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ZOOPLÂNCTON DE AMBIENTES LÓTICOS E LÊNTICOS DO RIO PARANÁ MÉDIO

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RESUMO

Foi realizada uma revisão dos conhecimentos sobre o zooplâncton dos diferentes ambientes aquáticos da planície de inundação do Rio Paraná Médio. Até o presente momento, foram registradas cerca de 300 espécies de rotíferos, cladóceros e copépodos. As espécies dominantes pertencem a estes grupos, e só ocasionalmente membros de outras taxa (Ciliophora, Suctoria, Turbelaria, Gastrotricha e Acari) são encontrados desenvolvendo grandes populações. Os rotíferos freqüentemente dominam em termos de número de indivíduos, tanto em ambientes láticos como lênticos. Os crustáceos são pouco abundantes no curso principal do rio, mas têm importância maior nos contribuintes, tributários, e particularmente nas lagoas. Embora algumas espécies sejam mais freqüentes nos ambientes lóticos (*Trichocerca rattus*, *Lecane proiecta*. *Notodiaptomus coniferoides*), não é possível afirmar que existe um potamozooplâncton muito diferenciado. A densidade de organismos varia de 10 a 148 ind.l^{-1}, no curso principal, com maiores valores na altura de Confluência, na margem que tem influência do Rio Paraguai. Nos ambientes lênticos a densidade varia de 10 a

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1100 ind.l^{-1}. Foram registrados valores mais elevados para o zooplâncton litoral. As variações temporais da composição e abundância são muito mais influenciadas pelo regime de inundação. Nos ambientes lóticos, tanto a velocidade da corrente quanto a turbidez da água, de origem fundamentalmente inorgânica, constituem os fatores ambientais mais importantes por sua influência no zooplâncton.

ABSTRACT - ZOOPLANKTON OF THE LOTIC AND LENTIC ENVIRONMENTS OF THE MIDDLE PARANA RIVER

This article presents a revision of knowledge of the zooplankton communities of the running waters and floodplain water bodies of the Middle Paraná River. About 300 species have been recorded belonging to the maior groups Rotifera, Cladocera and Copepoda. Though the common dominant species belong to these groups, members of other taxa (Ciliophora, Suctoria, Turbelaria, Gastrotricha and Acari) are occasionally found developing debse populations. Rotifers are often the most abundant zooplankters in both lentic and lotic waters. Crustacea are notably scarce in running waters. There is not a distinct potamozooplankton but some species (*Trichocerca rattus*, *Lecane proiecta*, *Notodiaptomus coniferoides*) are more frequent in lotic environments. Zooplankton density ranges from 10 to 148 ind.l^{-1} for the main channel and from 10 to 1100 ind.l^{-1} for the standing waters. Higher values have been recorded for littoral zooplankton. Variations in community composition and abundance are strongly influenced by flood regime. As well as the current velocity, the turbidity of the water (suspended sediments) are likely to be the most important environmental factors which govern the development of the zooplankton in running waters.

INTRODUCTION

The ecosystem of the Middle Paraná River shows highly complex characteristics due to its intricate and changeable, structural physical basis as much as for its rich biota, where proper adaptative aspects of terrestrial and aquatic organisms are superimposed.

From its confluence with the Paraguay River and all along its way, a wide floodplain extends and is crossed by anastomosed streams. Among them, island remain full of lentic water bodies (pond, swamp, ox-bows). The enormous kinetic energy of its running water (16000 m^3/s), annual average, not only causes a constant remodelling of the floodplain due to erosion and sedimentation, but greatly governs the development and flunctioning of the communities.

It could be said that there is a sort of gradient as regards water retention time in the basins which form the system, i.e., that there is a series which goes from lotic to lentic assuming as extremes, the main stream an on side and ponds with high degree of isolation on the other. Among them there is a great variety of water bodies which are sometimes difficult to be defined with in the common types of limnology and whose location in the lotic-lenitic gradient depends besides of the hydrologic stage of the river.

The main channel carries over the 80% of the discharge in a turbulent, high velocity flow (1-2 m/s). Secondary channels, with much inferior dimensions have much lower velocities; sometimes, greater water transparency and banks may be partially covered by aquatic vegetation, mainly floating vegetation.

For a correct interpretation of the data presented in this paper, the above mentioned characteristics of this system under study, must be kept in mind In spite of the intention of keeping the exposition for lotic environment separated from lentic ones, several items are to be considered which are common to both, since this heterogeneous group is at the same time, interrelated.

The most ancient and worthy antecedents about zooplankton are found in papers which do not specifically refer to the Middle Paraná River but to areas hydrologically related to it, as the Delta of the Paraná and the Paraguay Rivers (DADAY, 1905; PESTA, 1927). The studies on the zooplankton of the Middle Paraná River, principally the ecological ones are very recent in general, most of them appear in publications of the last twenty years. This coincides with the beginning of systematic research which started at the foundation of INALI. JOSÉ de PAGGI & PAGGI (1982) carried out a critical, systematic analysis of the available information up to 1982; further publications are considered in this paper.

FAUNAL COMPOSITION

When limnological research began in this region, the state of knowledge regarding taxonomy, constituted an important handicap for the studies on zooplankton. In RINGUELET's (1958) review on Copepoda we may find a few records about the main stream of the Middle Paraná. Nothing was found in OLIVIER's (1962, 1965) papers about Cladocera and Rotifera, respectively. Therefore, available data on the subject are quite new.

About 300 species have been recorded belonging to the major groups of the zooplankton (Tab. 1 and 2), though many taxonomic problems are still to be solved.

ROTIFERA

It is the most numerous and varied of the groups

Table 1 - Faunal composition of the zooplancton in the Middle Paraná. Number of species in parenthesis.

Rotifera	Asplanchnidae (3)	Moinidae (4)
Epiphanidae (2)	Dicranophoridae (1)	Daphnidae (17)
Brachionidae (39)	Testudinellidae (9)	Bosminidae (5)
Euchlanidae (10)	Flosculariidae (4)	Macrothricidae (11)
Mytilinidae (4)	Conochilidae (3)	Chydoridae (43)
Colurellidae (6)	Hexarthridae (2)	
Lecanidae (25)	Filiniidae (4)	Copepoda
Notommatidae (3)	Trochosphaeridae (2)	
Trichocercidae (15)	Collothecidae (1)	Boeckellidae (1)
Gastropodidae (4)	Cladocera	Diaptomidae (18)
Synchaetidae (7)	Sididae (10)	Cyclopidae (23)

comprising the zooplankton. The most abundant and widely distributed species belong to the genera: *Keratella*, *Brachionus*, *Polyarthra*, *Filinia*, *Conochilus*, *Synchaeta* and *Pompholix*. Other frequent elements are some species of the genera: *Anuraeopsis*, *Epiphanes*, *Asplanchna* and *Ascomorpha*. It is interesting to point out the richness of the genus *Brachionus* (25 species) and the occurrence of some species belonging to littoral genera adapted to the planktonic existence, *Trichocerca rattus*, conspicuous member of the potamoplankton possibly associated to the filaments of some diatom (*Melosira* spp) and *Lecane proiecta* also belonging to lentic environments whose globose body suggests an adaptation to the floating planktonic life.

Though there are some cases of Neotropical endemicity, specially in *Brachionus* (e.g. the "mirus" group), the majority of Rotifera inhabiting the middle Paraná, belong to cosmopolitan or tropicopolitan taxa.

Table 2 - List of common zooplankters of rivers and ponds of Middle Paranã.

Rotifera

Anuraeopsis fissa (Gosse)
Ascomorpha ecaudis Perty
Asplanchna brigtwelli Gosse
Beauchampiella eudactylota (Gosse)
Brachionus angularis (Gosse)
B. budapestinensis Daday
B. caudatus f. personatus Ahlst.
B. c. f. austrogenitus Ahlstrom
B. c. f. insuetus Ahlstrom
B. calyciflorus Pallas
B. dolabratus Harring
B. falcatus Zacharias
B. havanensis Rousselet
B. mirus mirus Daday
B. mirus voigti Hauer
B. patulus O.F.Muller
B. plicatilis O.F.Muller
B. quadridentatus Hermann
Conochiloides coenobasis Scoricoff
C. natans (Seligo)
C. unicornis (Rousselet)
Epiphanes clavulata (Ehrb.)
E. macrourus (Barrois & Daday)
Euchlanis dilatata (Ehrb.)
Filinia longiseta Ehrb.
F. opoliensis (Zacharias)
Hexarthra intermedia Wiszniewski
Keratella americana Carlin
K. cochlearis (Gosse)
K. lenzi Hauer
K. tropica (Apstein
Lecane curvicornis Murray
L. leontina Turner
L. papuana Murray
L. proiecta Hauer
L. (M) bulla (Gosse)
L. lunaris (Ehrb.)
Lepadella ovalis O.F.Muller
Mytilina ventralis (Ehrb.)
Platyias quadricornis (Ehrb.)
Ploesoma truncatum (Levander)
Polyarthra vulgaris Carlin
P. dolychoptera Idelson
Testudinella patina (Hermann)
Trichocerca rattus (O.F.Muller)
T. similis (Wierzejski)
Trichotria tetractis (Ehrb.)

Cladocera

Alona eximia Kieser
Bosmina hagmanni Stingelin
B. huaronensis Delachaux
B. longirostris (O.F.Muller)
Bosminopsis deitersi Richard
Ceriodaphnia cornuta Sars
Chydorus eurinotus Sars
C. pubescens Sars
Daphnia sp. (grupo *laevis*)
D. ambigua Scourfield
Diaphanosoma birgei Korinek
D. brevireme Sars
D. fluviatile Hansen
D. spinulosum Herbst
Guernella raphaelis Richard
Grimaldina brazzai Richard
Ilyocryptus spinifer Herrick
Moina micrura (Kurz)
M. minuta Hansen
M. reticulata (Daday)
Moinodaphnia macleayi (King)

Copepoda

Acanthocyclops robustus (Sars)
Argyrodiaptomus argentinus (Wright)
A. denticulatus (Pesta)
Boeckella bergi Richard
Diaptomus santafesinus Ringuelet y M.Ferrato
Diaptomus spiniger Brian
Eucyclops neumani (Pesta)
E. serrulatus (Fischer)
Mesocyclops longisetus (Thiebaud)
M. meridianus Kiefer
Metacyclops mendocinus (Wierzejski)
Microcyclops anceps (Richard)
Notodiaptomus anisitsi (Daday)
N. conifer (Sars)
N. coniferoides (Wright)
N. incompositus (Brian)
Thermocyclops decipiens Kiefer
T. minutus (Lowndes)

CLADOCERA

This group are represented by about 90 species. The most frequent and dominant are those belonging to the genera: *Diaphanosoma*, *Moina*, *Bosmina*, *Bosminopsis*, *Ceriodaphnia* and *Daphnia* (PAGGI, 1973a e b; 1978b, 1979a). Cladocera are not frequent in lotic waters. Some species of *Moina*, *Bosmina* and *Bosminopsis* may be found, but in low density populations.

Though Macrothricidae and Chydoridae have littoral habits, many species are occasionally recorded in open waters, probably as pseudoplankton. However, the occurrence of *Alona eximia* Kiser, is too frequent to be considered an adventitious form. A similar situation was found in other rivers (KISER, 1948; GREEN, 1962; FREY, 1974).

The genus *Daphnia* is poorly represented and members of the subgenus *Ctenodaphnia* are absent from the waters of the alluvial valley. It is probable that biogeographic as well as ecological (fish predation) reason explain this fact. It is reasonable to suspect that the cpmmon and abundant presence of *Moina* may be correlated to the poor presence of *Daphnia*. *Ceriodaphnia* is represented by several species (PAGGI, 1986). They are seldom recorded in open waters, except the common and pantropical *C. cornuta*.

As regards Bosminidae, only the members of the subgenus *Neobosmina* Lieder appear frequently in open waters. *Bosmina longirostris* rarely occurs and it seems to be confined to lotic environments.

There are no carnivorous Cladocera in the Paraná River, they are all herbivorous and detritivorous.

COPEPODA

As far as it is known, Copepoda comprises approximately 50 species of Calanoida y Cyclopoida. They are much more abundant and frequent in lentic environments than in running waters.

In general, it appears that Calanoida which are represented by Diaptomidae and Boeckellidae, are the most common and abundant in open waters, principally the species belonging to the genera *Argyrodiaptomus* Brehm and *Notodiaptomus* Kiefer, principally *N. incompositus* (Brian), *N. spiniger* (Brian), and *A. denticulatus* (Pesta). *Boeckella bergi* Richard, the sole representative of the family in the Paraná River, is occasionally collected in the open waters of ponds with poor vegetation, associated to species of Diaptomidae. It is interesting to point out that among the species of *Notodiaptomus*, *N. coniferoides* is the only one frequently found in lotic waters (PAGGI & JOSÉ de PAGGI, 1974).

As regards feeding habits calanoid copepods are principally herbivorous and detritivorous. Only occasionaly, rotifer rests have been observed in the intestinal content of large size species of *Argyrodiaptomus* (PAGGI, unpublished). There would not be raptorial calanoid copepods. Though the number of Cyclopidae species is relatively high (25), these copepods are scarcely represented in lotic waters and are rarely dominant in the composition of the zooplankton of lentic environments.

Cyclopoida in general, are found in pond and ox-bow plankton, principally as nauplius and copepods of species whose adult instars, as it seem probable may be found in littoral or bottom habitats. The most common species are those belonging to the genera: *Acanthocyclops*, *Mesocyclops*, *Metacyclops*, *Thermocyclops*, *Microcyclops*, *Eucyclops*, *Tropocyclops* and *Ectocyclops*.

OTHER PLANKTONIC INVERTEBRATES

The composition of the Middle Paranã zooplankton is dominated by the three major above mentioned groups, which are more common in the limnoplankton of the world. However, we may also find members of other groups which occasionally develop large populations in vegetated ponds and even in the open waters of the main stream.

Protozoa are represented by some species of Ciliophora and Suctoria. Among the first, species of the genus *Codonella* (Peritricha) are quite common in the plankton of some ponds, mainly in open waters. On the other hand, some unidentified species of Amphileptidae (Holotricha) occur as important element in vegetated ox-bows. In this same type of environments it is frequent to find turbelaria (*Catenula* cf. *lemnae*) developing brief summer pulses and neogoseid gastrotricha, *Neogossea fascicu lata* and *N. pauciseta*.

In ponds of Norhern floodplain, water mites (*Piona* spp) also occur living in open waters and preying upon cladocera.

MAIN AND SECONDARY CHANNELS

Spatial Distribution

As regards longitudinal distribution of the zooplankton along the potamic axis, the available data belong to JOSÉ de PAGGI (1978b, 1980) and CORRALES (1979). Only JOSÉ de PAGGI (1980) covers the middle stretch in teh whole, based on the study of samples taken each 15 km during a period of low waters. Data reveal the occurrence of two large zones and of a gradient of increasing tendency down-stream in several attributes of the community. The increasing gradient is more or less defined according to the considered parameter, biomass, density, diversity and richness. It could be related to the increase also occuring in the phytoplankton and primary productivity (Fig. 1). Apparently, this pattern of increasing longitudinal distribution downstream may not be a persistent phenomenon but restricted to the time of carrying out the sampling with a relatively reduced flow. Data obtained from intensive samplings carried out during long periods in front of Corrientes city (km 1208), that is the beginning of the middle stretch (BONETTO & CORRALES, 1984), in front of Paraná city (km 603-601), downstream from the above, PAGGI & JOSÊ de PAGGI (1974) and JOSÊ de PAGGI (1980) show not differences as regards annual average of the total density (Tab. 3). Regarding the number of species no considerable differences are observed either.

Table 3 - Mean values of zooplankton density (ind.l^{-1}) and richness in the main channel of the Paraná River. R: right margin, L: left margin, M: midchannel. Coeficient of variation in parenthesis.

Localities	Date	RM	MCh	LM	Spp	Authority
Upper Paraná	08/78-12/79		18*		55	Bonetto & Corrales 1985
Middle Paraná						
km 1208	04/76-12/79	41*	31*	22*	127	Bonetto & Corrales 1985
km 876	03/81-01/82	97*	-	101*	136	Bonetto & Corrales 1985
km 603	01/77-12/80	19(104)	21(109)	23(99)	109	José de Paggi 1980
km 601	09/71-01/73	-	31(118)	-	90	Paggi & J. de Paggi 1974

* without data of coefficient of variation.

According to the observations by JOSÊ de PAGGI (1980) from the confluence of the Paraná and Paraguay Rivers zone, the zooplankton show differences in its

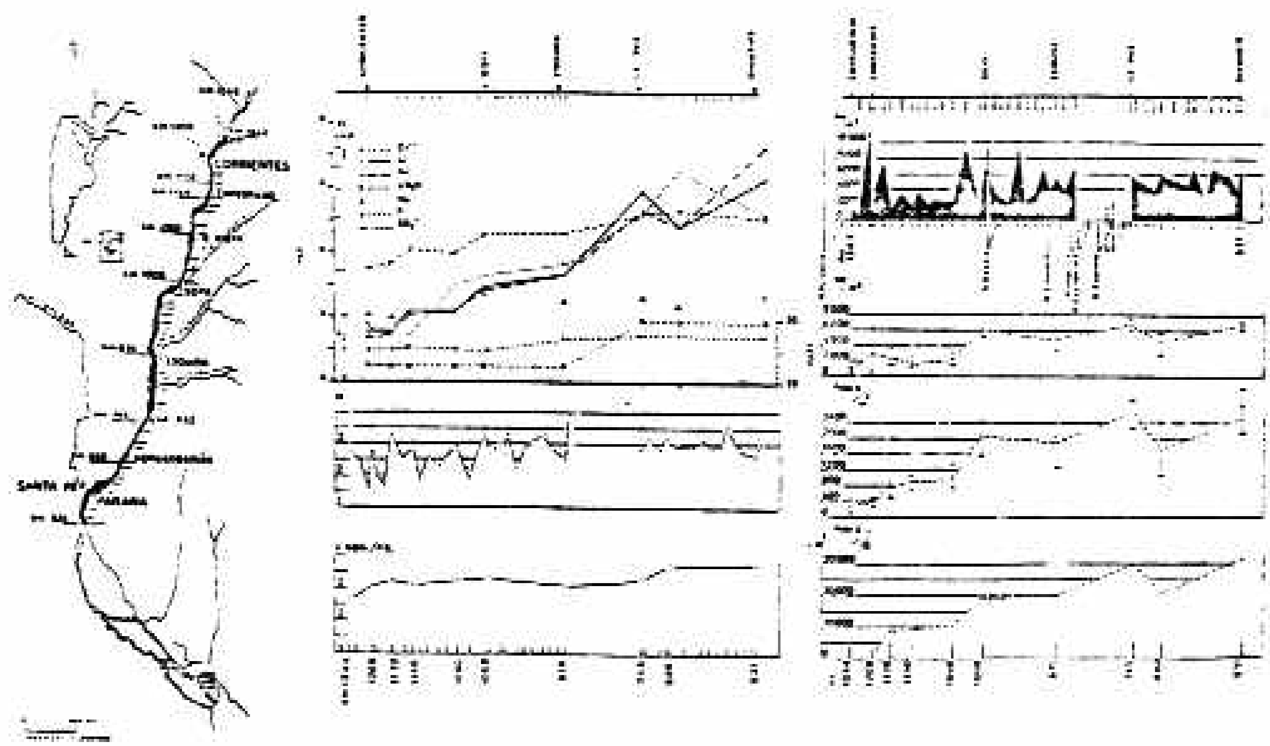

Figure 1 - Ionic composition, after DRAGO & VASALLO (1980) and Shannon Index calculated on number and biomass of the zooplankton taxa.

Density of the zooplankton in the main channel anabranches and tributaries. Biomass (PS= dry weight) in the transections of the main channel (mean, max. and min. values). Variations of the biomass relative to discharge.

ccmposition as well as in its abundance. This spatial diversity would be revealing the physicochemical differences of the waters of both rivers whose mixture does not occur inmediately. In the longitudinal sense, the influence of the Paraguay River gives rise to two zones: in the first 400 km downstream, density appears more fluctuating and the structure more heterogeneous (specific diversity: 1.57-3.89 bits; equitability: 0.22-1.00). The following 300 km exhibit greater homogeneity in the measured attributes (diversity: 2.67-3.00 bits; equitability: 0.42-0.67). Similarity among samples, in turn, according to Jaccard coefficient is lower (40%) in the upper stretch than in the inferior one (75%).

Although general composition and specific richness are not deeply modified, some changes occur at the specific level. Among Rotifera for example, *Trichocerca similis* is frequent and abundant uppstream (BONETTO & CORRALES, 1985), whereas downstream, it is apparently replaced by *T. rattus* which is an important element in the community. As regards *Keratella tropica* and *Lecane proiecta* also important in the zooplankton downstream, are either scarcely represented or absent upstream. Among cladocera, *Bosmina longirostris* commonly occur upstream but seldom occur down-stream where are dominant *B. huaronensis* and *B. hagmanni*. Several causes could be responsible for these changes, among them competence, variation in feeding resources, changes in the environmental conditions. Actual knowledge of this phenomenon which is not enough to allow a correct interpretation. It is possible however that the changes occurring in physical parameters, principally in the concentration of suspended solids, play an important role. Another interesting difference in the zooplankton composition is the greater number of the species *Brachionus* downstream (18), which practically doubles the number uppstream (11) Upper Paraná (7), and Paraguay River (8). This is probably influenced by tributaries, their influence, being responsible of the increases in density observed in their zone of influence (JOSÉ de PAGGI, 1980; 1983; in press; BONETTO & CORRALES, 1985).

Despite at this time not a little information is available concerning taxonomy and ecology of the zooplankton communities of Middle Paraná, much work remains to be done because of the large size and complexity of the ecosystem. Middle Paraná is clearly an integral part of a vast system hence more information on the zooplankton of the other reaches, upstream and downstream, would be achieved for a comprehensive understanding of its ecology.

Rotifers are dominant in lentic and lotic environments but the relative abundance of crustaceans is higher in standing waters. There is little evidence of major differences in community structure between lotic and lentic environments to consider the existence of a distinct "potamoplankton". However there is a number of species which seem to be better adapted to pelagic life subjected to extreme turbulence and high concentration of suspended sediments (Fig. 2).

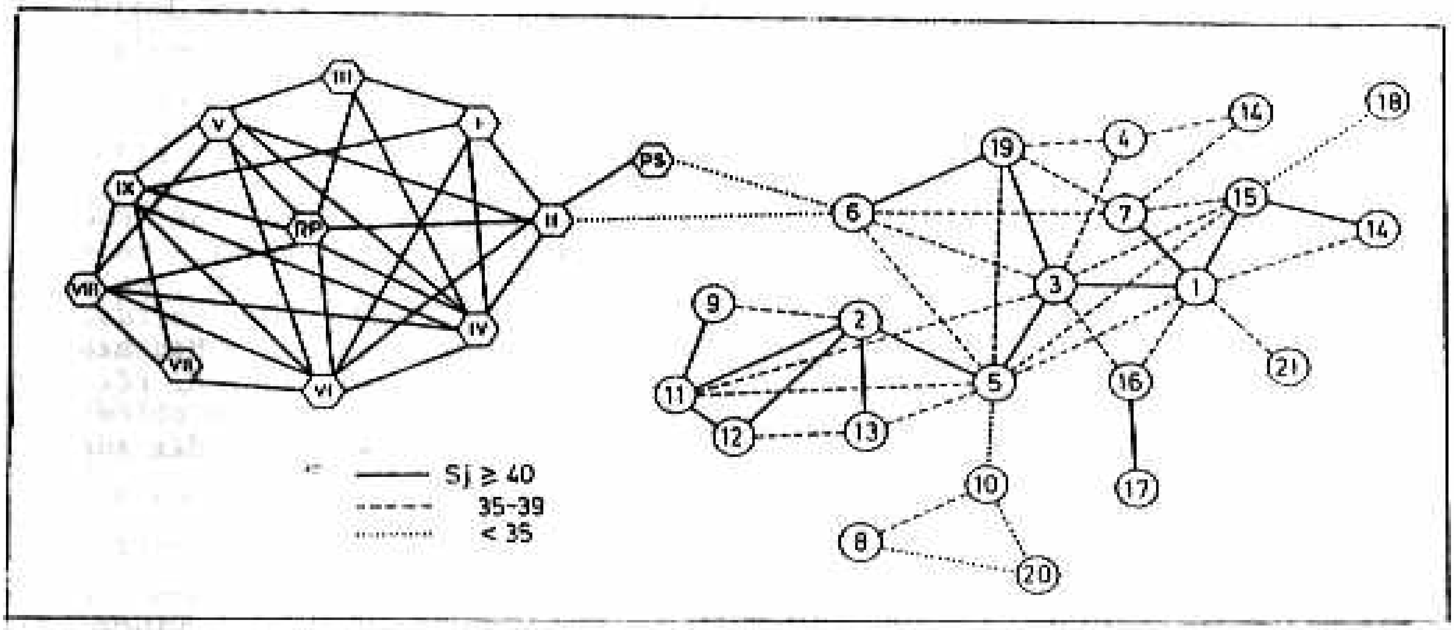

Figure 2 - Plexus diagram indicating the degree of affinity (Jaccard's Coefficient) among zooplankton assemblages from ponds (circles) and nearby river sampling stations (hexagons). Limnological Cruise Keratella I, see Table 6.

In general, a sort of transversal gradient with regard to water residence time may be observed which would have ponds at one extrema and the main stream at the other, with anabranches as intermediate. The greater to lesser gradient has its expression in the density and richness of species and in the proportion of dominance of crustacea.

Although there is a wide group of common taxa shared by the most of zooplankton communities, it is clear a correlation of the species composition with the limnological characteristics of their environments (Fig. 3).

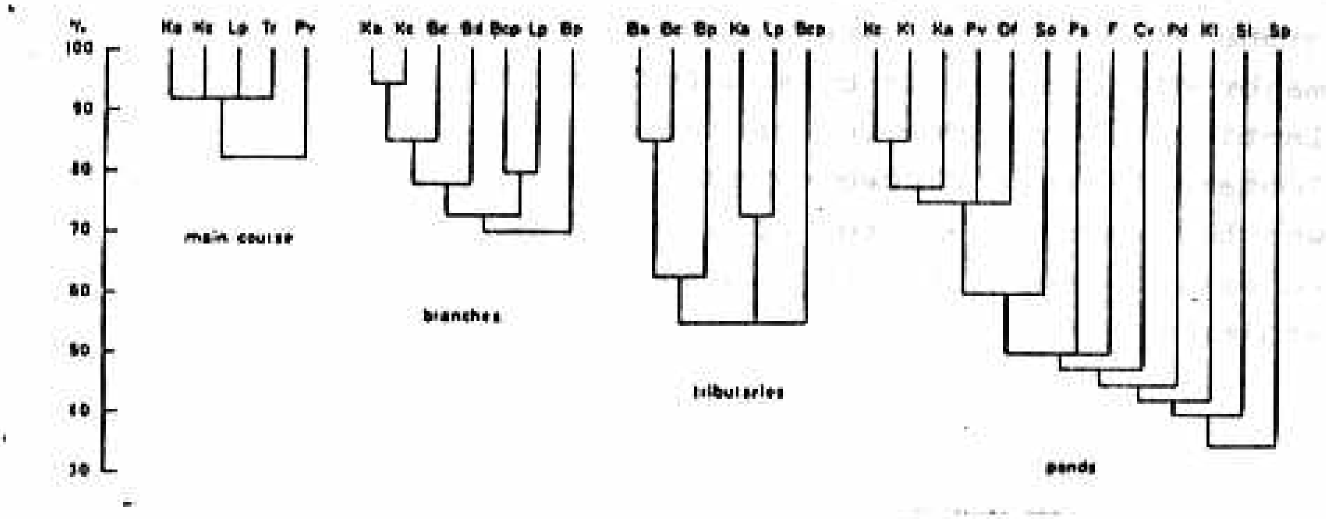

Figure 3 - Common zooplankton assemblages in the major units of the ecosystem (after JOSÉ de PAGGI, 1983 and PAGGI, 1980). Ka = *Keratella americana*, Kc = *K. cochlearis*, Kl = *K. lenzi*, Kt = *K. tropica*, Lp = *Lecane proiecta*, Tr = *Trichocerca rattus*, Pv = *Polyarthra vulgaris*, Pd = *P. dolychoptera*, Bc = *Brachionus calyciflorus*, Bcp = *B. caudatus personatus*, Bp = *B. plicatilis*, Df = *Diaphanosoma fluviatile*, So = *Synchaeta oblonga*, Sl = *S. longipes*, Sp = *S. pectinata*, Ps = *Phompholix sulcata*, F = *Filinia* spp., Cv = *Conochilus unicornis*.

Major changes in community structure and abundance of populations are mainly associated with seasonal fluctuations of water level. Physical factors (turbulence, principally from the right bank, being their alkaline waters favourable for the species of the genus.

As regards horizontal distribution in a transect of the confluence of the Upper Paraná and Paraguay, BONETTO & CORRALES (1985) find marked differences Zooplankton on the right bank, influenced by the Paraguay River, showed greater richness (101 spp) and density than the zooplankton on the left bank (75 spp). In front of Paraná city (km 603), downstream density and number of species show horizontal as well as vertical homogeneity (JOSÉ de PAGGI, 1984; 1985). Notwithstanding, during the period of high waters, vertical diversity increases, similitude values among samples according to Koch index, significantly correlate with the hydrometric level so much for rotifers as for crustaceans (r: 0.74, $P < 0.01$; r: 0.72, $P < 0.01$, respectively).

In secondary channels, density did not show variations in the horizontal sense, but the composition resulted somewhat different between the banks and the midchannel. These differences, surely related to the lower flow and size of channels, are produced by the occurrence of littoral species probably despoiled from marginal vegetation. Also in this case, the lesser faunistic affinity among the different points was recorded during the high water period.

Available data on horizontal distribution in other rivers (BEHNING, 1928; SHADIN, 1956; VRANOVSKY, 1974; DZYUBAN, 1979; SHIEL et alii, 1982) show different results and it is possible to assume that these distribution patterns greatly depend upon the hydrology characteristics of each fluvial system. In the case of the main stream and major secondary channels, the effect of water turbulence becomes evident. The mainstream, having greater flow and current velocity does not offer adequate conditions to differentiated distributions. On the other hand, in the smaller secondary branches having less flow and velocity, the effect of turbulence diminishes, and there are more possibilities of being influenced by external contributions.

Temporal Distributions

The main stream as much as the secondary channels presents in general, a similar pattern, sowing maximum density in the low water period, mainly in Spring (main channel, km 603: 148 ind.l^{-1}, anabranches, San Javier River: 327 ind.l^{-1}) and lower values in the high water period (10 ind.l^{-1} in both).

Table 4- Zooplankton density (ind.l^{-1}) in the main channel of Paraná river, secondary branches and tributaries (Goya-Diamante), in different period of the flow regime. After JOSÉ de PAGGI (1983, 1988).

	High waters			Mean waters		
	n	X	CV	n	X	CV
Main channel	(6)	10.72	52	(6)	54.37	43
Secondary branches	(10)	15.90	45	(10)	122.34	71
Left bank Tributaries	(4)	252.98	93	(4)	147.38	41
Wright bank Tributaries	(5)	387.89	128	(4)	153.77	65

Variations in the seasonal cycle, with changes in temperature and photoperiods are superimposed with these of the hydrologic regime, being quite difficult to discriminate the relative importance of the environmental factors involved. For example in the mainstream, during the years 1977, 1978, 1980 (JOSÉ de PAGGI, 1984) the highest values occured in Spring (temperature 18-21°C), in low water. However, during 1979, density peaks occurred in the same season but with high water. Seasonal pattern with highest values during Spring-Summer, and lowest values in Winter, has been observed in the Danube and some rivers of the United States (ZIVKOVIK, 1968; WILLIAMS, 1966).

Variations of the hydrologic regime are undoubtedly of great importance and main changes in a great number of environmental factors related to each other and the zooplankton, such as flow, current velocity, turbidity, composition of suspended solids, phytoplankton density, larvae density and fish.

As we have seen, zooplankton abundance shows an inverse relation to the water level. This level variations implies flow variation and therefore, in its two components: volume and current velocity. Volume increase has been cosidered as one of the causes of decrease in zooplankton density by simple dilution (BONETTO & CORRALES, 1985). However, observations carried out in the Santa Fe River (JOSÉ de PAGGI, 1981) based on flow estimates in situ, showed that the zooplankton decrease was greater than the decrease which ought to have occurred had dilution been taken as the only cause (Tab. 5).

Table 5 - Correlation between density of zooplankton ($ind.l^{-1}$) and current velocity.

Localities	r	P	Authority
Santa Fe river	-0.75	0.01	JOSÉ de PAGGI (1981)
Coronda river	-0.60	0.05	JOSÉ de PAGGI (1981)
Correntoso river	-0.70	0.01	JOSÉ de PAGGI (1981)
El Cordobés stream	-0.50	0.05	JOSÉ de PAGGI (1981)
Middle Paraná and secondary branches	-0.63	0.01	JOSÉ de PAGGI (1988)

Current velocity has been considered as one of the main environmental factors on abundance and even on the existence of the lotic zooplankton (RZOSKA, 1961; 1976; HYNES, 1970; PAGGI & JOSÉ de PAGGI, 1974; JOSÉ de PAGGI, 1981; 1983; 1984). Inverse relation between zooplankton density and current velocity was clear in the mainstream as well as in the secondary channels, not only with respect to temporal variations but in the local comparison.

Variations in the flow regime also imply changes in connection or isolation degree of the different water bodies of the alluvial valley, which means a kind of oscillation in the degree of complexity and actual size of the ecosystem. Higher hydrologic level implies a greater area covered by water. The effect of interconnection among the different environments would be more directly noted in the zooplankton density. It has been observed in the zooplankton, that the annual fluctuation range of water level, show a quite direct relation to the specific richness (JOSÉ de PAGGI, 1984), being this understood as the consequence of the incorporation of population coming from lentic water bodies of the floodplain to the lotic environments.

In lake ecology in general, the relation plankton-turbidity may be interpreted as being of the cause-effect type, but in running water ecology and, in our specific case, the relation is apparently reversed. The Middle Paraná, as other Southamerican rivers, is characterized by its turbid waters, fact that is related to the suspended solids (DRAGO & MARCHETTI, 1973) which are contributed by the Bermejo, a tributary of the Paraguay River (DRAGO & AMSLER, 1981). The particles composing that charge less to 16 um in diameter and almost exclusively of mineral origin (83 to 99% according to DRAGO & DEPETRIS, 1968), fall within the range of feeding size taken by the majority of the zooplankters. Therefore, the negative incidence of the abioseston on the organisms would occurr through two principal ways: indirectly, limiting by "shadowing" the development of the phytoplankton which would constitute one of the important feeding sources, and directly, by interfering the feeding mechanisms (KOFOID, 1908; SABANEFF, 1956) and or increasing the specific weight of the animals thats eat them (RYLOV, 1940). It is natural to assume that the filtrating and sedimenting zooplankton which are not capable of performing an efficient chemical selection, would suffer the consequences of a defficient energetic balance (ARRUDA et alii, 1983). On the other hand, it can be said under those conditions it would predominate only the species capables of performing a chemical selection of the food (de MOTT, 1986).

Though at least in one opportunity, a negative relation between zooplankton density and water turbidity (r: -0.68, $P < 0.01$) was found in the mainstream (PAGGI & JOSÉ de PAGGI, 1974), this environmental parameter would act more on the nature of the potamoplankton. Probably, the dominance of rotifers as well as the scarcity of adult calanoid copepods ought to be interpreted at least in part, as the result of two different energetic balances in relation to a similar capacity for the chemical selection of food.

As regards predators feeding on the zooplankton, there are not available data up to now, that let us infer their importance in running waters. It is reasonable to assume that the only important predators to be taken into account, would be fish. However, zooplanktophagous filterers in the Paraná River system are very scarce, even more in lotic waters.

It has also been proposed that turbidity could influence negatively on fish predation of the zooplankton (HART, 1986; 1988). Fish larvae and juveniles of greater importance in the ecosystem (e.g. *Prochilodus platensis* Holm.), appear in running waters in Spring coinciding with the period of greater abundance of zooplankton (OLDANI, personal communication). However, there are no data about the feeding habits of these organisms.

LENTIC ENVIRONMENTS

Zooplankton in lentic water bodies under more diversified environmental conditions than those of lotic water bodies, shows a series of features which are more difficult to be generalized. There are not many papers referring to the ecology of the zooplankton of ponds and ox-bows. The first studies were carried out by BONETTO & MARTINEZ de FERRATO (1966) and MARTINEZ de FERRATO (1967), followed by other contributions related to water bodies near Santa Fe City (DIONI, 1975, PAGGI & JOSÉ de PAGGI, unpublished). The majority of the studies are intensive. They are based on sampling which cover at least a year round cycle in one or more ponds. Extensive ones are not so numerous. One of them is the study done by the limnological cruise Keratella I (PAGGI, 1980) and another covering 30 ponds in nearby island to the Santa Fe city (PAGGI, unpublished).

Rotifers are dominant in density in the lentic environments too, showing the greatest number of species. However, crustaceans occur more constantly and develop denser populations than in lotic environments. The greater abundance and richness of copepods, especially calanoids, are comparatively manifest.

Zooplankton in 21 ponds along the Middle Paraná showed density values ranging betweer 10 and 1100 $ind.l^{-1}$, averaging 180 $ind.l^{-1}$, biomass between 8 and 420 $ug.l^{-1}$ de peso seco, averaging 95 $ug.l^{-1}$, (Tab. 6). Sampling carried out in other water bodies show that values may be even greater. In the pond La Cuarentena, locate at the Carabajal Island, the zooplankton reached values near to 4000 $ind.l^{-1}$ and in the pond El Tigre only the cladocera of the littoral

Table 6 - Zooplankton of flood plain ponds along Middle Paraná (Sept. 1975) (modified after PAGGI, 1980).

Location (1)	Density (i.p.l.)	Biomass (ug DW)	Shannon Index	Equitability	Richness	Limmnetic species %	Pond #
1216	57	39.37	3.07	1.00	12	92	1
1216	11	50.63	3.48	1.14	14	100	2
1170	68	41.18	1.90	0.38	13	92	3
1170	29	8.98	2.80	0.55	17	88	4
1129	100	47.24	2.65	0.57	14	100	5
1085	461	111.33	2.11	0.46	13	77	6
1027	368	261.59	0.613	0.14	14	93	7
960	38	8.47	1.43	0.50	6	67	8
960	161	73.58	2.27	0.54	12	92	9
913	683	138.09	1.13	0.23	9	100	10
847	173	104.71	2.23	0.50	13	77	11
825	852	421.59	1.69	0.23	15	100	12
820	24	45.29	2.76	0.86	11	100	13
811	76	56.69	2.83	0.56	18	78	14
781	205	87.46	2.59	0.62	13	92	15
706	65	30.88	2.84	0.83	12	69	16
706	-	-	-	-	12	25	17
655	24	8.27	2.01	0.42	13	54	18
652	61	25.74	2.54	0.40	20	80	19
620	58	30.87	1.64	0.36	11	55	20
533	1115	287.92	1.95	0.71	7	83	21

(1) distance from Buenos Aires

plankton, presented 1200 ind.l^{-1} (2500 ug.l^{-1} dry weight). The number of species by water body for a given moment is from 2 to 33 rotifers, 0 to 9 cladocera and 0 to 5 copepoda.

Zooplankton assemblage in the ponds is frequently "spoiled" by the prescense of elements from other communities or tychoplankters. Due to the fact that these ponds are not very deep and their generally abundant vegetation is shifted by wind, DIONI (1975) set the question about the existence of a true zooplankton in the ponds or whether it is an unstable mixture of elements from other communities. The taxocenosis of open water rotifers and those inhabiting the inter-rooting spaces of *Salvinia* sp. were compared, being observed that both were very well differentiated taxocenosis with scarce superpositions. Cumulative number of species along an annual cycle was not very different between both taxocenosis but while in the pleuston there is a group of constantly occurring species along time, in the plankton occur a rapid succession of strongly dominant taxa. This is expressed in the values of the Shannon index: plankton ≤ 2; pleuston ≥ 3.5. Similar results were obtained with crustacean. Appart from the differentiation of the pleustonic taxocenosis, basically composed by organisms that depend on a substratum, the existence of a littoral plankton, may also be defined. Comparative observations carried out in a pond of the alluvial valley among cladocera of open waters and areas covered by tall grasses, *Panicum* spp., confirm this (PAGGI, unpublished).

A parallelism at the generic level was observed since, while in open waters *Diaphanosoma birgei* or *D. fluviatile* and *Moina micrura* or *M. minuta* were recorded, *D. brevireme* or *D. spinulosum* and *M. reticulata* or *Moinodaphnia macleayi* were recorded in vegetated areas. This littoral plankton sometimes reaches considerable densities such as 1200 ind.l^{-1} of *Diaphanosoma brevireme*, being higher in several orders of magnitude compared to the recorded data for congeneric species, in open waters.

Notwithstanding the spatial seggregation recorded a number of littoral plankters is found in open waters, being its presence related to the variation in the hydrologic regime. The principal difficulty arising when one tries to generalize, is the number of conditions and combinations with respect to the state of the pond and the river before the connections, types and lasting of connections. A case which can be placed at the extreme of these types, is that observed at the ox-bow Negro. By the end of 1977 it was almost completely covered by *Eichhornia crassipes*. The sudden flooding of the river caused the shifting of vegetation from the basin and, for some time, it became a lotic water body. Therefore, the zooplankton which had been composed predominantly by *Polyarthra dolychoptera*, *Filinia saltator* and cyclopid copepods, was replaced by another typically fluvial composed by species of *Keratella*, *Brachionus* and *Bosmina*.

At the pond La Cuarentena, on the other hand, an area of 3 h placed on a bank island, and almost permanently connected to the river, the situation is different (PAGGI & JOSÉ de PAGGI, unpublished). The environmental structure of the is strongly conditioned by the hydrologic functioning of the river with zones of clear water lotic influence and other more isolated ones. The zooplankton composition then, showed a correlation with this zonation of the pond. In the period of mid water, the zooplankton was constituted by limnetic species, with dominance of rotifers, principally *Trichocerca rattus* in the zone of lotic influence and fundamentally, by crustaceans in the zones far from this influence. During the flooding period, zonation is changed abruptly and the community exhibit a certain "disorder". The most evident change is observed in the composition, with a strong increase of the specific richness due to the incorporation of individuals belonging to littoral species, genera *Lecane* and *Euchlanis* among rotifers and *Macrothrix* and *Chydorus* among cladocera. A similar phenomenon of richness increment after floodings has been also observed in ponds of the Upper Paraná, Amazonas, and Orinoco (CORRALES & FRUTOS, 1985; CARVALHO, 1983; VASQUEZ, 1984; respectively).

It has been observed that average similarity of the zooplankton from 21 ponds (PAGGI, 1980) increase if the littoral species are excluded from the analysis. This means that there is a group of species shared by the majority of ponds which would form the asocies having greatest dispersion, composed by *Keratella cochlearis*, *K. tropica*, *E. americana*, *Polyarthra vulgaris* and *Diaphanosoma fluviatile*. The correlation analysis among several attributes of the community and some environmental factors for those ponds, show several trends associated in the same sense: average similarity, specific diversity, proportion of limnetic species areas and deph. This suggest that the composition of the communities shoud be, in a certain way, influenced by basin morphometry expressed by depht and area. This may be understood through the relative importance of the ecotones between the zooplankton and other communities.

As regards temporal variations in the zooplankton density of the ponds in general, it is observed in a period of abundance which begins in Spring and lasts until Summer and a period of minimum values in Autum-Winter. In general terms, they follow a similar pattern to the lotic environments with a maximum during low water, fact that has been also observed in ponds of the Amazonas.

Sometimes, in isolated ponds during a greater period, the abundance peaks of the zooplankton may be observed just before Spring. This was also observed in the alluvial valley of Upper Paranā, Laguna La Sirena (CORRALES & FRUTOS, 1985).

The interpretation of these variations is erroneous if one considers ponds as "classical lake" and does not take into account a factor, really an environmental macrofactor, which is the hydrologic regime of the river. The consequence of the invasion of flooding waters in a pond produce alterations in the zooplankton succession which are not in general easy to evaluate and, that due to the current state of knowledge, are not easy to be generalized, either.

As regards predators of the zooplankton in lentic water bodies of the alluvial valley, not much is known; it is probable however, that these have more importance that in lotic bodies. Apparently several zooplankters are part of the diet of many small fish (OLIVEROS, 1980). In studies carried out on the feeding spectrum of small fish frequenting aquatic vegetation of ponds, it was observed that several species frequent integrants of the zooplankton (of the genera *Moina*, *Diaphanosoma*, *Ceriodaphnia*, *Bosmina*, *Argyrodiaptomus*, *Conochilus*, *Brachionus*, *Filinia*, *Keratella* and *Polyarthra*) were present in the intestinal content of 14 species.

It is to be noted that some taxa as *Aphyocharax albürnus*, *Prionobrama paraguayensis* and *Roeboides paranaensis* should have consumed almost exclusively calanoid copepods. *Phallatorynus victoriae* is also a predator with a strong tendency to consume cladocera and copepods, principally in vegetated areas (OLIVEROS, 1983).

The survival of these small fish should be greatly conditioned by the existence of aquatic vegetation refuge which protects them from ichthyophagous fish (OLDANI, personal communication). Therefore, the variations in the hydrologic level, widening or limiting the area of dispersion of these fish, would indirectly influence on the composition and density of the zooplankton.

TRIBUTARIES

The major part of data come from works of the extensive type and permit a certain knowledge about the principal characteristics of the zooplankton of these water bodies and the influence that would have on the main stream and secondary streams of the Paraná River (JOSÉ de PAGGI, 1980; 1981; 1983; in press; BONETTO & CORRALES, 1985; JOSÉ de PAGGI & KOSTE, 1988; JOSÉ de PAGGI, 1985; MARTÍNEZ & FRUTOS, 1986).

The zooplankton of the tributaties also present some differences so much for its density (Tab. 4) as for its composition with respect to the lotic water bodies of the floodplain. These are not too marked when they refer to outlet zones and even more during floding periods when the Paraná River may, due to its greater flow, influence in a reciprocally way, on its tributaries (JOSÉ de PAGGI, 1981; 1983; in press).

However, the differences may be of greater importance in the case of an hydrologically more independent unit of the Paraná Basin watershad as it is the case of the system Los Saladillos, and ancient alluvial valley of the Paraná River (TRIONDO, 1979; PAGGI & JOSÉ de PAGGI, 1985; JOSÉ de PAGGI & KOSTE, 1988). There, the 24% of the species of rotifers found, had not been previously recorded in the floodplain.

These differences are probably related to the chemical characteristics of the waters. The presence of dense populations of *Brachionus angularis* and *B. plicatilis* in tributaries of the West margin are correlated to the higher alkalinity of these waters (JOSÉ de PAGGI, 1983; in print). These species, traditionally considered as halobiont (AHLSTROM, 1940; HUTCHINSON, 1967) have been also found in the secondary channels next to the mouth of these tributaries, but evidently, they are not capable of thriving in this type of waters judging from their scarcity or absence downstream. Highedt value of density (1001 ind.l^{-1}) was recorded in El Ombú an small stream which is polluted by organic wastes.

The tributary having the greatest importance on the Middle Paraná River is undoubtedly the Paraguay River; however, it is probable that also the tributaries from the East margin which drain the waters of the Iberá system have discharge, turbidity) are the primary determinants of zooplankton ecology in running waters. On the other hand, biological interactions (development of aquatic plants, predations) would be more important environmental factors in ponds and ox-bows.

Even when the increase in water level is correlated with a decrease in zooplankton density, a phenomenon showing the characteristics of the Blue Nile (MOGHRABY, 1977) where the zooplankton completely disappears has not been observed. It is not infrequent to find gamogenetic populations specially in ponds and previously to flooding, but the production of diapause or resting eggs could difficulty be considered as the most important mechanisms for the recolonization of water bodies. Apparently, the persistence of the different populations and hence the diversity of the zooplankton is maintained by the environmental heterogeneity of the system.

The abundance of the zooplankton in the lower section of Middle Paranã is not too diferent from that of the upper section to postulate the increase of the populations downstream by reproduction *in situ*. Age of the water along Middle Paranã is about a week.

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