Zooplankton as an indicator of trophic conditions in two large reservoirs in Brazil

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Abstract

The physical and chemical variables of the water, and the composition and structure of the zooplankton communities, in Três Marias and Furnas Reservoirs in Minas Gerais, Brazil, were compared to characterize these environments in relation to their trophic state. Higher values of electrical conductivity and chlorophyll-*a,* total solids, suspended organic matter and total nitrogen concentrations were recorded in Três Marias Reservoir. Higher water transparency and nitrite and nitrate concentrations were observed in Furnas ($P < 0.000$). Higher zooplankton densities were always obtained in Três Marias Reservoir and, during the rainy period ($P < 0.000$), with mean values in the dry and rainy periods of 23 721 and 90 872 org m^{-3}, respectively, in Três Marias Reservoir and 9022 and 40 434 org m^{-3}, respectively, in Furnas Reservoir. Copepoda was the dominant group in both reservoirs, mainly the younger stages (nauplii and copepodids). Based on the absolute and relative values, the contribution of rotifers was higher in Três Marias Reservoir than in Furnas Reservoir. Although the Trophic State Index, based on water transparency and chlorophyll-*a* and total phosphorus concentrations, indicated an oligotrophic state for both reservoirs, the higher densities of the zooplankton community in Três Marias Reservoir, as well as the predominance of cyclopoids and smaller-sized species such as bosminids, characterized this environment as mesotrophic. Larger-sized species such as calanoids, daphniids and sidids in Furnas Reservoir characterized the better water quality of this reservoir.

Key words

trophic state, tropical reservoirs, water quality indicator, zooplankton.

INTRODUCTION

Complex interactions can occur among organisms (species, populations and communities) in reservoirs in response to their physical and chemical characteristics. These interactions are dynamic, resulting from constant responses to climate forces and effects produced by management of lake water levels.

Eutrophication is a growing problem in Brazilian reservoirs, attributable to urbanization and industrialization (point sources), and the extensive use of their basins for farming and cattle ranching (diffuse sources), which has compromised the quality of their water. Over the long term, eutrophication will lead to loss of biodiversity, thereby decreasing both the utility of a reservoir and its fish stocks (Straškraba & Tundisi 2000). Thus, studies on the physical, chemical and biological variables of reservoir water are fundamental to evaluating the impacts of these activities and to help formulate prevention and mitigation decisions.

The structure and abundance of the zooplankton community in a reservoir and its spatial distribution are influenced by abiotic factors and interactions among species. Rotifers and cladocerans generally are relatively more abundant in tropical aquatic ecosystems (Matsumura-Tundisi 1999). Changes in their physical and chemical conditions, however, may affect the phytoplankton composition, thereby also changing the zooplankton structure (Kozlowsky-Suzuki & Bozelli 2002; Jeppesen *et al.* 2005).

Although zooplankton do not depend directly on nutrients to survive, and are affected by the quantity and quality of algae, bacteria and detritus in a reservoir, its trophic state may influence the richness, structure, body size and productivity of this community (McCauley & Kalff 1981; Lathrop & Carpenter 1992).

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According to several authors (Gannon & Stemberger 1978; Ferdous & Muktadir 2009), if an aquatic environment does not exhibit clear oligotrophic or eutrophic conditions, zooplankton may be considered an indicator of its intermediate trophic characteristics. Because of the wide distributions of some species, however, these authors suggested the use of relative zooplankton abundance within the community as a more sensitive indicator than only their mere presence or absence. Matsumura-Tundisi *et al.* (2000), for example, studied the cascade system of the middle and lower Tietê River (state of São Paulo), observing changes in the relative abundances in zooplankton communities, wherein rotifers dominated over copepods in a eutrophic reservoir. The inverse occurred in a meso-oligotrophic reservoir.

Fish fauna also can influence the zooplankton structure because planktivorous fish can consume larger-bodied individuals, resulting in the dominance of smaller copepods and cladocerans (Carpenter *et al.* 1985), even though the microcrustacean biomass may not change (Quirós & Boveri 1999).

With the goal of increasing fish production in Três Marias and Furnas reservoirs, the project, 'Technical-Scientific Study to Delimit Aquaculture Areas in the Lakes of Furnas and Três Marias Reservoirs – Minas Gerais, Brazil' (SEAP/SECTES/FUNDEP-UFMG), of which this study is a part, was proposed to select areas with oligotrophic waters within these reservoirs in which to install cage systems for tilapia farming. Abiotic and biotic variables were measured to estimate the support capacity of these areas, with the objective of minimizing water quality impacts. The knowledge generated about the zooplankton will help guide the use of these organisms in the future as a food source for fish, as well as serving as possible bioindicators for monitoring water quality, thereby mitigating the impacts of fish production on aquatic communities.

In this context, the hypothesis examined in this study is that once the species richness is similar, the relative abundance of zooplankton is a more sensitive water quality indicator, allowing the use of this community in monitoring the water quality of Três Marias and Furnas Reservoirs (Minas Gerais State, Brazil).

MATERIAL AND METHODS

Study area

Três Marias (18°12′S and 45°15′W) and Furnas (46°19′W and 20°40′S) are two large reservoirs in the state of Minas Gerais in Brazil. Both were constructed ≈40 years ago, mainly for power generation and also being used for recreation, professional and sport fishing, irrigation and water supply. Três Marias Reservoir is located on the Upper São Francisco River in the central-western part of Minas Gerais. It was completed in 1960, with silting being the main impact compromising its power generation capacity and water quality, followed by the replacement of the vegetation along the shoreline by *Eucalyptus* plantations and large cattle ranches (Sampaio & López 2003). Furnas Reservoir is located in the Grande River basin in southern Minas Gerais, its north arm being represented by the Grande River and its south arm by the Sapucaí River. It was completed in 1962, and the main factors impacting it being monoculture crops and cattle ranching, sewage discharges, solid residues and loading of agricultural chemicals (Nogueira *et al.* 2008). Some morphometric characteristics of the two reservoirs are presented in Table 1.

Two arms with different surrounding land uses were selected in each reservoir (Fig. 1). The Barrão arm (Z_{max} = 21.8 m and containing preserved Cerrado, the Brazilian savanna) and the Extrema arm (Z_{max} = 20.9 m, with *Eucalyptus* monoculture) were selected in Três Marias Reservoir, being located between the Morada Nova de Minas and Três Marias municipalities. The Varjão arm (Z_{max} = 17.5 m, with its headwaters in Paredão Municipal Park, and coffee monoculture in its surroundings) and the Mendonça arm (Z_{max} = 25.5 m, with cattle ranching on native grasslands) were selected in Furnas Reservoir, being located between the Guapé and Capitólio municipalities. These arms were selected to reflect the different land uses around the reservoirs.

Procedures

Water samples were collected every 2 days over a 4-week interval, during two dry periods (July/August 2006 and July/August 2007) and two rainy periods (January/March 2007 and January/March 2008). These periods were

Table 1. Morphometric characteristics of Três Marias and Furnas Reservoirs, Minas Gerais

Characteristics	Três Marias Reservoir	Furnas Reservoir
Flooded area (km^2)	1100	1440
Volume (m^3)	15.27×10^9	17.21×10^9
Average outflow (m^3 s^{-1})	700	800
Retention time (days)	120	160
Maximum depth (m)	75	90
Mean depth (m)	12	13
Installed capacity (MW)	396	1126

(Source: CEMIG 2009; FURNAS 2009).

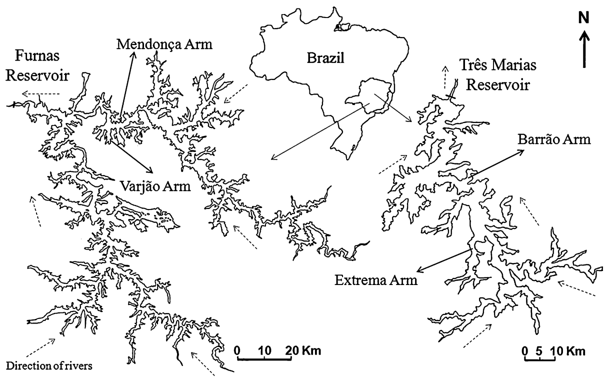

Fig. 1. Três Marias Reservoir (left, 1:10 000) and Furnas Reservoir (right, 1:20 000, Minas Gerais (arrows indicate arms studied; modified from López & Sampaio 2003 and Tundisi *et al.* 1993).

considered most representative of the temperature and precipitation variations. In the project, 'Technical-Scientific Study to Delimit Aquaculture Areas in the Lakes of Furnas and Três Marias Reservoirs – Minas Gerais, Brazil', the cages would be located within the arms to avoid the effects of reservoir management. Thus, samples were collected at the midpoint of each arm, in the limnetic region, far from the main channel of the São Francisco and Grande Rivers.

For all sample collection events, the water transparency was measured with a Secchi disc. Temperature (°C), dissolved oxygen concentration (mg L^{-1}) and electrical conductivity (μS cm^{-1}) profiles were taken with YSI multianalyzers (YSI30 and YSI55). Water samples were collected weekly from the subsurface, in order to determine chlorophyll-*a*, total phosphorus, total nitrogen, nitrite, nitrate, ammonium and total and organic suspended solids concentrations. The samples were analysed according to the procedures of Golterman *et al.* (1978) and Mackereth *et al.* (1978). Total nitrogen concentrations were determined only during the second year, according to the procedures of Wetzel and Likens (1991) and Strickland and Parsons (1972). The Trophic State Index (TSI) was calculated according to Carlson's modified Trophic Status Index (Mercante & Tucci-Moura 1999).

For the qualitative and quantitative zooplankton samples, vertical hauls were made with a plankton net (68 μm mesh size). Because of the presence of drowned original vegetation ('paliteiros') at the sampling sites, the hauls were made in the euphotic zone, as determined by Secchi disc measurements. Organisms were narcotized with gasified water, stained with Rose Bengal and preserved with 4% buffered formalin. Subsamples of 1.0 mL were counted in a Sedgwick–Rafter chamber with an Olympus (CBA) optical microscope. The data are presented as organisms per cubic metre. Rotifera, Cladocera and Copepoda were the three groups considered for the zooplankton community, with the samples counted according to the procedure of Bottrell *et al.* (1976).

The *Brachionus*:*Trichocerca* quotient ($Q_{B/T}$) (Sládeček 1983) and the Calanoida/Cyclopoida ratio (Tundisi *et al.* 1988) were estimated in order to relate the zooplankton structure and trophic state of reservoirs. Zooplankton diversity was evaluated using the Shannon–Wiener index (Magurran 1988). Pearson's correlations between environmental variables and zooplankton densities were calculated (Sampaio 2002).

Differences in environmental variables and zooplankton densities between arms, reservoirs and periods (dry and rainy) were tested with two-way analysis of variance, followed by a Tukey's *post hoc* comparison test. A Mann–Whitney non-parametric test was employed when the homogeneity assumption was not satisfied (Sampaio 2002). A principal components analysis (PCA) was performed to identify the environmental variables characterizing the reservoirs. The variables were log_{10}-transformed to satisfy the assumption of linearity (Valentin 2000). All statistical analyses were performed using Statistica 7.0 (StatSoft, Tulsa, OK, USA).

RESULTS

Environmental variables

Water transparency was higher during the dry period in both reservoirs ($F = 636.4$; $P < 0.000$) (Table 2), with the highest values always recorded in Furnas Reservoir ($F = 247.3$; $P < 0.000$). The water column was unstratified during dry periods, and stratified during rainy periods, with both periods exhibiting significant temperature differences ($F = 203.8$; $P < 0.000$). During the unstratified period, the dissolved oxygen concentrations and electrical conductivity did not exhibit differences through the water column. During the stratification period, hypoxia and lower electrical conductivity were observed in the deeper waters. Significant differences were observed in the dissolved oxygen concentrations between the dry and rainy periods ($F = 12.3$; $P = 0.003$), and for electrical conductivity between the reservoirs ($F = 153.9$; $P < 0.000$), with higher values observed in Três Marias Reservoir (Table 2).

Differences in water transparency, temperature, dissolved oxygen concentration and electrical conductivity were not significant between arms in the same reservoir ($F = 1.594$; $P = 0.2094$). During the second rainy period (January/March 2008), because of the lower precipitation

Table 2. Mean values of main environmental variables measured during dry (2006/07) and rainy (2007/08) periods in Três Marias and Furnas Reservoirs, Minas Gerais (mean precipitation related to sampling days, according to SIMGE/IGAM (2010); O = oligotrophic; M = mesotrophic)

	Três Marias Reservoir				Furnas Reservoir			
Variables	Dry/06	Rainy/07	Dry/07	Rainy/08	Dry/06	Rainy/07	Dry/07	Rainy/08
Secchi disc (m)	3.5 (O)	1.4 (M)	3.96 (O)	1.82 (M)	5.44 (O)	1.98 (M)	5.5 (O)	3.69 (O)
Temperature (°C)	22.52	26.70	23.30	27.04	22.01	26.84	21.91	26.23
Dissolved oxygen (mg L^{-1})	6.67	5.24	6.46	6.05	6.89	5.44	7.06	6.78
Electrical conductivity (μS cm^{-1})	55.20	50.53	53.84	62.70	34.02	31.25	33.95	34.74
Chlorophyll-*a* (μg L^{-1})	0.88 (O)	1.02 (O)	0.71 (O)	1.16 (O)	0.05 (O)	0.57 (O)	0.19 (O)	0.16 (O)
Total suspended solids (mg L^{-1})	2.61	4.00	2.23	3.54	0.55	2.91	1.18	8.50
Organic suspended solids (mg L^{-1})	1.13	1.73	1.52	1.68	0.49	1.24	0.44	2.63
Total phosphorus (μg L^{-1})	0.8 (O)	0.12 (O)	13.62 (O)	1.52 (O)	0.24 (O)	0.38 (O)	13.96 (O)	6.02 (O)
Nitrite (μg L^{-1})	0.19	2.07	1.45	2.37	1.29	4.24	1.64	2.51
Nitrate (μg L^{-1})	1.07	1.15	2.75	1.01	4.88	5.07	5.34	3.82
Ammonium (μg L^{-1})	1.08	30.96	22.74	nd	nd	8.03	7.35	nd
Total nitrogen (μg L^{-1})	–	–	691.20	707.00	–	–	636.60	497.00
Mean precipitation (mm)	5.0	315.0	4.7	253.0	7.3	180.1	5.2	137.0

during this year (Table 2; SIMGE/IGAM, 2010), there was a smaller reduction in the water transparency in Furnas Reservoir and a concentration of ions in Três Marias Reservoir. Measurements taken during 2006 and 2007 during the 'Aquaculture Areas Project' by Pinto-Coelho (2006) indicated pH values oscillating between 8.0 and 8.5 in Três Marias Reservoir, and between 7.3 and 8.3 in Furnas, with no significant differences ($F = 1.746$; $P = 0.2109$).

Higher chlorophyll-*a* concentrations were observed in Três Marias Reservoir ($F = 103.1$; $P < 0.000$) and in the rainy period for both reservoirs ($F = 52.5$; $P < 0.000$) (Table 2). The total and organic suspended solids concentrations were always higher in Três Marias Reservoir ($F = 10.3$; $P < 0.000$ and $F = 16.7$; $P < 0.000$, respectively). The exception was the rainy period in 2008, when the lower precipitation increased the concentrations of these variables in Furnas Reservoir ($F = 8.17$; $P = 0.007$ and $F = 9.00$; $P < 0.000$, respectively). Differences between arms of the same reservoir were not significant ($F = 0.1333$; $P = 0.7163$).

The total phosphorus concentrations were always low (0.0–27.1 μg L^{-1}), with no significant differences between the reservoirs. Higher concentrations ($F = 24.5$; $P < 0.000$) were obtained in the second dry (July/August 2007) and rainy (January/March 2008) periods, probably as an effect of the decreased precipitation. The nitrite and nitrate concentrations were higher in Furnas Reservoir ($F = 9.66$; $P = 0.002$ and $F = 37.6$; $P < 0.000$, respectively), although only nitrite exhibited differences between periods ($F = 26.3$, $P < 0.000$). By contrast, higher concentrations of ammonium ($U = 346.5$; $Z = 2.45$; $P = 0.014$) and total nitrogen ($F = 6.37$; $P = 0.017$) were observed in Três Marias, with no significant differences in periods. Differences between arms of the same reservoir also were not significant ($F = 0.3028$; $P = 0.5846$).

The TSI classified the arms in Três Marias Reservoir as oligo-mesotrophic, based on the water transparency, and oligotrophic, based on the chlorophyll-*a* and total phosphorus concentrations. In Furnas Reservoir, the arms were classified as oligotrophic for all parameters, with exception of the Mendonça arm, which was classified as mesotrophic based on the water transparency in the rainy period in 2007.

The principal components analysis (Fig. 2) distinguished two groups of environmental variables. The former, represented by factor 1 (which explained 44.4% of the variance), was related to seasonality in the reservoirs, where temperature (−0.881), chlorophyll-*a* (−0.757), total (−0.731) and organic (−0.769) suspended solids concentrations were negatively correlated, while water transparency as measured by Secchi disc (0.897) was positively correlated. Factor 2 (which explained 23.4% of the variance) represented the difference between the reservoirs, where the nitrite (−0.844) and nitrate (−0.718) concentrations were negatively correlated and the electrical conductivity (0.771) was

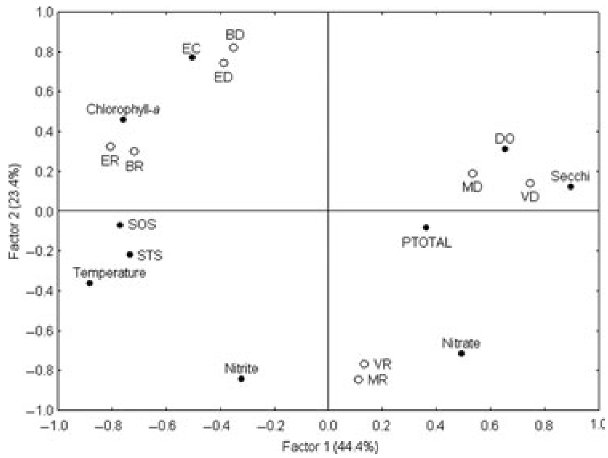

Fig. 2. Principal components analysis for environmental variables of Três Marias and Furnas Reservoirs, Minas Gerais (● = variables: DO = dissolved oxygen concentration, CE, electrical conductivity; STS and SOS, total and organic suspended solids concentrations; PTOTAL, total phosphorus concentration; ○, arms and periods of samplings: B, Barrão Arm; E, Extrema Arm; V, Varjão Arm; M, Mendonça Arm; D and R, dry and rain periods, respectively).

positively correlated. The two factors together explained 67.8% of the variance.

Zooplankton community

Sixty-two species were identified in Três Marias Reservoir (5 Copepoda, 11 Cladocera and 46 Rotifera), and 65 species in Furnas (7 Copepoda, 15 Cladocera and 43 Rotifera). The species list and occurrence (Três Marias Reservoir = TM and Furnas Reservoir = F) are as follows: Copepoda species: *Mesocyclops* sp. (TM), *Microcyclops anceps* (TM, F), *Paracyclops* sp. (F), *Thermocyclops minutus* (TM, F), *T. decipiens* (TM, F), *Notodiaptomus henseni* (F), *N.* cf. *spinuliferus* (TM), and non-identified Harpacticoida. Cladocera species: *Bosmina (S.) freyi* (TM, F), *B. hagmanni* (TM, F), *B. tubicen* (TM, F), *Bosminopsis deitersi* (TM, F), *Ceriodaphnia cornuta* (TM, F), *C. silvestrii* (TM, F), *Chydorus eurynotus* (TM, F), *Daphnia ambigua* (F), *D. laevis* (TM), *Diaphanosoma brevirreme* (F), *D. fluviatile* (F), *D. spinulosum* (TM, F), *Illyocryptus spinifer* (TM, F), *Moina minuta* (TM, F), *Macrothrix* sp. (F), *Simocephalus* sp. (F). Rotifera species: *Ascomorpha saltans* (TM), *A. ecaudis* (F), *Ascomorpha* sp. (TM), *Asplanchna* sp. (TM, F), *Anuraeopsis fissa* (TM), *A. navicula* (TM), *Brachionus angularis* (TM), *B. caliciflorus* (TM, F), *B. dolabratus* (TM, F), *B. falcatus* (TM, F), *B. mirus* (TM, F), *Brachionus* sp. (TM, F), *Conochilus coenobasis* (TM, F), *Conochilus* sp. (F), *Collotheca* sp1 (TM, F) and sp2 (F), *Collurella* sp. (TM), *Cephalodella mucronata* (F), *Euchlanis meneta* (TM, F), *Filinia longiseta* (TM, F), *F. opoliensis* (TM, F), *Gastropus* sp. (TM, F), *Hexarthra intermedia* (TM, F), *Keratella americana* (TM, F), *K. cochlearis* (TM, F), *K. lenzi* (TM, F), *K. tropica* (TM, F), *Keratella* sp. (TM), *Kellicottia bostoniensis* (TM, F), *Lecane bulla* (TM, F), *L. curvicornis* (TM, F), *L. leontina* (TM, F), *L. lunaris* (TM, F), *L. monostyla* (F), *L.* cf *papuana* (F), *L. proiecta* (TM, F), *L. signifera* (TM), *Lecane* sp. (F), *Lepadella* sp. (TM), *Macrochaetus collinsi* (TM), *Macrochaetus* sp. (F), *Platyas* sp. (F), *Monomata* sp. (TM), *Platyonus patulus* (TM), *Ploesoma truncatum* (TM, F), *Polyarthra* sp. (TM, F), *Ptygura* sp. (TM, F), *Sinantherina verrucosa* (TM, F), *Sinantherina* sp. (TM, F), *Testudinella patina* (TM), *Trichocerca pusilla* (TM, F), *T. similis* (TM, F), *Trichocerca* sp1 (TM, F), sp2 (TM, F), sp3 (F) and non-identified Bdelloidea (TM, F).

Higher zooplankton densities were always observed in Três Marias Reservoir (F = 18.6; P < 0.0001), and in the rainy period (F = 132.5; P < 0.000) for both reservoirs (mean values in dry and rainy periods for Três Marias Reservoir = 23 721 org m^{-3} and 90 872 org m^{-3}, respectively; the mean values for Furnas Reservoir were 9022 org m^{-3} and 40 434 org m^{-3}, respectively) (Fig. 3). Between the arms, higher densities were observed in Barrão during the dry period and in Extrema during the rainy period in Três Marias Reservoir, although the differences were not significant (t = 0.0584; P = 0.953). The Mendonça arm in Furnas Reservoir exhibited higher zooplankton densities in both periods (t = 2.062; P = 0.0416).

Copepoda was dominant in Três Marias Reservoir, comprising 50.6% of the zooplankton community (mean density of 31 022 org m^{-3}), 34% (20 171 org m^{-3}) being naupliar stages. The next most numerous group was Rotifera, comprising 40.1%, and finally the Cladocera 9.3% (mean densities 20 569 and 5561 org m^{-3}, respectively) (Fig. 3). *Thermocyclops minutus* was the most abundant zooplankton species, comprising 15.5% (10 505 org m^{-3}, copepodids and adults). Among the Rotifera, Bdelloidea, *Conochilus coenobasis*, *Collotheca* sp., *Hexarthra intermedia*, *Keratella americana*, *K. cochlearis*, *Polyarthra* sp., *Ptygura* sp., and *Sinantherina* sp. comprised 5% (mean density of 2787 org m^{-3}) in at least one sampling period. *Bosmina hagmanni*, *Bosminopis deitersi*, *Ceriodaphnia cornuta* and *Moina minuta* were the most abundant cladoceran species, representing between 2% and 5% (1683 org m^{-3}) of the abundance in at least one sampling period.

Copepods were also dominant in the zooplankton community in Furnas Reservoir, comprising 62.5% (mean density of 16 373 org m^{-3}); 38.4% (10 329 org m^{-3}) of them being nauplii, followed by Rotifera (20.6%) and Cladocera (16.9%) (mean densities: 4617 and 3738 org m^{-3},

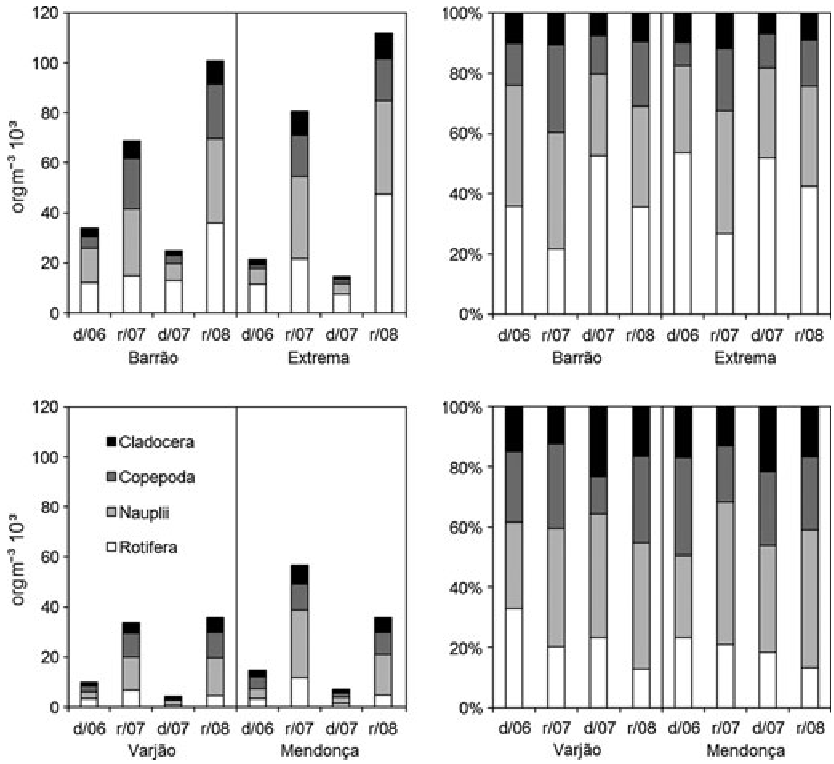

Fig. 3. Mean density (org m^{-3} 10^3) and relative abundance (%) of nauplii and main zooplankton groups in Três Marias Reservoir (Barrão and Extrema arms, above) and Furnas Reservoir (Varjão and Mendonça, below), Minas Gerais (*d*/06 = dry period 2006; *r*/07 = rainy period 2007; *d*/07 = dry period 2007; *r*/08 = rainy period 2008).

respectively). *Thermocyclops minutus* and *Notodiaptomus henseni* were the most abundant species in this reservoir, comprising 16.5% (7598 org m^{-3}, copepodids and adults) and 6.6% (2041 org m^{-3}, copepodids and adults) of the zooplankton, respectively. *Brachionus mirus*, *Conochilus coenobasis*, *Collotheca* spp. and *Lecane proiecta* were the most abundant rotifer species (mean densities: 1130 org m^{-3}), and *Bosmina (S.) freyi*, *B. hagmanni*, *Bosminopsis deitersi*, *Ceriodaphnia cornuta*, *C. silvestrii*, *Daphnia ambigua*, *Diaphanosoma fluviatile*, *D. spinulosum* and *Moina minuta* dominated among cladocerans, comprising between 2.0 and 5.2% (862 org m^{-3}) during the sampling periods.

The *Brachionus*:*Trichocerca* quotient was 1.25 for Três Marias Reservoir, classifying it as mesotrophic ($1 < Q_{B/T} < 2$). It was 0.80 for Furnas Reservoir, classifying it as oligotrophic ($Q_{B/T} < 1$).

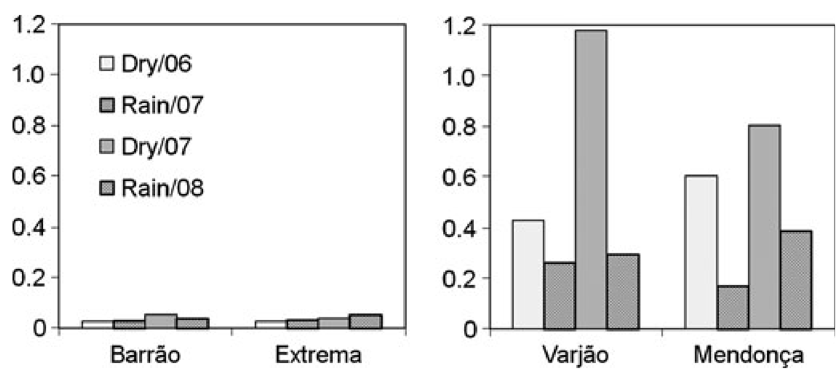

Fig. 4. Calanoida/Cyclopoida ratios in the four sampling periods in Três Marias Reservoir (Barrão and Extrema arms, left) and Furnas Reservoir (Varjão and Mendonça, right).

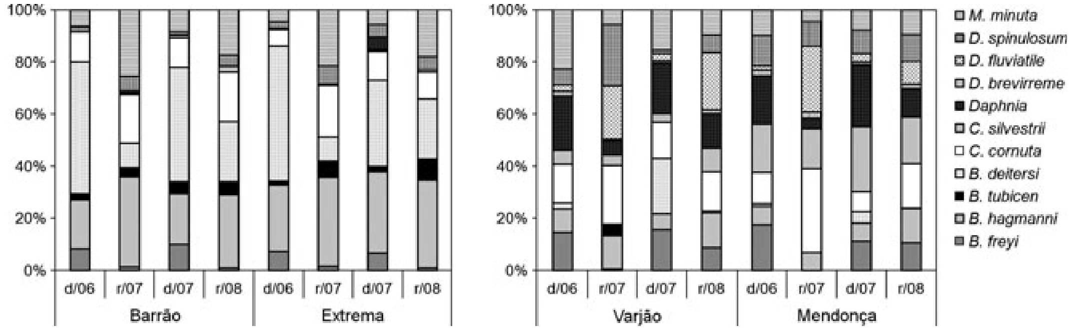

Fig. 5. Relative abundance (%) of main species of Cladocera in Três Marias Reservoir (Barrão and Extrema arms, left) and Furnas Reservoir (Varjão and Mendonça, right) (*d*/06 = dry period 2006; *r*/07 = rainy period 2007; *d*/07 = dry period 2007; *r*/08 = rainy period 2008; *Daphnia laevis* in Três Marias Reservoir; *D. ambigua* in Furnas Reservoir).

The Calanoida/Cyclopoida ratio (Fig. 4) reflected the predominance of Cyclopoida (values below 1), mainly in Três Marias Reservoir, indicating a meso-eutrophic condition. Although the ratio sporadically exceeded 1 in Furnas Reservoir, it always was higher in this reservoir, mainly in the dry period, reflecting more oligotrophic conditions.

With respect to the main species of Cladocera (Fig. 5), smaller-bodied species (mean size: 210–240 μm) (bosminids) dominated in Três Marias Reservoir, while larger-bodied species such as daphniids (mean size: 550–960 μm) and sidids (mean size: 520–665 μm) dominated in Furnas Reservoir.

The diversity index did not exhibit significant differences between the dry and rainy periods, arms or reservoirs. Larger differences were observed within each sampling period (Barrão arm from 1.64 to 2.80 bits; Extrema arm from 1.73 to 2.99 bits; and the Varjão and Mendonça arms from 1.81 to 2.85 bits). When calculated by groups, significant differences between reservoirs were observed for Cladocera ($F = 86.558$; $P < 0.0001$), Rotifera ($F = 15.004$; $P < 0.0001$) and Copepoda ($F = 258.41$; $P < 0.0001$). For Cladocera and Copepoda, higher indexes were estimated for Furnas Reservoir (1.89 and 0.63 bits, respectively), and for Rotifera, higher indexes were estimated for Três Marias Reservoir (2.28 bits).

DISCUSSION

The influence of the periods was evident in both reservoirs, with higher water transparency and dissolved oxygen concentrations in the dry periods, and temperature, and chlorophyll-*a*, total and organic suspended solids concentrations in the rainy periods. A similar pattern has been observed for other large reservoirs, such as São Simão Reservoir (Pinto-Coelho *et al.* 2005a) and Salto Grande Reservoir (Zanata & Espíndola 2002), where the total phosphorus concentration and water turbidity were also higher in rainy periods.

The differences between the environments were clear, with higher values of electrical conductivity and chlorophyll-*a*, ammonium, total nitrogen and total and organic suspended solids concentrations in Três Marias Reservoir. Only water transparency and nitrite and nitrate concentrations were higher in Furnas Reservoir. This difference is a reflection of the silting process that occurs throughout the entire São Francisco River basin (Tundisi *et al.* 1993; Sampaio & López 2003). Although they are the same age, the size and morphology of Furnas Reservoir probably contribute to the dilution of phosphorus and nitrogen in the waterbodies, decreasing the effects of these nutrients on the plankton and maintaining their oligotrophic state.

Although it was classified as oligotrophic based on its chlorophyll-*a* concentrations, based on the TSI, Três Marias Reservoir (in samples taken in the same arms as the present study) exhibited a dominance of cyanobacteria. It comprised up to 86.7% of the phytoplankton (14 803 ind mL^{-1}), followed by 7.88% of the Cryptophyceae (1347 ind mL^{-1}) and 1.97% of the Bacillariophyceae (184 ind mL^{-1}). Crysophyceae, Chlorophyceae and Zygnemaphyceae did not reach 1% (Pinto-Coelho & Greco 2007a). In the present study, cyanobacterial blooms were constantly observed in all sampling events in rainy periods in Três Marias Reservoir. The cyanobacterial densities in Furnas Reservoir were generally about one-sixth the levels (2251 ind mL^{-1}) found in Três Marias Reservoir (Pinto-Coelho & Greco 2007b). In Furnas Reservoir, cyanobacteria comprised more than 50% of the phytoplankton community in terms of cell percentage. Chlorophyceae, Bacillariophyceae and Crysophyceae were the most numerous groups in terms of biovolume.

The zooplankton species richness recorded in Três Marias and Furnas Reservoirs is consistent with those found in other Brazilian reservoirs, especially those of the same age and general area. Jurumirim and Barra

Bonita Reservoirs (both in the state of São Paulo) are good examples, exhibiting 60 and 57 species, respectively (Rocha *et al.* 1999). Former studies indicated the highest richness in oligo-mesotrophic reservoirs (Arcifa 1984), although recent studies indicated greater richness in eutrophic environments (Matsumura-Tundisi & Tundisi 2005), or no difference (Pinto-Coelho *et al.* 2005b).

The high species richness of Rotifera is also a general condition in tropical aquatic ecosystems (Matsumura-Tundisi 1999; Starling 2001). The dominance of rotifers in reservoirs is attributed to hydrodynamics, which removes individuals from the deep and littoral zones to the limnetic zone, mainly the genera *Lecane*, *Platyas*, *Lepadella*, *Colurella* and *Cephalodella* (Velho *et al.* 2005).

As a quantitative index, not considering the species composition (Buckland *et al.* 2005), the zooplankton diversity was estimated by group in order to corroborate differences between reservoirs. In Furnas Reservoir, the estimated diversity was higher for Cladocera and Copepoda, because these groups exhibited more species with well-distributed proportions. For Três Marias Reservoir, the Rotifera was the most diverse group. In Três Marias Reservoir, the dominance of *B. deitersi* and *B. hagmanni* among the cladocerans (Fig. 5), and of *T. minutus* among the copepods, explains the lower diversity calculated for these groups.

Higher zooplankton densities in the rainy periods are generally attributed to higher temperatures (which decrease generation times), as well as to greater food availability (algae and/or suspended solids) (Sampaio *et al.* 2002; Whitman *et al.* 2004; Melão *et al.* 2005). In fact, the correlations between zooplankton densities and water temperature ($r = 0.806$), and chlorophyll-*a* ($r = 0.612$), total ($r = 0.576$) and organic ($r = 0.589$) suspended solids concentrations were positive and significant ($P < 0.0001$) in both reservoirs. The nutrient correlations were not significant, with only water transparency being negative ($r = -0.747$), because higher water transparency reflects lower quantities of suspended matter in the dry months, and probably less available food.

Although several investigators have indicated that rotifers are numerically dominant in reservoirs (Nogueira 2001; Almeida *et al.* 2009), the copepods were dominant in Três Marias and Furnas Reservoirs, mainly because of the large numbers of nauplii. A predominance of copepods (especially nauplii and copepodids) also was observed by Espíndola *et al.* (2000) in Tucuruí Reservoir (State of Tocantins), by Ramos *et al.* (2008) in Emborcação Reservoir (Minas Gerais), by Takahashi *et al.* (2009) in Corumbá Reservoir (state of Goiás) and by Lansac-Tôha *et al.* (2005) in most of 30 reservoirs in the state of Paraná.

According to Panarelli *et al.* (2003) and Lansac-Tôha *et al.* (2005), the longer retention time may favour copepods because of their longer life cycles. According to Velho *et al.* (2005), the dominance of rotifers in tropical reservoirs cannot be considered the general rule. Moreover, considering the large size of reservoirs in the present study, and the locations of the sampling points in the arms, the predominance of copepods can be explained by a smaller effect of reservoir management (e.g. changes in outflow) on these species, which need more-constant habitats to complete their longer life cycles and are not as opportunistic as rotifers (Velho *et al.* 2001; Takahashi *et al.* 2009).

Rotifera was the second most abundant group. The dominance of rotifers in reservoirs is attributed to the instability of these environments, as well as to their short life cycles (*r*-strategy) (Matsumura-Tundisi 1999) and generalist food habits (Pourriot 1977).

López and Sampaio (2003), also working in Três Marias Reservoir, observed the same zooplankton structure, where *T. minutus* was the most abundant (30–40%), as well as the rotifers *H. intermedia*, *B. patulus*, *Ptygura libera*, *K. americana* and *C. coenobasis* and the cladocerans *B. deitersi*, *M. minuta*, *C. cornuta* and *B. hagmanni*.

Cyclopoid copepods, which are considered omnivorous, can manipulate particles larger than 20 μm (microphytoplankton), and *T. minutus* can feed on cyanobacterial colonies, including *Microcystis*, *Botryococcus* and *Aphanocapsa* (Matsumura-Tundisi *et al.* 1997), which may account for its dominance in Três Marias Reservoir. Pinto-Coelho *et al.* (2003) demonstrated that phytoplankton of low nutritional quality, combined with the toxicity of *Microcystis* blooms, which are also constant in Três Marias Reservoir, were responsible for the collapse of a population of *Daphnia laevis* in a eutrophic urban reservoir (Pampulha Reservoir in Minas Gerais).

The better-quality phytoplankton in Furnas Reservoir, in addition to the higher water transparency and lower concentrations of total phosphorus and nitrogen, allow higher densities of larger-bodied species (>500 μm). Tundisi *et al.* (2008) and Almeida *et al.* (2009) also observed that calanoids showed higher abundance in environments with low electrical conductivity (in Três Marias Reservoir, the conductivity values are twice as high as in Furnas Reservoir). Pinto-Coelho *et al.* (2005c) also found higher abundances of calanoids and larger-bodied cladocerans (*Daphnia*, *Diaphanosoma* and *Moina*) next to the dam in Furnas Reservoir, where oligotrophic conditions predominate.

With respect to the effects of fish on zooplankton in Três Marias Reservoir, *Anchoviella vaillanti*, a common zooplanktivorous species, is the major food source for *Acestrorhynchus britskii* and *A. lacustris* ('peixes-cachorro'), *Pachyurus squamipennis* ('corvina') and the peacock bass *Cichla ocellaris* ('tucunaré'), all piscivorous species that control the forage fish populations. *A. vaillanti* is a key species in trophic interactions involving fish and other aquatic organisms (Gomes & Verani 2003).

In Furnas Reservoir, Santos and Formagio (2007) observed that only four of 53 fish species ingest mainly aquatic invertebrates (testate amoebae, rotifers, nematodes, microcrustaceans, molluscs and small insect larvae). Three of the four fish species are benthophagous, and one is omnivorous. Thus, the presence of a truly zooplanktivorous species in Três Marias Reservoir may be another factor promoting smaller-bodied species in this reservoir.

Zooplankton as an indicator of trophic conditions

Considering that both reservoir samples were collected outside the main body, in areas less influenced by reservoir management efforts, the higher relative abundance of rotifers in Três Marias Reservoir (where this group comprised 40.1% of the zooplankton community), compared with Furnas Reservoir (with only 20.6%; the absolute density of rotifers is almost five times higher in Três Marias Reservoir), seems to be a better indicator of enrichment than the presence of any particular species, as pointed out by Fuller *et al.* (1977) and Matsumura-Tundisi *et al.* (2000).

The *Brachionus*:*Trichocerca* quotient also indicated a mesotrophic condition for Três Marias Reservoir and an oligotrophic condition for Furnas Reservoir. Moreover, higher densities of *B. angularis*, *B. falcatus*, *B. calyciflorus*, *H. intermedia*, *K. cochlearis*, *C. coenobasis*, *Polyarthra* sp., and Bdelloidea, all considered typical of meso-eutrophic environments (Attayde & Bozelli 1998; Duggan *et al.* 2001), were recorded in Três Marias Reservoir.

Differences in the abundance of Copepoda between the reservoirs can also be explained by their trophic state. According to several authors (Matsumura-Tundisi & Tundisi 2003; Pinto-Coelho *et al.* 2005b), calanoids are associated with more oligotrophic ecosystems (especially low conductivity and neutral pH), while cyclopoids and cladocerans are associated with more eutrophic lakes and reservoirs. Even in oligo-mesotrophic ecosystems, dominant Calanoida species can be found, as the higher densities of *N. henseni* in Furnas Reservoir, and the changes in species composition observed by Matsumura-Tundisi and Tundisi (2003) in reservoirs of São Paulo State over the last two decades. Considering only Cyclopoida, *T. minutus* is typical of oligo-mesotrophic environments, whereas its congener *T. decipiens* (present in low densities in both study reservoirs) dominates in more eutrophic waters (Landa *et al.* 2007).

Finally, the abundance of smaller-bodied cladocerans, especially bosminids (<500 μm) in Três Marias Reservoir, reflects the advantage of these species in enriched environments. The presence of colonial and filamentous algae that clog the filtering apparatus of larger-bodied cladocerans such as *Daphnia* and *Diaphanosoma* (Lampert 1987) explains the lower densities of members of these genera in Três Marias Reservoir. The same species may be favoured by phytoplankton in Furnas Reservoir, predominated by chlorophyceans and chrysophyceans, which provide better nutritional quality.

In oligotrophic environments with higher water transparency, lower nutrient concentrations and electrical conductivity, the nanophytoplankton is the dominant fraction, allowing high abundances of herbivorous zooplankton (i.e. filter-feeders such as calanoids and large cladocerans (daphniids and sidids)) (Xu *et al.* 2001; Sampaio *et al.* 2002).

Meso-eutrophic environments, with higher concentrations of detritus and nutrients, allow increased growth of bacteria and protozoa, important food sources for small filter-feeders such as nauplii, rotifers and small-bodied cladocerans (bosminids). Moreover, the predominance of colonial and filamentous cyanobacteria favours cyclopoids, whose raptorial habit makes it possible to feed on these algae, and uses microzooplankton as a food source (Esteves & Sendacz 1988; Matsumura-Tundisi *et al.* 2002).

The data obtained in the present study allow us to conclude that although they are both considered oligotrophic, and have similar ages and areas, these reservoirs exhibited marked differences in zooplankton structure. Três Marias Reservoir supports a community typical of mesotrophic environments, with a predominance of cyclopoids and small cladocerans and higher densities of rotifers. In contrast, the greater participation of larger-bodied species (calanoids, daphniids and sidids) in Furnas Reservoir may be an indicator of phytoplankton control by herbivory, characterizing an environment with better water quality.

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