

Life history, biomass and production of two planktonic cyclopoid copepods in a shallow subtropical reservoir

MARIA DA GRAÇA GAMA MELÃO* AND ODETE ROCHA¹

DEPARTAMENTO DE HIDROBIOLOGIA AND ¹DEPARTAMENTO DE ECOLOGIA E BIOLOGIA EVOLUTIVA, UNIVERSIDADE FEDERAL DE SÃO CARLOS (UFSCAR), 13565-905, SÃO CARLOS, SP, BRAZIL

*CORRESPONDING AUTHOR: dmgm@power.ufscar.br

Received December 15, 2003; accepted in principle February 11, 2004; accepted for publication March 24, 2004; published online April 30, 2004

*Two planktonic cyclopoid copepods (*Tropocyclops prasinus* and *Mesocyclops longisetus*) were raised in the laboratory to obtain life history information (duration of embryonic and post-embryonic development, reproductive performance, longevity, and stage-specific length and weight values). Animals were maintained at 20 and 25°C, and fed ad libitum. Development times were temperature dependent when food was not limiting, with shorter periods of embryonic and post-embryonic development and decreased longevity at 25°C. 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 biomass and production of these species in a shallow reservoir, Lagoa Dourada, Brazil. The maximum production rate of *T. prasinus*, attained during summer, was 2.8 mg dry weight (DW) m⁻³ day⁻¹ and the highest daily production:biomass (P:B) ratio was 0.29, whereas for *M. longisetus* the maximum production rate was 1.4 mg DW m⁻³ day⁻¹ and the highest daily P:B ratio was 0.39, in the winter. Over short time intervals (every other day), there was great variability of the species production rates. Species production rates were low compared to values reported in the literature for the same or other species of equivalent sized copepods from both tropical and subtropical regions.*

INTRODUCTION

Basic knowledge on the life history and biomass of different zooplankton species provides the necessary data for the calculation of secondary production, as well as information about the competitive strategies responsible for their success in a given environment. The study of secondary production has an important place in biological research. Assessing the balance between input and output of matter and energy of populations is vital for a complete understanding of the ecosystem's dynamics.

Although copepods play an important role in freshwater trophic chains, studies focusing on their population dynamics and production, especially in tropical and subtropical areas, are rare. This gap in knowledge is partly due to the lack of a database on the life history of regional zooplankton species, since the calculation of production usually requires experimental estimates of growth rates or development times. In Brazil, the only work on secondary production of a copepod population in freshwater is that regarding production of

Argyrodiaptomus furcatus (calanoid copepod), a dominant species in Lobo reservoir (Rocha and Matsumura-Tundisi, 1984).

The present work was intended to quantify field biomass and secondary production of *Tropocyclops prasinus* and *Mesocyclops longisetus*, the only planktonic copepod species occurring in Lagoa Dourada, an oligotrophic reservoir, analysing short-term species fluctuations in the rainy and dry seasons, over 1 year. In addition, copepods were raised under laboratory conditions, to obtain life history information such as the duration of embryonic and post-embryonic development, reproductive performance, longevity, and stage-specific length and weight relationships.

METHOD

Lagoa Dourada is a small, shallow reservoir located in the subtropical region of Brazil (22°11'33"S; 47°55'2"W), Brotas District, São Paulo State (Figure 1).

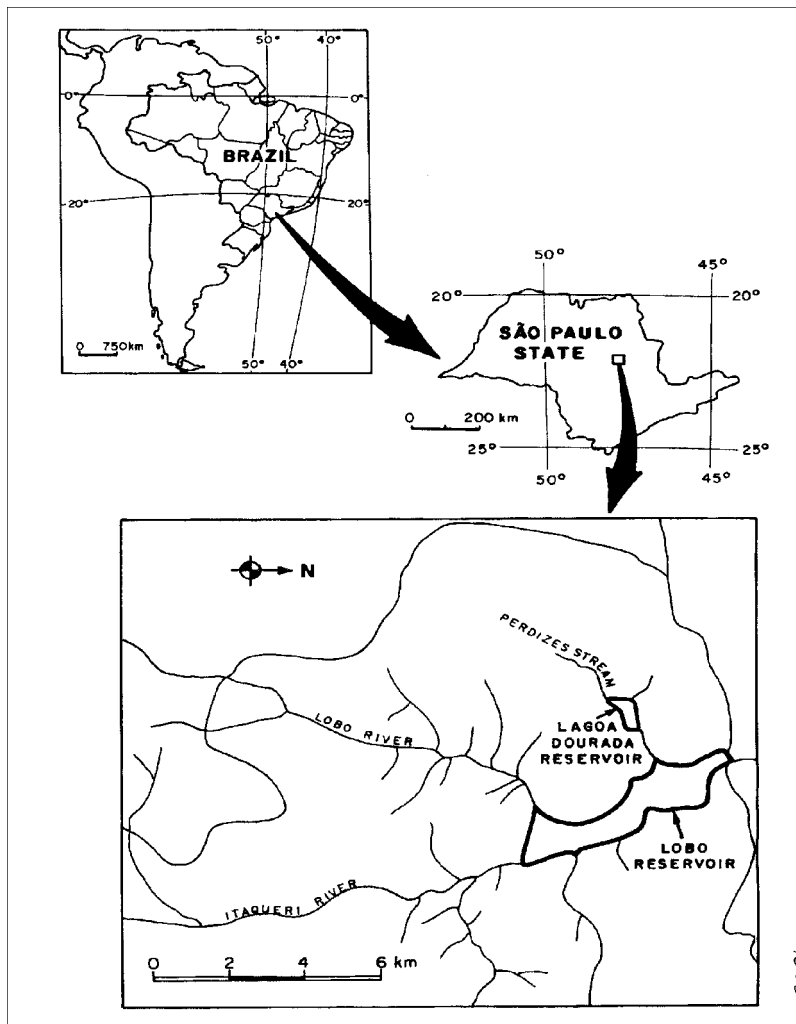


Fig. 1. Map of the Lobo watershed with the location of Lagoa Dourada reservoir, Brazil.

As this environment is near a transition region, its characteristics are very close to tropical ones. It has a surface area of 76 815 m², with a mean depth of 2.6 m, maximum depth of 6.3 m and volume of 202 743 m³, and is located at an altitude of 715 m.

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

Zooplankton samples were collected with a low-rotation motorized pump. Volumes of 300 and 100 L of

water, for zooplankton and phytoplankton, respectively, were obtained, integrating the water column from 0 to 4.5 m depth, sieved on a 68- μ m-mesh net and preserved in 4% formaldehyde.

The cyclopoid species were also raised in the laboratory, using the techniques described by Bottrell *et al.* (Bottrell *et al.*, 1976) and Vijverberg (Vijverberg, 1989). Culture vessels of 15 and 60 mL were used for *T. prasinus* and *M. longisetus*, respectively. Copepods were fed with reservoir seston enriched with algae from laboratory cultures at 10⁵ cells mL⁻¹ (*Chlamydomonas* sp., *Scenedesmus bijugus* and *Monoraphidium pusillum*) and protozoans at 2 \times 10³ cells mL⁻¹ (*Colpidium campyllum*, *Colpidium colpoda* and *Paramecium caudatum*). Cultures were kept at 20 and 25°C \pm 1°C, close to local winter and summer mean temperatures (18.10 and 26.86°C), with a 12 h photoperiod. Culture medium replacement and observations were performed every 24 h.

Biomasses were obtained using length–weight relationships for each species, obtained by measuring and weighing non-preserved animals (dried at 60°C over 24 h) on a Mettler MT-5 microanalytical balance (accuracy of 0.1 µg).

Secondary production (P) was calculated by the biomass increment method (Winberg *et al.*, 1965), which takes into account biomass increment ($\Delta\omega$), development time (T) and number of individuals (N) of each instar (subscripts: nauplii = n, copepodids = c and adults–eggs = e), using the following equation:

$$P = (N_e \Delta\omega_e)T_e^{-1} + (N_n \Delta\omega_n)T_n^{-1} + (N_c \Delta\omega_c)T_c^{-1}$$

The adult mean weight was taken as the final value for copepodids, whereas $\Delta\epsilon_e$ is the egg weight (or initial weight of nauplii).

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 and Duncan (Rocha and Duncan, 1985). Algal volumes were obtained by 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

Tables I and II summarize the life history data (mean values) of *T. prasinus* and *M. longisetus* raised under laboratory conditions (20 and 25°C ± 1°C). Mean weights are given in Table III and lengths in Table IV, for different stages of development. These data were used for the calculation of field copepod production.

Field results: population dynamics, standing stock and production of *T. prasinus* and *M. longisetus*

Figure 2 compares the daily numerical density [individuals (ind.) m⁻³] of the two cyclopoid species under study 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. Among microcrustaceans, *Bosminopsis deitersi* (Cladocera) was dominant in all samples, followed by *T. prasinus*, which was dominant in the summer (up to 31 500 ind. m⁻³), and *M. longisetus*, dominant in the winter (maximum of 3000 ind. m⁻³). Of the rotifers, *Hexarthra intermedia* was abundant in the summer, whereas *Polyarthra vulgaris* predominated in the winter. Copepods had a mean relative numeric abundance of 15.89% in the summer, decreasing to 9.38% in the winter.

Table I: Life history data (mean values) of *T. prasinus* and *M. longisetus* raised under laboratory conditions (20 and 25°C ± 1°C)

| Species | | De | CS | N | E % | ICI |
|-------------------------------|----|------|-------|-------|-------|------|
| <i>Tropocyclops prasinus</i> | | | | | | |
| 20°C | X | 2.28 | 12.68 | 12.00 | 95.41 | 2.62 |
| | Sx | 0.69 | 2.51 | 2.31 | 9.37 | 0.99 |
| | n | 46 | 34 | 34 | 34 | 40 |
| 25°C | X | 1.61 | 10.68 | 9.97 | 93.55 | 2.14 |
| | Sx | 0.59 | 2.60 | 2.61 | 10.19 | 0.82 |
| | n | 47 | 31 | 31 | 31 | 32 |
| <i>Mesocyclops longisetus</i> | | | | | | |
| 20°C | X | 2.93 | 41.55 | 36.82 | 87.45 | 5.42 |
| | Sx | 0.56 | 8.50 | 11.97 | 21.80 | 0.45 |
| | n | 14 | 11 | 11 | 11 | 5 |
| 25°C | X | 1.84 | 44.91 | 43.23 | 96.23 | 3.76 |
| | Sx | 0.47 | 11.24 | 11.46 | 9.81 | 0.90 |
| | n | 35 | 22 | 22 | 22 | 10 |

De, embryonic development time (days); CS, clutch size; N, number of ecloded nauplii; E %, percentage of eclosion; ICI, inter-clutch interval (days); X, mean; Sx, standard deviation; n, number of replicates.

Table II: Life history data (mean values) of *T. prasinus* and *M. longisetus* raised under laboratory conditions (20 and 25°C ± 1°C)

| Species | Dpe | | | | | | | | | N-Fe | e-e | L | | | | |
|----------------------|-----|------|--------|--------|------|-----|-----|------|-----|------|------|------|------|------|------|------|
| | N-I | I-II | II-III | III-IV | IV-V | V-M | N-M | V-F | N-F | | | M | | F | | |
| | | | | | | | | | | | | X | max | X | max | |
| <i>T. prasinus</i> | | | | | | | | | | | | | | | | |
| 20°C | X | 6.4 | 1.7 | 1.4 | 1.6 | 1.6 | 1.6 | 14.4 | 3.7 | 16.8 | 19.1 | 21.5 | 43.9 | 60.4 | 64.8 | 98.7 |
| | Sx | 1.6 | 0.7 | 0.6 | 0.8 | 0.9 | 0.6 | 1.8 | 1.3 | 1.6 | 2.3 | 2.5 | 16.8 | | 17.6 | |
| | n | 11 | 11 | 11 | 11 | 11 | 10 | 10 | 11 | 11 | 10 | 10 | 4 | | 6 | |
| 25°C | X | 4.8 | 1.3 | 1.0 | 1.1 | 1.3 | 0.8 | 10.3 | 2.7 | 12.1 | 14.9 | 16.5 | 30.9 | 54.1 | 52.4 | 61.1 |
| | Sx | 1.7 | 0.5 | 0.3 | 0.4 | 0.7 | 0.4 | 2.3 | 1.5 | 2.7 | 2.6 | 2.7 | 13.6 | | 11.0 | |
| | n | 13 | 13 | 12 | 12 | 12 | 11 | 12 | 10 | 11 | 9 | 9 | 9 | | 6 | |
| <i>M. longisetus</i> | | | | | | | | | | | | | | | | |
| 20°C | X | 6.7 | 2.7 | 2.0 | 2.6 | 3.1 | 2.5 | 20.5 | 5.3 | 26.1 | 31.5 | 34.4 | 45.6 | 47.0 | 53.7 | 90.9 |
| | Sx | 1.5 | 0.9 | 0.8 | 1.4 | 1.6 | 0.7 | 1.4 | 1.7 | 2.8 | 0.6 | 0.7 | 1.5 | | 16.6 | |
| | n | 8 | 9 | 9 | 9 | 8 | 2 | 2 | 8 | 8 | 5 | 5 | 5 | | 8 | |
| 25°C | X | 3.8 | 1.8 | 1.8 | 1.6 | 2.6 | 1.6 | 14.1 | 3.7 | 22.4 | 29.6 | 31.2 | 42.8 | 44.1 | 49.3 | 57.4 |
| | Sx | 0.5 | 0.7 | 1.0 | 0.8 | 1.5 | 0.6 | 1.9 | 2.1 | 2.7 | 2.7 | 2.5 | 1.3 | | 5.8 | |
| | n | 6 | 12 | 12 | 12 | 12 | 3 | 3 | 9 | 10 | 9 | 9 | 3 | | 8 | |

Dpe, post-embryonic development of nauplii to copepodid I (N-I); copepodids I-II, II-III, III-IV, IV-V, V to male (V-M), nauplii to male (N-M), V to female (V-F), nauplii to female (N-F), nauplii to female with eggs (N-Fe); e-e, egg to egg time; mean and maximum longevity of males (M) and females (F); X, mean; Sx, standard deviation; n, number of replicates. The values are expressed in days.

The mean contribution of each developmental stage to total copepod production is presented in Figure 3. Numerical density (ind. m⁻³), biomass and production of each stage of development (nauplii, copepodids and adults) are summarized in Figures 4 and 5 for *T. prasinus* and Figures 6 and 7 for *M. longisetus* (summer and winter, respectively). Naupliar and copepodid production is

somatic, while adult production is reproductive. In general, numbers of nauplii surpassed those of other stages in both species. In the summer, densities of both copepodids and adults of *M. longisetus* were higher than in the winter. There was a large variability in densities recorded daily, especially for nauplii. The regularity of peaks and subsequent decreases suggests that it could be

Table III: Dry weight (µg) of eggs, nauplii and adults of *T. prasinus* and *M. longisetus* raised under laboratory conditions (20 and 25°C ± 1°C)

| Species | Eggs | Nauplii | Cop. I | Cop. II | Cop. III | Cop. IV | Cop. V | Male | Female (no eggs) | Female (+ eggs) |
|----------------------|---------|---------|--------|---------|----------|---------|--------|--------|------------------|-----------------|
| <i>T. prasinus</i> | | | | | | | | | | |
| X | 0.20 | 0.27 | 0.39 | 0.56 | 0.70 | 0.83 | 1.31 | 0.88 | 2.24 | 3.14 |
| Sx | 0.02 | 0.06 | 0.01 | 0.08 | 0.10 | 0.13 | 0.34 | 0.54 | 0.80 | 1.67 |
| n | 5 (155) | 4 (92) | 2 (20) | 4 (49) | 4 (52) | 4 (50) | 3 (15) | 6 (57) | 7 (30) | 7 (31) |
| <i>M. longisetus</i> | | | | | | | | | | |
| X | 0.39 | 0.46 | 1.11 | 1.68 | 2.82 | 5.03 | 6.87 | 4.33 | 14.00 | 31.50 |
| Sx | 0.22 | 0.19 | 0.24 | 0.22 | 1.14 | 0.97 | 0.40 | 0.60 | 2.00 | 9.47 |
| n | 3 (112) | 6 (106) | 4 (25) | 4 (16) | 4 (18) | 4 (16) | 4 (20) | 3 (14) | 3 (3) | 4 (4) |

X, mean; Sx, standard deviation; n, number of replicates. The numbers in parentheses are the total number of individuals weighed.

Table IV: Mean values (μm) of egg diameters and lengths of nauplii, copepodids and adults of *T. prasinus* and *M. longisetus* raised under laboratory conditions (20 and $25^\circ\text{C} \pm 1^\circ\text{C}$)

| Species | Eggs | Nauplii | | Cop. I | Cop. II | Cop. III | Cop. IV | Cop. V | Male | Female | |
|----------------------|------|---------|-----|--------|---------|----------|---------|--------|------|--------|------|
| | | A | B | | | | | | | | |
| <i>T. prasinus</i> | | | | | | | | | | | |
| 20°C | X | 39 | 120 | 177 | 272 | 334 | 362 | 397 | 462 | 419 | 536 |
| | Sx | 0 | 28 | 17 | 19 | 23 | 17 | 25 | 21 | 34 | 35 |
| | n | 3 | 8 | 12 | 9 | 7 | 6 | 7 | 7 | 4 | 10 |
| 25°C | X | 39 | 120 | 167 | 266 | 323 | 360 | 406 | 461 | 407 | 520 |
| | Sx | 0 | 28 | 13 | 21 | 19 | 18 | 14 | 31 | 27 | 16 |
| | n | 3 | 8 | 6 | 7 | 8 | 7 | 5 | 9 | 6 | 6 |
| <i>M. longisetus</i> | | | | | | | | | | | |
| 20°C | X | 86 | 179 | 286 | 480 | 654 | 838 | 1026 | 1346 | 917 | 1603 |
| | Sx | 12 | 19 | 35 | 32 | 38 | 48 | 75 | 30 | 25 | 63 |
| | n | 5 | 15 | 12 | 11 | 13 | 9 | 9 | 8 | 4 | 6 |
| 25°C | X | 86 | 175 | 286 | 442 | 610 | 868 | 991 | 1217 | 917 | 1560 |
| | Sx | 12 | 19 | 35 | 28 | 26 | 19 | 89 | 162 | 25 | 72 |
| | n | 5 | 19 | 12 | 8 | 9 | 8 | 10 | 10 | 4 | 8 |

The values for copepodids and adults correspond to the whole body (metasome + urosome). Nauplii: A, I–III, B, IV–V. X, mean; Sx, standard deviation; n, number of replicates.

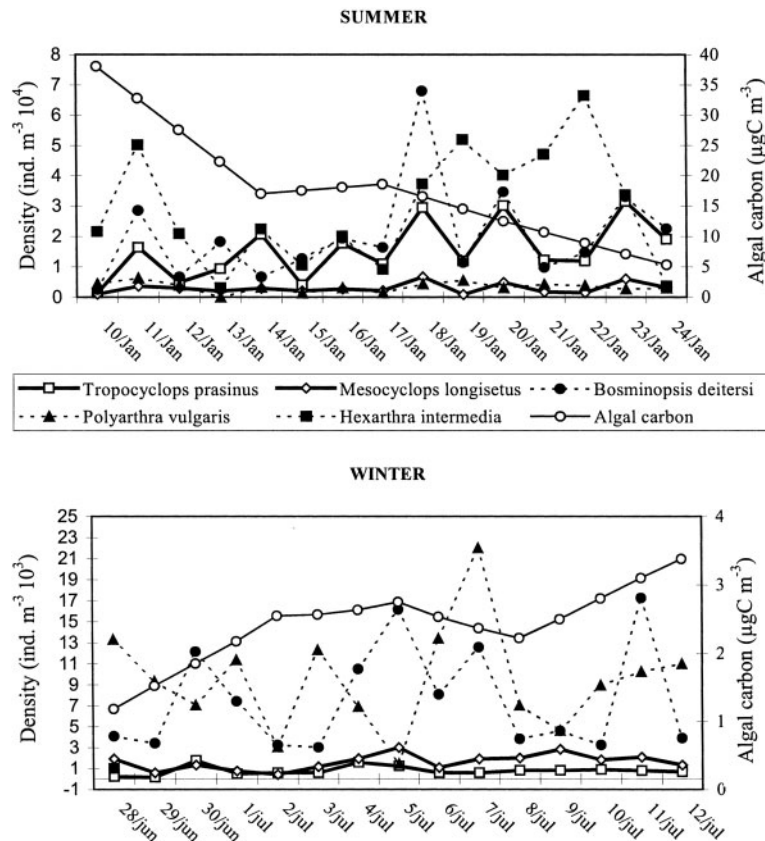


Fig. 2. Comparison between daily numerical densities (ind. m^{-3}) of *T. prasinus* and *M. longisetus* and those of the dominant zooplanktonic species in Lagoa Dourada during the summer and winter of 1995, as well as the algal carbon concentration in the environment at this period.

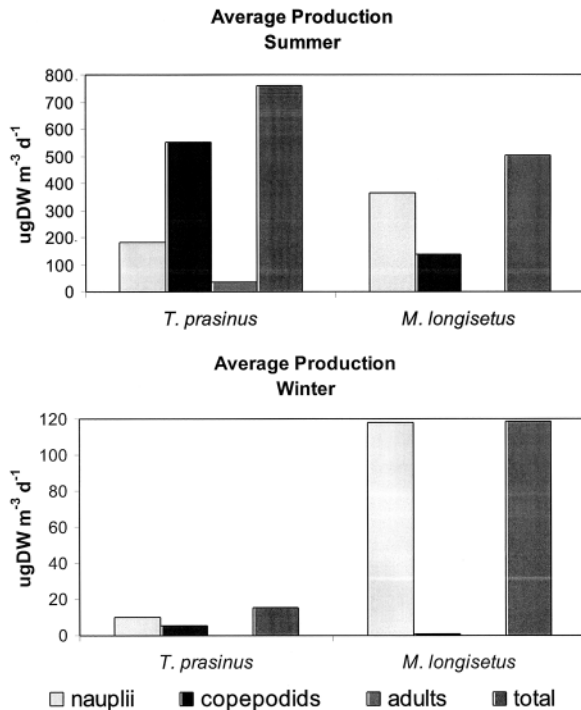


Fig. 3. Mean contribution of each developmental stage to total copepod production in Lagoa Dourada during the summer and winter of 1995.

caused by recruitment from eggs followed by predation, and partially by drift losses. Higher biomass values were found in the summer than in the winter for both species. For *T. prasinus*, the mean values were 4.0 mg dry weight (DW) m⁻³ (from 0.2 to 14.3 mg DW m⁻³) in the summer and 0.19 mg DW m⁻³ (from 0 to 0.6 mg DW m⁻³) in the winter. For *M. longisetus*, the equivalent mean values were 1.7 mg DW m⁻³ (from 0.5 to 4.2 mg DW m⁻³) and 0.8 mg DW m⁻³ (from 0.2 to 1.4 mg DW m⁻³), respectively. Copepod biomass was, on average, 41% of total zooplankton biomass in the summer and 19% in the winter.

Production rates of *T. prasinus* were higher in the summer, whereas for *M. longisetus* maximum rates occurred in the winter. Mean production rates for *T. prasinus* in the summer were almost twice that of *M. longisetus*. Conversely, the mean production rate of *M. longisetus* in the winter was one order of magnitude higher than that of *T. prasinus* (Figures 4–7).

For *T. prasinus*, the maximum production rate during the periods of study was 2.8 mg DW m⁻³ day⁻¹ and the highest P:B ratio was 0.29 (3.4 days for biomass turnover), while for *M. longisetus*, the maximum production rate was 1.4 mg DW m⁻³ day⁻¹ and the highest P:B ratio was 0.39 (2.6 days for biomass turnover). The mean P:B rates were 0.18 and 0.08 for *T. prasinus*, and 0.35

and 0.21 for *M. longisetus*, in the summer and winter, respectively.

DISCUSSION

Laboratory studies

Life history

Raising plankton species in the laboratory contributes to ecological studies by supplying important information on the physiological processes, growth and competitive interactions under controlled conditions. According to Herzig (Herzig, 1983), the duration of embryonic development in planktonic freshwater copepods is primarily a function of temperature; the thermal history of the species population influences the relationship between temperature and duration of embryonic development. Life history data available for copepods from tropical and subtropical regions are limited. Results of development times obtained in this study were close to those obtained by other authors (Table V) and follow the general trend of an inverse relationship between temperature and development time or longevity as reported by other authors (Sarvala, 1979; Herzig, 1983; Hart, 1990).

Post-embryonic duration is mainly affected by temperature and quality/quantity of food. There are, however, divergent responses among copepod species regarding the influence of food concentration on naupliar development. Naupliar durations appeared to be relatively independent of food concentrations, although food supply largely influenced copepodid development times in calanoid freshwater copepods (Hart, 1990; Hart *et al.*, 1995). On the other hand, Hansen and Santer (Hansen and Santer, 1995) have found that naupliar development times of *Cyclops vicinus* and *Mesocyclops leuckarti* were inversely related to food concentration (motile algae). Indeed, Santer and van den Bosch found that nauplii of *C. vicinus* need a much higher food concentration for development than copepodids (Santer and van den Bosch, 1994). Additionally, Jamieson and Santer, studying maternal aging in *Cyclops kolensis*, showed that egg sizes and naupliar development times are dependent on the age of the mother: as females aged, egg size and clutch size decreased, because they are constrained by the energy reserves available (Jamieson and Santer, 2003).

Under non-limiting food levels, as in the present experimental study, post-embryonic development times are highly dependent on temperature. There was an inverse relationship between temperature and post-embryonic duration of cyclopoids from Lagoa Dourada reservoir (Table II). The occurrence of similar development

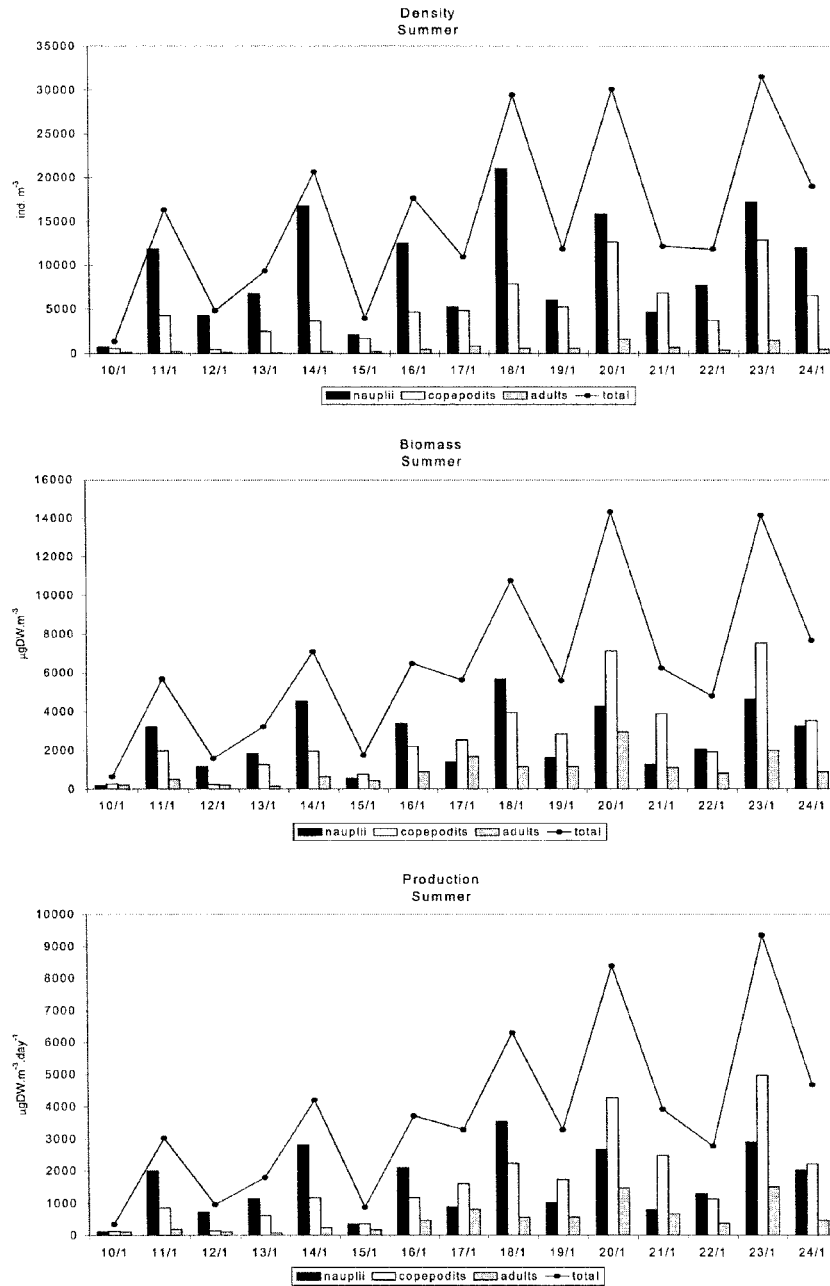


Fig. 4. Numerical density (ind. m^{-3}), standing stock ($\mu\text{g DW m}^{-3}$) and production ($\mu\text{g DW m}^{-3} \text{ day}^{-1}$) of each stage of development (nauplii, copepodites and adults) of *T. prasius* in Lagoa Dourada in the summer of 1995.

times among the copepodid stages suggests an isochronal development at this stage, in agreement with Omori and Ikeda (Omori and Ikeda, 1984). However, according to Hart (Hart, 1990), isochronality must be rejected as a general pattern in copepods; relative stage duration is, nevertheless, quite similar for a number of copepod species, across a broad range of temperatures and food levels. Hart suggested that equiproportional development is a generally valid growth rule in copepods (at

least for non-diapausing species) as long as the minimal energetic food threshold is provided (Hart, 1994, 1998).

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 the values vary with the temperature, quality and quantity of food and

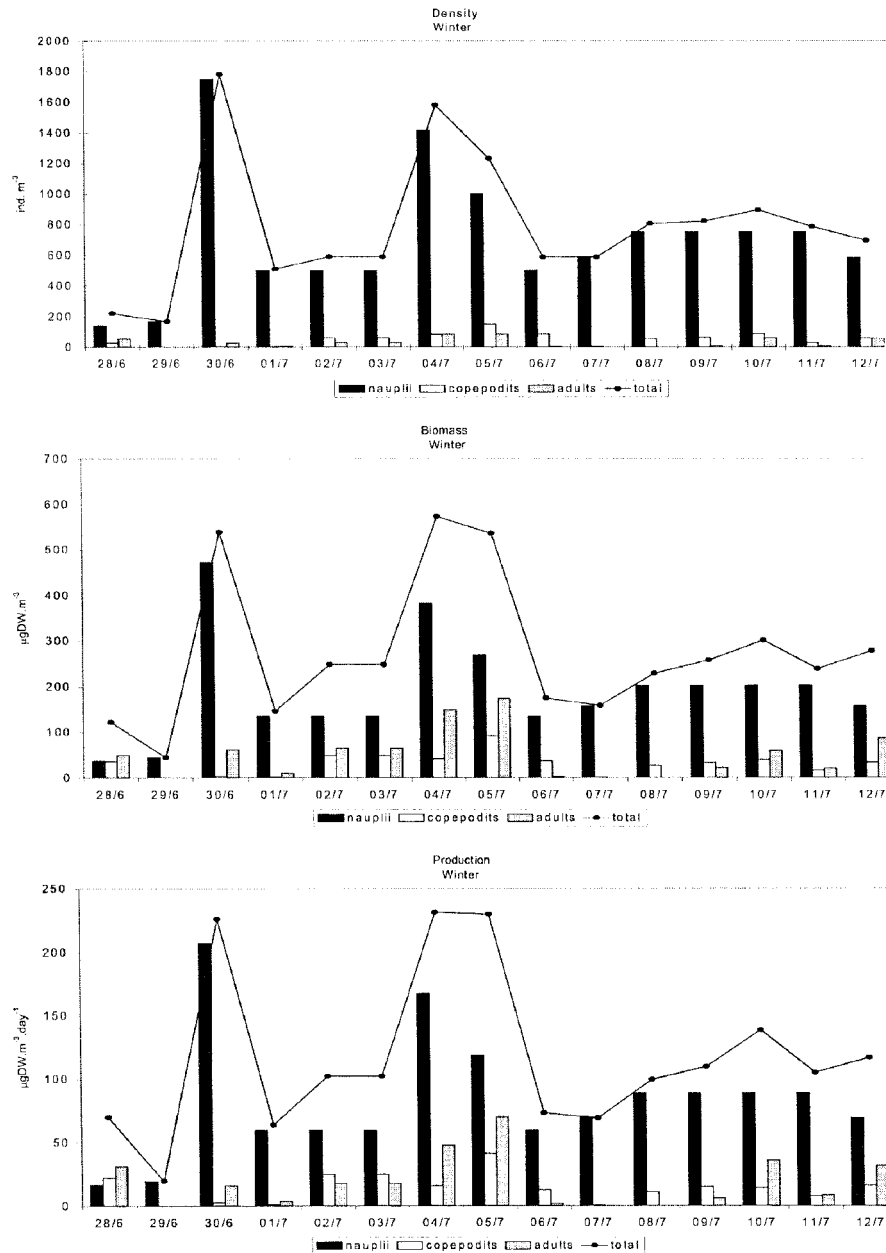


Fig. 5. Numerical density (ind. m^{-3}), standing stock ($\mu\text{g DW m}^{-3}$) and production ($\mu\text{g DW m}^{-3} \text{ day}^{-1}$) of each stage of development (nauplii, copepodites and adults) of *T. prasinus* in Lagoa Dourada in the winter of 1995.

genotype of the local population. Table VI shows some stage-specific DW data obtained by authors for the same species studied here. Differences among those and the present results might be related to differences in nutritional state or environmental temperatures. According to Rocha, weight can vary between individuals of the same size, depending on the nutritional state, stage of the life cycle and reproductive condition (Rocha, 1983). Indeed, intrinsic differences of populations should be considered.

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).

The feeding of freshwater cyclopoid copepods on a wide spectrum of food is well known from the classic study of Fryer (Fryer, 1957). According to this author,

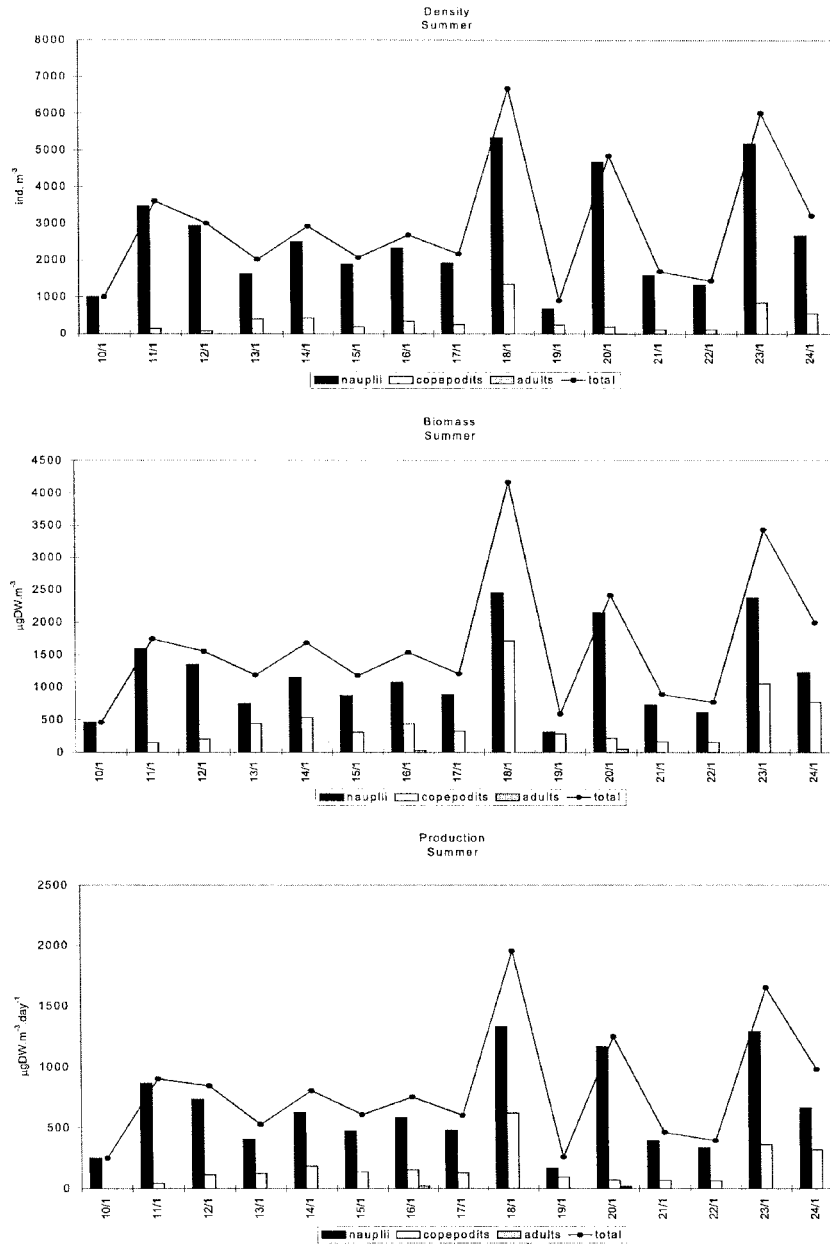


Fig. 6. Numerical density (ind. m^{-3}), standing stock ($\mu\text{g DW m}^{-3}$) and production ($\mu\text{g DW m}^{-3} \text{ day}^{-1}$) of each stage of development (nauplii, copepodites and adults) of *M. longisetus* in Lagoa Dourada in the summer of 1995.

algae are considered a more important food source for juvenile stages of planktonic cyclopoid copepods, while adults are mainly carnivorous. A different picture appears, however, from recent studies regarding cyclopoid feeding habits and life cycle strategies. Adrian and Frost provided evidence that cyclopoid copepods must be considered omnivorous (Adrian and Frost, 1992). According to them, animal body size appears to be an important factor determining the relative importance of both algal and animal prey on its feeding ecology; they

have found that *Tropocyclops prasinus mexicanus* is omnivorous, but due to its small size, it exhibits a greater dependence on algal food than other large-bodied cyclopoids (*C. kolensis* and *C. vicinus*). Also, Adrian and Frost, evaluating omnivory in three cyclopoid species (*T. p. mexicanus*, *Diacyclops thomasi* and *Mesocyclops edax*), demonstrated that the extension of herbivory is dependent on species body size: small species were much more dependent on algae than the larger species, for whom invertebrate prey had a greater importance (Adrian and Frost, 1993). Thus,

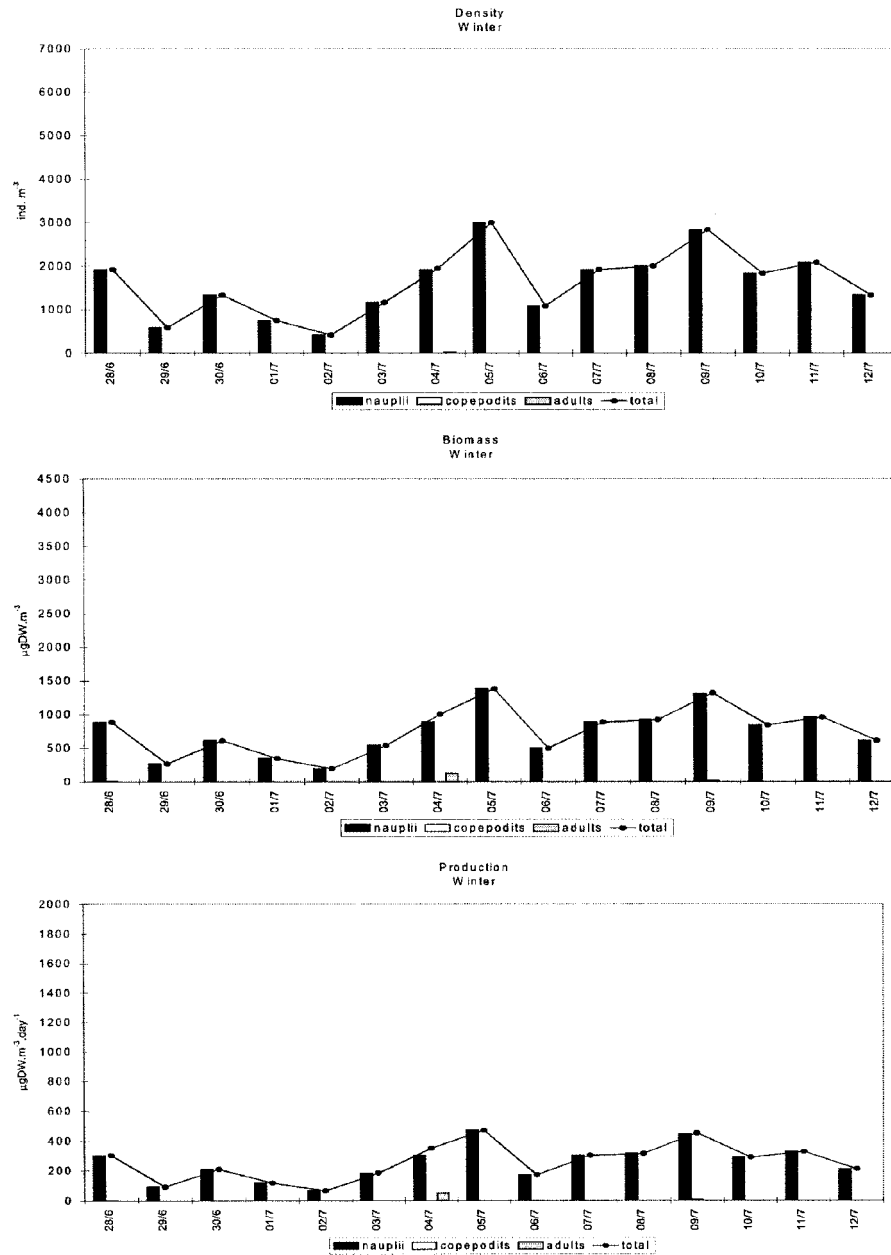


Fig. 7. Numerical density (ind. m^{-3}), standing stock ($\mu\text{g DW m}^{-3}$) and production ($\mu\text{g DW m}^{-3} \text{ day}^{-1}$) of each stage of development (nauplii, copepodites and adults) of *M. longisetus* in Lagoa Dourada in the winter of 1995.

cyclopoid copepods potentially should be able to derive their energy from either animal or algal sources, suggesting that omnivory is an advantageous feeding strategy, since zooplankton communities are often under food limitation (Adrian and Frost, 1992, 1993). Santer and van den Bosch described the purely herbivorous nutrition of *C. vicinus*, which differed from the current knowledge on feeding habits of planktonic cyclopoid copepods (Santer and van den Bosch, 1994). Also, Hansen and Santer investigated the food requirements of juveniles of

two cyclopoid species (*C. vicinus* and *M. leuckarti*) and evaluated the importance of algae for predaceous adults (Hansen and Santer, 1995). They found that nauplii of both species developed into copepodites when fed motile algae. However, while copepodites of *C. vicinus* were able to develop into adults on a pure algal diet, the second species required a prey supply (rotifers), although copepodite survivorship of both species was higher in the presence of prey. *Mesocyclops leuckarti* females had lower reproductive performance on pure algal diets.

Table V: Life history data of copepod cyclopoids from several sources

| Taxa | T (°C) | Life history data | Locality | Author |
|----------------------------------|-----------|---|-------------------------|-------------------------------|
| Cyclopoid copepods | 24.3/26.5 | De = 1.67/1.43 | Lanao (Philippines) | Lewis (1979) |
| <i>Thermocyclops minutus</i> | 23 | CS = 14.0 | B. Bonita (Brazil) | Rietzler (1995) |
| <i>Mesocyclops longisetus</i> | 23 | De = 2.48 N-I = 7.2 Cop I-F = 23 Cop I-M = 20 CS = 59.2 | B. Bonita (Brazil) | Rietzler (1995) |
| <i>Mesocyclops longisetus</i> | 25 | De = 1.75 | B. Bonita (Brazil) | Rietzler (1995) |
| <i>Mesocyclops longisetus</i> | 25 | Cop I-F = 18.3 Cop I-M = 22.3 CS = 70.2 | L. Valencia (Venezuela) | Wyngaard <i>et al.</i> (1994) |
| <i>Tropocyclops prasinus</i> | 16 | De = 3.3 | L. Placid (Canada) | Peacock and Smyly (1983) |
| <i>Mesocyclops leuckarti</i> | 22 | De = 2.33 | L. Chad (Africa) | Gras and Saint-Jean (1969) |
| <i>Mesocyclops leuckarti</i> | 25/24 | De = 1.58 N-I = 18 Cop I-F = 16 Cop I-M = 13 | L. Chad (Africa) | Gras and Saint-Jean (1969) |
| <i>Thermocyclops neglectus</i> | 22 | De = 2.04 | L. Chad (Africa) | Gras and Saint-Jean (1969) |
| <i>Thermocyclops neglectus</i> | 25/24 | De = 1.54 N-I = 16 Cop I-F = 13 Cop I-M = 17.5 | L. Chad (Africa) | Gras and Saint-Jean (1969) |
| <i>Th. incisus circusi</i> | 22/25 | De = 2.13/1.67 | L. Chad (Africa) | Gras and Saint-Jean (1969) |
| <i>Th. incisus circusi</i> | 20/25 | De = 2.79/1.67 | L. Chad (Africa) | Gras and Saint-Jean (1976) |
| <i>Thermocyclops neglectus</i> | 20/25 | De = 2.57/1.58 | L. Chad (Africa) | Gras and Saint-Jean (1976) |
| <i>Mesocyclops leuckarti</i> | 20/25 | De = 3.0/1.58 | L. Chad (Africa) | Gras and Saint-Jean (1976) |
| <i>Thermocyclops neglectus</i> | 24 | De = 1.71 N-I = 16.0 Cop I-Ad = 31.5 | L. Chad (Africa) | Gras and Saint-Jean (1983) |
| <i>Mesocyclops leuckarti</i> | 24 | De = 1.77 N-I = 18.0 Cop I-Ad = 33.0 | L. Chad (Africa) | Gras and Saint-Jean (1983) |
| <i>Tropodiptomus cunningtoni</i> | 26 | De = 2.0 N-I = 5.0 Cop I-Ad = 11.5 | L. Malawi (Africa) | Irvine and Waya (1999) |
| <i>Mesocyclops aequatorialis</i> | 26 | De = 1.8 Cop I-Ad = 19 | L. Malawi (Africa) | Irvine and Waya (1999) |
| <i>Thermocyclops neglectus</i> | 26 | De = 2.5 N-I = 7.0 Cop I-Ad = 13.6 | L. Malawi (Africa) | Irvine and Waya (1999) |
| <i>Tropodiptomus cunningtoni</i> | 26.5 | N-I = 3.97-5.14 N-F = 12.77-31.58 N-M = 11.89-32.03 CS = 1-8 | L. Malawi (Africa) | Hart <i>et al.</i> (1995) |

Temperature (T °C). De, embryonic development; N-I, development time from nauplii to copepodid I (days); N-F, N-M, development time from nauplii to female and male, respectively (days); Cop I-F, Cop I-M, Cop I-Ad, development time from copepodid I to female, male and adult, respectively (days); CS, clutch size (eggs female⁻¹).

Table VI: Weight values of copepod cyclopoids from several sources

| Species | Dry weight | Author |
|--|-------------------------------|-------------------------------|
| <i>Mesocyclops longisetus</i> | Egg = 0.04 | Wyngaard <i>et al.</i> (1994) |
| <i>Mesocyclops leuckarti</i> | C = 3.7 F = 7.2 M = 2.7 | Dumont <i>et al.</i> (1975) |
| <i>Tropocyclops prasinus</i> | F = 3.3 M = 1.8 | Dumont <i>et al.</i> (1975) |
| <i>Tropocyclops prasinus</i> | Egg = 0.075 F = 2.33 | Maier (1994) |
| <i>Tropocyclops prasinus mexicanus</i> | F = 0.57 M = 0.28 | Lawrence <i>et al.</i> (1987) |

Dry weight (μg DW) of eggs, copepodids (C), males (M) and females (F).

Although there were no previous detailed studies on the feeding ecology of *T. prasinus* and *M. longisetus* in Lagoa Dourada reservoir, they were considered omnivorous, since both grew well with a mixture of algae and ciliates as food source. The relative importance of herbivory and predation remains to be examined. In pilot experiments, nauplii and young copepodites of *T. prasinus*, an especially small cyclopoid, could be raised with pure algae, but predation by adults on *B. deitersi* was observed in the laboratory, which partially differed from the results of Peacock and Smyly who found, in experimental feeding studies in a temperate oligotrophic lake, that *T. prasinus* was omnivorous in the later instars but this species was neither cannibalistic nor did it prey on other microcrustaceans (Peacock and Smyly, 1983). *Mesocyclops longisetus*, a much larger species, is a well-known carnivorous species, at least in copepodid and adult stages (Matsumura-Tundisi *et al.*, 1990).

In many tropical and subtropical water bodies, the alternation of rainy calm summers with dry windy winters constitutes, in most of the cases, the main factor promoting seasonal changes in the plankton community. In Lagoa Dourada, there were great changes between summer and winter phytoplankton populations, related to the rainfall. In the summer, intensified production and decomposition processes, following nutrient release, stimulate 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 the summer ($17.5\text{--}18.3\text{ mg C m}^{-3}$) and algal carbon in summer (7.5 times that of winter) is associated with small sizes of algae (Peridinales) compared to those in winter (Desmidiaceae) (Melão and Rocha, 2000). Although in freshwaters it is rare to find copepods grazing on dinoflagellates (Santer, 1996), due to their presumed low nutritional values, some

studies have already demonstrated that it can be an important food source for predatory stages of freshwater cyclopoids (Adrian and Frost, 1993; Santer and van den Bosch, 1994; Santer, 1996). It is probable, therefore, that in Lagoa Dourada, *Peridinium* spp. can be an important food source for *T. prasinus* in summer. Adrian and Frost found that, under *in situ* food conditions, *T. p. mexicanus* depends mainly on algae rather than invertebrate prey, especially consuming *Peridinium* spp., which served as the sole food source for extended periods (Adrian and Frost, 1992). According to these authors, besides the minor importance of predation, the algae's mobility might be advantageous for those cyclopoid species. The preference of motile over non-motile algae by *T. prasinus* in food selection experiments was found by DeMott and Watson (DeMott and Watson, 1991), a fact that can be attributed to their raptorial feeding habits, visually selecting prey items. Under enriched food availability, they demonstrated that *T. p. mexicanus* has the potential to capture a wide variety of invertebrate prey when that is abundant and is of adequate size.

Predatory cyclopoid copepods may have a substantial impact on the survival of planktonic prey. In the summer, a relationship between the populations of *T. prasinus* and *B. deitersi* was observed, probably reflecting a predator relationship (predation was actually observed in the laboratory during this study). In addition, *T. prasinus* may have used rotifer populations as food source, which were also high at this time of the year.

Tropocyclops prasinus, the smaller species with a shorter generation time and smaller clutch size, predominated in the summer. Dumont asserts that smaller species present a lower food demand and larger visual protection from predators, which can be an advantage in tropical areas (Dumont, 1994).

Standing stock

Standing stock data for tropical and subtropical copepod species found in the literature show large variability. Burgis (Burgis, 1974) recorded mean annual standing stock values of 559 mg DW m⁻² for *Thermocyclops hyalinus*, the predominant zooplankton species in Lake George (Uganda); Gras and Saint-Jean (Gras and Saint-Jean, 1983) estimated for cyclopoid species in Lake Chad standing stock values ranging from 13.6 to 243.9 mg DW m⁻², under temperatures ranging from 19.1 to 25.6°C, close to summer and winter temperatures in Lagoa Dourada.

At Lake Malawi, Irvine and Waya obtained a mean standing stock of 1.6 g DW m⁻² (ranging from 0.9 to 2.4 g DW m⁻²) for total crustacean zooplankton (Irvine and Waya, 1999). Maximum values were 1635 mg DW m⁻² for *Tropodiptomus cunningtoni*, 382 mg DW m⁻² for *Mesocyclops aequatorialis aequatorialis*, 317 mg DW m⁻² for *Thermocyclops neglectus* and 319 mg DW m⁻² for nauplii. The standing stock of copepod species in Lagoa Dourada is quite low compared to the figures just reported: mean production of *T. prasinus* (integrated for a water column of 4.5 m depth) was 18.0 mg DW m⁻² in summer and 0.9 mg DW m⁻² in winter. For *M. longisetus*, the corresponding values were 7.6 mg DW m⁻² in summer and 3.6 mg DW m⁻² in winter.

Evaluating the production of planktonic crustaceans in Lake Naivasha (Kenya), a moderately eutrophic water body, Mavuti found an annual mean biomass of 120.45 mg DW m⁻³ for *Thermocyclops oblongatus* under a mean annual temperature of 22°C (Mavuti, 1994). The standing stock was higher in the rainy season, similar 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 56.4 mg DW m⁻³ (annual mean temperature of 26°C) for *T. neglectus* in Lake Chad (oligotrophic). The standing stock of copepods in Lagoa Dourada is low when compared to these data.

Detailed standing stock data including the different stages of development are not common. Lewis recorded values of 31.8, 67.5, 21.6, 28.7 and 0.9 mg DW m⁻³ for the nauplii, copepodids, males, females and eggs of *T. hyalinus* (Lake Lanao), respectively (Lewis, 1979). Burgis found mean values of 4, 10, 164 and 74 mg DW m⁻³ for eggs, nauplii, copepodids and adults of *T. hyalinus* (Lake George), respectively (Burgis, 1974).

In the present work, standing stock values of developmental stages were very low for both species investigated. The predominance of nauplii in the winter indicates a larger mortality of copepodids, which may be due to worse feeding conditions and perhaps to lower mean temperatures, corresponding to 26.86 and 18.10°C in summer and winter, respectively (Melão, 1997; Melão and Rocha, 2000).

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, accumulate little biomass, yet 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. Gras and Saint-Jean estimated the production of crustacean zooplankton in Lake Chad (Africa) and found, for cyclopoid copepods, daily productions ranging from 1.3 to 60.6 mg DW m⁻², under temperatures ranging from 19.1 to 25.6°C (Gras and Saint-Jean, 1983). Burgis recorded an annual mean production of 44 mg DW m⁻² day⁻¹ for a population of *T. hyalinus* in Lake George (Africa), which the author considered to be low and due to the bad quality of the phytoplankton as food for the zooplankton in that environment (Burgis, 1974). In Lagoa Dourada, integrated daily production ranged from 0.01 to 12.5 mg DW m⁻² for *T. prasinus* and from 0.2 to 6.3 mg DW m⁻² for *M. longisetus*, under temperatures varying from 17.8 to 27.8°C.

Irvine and Waya reported annual production values ranging from 39.5 to 42.8, from 3.2 to 7.0 and from 1.6 to 3.2 g DW m⁻² for *T. cunningtoni*, *M. a. aequatorialis* and *T. neglectus*, respectively, along 2 year full-lake cruises in the oligotrophic Lake Malawi (Irvine and Waya, 1999).

In general, the copepod 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 commonly used productivity index and is the reciprocal of the time of renewal of a species, under given conditions. Rocha and Matsumura-Tundisi found a daily P:B ratio of 0.10 for *A. furcatus* in Broa reservoir (Brazil), which is very similar to the mean values registered for cyclopoid copepods in this study (Rocha and Matsumura-Tundisi, 1984). Both cyclopoid species had higher P:B ratios and shorter turnover times in summer, thus suggesting that this is the most favourable condition for these species in the reservoir.

Gras and Saint-Jean estimated for cyclopoid species in Lake Chad daily P:B ratios ranging from 0.10 to 0.25, under temperatures ranging from 19.1 to 25.6°C (Gras and Saint-Jean, 1983). Mavuti (Mavuti, 1994) obtained

a P:B ratio of 0.09 (turnover time of 11.1 days) for *T. oblongatus* in Lake Naivasha (Kenya). Burgis (Burgis, 1974) found a daily P:B ratio of 0.078 (turnover time of 12.8 days or 8% of the biomass a day) for *T. hyalinus* in Lake George (Africa). Hart (Hart, 1987) registered values of P:B ratio ranging from 0.15 to 0.16 for *Metadiaptomus meridianus* and *Lovenula excellens* in Lake Le Roux (South Africa).

Thus, in spite of the low biomass and productivity values, copepods studied in the present work show relatively high turnover rates when compared with other species, both cyclopoids and calanoids. This clearly has important consequences for the maintenance of the food chain of Lagoa Dourada reservoir.

ACKNOWLEDGEMENTS

This work was partially supported by FAPESP, SP, Brazil under contracts 2002/11582–6. We acknowledge the critical comments and suggestions of anonymous referees, which greatly improved this manuscript.

REFERENCES

- Adrian, R. and Frost, T. M. (1992) Comparative feeding ecology of *Tropocyclops prasinus mexicanus* (Copepoda, Cyclopoida). *J. Plankton Res.*, **14**, 1369–1382.
- Adrian, R. and Frost, T. M. (1993) Omnivory in cyclopoid copepods: comparisons of algae and invertebrates as food for three, differently sized species. *J. Plankton Res.*, **15**, 643–658.
- Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. and Weglenska, T. (1976) A review of some problems in zooplankton production studies. *Borv. J. Zool.*, **24**, 419–456.
- Burgis, M. J. (1974) Revised estimates for the biomass and production of zooplankton in Lake George, Uganda. *Freshwater Biol.*, **4**, 535–541.
- DeMott, W. R. and Watson, M. D. (1991) Remote detection of algae by copepods: responses to algal zooplankton. *J. Plankton Res.*, **13**, 1203–1222.
- Dumont, H. J. (1994) On the diversity of the Cladocera in the tropics. In Dumont, H. J., Green, J. and Masudire, H. (eds), *Studies on the Ecology of Tropical Zooplankton*. *Hydrobiologia*, **272**, 27–38.
- Dumont, H. J., Van De Velde, I. and 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 (Berlin)*, **19**, 75–97.
- Fryer, G. (1957) The food of some freshwater cyclopoid copepods and its ecological significance. *J. Anim. Ecol.*, **26**, 263–286.
- Gras, R. and Saint-Jean, L. (1969) Biologie des crustacés du Lac Tchad. *Cah. O.R.S.T.O.M. Sér. Hydrobiol.*, **3**, 43–60.
- Gras, R. and 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. Sér. Hydrobiol.*, **10**, 233–254.
- Gras, R. and Saint-Jean, L. (1983) Production du zooplancton du Lac Tchad. *Rev. Hydrobiol. Trop.*, **16**, 47–77.
- Hansen, A. M. and Santer, B. (1995) The influence of food resources on the development, survival and reproduction of the two cyclopoid copepods: *Cyclops vicinus* and *Mesocyclops leuckarti*. *J. Plankton Res.*, **17**, 631–646.
- 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.
- Hart, R. C. (1990) Copepod post-embryonic durations: pattern, conformity, and predictability. The realities of isochronal and equiproportional development, and trends in the copepodids-naupliar duration ratio. *Hydrobiologia*, **206**, 175–206.
- Hart, R. C. (1994) Equiproportional temperature–duration responses and thermal influences on distribution and species switching in the copepods *Metadiaptomus meridianus* and *Tropodiaptomus spectabilis*. *Hydrobiologia*, **272**, 163–183.
- Hart, R. C. (1998) Copepod equiproportional development: experimental confirmation of its independence of food supply level, and a conceptual model accounting for apparent exceptions. *Hydrobiologia*, **380**, 77–85.
- Hart, R. C., Irvine, K. and Waya, R. (1995) Experimental studies on food dependency of development times and reproductive effort (fecundity and egg size) of *Tropodiaptomus cunningtoni* in relation to its natural distribution in Lake Malawi. *Arch. Hydrobiol.*, **133**, 23–47.
- Herzig, A. (1983) The ecological significance of the relationship between temperature and duration of embryonic development in planktonic freshwater copepods. *Hydrobiologia*, **100**, 65–91.
- Irvine, K. and Waya, R. (1999) Spatial and temporal patterns of zooplankton standing biomass and production in Lake Malawi. *Hydrobiologia*, **407**, 191–205.
- Jamieson, C. D. and Santer, B. (2003) Maternal aging in the univoltine freshwater copepod *Cyclops kolensis*: variation in egg sizes, egg development times, and naupliar development times. *Hydrobiologia*, **510**, 75–81.
- Lawrence, S. G. *et al.* (1987) Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. *Can. J. Fish. Aquat. Sci.*, **44**, 264–274.
- 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, 163 pp.
- Maier, G. (1994) Patterns of life history among cyclopoid copepods of central Europe. *Freshwater Biol.*, **31**, 77–86.
- Matsumura-Tundisi, T., Rietzler, A. C., Espíndola, E. L. G., Tundisi, J. G. and Rocha, O. (1990) Predation on *Ceriodaphnia cornuta* and *Brachionus calyciflorus* by *Mesocyclops* species coexisting in Barra Bonita reservoir (SP, Brazil). *Hydrobiologia*, **198**, 141–151.
- 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. In Dumont, H. J., Green, J. and Masudire, H. (eds), *Studies on the Ecology of Tropical Zooplankton*. *Hydrobiologia*, **272**, 27–38.
- Melão, M. G. G. (1997) A comunidade planctônica (fitoplâncton e zooplâncton) e produtividade secundária do zooplâncton de um reservatório oligotrófico. Thesis, Universidade Federal de São Carlos, São Carlos, 152 pp.
- Melão, M. G. G. and 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. and Rocha, O. (2000) Productivity of zooplankton in a tropical oligotrophic reservoir over short periods of time. *Verh. Int. Ver. Limnol.*, **27**, 2879–2887.
- Omori, M. and Ikeda, I. (1984) *Methods in Marine Zooplankton Ecology*. John Wiley and Sons, Tokyo, 332 pp.
- Peacock, A. and Smyly, W. J. P. (1983) Experimental studies on the factors limiting *Tropocyclops prasinus* (Fischer) 1860 in an oligotrophic lake. *Can. J. Zool.*, **61**, 250–265.
- Rietzler, A. C. (1995) Alimentação, ciclo de vida e análise da coexistência de espécies de Cyclopoida na represa de Barra Bonita, São Paulo. Thesis, EESC/USP, São Carlos, 385 pp.
- Rocha, O. (1983) The influence of food–temperature combinations on the duration of development, body size, growth and fecundity of *Daphnia* species. Thesis, Royal Holloway College, London, 337 pp.
- Rocha, O. and 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. and Matsumura-Tundisi, T. (1984) Biomass and production of *Argyrodiaptomus furcatus*, a tropical calanoid copepod in Broa Reservoir, southern Brazil. *Hydrobiologia*, **113**, 307–311.
- Santer, B. (1996) Nutritional suitability of the dinoflagellate *Ceratium furcoides* for four copepod species. *J. Plankton Res.*, **18**, 323–333.
- Santer, B. and van den Bosch, F. (1994) Herbivorous nutrition of *Cyclops vicinus*: the effect of a pure algal diet on feeding, development, reproduction and life cycle. *J. Plankton Res.*, **16**, 171–195.
- Sarvala, J. (1979) Effect of temperature on the duration of egg, nauplius and copepodite development of some freshwater benthic Copepoda. *Freshwater Biol.*, **9**, 513–534.
- 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. and Shushkina, E. A. (1965) Production of planktonic crustaceans in three lakes of different type. *Zool. Zh.*, **44**, 676–687.
- Wyngaard, G. A., Goulden, C. E. and Nourbakhsh, A. (1994) Life history traits of the tropical freshwater copepod *Mesocyclops longisetus* (Crustacea: Copepoda). *Hydrobiologia*, **292/293**, 423–427.

