SPATIAL HETEROGENEITY OF THE TUCURUÍ RESERVOIR (STATE OF PARÁ, AMAZONIA, BRAZIL) AND THE DISTRIBUTION OF ZOOPLANKTONIC SPECIES

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ABSTRACT

With the purpose of analyzing the horizontal distribution of the zooplankton community of the Tucuruí Reservoir in the State of Pará, Brazil, collections were made at 16 stations during August 1988. The stations cover the regions called Caraipé (C), Araçagi (B) and Ararão (A), and represent the different compartments of this ecosystem in regard to the morphometry and the presence or absence of "flooded forest". Our findings showed the existence of three compartments with different limnological characteristics determined as a function of the system's morphometry, a factor that may have influenced the horizontal circulation of the reservoir's water and, consequently, led to physical, chemical and biological differences at each of the sampled stations. All the stations presented physical and chemical stratification and layers of total anoxia or reduced concentrations of oxygen dissolved at depths corresponding to the limit of the euphotic zone. With regard to the zooplankton, a differentiated distribution that was mainly quantitative was found among the compartments (density of organisms and proportion among the species) in the case of Cladocera and Copepoda, and basically qualitative in the case of Rotifera. On the other hand, the greatest densities of organisms for all the groups were recorded at the Caraipé stations. As for the spatial distribution, some species were more restricted or more abundant at given stations. Among the Cladocera, there was a greater abundance of *Moina minuta*, *Bosmina hagmani* and *Bosminopsis deitersi* at the Araçagi stations, while *C. cornuta intermedia*, *C. cornuta rigaudi* and *C. cornuta cornuta* were more plentiful in the Caraipé and *Diaphanosoma birgei* in the Ararão. Among the Rotifera, *Trochosphaera aequatoriales* and *Lecane proiecta*, *Ascomorpha ecaudis*, besides *Polyartha* cf *vulgaris* were restricted, respectively, to the Caraipé, Araçagi and Ararão stations, while the others, such as *Keratella americana* and *Collotheca* sp., were more broadly distributed. As regards Copepoda Calanoida, the dominating species was found to be *Notodiaptomus maracaibenses*, followed by *Notodiaptomus henseni* and *Argyrodiaptomus azevedoi*. The most abundant Cyclopoda species was *Thermocyclops minutus*, although *Thermocyclops decipiens*, *Mesocyclops longisetus*, *Mesocyclops meridianus* e *Metacyclops* sp. were also found.

Key words: zooplankton, horizontal distribution, spatial heterogeneity, reservoirs.

RESUMO

Heterogeneidade espacial do Reservatório de Tucuruí (Estado do Pará, Amazônia, Brasil) e a distribuição das espécies zooplanctônicas

Com o objetivo de analisar a distribuição horizontal da comunidade do zooplâncton no Reservatório de Tucuruí, Pará, foram efetuadas coletas em 16 estações durante o período de agosto de 1988. As estações compreenderam as regiões denominadas de Caraipé (C), Araçagi (B) e Ararão (A), as quais representam diferentes compartimentos desse ecossistema em relação à morfometria e à presença ou ausência da “mata afogada”. Os resultados obtidos mostraram a existência de três compartimentos com distintas características limnológicas determinadas em função da morfometria do sistema, fator este que pode ter influenciado na circulação horizontal da água no reservatório e, conseqüentemente, levado a diferenças físicas, químicas e biológicas em cada estação amostrada. Todas as estações apresentaram estratificações física e química e camadas de total anoxia ou reduzida concentração de oxigênio dissolvido em profundidades correspondentes ao limite da zona eufótica. Em relação ao zooplâncton, verificou-se uma distribuição diferenciada entre os compartimentos, diferença esta principalmente quantitativa (densidade de organismos e proporção entre as espécies) no caso de Cladocera e Copepoda, enquanto essencialmente qualitativa no caso de Rotifera. Por outro lado, as maiores densidades de organismos para todos os grupos foram registradas nas estações do Caraipé. Quanto a distribuição espacial, algumas espécies mostraram-se restritas ou mais abundantes em determinadas estações. Entre os Cladocera, *Moina minuta, Bosmina hagmani* e *Bosminopsis deitersi* foram mais abundantes nas estações do Araçagi, *C. cornuta intermedia, C. cornuta rigaudi* e *C. cornuta cornuta,* no Caraipé e *Diaphanosoma birgei,* no Ararão. Entre Rotifera, *Trochosphaera aequatoriales* e *Lecane proiecta, Ascomorpha ecaudis,* além de *Polyartha* cf *vulgaris,* estiveram restritas às estações do Caraipé, Araçagi e Ararão, respectivamente, enquanto outras apresentaram distribuição mais ampla como *Keratella americana* e *Collotheca* sp. Quanto a Copepoda Calanoida, *Notodiaptomus maracaibenses* foi a espécie dominante, seguida de *Notodiaptomus henseni* e *Argyrodiaptomus azevedoi*. *Thermocyclops minutus* foi a espécie mais abundante dentre Cyclopoida, tendo sido também encontrados *Thermocyclops decipiens, Mesocyclops longisetus, Mesocyclops meridianus* e *Metacyclops* sp.

Palavras-chave: zooplâncton, distribuição horizontal de organismos, heterogeneidade espacial, reservatórios.

INTRODUCTION

Reservoirs are intermediate ecosystems between rivers and lakes. Besides being subject to the action of climatological forces such as precipitation, wind and solar radiation, are also closely related to the operational mechanisms of dams (outflow and retention time). These, together with the system’s morphometry, produce differences in the horizontal and vertical circulation throughout a spatial gradient (compartmentalization), making them extremely dynamic environments with a high spatial and temporal variability of their physical and chemical characteristics (Tundisi, 1981; Tundisi, 1990; Armengol & Saab, 1990) and producing differences in the qualitative and quantitative structural organization of their communities (Burgis, 1969; Watson & Carpenter, 1974; Hart, 1978; Hayward & Van Den Avyle, 1986; Cryer & Townsend, 1988; Infante, 1995). Another factor to be considered is the input of nutrients via affluents, which become diluted toward the main axis, and the many secondary water sources along the hydrographic basin that flow into the reservoir and contribute not only to the eutrophication of the system but also to the formation of compartments with different environmental conditions. However, although they recognize the horizontal heterogeneity and the compartmentalization of the abiotic factors, most studies of biological communities are still carried out descriptively, evaluating the temporal distribution of communities in seasonal cycles, emphasizing their structural alterations (composition and density) or determining metabolic processes in a single season, all of which is information considered to be representative of the system under study (Stavn, 1971; Soto *et al.*, 1984; Jones *et al.*, 1995).

Organisms, present spatial and temporal variations related to the physical and chemical gradients imposed not only by the difference in the longitudinal axis produced by the transition from river to lake but also by the system’s morphometric differences. Thus, in their natural environment, organisms are not distributed homogeneously and present considerable differences in their vertical and horizontal distribution, such as aggregated distribution (Hutchinson, 1967; Stavn, 1971).

Taking into account this spatial variability and the importance of the planktonic community in the food chain, we sought to characterize the distribution and spatial heterogeneity of the organisms in the Tucuruí (State of Pará) Reservoir, with emphasis on the zooplankton community and its relation to some environmental variables.

AREA OF STUDY

The Tucuruí hydroelectric power plant, formed by the damming of the Tocantins river, is the second largest hydroelectric plant established essentially in Brazilian territory, and is located in the State of Pará, at an altitude of 72 m, between the latitudes of 3°45' and 5°15' South and longitudes 49°12' and 50°00' West. The basin's drainage area spreads over 758,000 km^2 and the area of the reservoir is 2,430 km^2, with a maximum width of 40 km and an average width of 14.3 km. It is 170 km long and has a maximum depth of 75.0 m and average depth of 18.9 m. The affluent inflow is 11,090 m^3/s, with an average residence time of 47.8 days. The magnitude of the outflow, according to information obtained by ELETRONORTE allows for the total renewal of the reservoir's waters in less than two months, since the Tocantins River's average outflow at Tucuruí is considered high, and has been recorded as 3,500 m^3/s during the dry season and as 35,000 m^3/s during the rainy season.

According to information from ELETRONORTE, a great phytomass was flooded as a result of the damming of the Tocantins waters, and this material is undergoing a gradual process of decomposition until its complete mineralization and humification owing to the fact that this process is taking place under a dense layer of inorganic sediments deriving from upstream erosion. Another important consequence was the formation of innumerable islands (around 600) around the borders of the reservoir, which, associated with or without prior deforestation, form different compartments in the system and contribute toward increased environmental heterogeneity.

MATERIAL AND METHODS

Due to the reservoir's size, the collections were made in areas closer to the dam, considering two principal aspects: the presence or absence of previously deforested areas and the system's morphometry (the presence or absence of islands). The collections were carried out during the dry season on August 24, 25 and 26, 1988 at 16 stations called the Caraipé (from C_1 to C_7), Araçagi (from B_1 to B_5) and Ararão (from A_1 to A_4) stations, as shown in Fig. 1.

The zooplankton samples were collected by means of vertical dragging in the water column, with the material concentrated in a 68 mm sized mesh plankton net. The material collected was fixed with 4% formalin and analyzed in a laboratory, considering the composition and density of the organisms. Identification of the organisms, including the Cladocera, Copepoda (Cyclopoida and Calanoida) and Rotifera species, was carried out based on the following references: Pennak (1953), Edmondson (1959), Smirnov (1974), Smirnov & Timms (1983), Rocha & Matsumura-Tundisi (1976), Koste (1978a, 1978b), Reid (1985) and Matsumura-Tundisi (1984, 1986), Montú & Goeden (1986). The density of the organisms was determined by counting the sub-samples (enumerating at least 100 organisms of the most abundant species) or by total sample, as a function of organism density in each sample. Quantification of the rotifers was carried out by Sedgwick-Rafter slide while the density of the copepods and cladocerans was determined using the methods of Edmondson & Winberg (1971). The Copepoda, particularly, were analyzed considering the nauplius, copepodit and adult phases (males, females and spawning females).

Other organisms present in the samples were also included in the analysis, such as insect larvae, alevins, turbellarians and ostracods. The findings were expressed in numbers of individuals per m^{-3}. The volume of water filtered by the net was calculated according to Edmondson & Winberg (1971).

The indexes of species diversity was calculated based on the composition and density data, using the Shannon & Weaver (1949) index,

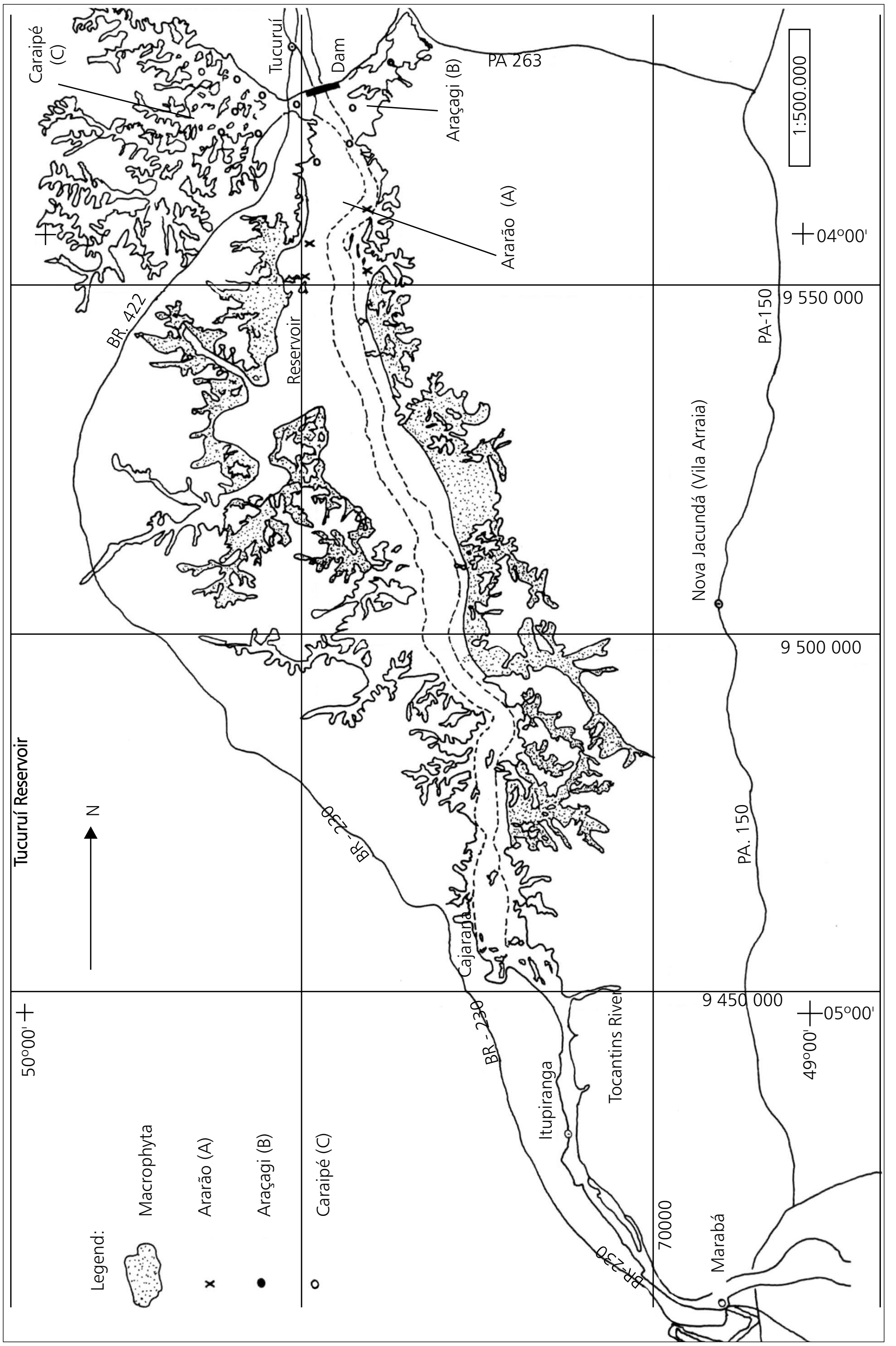

Fig. 1 — Morfometry of the Tucuruí Reservoir and the locations of the Caraipé, Araçagi and Ararão stations.

while the index of similarity was calculated using Sorensen's Index of Similarity (1948).

To evaluate the plankton biomass (in terms of dry weight), samples were collected be vertical dragging using a 68 mm mesh plankton net. The material thus collected was filtered using a MILLIPORE AP20 filter (with 47 mm diameter e 0,45 mm hole pore openings), previously calcined in a muffler at 460°C for 2 hours and weighed to reach Weight 01. After filtering, the filters were left in an oven at 60°C for 24 hours, after which they were weighed to find the total weight of the material, determined as Weight 02, using the difference in weight to estimate the dry weight of the organic material.

Water samples were collected at three depths (surface, limit of the euphotic zone and aphotic zone) to determine the pH (using a MICRONAL B-382 potentiometer), conductivity (using a DIGIMED CD-20 conductivimeter), dissolved oxygen (using the Winkler method described in Golterman *et al.*, 1978) and chlorophyll *a* + phaeopigments (Golterman *et al.*, 1978). Measurements were also made of the local depth, water temperature profiles (using a Toho Dentan thermistor), water transparency (by Secchi disc) and the extent of the euphotic zone (defined as the point of disappearance of the Secchi disc multiplied by three, according to Esteves, 1988).

RESULTS

Limnological characterization of the Tucuruí Reservoir

The findings of some of the limnological variables summarized in Table 1 indicate that the pH and conductivity values of the sampled stations did not differ significantly. The pH values found for Caraipé lay between 6.59 and 7.06, those of Araçagi ranged from 6.94 to 7.22 and those of Ararão were between 7.06 to 7.14, while conductivity values were from 47.6 to 52.7 $\mu S.cm^{-1}$ at Caraipé, 47.6 to 50.2 $\mu S.cm^{-1}$ at Araçagi and 52.1 to 53.0 $\mu S.cm^{-1}$ at Ararão. However, a vertical chemical gradient was found at all the stations, with lower pH values and higher conductivity values at depths corresponding to the aphotic zone. The dissolved oxygen concentrations varied from 3.90 to 4.99 $\mu g.L^{-1}$ at Caraipé, from 4.82 to 5.69 $\mu g.L^{-1}$ at Araçagi and from 4.90 to 5.0 $\mu g.L^{-1}$ at Ararão, and layers of total anoxia were found at most of the stations. With regard to water transparency, lower values were found at the Caraipé stations due to the high contribution of organic material, leading to a reduction of the euphotic zone at these sites. The temperature profiles showed a difference of 4°C between the surface and the bottom at the Caraipé stations and of 2.4°C and 2.6°C, respectively, at the Araçagi and Ararão stations.

The variation in chlorophyll a concentrations, considering the mean values between the depths sampled (Fig. 2), showed a greater phytoplanktonic biomass at the Caraipé stations (between 3.73 and 9.41 $\mu g.L^{-1}$), with values ranging from 3.22 to 4.28 $\mu g.l^{-1}$ at the Araçagi and from 3.11 to 4.02 $\mu g.L^{-1}$ at the Ararão stations. The planktonic biomass, estimated in dry weight (Fig. 3) was also higher at the Caraipé stations, with values varying from 5.85 to 35.93 $mg.m^{-3}$. The variation at the Araçagi stations ranged from 5.40 to 17.02 $mg.m^{-3}$, while at the Ararão stations it was between 9.34 and 25.97 $mg.m^{-3}$.

Composition, abundance and dominance of the zooplankton community

Table 2 shows the composition and density (ind/m^3) of zooplankton species found at the 16 stations analyzed. Thirty-four species of Rotifera, 15 species of Cladocera and 8 species of Copepoda were found, besides Turbellaria, Ostracoda and *Chaoborus*.

The dominance of the Copepoda group over the Rotifera was observed at the all stations. Table 3 summarizes the relative abundance of the most common zooplankton groups in the samples taken from the three sites, Araçagi, Ararão and Caraipé. There was an evident dominance of copepods at all the sites, particularly those of the Ararão stations, where this group's dominance was 70.7%. However, the highest density was found at the Caraipé stations.

The Caraipé stations were dominated by the Cladocera species *Ceriodaphnia cornuta* (87%) in the following three varieties: *cornuta, intermedia* and *righaudi* and by *Diaphanosoma birgei* (15.9%). The stations of Ararão were also dominated by *Ceriodaphnia cornuta* (67%), but only two of its forms: *cornuta* and *intermedia.*

TABLE 1

Depth, secchi, temperature, pH, conductivity and dissolved oxygen found at the three locations (Caraipé, Araçagi and Ararão) in the Tucuruí Reservoir.

Station – Depth. (m)	Secchi (m) e Depth. (m)	Temp (°C)	pH	Cond. (μS.cm^{-1})	DO (mg.L^{-1})
C1 – 0.0 5.0 10.0	3.30 – (24.0)	26.8-30.8	6.52 6.48 6.77	48.5 52.6 48.9	7.22 4.14 0.35
C2 – 0.0 4.0 8.0	3.00 – (18.0)	28.4-31.4	7.12 6.97 6.66	48.6 48.6 49.5	7.05 5.46 0.44
C3 – 0.0 4.0 8.0	3.10 – (27.0)	27.5-30.8	7.05 7.06 6.62	47.7 48.0 48.7	6.61 6.61 0.79
C4 – 0.0 3.5 7.0	2.50 – (23.0)	27.5-31.2	7.16 7.20 6.70	47.9 47.8 47.2	7.31 7.05 0.53
C5 – 0.0 4.0 8.0	3.00 – (28.0)	27.0-29.6	7.14 7.21 6.84	48.0 48.5 48.8	5.73 7.22 2.03
C6 – 0.0 4.0 8.0 15.0	3.10 – (21.0)	28.3-30.8	7.21 7.20 6.88 6.52	49.0 49.2 50.6 62.0	7.84 7.14 2.29 0.00
C7 – 0.0 4.0 8.0 15.0	3.00 – (40.0)	27.9-30.2	7.08 7.10 6.90 6.67	48.7 48.3 49.6 54.5	7.66 7.22 3.44 0.35
A1 – 0.0 6.0 12.0	4.70 – (45.0)	28.4-29.5	7.26 7.14 6.78	51.6 51.2 53.5	7.22 6.99 0.79
A2 – 0.0 7.0 15.0	5.75 – (21.0)	28.5-29.8	7.31 7.26 6.87	52.9 53.0 53.0	7.22 7.05 1.14
A3 – 0.0 7.0 15.0	5.70 – (37.0)	28.3-30.2	7.26 7.26 6.95	52.5 53.3 53.2	6.87 6.61 1.23
A4 – 0.0 6.0 12.0	4.30 – (38.0)	28.2-30.8	7.20 7.20 6.97	52.6 52.5 52.5	6.78 6.16 2.20
B1 – 0.0 6.0 12.0	4.30 – (15.0)	28.6-29.5	7.43 7.40 6.83	48.8 49.0 49.7	7.84 7.49 1.76
B2 – 0.0 6.0 12.0 20.0	4.10 – 60.0)	28.2-29.5	7.36 7.27 6.96 6.86	49.4 49.5 49.6 52.5	7.57 7.22 3.26 2.20
B3 – 0.0 7.0 15.0 20.0	5.40 – (76.0)	28.3-29.2	7.25 7.25 7.10 6.85	49.8 49.7 50.3 50.5	7.22 6.87 4.49 2.03
B4 – 0.0 6.0 12.0	4.20 – (17.0)	28.5-30.8	7.09 6.95 6.80	47.0 48.2 47.6	6.08 4.40 2.29
B5 – 0.0 5.0 11.0 15.0	4.00 – (29.0)	28.2-30.6	7.24 7.13 6.97 6.84	48.0 49.0 48.6 48.0	7.22 5.72 3.70 2.64

TABLE 2

Composition, abundance (Ind.m^{-3}) and distribution of the zooplankton in the Tucuruí Reservoir.

Species	C1	C2	C3	C4	C5	C6	C7	A1	A2	A3	A4	B1	B2	B3	B4	B5
CLADOCERA																
Alona retangula pulchra	–	–	–	–	–	–	–	2	1	1	1	–	–	–	–	–
Bosminopsis deiters	169	110	142	113	235	122	70	421	8	14	2	765	205	143	232	441
Bosmina hagman	51	91	60	80	190	85	20	32	16	7	6	296	29	23	192	240
C. cornuta rigaud	90	85	124	97	120	106	201	5	1	5	5	21	4	8	70	192
C. cornuta intermedia	54	173	461	250	369	130	16	29	2	4	14	29	4	4	50	74
C. cornuta cornuta	750	100	58	118	449	263	44	515	100	75	204	115	28	23	129	182
Ceriodaphnia reticulata	–	–	6	–	–	8	–	–	–	–	–	–	–	–	–	–
Diaphanosoma birgei	64	396	157	240	490	481	83	399	120	94	71	346	53	98	53	79
Diaphanosoma spinulosum	–	65	16	17	21	17	1	–	4	13	15	23	3	12	3	–
Daphnia gessneri	90	28	1	–	7	8	–	2	–	–	98	–	–	–	–	–
Grimaldina brazza	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–
Ilyocryptus spinifer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Latonopsis fasciculata	–	–	–	–	–	–	–	–	3	5	22	–	–	–	–	–
Moina minuta	25	11	63	50	59	7	20	8	7	14	1	403	13	38	140	155
Simoceplallus serrulatus	14	3	–	–	–	–	–	–	1	8	–	–	–	–	–	
COPEPODA																
Notodiaptomus henseni	492	448	599	345	52	116	7	368	120	115	303	140	19	18	15	14
N. maracaibensis	474	283	453	204	61	94	27	423	207	130	433	176	47	41	53	28
Argyrodiaptomus azevedoi	56	41	53	4	–	6	34	1	2	1	4	–	7	2	2	2
Thermocyclops minutus	514	771	939	360	144	171	477	145	810	563	104	212	401	606	205	115
T. decipiens	4	–	–	5	5	–	–	–	6	10	9	2	6	3	–	1
Mesocyclops meridianus	–	–	–	1	–	–	–	–	–	–	–	2	–	–	–	–
M. longisetus	2	–	–	–	2	2	–	–	2	–	1	4	2	–	–	–
Metacyclops sp.	–	–	–	–	–	—	–	–	–	–	–	10	–	–	–	–
Nauplii of Calanoida	467	956	644	917	536	102	314	103	978	373	632	597	348	299	607	509
Nauplii of Cyclopoida	303	397	365	297	428	619	189	367	288	123	924	355	563	214	294	275
Copepodites of Calanoida	347	478	239	422	237	180	88	775	669	477	622	220	202	163	308	253
Copepodites of Cyclopoida	574	127	126	773	129	123	283	541	502	477	538	283	216	362	661	473
ROTÍFERA																
Ascomorpha ecaudis	–	–	–	–	–	–	–	–	–	4	–	268	19	44	–	35
Ascomorpha ovalis	16	28	91	–	–	–	14	–	25	53	41	–	33	–	57	–
Ascomorpha saltans	25	28	10	10	–	–	4	8	50	12	7	26	5	29	57	11
Asplanchna sp.	–	42	61	–	–	–	–	–	–	–	–	–	–	–	38	–
Bdelloidea sp.	–	–	–	–	–	–	–	46	–	–	–	–	–	–	–	–
Brachionus dolabratus	8	99	71	38	128	–	32	–	–	–	–	–	–	–	160	70
B. falcatus	16	–	20	10	14	85	–	–	–	–	–	–	–	–	9	35

TABLE 2 (*continued*)

Species	**C1**	**C2**	**C3**	**C4**	**C5**	**C6**	**C7**	**A1**	**A2**	**A3**	**A4**	**B1**	**B2**	**B3**	**B4**	**B5**
B. patulus	8	14	51	–	235	66	36	–	–	–	–	–	–	–	–	–
B. mirus angustu	–	14	–	–	–	19	4	–	–	–	–	38	–	37	207	224
B. zahniseri	–	28	30	10	36	28	7	–	–	–	–	281	104	124	415	271
Collotheca sp.	58	198	304	76	156	255	128	39	6	114	–	38	5	11	170	141
Conochilus coenobasi	–	28	61	10	29	28	7	69	38	29	61	13	–	–	19	23
C. unicorni	–	–	20	–	–	28	–	69	38	8	34	–	–	–	85	35
Filinia longiseta	–	42	30	–	29	–	11	–	–	–	–	–	–	4	19	23
F. terminalis	8	14	91	10	78	57	29	8	–	–	–	–	–	–	–	–
Horaella sp.	–	–	–	–	–	–	–	31	–	–	–	38	24	37	57	–
Hexarthra int. brasiliensis	16	28	51	19	14	38	–	46	25	41	62	383	85	44	217	247
Keratella americana	8	14	51	28	114	113	50	8	44	61	62	217	19	26	566	354
K. lenzi	16	28	30	–	43	47	50	23	–	12	21	–	28	26	57	23
K. paludosa	–	14	–	–	7	9	–	8	–	20	14	–	–	–	–	–
Lecane arcuata	–	–	–	–	–	–	–	–	–	4	7	–	–	4	–	–
L. chankensis	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–
L. hamata	–	–	30	28	57	19	28	8	–	4	–	13	–	–	–	–
L. proiecta	66	297	637	86	856	405	264	8	–	–	–	–	–	–	–	–
Machrochaetus serricus	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–
Polyathra vulgaris	–	–	–	–	–	–	–	100	19	253	82	89	156	95	85	130
Ptygura sp.	–	42	–	10	–	–	7	31	13	65	96	–	–	–	9	23
Sinantherina socialis	8	28	–	–	14	–	7	54	–	16	21	–	–	–	28	–
Synchaeta stylata	25	99	51	–	14	–	11	–	13	4	75	–	14	–	38	23
Testudinella sp.	–	28	40	10	107	47	39	–	–	82	41	153	14	11	–	23
Trichocerca sp.	8	–	20	–	7	–	7	–	13	–	–	–	9	–	–	12
Trichocerca chattoni	25	28	20	19	29	75	28	15	13	25	27	178	38	26	47	106
Trochosphaera aequatorialis	712	240	384	601	14	274	7	–	6	–	–	–	–	–	–	–
Vonoyella globosa	8	14	–	10	21	–	–	–	–	4	–	–	–	–	–	–
OTHER ORGANISMS																
Chaoborus	3	3	2	7	10	3	2	–	–	2	3	–	–	1	1	1
Turbellari	6	11	1	3	–	37	–	–	–	1	5	–	–	1	1	2
Ostracoda	6	25	83	167	17	14	4	–	–	–	3	5	1	–	1	–

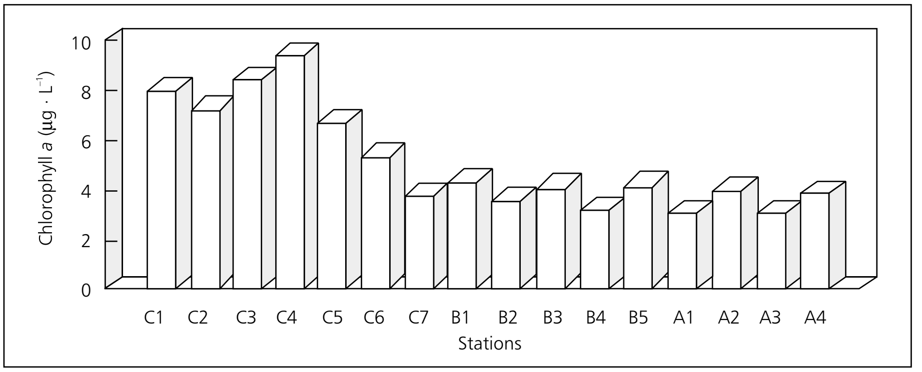

Fig. 2 — Chlorophyll *a* concentration at the Caraipé (C), Araçagi (B) and Ararão (A) stations in the Tucuruí Reservoir.

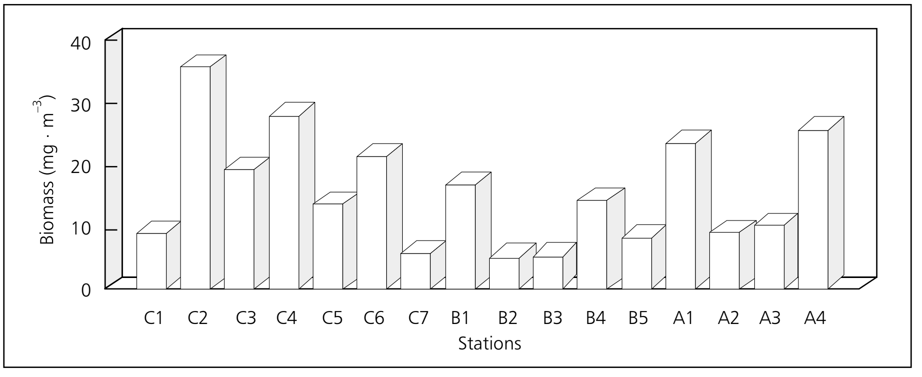

Fig. 3 — Biomass of the zooplankton at the Caraipé (C), Araçagi (B) and Ararão (A) stations in the Tucuruí Reservoir.

TABLE 3

Average values for copepods, cladocerans and rotifers (excluding nauplii) for the stations of each site.

	Araçagi		Ararão		Caraipé	
Groups	**Ind/m³**	**%**	**Ind/m³**	**%**	**Ind/m³**	**%**
Copepoda (adults + copepodits)	2,030	46.1	2,832	70.7	3,121	49.9
Cladocer	984	22.4	589	14.7	1,722	27.5
Rotifer	1,388	31.5	585	14.6	1,417	22.6
Total	4,402		4,006		6,260	

The Araçagi stations were dominated by three species: *Bosminopsis deitersi* (36.3%), *Bosmina hagmani* (15.8%) and *Diaphanosoma birgei* (12.8%).

Fig. 4 shows the distribution of the most abundant species of Cladocera along the reservoir. It can be seen that, among the varieties of *Ceriodaphnia cornuta*, the *cornuta* form dominated at some of the Caraipé stations and at all the Ararão stations, whereas the other two forms, *righaudi* and *intermedia*, were present in significant numbers only at the Caraipé stations.

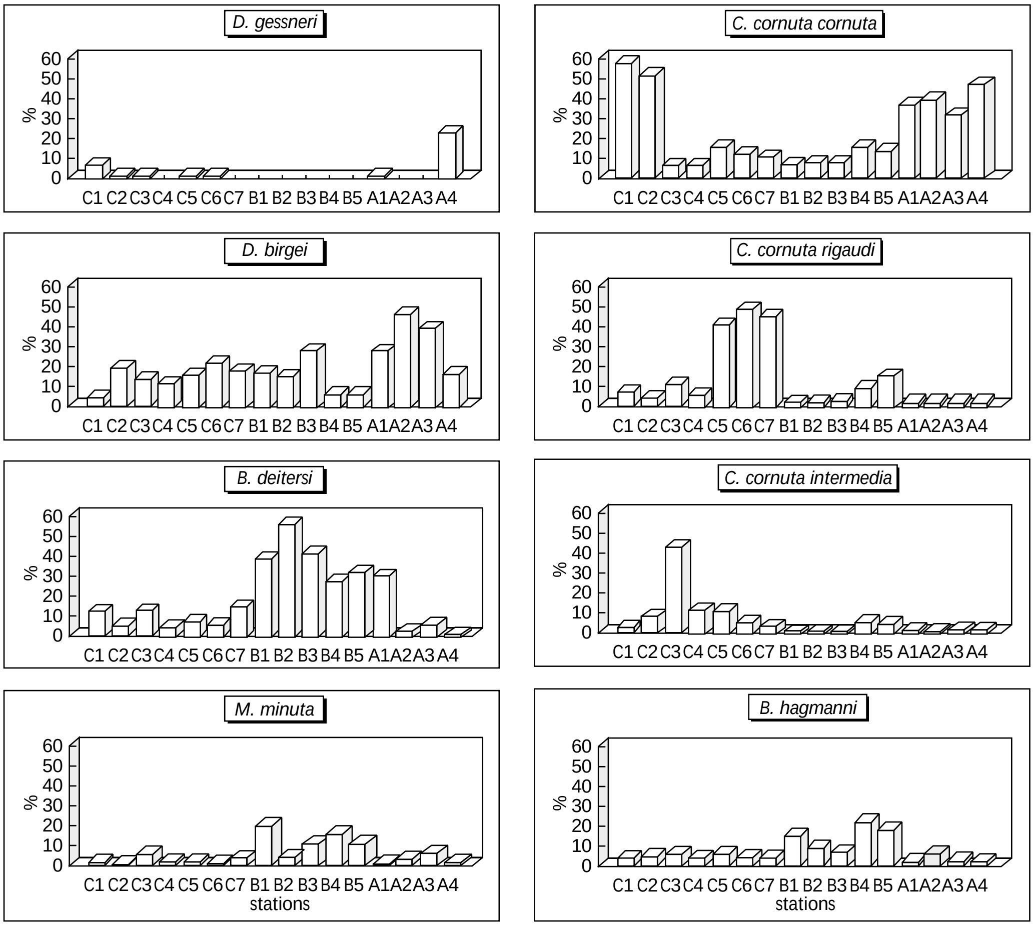

Fig. 4 — Horizontal distribution of the most abundant Cladocera species in the Tucuruí Reservoir (C = Caraipé, B = Araçagi and A = Ararão).

Bosminopsis deitersi was characteristic of the Araçagi stations. Other species such as *Diaphanosoma birgei, Bosmina hagmani* and *Moina minuta* were evenly distributed throughout the reservoir. *Daphnia gessneri* was present at some of the Caraipé stations and at two of the Ararão stations, but in very reduced numbers.

Some of the Rotifera species, such as *Lecane proiecta* and *Trocosphaera aequatoriales*, predominated at the Caraipé stations, while *Polyarthra vulgaris* and *Keratella americana* predominated at the Araçagi and Ararão stations. As can be observed in Fig. 5, *Collotheca* sp. was distributed homogeneously at every station of the three sites, although *Ascomorpha aecaudis* was restricted to the Araçagi stations. At the Ararão stations, besides the dominance of *Keratella americana,* two other species were also found to dominate: *Hexarthra intermedia brasiliensis* and *Brachionus zahniseriu,* the latter typical of the Amazonian region. The density of Rotifera was highest at the Araçagi stations (517 to 2,339 ind.m^{-3}). The other sites showed densities ranging from 769 to 2,004 ind.m^{-3} (Caraipé) and from 308 to 813 ind.m^{-3} (Ararão). Cyclopoida dominated over Calanoida at all the stations of the three sites. This domination was more evident at Araçagi, where Cyclopoida represented 91.8%. Table 4 shows the relative abundance of Cyclopoida and Calanoida at the three sites.

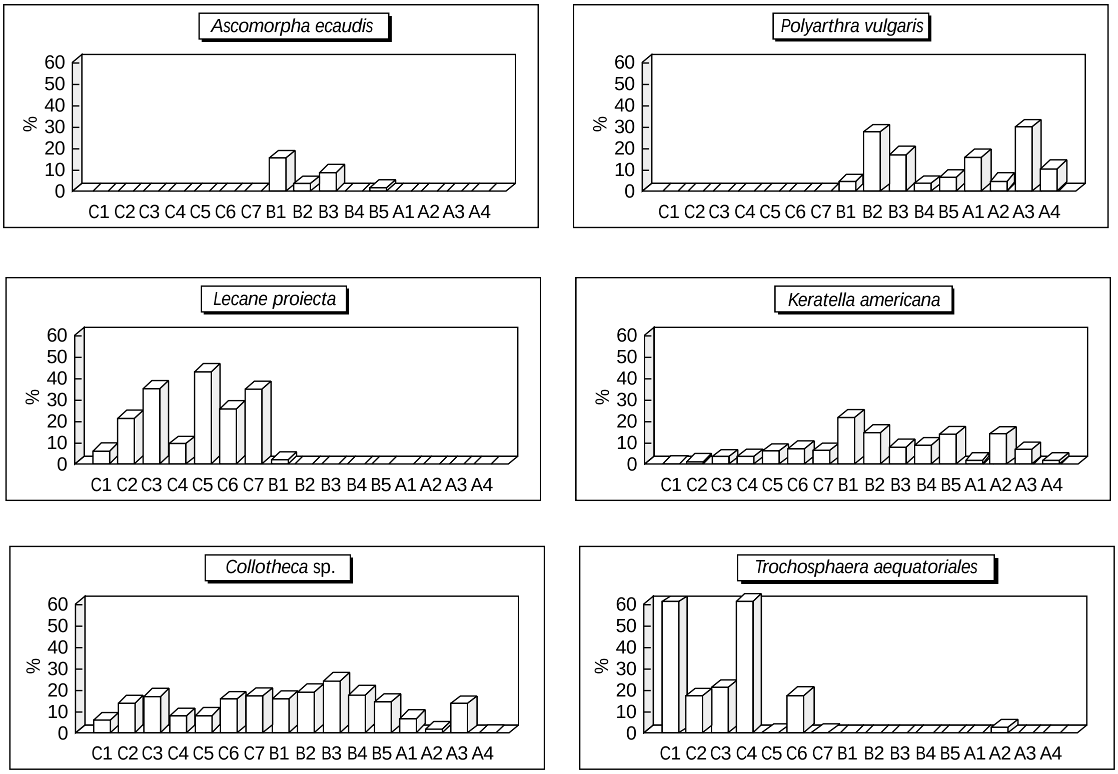

Fig. 5 — Horizontal distribution of the most abundant Rotifera species in the Tucuruí Reservoir (C = Caraipé, B = Araçagi and A = Ararão).

TABLE 4

Relative abundance of Cyclopoida and Calanoida at the Caraipé, Ararão and Araçagi stations (only adult stages were considered).

	Caraipé	Ararão	Araçagi
Calanoida	38.2%	31.1%	1.2%
Cyclopoida	61.8%	68.9%	91.8%

Thermocyclops minutus was the dominant Cyclopoida species. Other species such as *Thermocyclps decipiens*, *Mesocyclops longisetus* and *Metacyclops* sp occurred, albeit in much fewer numbers. With regard to Calanoida, three species were present: *Notodiaptomus maracaibensis, Notodiaptomus henseni* and *Argyrodiaptomus azevedoi*. At the Caraipé stations, the dominant species was *Notodiaptomus henseni,* while at the Ararão and Araçagi stations, *Notodiaptomus maracaibensis* predominated. Fig. 6 shows the distribution of the dominant Calanoida species along the reservoir.

Comparison of the distribution of the developmental stages of Copepoda at the three sites of the reservoir

As regards the distribution of the developmental stages of Calanoida and Cyclopoida at the three sites of the reservoir, it can be observed that Copepods produce a large number at the larval stage (nauplii) but significant mortality occurs before they reach the copepodit stage. The rate of the copepodit to the nauplii stage was four or five times less for Cyclopoida, whereas the rate for Calanoida was double or equal. This index is far more marked in the Cyclopoida, as can be seen in Table 5.

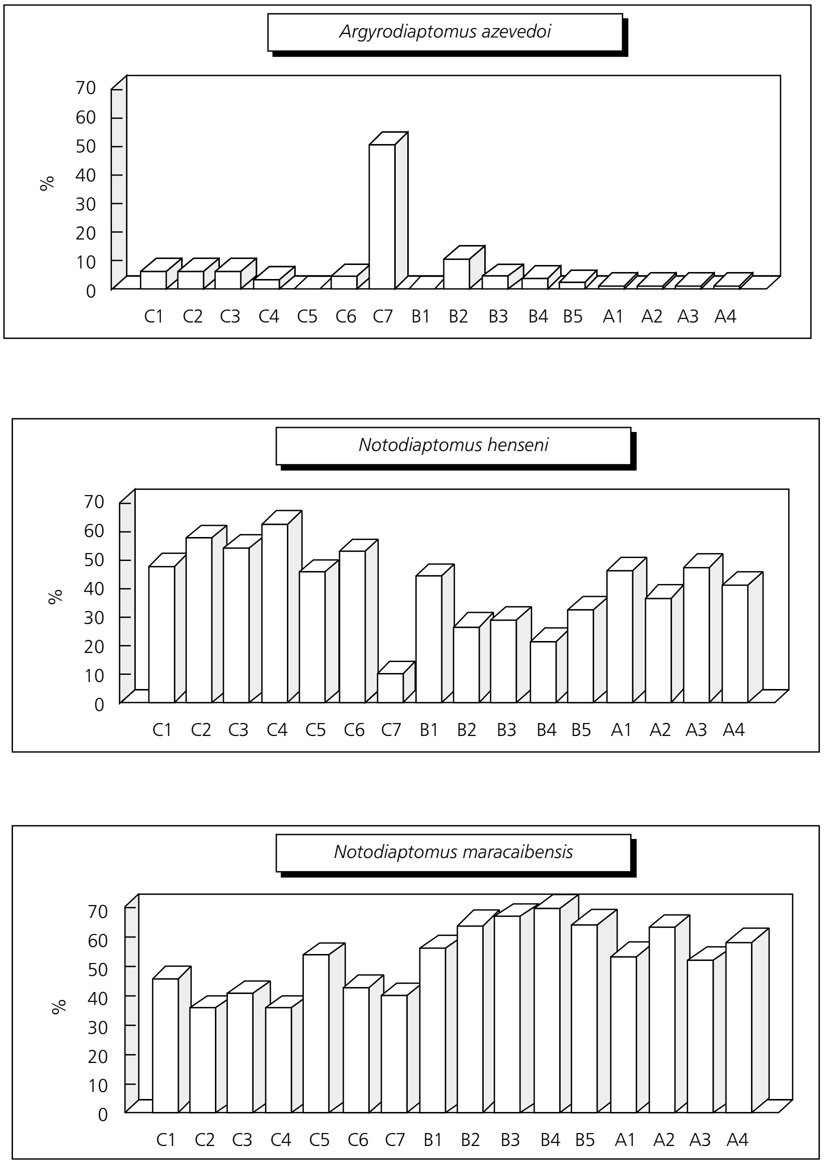

Fig. 6 — Relative abundance and horizontal distribution of Calanoida at the Caraipé (C), Araçagi (B) and Ararão (A) stations in the Tucuruí Reservoir.

If an analysis had been made of the relation between adults, copepodits and nauplii from the three sites, it would have been found that, in the case of Calanoida, the adults are more abundant at the Caraipé stations, there is a greater abundance of copepodits in Ararão, with nauplii predominating in Araçagi. A higher contribution of females with eggs sacs of *Notodiaptomus maracaibensis* was observed in Caraipé (19.7% of the total Calanoida) than in other regions, and females with egg sacs of *Notodiaptomus henseni* and *Argyrodiaptomus azevedoi* abounded more at in the Araçagi stations (20.4% and 61.5%, respectively).

There was a greater abundance of the adult stage of Cyclopoida, represented mainly by *Thermocyclops minutus*, at the Araçagi and Ararão stations, while there were fewer nauplii and copepodits.

TABLE 5

Percentage (%) of adult, copepodit and naupliae phases of Calanoida and Cyclopoida found at the three sites of the Tucuruí Reservoir.

	Calanoida	Cyclopoida
ARARÃO		
adult	27.5	26.5
copepodit	33.2	14.0
nauplii	39.3	59.0
ARAÇAGI		
adult	13.9	31.3
copepodit	28.2	9.8
nauplii	58.0	58.8
CARAIPÉ		
adult	35.9	16.0
copepodit	18.6	17.2
nauplii	45.4	66.8

Females of *Thermocyclops minutus* with egg sacs were found in a higher proportion at the Ararão stations and those with *Thermocyclops decipiens* egg sacs were more plentiful at Caraipé. This evidence indicates that closely related species preferentially use different sites to reproduce, possibly to avoid interspecific competition.

Diversity and similarity of the zooplankton species at the three sites

Table 6 presents the indexes of similarity and diversity of species, calculated for Cladocera and Rotifera. The highest indexes of diversity were found at the Ararão and Araçagi stations, mainly for Rotifera, which presented greater equability at these stations (between 0.81 and 0.91), while less equability was found at the Caraipé stations (between 0.39 and 0.82), demonstrating a higher contribution from few species.

The indexes of similarity varied from 70 to 100 for Cladocera and from 21 to 44 for Rotifera, pointing to a more differentiated composition and distribution of the Rotifera species and a broader and more similar distribution of the Cladocera species in the Tucuruí Reservoir. In the cases of both Cladocera and Rotifera, the closest similarity was observed among the stations corresponding to the areas delimited as Caraipé (C1 to C7), Araçagi (B1 to B5) and Ararão (A1 to A4), while analyses showed less similarity occurring between the Caraipé and Araçagi stations and between the Araçagi and the Ararão stations.

TABLE 6

Maximum and minimum values found for the index of similarity (S), equitability (E) and species diversity (H' = bits/ind) at the Caraipé, Araçagi and Ararão stations.

Stations	Rotifera		Cladocera	
	Similarity: 21-44		Similarity: 90-100	
	Diversity	Equitability	Diversity	Equitability
Caraipé	1.75-3.75	0.39-0.83	1.99-2.50	0.65-0.77
Ararão	3.48-3.65	0.79-0.91	1.89-2.45	0.55-0.71
Araçagi	3.12-3.52	0.81-0.86	1.85-2.64	0.62-0.92

DISCUSSION

According to Rocha *et al.* (1999), reservoirs are considered favorable environments for the development of zooplankton communities. The complex structure of reservoirs derives from the trophic state (related to the time of formation and artificial enrichment), the morphometry (related to shape and size) and operational regimen (retention time and outflow), which lead to the formation of different compartments within the same system.

From this standpoint, the physical, chemical and biological differences found at each station and study area characterize the different compartments that exist at the Tucuruí Reservoir, such as the Ararão, Araçagi and Caraipé. Each compartment has physical peculiarities (morphometry and areas previously deforested or not) that influence the water flow, the retention time of materials, the incorporation of nutrients, the production of organic matter, and the establishment of populations.

The water in the Ararão compartment, located in a more open area in the upper portion of the reservoir, stays there less time (greater flow). It is an area devoid of islands where the water circulates more freely, but it contains flooded forest with layers of anoxic water or reduced amounts of oxygen and a greater thermal homogeneity. The lower values of chlorophyll and zooplanktonic biomass indicate the establishment of smaller species with a faster reproductive cycle, such as the rotifers (*Ascomorpha ecaudis* and *Polyarthra* cf *vulgaris*) and small cladocerans (such as *Bosmina hagmanni* and *Moina minuta*). The Araçagi compartment corresponds to the area closest to the dam, with prior deforestation and deeper stations, higher values of oxygen in comparison to the Ararão, and a smaller zooplanktonic biomass, demonstrating the effect of low water retention time in the structuring of its populations. Both compartments, however, despite the smaller zooplanktonic biomass, presented a greater diversity due to the equability among species in comparison to the Caraipé.

The Caraipé compartment is shallower and has extensive areas not deforested before being flooded. The compartment contains several islands and its edges are markedly dendritical. These factors lead to longer retention times and, therefore, to a greater material cycling among the system's biotic components, which contributes to increased organic production. The sampled stations in this area presented physical and chemical stratification, with low oxygen levels and anoxia at several stations. It was also noted that the larger species, such as *Argyrodiaptomus azevedoi* (Calanoida), *Mesocylops longisetus* (Cyclopoida), *Trocosphaera aequatorialis* (Rotifera) and *Daphnia gessneri* (Cladocera) were only present or were more abundant at the Caraipé stations, a fact that may be related to the greater availability of food as well as to the presence of larger refuge areas. In the case of the planktonic populations, some papers have demonstrated the influence of the presence of subsystems lateral to the principal axis of reservoirs (Kimmel *et al.*, 1990; Betsil & Van Den Avyle, 1994), a situation similar to the Caraipé region.

The compartmentalization of the Tucuruí Reservoir, as it concerns the system's biotic components, is related to the reservoir's morphometry and the presence or absence of prior deforestation.

These factors contribute toward a reduction of the water flow and to the increase of areas that favour colonization by autotrophic organisms, such as periphytic and macrophytic aquatic algae, which forms differentiated niches for the establishment of other communities, contributing to species diversity and biomass production. The distribution and abundance of organisms and their relation to the presence of macrophytes have been mentioned by several authors (Gehrs, 1974; Rocha, 1978). Gehrs (1974), for instance, mentions the relation between the distribution of *Diaptomus clavipes* and the presence of the macrophyte *Potamogeton foliosus* in a small reservoir in the United States and under experimental conditions, while Rocha (1978) discusses the macrophytic regions in the Represa do Lobo (State of São Paulo), an area of greater reproduction for Copepoda Calanoida *Argyrodiaptomus furcatus*.

Within this diversity of the system's habitats, the establishment of different species is a consequence of the environmental factors that can, directly or indirectly, influence the reproduction and survival of organisms, as postulated by the Theory of the Environment (Andrewarthra & Birch, 1984). Thus, reproductive strategies and adaptations of species to abiotic (such as pH, temperature, dissolved oxygen, water flow, etc.) and biotic (predation and competition for food resources) environmental factors must be taken into account in distribution analyses (occurrence and density) of a system's species. Studies developed by several authors have shown the magnitude of environmental effects, principally temperature, food and predation, on the life cycle of species. This can be observed by the differences in average fecundity, development time of the different life cycles, longevity and size of organisms (Espíndola & Niselli, 1996; Rietzler, 1991; Rietzler & Espíndola, 1998).

One must also consider that areas with a greater horizontal water circulation, such as Ararão and Araçagi, can have a stronger effect on the structure of the zooplanktonic community, since the constant input of water leads to changes in the environmental conditions, as explained by Threlkeld (1983, 1986). Other factors, such as wind, whose influence is more effective in more open areas, may contribute toward the spatial heterogeneity of populations.

The findings of this study allow one to conclude that, despite the apparent homogeneity of the planktonic community, the organisms have a differentiated spatial distribution with a greater or lesser number of species, biomass or density, depending on environmental conditions, as also discussed by Riley (1976), Urabe & Murano (1986), Betsil & Van Den Avyle (1994), among others. Therefore, studies involving biological communities should comprehend the largest possible number of samplings in order to better characterize the structure of communities, as well as the other metabolic processes deriving from the workings of an ecosystem. Otherwise, according to Lind *et al.* (1993), samples taken from a single sampling station may be inadequate, to characterize spatially and temporarily heterogeneous and dynamic systems.

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REFERENCES

ANDREWARTHRA, M. C. & BIRCH, L. C., 1984, *The ecological web: more on the distribution and abundance of animals*. The University of Chicago Press, Chicago.

ARMENGOL, J. & SAAB, F., 1990, Annual and longitudinal changes in the environmental conditions in three consecutive reservoirs of Guadiana river (W.Spain). *Arch. Hydrobiol. Beih., 33*: 679-687.

BETSIL, R. K. & VAN DEN AVYLE, M. J., 1994, Spatial heterogeneity of reservoir zooplankton: a matter of timing? *Hydrobiologia, 277*: 63-70.

BURGIS, M. J., 1969, A preliminary study of the ecology of zooplankton in Lake George, Uganda. *Verh. Internat. Verein. Limnology, 17*: 297-302.

CRYER, M. & TOWNSEND, C. R., 1988, Spatial distribution of zooplankton in a shallow eutrophic lake, with a discussion of its relation to fish predation. *Journal of Plankton Research, 10*(3): 487-501.

EDMONDSON, W. T. & WINBERG, G. G., 1971, *A manual of methods for the assessmemnt of secondary productivity in freshwater*. Blackwell Scientific Publications, Oxford, Handbook 17, IBP.

EDMONDSON, W. T., 1959, *Freshwater Biology*. John Wiley & Sons Inc., New York, 1248p.

ESPÍNDOLA, E. L. G. & NISELLI, R., 1996, Análise da dinâmica populacional de Notodiaptomus conifer, Sars, 1901 (Copepoda Calanoida): uma abordagem experimental. *Acta Limnológica Brasiliensia, 8*: 1-12.

ESTEVES, F. A., 1988, *Fundamentos de Limnologia*. Editora Interciência/FINEP, Rio de Janeiro, 575p.

GEHRS, C. W., 1974, Horizontal distribution and abundance of Diaptomus clavipes Schacht in relation to Potamogeton foliosus in a pond and under experimental conditions. *Limnology and Oceanography, 19*(1): 100-104.

GOLTERMAN, H. L., CLYMO, R. S. & ONHSTAD, M. A. M., 1978, *Methods for physical and chemical analysis of freshwater*. 2th ed. Blackwell Scientific Publication, Oxford, 213p.

HART, R. C., 1978, Horizontal distribution of the Copepod *Pseudodiaptomus hessei* in a subtropical Lake Sibaya. *Freshwater Biology, 8*(5): 415-422.

HAYWARD, R. S. & VAN DEN AVYLE, M. J., 1986, The nature of zooplankton spatial heterogeneity in a nonriverine impoundment. *Hydrobiologia, 131*: 261-271.

HUTCHINSON, G. E., 1967, *A treatise on limnology (Introduction to lake biology and the limnoloplankton)*. John Wiley & Sons, Inc., New York, 2 vol., 1115p.

INFANTE, A. G., 1995, Vertical and horizontal distribution of the zooplankton in lake Valencia. *Acta Limnologica Brasiliensia*, *6*: 97-105.

JONES, R. I., FULCHER, A. S., JAYAKODY, J., LAYBOURN-PARRY, J., SHINE, A. J., WALTON, M. C. & YOUNG, J. M., 1995, The horizontal distribution of plankton in a deep, oligotrophic lake – Loch Nees, Scotland. *Freshwater Biology*, *33*: 161-170.

KIMMEL, B. L., LIND, O. T. & PAULSON, L. J., 1990, *In*: K. W. Thornton, B. L. Kimmel & E. F. Payne (eds.), *Reservoir limnology: ecological perspectives*. A Wiley-Intersciewnce Publication. John Wiley & Sons, Inc., 246p.

KOSTE, W., 1978a, *Rotatorie die Radertiere Mitteuropas*. I. Texband Gebruder Borntraeger, Stuttgart, 673p.

KOSTE, W., 1978b, *Rotatoria. Die radertiere mitteuropas II*. Textband. Gebruder Borntrauger, Berlim, Stuttgart, 237p.

LIND, O. T., TERREL, T. T. & KIMMEL, B. L., 1993, *In*: M. Straškraba, J. G. Tundisi & A. Duncan (eds.), *Comparative reservoir limnology and water quality management*. Kluwer Academic Publishers. Dordrecht. The Netherlands, pp. 57-67.

MATSUMURA-TUNDISI, T., 1984, Occurence of species of the genus *Daphnia* in Brazil. *Hydrobiologi*a, *112*: 161-165.

MATSUMURA-TUNDISI, T., 1986, Latitudinal distribution of Calanoida Copepods in freshwaters aquatic systems of Brazil. *Rev. Brasil. Biol*., *46*(3): 527-553.

MONTÚ, M. & GOEDEN, I. M., 1986, Atlas dos Cladocera e Copepoda (Crustacea) do estuário da Lagoa dos Patos (Rio Grande, Brasil). *Nerítica*, *1*(2): 1-34.

PENNAK, G. E., 1953, *Freshwater invertebrates of the United States*. The Ronald Press Company, New York, 769p.

REID, J. W., 1985, Calanoid copepods (Diaptomidae) from Costal lakes, State of Rio de Janeiro, Brazil. *Proc. Biol. Soc. Was*., *98*(3): 574-590.

RIETZLER, A. C. & ESPÍNDOLA, E. L. G., 1998, *Microcystis* as a food source for copepods in a subtropical eutrophic reservoir. *Verh. Internat. Verein. Limnol*., *26*: 2001-2005.

RIETZLER, A. C., 1991, *Estudo da dinâmica de populações de Copepoda Calanoida na Represa do Lobo ("Broa")*. Dissertação de Mestrado, EESC/USP, São Carlos, 196p.

RILEY, G. A., 1976, A model of plankton patchiness. *Limnology and Oceanography*, *21*(6): 873-880.

ROCHA, O. & MATSUMURA-TUNDISI, T., 1976, *Atlas do zooplâncton da Represa do Lobo (Broa)*. UFSCar, São Carlos, Série Atlas, 1 vol., 68p.

ROCHA, O., 1978, *Flutuação sazonal e distribuição da população de Diaptomus furcatus, Sars (Copepoda Calanoida) na Represa do Lobo ("Broa"), São Carlos, SP*. Dissertação de Mestrado, USP, São Carlos, 147p.

ROCHA, O., MATSUMURA-TUNDISI, T., ESPÍNDOLA, E. L. G., ROCHE, K. F. & RIETZLER, A. C., 1999, Ecological theory applied reservoir zooplankton. *In:* J. G. Tundisi & M. Straškraba (eds.), *Theoretical reservoir ecology and its applications*. São Carlos, São Paulo, 592p.

SHANNON, C. E. & WEAVER, W., 1949, *The mathematical theory of communication*. Urbana, Univer: Illinois Press, 125p.

SMIRNOV, N. N. & TIMMS, B. V., 1983, A revision of the Australian Cladocera (Crustacea). *Record of the Australian Museum*, Suppl 1, 132p.

SMIRNOV, N. N., 1974, *Fauna of the USSR – Crustacea (Chydoridae)*. Jerusalém: Peter Publishing House Ltd, 644p.

SORENSEN, T., 1948, A method of stablishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of vegetation on Danish commons. *Biol. Skr*, *5*(4): 1-34.

SOTO, D., VILA, I. & VILLALOBOS, B., 1984, Temporal and spatial distribution of Rotifera in a Chilean reservoir: a possible effect of impoundment hydrodynamics. *Hydrobiologia*, *114*: 67-74.

STAVN, R. H., 1971, The horizontal-vertical distribution hypothesis: Langmuir circulations and *Daphnia* distribution. *Limnology and Oceanography*., *16*(2): 453-466.

THRELKELD, S. T., 1983, Spatial and temporal variation in the summer zooplankton community of a riverine reservoir. *Hydrobiologia*, *107*: 249-254.

THRELKELD, S. T., 1986, Life table responses and population dynamics of four cladoceran zooplankton during a reservoir flood. *Journal of Plankton Research*, *8*(4): 639-647.

TUNDISI, J. G., 1981, Typology of reservoirs in Souther Brazil. *Verh. Internat. Verein. Limnology*, *21*: 1031-1039.

TUNDISI, J. G., 1990, Distribuição espacial, seqüência temporal e ciclo sazonal do fitoplâncton em represas: fatores limitantes e controladores. *Rev. Brasil. Biol*., *50*(4): 937-955.

URABE, J. & MURANO, M., 1986, Seasonal and horizontal variations in the zooplankton community of Ogochi Reservoir, Tokyo. *Bolm of Plankton Society of Japan*, *33*(2): 101-112.

WATSON, N. H. F. & CARPENTER, G. F., 1974, Seasonal abundance of crustacean zooplankton and net plankton biomass of lakes Heron, Erie and Ontario. *J. Fish. Res. Board of Canada*, *31*(3): 309-317.