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 µg l⁻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: CALANOIDEA) EN EL COMPLEJO ESTUARINO-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. Ésta 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-Shader variaron entre 0.0002 ± 0.0006 y 1.115 ± 0.261 mgC m⁻³ d⁻¹ (media ± SD). Los cocientes P/B varían entre 0.17 y 0.45 d⁻¹. Estos resultados muestran que *T. turbinata* constituía, 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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**TEMORA TURBINATA IN CANANÉIA, BRAZIL**
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 (Hirotā, 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 µm 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.](image-url)
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*, one-way 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 (\(DW, \mu g\)) calculated from prosome body length (\(PL, \mu m\)) using a length-weight regression equation (Ara, 1998, 2001b) given as:

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

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

Production rate (\(P_c, \text{mgC m}^{-3} \text{d}^{-1}\)) was estimated by the following equation:

\[
P_c = \sum N \times W_c \times G
\]

where \(N\) is abundance (ind. m\(^{-3}\)), \(W_c\) is individual weight (\(\mu g\)) 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:

\[
G = 1.0583 \times W_c^{-0.2962} / 13.6616
\]

where \(T\) is temperature (°C).

**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 \(\mu g l^{-1}\) (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.
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 $2 \pm 4$ to $7.2 \times 10^3 \pm 2.6 \times 10^3$ ind. m$^{-3}$ (mean ± 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 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>
<thead>
<tr>
<th>Stage/sex</th>
<th>$T$</th>
<th>$S$</th>
<th>Chl</th>
<th>TH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>-0.59***</td>
<td>0.744***</td>
<td>-0.617***</td>
<td>0.144</td>
</tr>
<tr>
<td>C1</td>
<td>-0.563***</td>
<td>0.716***</td>
<td>-0.570***</td>
<td>0.168</td>
</tr>
<tr>
<td>C2</td>
<td>-0.536***</td>
<td>0.723***</td>
<td>-0.621***</td>
<td>0.180</td>
</tr>
<tr>
<td>C3</td>
<td>-0.552***</td>
<td>0.712***</td>
<td>-0.581***</td>
<td>0.156</td>
</tr>
<tr>
<td>C4 Females</td>
<td>-0.574***</td>
<td>0.700***</td>
<td>-0.509***</td>
<td>0.145</td>
</tr>
<tr>
<td>C4 Males</td>
<td>-0.566***</td>
<td>0.722***</td>
<td>-0.571***</td>
<td>0.144</td>
</tr>
<tr>
<td>C5 Females</td>
<td>-0.537***</td>
<td>0.640***</td>
<td>-0.447***</td>
<td>0.112</td>
</tr>
<tr>
<td>C5 Males</td>
<td>-0.623***</td>
<td>0.674***</td>
<td>-0.462***</td>
<td>0.142</td>
</tr>
<tr>
<td>C6 Females</td>
<td>-0.533***</td>
<td>0.503***</td>
<td>-0.440***</td>
<td>0.0422</td>
</tr>
<tr>
<td>C6 Males</td>
<td>-0.632***</td>
<td>0.549***</td>
<td>-0.458***</td>
<td>0.0372</td>
</tr>
<tr>
<td>F / F+M (C4)</td>
<td>0.0351</td>
<td>-0.0906</td>
<td>0.176</td>
<td>0.00179</td>
</tr>
<tr>
<td>F / F+M (C5)</td>
<td>0.352**</td>
<td>-0.222</td>
<td>0.0871</td>
<td>-0.120</td>
</tr>
<tr>
<td>F / F+M (C6)</td>
<td>0.351**</td>
<td>-0.233</td>
<td>0.116</td>
<td>-0.0338</td>
</tr>
</tbody>
</table>
atures lower than ca. 24°C, salinities higher than ca. 20 psu and chlorophyll a concentrations lower than ca. 8 µg 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 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±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 estima-

<table>
<thead>
<tr>
<th>Stage/sex</th>
<th>Multiple regression equation (PL vs. T, S and Chl)</th>
<th>r</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>( PL = 276.46 + 0.0349T - 0.0768S - 0.393Chl )</td>
<td>0.376*</td>
<td>56</td>
</tr>
<tr>
<td>C2</td>
<td>( PL = 342.01 - 0.0061T - 0.176S - 0.438Chl )</td>
<td>0.425**</td>
<td>63</td>
</tr>
<tr>
<td>C3</td>
<td>( PL = 421.15 - 0.342T + 0.0195S - 0.215Chl )</td>
<td>0.441**</td>
<td>61</td>
</tr>
<tr>
<td>C4 Female</td>
<td>( PL = 447.12 - 0.264T + 0.234S + 0.208Chl )</td>
<td>0.432**</td>
<td>57</td>
</tr>
<tr>
<td>C4 Male</td>
<td>( PL = 486.96 - 0.475T + 0.120S + 0.086Chl )</td>
<td>0.551***</td>
<td>58</td>
</tr>
<tr>
<td>C5 Female</td>
<td>( PL = 601.86 - 0.353T + 0.0827S + 0.152Chl )</td>
<td>0.399*</td>
<td>59</td>
</tr>
<tr>
<td>C5 Male</td>
<td>( PL = 597.33 - 0.452T + 0.0131S + 0.190Chl )</td>
<td>0.446**</td>
<td>63</td>
</tr>
<tr>
<td>C6 Female</td>
<td>( PL = 778.09 - 0.439T + 0.0239S + 0.184Chl )</td>
<td>0.446**</td>
<td>63</td>
</tr>
<tr>
<td>C6 Male</td>
<td>( PL = 822.90 - 0.631T - 0.182S - 0.0844Chl )</td>
<td>0.563***</td>
<td>63</td>
</tr>
</tbody>
</table>
ed production rates varied from 0.0002 ± 0.0006 to 1.115 ± 0.261 mgC m⁻³ d⁻¹ (daily mean ± 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 Gloden, 1995; De La Rocha, 1998), nothing has been known about 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...
youngster 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 Euterpinia 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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