Life history, population dynamics, standing biomass and production of Bosminopsis deitersi (Cladocera) in a shallow tropical reservoir.

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ABSTRACT: Life history, population dynamics, standing biomass and production of Bosminopsis deitersi (Cladocera) in a shallow tropical reservoir. Reproductive performance, life history parameters (duration of embryonic and post-embryonic development and longevity) and stage-specific length and weight values were measured for a planktonic tropical cladoceran species, Bosminopsis deitersi, from a shallow Brazilian reservoir (Lagoa Dourada). This species was reared in laboratory under 20ºC and 25ºC and fed ad libitum on natural seston enriched with algae from laboratory cultures at 10^5 cells mL^{-1}. Laboratory data on the duration of development and biomass, together with population dynamics data obtained in the field, were used to estimate summer and winter standing stock and production of B. deitersi in Lagoa Dourada reservoir. Development times were mainly temperature dependent, once food was not limiting, with shorter periods of embryonic and post-embryonic development and decreased longevity at 25ºC. Mean weights of neonates, juveniles and adults were 0.23, 0.55 and 0.80mg, respectively. B. deitersi showed better reproductive performance in laboratory cultures with higher mean clutch-size (1.47 and 1.60 eggs per female at 20ºC and 25ºC, respectively) than field populations (1.12 and 1.11 eggs per female in winter and summer, respectively). Maximum production rate of B. deitersi in the field, attained during summer, was 5.08mgDW m^{-3} day^{-1} and the highest daily production: biomass (P:B) ratio was 0.35. Over short-time intervals (every other day) there was great variability on species' production rates. Although this is the very first experimental study undertaken on this species, B. deitersi production rates were low compared to values reported in the literature for other cladocerans, from both tropical and subtropical regions.

Key-words: secondary production, growth, reproduction, seasonal variation, tropical cladoceran.

RESUMO: Bionomia, dinâmica populacional, biomassa e produção de Bosminopsis deitersi (Cladocera) em um reservatório tropical raso. O desempenho reprodutivo, parâmetros da bionomia (duração do desenvolvimento embrionário e pós-embrionário, e longevidade) e valores de comprimento e peso dos diferentes estádios foram medidos em uma espécie planctônica de cladócero tropical, Bosminopsis deitersi, de um reservatório raso brasileiro (Lagoa Dourada). Essa espécie foi cultivada em laboratório a 20ºC e 25ºC, e alimentada ad libitum com seston natural enriquecido com algas cultivadas em laboratório à concentração de 10^5 células mL^{-1}. Dados obtidos em laboratório para duração do desenvolvimento e biomassa, juntamente com dados de dinâmica populacional obtidos em campo, foram usados para estimar a biomassa e produção de B. deitersi na Lagoa Dourada. Os tempos de desenvolvimento foram principalmente dependentes da temperatura, já que o alimento não foi limitante, com períodos de desenvolvimento embrionário e pós-embrionário mais curtos e um decréscimo da longevidade a 25ºC. Os pesos médios das neonatas, jovens e adultos foram 0.23, 0.55 e 0.80mg, respectivamente. B. deitersi teve um maior desempenho reprodutivo quando cultivado no laboratório, apresentando maiores ninhadas (médias de 1.47 e 1.60 ovos por fêmea a 20ºC e 25ºC, respectivamente) do que a população de campo (1.12 e 1.11 por fêmea no inverno e no verão, respectivamente). A taxa de produção máxima obtida para B. deitersi no campo, alcançada durante o verão, foi de 5.08mgPS.m^{-3}.dia^{-1} e a maior razão produção:biomassa (P:B) foi 0.35. Em curtos intervalos de tempo (diariamente) houve grande variabilidade nas taxas de produção da espécie. Embora este seja o primeiro estudo experimental realizado com essa espécie, as taxas de produção de B. deitersi

foram baixas quando comparadas a valores reportados na literatura para outros cladóceros, tanto de regiões tropicais quanto subtropicais.
Palavras-chave: produção secundária, crescimento, reprodução, variação sazonal, cladócero tropical.

Introduction

Much effort has been done in order to uncover the role of particular species on zooplankton communities of a variety of aquatic ecosystems, once they are an important component in the trophic chains of these environments. Studies, including those on life histories, standing biomass and production, contribute to the understanding of the aquatic ecosystem's trophic dynamics, regarding the balance between input and output of matter and energy in natural populations. Knowledge about zooplankton growth and development rates are particularly important in population dynamics, production and food web studies (Vijverberg, 1989).

This paper presents part of a study on the production of zooplankton in Lagoa Dourada, a shallow oligotrophic reservoir in the south-east of Brazil, which analyzed short term species fluctuations in the rainy and dry seasons, over one year. Earlier articles have dealt with zooplankton populations' structure, dynamics, abundance, standing biomass and total production by the addition of production values for each of the main rotifers, cladocerans and copepods species occurring in the reservoir (Melão & Rocha, 2000); and life histories, standing biomass and production of two planktonic cyclopoid copepods, Tropocyclops prasinus and Mesocyclops longisetus (Melão & Rocha, 2004). Production was calculated for each species separately, using the method based on their population dynamics. In order to analyze the factors regulating the production, population dynamics were related to environmental factors. The results of these analysis in regard to dominant cladoceran species, Bosminopsis deitersi Richard, 1895 (Anomopoda, Branchiopoda), were presented here. Since this species shows continuous recruitment, a population dynamics model is used to integrate field data with laboratory data on development rates and length/weight relationships. This involves the use of data as duration of the egg, juvenile and adult stages, at different temperatures, which are examined in this paper.

Despite the importance of cladocerans in freshwater trophic chains, studies focusing on their production, especially in tropical and subtropical areas, are rare. In Brazil, papers regarding production of cladoceran populations in freshwater environments are basically inexistent. Although there are a few studies regarding life history characteristics, standing biomass or production for some cladocerans zooplankters in tropical and subtropical environments in the world (Gras & Saint-Jean, 1969, 1976, 1983; Hart, 1985; 1987; Hardy & Duncan, 1994; Irvine & Waya, 1999; Lewis, 1979; Mavuti, 1994; Saint-Jean & Saint-Jean Bonou, 1994), the present work is the first one focusing these aspects for Bosminopsis deitersi, a species currently found in these ecosystems.

Material and methods

Lagoa Dourada is a small, shallow reservoir located in the tropical region of Brazil (22° 11' 33" S; 47° 55' 2"W), Brotas District, São Paulo State (Fig. 1). As this environment is near a transition region, its characteristics are very similar to the tropical ones. It has a surface area of 76,815m^2, with a mean depth of 2.6m, maximum depth of 6.3m, and volume of 202,743m^3. It is located at an altitude of 715m.

The season with the lowest rainfall lasts from April to September (dry cold season) while that with the highest goes from December to February (rainy hot season). Soil in the surrounding area of the reservoir is acid and sandy, and the typical vegetation is "cerrado", the Brazilian savannah. The reservoir has great transparency; its bed is largely covered by macrophytes and the freshwater sponge Metania spinata (Melão & Rocha, 1999). Daily sampling was carried out during 15 days, both in summer (January 10-24, 1995) and winter (June 28 – July 12, 1995) at the limnetic region (5.2m depth, without macrophytes).

Zooplankton samples were collected with a low-rotation motorized pump. Volumes

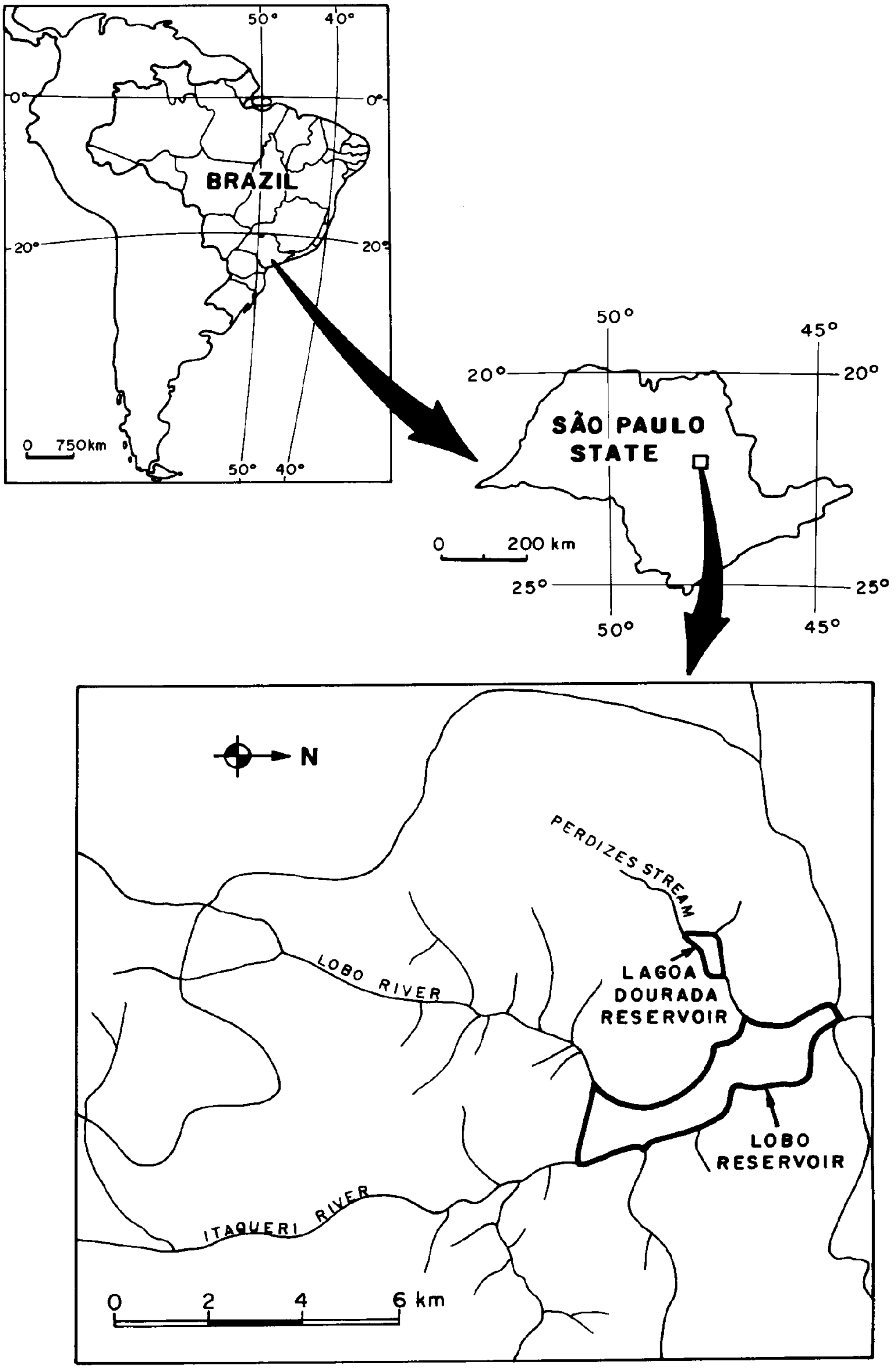

Figure 1: Map of the Lobo watershed with the location of Lagoa Dourada reservoir, Brazil.

of 300 and 100 L of water, for zooplankton and phytoplankton, respectively, were obtained, integrating the water column from 0 to 4.5m depth, sieved on 68 and 20mm-mesh nets and preserved in 4% formaldehyde.

B. deitersi, the dominant planktonic cladoceran species, was also raised in the laboratory, using the techniques described by Bottrell et al. (1976) and Vijverberg (1989). Culture vessels of 15mL were used for cultures. Animals were fed with reservoir seston enriched with algae from laboratory cultures at 10^5 cells mL^{-1} (Chlamydomonas sp, Scenedesmus bijugus and Monoraphidium pusillum). Cultures were kept at 20 and 25°C ± 1, close to local winter and summer mean temperatures (18.10 and 26.86°C, respectively), with a 12h photoperiod. Culture medium replacement and observations were performed every 24 hours.

Biomasses were calculated using length-weight relationships obtained by measuring and weighing non-preserved animals (dried at 60°C over 24 hours) on a Mettler MT-5 microanalytical balance (accuracy of 0.1mg).

Secondary production (P) was calculated by the biomass increment method (Winberg et al., 1965), which takes into account biomass increment (Dv), development time (T) and number of individuals (N) of each instar or, in this case, size classes (neonates = n, juveniles = j and adults = a), using the following equation:

$$P = (Nn.\,Dvn)\,Tn^{-1} + (Nj.\,Dvj)\,Tj^{-1} + (Na.\,Dva)\,Ta^{-1}$$

The production:biomass (P:B) ratio and turnover time ($(P:B)^{-1}$) were also determined.

The algal carbon concentration for the dominant phytoplankton species in the environment was calculated from a cell carbon and cell volume relationship provided by Rocha & Duncan (1985). Algal volumes were obtained adopting the nearest geometric form of each species for calculations, and multiplying individual species biovolume by population densities in the samples.

Results

Laboratory results: life history

Table I summarizes the life history data (mean values) of B. deitersi raised under laboratory conditions (20 and 25°C ± 1). Mean lengths are given in Table II and weights in Table III, for different age classes. These data were used for the calculation of field cladoceran production.

Field results: population dynamics, standing stock and production of B. deitersi

Figure 2 compares the daily numerical density (individuals (ind.) m^{-3}) of B. deitersi with that of the dominant zooplankton species in the reservoir during the summer and winter of 1995, as well as the algal carbon concentration in the water over the same period (see also Melão & Rocha, 2004). Among microcrustaceans, B. deitersi was dominant in all samples (up to 68000 ind. m^{-3} in summer and 17250 ind. m^{-3} in winter), followed by the copepods Tropocyclops prasinus in summer and Mesocyclops longisetus in winter (Melão & Rocha, 2004). Among rotifers, Hexarthra intermedia was abundant in summer, whereas Polyarthra vulgaris predominated in winter (Melão & Rocha, op cit.). The cladoceran under study had a mean relative numeric abundance of 24.5% in summer and 32.2% in winter.

Table I: Life history data (mean values) of B. deitersi raised under laboratory conditions (20°C and 25° C ± 1° C).

T		De	CS	N	E %	ICI	PA	IP	TI	MI	L	ML
	M	1.62	1.47	1.21	83.33	1.88	4.56	2.00	4.47	7	11.85	19.55
20°C	SD	0.53	0.59	0.62	30.80	0.76	0.72	0.00	1.26	-	4.25	-
	n	48	66	66	66	38	19	19	19	-	20	-
	M	1.21	1.60	1.47	93.51	1.48	2.74	2.00	5.37	8	9.41	16.60
25°C	SD	0.51	0.69	0.72	20.44	0.61	0.87	0.00	1.71	-	3.22	-
	n	66	77	77	77	45	14	19	19	-	18	-

T = Temperature (°C); De = embryonic development time (days); CS = clutch-size; N = number of ecloded neonates; E % = percentage of eclosion; ICI = inter-clutch interval (days); PA = primiparous age; IP = number of instars until primiparous; TI = total number of instars; MI = maximum number of instars; L = mean longevity; ML = maximum longevity. M = mean; SD = standard deviation; n = number of replicates.

Table II: Mean values (mm) of length and width of eggs, length of neonates and successive moults of B. deitersi raised under laboratory conditions (20 and 25°C ± 1°C).

T		Eggs length	Eggs width	Neonates	1st Mo	2nd Mo	3rd Mo	4th Mo	5th Mo	6th Mo	7th Mo	8th Mo
	M	138.67	99.67	185.25	240.50	282.29*	308.29	338.00	364.00	372.67	-	-
20°C	SD	13.43	10.61	16.66	18.38	23.39	9.83	26.00	0.00	15.01	-	-
	n	6	6	8	8	7	7	3	3	3	-	-
	M	136.50	91.00	208.00	253.50	293.43*	312.00	320.67	351.00	351.00	390.00	390.00
25°C	SD	12.04	12.04	21.23	12.04	19.65	0.00	15.01	15.01	18.38	0.00	-
	n	8	8	7	8	7	6	3	4	2	2	1

Numbers marked with * correspond to primiparous females' length. T = Temperature (°C); M= mean; SD = standard deviation; n = number of replicates; Mo = moult.

Table III: Dry weight (mg) of eggs, neonates, juveniles and adults of B. deitersi raised under laboratory conditions (20 and 25°C ± 1°C).

	Eggs	Neonates	Juveniles	Female (no eggs)	Female (+ eggs)
M	0.10	0.23	0.55	0.70	0.80
SD	0.00	0.12	0.02	0.10	0.08
n	3 (57)	5 (106)	3 (42)	3 (71)	4 (41)

M = mean; SD = standard deviation; n = number of replicates. Numbers in brackets are the total number of individuals weighed.

The mean contribution of each age class to total B. deitersi numerical density, standing stock and production is presented in Figure 3. All mean values were higher in summer than in winter. There was a predominance of adults (including females with and without eggs) both in summer and winter. In summer, the female with eggs class represented approximately 28% of adults, while in winter, 17%, evidenced the higher reproductive potential in the first period.

Numerical density (ind. m^{-3}), standing stock and production of each age class (neonate, juvenile and adult) during the fifteen sampling days in summer and winter of 1995, are summarized in Figure 4. Neonate and juvenile's production is somatic growth, while for adult, only the reproductive production was considered. In general, adult numbers surpassed those of other age classes in summer (Fig. 4). In winter, although adult predominated as a mean (Fig. 3), daily juvenile densities were similar or slightly higher than adults in several sampling days (Fig. 4). There was a large variability in densities recorded daily. Total daily densities varied up to 25 times in summer and 6 times in winter. The regularity of peaks and subsequent decreases suggests that it could be caused by recruitment from eggs followed by predation, and partially by drift losses.

Among the microcrustaceans, B. deitersi displays the highest biomass values in both sampling periods (compare with Melão & Rocha, 2004). Mean values of 11.8mgDW m^{-3} (ranging from 1.5 to 42.3mgDW m^{-3}) were found in summer and of 1.7mgDW m^{-3} (ranging from 1.7 to 9.1mgDW m^{-3}) in winter. Cladoceran biomass represented, in average, 54.66% of the total zooplankton biomass in summer and 75.09% in winter. B. deitersi, the most abundant cladoceran species in all sampling days, represented, as a mean, 97.36% of the cladoceran biomass in summer and 92.41% in winter. Adult biomass predominated both in summer and in winter, while neonates' biomass was lower throughout the sampling period.

Mean production rate of B. deitersi was almost four times higher in summer than in winter. In summer, the mean value of 2.13mgDW m^{-3} day^{-1} (ranging from 0.29 to 5.08mgDW m^{-3} day^{-1}) represents 47.46% of

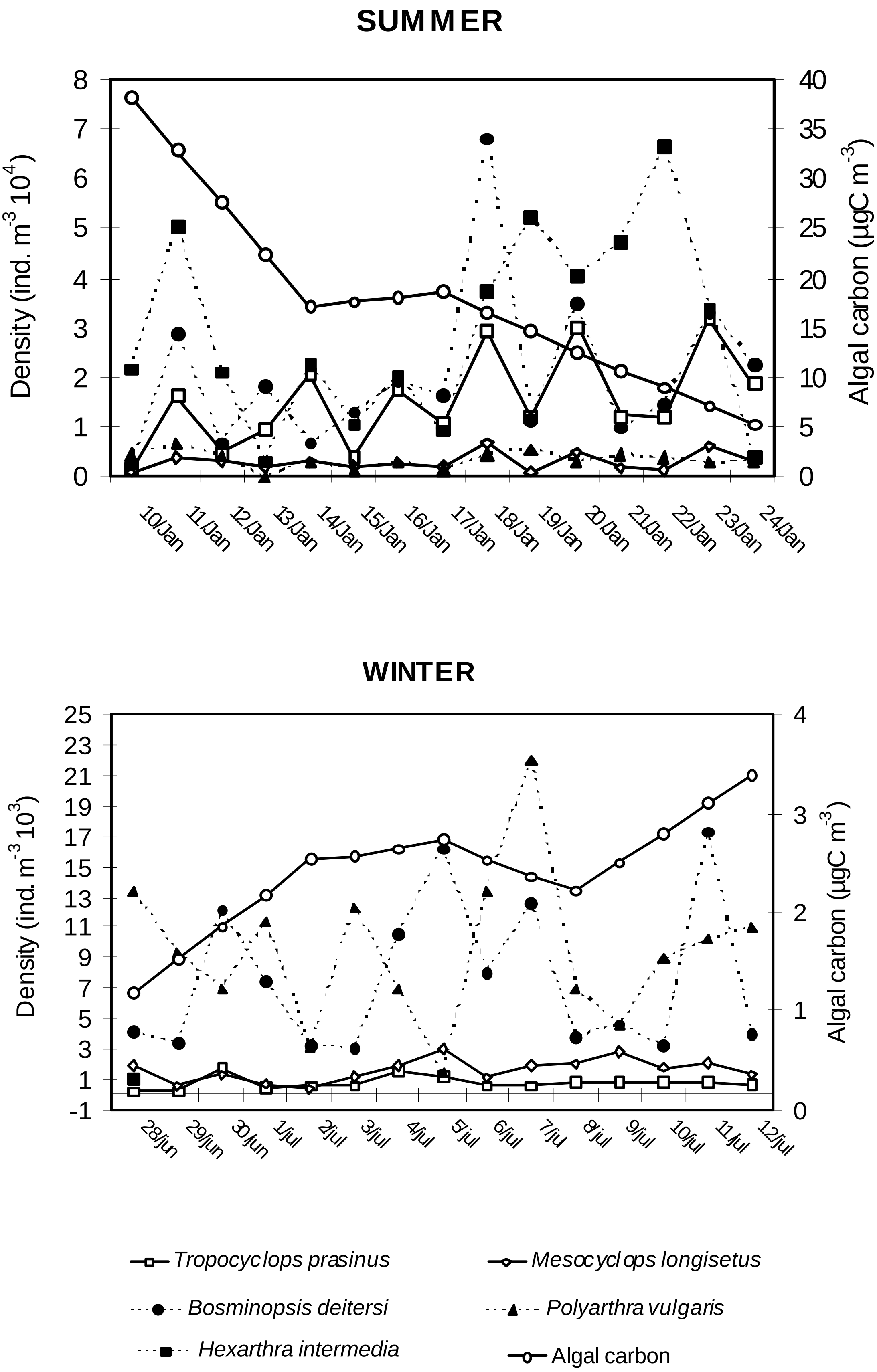

Figure 2: Comparison between daily numerical densities (ind. m^{-3}) of B. deitersi and those of the dominant zooplanktonic species in Lagoa Dourada during summer and winter of 1995, as well as the algal carbon concentration in the environment at this period (see also Melão & Rocha, 2004).

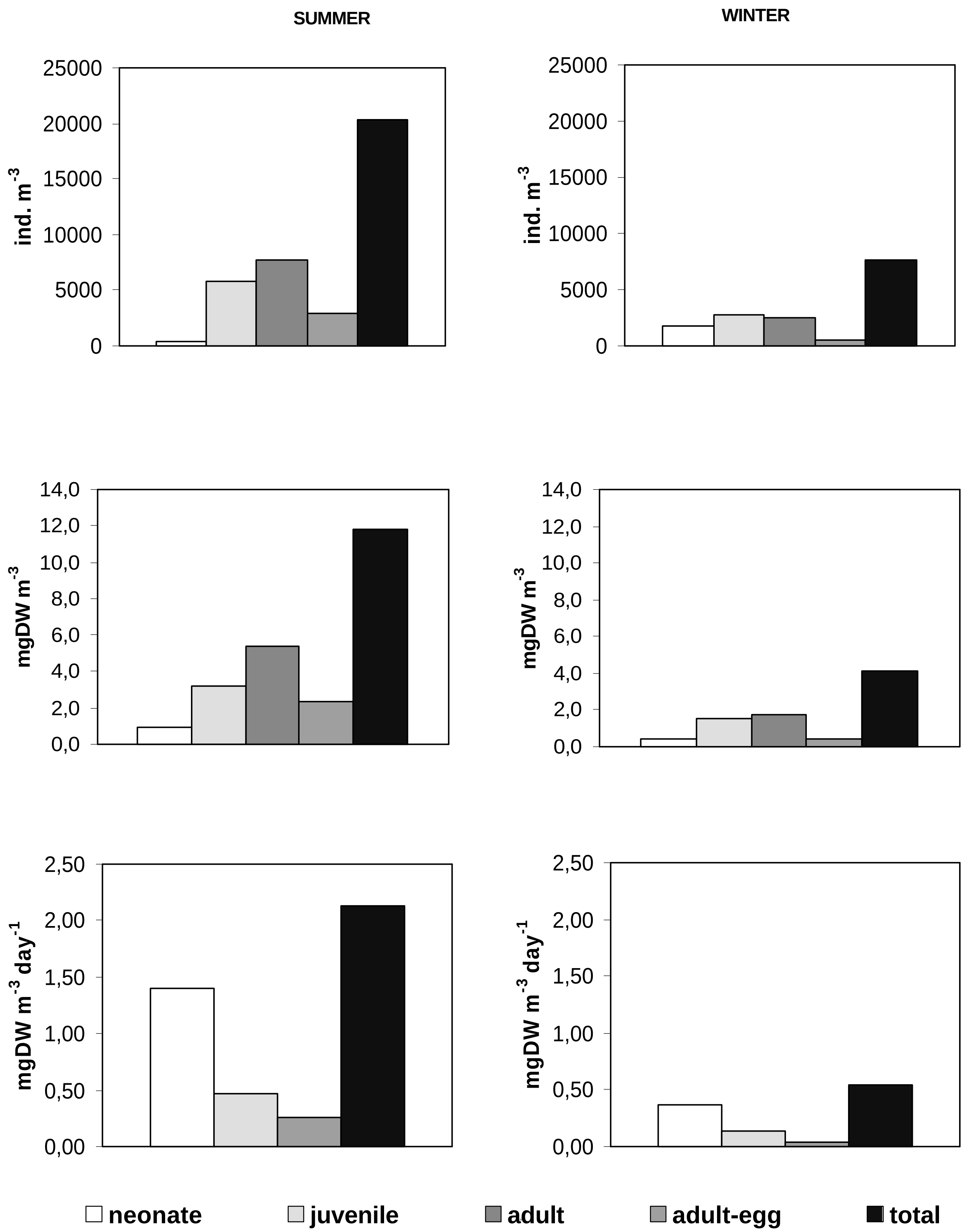

Figure 3: Mean contribution of each age class to total B. deitersi numerical density (a), standing stock (b) and average productivity (c) in Lagoa Dourada during summer and winter of 1995.

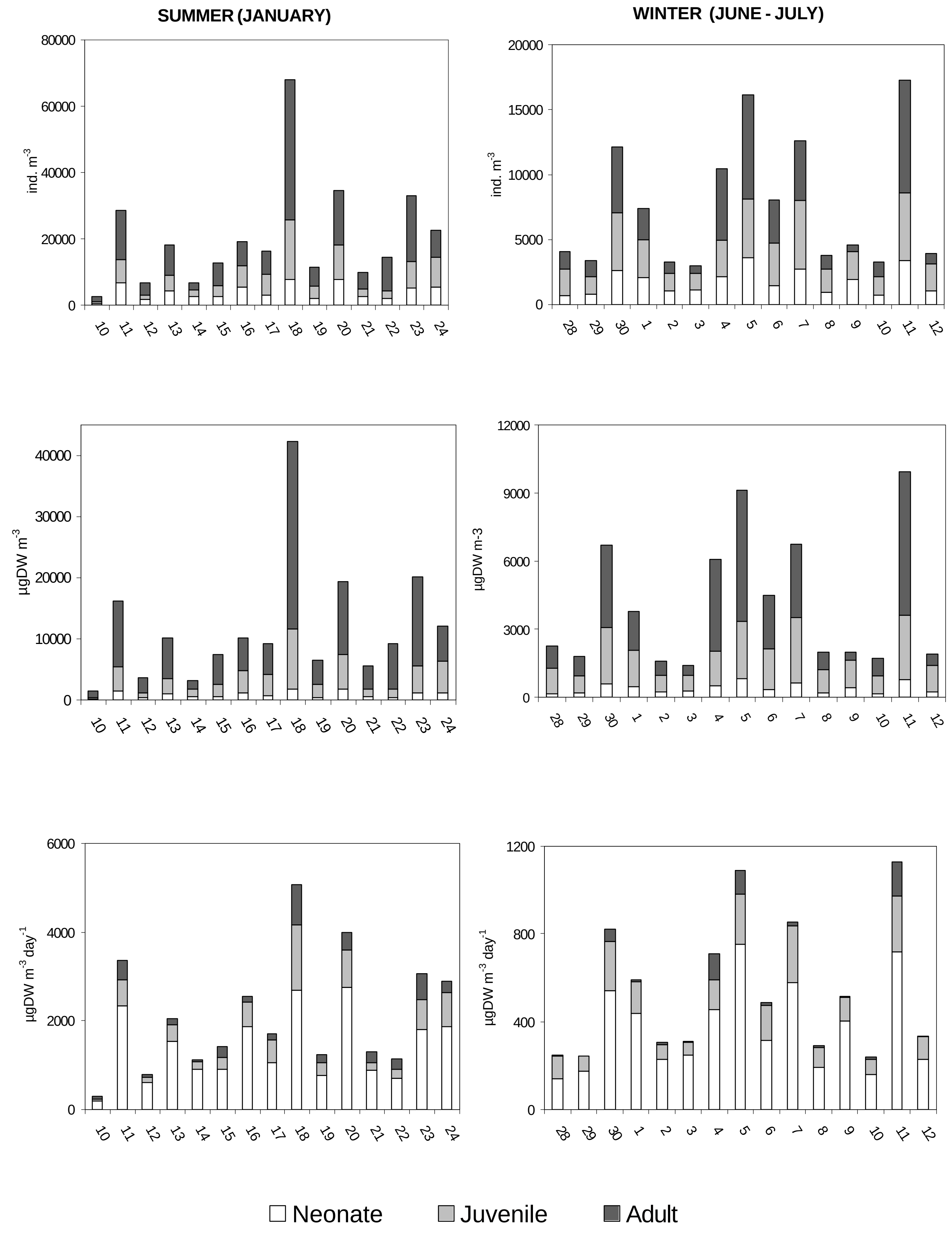

Figure 4: Daily numerical density (a), daily standing stock (b) and daily productivity (c) of each age class (neonate, juvenile and adult) of B. deitersi in Lagoa Dourada during fifteen sampling days in summer (January) and winter (June - July) of 1995.

total zooplankton production and, in winter, the mean of 0.54mgDW m^{-3} day^{-1} (ranging from 0.24 to 1.13mgDW m^{-3} day^{-1}) represents 63.33% of total zooplankton production. B. deitersi presented as a mean 97.36% of cladoceran production in summer and 92.41% in winter. The only other truly planktonic cladoceran species found in the samples, Ceriodaphnia cornuta, represented only 0.46% of cladocerans' production in summer and 0.08% in winter. Other cladocerans species, not typically planktonic, found in the samples (Simocephalus serrulatus, Acroperus harpae, Ilyocryptus spinifer, Macrothrix pectinata, Macrothrix rosea, Chydorus spp) represented altogether 2.18% of cladocerans' production in summer and 7.51% in winter.

For B. deitersi there was a tendency of decline in the P:B ratios in winter. The highest P:B ratio was 0.35 (2.86 days for biomass turnover) in summer and 0.26 (3.85 days for biomass turnover) in winter. Mean P:B rates were 0.20 and 0.15 (5.00 and 6.67 days for biomass turnover) in summer and winter, respectively.

Table IV shows a comparison of B. deitersi production related to reproduction (Pr) between laboratory (20 and 25°C± 1°C) and natural conditions (winter and summer). This production was obtained by multiplying the mean clutch-size, both in laboratory and in the reservoir, by egg weight.

Table IV: Comparison of production related to reproduction (Pr) of B. deitersi between laboratory and natural conditions (20°C and 25°C ± 1°C in laboratory which are near to mean winter and summer temperatures in the field).

T°C		CS-lab	CS-field	Pr-lab	Pr-field
20°C /	M	1.47	1.12	0.15	0.11
Winter	SD	0.59	0.33	-	-
	n	66	107	-	-
25°C /	M	1.60	1.11	0.16	0.11
Summer	SD	0.69	0.31	-	-
	n	77	70	-	-

CS-lab = clutch-size in laboratory conditions; CS-field = clutch-size in the reservoir; Pr-lab = production relating to reproduction in laboratory conditions; Pr-field = production relating to reproduction in the reservoir. Pr (mgDW) = CS x egg weight (0.10mg). M = mean; SD = standard deviation; n = number of replicates.

Discussion

B. deitersi is a truly tropical cladoceran species and has been commonly recorded in Brazilian freshwaters (Arcifa, 1984; Nogueira, 2001; Branco et al., 2000; Lima et al., 1996, 1998). Most of the citations for this species refer to studies regarding zooplankton composition and distribution (Arcifa, 1984.; Egborge, 1994; Lin et al., 2003; Nogueira, 2001; Branco et al., 2000; Lima et al., 1996, 1998), of morphology (Kotov, 1997) or predation impact (Chang et al., 2004; Chang & Hanazato, 2005; Mandima, 1999). The present study is the first providing data on life history and production of this species

Laboratory studies

Life history

Raising zooplankton species in laboratory is important to secondary production studies by supplying accurate information on development times under controlled conditions. According to Seitz (1979, in Hart 1985), some population dynamics parameters, like finite and instantaneous birth and death rates, may be greatly distorted by errors in egg development rates. The duration of embryonic development (De) in planktonic freshwater cladocerans is mainly dependent on temperature. Egg development rates for this group, as well as for copepods, have been reviewed by Bottrell et al. (1976). Nevertheless, some authors found that the quantity of food could also be an important factor for the duration of embryonic development of some tropical planktonic cladoceran species: they show some evidence that low food level affects De, which might be longer under lower values, due to the poor nutritional condition of the mother (Hardy & Duncan, 1994).

Life history data available for cladocerans from tropical and subtropical regions are limited, especially for non-daphnids. Particularly for B. deitersi, there are no data available in literature. Despite this, Bottrell et al. (1976) show that the mean development time for non-daphnids cladocerans, at 25°C, is not much longer than one day, which is close to what we obtained in this study (1.21 days). Temperature was the main factor controlling the duration of embryonic development of B. deitersi reared on a high food level (ad-libitum). Despite the lack of data for this species, the results on development times obtained in this study were consistent compared to those found in literature for some other planktonic cladoceran species, especially for those of approximately equivalent size (Tab. V), and follow the general trend of an inverse relationship between temperature and development time, as reported by other authors (Rocha & Matsumura - Tundisi, 1990; Hardy & Duncan, 1994; Melão, 1999), as well as for longevity.

Table V: Comparison of tropical cladoceran life history data; T = temperature; De = embryonic development duration and Dj = postembryonic development duration (juvenile from birth to primiparous) in days; CS = clutch size (eggs female^{-1}); L = mean longevity (days) and LM = maximum longevity (days).

Taxa	T	Life history data	Food conditions	Origin of animals	Author
Bosminopsis deitersi	20°C/25°C	De = 1.62 / 1.21 Dj = 4.56 / 2.74 CS = 1.47 / 1.60 L = 11.85 / 9.41	Seston + algae 10^5cels. mL^{-1} (Chlamydomonas sp., Scenedesmus bijugus, Monoraphidium pusillum),.	Lagoa Dourada reservoir (Brazil)	This study
Ceriodaphnia cornuta	20°C/25°C	De = 3.24 / 1.66 Dj = 4.76 / 3.83 CS = 2.22 / 1.76	Seston + algae 10^5cels. mL^{-1} (Chlamydomonas sp., Scenedesmus bijugus, Monoraphidium pusillum),.	Lagoa Dourada reservoir (Brazil)	Melão, 1999
Daphnia laevis	25°C	De = 2.00 Dj = 4.92 CS = 14.30	Scenedesmus bijugatus - 10^5 cels.mL^{-1}	São Paulo (Brazil)	Rocha & Matsumura - Tundisi, 1990
Daphnia gessneri	18°C/25°C	De = 3.39 / 2.00 Dj = 12.27 / 4.30 CS = 9.17 / 9.07	Scenedesmus bijugatus - 10^5 cels.mL^{-1}	São Paulo (Brazil)	Rocha & Matsumura - Tundisi, 1990
Daphnia ambigua	25°C	De = 2.0 Dj = 4.25 CS = 7.12	Scenedesmus bijugatus - 10^5 cels.mL^{-1}	São Paulo (Brazil)	Rocha & Matsumura - Tundisi, 1990
Diaphanosoma birgei	20°C/25°C	De = 2.44 / 1.36 Dj = 7.19 / 3.17 CS = 1.57 / 2.39	Seston (< 100mm)	Barra Bonita reservoir (Brazil)	Rietzler, 1998 in Fonseca & Rocha 2004
Ceriodaphnia silvestrii	20°C/25°C	De = 2.32 / 1.33 Dj = 5.45 / 4.50 CS = 2.02 / 4.13 L = 17.22	Seston (< 100mm)	Barra Bonita reservoir (Brazil)	Rietzler, 1998 in Fonseca & Rocha 2004
Daphnia gessneri	22°C/27°C/32°C	De = 2.08 to 2.63* / 1.58 to 2.25* / 1.0 to 1.29* Dj = 7.38 to 10.0* / 6.5 to 8.25* / 5.5 to 10.25*	Several diets Continuous flow cultures.	Lake Jacaretinga (Brazil)	Hardy & Duncan, 1994
Moina reticulatada	27°C	De = 1.0 to 2.13* Dj = 2.0 to 3.75	Several diets Continuous flow cultures.	Lake Jacaretinga (Brazil)	Hardy & Duncan, 1994
Diaphanosoma sarsi	27°C	De = 1.0 to 1.83* Dj = 3.0 to 5.25*	Several diets Continuous flow cultures.	Lake Jacaretinga (Brazil)	Hardy & Duncan, 1994
Ceriodaphnia silvestrii	25°C	CS = 9.46 L = 29.8	Monoraphidium dibowiskii- 10^5 cels. mL^{-1}	Tanks, S. Carlos (Brazil)	Fonseca & Rocha, 2004
Daphnia laevis	25°C	CS = 1.57 to 2.36	Monoraphidium dibowiskii- 10^5 cels. mL^{-1}	Tanks, S. Carlos (Brazil)	Fonseca, 1998

Table 5: Cont.

Taxa	T	Life history data	Food conditions	Origin of animals	Author
Ceriodaphnia cornuta	29°C	De = 1.27 Dj = 2.5 LM = 25	Natural	Lake Calado, (Brazil)	Hardy & Caraballo, 1995
Daphnia gessneri	29°C	Dj = 4.8 LM = 21	Natural	Lake Calado, (Brazil)	Hardy & Caraballo, 1995
Moina micrura	25°C	Dj = 1.09 to 1.42 L = 4.58 to 5.57	Several diets	Fish ponds, (Brazil)	Sipaúba-Tavares & Bachion, 2002.
Diaphanosoma birgei	25°C	Dj = 2.27 to 2.75 L = 13.51 to 16.21	Several diets	Fish ponds (Brazil)	Sipaúba-Tavares & Bachion, 2002.
Moina micrura	25°C	De = 2.15	Natural	Lake Lanao (Philippines)	Lewis, 1979
Bosmina fatalis	25°C	De = 1.42	Natural	Lake Lanao (Philippines)	Lewis, 1979
Daphnia gibba	24°C 19.1°C	De = 2.16* De = 3.0*	Seston (< 35mm) + Chlorella sp.	Lake le Roux (South Africa)	Hart, 1985
Daphnia barbata	24°C 19°C	De = 1.89* De = 2.95*	Seston (< 35mm) + Chlorella sp.	Lake le Roux (South Africa)	Hart, 1985
Daphnia longispina	24°C 20°C	De = 1.95* De = 2.54*	Seston (< 35mm) + Chlorella sp.	Lake le Roux (South Africa)	Hart, 1985
Moina brachiata	26.7°C 23.6°C 21.1°C 18.7°C	De = 1.02* De = 1.36* De = 1.73* De = 2.56*	Seston (< 35mm) + Chlorella sp.	Lake le Roux (South Africa)	Hart, 1985

* Values originally supplied in hours by the author.

The post-embryonic development time (Dj) was considered as the juvenile duration, from birth of neonates to the primiparous female. Thus, the duration of the juvenile stage also estimates the age of the primipara female.

Post-embryonic duration is mainly affected by temperature and quality/quantity of food. Hardy & Duncan (1994), studying three tropical cladoceran species, showed that the response to severe conditions of both, high temperatures and low food level (which could represent common conditions for tropical species), involves the increase in the number of juvenile instars, delaying the primipara's stage and, consequently, increasing her longevity. Indeed, the authors found that threshold concentration was affected by temperature. However, according to Bottrell et al. (1976), under non-limiting food levels, as in the present experimental study, post-embryonic development times are highly dependent on temperature. Like for embryonic durations, there was an inverse relationship between temperature and post-embryonic duration of B. deitersi from Lagoa Dourada reservoir (Tab. I). Females became primiparous, being able to produce a brood of young, after two moults, in both experimental temperatures.

According to Lei & Armitage (1980), an increase in post-embryonic development time could be due to either an increase in the number of juvenile instars or an increase in each instar duration or, yet, an increase in both. Apparently, B. deitersi has a lengthened longevity at 20°C by increasing the duration of the each individual instar, once the total number of instars was lower at 20°C than at 25°C, although the longevity in the first temperature was longer (Tabl. I and II).

Comparing post-embryonic development times of B. deitersi in the present experimental study with data available for other tropical species also raised under non-limiting food conditions (Tab. V), this small-size cladoceran seems to develop and attain maturity faster than larger animals, thus providing additional evidence to support the hypothesis that body size and duration of post-embryonic development of cladocerans are positively related (Hall et al., 1976 and Allan & Goulden, 1980 in Hardy & Duncan 1994).

In relation to the reproductive potential of B. deitersi, the difference between field and laboratory clutch sizes and, consequently, between production related to reproduction (Tab. IV) was found to be greater than the differences obtained at the two experimental temperatures. This is a consequence of the lower food availability in field (Lagoa Dourada is an oligotrophic environment), once the number of eggs produced by females are closely related to the quantity/quality of food. According to Vijverberg (1989), most species do not achieve their growth and reproduction potential in natural conditions because, frequently, there is limitation of food.

Most zooplankton studies evaluate species' abundance only in terms of the number of organisms per unit volume or area, rarely showing values of biomass (Dumont et al., 1975). Biomass information for local species is important, however, because it may vary with temperature, quality and quantity of food and the genotype of the local population. These data are also necessary in food web and secondary production studies. Although other weight data for B. deitersi were not found for comparison, Table VI shows some stage-specific dry-weight data available for some planktonic cladocerans, for comparison.

Table VI: Weight values of planktonic cladocerans, from several sources. Dry weight (mgDW) of eggs, neonates (N), primipara (P), adult females (F) and mean of mixed sizes (M).

Species	Dry weight (µgDW)	Origin of animals	Author
Ceriodaphnia silvestrii	N = 1.8 P = 8.4	Fish ponds, SP (Brazil)	Rocha & Sipaúba-Tavares, 1994
Ceriodaphnia silvestrii	N = 3.8 P = 9.7	Tanks, S. Carlos (Brazil)	Fonseca & Rocha, 2004
Ceriodaphnia richardi	N = 0.5 P = 4.9	Lake Monte Alegre (Brazil)	Bunioto & Arcifa in Fonseca & Rocha 2004
Ceriodaphnia reticulata	Egg = 0.26 F = 1.04 to 9.58 (0.4 to 1.2 mm)	Ag. Sidi Ali (Morocco)	Dumont et al., 1975
Ceriodaphnia quadrangula	Egg = 0.35 F = 1.32 to 15.86 (0.4 to 1.2 mm)	Lake Donk (Belgium)	Dumont et al., 1975
Moina micrura	M = 1.35	Lake George (Uganda)	Burgis, 1974
Ceriodaphnia cornuta	M = 1.13	Lake George (Uganda)	Burgis, 1974
Daphnia barbata	M = 2.75	Lake George (Uganda)	Burgis, 1974
Moina micrura	M = 2.3	Lake Chad (Africa)	Gras & Saint-Jean, 1983
Diaphanosoma excisum	M = 2.5	Lake Chad (Africa)	Gras & Saint-Jean, 1983
Bosmina longirostris	M = 0.75	Lake Chad (Africa)	Gras & Saint-Jean, 1983
Daphnia barbata	M = 2.9	Lake Chad (Africa)	Gras & Saint-Jean, 1983
Bosmina longirostris	M = 0.86	Lake Kariba (Zimbabwe)	Masundire, 1994
Ceriodaphnia cornuta	M = 1.56	Lake Kariba (Zimbabwe)	Masundire, 1994
Diaphanosoma excisum	M = 1.81	Lake Kariba (Zimbabwe)	Masundire, 1994
Daphnia lumholtzi	M = 6.5	Lake Kariba (Zimbabwe)	Masundire, 1994

Field studies

Population dynamics and biological interactions

The regulation of the number of organisms in a population is frequently seen as being due to predation (top-down) or to food resource availability (bottom-up), but these two types of regulation are related (Leibold, 1989).

Although there were no previous detailed studies on feeding ecology of B. deitersi, taking into account its population dynamics in Lagoa Dourada (Melão, 1997) as well as laboratory cultures maintained in this study, we can consider it as a filtering species, feeding mainly on algae, bacteria and detritus, i.e. the typical food source of major part of cladocerans' species (Wylie & Currie, 1991). During the present study, it grows well with algae as food source in a culture medium not free of bacteria and appears to have a positive relation, in the field, with algae and possible bacteria increases. Nevertheless, the relative importance of algae and bacteria for this species remains to be examined.

In many tropical and subtropical water bodies, the alternation of rainy calm summers with dry windy winters constitutes, in most cases, the main factor promoting seasonal changes in plankton communities. In Lagoa Dourada, there were great changes between summer and winter phytoplankton populations, related to the rainfall. In summer, intensified production and decomposition processes, following nutrient loading stimulates secondary production. Primary production seems to be the main limiting factor for zooplankton growth in this reservoir, since algal carbon is very low, even in summer (17.5 to 18.3mgC m^{-3}) and algal carbon in summer (7.5 times that of winter) is associated to relatively small sizes of algae (Peridiniales) compared to those in winter (Desmidiaceae) (Melão, 1997; Melão & Rocha, 2000, 2004).

Food & temperature are essential factors to determine zooplankton temporal dynamics in freshwater ecosystems. In Lagoa Dourada, we could observe that B. deitersi daily fluctuations, although quite irregular, evidencing several food sources, it is possible to see some peaks related to algae cellular carbon concentration and with the dynamics of the potential predators' populations (see Fig. 2). In summer, for example, the peaks for this cladoceran population followed the peaks for algal carbon concentrations and the highest peak abruptly fell down when algae began to decrease. One last peak occurred when algal carbon concentration was already decreasing, but this was preceded by an increase of total and organic material and, possibly, bacterial populations related to high decomposition rates in the reservoir during rainy periods (Melão & Rocha, 2000). Bacteria populations must represent an important alternative food source for planktonic cladocerans in Lagoa Dourada. The importance of bacteria on maintenance of cladoceran populations was pointed out by Wylie & Currie (1991), who suggested that either algae or bacteria populations could result in the same carbon transfer rates by a time unit in crustaceans.

In our field data, it was also possible to identify a probable prey-predator relationship between the populations of B. deitersi and Tropocyclops prasinus (a small cyclopoid copepod), reflecting a potential impact on the survival of this planktonic prey (see also Melão & Rocha, 2004). In fact, predation on this cladoceran by this cyclopoid species was observed in laboratory experimental studies by Melão & Rocha (2004). On the other hand, in winter, the cyclopoid Mesocyclops longisetus had a relative higher importance on the daily fluctuations of B. deitersi, once populations of the first predator (T. prasinus) decreased in this period (Melão & Rocha, 2004). Chang & Hanazato (2005) studying the vulnerability of three small cladoceran species, including B. deitersi, to predation by Mesocyclops sp. found that this cyclopoid rejected prey higher than 0.35mm of the two larger studied species, whereas most individuals of B. deitersi were consumed. Indeed, according to these authors, the greatest vulnerability and shorter prey handling is during the juvenile period, thus Mesocyclops sp. ingest small juveniles more efficiently than larger individuals. In Lagoa Dourada, the period in which M. longisetus replaces T. prasinus (winter) coincides with a larger proportion of neonates and juveniles in relation to adults of B. deitersi (although numeral densities are smaller than in summer), what might have favoured the first predator species in winter. Thus, it is possible to verify that decreases in B. deitersi population density were, in this study, frequently followed by increases in both predators' populations. As pointed out by Gliwicz & Pijanowska (1989), the predation intensity has a determinant role in succession events of zooplankton populations, together with abiotic factors and food availability (quantity and quality).

Standing stock

Studies on zooplankton standing stock are useful to supply information about available material in each trophic level, besides of being a more suitable measure of organisms' growth, once lengths do not take into account the nutritional reserves. Nevertheless, the difficulties involved in obtaining these values explain why so few zooplankton biomass estimates are available for tropical environments (Payne, 1986).

Standing stock data for tropical and subtropical cladocerans species found in the literature show large variability. Gras and Saint-Jean (1983) estimated for eight cladoceran species in Lake Chad (Africa), under mean temperature of 26.2°C, the following mean standing stock values for two consecutive years of study: 16.5mgDW m^{-3} for Moina micrura; 27.5mgDW m^{-3} for

Diaphanosoma excisum; 29.6mgDW m^{-3} for Bosmina longirostris; 27.8mgDW m^{-3} for three Daphnia species and 23.1mgDW m^{-3} for two Ceriodaphnia species. In Lagoa Dourada, under mean temperatures of 19.1ºC to 25.6ºC in winter and summer, respectively, we found lower mean standing stock values (4.1 and 11.8mgDW m^{-3}), which could be explained by lower food availability (20 to 280 mg chlorophyll a m^{-3} in L. Chad and 1.8 mg chlorophyll a m^{-3} in Lagoa Dourada – Melão & Rocha, 2000), besides the smaller size of B. deitersi and differences in temperatures. However, the values are closer to those obtained by Lewis (1979) for three cladoceran species from Lake Lanao (Philippines), under mean temperature of 24ºC (20mgDW m^{-3} for Diaphanosoma modigliani; 2.7mgDW m^{-3} for Moina micrura and 3.7mgDW m^{-3} for Bosmina fatalis), especially for the small ones.

At Lake Malawi, Irvine & Waya (1999) obtained a mean standing stock of 55.5mgDW m^{-2} (ranging from 15 to 123mgDW m^{-2}) for Diaphanosoma excisum, the dominant cladoceran species. In this environment, the smaller cladoceran, Bosmina longirostris, contributed little to overall biomass, usually with less than 10mgDW m^{-2}. The standing stock of the dominant cladoceran species in Lagoa Dourada is quite comparable to the figures just reported: mean production (integrated for a water column of 4.5m depth) were 53.05mgDW m^{-2} in summer and 18.45mgDW m^{-2} in winter.

Evaluating the production of planktonic crustaceans in Lake Naivasha (Kenya), a moderately eutrophic tropical water body, Mavuti (1994) found an annual mean biomass of 87.7mgDW m^{-3} for Diaphanosoma excisum under a mean annual temperature of 22ºC. The standing stock was higher in the rainy season, similarly to what was found in Lagoa Dourada in the present study. Lévêque and Saint-Jean (1979 in Mavuti, 1994) found a mean annual biomass of 27.5mgDW m^{-3} (annual mean temperature of 26ºC) for D. excisum in Lake Chad (oligotrophic). Cladocerans' mean standing stock in Lagoa Dourada is low when compared to these data. However, B. deitersi shows, in the summer, standing biomass peaks (up to 42.3mgDW m^{-3}) comparable to those for the cladoceran from Lake Chad, although this is a smaller species.

Hart (1987) also recorded data comparable to those from Lagoa Dourada, studying the population dynamics and production of five planktonic crustaceans' species from lake Le Roux (South Africa), a reservoir with distinct turbidity characteristics, during two years. For cladocerans, the author found the following standing biomass values, in the years of higher and lower turbidity, respectively: 1.1 and 9.7mgDW m^{-3} for Daphnia gibba; 0.4 and 0.6mgDW m^{-3} for Moina brachiata and 0 and 0.8mgDW m^{-3} for Daphnia barbata. The standing biomass values were, therefore, higher in the year with the lowest turbidity.

Detailed zooplankton standing stock data including the different stages of development are not common. The predominance of each stage is much related with the local environmental conditions. Lewis (1979) recorded values of 3.60 mgDW m^{-3} for juveniles and adults and 0.11mgDW m^{-3} for eggs and embryos of Bosmina fatalis (Lake Lanao).

In the present study, for B. deitersi, the dominant cladoceran species in Lagoa Dourada, the standing stock values of developmental stages were found to be higher than those recorded for copepods (Melão & Rocha, 2004) and also higher than those data reported by Lewis (1979). We found maximum values of 2.6, 10.5 and 30.6mgDW m^{-3} for neonates, juveniles and adults (including females with eggs), respectively. The predominance of adults, in summer or in winter, indicates that the environmental conditions are suitable for growth and reproduction of this species. Also, the very short development time of the neonate must contribute for a minor participation of this developmental stage in the total standing stock, as found for this species in Lagoa Dourada.

Production

The standing stock of the organisms present at a certain moment in an environment does not necessarily reflect the production rate of new material or the rate of energy transfer. The zooplankton, for example, accumulates little biomass compared to bigger animal species, but, on the other hand, they have a short generation time. Thus, productivity is a more realistic measure of the contribution of each species to the energy and the available resources in the ecosystem.

Although there are several estimates for zooplankton production in African lakes and reservoirs, in South America they are almost non-existent. Production rates display great variation even among species of similar sizes or closely related species. Lévêque & Saint-Jean (1983 in Payne, 1986), quantifying the zooplankton production of Lake Chad (Africa), found a mean cladoceran production of 41.9 mgDW m^{-3} day^{-1} (ranging from 9.6 a 98.8 mgDW m^{-3} day^{-1}), being Moina micrura, Bosmina longirostris and Diaphanosoma excisum the three most important species, in terms of production, of this environment (40 to 66% of the total crustacean production). In Lagoa Dourada we found much lower values for crustaceans (Melão & Rocha, 2000, 2004). Particularly for B. deitersi, which represented more than 90% of cladoceran production, the mean values were not higher than 2.13mgDW m^{-3} day^{-1} (in summer), with a maximum value of 5.08mgDW m^{-3} day^{-1}.

Gras & Saint-Jean (1983) also estimated the production of crustacean zooplankton in Lake Chad, and found for cladocerans, under a mean temperature of 26.2°C, the following annual production values: 3118.1mgDW m^{-3} $year^{-1}$ for Moina micrura; 3242.4mgDW m^{-3} $year^{-1}$ for Diaphanosoma excisum; 2123.1mgDW m^{-3} $year^{-1}$ for Bosmina longirostris; 2101.8mgDW m^{-3} $year^{-1}$ for three Daphnia species and 3494.9mgDW m^{-3} $year^{-1}$ for two Ceriodaphnia species. Converting B. deitersi production to the same unit, we have 195.8 and 768.4mgDW m^{-3} $year^{-1}$, in winter and summer, respectively. Again, the values found in Lagoa Dourada were much lower, probably as a consequence of a lower trophic state, reflecting the lower food availability, among other factors such as temperature and species' particularities.

Irvine and Waya (1999) reported annual production values of 8.0 and 8.6gDW m^{-2} for Diaphanosoma excisum in two consecutive years full lake cruises in Lake Malawi. In Lagoa Dourada, the water column integrated mean daily production of B. deitersi was 2.45 and 9.61mgDW m^{-2} day^{-1}, under mean temperatures of 17.8°C and 27.8°C (winter and summer, respectively). In annual basis, mean production of this cladoceran is 2.17gDW m^{-2} $year^{-1}$ (0.88 and 3.46gDW m^{-2} $year^{-1}$ in winter and summer, respectively) which is approximately four times lower than the values found by that author for that larger sized cladoceran species in the also oligotrophic, Lake Malawi.

Mavuti (1994) recorded a mean production rate of 5.96mgDW m^{-3} day^{-1} for Diaphanosoma excisum, the dominant planktonic cladoceran species from the slightly eutrophic Lake Naivasha (Kenya), in a mean temperature of 22.5°C. Like in Lagoa Dourada, the production was continuous but with irregular peaks, especially in the rainy season when planktonic standing biomass was higher. For the different developmental stages of D. excisum, the author registered mean annual production values of 0.44mgDW m^{-3} day^{-1} for eggs (7.4% of total production), 3.72mgDW m^{-3} day^{-1} for juveniles (62.4% of total production) and 1.80mgDW m^{-3} day^{-1} for adults (30.2% of total production). For B. deitersi, we found lower mean values (0.3 / 0.03, 1.4 / 0.4 and 0.5 / 0.1mgDW m^{-3} day^{-1}, for adults with eggs, neonates and juveniles, in summer and winter, respectively), what could certainly be expected due to the different trophic state of the environments as well as the intra-specific characteristics. However, the maximum values found in Lagoa Dourada for the developmental stages (0.9mgDW m^{-3} day^{-1} for eggs, considered as the adult production, 4.1mgDW m^{-3} day^{-1} for neonates and 1.6mgDW m^{-3} day^{-1} for juveniles) seem to be closer to the author's data.

In general, the cladoceran production rates in Lagoa Dourada were low compared to values recorded in the literature for tropical and subtropical regions.

P:B ratio

The P:B ratio is a productivity index commonly used and it is expressed as the reciprocal of the renewal time of a species population, under given conditions. Great differences have been found for the renewal rates among zooplankton species, although the reasons for that are not well understood.

Gras & Saint-Jean (1983) estimated mean daily P:B ratios for several cladocerans from Lake Chad. He found the values of 0.21, 0.20, 0.32, 012 and 0.52, respectively for: three species of Daphnia together, Bosmina longirostris; Diaphanosoma excisum; two Ceriodaphnia species and Moina micrura dubia, under a mean temperature of 26.2°C. Mavuti (1994) obtained a P:B ratio of 0.07 (turnover time of 13.7 days) for Diaphanosoma excisum in Lake Naivasha (Kenya). For this same species, Lévêque and Saint-Jean (1979 in Mavuti, 1994) reported a mean daily P:B ratio of 0.32 (turnover time of 3.1 days) in Lake Chad and

Irvine & Waya (1999) of 0.42 (original data on annual basis) in Lake Malawi, both in Africa. Hart (1987) registered values of P:B ratio ranging from 0.005 to 0.008 for two Daphnia species and 0.13 to 0.21 for Moina brachiata in Lake Le Roux (South Africa). Moina micrura from Lake Chad was found to have 27% to 87% of biomass renewal per day (Lévêque & Saint-Jean, 1983 in Payne, 1986). Lewis (1979) reported for three cladoceran species from Lake Lanao (Philippines), under mean temperature of 24°C, the following mean daily P:B ratio values: 0.24 for Diaphanosoma modigliani; 0.29 for Moina micrura and 0.21 for Bosmina fatalis.

Thus, in spite of the low biomass and productivity values, Bosminopsis deitersi, the species studied in the present study, shows a continuous reproduction along the year, with relatively high turnover rates when compared to other cladoceran species, reflecting both, high reproductive rates and short development time. It has an important role for the maintenance of the food chain of the oligotrophic Lagoa Dourada reservoir.

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References

Arcifa, M.S. 1984. Zooplankton composition of ten reservoirs in southern Brazil. Hydrobiologia, 113:137-145.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. & Weglenska, T. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool., 24:419-456.

Branco, C.W.C., Esteves, F.A. & Kozlowsky-Suzuki, B. 2000. The zooplankton and other limnological features of a humic coastal lagoon (Lagoa Comprida, Macaé, RJ) in Brazil. Hydrobiologia, 437:71-81.

Burgis, M.J. 1974. Revised estimates for the biomass and production of zooplankton in Lake George, Uganda. Freshwater Biol., 4:535-541.

Chang, K.H. & Hanazato, T. 2005. Prey handling time and ingestion probability for Mesocyclops sp. Predation on small cladoceran species Bosmina longirostris, Bosminopsis deitersi, and Scapholeberis mucronata. Limnology, 6:39-44.

Chang, K.H., Nagata, T. & Hanazato, T. 2004. Direct and indirect impacts of predation by fish on the zooplankton community: an experimental analysis using tanks. Limnology, 5:121-124.

Dumont, H.J., Van De Velde, I. & Dumont, S. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia, 19:75-97.

Egborge, A.B.M., Onwudinjo, E. & Chigbu, P.C. 1994. Cladocera of coastal rivers of western Nigeria. Hydrobiologia, 272:39-46.

Fonseca, A.L. 1998. The life cycle of Ceriodaphnia silvestrii (Daday 1902) and Daphnia laevis (Birge 1878) (Crustacea, Cladocera) reared under different pH conditions. Verh. Int. Verein. Limnol., 26:1918-1921.

Fonseca, A.L. & Rocha, O. 2004. The life-cycle of Ceriodaphnia silvestrii Daday, 1902, a Neotropical endemic species (Crustacea, Cladocera, Daphnidae). Acta Limnol. Bras., 16:319-328.

Gliwicz, Z.M. & Pijanowska, J. 1989. The role of predation in zooplankton succession. In: Sommer, U. (ed.) Plankton ecology: sucession in plankton communities. Springer Verlag, Berlin. p.253-296.

Gras, R. & Saint-Jean, L. 1969. Biologie des crustacés du Lac Tchad. Cah. O R S T O M Ser. Hydrobiol., 3:43-60.

Gras, R. & Saint-Jean, L. 1976. Durée du développement embryonnaire chez quelques espèces de cladocères et de copépodes du Lac Tchad. Cah. O R S T O M Ser. Hydrobiol., 10:233-254.

Gras, R. & Saint-Jean, L. 1983. Production du zooplancton du Lac Tchad. Rev. Hydrobiol. Trop., 16:47-77.

Hardy, E.R. & Caraballo, P. 1995. Fluctuatión diaria de las poplaciones de Daphnia gessneri Herbst y Ceriodaphnia cornuta Sars (Crustacea-Cladocera) en el lago Calado. Bol. Cient., 379-396.

Hardy, E.R. & Duncan, A. 1994. Food concentration and temperature effects on life cycle characteristics of tropical Cladocera (Daphnia gessneri Herbst, Diaphanosoma sarsi Richard, Moina reticulata (Daday)): I. Development time. Acta Amazonica, 24:119-134.

Hart, R.C. 1985. Embryonic development times of entomostracan zooplankton from Lake le Roux (Orange River, South Africa), and their possible relationships to seasonal succession. Hydrobiologia, 127:17-26.

Hart, R.C. 1987. Population dynamics and production of five crustacean zooplankters in a subtropical reservoir during years of contrasting turbidity. Freshwater Biol., 18:287-318.

Irvine, K. & Waya, R. 1999. Spatial and temporal patterns of zooplankton standing biomass and production in Lake Malawi. Hydrobiologia, 407:191-205.

Kotov, A.A. 1997. Structure of thoracic limbs in Bosminopsis deitersi Richard, 1895 (Anomopoda, Branchiopoda). Hydrobiologia, 360:25-32.

Lei, C & Armitage, K.B. 1980. Growth, development and body size of field and laboratory populations of Daphnia ambigua. Oikos, 35:31-48.

Leibold, M.A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. Am. Nat., 134:922-949.

Lewis, W.M. 1979. Zooplankton community analysis: studies on a tropical system. Springer-Verlag, New York. 163p

Lima, A.F., Lansac-Toha, F.A. & Bonecker, C.C. 1996. Zooplankton in the floodplains of a tributary to the Paraná river in Mato Grosso do Sul, Brazil. Stud. Neotrop. Fauna Environ., 31:112-116.

Lima, A.F., Lansac-Toha, F.A., Velho, L.F.M. & Bini, L.M. 1998. Environmental influence on planktonic cladocerans and copepods in the floodplain of the Upper River Paraná, Brazil. Stud. Neotrop. Fauna Environ., 33:188-196.

Lin, Q.Q., Duan, S.S., Hu, R. & Han, B.P. 2003. Zooplankton distribution in tropical reservoirs, South China. Internat. Rev. Hydrobiol., 88:602-613.

Mandima, J.J. 1999. The food and feeding behavior of Limnothrissa miodon (Boulenger, 1906) in Lake Kariba, Zimbabwe. Hydrobiologia, 407:175-182.

Masundire, H.M. 1994. Mean individual dry weight and length-weight regressions of some zooplankton of Lake Kariba. Hydrobiologia, 272:231-238.

Mavuti, K.M. 1994. Durations of development and production estimates by two crustacean zooplankton species Thermocyclops oblongatus Sars (Copepoda) and Diaphanosoma excisum Sars (Cladocera), in Lake Naivasha, Kenya. Hydrobiologia, 272:185-200.

Melão, M.G.G. 1997. A comunidade planctônica (fitoplâncton e zooplâncton) e produtividade secundária do zooplâncton de um reservatório oligotrófico. São Carlos, UFSCar, 152p (PhD Thesis).

Melão, M.G.G. 1999. Desenvolvimento e aspectos reprodutivos de Cladóceros e Copépodos de águas continentais brasileiras. In: Pompeo, M.L.M (ed.) Perspectivas da Limnologia no Brasil. Gráfica e Editora União, São Luís. p.45-57.

Melão, M.G.G. & Rocha, O. 1999. Biomass and productivity of the freshwater sponge Metania spinata (Carter, 1881) (Demospongiae: Metaniidae) in a Brazilian reservoir. Hydrobiologia, 390:1-10.

Melão, M.G.G. & Rocha, O. 2000. Productivity of zooplankton in a tropical oligotrophic reservoir over short periods of time. Verh. Int. Verein. Limnol., 27:2879-2887.

Melão, M.G.G. & Rocha, O. 2004. Life history, biomass and production of two planktonic cyclopoid copepods in a shallow subtropical reservoir. J. Plankton Res., 26:909-923.

Nogueira, M.G. 2001. Zooplankton composition, dominance and abundance as indicators of environmental compartmentalization in Jurumirim Reservoir (Paranapanema River), São Paulo, Brazil. Hydrobiologia, 455:1-18.

Payne, A.I. 1986. The ecology of tropical lakes and rivers. John Wiley, Chichester. 301p.

Rocha, O. & Duncan, A. 1985. The relationship between cell carbon and cell volume in freshwater algal species used in zooplanktonic studies. J. Plankton Res., 7:279-294.

Rocha, O & Matsumura-Tundisi, T. 1990. Growth rate, longevity and reproductive performance of Daphnia laevis Berge, D. gessneri Herbst and D. ambigua Scounfield in laboratory cultures. Rev. Bras. Biol., 50:915-921.

Rocha, O. & Sipaúba-Tavares, L.H. 1994. Cultivo em larga escala de organismos planctônicos para alimentação de larvas e alevinos de peixes: II – organismos zooplanctônicos. Biotemas, 7:94-109.

Saint-Jean, L & Saint-Jean, B. 1994. Growth, production, and demography of Moina micrura in brackish tropical fishponds (Layo, Ivory Coast). Hydrobiologia, 272:125-146.
Sipaúba-Tavares, L.H. & Bachion, M.A. 2002. Population growth and development of two species of Cladocera, Moina micrura and Diaphanosoma birgei, in laboratory. Braz. J. Biol., 62:701-711.
Vijverberg, J. 1989. Culture techniques for studies on the growth, development and reproduction of copepods and cladocerans under laboratory and in situ conditions: a review. Freshwater Biol., 21:317-373.
Winberg, G.C., Pechen, G.A. & Shushkina, E.A. 1965. Production of planktonic crustaceans in three lakes of different type. Zoologicheskii Zhurnal, 44:676-687.
Wylie, J.L. & Currie, D.J. 1991. The relative importance of bacteria and algae as food sources for crustacean zooplankton. Limnol. Oceanogr., 36:708-728.

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