

Secondary productivity of main microcrustacean species of two tropical reservoirs in Brazil and its relationship with trophic state

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ABSTRACT

In view of the importance of the zooplankton community in energy transfer between trophic levels, this study had as objective to estimate the secondary productivity rates of the main microcrustacean in two large tropical reservoirs, Três Marias and Furnas, state of Minas Gerais, Brazil. We included *Thermocyclops minutus*, *Bosminopsis deitersi*, *Bosmina haggmani*, *Ceriodaphnia cornuta* and *Moina minuta* in Três Marias Reservoir; and, in Furnas, these species and also *Notodiaptomus henseni*, *Daphnia ambigua*, *Ceriodaphnia silvestrii*, *Diaphanosoma spinulosum*, *D. fluviatile* and *Bosmina freyi*. With respect to total productivity, higher rates were obtained in the rainy period in both reservoirs ($P < 0.000$), with mean values during the dry and rainy periods of 0.44 and 1.80 mg DW m⁻³ d⁻¹ for Três Marias Reservoir and 1.50 and 3.10 mg DW m⁻³ d⁻¹ for Furnas Reservoir, respectively. *Thermocyclops minutus* was the most important species in terms of density and biomass in Três Marias Reservoir; and *M. minuta* showed the highest rates of secondary productivity, especially during the rainy period. In Furnas, *N. henseni* and *D. ambigua* showed the highest productivity rates in both periods, and *C. silvestrii*, *C. cornuta*, *D. spinulosum* and *D. fluviatile* were also important during the rainy period. Values of the productivity:biomass ratio were usually lower for the copepods; the cladoceran *M. minuta* showed the highest values in both reservoirs. The higher microcrustacean secondary productivity rates in Furnas Reservoir are probably the result of greater efficiency in energy transfer between trophic levels, due to the presence of phytoplankton species with better nutritional quality in this environment.

Key words: Secondary productivity; microcrustacean; tropical reservoirs; trophic state.

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INTRODUCTION

Secondary productivity is an important tool to understand biological communities, by means of population and reproductive parameters or by the cycling of matter and energy flow. Because secondary productivity is a measure of the amount of new material formed, knowledge of this quantity allows an estimate of the portion of the biomass that is renewed per unit time (Lampert and Sommer, 2007). For zooplankton, productivity has a special importance, because it is characterized by species with short life cycles and high reproductive rates; parameters such as density or biomass alone cannot reflect all the responses of this community to environmental variables and biotic interactions (Edmondson, 1974). Moreover, secondary productivity provides supporting information in studies of trophic cascades, due to the importance of zooplankton in transferring energy from producers (phytoplankton) to higher trophic levels (e.g., fish). Several methods are described in the technical literature to estimate secondary productivity. However, in natural populations it is difficult to precisely quantify the feeding habits of filtering and omnivorous organisms, as well as the portion of biomass that is lost through physiological processes and predation

(Allan and Castilho, 2007). In this context, indirect population methods such as cohorts (Allen, 1951) and the sum of increments (Edmondson and Winberg, 1971) are commonly used. Other methods involve the product of the growth rates of species and their biomass (Hart, 1987).

Among the factors that influence productivity are the intrinsic characteristics of each species, such as biomass, fecundity, rates of development and growth, starvation, resistance to environmental pressures, vulnerability to predation, and competition. Environmental factors also influence secondary productivity and must be considered in order to understand its variations through time: seasonality, hydrological variations, morphometric characteristics of the water body (Peláez-Rodríguez and Matsumura-Tundisi, 2002; Rietzler *et al.*, 2004), and the interactions among species, particularly phytoplankton (available food source) and predation pressures (Melão and Rocha, 2004). The trophic state of lakes or reservoirs also can influence zooplankton productivity, where higher density and biomass of Cladocera and Copepoda were observed in eutrophic environments both in tropical and temperate regions (Pinto-Coelho *et al.*, 2005; Ejsmont-Karabin and Karabin, 2013). However, this relationship still needs more investigation

since an increase in phytoplankton production does not reflect a proportional increase in zooplankton production (Pedersen *et al.*, 1976; Kang *et al.*, 2009). Some aspects, such as the structure of phytoplankton community or other food resources available (specially comparing environments within same trophic state), must be evaluated concomitantly with zooplankton productivity rates. Several estimates of secondary productivity of tropical zooplankton have been made for large African lakes (Burgis, 1974; Hart and Allanson, 1975; Mavuti, 1994). Despite the scarcity of similar studies in Brazilian aquatic ecosystems in past decades (Rocha and Matsumura-Tundisi, 1984), the number of studies has been growing (Maia-Barbosa, 2000; Peláez-Rodríguez, and Matsumura-Tundisi, 2002; Melão and Rocha, 2004 and 2006; Rietzler *et al.*, 2004; Santos-Wisniewski and Rocha, 2007; Panarelli *et al.*, 2010; Santos *et al.*, 2010).

The aim of this study was to estimate the secondary productivity rates of the main microcrustacean species of two tropical reservoirs, Três Marias and Furnas in the state of Minas Gerais (Brazil), during the dry and rainy periods. Once reservoirs are similar in age, surface area and morphology, our hypothesis is the differences in the secondary productivity of microcrustaceans are associated to food sources available and trophic state of these environments. Secondary productivity data in Brazilian aquatic ecosystems at different trophic states are presented.

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 (Brazil). Both were constructed ca. 50 years ago, mainly for power generation, and are also 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 (Brazil). The reservoir was completed in 1960, and silting is the main impact that compromises its power generation and water quality, followed by the replacement of the vegetation along the shore by *Eucalyptus* plantations and large cattle ranches (Sampaio and López, 2003). Furnas Reservoir is located in the Grande River basin in southern Minas Gerais (Brazil); its north arm is represented by the Grande River, and the south arm by the Sapucaí River. This reservoir was completed in 1962, and the main impacts are monoculture crops and cattle ranching, sewage discharge, solid residues, and loading of agricultural chemicals (Nogueira *et al.*, 2008). Some morphometric characteristics of the two reservoirs are presented in Tab. 1.

In each reservoir, we selected two arms with different surrounding land uses (Fig. 1). In Três Marias Reservoir, we selected the Barrão arm (Z_{\max} =21.8 m, with preserved

Cerrado, the Brazilian savanna) and Extrema arm (Z_{\max} =20.9 m, with *Eucalyptus* monoculture), located between Morada Nova de Minas and Três Marias municipalities. In Furnas Reservoir, we selected the Varjão arm (Z_{\max} =17.5 m, with headwaters in Paredão Municipal Park and coffee monoculture in the surroundings) and the Mendonça arm (Z_{\max} =25.5 m, with cattle ranching on native grasslands), located between Guapé and Capitólio municipalities. These arms were selected in order to reflect the different land uses around the reservoirs.

Procedures

Samples were collected every two days, during four weeks, in two dry periods (July/August 2006 and July/August 2007) and two rainy periods (January/March 2007 and January/March 2008) totaling 14 samples for each sampling period in each arm of reservoir. These periods were considered to be the most representative of the annual variations in temperature and precipitation. The collections were made at the deepest point of the limnetic zone in each arm.

For the qualitative and quantitative zooplankton samples, vertical hauls were made with a plankton net of 68 μm mesh size. Because of the presence of drowned original vegetation (*paliteiros*) at the sampling stations, hauls were made in the euphotic zone as determined by Secchi disk. 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, under an Olympus (CBA) optical microscope. The data are presented as organisms per m^3 . During the counts, nauplii, copepodids, and adults were separated for each species of Copepoda, and neonates, juveniles and adults of each species of Cladocera were counted. Females with eggs and the number of eggs or embryos for each female also were quantified for both groups. For this contribution, we considered the most abundant microcrustacean species (those that comprised at least 5% of the zooplankton community during the sampling seasons): *Thermocyclops minutus* Lowndes,

Tab. 1. Morphometric characteristics of Três Marias and Furnas reservoirs, Minas Gerais (Brazil). Sources: Cemig (2015) and Furnas (2015).

Reservoir	Três Marias	Furnas
Flooded area	1100 km ²	1440 Km ²
Volume	15.27x10 ⁹ m ³	17.21x10 ⁹ m ³
Average outflow	700 m ³ s ⁻¹	800 m ³ s ⁻¹
Retention time	120 days	160 days
Maximum depth	75 m	90 m
Mean depth	12 m	13 m
Installed capacity	396 MW	1126 MW

Bosminopsis deitersi Richard, *Bosmina hagmanni* Stin-gelin, *Ceriodaphnia cornuta* Sars, and *Moina minuta* Hansen in Três Marias Reservoir; and in Furnas Reser-voir, in addition to these species, we also considered *No-todiaptomus henseni* Dahl, *Daphnia ambigua* Scourfield, *Ceriodaphnia silvestrii* Daday, *Diaphanosoma spinulo-sum* Herbst, *D. fluviatile* Hansen, and *Bosmina freyi* De Melo and Hebert. Detailed descriptions of the zooplank-ton communities of Três Marias and Furnas reservoirs can be found in Brito *et al.* (2011).

Secondary productivity was estimated according to Hart (1987), first determining the finite birth rate *per capita*, β :

$$\beta = E N^{-1} De^{-1} \tag{eq. 1}$$

where:

E=egg density

N=population density

De=embryonic development time.

To determine embryonic development time, adult fe-males were collected from Três Marias and Furnas Reser-voirs and kept alive in laboratory. Females were cultivated in 6-well acrylic plates with transparent covers, filled with

reservoir water filtered through a plankton net of 68 μ m mesh size. The plates were kept in a growth chamber (Eletrolab EL202) at 22 and 26 \pm 1 $^{\circ}$ C (mean water temper-atures during the dry and rainy periods) and a 12h/12h light/ dark period. The water in the plates was replaced daily and observations were made every 12 h; females were monitored from egg production until the birth of neonates. For *T. minutus*, *N. henseni*, *B. freyi*, *B. hag-manni* and *B. deitersi*, embryonic development time could not be estimated, so the formula proposed by Bottrell *et al.* (1976) for Cyclopoida, Calanoida and other species of Cladocera was used:

$$\ln De = \ln a + b \ln T + c (\ln T)^2 \tag{eq. 2}$$

where:

De=embryonic development time

T=temperature

a, b, c=polynomial constants.

The values of polynomial constants are provided by Bottrell *et al.* (1976): for Cyclopoida $\ln a=4.1301$; $b=-0.4141$; $c=-0.2159$; for Calanoida $\ln a=3.9650$; $b=-0.4049$; $c=-0.1909$; for other Cladocera $\ln a=2.3279$; $b=1.2472$; $c=-0.5647$.

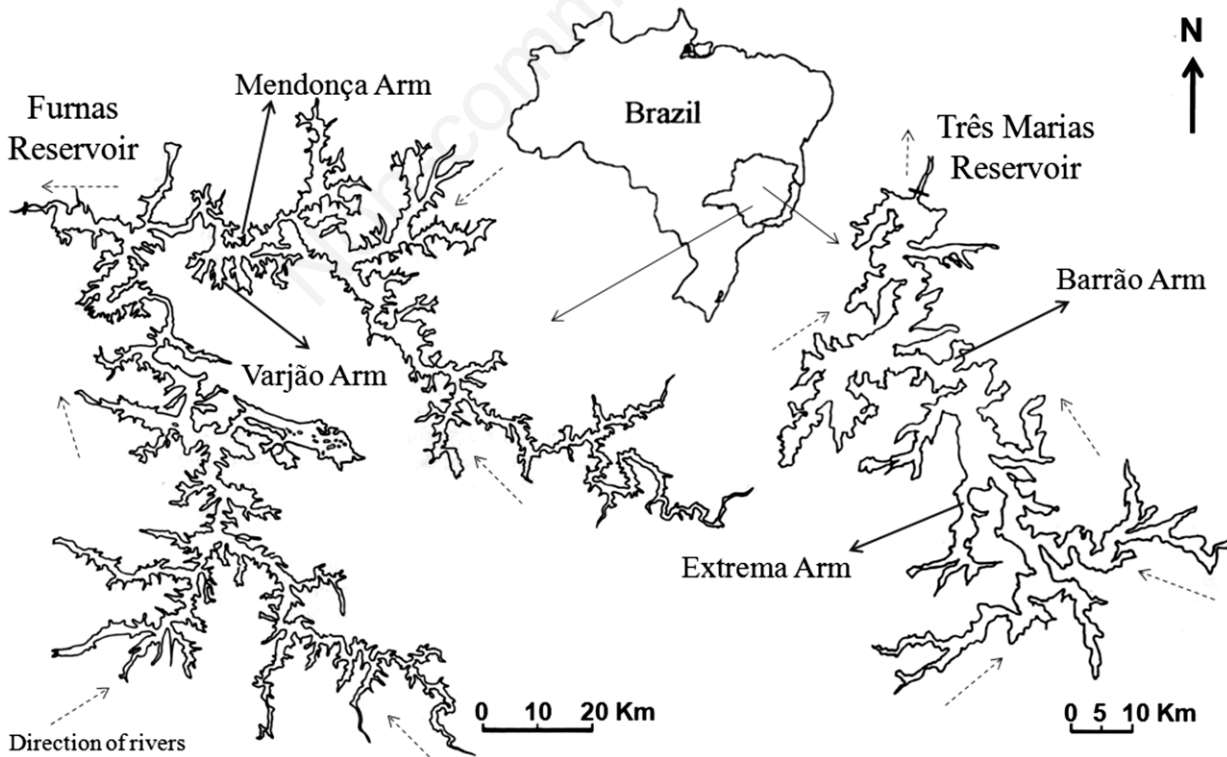


Fig. 1. Três Marias (right, 1:10.000) and Furnas (left, 1:20.000) reservoirs, Minas Gerais (Brazil). Solid arrows indicate arms studied. Dotted arrows indicate direction of river flow. Modified from: López and Sampaio, 2003; and Tundisi *et al.*, 1993.

The secondary productivity (P) was calculated by the product of the finite birth rate *per capita* (β) and the biomass (B) (Hart, 1987):

$$P = \beta B \quad (\text{eq. 3})$$

Biomass data can be found in Brito *et al.* (2013). Differences in values of productivity were tested through two-way Analysis of Variance, followed by a Tukey's *post-hoc* comparison test. Two analysis were performed: one between reservoirs and seasons and another between arms and seasons for each reservoir. Pearson's correlations were performed between temporal fluctuation of productivity of each species and environmental data (available in Brito *et al.*, 2011): temperature, dissolved oxygen, electrical conductivity, chlorophyll-*a*, total suspended solids, organic suspended solids, total phosphorus, nitrite, nitrate, ammonium and total nitrogen. All the analyses were performed with Statistica 7.0 (StatSoft).

RESULTS

The embryonic development time showed the same pattern for the microcrustacean species in general, with longer durations in low temperatures (22°C) and for species with larger body size (*D. ambigua* and *D. spinulosum*) (Tab. 2).

Mean values of productivity of the main microcrustacean of Três Marias and Furnas reservoirs are presented Fig. 2 (grouped by Cladocera and Copepoda) and in Tab. 3 (for each species). Considering the total microcrustacean productivity, higher rates were obtained in the rainy period, and in Furnas reservoir (F=28.19; P<0.0001). The mean values in the dry and rainy periods were 0.44 and 1.80 mg DW m⁻³d⁻¹ for Três Marias Reservoir and 1.05 and 3.10 mg DW m⁻³d⁻¹ for Furnas, respectively. Comparing arms and seasons, in Furnas higher values of secondary productivity were observed in rainy period, in Mendonça arm (F=9.30; P<0.0001). In Três Marias, the differences between arms were not significant (P>0.981). Cladocera contributed most to the microcrustacean productivity, ranging between 42-81% in Três Marias and 47-65% in Furnas.

In Três Marias Reservoir, *T. minutus* (mean values in dry and rainy periods: 0.18 and 0.62 mg DW m⁻³d⁻¹) followed by *M. minuta* (mean values in dry and rainy periods: 0.04 and 0.62 mg DW m⁻³d⁻¹) were the species that most contributed to secondary productivity (Tab. 3). In Furnas, *N. henseni* (mean values in dry and rainy periods: 0.35 and 0.98 mg DW m⁻³d⁻¹) and *D. ambigua* (mean values in dry and rainy periods: 0.30 and 0.53 mg DW m⁻³d⁻¹) was the most important species for secondary productivity (Tab. 3).

Mean values of the productivity:biomass ratio (P:B) are presented in Tab. 4. Generally, lower values were observed for copepod species, probably due to their longer life cycles with several development stages. *M. minuta* showed the highest values of the P:B ratio in both reser-

voirs (mean values 0.66 and 0.72 in Três Marias; 0.44 and 0.48 in Furnas, in the dry and rainy periods, respectively). For *M. minuta*, the rates of biomass renewal ($[P:B]^{-1}$) were 1.51 and 1.39 days in Três Marias, and 2.27 and 2.08 days in Furnas, in the dry and rainy periods, respectively.

C. cornuta and *B. deitersi* also showed higher P:B ratios in Três Marias, with 0.64 and 0.52, and renewal rates of 1.56 and 1.92 days, respectively. In Furnas Reservoir, *D. ambigua* (0.63), *C. silvestrii* (0.68) and *D. spinulosum* (0.55) also showed higher P:B ratios, with renewal rates of 1.58; 1.47 and 1.81 days, respectively.

Correlations were significant between total productivity and temperature ($r=0.67$; P<0.0001) and total suspended solids ($r=0.41$; P<0.0001) in Três Marias reservoir. In Furnas, total productivity was significant correlated to temperature ($r=0.62$; P<0.0001) and chlorophyll-*a* ($r=0.43$; P<0.0001). For each species in both reservoirs, most of correlations were significant to temperature, even Pearson's coefficient showed lower values. In Três Marias, the exceptions were *B. deitersi*, significantly correlated to

Tab. 2. Embryonic development time (days) determined for Cladocera species in Três Marias and Furnas reservoirs, Minas Gerais (Brazil).

	Três Marias		Furnas	
	22±1°C	26±1°C	22±1°C	26±1°C
<i>Daphnia ambigua</i>			2.50	2.00
<i>Ceriodaphnia silvestrii</i>			2.00	1.63
<i>Ceriodaphnia cornuta</i>	2.07	1.50	2.00	1.67
<i>Moina minuta</i>	1.94	1.55	2.00	1.64
<i>Diaphanosoma spinulosum</i>			2.33	1.55
<i>Diaphanosoma fluviatile</i>			1.67	1.50

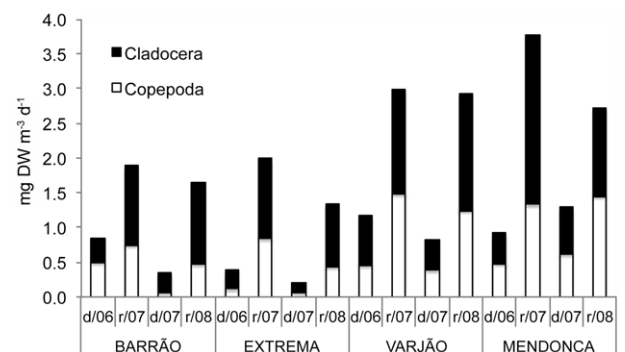


Fig. 2. Means values of productivity (mg DW m⁻³d⁻¹) of Copepoda and Cladocera of Três Marias (Barrão and Extrema arms, right) and Furnas (Varjão and Mendonça arms, left) d/06, dry season 2006; r/07, rainy season 2007; d/07, dry season 2007; r/08, rainy season 2008.

electrical conductivity ($r=0.49$; $P<0.0001$) and *M. minuta* to organic suspended solids ($r=0.67$; $P<0.0001$). In Furnas, the productivity of *T. minutus*, *C. silvestrii*, *C. cornuta*, *D. spinulosum* and *B. hagmanni* was also significantly correlated to chlorophyll-*a* (r values: 0.46, 0.55, 0.57, 0.58,

0.51; $P<0.0001$, respectively) while correlations for *N. henseni* and *M. minuta* were significant to organic suspended solids (r values: 0.42, 0.53; $P<0.0001$, respectively). *D. ambigua* and *B. deitersi* showed no significant correlations to environmental data.

Tab. 3. Mean values of productivity ($\text{mg DW m}^{-3} \text{d}^{-1}$) for the main microcrustacean species in Três Marias and Furnas reservoirs, Minas Gerais (Brazil).

Três Marias	Barrão				Extrema			
	d/06	r/07	d/06	r/07	d/06	r/07	d/06	r/07
<i>Thermocyclops minutus</i>	0.49	0.75	0.07	0.47	0.11	0.84	0.06	0.43
<i>Bosminopsis deitersi</i>	0.14	0.07	0.08	0.27	0.14	0.06	0.04	0.14
<i>Bosmina hagmanni</i>	0.08	0.26	0.08	0.17	0.09	0.21	0.06	0.19
<i>Ceriodaphnia cornuta</i>	0.07	0.14	0.06	0.16	0.02	0.14	0.02	0.11
<i>Moina minuta</i>	0.06	0.67	0.07	0.58	0.02	0.74	0.02	0.47
Furnas	Varjão				Mendonça			
	d/06	r/07	d/06	r/07	d/06	r/07	d/06	r/07
<i>Thermocyclops minutus</i>	0.17	0.37	0.06	0.36	0.12	0.53	0.18	0.31
<i>Notodiaptomus henseni</i>	0.28	1.11	0.33	0.88	0.36	0.80	0.44	1.14
<i>Daphnia ambigua</i>	0.32	0.28	0.32	0.75	0.12	0.66	0.43	0.41
<i>Ceriodaphnia silvestrii</i>	0.07	0.29	0.01	0.16	0.07	0.41	0.08	0.19
<i>Ceriodaphnia cornuta</i>	0.04	0.15	0.01	0.05	0.01	0.37	0.03	0.06
<i>Moina minuta</i>	0.16	0.15	0.05	0.18	0.06	0.10	0.03	0.21
<i>Diaphanosoma spinulosum</i>	0.07	0.27	0.01	0.17	0.11	0.49	0.07	0.24
<i>Diaphanosoma fluviatile</i>	0.02	0.31	0.01	0.26	0.01	0.35	0.01	0.07
<i>Bosmina freyi</i>	0.03		0.01	0.06	0.03		0.01	0.06
<i>Bosmina hagmanni</i>	0.02	0.06	0.01	0.05	0.02	0.05	0.01	0.03
<i>Bosminopsis deitersi</i>			0.01				0.01	

d/06, dry season 2006; r/07, rainy season 2007; d/07, dry season 2007; r/08, rainy season 2008.

Tab. 4. Mean values of productivity:biomass ratio (P:B) for the main microcrustacean species in Três Marias and Furnas reservoirs, Minas Gerais (Brazil).

Três Marias	Barrão				Extrema			
	d/06	r/07	d/07	r/08	d/06	r/07	d/07	r/08
<i>Thermocyclops minutus</i>	0.10	0.05	0.03	0.03	0.05	0.06	0.04	0.03
<i>Bosminopsis deitersi</i>	0.19	0.22	0.18	0.52	0.27	0.30	0.28	0.33
<i>Bosmina hagmanni</i>	0.17	0.13	0.28	0.08	0.24	0.10	0.25	0.08
<i>Ceriodaphnia cornuta</i>	0.44	0.28	0.64	0.24	0.33	0.21	0.42	0.30
<i>Moina minuta</i>	0.63	0.83	0.84	0.81	0.52	0.82	0.67	0.68
Furnas	Varjão				Mendonça			
	d/06	r/07	d/07	r/08	d/06	r/07	d/07	r/08
<i>Thermocyclops minutus</i>	0.12	0.06	0.13	0.05	0.05	0.06	0.19	0.05
<i>Notodiaptomus henseni</i>	0.15	0.15	0.33	0.10	0.08	0.12	0.18	0.14
<i>Daphnia ambigua</i>	0.43	0.38	0.48	0.29	0.12	0.63	0.36	0.20
<i>Ceriodaphnia silvestrii</i>	0.68	0.52	0.27	0.18	0.10	0.22	0.14	0.11
<i>Ceriodaphnia cornuta</i>	0.28	0.24	0.14	0.09	0.08	0.24	0.34	0.10
<i>Moina minuta</i>	0.65	0.68	0.42	0.32	0.34	0.41	0.34	0.53
<i>Diaphanosoma spinulosum</i>	0.55	0.30	0.50	0.35	0.29	0.47	0.37	0.27
<i>Diaphanosoma fluviatile</i>	0.36	0.25	0.29	0.21	0.22	0.22	0.18	0.13
<i>Bosmina freyi</i>	0.24		0.14	0.19	0.11		0.12	0.14
<i>Bosmina hagmanni</i>	0.26	0.32	0.16	0.10	0.15	0.16	0.13	0.07
<i>Bosminopsis deitersi</i>			0.14				0.16	

d/06, dry season 2006; r/07, rainy season 2007; d/07, dry season 2007; r/08, rainy season 2008.

DISCUSSION

Knowledge of the secondary productivity of zooplankton species in aquatic ecosystems allows us to elucidate the dynamics of these environments, because this group of organisms is an important link between primary producers and the higher trophic levels.

The values of embryonic development time obtained in this study were similar to those found in other studies in Brazil. For *D. ambigua*, Rocha and Matsumura-Tundisi (1990 apud Melão 1999b) also observed a development time of 2.0 days, at 25°C. Similar values were also obtained by Santos *et al.* (2006) for *C. silvestrii* at 25°C, varying between 1.61 and 1.73 days in different treatments with different media and food sources. For this same species, Rietzler (1998 apud Melão, 1999b) observed higher values at 20°C (2.32 days) and lower at 25°C (1.33 days). For *C. cornuta*, Melão (1997) estimated development times of between 3.24 and 1.66 days (at 20 and 25°C, respectively); while Maia-Barbosa (2000) estimated 1.57 days; and for *M. minuta* 1.84 days (at 25°C). Both authors found very similar values for the development time of *B. deitersi* at 25°C (1.21 and 1.10 days, by Melão, 2006 and Maia-Barbosa, 2000, respectively). Formulas for embryonic development time proposed by Bottrell *et al.* (1976), which are generalizations for large groups, are not considered appropriate for cladocerans and copepods of Brazilian continental waters, which are typically tropical. Studies in Brazil, despite the different conditions where they were conducted, *i.e.*, with different culture media; natural or reconstituted water; or with or without algae addition, especially chlorophytes, showed similar responses by the same species, allowing patterns to be determined.

Some authors (Margalef, 1983; Melão, 1999a) have stated that temperature and food availability are the main factors that affect zooplankton productivity. In Três Marias and Furnas reservoirs, higher values of density, biomass and productivity were observed in the rainy period. Higher temperatures reduce generation time and body size, causing the individuals to reach reproductive age more rapidly and increase their densities within a few weeks (Gillooly, 2000; Gillooly *et al.*, 2002). Furthermore, greater food availability in Três Marias and Furnas reservoirs (chlorophyll-*a* and organic suspended solids, according to Brito *et al.*, 2011) led to a better nutritional status of organisms, increasing the proportion of egg-bearing females (Klein-Breteler *et al.*, 1990; Melão, 1999b; Santos *et al.*, 2006), especially for cladocerans. Although higher densities were recorded in Três Marias Reservoir, higher microcrustacean productivity was observed in Furnas. Primary productivity (estimated in the same sites and periods of this study) also showed higher values in Três Marias (between 4.68 and 4831.78 mg C m⁻² day⁻¹ and between 4.27 and 100.89 mg C m⁻² day⁻¹ in Furnas, according to Carvalhais-Júnior *et al.*, 2007). According to Hillbricht-Ilkowska (1972, apud Pederson *et al.*,

1976) the efficiency of energy transfer between primary and secondary producers tends to decrease with the increase of trophic state, because more-eutrophic environments show high densities of cyanobacteria and larger-sized algae. Although it is considered oligotrophic (Sampaio and López, 2003), in Três Marias, cyanobacteria comprised more than 80% of the phytoplankton (Brito *et al.*, 2011); this group of algae is difficult for microcrustaceans to digest (Lampert, 1987). In Furnas, due to the higher contribution of chlorophytes, bacillariophytes and chrysophytes (Campos, 2008), as well as the positive correlations between productivity and chlorophyll-*a*, indicates that microcrustaceans may be able to assimilate more efficiently the energy produced by phytoplankton, and therefore showed higher secondary productivity in this environment.

Other factors that could influence microcrustacean productivity are water quality and land use surrounding each arm of reservoirs. In Três Marias, secondary productivity has no difference between arms, even Barrão's vegetation covering is preserved as *Cerrado* (Brazilian savannah). Although classified as oligotrophic by Trophic State Index, Três Marias showed lower water transparency and higher values of electrical conductivity, chlorophyll-*a*, ammonium, total nitrogen, total and organic suspended solids (Brito *et al.*, 2011). Additionally, the *Eucalyptus* monoculture (Extrema arm) also can impact negatively the zooplankton community either by the volatile compounds of its leaves (which ecotoxicological effects were observed in *Daphnia* by Araújo *et al.*, 2010, in Southeast of Minas Gerais State) or by the pesticides applied on the plantations and brought to aquatic environment through runoff. In Furnas, despite the impacts of land use, it showed a better water quality, with higher transparency and dissolved oxygen concentrations. The predominance of coffee monoculture in the landscape, could be a positive factor, once this permanent plantation protects the soil, decreasing the silting effect (like observed in Três Marias). The presence of this monoculture and the cattle on native grassland, could be observed through higher nitrite and nitrate concentrations (Brito *et al.*, 2011). Among the cladoceran species in Três Marias Reservoir, *M. minuta* showed the highest productivity. Temperature has an important role, because the population of egged females (mean 27%; maximum 37%) and the mean number of eggs per female (mean 1.38 eggs, maximum 2.0 eggs) were higher in the warm rainy period. Furthermore, the correlations between productivity of this species and concentrations of organic suspended solids in Três Marias and Furnas reservoirs indicate an additional source of food for this species, as observed for *M. micrura* by Ferrão-Filho *et al.* (2005). These authors observed that only this species showed similar growth rates to a control treatment, when different food sources were offered: only chlorophytes, only seston, or seston+chlorophytes.

B. deitersi contributed 43% of the productivity at a station impacted by mine tailings in Batata Lake, state of Pará (Brazil) (Maia-Barbosa, 2000), and is the main species in Lagoa Dourada Reservoir, state of São Paulo (Brazil), where it has contributed 92.41 and 97.36% of the productivity at different times (Melão and Rocha, 2006). In Três Marias, *B. deitersi* contributed 51% of productivity in the dry period, and was always present in all samples, in contrast to Furnas, where it was less abundant or even absent. Melão and Rocha (2006) observed percentages between 17 and 28% of egged females for this species, and in Três Marias the percentages ranged between 8 and 30%. Furthermore, the positive correlations between the productivity of *B. deitersi* and electrical conductivity in Três Marias reservoir (which values are almost double of Furnas) indicates that this species would use other food sources on this environment more rich, probably bacteria, as well as observed by Melão and Rocha (2006). While Maia-Barbosa (2000) observed a higher contribution of *B. haggmani* ($0.88 \text{ mg DW m}^{-3} \text{ d}^{-1}$) and *D. birgei* ($0.77 \text{ mg DW m}^{-3} \text{ d}^{-1}$) to secondary productivity at a natural (unimpacted) station in Batata Lake; in the present study, with the exception of *B. deitersi* in Três Marias, bosminids and *C. cornuta* contributed least to secondary productivity. Despite its higher density and biomass, *T. minutus* showed lower productivity in both reservoirs, probably due to fewer spring compared with other copepod species. According to Reid and Pinto Coelho (1994), this smaller-sized species has a low reproductive potential, with a mean number of 5.7 eggs per female. Even lower means were recorded in Três Marias and Furnas reservoirs (5.3 and 4.2 eggs per female, respectively). In Lagoa Dourada Reservoir, *Tropocyclops prasinus*, another small-bodied cyclopoid, showed higher productivity (up to $2.8 \text{ mg DW m}^{-3} \text{ d}^{-1}$ during summer), and also more eggs per female, between 10.7 and 12.7 (Melão and Rocha, 2004). *N. henseni*, despite a lower mean number of eggs (2.4) always showed higher proportions of egged females than *T. minutus* in Furnas (0.27 and 0.19, respectively), contributing to a higher finite birth rate *per capita* (β) and consequently higher rates of productivity, especially in rainy periods. Larger cladocerans (like daphnids and sidids) that dominated in biomass and productivity in Furnas Reservoir (*D. ambigua*, *C. silvestri*, *D. spinulosum* and *D. fluviatile*) generally invest less in body growth, producing larger offspring (Melão, 1999b), thus gaining a competitive advantage over other smaller cladocerans species, like bosminids. These species also showed the higher productivity:biomass ratio related to the other microcrustacean species in this reservoir.

Generally, secondary productivity values recorded for Três Marias and Furnas reservoirs were within the same order of magnitude as those observed for other oligotrophic environments such as Lagoa Dourada Reservoir

(Melão *et al.*, 2004 and 2006) and the natural station of Lake Batata (Maia-Barbosa, 2000) (Tab. 5). The impacted station of Lake Batata showed intermediate values, because this station is mesotrophic due to bauxite tailings. A similar pattern was observed by Panarelli *et al.* (2010), comparing two marginal lakes of the Paranapanema River in São Paulo (Brazil). Conversely, Rietzler *et al.* (2004) found much higher values in the eutrophic Salto Grande Reservoir in São Paulo (Brazil). An earlier study in Furnas, Santos *et al.* (2010) observed higher values of productivity for the same species of Cladocera as in this study. The authors worked in the Sapucaí arm, a mesotrophic region in Furnas reservoir, which drains Alfenas and Varginha, some of the most populous municipalities of Minas Gerais State. This relationship between the increasing of microcrustacean productivity with the increasing of trophic state (Tab. 5) recurs in other Brazilian aquatic ecosystems. All studies in Brazilian lakes and reservoirs used the biomass increment method of Winberg *et al.* (1965) and the present study applied the method of Hart (1987), and both direct (Maia-Barbosa, 2000; Melão *et al.*, 2004 and 2006; Rietzler *et al.*, 2004; Santos-Wisniewski and Rocha, 2007) and indirect (Panarelli *et al.*, 2010; Santos *et al.*, 2010) methods were employed to estimate the zooplankton biomass. In spite of these methodological differences, the values of secondary productivity were compatible with each other. Even eutrophic environments have higher rates of primary productivity, there is a decreasing of the energy transfer from phytoplankton to zooplankton. However eutrophic environments, may provide other food resources as detritus, particulate organic matter and bacteria and protozoans, able to sustain higher zooplankton productivity (Rocha *et al.*, 1995; Rocha *et al.*, 1997). Still comparing these studies, the higher values of microcrustacean productivity were observed in rainy season (November to March - late spring and during the summer in Brazil) independently the trophic state of the aquatic environment. The only exception was observed in the study of Rietzler *et al.*, (2004) for Copepoda, where its productivity was higher in winter in two of four sampling stations. As discussed for Três Marias and Furnas reservoirs, the higher water temperatures (typical of these months) and more abundant nutrients and food resources (brought by drainage) in the rainy period, contributed to this pattern. Zooplankton productivity in temperate aquatic environments are also influenced mainly by temperature, however different from tropical environments, there is a huge decrease during the winter, when the biomass and production are often undetectable (Lehman, 1988, Shuter and Ing, 1997). Comparing 54 lakes in northern hemisphere, Lacroix *et al.* (1999) found linear relationships between phytoplankton and zooplankton productions, however, the ecological efficiencies (Pzoo/Pphyto) do not vary significantly with the trophic state of the lakes. As in tropical aquatic ecosystems, there

is a tendency in increasing of microcrustacean production with eutrophication. In low nutrients alpine lakes (Paione Superiore and Malghette, Italy), Manca *et al.*, (1999) observed low values of productivity for two species of Copepoda (*Acanthodiaptomus denticornis*, *Cyclops abyssorum*) and one of Cladocera (*Daphnia longispina*) (Tab. 5). In a warm temperate estuary in South Africa (Sundays River) Jerling and Wooldridge (1991) observed a gradient between the upper estuary (contaminated by the residues and fertilizers used in the citrus orchards and sheep farming) and the estuary mouth. The productivity of *Pseudodiaptomus hessei* varied more 10 times from contaminated to diluted waters in mouth estuary. Even grown in laboratory (18-21°C), *Daphnia magna* showed low productivity values in a nutrient-poor diet contrasting with higher values in a nutrient-rich diet (Gómez *et al.*, 2012) (Tab. 5). In lake Cheongpyeong, a mesotrophic reservoir in Korea, lower values of secondary productivity were observed for *Daph-*

nia galeata, *Bosmina longirostris* and *Cyclops* sp when compared with lake Paldang, a nearby reservoir characterized by eutrophic waters (Kang *et al.*, 2009). Other eutrophic environments also showed higher values of secondary productivity: for hole zooplankton community (in lake Manzala, in Egypt) (Mageed, 2006), and *Arctodiaptomus spinosus* and *Diaphanosoma mongolianum* in the eutrophic, shallow, well mixed Neusiedler See lake, in Austria (Akbulut, 2000) (Tab. 5). Also in areas known as more productive, as the upwelling area of Antofagasta, northern Chile, productivity of *Calanus chilensis* showed higher rates and continuous growth through the year (Escribano and McLaren, 1999). Despite the differences on climatic conditions or species composition (Lehman, 1988), tropical and temperate aquatic ecosystems seems to show higher rates of secondary productivity with the trophic state increasing. Microcrustaceans of lakes and reservoirs in tropical areas show continuous productivity

Tab. 5. Mean values of secondary productivity (mg DW m⁻³ d⁻¹) in several lakes and reservoirs of Brazil, considering their trophic state. Transformations were made to convert all measures in a common unity.

Brazilian environments	Range (mg DW m ⁻³ d ⁻¹)	Authors	Trophic state*
Três Marias (MG)	Cladocera: 0.13-1.19 Copepoda: 0.06-0.84	This study	Oligotrophic
Furnas (MG) Rio Grande Arm	Cladocera: 0.44-2.43 Copepoda: 0.38-1.48	This study	Oligotrophic
Furnas (MG) Rio Sapucaí Arm	Cladocera: 0.02-28.6	Santos <i>et al.</i> , 2010	Oligotrophic
Lagoa Dourada (SP)	Cladocera: 0.455-1.970 Copepoda: 0.152-1.428	Melão <i>et al.</i> , 2004 Melão <i>et al.</i> , 2006	Oligotrophic
Lake Coqueiral (SP)	Cladocera: 0.017-0.510	Panarelli <i>et al.</i> , 2010	Oligotrophic
Lake Batata (PA)	Cladocera, natural station: 2.72	Maia-Barbosa, 2000	Oligotrophic
Lake Batata (PA)	Cladocera, impacted station: 7.48	Maia-Barbosa, 2000	Mesotrophic
Salto Grande (SP)	Cladocera: 22.97-61.15 Copepoda: 46.22-53.55	Rietzler <i>et al.</i> , 2004	Eutrophic
Lake Camargo (SP)	Cladocera: 3.036-33.466	Panarelli <i>et al.</i> , 2010	Eutrophic
Barra Bonita (SP)	Copepoda: 14.0-23.61	Santos-Wisniewski and Rocha, 2007	Eutrophic
Temperate environments	Range (mg DW m ⁻³ d ⁻¹)	Authors	Trophic state*
Lakes Paione Superiore and Malghette (Italy)	Cladocera: 0.992 Copepoda: 0.169-0.204	Manca <i>et al.</i> , 1999	Low nutrients
Mouth of Sunday estuary (South Africa)	Copepoda: 0.00-8.72	Jerling and Wooldridge, 1991	Low nutrients
Nutrient-poor diet (laboratory)	Cladocera: 0.368	Gómez <i>et al.</i> , 2012	Low nutrients
Lake Cheongpyeong (Korea)	Cladocera: 6.75-11.0 Copepoda: 0.50-3.25	Kang <i>et al.</i> , 2009	Mesotrophic
Nutrient-rich diet (laboratory)	Cladocera: 0.719	Gómez <i>et al.</i> , 2012	Eutrophic
Upwelling area of Antofagasta (Chile)	Copepoda: 1.57	Escribano and McLaren, 1999	Eutrophic
Lake Manzala (Egypt)	Cladocera 2.18-5.18 Copepoda 4.56-17.84	Mageed, 2006	Eutrophic
Upper Sunday estuary (South Africa)	Copepoda: 0.08-21.19	Jerling and Wooldridge, 1991	Eutrophic
Lake Neusiedler See (Austria)	Cladocera 0.724-5.00 Copepoda 9.88-30.39	Akbulut, 2000	Eutrophic
Lake Paldang (Korea)	Cladocera: 4.5-192 Copepoda: 1.75-33.75	Kang <i>et al.</i> , 2009	Eutrophic

*Trophic state according to the authors of each manuscript.

while in temperate environments, it is limited mainly to growing season. In both environments, the trophic state and food resources are the other factors that most influence microcrustacean production.

CONCLUSIONS

The data evaluated indicated that, besides temperature, microcrustacean productivity is also influenced by the food sources (chlorophyll-a and organic suspended solids) available in the tropical reservoirs of this study. Furthermore, in a boarder scale, the secondary productivity in Brazilian lakes and reservoirs also can be influenced by seasonality and trophic state, with higher values observed in rainy period and eutrophic environments.

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