Temporal variability and production of *Temora turbinata* (Copepoda: Calanoida) in the Cananéia Lagoon estuarine system, São Paulo, Brazil*

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SUMMARY: Diel and seasonal variations in abundance, population structure, biomass and production rate of the planktonic calanoid copepod *Temora turbinata* were studied in the Cananéia Lagoon estuarine system, São Paulo, Brazil. Zooplankton sample collections were carried out at 4-h intervals over multiple 24-h periods, from February 1995 to January 1996. *Temora turbinata* was present in the plankton all year round (temperature, 18.6-29.6°C; salinity, 8-33 psu; chlorophyll *a* concentration, 1.32-15.33 μ gl⁻¹). *Temora turbinata* showed considerable diel variations in abundance. Abundance of *T. turbinata* was higher from June to October when temperature was lower than ca. 24°C and salinity was higher than ca. 20 psu. The biomass varied from 0.0005 ± 0.0014 to 3.715 ± 2.360 mgC m⁻³ (daily mean ± SD). The daily production rates estimated by the Hirtst-Sheader models varied from 0.0002 ± 0.0006 to 1.115 ± 0.261 mgC m⁻³ d⁻¹ (mean ± SD). The P/B ratios varied from 0.17 to 0.45 d⁻¹. These results showed that *T. turbinata* constituted 8.3 and 7.8% of the annual copepod community biomass and production rate respectively.

Key words: Temora turbinata, temporal variation, population structure, production, Cananéia Lagoon estuarine system, Brazil.

RESUMEN: VARIABILIDAD TEMPORAL Y PRODUCCIÓN DE *TEMORA TURBINATA* (COPEPODA: CALANOIDA) EN EL COMPLEJO ESTUA-RINO-LAGUNAR DE CANANÉIA, SÃO PAULO, BRASIL. – Variaciones diurnas y estacionales en la abundancia, estructura de población, biomasa y tasa de producción del copépodo calanoide planctónico *Temora turbinata* fueron estudiadas en el sistema estuarino Cananéia Lagoon, São Paulo, Brasil. Muestras de zooplancton fueron obtenidas a intervalos de 4 horas a lo largo de múltiples períodos de 24 h desde febrero 1995 hasta enero 1996. *T. turbinata* estuvo presente en el plancton durante todo el año (temperatura, 18.6–29.6°C; salinidad, 8-33 psu; concentración de clorofila *a*, 1.32-15.33 µg l⁻¹). *T. turbinata* mostró considerables variaciones diurnas en su abundancia. Esta fue mayor de junio a octubre cuando la temperatura era inferior a alrededor de 24°C y la salinidad era superior a alrededor de 20 psu. La biomasa varió entre 0.0005±0.0014 y 3.715 ±2.360 mgC m⁻³ (media diaria ±SD). Las tasas de producción diaria estimadas por los modelos de Hirtst-Sheader variaron entre 0.0002±0.0006 y 1.115±0.261 mgC m⁻³ d⁻¹ (media ±SD). Los cocientes P/B variaron entre 0.17 y 0.45 d⁻¹. Estos resultados muestran que *T. turbinata* constituyó, respectivamente, el 8.3% y el 7.8% de la biomasa anual de la comunidad de copépodos y de la tasa de producción.

Palabras clave: Temora turbinata, variación temporal, estructura poblacional, complejo estuarino-lagunar de Cananéia, Brasil.

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INTRODUCTION

Planktonic copepods of the family Temoridae are widely distributed in tropical, subtropical, temperate and subboreal waters, and are one of the conspicuous members of the surface and near-surface mesozooplankton communities in estuarine, neritic and oceanic waters.

Along the western coast of the Atlantic, 3 species of the genus *Temora* (*T. longicornis*, *T. stylifera* and *T. turbinata*) have been recorded (Bradford-Grieve *et al.*, 1999). Among these, *Temora turbinata* (Dana, 1849) is widely distributed in tropical, subtropical and temperate waters of the Atlantic, Pacific and Indian Oceans, except in the eastern Pacific (Fleminger, 1975; Haedrich and Judkins, 1979; Bradford-Grieve *et al.*, 1999), and is often predominant in the mesozooplankton communities of tropical, coastal and oceanic environments of the Gulf of Mexico and the Caribbean Sea (Suárez-Morales and Gasca, 1997, 2000; López-Salgado and Suárez-Morales, 1998).

In recent years, T. turbinata has been found to appear in various estuarine and neritic waters of Brazil (e.g. Araújo and Montú, 1993; Muxagata and Gloeden, 1995; De La Rocha, 1998; Ara, 1998). The immigration of estuarine zooplankters (e.g. copepods) can be caused by ships, which carry millions of cubic meters of ballast water, transporting entire holo- and meroplankton assemblages (e.g. Orsi et al., 1983; Fleminger and Kramer, 1988; Cordell and Morrison, 1996). The introduction of exotic species that invade their new environments usually results in changes in native assemblages. In the Cananéia Lagoon estuarine system, a mangrove-surrounded estuary situated near the southern border of São Paulo State, Brazil, T. stylifera, which was formerly one of the principal copepod species (Matsumura-Tundisi, 1972), was recently substituted by T. turbinata (Luz Amelia Vega-Pérez, Universidade de São Paulo, personal communication).

The biology and ecology of *T. turbinata* have been studied, e.g. developmental time and growth rate (Binet, 1977; Chisholm and Roff, 1990b; Roff *et al.*, 1995; Hopcroft *et al.*, 1998b; Hopcroft and Roff, 1998b), length-weight relationship (Chisholm and Roff, 1990a; Ara, 1998, 2001b), body chemical content (Hirota, 1981; Bandaranayake and Gentien 1982; Uye, 1982; Ara, 1998, 2001b), egg production rate (Hopcroft and Roff, 1998a), and biomass and production rate (Chisholm and Roff, 1990b; Hopcroft *et al.*, 1998a). However, for *T. turbinata*, there have been no studies on the temporal variation in population production rate.

The objective of the present study was to obtain quantitative information on *Temora turbinata*, analysing the diel and seasonal variations in abundance and population structure in relation to the environmental variables, as well as to evaluate the biomass and production rate of this species in the Cananéia Lagoon estuarine system.

MATERIALS AND METHODS

A series of field investigations and sample collections were carried out at a fixed sampling station (25°01'11"S, 47°55'43"W, 10-12 m in depth depending on the tidal phase) situated in Mar de Cananéia (Fig. 1), from February 1995 to January 1996. On each sampling date, sampling was carried out at intervals of 4-h during multiple 24-h periods. Zooplankton samples were taken by vertical hauls from the bottom to the surface, using a plankton net (50 cm in mouth diameter, 150 μ m in mesh size) equipped with a flowmeter. Net samples were immediately preserved in 5-10% formalin-seawater solution.

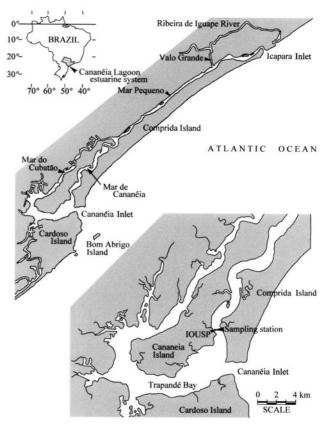


FIG. 1. – Map showing the sampling station in the Cananéia Lagoon estuarine system.

Water samples were collected every 2 m from the surface to the bottom, using a 3 litre-Van Dorn bottle. Water temperature was recorded with an electronic thermometer and salinity was determined using an optical refractometer. Water aliquots (volume: 200–500 ml) collected from 0, 2, 6 and 10-m depth were filtered through a glass-fibre filter (Whatman, GF/F) for spectrophotometric determination of chlorophyll *a* concentration (Lorenzen, 1967). Tidal height was cited from the tide tables given by Mesquita and Harari (1993) and Harari and Mesquita (1995).

Temora turbinata from split samples (1.25 to 40% of the original samples) was staged, sexed and counted under a microscope. Total body length of the copepodite stages C1–5 and C6 (adults) were measured using an eyepiece micrometer.

For statistical comparison between daytime (08:00, 12:00 and 16:00 h) and nighttime (20:00, 00:00 and 04:00 h) abundances of T. turbinata, oneway ANOVA was applied: a p-value of less than 0.05 was considered statistically significant (Sokal and Rohlf, 1981). Correlation between abundances of T. turbinata and the environmental variables (temperature, salinity, chlorophyll a concentration and tidal height) was examined by Spearman rank correlation analysis. The correlation between total body length of T. turbinata and the environmental variables was analysed by multiple linear regression. Biomass was estimated by the multiplication of abundances and individual dry weights (DW, μ g) calculated from prosome body length (*PL*, μ m) using a length-weight regression equation (Ara, 1998, 2001b) given as:

$$DW = 1.471 \times 10^{-8} PL^{3.064}$$
 ($r = 0.972, p < 0.0001$).

Carbon content was assumed to be 44.6% of dry weight (Ara, 1998, 2001b).

Production rate (Pc, mgC m⁻³ d⁻¹) was estimated by the following equation:

$$Pc = \sum N \times Wc \times G$$

where *N* is abundance (ind. m⁻³), *Wc* is individual weight (μ gC) and *G* is individual weight-specific growth rate (d⁻¹). Here, *G* was estimated using the model proposed by Hirst and Sheader (1997), expressed as:

$$G = 1.0583^T \times Wc^{-0.2962} / 13.6616$$

where *T* is temperature ($^{\circ}$ C).

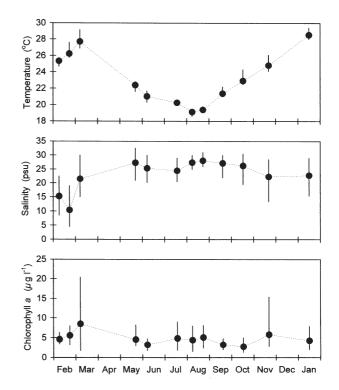


FIG. 2. – Seasonal variations in water temperature, salinity and chlorophyll *a* concentration in the Cananéia Lagoon estuarine system, from February 1995 to January 1996. Closed symbols and vertical bars denote mean values in the water column and their ranges respectively.

RESULTS

Environmental variables

Water temperature showed seasonal variation, ranging from 18.6°C on 8 August to 29.6°C on 15 January (Fig. 2). No thermal stratification was found throughout the year. Salinity varied from 4.5 to 33.0 psu, and was much lower in February (Fig. 2), due to the heavy local rains. Chlorophyll *a* concentration fluctuated from 1.32 to 20.42 μ g l⁻¹ (Fig. 2). Salinity and chlorophyll *a* concentration varied dramatically with depth and time. The variations in salinity were associated with the tidal cycle, whereas those in chlorophyll *a* concentration were inconsistent in pattern.

Abundance

On each sampling date, the abundance of *T. turbinata* varied considerably with time: coefficients of variation (SD) were 36.4-264.6% (mean 86.5%) of daily mean abundance. On most sampling dates, there was no consistent trend of diel variation in abundance: peak abundance was randomly observed

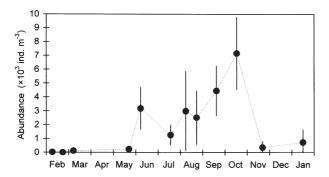


FIG. 3. – Monthly variation in abundance of *Temora turbinata* (C1-6) in the Cananéia Lagoon estuarine system, from February 1995 to January 1996. Abundance is expressed as daily mean ± SD (vertical bars).

with respect to time. There was no statistically significant difference between daytime and nighttime abundances (ANOVA, p>0.05). The night:day abundance ratio varied from 0.58 in June to 4.62 in November, with an overall mean of 1.11. On most sampling dates, higher abundances of *T. turbinata* were recorded at times when salinity was higher.

Daily mean abundance of *T. turbinata* varied from 2 ± 4 to $7.2 \times 10^3 \pm 2.6 \times 10^3$ ind. m⁻³ (mean \pm SD) (Fig. 3). The population densities were higher in October, but lower from February to May and from November to January.

Population structure

All of the copepodites (C1-5) and adults (C6) were abundant from June to October, but were rare from February to May and from November to January. These stages showed a similar pattern of temporal variation in abundance, although stages C1-3 were more abundant than the older stages (C4-6), in particular in September and October (Fig. 4). The

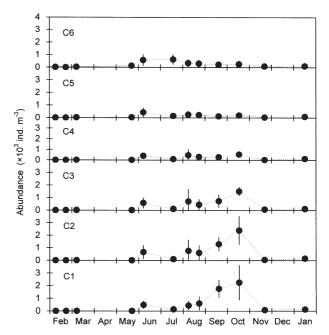


FIG. 4. – Monthly variation in abundance of the stages C1-6 of *Temora turbinata* in the Cananéia Lagoon estuarine system, from February 1995 to January 1996. Abundance is expressed as daily mean ± SD (vertical bars).

mean relative abundances of stages C1-6 were 25.7, 26.5, 18.7, 10.2, 6.9 and 11.9% respectively.

While the sex composition of C4-6 showed irregular variations, males were slightly more abundant than females: the mean percentage of females in C4, C5 and C6 were 43.2, 40.8 and 43.1% respectively.

Effects of the environmental factors

Temora turbinata was present in the plankton over wide ranges of the environmental variables, but its higher densities were frequently found at temper-

TABLE 1. – Coefficients of Spearman rank correlation between abundance of *Temora turbinata* and the environmental variables (tidal height and mean temperature, salinity and chlorophyll *a* concentration in the water column) in the Cananéia Lagoon estuarine system, from February 1995 to January 1996. *T*: temperature (°C); *S*: salinity (psu); Chl: chlorophyll *a* concentration (μ gl⁻¹); TH: tidal height (m); C: copepodite stage; F: female; M: male. Significant correlation: * 0.01 < *p* < 0.05; ** 0.001 < *p* < 0.01; *** *p* < 0.001.

Stage/sex	Т	S	Chl	TH
Total	-0.590***	0.744***	-0.617***	0.144
C1	-0.563***	0.716***	-0.570***	0.168
C2	-0.536***	0.723***	-0.621***	0.180
C3	-0.552***	0.712***	-0.581***	0.156
C4 Females	-0.574***	0.700***	-0.509***	0.145
C4 Males	-0.566***	0.722***	-0.571***	0.144
C5 Females	-0.537***	0.640***	-0.447***	0.112
C5 Males	-0.623***	0.674***	-0.462***	0.142
C6 Females	-0.533***	0.503***	-0.440***	0.0422
C6 Males	-0.632***	0.549***	-0.458***	0.0372
F / F+M (C4)	0.0351	-0.0906	0.176	0.00179
F / F+M (C5)	0.352**	-0.222	0.0871	-0.120
F / F+M (C6)	0.351**	-0.233	0.116	-0.0338

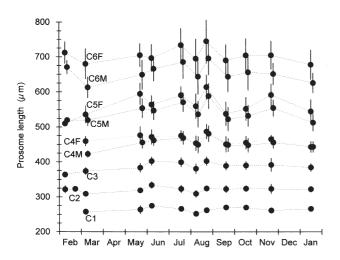


FIG. 5. – Monthly variation in prosome length of the stages C1-6 of *Temora turbinata* in the Cananéia Lagoon estuarine system, from February 1995 to January 1996. Prosome length is expressed as mean ± SD (vertical bars). F: female; M: male.

atures lower than ca. 24° C, salinities higher than ca. 20 psu and chlorophyll *a* concentrations lower than ca. 8 μ g l⁻¹. However, it did not show preferential ranges related to tidal height.

Coefficients of correlation between the abundances of C1-6 and the environmental variables are presented in Table 1. The abundance of C1-6 showed significantly positive correlations with salinity and negative correlations with temperature and chlorophyll a concentration. Sex composition (females:total) of C5-6 was positively correlated with temperature.

Body length

Prosome length of stages C1-6 showed seasonal fluctuation, in particular in older stages (Fig. 5). Their body lengths were generally larger in winter

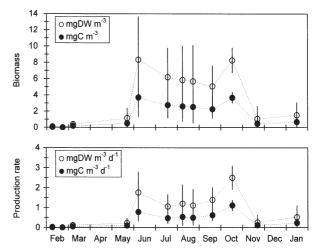


FIG. 6. – Monthly variations in biomass (uppermost) and production rate (lower) of *Temora turbinata* (C1-6) in the Cananéia Lagoon estuarine system, from February 1995 to January 1996. Biomass and production rate are expressed as daily mean ± SD (vertical bars).

and smaller in summer. The correlation between prosome length and the environmental variables (temperature, salinity and chlorophyll *a* concentration) varied depending on the stage and sex. Among these environmental factors, the main factor to explain the size variation was temperature for C3-6, whereas it was chlorophyll *a* concentration for C1-2 (Table 2).

Biomass and production rate

Biomass varied from 0.0012 ± 0.0031 to 8.335 ± 5.296 mgDW m⁻³ (daily mean \pm SD), or from 0.0005 ± 0.0014 to 3.715 ± 2.360 mgC m⁻³. Biomass was higher from June to October, and was lower from February to May and from November to January (Fig. 6).

The pattern of temporal variations in production rate was similar to that of biomass, and the estimat-

TABLE 2. – Multiple linear regression equations of the relationships between prosome length of the developmental stages C1-6 of *Temora turbinata* and the environmental variables (temperature, salinity and chlorophyll *a* concentration) in the Cananéia Lagoon estuarine system, from February 1995 to January 1996. *PL*: prosome length (μ m); *T*: mean temperature (°C) in the water column; *S*: mean salinity (psu) in the water column; *Chl*: mean chlorophyll *a* concentration (μ g l⁻¹) in the water column; *r*: coefficient of correlation; *n*: number of cases. Significant correlation: * 0.01 < *p* < 0.05; ** 0.001 < *p* < 0.01; *** *p* < 0.001.

Stage/sex	Multiple linear regression equation (PL vs. T, S and Chl)	r	n
C1	PL = 276.46 + 0.0349T - 0.0768S - 0.393Chl	0.376*	56
C2	PL = 342.01 - 0.0061T - 0.176S - 0.438Chl	0.425**	63
C3	PL = 421.15 - 0.342T + 0.0195S - 0.215Chl	0.441**	61
C4 Female	PL = 447.12 - 0.264T + 0.234S + 0.208Chl	0.432*	57
C4 Male	PL = 486.96 - 0.475T + 0.120S + 0.0860Chl	0.551***	58
C5 Female	PL = 601.86 - 0.353T + 0.0827S + 0.152Chl	0.399*	59
C5 Male	PL = 597.33 - 0.459T + 0.0893S + 0.148Chl	0.502***	61
C6 Female	PL = 778.09 - 0.452T + 0.0131S + 0.190Chl	0.446**	63
C6 Male	PL = 822.90 - 0.631T - 0.182S - 0.0844Chl	0.563***	63

ed production rates varied from 0.0002 ± 0.0006 to $1.115 \pm 0.261 \text{ mgC} \text{ m}^{-3} \text{ d}^{-1}$ (daily mean $\pm \text{SD}$) (Fig. 6). The mean ratio of daily production rate to biomass (daily P/B ratio) varied from 0.17 to 0.45 d⁻¹.

DISCUSSION

Although Temora turbinata has been found to appear recently in various estuarine waters of Brazil (e.g. Araújo and Montú, 1993; Muxagata and Gloeden, 1995; De La Rocha, 1998), nothing has been known on the diel and seasonal occurrence of this species in these waters. Abundance of T. turbinata varied considerably during the 24-h periods, not showing a consistent trend of diel variation in abundance in relation to time of day, as similarly observed for marine zooplankton (e.g. copepods) in the Cananéia Lagoon estuarine system (Ara, 1998, 2001a, c) and in other estuarine and neritic environments (Sameoto, 1975: Lee and McAlice, 1979: Gagnon and Lacroix, 1981; Dauvin et al., 1988). On most sampling dates, its higher population densities were recorded at times when salinities were higher. Therefore, in the Cananéia Lagoon estuarine system the position of its population centre might move depending on the tidal condition. During the study period, T. turbinata appeared in the plankton over wide ranges of temperature and salinity, but its higher population densities were found from autumn to early spring. A similar seasonal occurrence of T. turbinata was observed in previous studies carried out in subtropical waters along the eastern coast of the U.S.A. and Mexico (Woodmansee, 1958; Suárez-Morales and Gasca, 1996). However, T. turbinata was found to be abundant throughout the year in Kingston Harbour, Jamaica, where there is little annual variation in temperature (27-30°C) and salinity (34-36%) (Hopcroft et al., 1998a). Judging from these seasonal occurrences of T. turbinata mentioned above, temperature could be less limiting to the occurrence of *T. turbinata* than salinity.

One of the characteristic aspects of calanoid copepods is their stage composition that is commonly skewed toward younger stages rather than older stages (e.g. adults), as observed for T. turbinata (see Fig. 5). In the present study, when population density of T. turbinata decreased, the proportion of C6 increased proportionally (r = 0.475, p < 0.01), as contrary did the proportion of C1 (r = 0.500, p <(0.01). This indicates that older stages might have higher tolerance to environmental stress than their

Reference	Bakker <i>et al.</i> , 1977 Allan <i>et al.</i> , 1976 Bakker <i>et al.</i> , 1976 Burkill and Kendall, 1982 Castel and Feurtet, 1993 Escaravage and Soctaert, 1993 Escaravage and Soctaert, 1995 Peitch, 1995 McLaren and Corkett, 1981 Middlebrook and Roff, 1986 Fransz <i>et al.</i> , 1984 Aksnes and Magnesen, 1988 Kiørboe and Nielsen, 1990 Peterson <i>et al.</i> , 1991 Razouls, 1974 Chisholm and Roff, 1990b Hopcroft <i>et al.</i> , 1998a This study
Temp. (°C)	ca. 6-19.5 ND 6.5-14.4 ND ND 8-20 8-20 8-18 8-20 8-18 ca. 1-12 ND ND ND ND ND ND ND ND ND ND ND ND ND
P/B ratio (d ⁻¹)	ND 0.037-0.8 ND 0.03-0.13 0.03-0.13 0.07* mean 0.07* mean 0.11 ca. 0.16-0.17* ND 0.05-0.11 ca. 0.02-0.084 0.023-0.084 ND mean 0.17-0.45 mean 0.17-0.45
Production rate	ND 0.01-20.47b ND 0.00005-0.00066 7-42.6b ca. 0-18.7b ca. 0-18.7b ca. 1-13b ca. 1-13b ca. 1-13b ca. 1-13b ca. 1-13b ca. 1-13b ca. 1-13b ca. 1-13b nan 2.7-34f 0.1188bs 0.035-0.205bs mean 7.33c mean 7.33c mean 0.0005-2.502bs mean 0.0005-2.502bs
Biomass	mean 0-22 ⁴ 0.04-218.62 ^b mean 0-5546 ^{4*} 0.0007-0.022 ^b ?-343 ^b ca. 0-365 ^b ca. 3-355 ^b ca. 3-355 ^b ca. 3-355 ^b ca. 3-356 ^b ca. 3-366 ^b mean 100-141 ^e 0.4-7,4 ^b 0.792-4.786 ^{b*} ND mean 0.0012-8.335 ^b mean 0.0002-3.715 ^d mean 0.0002-3.715 ^d
Region	Westerschelde estuary, Netherlands Chesapeake Bay', USA Westerschelde estuary, Netherlands Bristol Channel, UK Gironde estuary, France Westerschelde estuary, Netherlands Westerschelde estuary, Netherlands Westerschelde estuary, Netherlands Halifax, Canada Passamaquoddy Bay, Canada North Sea North Sea Nort
Stage	CI-6 CI-6 CI-6 CI-6 CI-6 CI-6 CI-6 CI-6
Species	Eurytemora americana Eurytemora affinis Eurytemora affinis Temora longicornis Temora longicornis Temora turbinata Temora turbinata Temora turbinata

Biomass, daily production rate and daily P/B ratio of the family Temoridae in various estuarine, lagoon and neritic waters.

TABLE 3. -

E: egg; N: nauplius; C: copepodite; ND: no data; * calculated from data; * biomass (mg wet weight m⁻³); * biomass (mg dry weight m⁻³); * biomass (mg dry weight m⁻³); * biomass (mg dry weight m⁻³) and production rate (mg dry weight m⁻³); * biomass (mg dry weight m⁻² d⁻¹); * biomass (mg ash-free dry weight m⁻² d⁻¹); * biomass (mg dry weig Rhode River subestuary

younger stages. During periods of low population density, the dominance of adults is advantageous to recover its population size (Heinle, 1970; Sabatini, 1990; Zaballa and Gaudy, 1996).

Biomass determinations have been done for some *Temora* and *Eurytemora* species of the family Temoridae in various estuarine, lagoonal and neritic waters around the world. Although in the present study the biomass of *T. turbinata* was determined only for C1-6, not including the eggs and naupliar stages, the biomasses were higher than those obtained for *Temora* species, but were much lower than those obtained for *Eurytemora* species (see Table 3).

The maximum production rates of *T. turbinata* obtained in the present study were higher than those obtained for *Temora* species, but were lower than those obtained for *Eurytemora* species (Table 3). However, daily P/B ratios obtained for *T. turbinata* in the present study were higher than those obtained for all species of the Temoridae family in other estuarine, lagoonal and neritic waters (Table 3). This can be attributed to higher temperatures in the Cananéia Lagoon estuarine system than in other waters (Table 3).

During the study period, *T. turbinata* constituted 6.0, 8.3 and 7.8% of the annual copepod community abundance, biomass and production rate respectively. This indicates that in the Cananéia Lagoon estuarine system *T. turbinata* was one of the important copepod species such as *Acartia lilljeborgi*, *A. tonsa*, *Oithona hebes*, *O. oswaldocruzi*, *Pseudodiaptomus acutus*, *Paracalanus crassirostris* and *Euterpina acutifrons* (Ara, 1998, 2001a, c). The present study showed that the exotic copepod *T. turbinata*, which recently immigrated into the Cananéia Lagoon estuarine system, played an important role as a secondary producer in this environment.

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