer populations, as in other floodplain lakes (KOSTE and ROBERTSON 1983, VASQUEZ 1984), however there may have been a population reduction by passage of flood water through littoral macrophytes, as in Orinoco floodplain lakes (HAMILTON *et al.* 1990).

The highest rotifer densities were recorded at low water levels during the isolation phase (Table V). The relation between water level and abundance of rotifer was more significant in the limnetic stations than in the littoral (Table VI).

Oxygen concentration, although its influence on the occurrence of many species has been pointed out (ELLIOT 1977, HERZIG 1987), was not found to have direct effects on the taxa of this lake. Because of the low values of oxygen recorded in some instances, a range of tolerance by the species is presumed, mainly in station W. In studies of diel migration of rotifers on the same lake, a wide range of tolerance to low concentrations was observed (JOSE DE PAGGI, unpublished). BERZINS and PEJLER (1989) found that for warm-stenothermal species there are no close connections with oxygen content.

Conductivity was lower than 310 µmS/cm and had no relation with the richness or abundance observed.

TABLE VI

Correlation coefficients between abundance or rotifers and environmental factors

Corrélations entre abondance de rotifères et variables de l'environnement

Station	n	H	T°C	SD	Cond.	Oxygen
C	26	- 0.73**	0.60**	- 0.18	0.35	- 0.19
S	23	- 0.75**	0.59**	- 0.73**	0.44*	0.03
W	25	-0.36	0.60**	- 0.58**	0.08	- 0.16
E	25	-0.12	0.36	- 0.58**	0.07	- 0.10
N	25	- 0.49	0.59**	- 0.50*	0.22	- 0.18

**P < 0,01

n = data, H = water level ; SD = Secchi disc ; Cond = water conductivity

n = nombre de données, H = niveau de l'eau, SD = disque de Secchi ; Cond = conductivité

DISCUSSION

It is evident that the weedy littoral area contributed to greater environmental heterogeneity, i.e. a larger number of niches are available, there is finer spatial partitioning, and consequently lower interspecific competition (HASLER and JONES 1949, PENNAK 1966, GREEN 1972, LEMLY and DIMICK 1982). Notably, the weedy littoral provides two feeding resources : periphyton and suspended particles (phytoplankton and detritus). Consequently, conditions are created that favour detritivorous species such as *Lepadella ovalis*, *Euchlanis dilatata* and species of *Colurella* and *Cephalodella*. Structural complexity of the floodplain weedy lakes thus plays an important role in the species richness. The number of species of El Tigre is high, as in other floodplain lakes (KOSTE *et al.*, 1984, SHIEL and KOSTE 1986)

Some authors have observed relationships between macrophytes and composition of the rotifer community. Some of the results obtained in El Tigre support those found by SUDZUKI *et al.* (1983), for example, *F. longiseta* density was negatively correlated with *E. crassipes* density. In El Tigre, *F. longiseta* had an occurrence of 61 % in open water and was very abundant, but of only 16 % in the station with *E. crassipes*. Conversely, *B. quadridentatus* was found in El Tigre almost exclusively in weedy zones, and is reported elsewhere to prefer littoral habitats (PEJLER and BERZINS 1989).

Faunistic similarity between stations throughout the study was very low, reflecting the spatial heterogeneity of the lake. The presence of some limnetic species in littoral areas and *vice versa* would indicate also the existence of a wide ecotonal zone between open and weedy waters. Station S, because of its composition and dominant species, is indicative of such a transitional zone. Such zones are maintained by wind causing water circulation, which is important in small lakes with a wide weedy littoral like El Tigre (cf. GLIWICZ and RYBAK 1976). TAIT *et al.* (1984) and SHIEL *et al.* (1986) found also a large proportion of littoral species in billabong's open water as consequence of level fluctuations and the strong influence of marginal macrophytes.

In terms of seasonality and causal factors, the same trends in abundance, richness and diversity patterns were observed in the two areas. Nevertheless, the changes were more attenuated in the littoral and transition areas (Table VII). It is likely that the

TABLE VII

Annual means (X) and coefficient of variation (CV) of abundance, richness, and diversity in the different stations
Moyennes annuelles et coefficients de variations (CV) de l'abondance, de la richesse et de la diversité aux cinq stations

Stations		C	S	N	W	E
Abundance	X	638.33	260.45	292.20	521.04	503.08
	CV	135	81	65	77	94
Richness	X	8.43	9.58	9.30	9.19	10.20
	CV	62	53	53	58	45
Diversity	X	1.88	2.21	2.53	2.31	2.49
	CV	63	38	34	38	34

factors which control changes are not the same in the two areas. On the basis of hydrologic events, the most important changes occur at the time of inundation : the rotifer density and richness in station C is the lowest (i.e. a dilution), there are less resources in phytoplankton, temperatures are lower, and competition with copepods is likely. The lowest density of rotifers coincided with a marked increase in copepod populations, and, more generally, rotifers and calanoid copepods had alternating population fluctuations in the lake (Fig. 8). *Notodiaptomus carteri*, *N. incompositus* and *Diaptomus spiniger* were the dominant species. Calanoid copepods of the family Diaptomidae, even the smaller suspension-feeding diaptomid species, may prey on rotifers, and the predation may be intense and selective. *Diaptomus pallidus*, for example, can seriously affect rotifer populations (WILLIAMSON and BUTLER 1986, WILLIAMSON 1987). In El Tigre there is not direct evidence for the mechanism responsible for the alternating seasonal population fluctuations. Species interactions by exploitative competition, and by mechanical interference, may be operating.

In the littoral area, the rotifer densities decreased during June-July, and during this time important densities were reached by the cyclopoids, *Tropocyclops*, *Mesocyclops* and *Microcyclops* (Fig. 8). Gut content analysis of adults and late instars of cyclopoids at this time revealed consumption of *Filinia*, *Trichocerca* and *Testudinella*. Other studies have shown that these copepods prey on rotifers (WILLIAMSON, 1983).

In the isolation phase, a gradual decrease in water level and transparency were observed, as in other floodplain lakes (TWOMBLY and LEWIS 1987), with increases in conductivity and phytoplankton (G. de EMILIANI, pers. commun.). Resuspended sediments are not important in El Tigre because of the short fetch, velocity of the winds and vegetation which rings the lake (DRAGO, pers. commun.). The isolation period is characterized by high abundance of rotifers and species richness in the limnetic and littoral areas.

Notably, higher rotifer densities coincided with lower concentrations of cyclopoids in the weedy waters and of calanoids in the limnetic area during the isolation period. Predation and competition probably are reduced, and the higher temperatures and abundance of phytoplankton are favorable to rotifers.

Information on feeding of fish in the lake suggests that during the isolation period they prey more selectively on microcrustacea — only *Diapoma* sp. had rotifers in their digestive tract (OLIVEROS, pers. commun.). ANDERSON (1980) showed that rotifers were more affected by cyclopoids than by fish. Similar selectivity may occur in El Tigre.

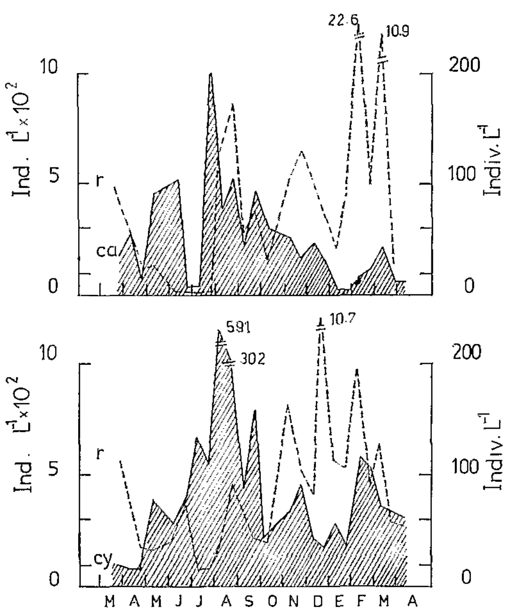

FIG. 8. — Seasonal variations in calanoids (ca) and cyclopoids (cy) abundance, and rotifers (r) abundance, at limnetic (top) and littoral (bottom) stations, respectively (mean values). Right scale for rotifers and left scale for copepods.
Variations des abondances de calanoïdes (ca), cyclopides (cy) et de rotifères (r) dans la station centrale (en haut) et littorale (en bas). Échelle de droite pour les rotifères, et de gauche pour les copépodes.

In conclusion, the evidence indicates that rotifer seasonality in the lake was determined mainly by hydrologic events. Interactions with calanoids in the limnetic area and intrazooplanktonic predation in littoral area are, by implication, important factors.

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