Population biology and secondary production of the stout razor clam
*Tagelus plebeius* (Bivalvia, Solecurtidae) on a sandflat in southeastern Brazil

Jolnnye R. Abrahão¹, ³; Ricardo S. Cardoso²; Leonardo Q. Yokoyama¹ & A. Cecilia Z. Amaral¹, ³

¹ Laboratório de Biologia Marinha, Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas. Caixa Postal 6109, 13083-970 Campinas, São Paulo, Brasil.
² Laboratório de Ecologia Marinha, Departamento de Ecologia e Recursos Marinhos, Universidade Federal do Estado do Rio de Janeiro. 22290-240 Rio de Janeiro, Rio de Janeiro, Brasil.
³ Corresponding authors. E-mail: jolnnye@yahoo.com.br; ceamaral@unicamp.br

ABSTRACT. The population biology and production of the stout razor clam *Tagelus plebeius* Lightfoot, 1786 were investigated on an intertidal sandflat on the southeast coast of Brazil (Enseada Beach, São Sebastião, state of São Paulo) between April 1997 and April 1998. Two rectangular sites of 50 X 10 m parallel to the waterline were established, site A (upper intertidal level) and site B (middle intertidal level), where the samples were taken in an 0.5 x 0.5 m quadrat. High abundances were recorded in winter and spring, with no significant differences between the sites. The high bivalve abundances were related to the presence of very fine homogeneous sediment with low salinities. *Tagelus plebeius* had negative allometric growth, characteristic of deep burrowers for the relationships DM/SL and AFDM/SL. Parameters of the modified von Bertalanffy growth function were: \( L_\infty = 67.01 \text{ mm}, \ K = 1.73 \text{ year}^{-1}, t_0 = -0.11 \text{ year}, C = 0.43, WP = 0.96. \) The instantaneous mortality \( (Z) = 3.12 \text{ year}^{-1}, \) relatively high in comparison to other tropical bivalve populations. Secondary production was 1.53 g AFDM m\(^{-2}\) year\(^{-1}\), with a P/B ratio reaching 1.37 year\(^{-1}\). This high turnover ratio \( (P/B) \) was related to a rapid population replacement, connected with the short life span and high mortality of the species.

KEY WORDS. Abundance; growth; intertidal zone; mortality.
in Maceió, and Abrahão & Amaral (1999) described its abundance and spatial distribution in a beach on the northern coast of São Paulo. In this context, the present study aimed to analyze the population dynamics and secondary production of *T. plebeius* at an intertidal zone of a sandflat in southeast Brazil.

**MATERIAL AND METHODS**

Enseada Beach, located at the southern end of the Caraguatatuba Bay on the northern coast of São Paulo (23°43’S, 45°25’W), Brazil, is a sheltered and dissipative beach approximately 2 km long (Omena & Amaral 1997). This extensive intertidal sandflat is formed by a gentle slope (1° to 2°), with a low tidal amplitude of less than 1 m (Omena & Amaral 2000). The upper and middle level of the intertidal region at Enseada has a sediment composed by very fine, well-sorted sand, with mean grain size ranging from 3 to 5 μ, low percentage of silt and clay (0.2 to 0.4%), and low organic matter content (1.3 to 1.7%) (Abrahão & Amaral 1999, Arruda et al. 2003). A predominance of very fine and well-sorted sediments denoted the hydrodynamic stability of the study areas. In addition, the Enseada Beach is subject to anthropogenic interference because it is located near to an urban center. The freshwater influx and a waste water discharge, which flow onto the middle level of the intertidal region caused a high range of salinity and increased the amount of organic matter dissolved in the water, especially during summer.

The stout razor clams were sampled monthly between April 1997 and April 1998, during low tide, at two rectangular sites of 50 x 10 m, parallel to the waterline and separated by a distance of approximately 50 m: Site A (upper intertidal level) and Site B (middle intertidal level). Monthly, at each site, five random samples were obtained with a 0.5 x 0.5 m². The sediment was removed to a depth of 50 cm and washed through a 1.0 mm mesh net. Live razor clams were separated from dead clams were determined in previous studies and considered to be homogeneous in the two sites (Abrahão & Amaral 1999, Arruda et al. 2003), only the interstitial water salinity was measured during every sample series (five samples per month) for both sites. To increase the number of individuals for the analyses of size distribution and growth, other clams were randomly collected in areas surrounding the original sites, always taking into account the tidal level where the sites were located.

In the laboratory, the antero-posterior length of each individual (alive and dead) was measured with a digital caliper with a 0.01 mm precision. The soft tissues of the clams were separated from the shells and dried at 80°C until constant weight to obtain the dry mass (DM). The ash-free dry mass (AFDM) resulted from the loss after the soft dried tissues were incinerated at 550°C for five hours (Urban & Campos 1994).

Cochran’s test (Underwood 1997) was used to test the homogeneity of variances, and to remove any heterogeneity; data were log_{10}x+1 transformed. The mean values of the parameters interstitial salinity, abundance of live clams, and abundance of dead clams were compared between the sites with a paired Student’s t-test. A correlation between the interstitial salinity and the mean monthly abundance of live clams for each site was verified with the Pearson correlation coefficient. In all statistical analyses, a significance level of 5% was adopted (Zar 1996).

The relationships between the shell length (SL) versus dry mass (DM) and ash-free dry mass (AFDM) were defined through exponential regressions: DM = aSL^b and AFDM = aSL^b, where a and b are constants. For both regressions, SL was considered the independent variable. To confirm if the values of b obtained in the exponential regressions were significantly different from the isometric values (b = 3), a t-test (Ho, b = 3) was applied (Gaspar et al. 2001). The mean shell lengths of *T. plebeius* at sites A and B were compared.

To perform the growth analysis, the monthly shell length-frequency distributions of live clams were used, according to procedures suggested by Gómez & Defeo (1999) and Defeo et al. (2001). This procedure consists of: (1) separate shell length-frequency distributions using the NORMSEP routine of the FISAT statistical program (Gayanilo et al. 1996); (2) assign absolute ages for the respective cohorts (lengths) and build the relation age-length key; and (3) use the age-length results to fit the von Bertalanffy growth curve modified for seasonal oscillation in growth (VBGF: Gayanilo et al. 1996) by non-linear least-squares:

\[
L_t = L_{\infty} \left[1 - e^{-\left(K/2\pi\sin\pi (t-t_0)/W\right)}\right]
\]

where \(L_t\) is the shell length at age \(t\); \(L_{\infty}\) is the maximum theoretical shell length for the species; \(K\) is the curvature parameter; \(C\) is the constant of amplitude of the seasonal oscillation growth; \(t_0\) is the theoretical age at size 0; and \(W\) is the wintertime point, i.e., period of growth reduction, expressed as a decimal fraction of the year. The growth index phi-prima (\(\phi'\)), defined as:

\[
\phi' = 2\log_{10}(L_{\infty}) + \log_{10}K
\]

(Pauly & Munro 1984, Defeo et al. 1992) was employed as a measure of overall growth performance.

The instantaneous mortality rate (Z) was calculated by the single negative exponential model using the length-converted catch curve method (Pauly et al. 1995) provided by the FISAT program (Gayanilo et al. 1996). The estimation of Z was given by: \(\ln(N) = g-Zt\), where \(N\) is the number of individuals; \(g\), the regression intercept, \(Z\) in module, the unbiased mortality estimated; and \(t\), the estimated age in each cohort (Pauly et al. 1995).

Life span was estimated by the growth parameters of VBGF and on the basis of the length representing the 99th percentile of the population, \(L_{99\%}\) (Cardoso & Veloso, 1996).

Production was estimated by the weight-specific growth rate method (Crisp 1984), given by the equation \(P = \sum f_i G_i W_i \Delta t\), where \(f_i\) is the mean number of individuals in size class \(i\) during period \(\Delta t\), \(G_i\) is the mass-specific growth rate in size class \(i\),...
and Δt is the time range. \( G_i = bK[(L_i/L_i)-1] \), where \( b \) is the exponent of the weight-length ratio, \( K \) and \( L_i \) are parameters of the VBG equation, and \( L_i \) is the mean length in size class \( i \). The mean annual biomass was calculated as: \( B = \sum W_i \Delta t \).

**RESULTS**

The mean salinity at site A was 16.6 ± 6.1, ranging between 11.2 (October 1997) and 34.4 (July 1997). At site B the mean salinity was 5.4 ± 1.5, ranging from 3.6 (January 1998) to 25.4 (August 1997). Salinities were significantly different between sites (\( t = 4.896, \text{df} = 10, p = 0.001 \)).

At site A, 831 individuals of *Tagelus plebeius* were obtained: 264 alive and 567 dead. At site B, 191 live and 350 dead individuals were collected, totaling 541 clams. At the former, the highest abundance was recorded in winter (July 1997), and the lowest in autumn (May 1997) and summer (February 1998) (Fig. 1). For site B, the highest abundance was observed in spring (October 1997) and the lowest in autumn (June 1997) and the end of winter (September 1997) (Fig. 1). There was no significant difference in abundance between the two sites (\( t = 0.839; \text{gl} = 12; p = 0.418 \)).

Negative allometry was observed for the relationships DM/SL and AFDM/SL, with the shell length increasing faster than the body mass (Tab. I).

The mean shell lengths of *Tagelus plebeius* at sites A and B were 48.76 mm ± 7.22 and 52.02 mm ± 9.80, respectively. The populations at both sites were composed by similar size classes, with a dominance of adult individuals (Fig. 2). At site A, the smallest clam was 13.16 mm long and the maximum shell length observed was 63.19 mm; at site B a maximum shell length of 65.97 mm and a minimum of 10.85 mm were recorded.

![Figure 1. *Tagelus plebeius*. Temporal variation of abundance of live individuals (ind m⁻²). Vertical bar: standard error.](image1.png)

![Figure 2. *Tagelus plebeius*. Size frequency distribution in the sites A and B of Enseada Beach.](image2.png)

Regarding dead clams, at site A, the high and low peaks of abundances were recorded in April and June 1997, respectively. At site B, the highest abundances were observed in autumn (March and April 1998) and the lowest over the entire year. Mean annual abundances of dead clams were significantly different between the sites (\( t = 5.308; \text{df} = 12, p = 0.000 \)). The correlation between the number of individuals (mean abundance) and the salinity was not significant (\( r = -0.050, p = 0.825 \)).
Figure 3. *Tagelus plebeius*. Frequency distribution of size class shell in the sites grouped in the differences months of study in the Enseada Beach.
Three overlapping cohorts were distinguished in the size-frequency distributions of *T. plebeius* (Fig. 3). The population had a unimodal distribution between May and July 1997, with cohort 1 growing continuously from size class 50.1 mm to high length classes over the months until January 1998, when a decrease occurred in the abundance, with few individuals represented. From September 1997, the size-frequency distribution became bimodal, represented by cohorts 1 (size class 57.6 mm) and 2 (size class 47.6 mm). In January 1998, the population still had a bimodal distribution, with the displacement of the mode, now of cohort 2 (52.6 mm), and a new mode represented by cohort 3 (30.1 mm).

The growth analysis revealed an asymptotic size of 67.01 mm for *T. plebeius*. The estimate of growth parameters was significant (*p* < 0.001, Tab. II), except for *C* and *t*<sub>0</sub>. The clams grew rapidly in their first years, reflected by the annual growth rate (*K* = 1.73 year<sup>-1</sup>), with the rate declining as they approached the asymptotic size (Fig. 4). The “winter point” (WP) indicated a decrease in growth by the end of October 1997 (0.9 x 12 = 10.8 months). Although not significant, parameter *C* indicated a small oscillation in growth (Tab. II, Fig. 4). The growth intensity (φ') was 3.89. Life expectancy on the basis of *L*<sub>99%</sub> was 19 months, and the life span of the largest individuals found (65.97 mm) was estimated as 27 months. The instantaneous mortality rate (*Z*) calculated for *T. plebeius* was 3.12 year<sup>-1</sup>.

The mean monthly density of the population of *T. plebeius* in Enseada Beach ranged between 16.00 and 41.60 ind.m<sup>-2</sup>, representing a mean annual biomass of 1.12 g AFDM m<sup>-2</sup>. The highest value of biomass was recorded in October 1997 (1.90 g AFDM m<sup>-2</sup>). The production ranged between 0.08 g and 0.21 g AFDM m<sup>-2</sup> year<sup>-1</sup>, with total production of 1.53 g AFDM m<sup>-2</sup> year<sup>-1</sup>, giving a P/B ratio of 1.37 year<sup>-1</sup>.

![Figure 4. Tagelus plebeius. VBG growth curve with seasonal oscillation. The bars represent the standard error of the mean.](image)

### DISCUSSION

The abundances of live individuals of *T. plebeius* in the population at Enseada Beach showed significant fluctuations over the months of sampling. The maximum density reached 79 ind m<sup>-2</sup>. Abundances reported for other extant populations are much higher: up to 300 ind m<sup>-2</sup> in estuaries along the northwestern Atlantic and the Gulf of Mexico (Chanley & Castagna 1971); 138 ind m<sup>-2</sup> in an estuary in Maceió, Brazil (O. Viégas pers. comm.); 128 ind m<sup>-2</sup> in Florida, USA (Sheridan & Livingston 1983); and up to 200 ind m<sup>-2</sup> in the Mar Chiquita lagoon, Argentina (Iribarne et al. 1998). However, these high abundances were not found in other populations. The maximum mean density recorded by Holland & Dean (1977b) was 72 ind m<sup>-2</sup>.
There is thus a wide range of abundance between the populations studied, regardless of latitude.

The sediment composition is very important for the distribution and abundance of *T. plebeius*. Hollando & Dean (1997a, b) observed that the species only occurred in sediments with grain diameter ranging from 2 to over 6b and that high abundances were observed in areas where the sediments were composed of at least 2% silt and clay. The grain diameter, ranging from 3 to over 5b and the low percentage of silt and clay in the sediment of Enseada Beach (Abrahão & Amaral, 1999), characterized the upper and middle levels as more suitable habitats for *T. plebeius*. The lower level is less stable and undergoes regular alterations caused by the constant deposition of sand, forming small temporary beds and impeding the development of the species.

The abundance of the trophic group SDS (suspension feeding, restricted mobility, inhalant siphon, and ctenidium) in Enseada Beach is related to the presence of very fine homogeneous sediment and low salinities (Arruda et al. 2003). The correlation between the SDS group and low salinities may be a factor in the high abundance of *T. plebeius*, a suspension-feeding bivalve, in Enseada Beach. The middle level of this beach receives domestic sewage discharge, reducing the salinity and increasing the suspended organic-matter content. According to Lima et al. (2000), great variations in salinity have a strong effect on the population dynamics of *Mesodesma mactroides* Deshayes, 1854. Defeo (1993) observed that an intense freshwater discharge from the Andreoni Channel (Uruguay) was responsible for the reduction in the density of adult individuals of *M. mactroides*.

There was no correlation between the abundance of *T. plebeius* and salinity. Although there was no mention of an optimal condition for the survivorship of the species, Castagna & Chanley (1973) reported that feeding and burrowing activities were reduced in salinities below 10, with low survivorship between salinities of 2.5 and 5.0. The temporal fluctuation in abundance may be associated with biological factors such as recruitment, mortality, and intra- and interspecific competition. High abundances of *T. plebeius* in South Carolina (USA) were observed in conjunction with the spring recruitment (Holland & Dean 1977b). These authors observed that recruitment occurred mainly in low areas of the intertidal zone because of environmental and biological factors such as: enhanced physiological stress, predation by birds and other animals after larval settlement, and selective larval settlement pattern determined by the adult population. Viégas (pers. comm.) reported an inverse situation, with recruitment marked by a high abundance of juveniles in the permanently exposed area. The high recruitment in this area compared to the submerged area may result from the elimination of the larvae by the dense populations of adult *T. plebeius* and other filtering bivalves. Lima et al. (2000) observed an interaction between individuals of the population of *M. mactroides*, where adults reduced recruitment by passive filtration of their own larvae.

Other climatic and biotic factors besides salinity could affect the abundance of this species in Enseada Beach. No significant variations were observed in the abundance of live clams between the sites; however, the same was not observed for the dead clams. Site A showed a high number of dead clams, related to the occurrence of an increased desiccation rate in the upper level. The small numbers of dead clams found at site B, adjacent to a stream, indicate that this is a suitable area for the development of the species, because of the low desiccation rate and high food availability. Besides the reduced salinity, which might affect the feeding activities of the clams, individuals with a large mean size were dominant at site B. Only in October 1997, and February and March 1998 was an increase in the number of dead clams observed. Coarse sediment transported in by rainfall may have increased the instability of the substrate and consequently compromised the integrity of the clams’ siphon tubes, interfering with their feeding.

In this study, *T. plebeius* showed a negative allometry for the relationships DM/SL and AFDM/SL, which differed from the isometric growth for DM/SL observed in the South Carolina populations (Holland & Dean 1977b). Lomovaski et al. (2006) found negative allometry for the height/length (H/SL) and width/length (W/SL) relationships of *T. plebeius*. Gaspar et al. (2002) reported discrepancies in the allometric relationships of *Pharus legumen* Linnaeus, 1758 (Bivalvia, Solecurtidae), which, in spite of being considered a great burrower, displays negative allometry for H/SL and is isometric for W/SL. The differences in relative growth observed in *T. plebeius* may be related to particular ecological characteristics of the species in each environment. Gaspar et al. (2002) stated that the differences observed in the relative growth of *P. legumen* are a result of the ecological characteristics of the species, which showed a wide depth distribution in the study area. Discrepancy in the morphometric relationships may be a consequence of distinctive hydrological and sedimentological patterns between the areas (Gaspar et al. 2002). The sediment characteristics found at Enseada Beach (see Abrahão & Amaral 1999) were similar to those recorded by Holland & Dean (1977a), and relative growth could be influenced by other abiotic factors, such as salinity.

The negative allometry detected for *T. plebeius* reveals a morphological adaptation found in deep burrowers, which normally possess elongated shells. Urban (1994) verified this relationship for *Tagelus dombeii* Lamarck, 1818. Elongated-shelled bivalves normally predominate in compact sediments because of their high capacity to burrow (Eagar 1978), expending less energy (Trueman 1966, Stanley 1970). The long thin shells of deep burrowers could be an advantage because less energy is invested in shell growth (Urban 1994). Species of the family Solecurtidae can burrow at least 50 cm in the substrate (Farinati et al. 1992), as also observed by Abrahão & Amaral (1999) and Arruda et al. (2003).

The population of *T. plebeius* showed three annual merging cohorts. January 1998 was the single period with a four age-class structure in Enseada Beach. Two recruitment peaks
were recorded, one at the end of winter and beginning of spring (September 1997), and another in summer (February 1998). The pattern of three annual cohorts was similar to the age structure observed by Holland & Dean (1977b); however, the authors observed the formation of four age classes in the area below the low intertidal level, and assumed that the absence of human exploitation was the main cause for it.

The asymptotic size of *T. plebeius* (67.01 mm) is larger than the values estimated by Holland & Dean (1977b), 65 mm, and Viégas (1982), 51.73 mm. However, it is smaller than that estimated for *T. dombeii* (Urban 1996), 88.50 mm (Tab. III). *Ensis siliqua* Linnaeus, 1758 had different values of *L*ₙ between populations in the United Kingdom (Henderson & Richardson 1994), Portugal (Gaspar et al. 1994) and Ireland (Fahy & Gaffney 2001). Differences in the growth rates of some bivalves might be related to the structure of the sediment (Henderson & Richardson 1994), thus influencing *L*ₙ. *Ensis ensis* Linnaeus, 1758 had a smaller size than *E. siliqua*; the former occurs in fine sediments and the latter in coarse sediments (Henderson & Richardson 1994). Furthermore, high organic-matter content and fine sediments reflect a high stability of the substrate (Grant & Daborn 1994), and such conditions would enhance growth and body condition for suspension-feeding bivalves (Lomovasky et al. 2006). Similarly, a positive influence on the population of *T. plebeius*, which lives in fine sediments in Enseada Beach, is expected.

The availability of food and other resources can affect the physiological costs and also influence the maximum size of bivalves. Regarding abiotic conditions, temperature seems to be the effective controlling factor (Bachelet 1980). However, differences in feeding conditions over the area of distribution can be more important than temperature (Cardoso et al. 2007). These authors observed that feeding conditions for *Macoma balthica* Linnaeus, 1758 of similar age classes were more favorable in areas below the low-tide level. In these locations, shell growth was rapid because individuals were continuously submersed, in contrast with those in the intertidal zone. In other bivalves such as scallops, mussels, and oysters, the growth rate also seems to be controlled by food availability (Bayne & Worral 1980, Borrero 1987, Navarro et al. 2000, Paterson et al. 2003).

Clams at Site B showed a greater mean length (52.02 mm) than clams at Site A (mean length 48.58 mm). This difference might be related to high availability of food at Site B, since the constant influx from a stream maintains a high feeding activity; and the domestic sewage discharge furnished a high organic-matter input. By contrast, at Site A, the physiological stress from extended periods of air exposure and the impossibility of frequent feeding seem to have reduced the growth rate.

The maximum length recorded at Enseada (65.97 mm) was smaller than the maximum lengths reported for other localities: 70 and 91 mm in South Carolina (Holland & Dean 1977b) and 69 mm at Maceió (Viégas 1982). Individuals of *T. plebeius* are capable of attaining 50 mm in eight months with the estimated growth rate (K = 1.73 year⁻¹). Holland & Dean (1977b)

<table>
<thead>
<tr>
<th>Species</th>
<th>K (yr⁻¹)</th>
<th>Lₙ (mm)</th>
<th>²a'</th>
<th>Z (yr⁻¹)</th>
<th>Climate area</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tagelus plebeius</em></td>
<td>1.73</td>
<td>67.01</td>
<td>3.89</td>
<td>3.12</td>
<td>Subtropical (23°43’S)</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Gari solida</em></td>
<td>1.34</td>
<td>57.90</td>
<td>3.65</td>
<td>1.45</td>
<td>Tropical (14°15’S)</td>
<td>Urban &amp; Tarazona (1996)</td>
</tr>
<tr>
<td><em>Gari solida</em></td>
<td>0.67</td>
<td>77.50</td>
<td>3.60</td>
<td>1.64</td>
<td>Tropical (14°15’S)</td>
<td>Urban &amp; Tarazona (1996)</td>
</tr>
<tr>
<td><em>Gari solida</em></td>
<td>0.49</td>
<td>101.60</td>
<td>3.74</td>
<td>1.18</td>
<td>Tropical (14°15’S)</td>
<td>Urban &amp; Tarazona (1996)</td>
</tr>
<tr>
<td><em>Gari solida</em></td>
<td>0.35</td>
<td>101.60</td>
<td>3.55</td>
<td>1.30</td>
<td>Tropical (14°15’S)</td>
<td>Urban &amp; Tarazona (1996)</td>
</tr>
<tr>
<td><em>Donax hanleyanus</em></td>
<td>0.90</td>
<td>28.50</td>
<td>2.86</td>
<td>1.55</td>
<td>Tropical (23°03’S)</td>
<td>Cardoso &amp; Veloso (2003)</td>
</tr>
<tr>
<td><em>Donax hanleyanus</em></td>
<td>0.80</td>
<td>26.40</td>
<td>2.75</td>
<td>1.70</td>
<td>Tropical (23°03’S)</td>
<td>Cardoso &amp; Veloso (2003)</td>
</tr>
<tr>
<td><em>Tagelus dombeii</em></td>
<td>0.23</td>
<td>88.50</td>
<td>3.26</td>
<td>0.84</td>
<td>Temperate (36°5’S)</td>
<td>Urban (1996)</td>
</tr>
<tr>
<td><em>Venus antique</em></td>
<td>0.22</td>
<td>73.90</td>
<td>3.08</td>
<td>1.08</td>
<td>Temperate (36°5’S)</td>
<td>Urban (1996)</td>
</tr>
<tr>
<td><em>Ensis macha</em></td>
<td>0.21</td>
<td>189.90</td>
<td>3.88</td>
<td>1.09</td>
<td>Temperate (36°5’S)</td>
<td>Urban (1996)</td>
</tr>
<tr>
<td><em>Gari solida</em></td>
<td>0.31</td>
<td>89.60</td>
<td>3.39</td>
<td>0.85</td>
<td>Temperate (36°32’S)</td>
<td>Urban &amp; Campos (1994)</td>
</tr>
<tr>
<td><em>Semele solida</em></td>
<td>0.29</td>
<td>78.00</td>
<td>3.26</td>
<td>0.92</td>
<td>Temperate (36°32’S)</td>
<td>Urban &amp; Campos (1994)</td>
</tr>
<tr>
<td><em>Prototacha thaca</em></td>
<td>0.17</td>
<td>82.20</td>
<td>3.07</td>
<td>0.63</td>
<td>Temperate (36°32’S)</td>
<td>Urban &amp; Campos (1994)</td>
</tr>
<tr>
<td><em>Venus antique</em></td>
<td>0.18</td>
<td>80.00</td>
<td>3.06</td>
<td>0.66</td>
<td>Temperate (43°07’S)</td>
<td>Clasing et al. (1994)</td>
</tr>
<tr>
<td><em>Ensis siliqua</em></td>
<td>0.26</td>
<td>178.20</td>
<td>3.91</td>
<td>–</td>
<td>Temperate (53°08’N)</td>
<td>Fahy &amp; Gaffney (2001)</td>
</tr>
<tr>
<td><em>Ensis siliqua</em></td>
<td>0.53</td>
<td>154.70</td>
<td>4.10</td>
<td>–</td>
<td>Temperate (53°08’N)</td>
<td>Henderson &amp; Richardson (1994)</td>
</tr>
<tr>
<td><em>Ensis ensis</em></td>
<td>0.56</td>
<td>131.60</td>
<td>3.99</td>
<td>–</td>
<td>Temperate (53°17’N)</td>
<td>Henderson &amp; Richardson (1994)</td>
</tr>
</tbody>
</table>
reported that individuals attain a shell length of approximately 50 mm in seven months, and Viegas (1982) reported a similar size within a period of 12 months. In the latter case, intraspecific competition was the main factor affecting the growth of the clams. The homogeneity in the granulometric composition of Enseada Beach reported by Abrãão & Amaral (1999) would enhance the growth of the clams in the studied area.

The value of K (1.73 year\(^{-1}\)) for T. plebeius was high compared to some of the values determined by Viegas (1982: 0.25 year\(^{-1}\)) for the same species, and by Urban (1996) for T. dombei (0.23 year\(^{-1}\)) (Tab. III). These differences could be a result of the differing latitudinal gradients, physiological levels of tolerance of each species for different environmental conditions, and methods used to calculate growth. Growth performance can be best compared using the index of growth (\(\phi^\prime\)), especially in bivalves (Vakily 1992). The index for T. plebeius was estimated as 3.89, and 2.83 (Viegas 1982), and 3.26 for T. dombei (Urban 1996). According to Vakily (1992), bivalves grow faster in low latitudes because the higher temperatures increase their metabolic rates. Furthermore, there is evidence that growth rates of bivalves that inhabit the intertidal zone decrease with the reduction in the period of immersion (Gillmor 1982, Peterson & Black 1988, Lomovasky et al. 2006).

The Z value obtained in this study was higher than the values obtained for the majority of bivalves, especially in temperate regions (Tab. III). This high value is explained by the large numbers of individuals found dead in the sediment, a consequence of the presence of large numbers of predators, especially birds, during low-tide periods. According to Abrãão & Amaral (1999) the presence of predators such as hawks, vultures, sandpipers, and crustaceans could be responsible for the population mortality of T. plebeius. Urban et al. (1998) reported that the American oystercatcher Haematopus palliatus Temminck, 1820 was an important source of T. plebeius mortality in Argentinean estuaries. Similar conditions were observed for T. dombei in the tidal flat of Corhuín, Chile (Lardies et al. 2001). No individuals of M. bullithca over five years old were observed in the intertidal areas, reflecting the high mortality of adults predated upon by birds (Cardoso et al. 2007).

Mortality rate can also be related to the human exploitation of clams, which are collected for food at Enseada Beach (Abrãão & Amaral 1999). Clasing et al. (1994) found that the increased mortality of Venus antiqua King & Broderip, 1832 in Chile was the result of intense human exploitation of the natural beds. In conjunction with the intense exploitation, the physical stress caused by sediment disturbance during harvesting changes the substrate penetrability and decreases larval settlement. This restricts the burrowing movements of T. plebeius and may increase mortality. DeFeo & de Alava (1995) and DeFeo (1998) made similar observations in for another species, M. mactroides.

The estimated value of secondary production for T. plebeius was 1.53 g AFDM m\(^{-2}\) year\(^{-1}\), lower than the values observed for the same species by Viegas (1982), (2.19 g AFDM m\(^{-2}\) year\(^{-1}\)), and for T. dombei by Urban (1996), (7.8 AFDM m\(^{-2}\) year\(^{-1}\)). However, the population of T. plebeius at Enseada Beach showed a high P/B ratio compared to the former populations (Tab. IV).

### Table IV. Comparison of secondary production (P, g AFDM m\(^{-2}\) year\(^{-1}\)) and production-to-biomass (P/B) ratio of several bivalves species from different geographical regions.

<table>
<thead>
<tr>
<th>Species</th>
<th>P</th>
<th>P/B</th>
<th>Climate area</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tagelus plebeius</td>
<td>1.53</td>
<td>1.37</td>
<td>Subtropical (23°43’S)</td>
<td>Present study</td>
</tr>
<tr>
<td>Tagelus plebeius</td>
<td>2.19</td>
<td>1.23</td>
<td>Tropical (9°37’S)</td>
<td>Viegas (1982)</td>
</tr>
<tr>
<td>Donax serra</td>
<td>273.20</td>
<td>1.60</td>
<td>Tropical (22°47’S)</td>
<td>Laudien et al. (2003)</td>
</tr>
<tr>
<td>Donax serra</td>
<td>356.60</td>
<td>1.20</td>
<td>Tropical (22°47’S)</td>
<td>Laudien et al. (2003)</td>
</tr>
<tr>
<td>Donax serra</td>
<td>166.90</td>
<td>1.20</td>
<td>Tropical (22°59’S)</td>
<td>Laudien et al. (2003)</td>
</tr>
<tr>
<td>Donax serra</td>
<td>637.30</td>
<td>1.20</td>
<td>Tropical (22°59’S)</td>
<td>Laudien et al. (2003)</td>
</tr>
<tr>
<td>Donax hanleyanus</td>
<td>0.76</td>
<td>1.59</td>
<td>Tropical (23°03’S)</td>
<td>Cardoso &amp; Veloso (2003)</td>
</tr>
<tr>
<td>Donax hanleyanus</td>
<td>3.67</td>
<td>1.45</td>
<td>Tropical (23°03’S)</td>
<td>Cardoso &amp; Veloso (2003)</td>
</tr>
<tr>
<td>Ensis macha</td>
<td>9.70</td>
<td>0.22</td>
<td>Temperate (36°S)</td>
<td>Urban (1996)</td>
</tr>
<tr>
<td>Tagelus dombei</td>
<td>7.80</td>
<td>0.29</td>
<td>Temperate (36°S)</td>
<td>Urban (1996)</td>
</tr>
<tr>
<td>Venus antiqua</td>
<td>22.00</td>
<td>0.18</td>
<td>Temperate (36°S)</td>
<td>Urban (1996)</td>
</tr>
<tr>
<td>Gari solida</td>
<td>27.60</td>
<td>0.33</td>
<td>Temperate (36°32’S)</td>
<td>Urban &amp; Campos (1994)</td>
</tr>
<tr>
<td>Prototachaca thaca</td>
<td>16.90</td>
<td>0.27</td>
<td>Temperate (36°32’S)</td>
<td>Urban &amp; Campos (1994)</td>
</tr>
<tr>
<td>Semele solida</td>
<td>4.80</td>
<td>0.19</td>
<td>Temperate (36°32’S)</td>
<td>Urban &amp; Campos (1994)</td>
</tr>
<tr>
<td>Venus antiqua</td>
<td>42.00</td>
<td>0.57</td>
<td>Temperate (43°07’S)</td>
<td>Clasing et al. (1994)</td>
</tr>
</tbody>
</table>
A pattern of turnover (P/B ratio) increase from temperate to tropical regions is evident when ratios from different geographical regions are compared (Tab. IV). However, this does not apply to all species and systems. Cardoso & Veloso (2003) observed that the wide range of production and biomass between species of Donax resulted from the influence of a latitudinal temperature gradient and food availability. High somatic production of Venus antiqua was associated with an extended period of primary production in Yaldad Bay, Chile (Las ing et al. 1994). Upwelling was responsible for high production of Donax serra Röding, 1798 on the Namibian coast (Africa), increasing the nutrients in the water and favoring growth (Laudien et al. 2003). The high P/B estimated for Tagelus plebeius at Enseada may be related to high food availability and organic matter supplied by domestic-sewage discharge.

The productivity of a population can vary because of oscillations in its density and size structure (recruitment periods), as well as other intrinsic characteristics (growth) (Caetano et al. 2006). Populations with a high P/B ratio are composed of small individuals with rapid growth and short life span, whereas low values of P/B are associated with large individuals, low growth rate, and long life span (Cardoso & Veloso 2003). The low P/B ratios recorded for Gari solida Gray, 1828, Semele solida Gray, 1828, and Protothaca thaco Molina, 1782 in the Bay of Dichtato (Chile) resulted from the small number of recruits, producing populations of old individuals with low secondary production (Urban & Campos 1994). Cardoso & Veloso (2003) reported that the elevated production of Donax hanleyanus Phillipi, 1845 at Restinga da Marambaia Beach (Brazil) was associated with high densities. Urban & Campos (1994) observed that the difference in P/B ratios between populations of V. antiqua in two regions of Chile was caused by different rates of exploitation at fishery sites. High mortality induced by human exploitation was responsible for the high P/B ratio of V. antiqua in comparison to other species of the superfamily Veneracea (Las ing et al. 1994).

Tagelus plebeius showed a P/B ratio typical of highly productive environments, attributed to high levels of organic matter from domestic-sewage discharge at Enseada Beach, which is not an estuarine region. Furthermore, this high P/B ratio may also be a consequence of rapid population replacement together with a short life span (27 months) and high mortality rate. Part of the secondary production by this clam is consumed by crabs, fish, and especially birds (Abrahao & Amaral 1999), and may constitute an important food resource for human populations. The present results have shown that T. plebeius is an essential trophic link in this coastal ecosystem.

ACKNOWLEDGMENTS

This study is part of the extensive program “Environmental Monitoring of Sandy Beach Fauna of São Sebastião Channel”, which could not have been completed without the collaboration of a team of students, technicians, and colleagues. We thank Alexander Turra and Márcia Denadai for their assistance in data analysis. We also thank to anonymous referees for valuable comments on the manuscripts. Thanks also to J.W. Reid for revision of the English text. We express our sincere thanks to E. Soares Marinho, A. Maximo Rosa, and the CEBIMar technicians who assisted in the field work. We are also grateful to the Centro de Biologia Marinha (CEBIMar-USP), and IB/UNICAMP for their assistance with logistics. Financial support for this study was provided by CNPq and FAEP UNICAMP.

LITERATURE CITED


Carmichael, R.H.; A.C. Shriver & I. Valiela. 2004. Changes in shell and soft tissue growth, tissue composition, and survival of quahogs, Mercenaria mercenaria, and softshell clams, Mya arenaria, in response to eutrophic-driven changes in food...


Honkoop, P.J.C. & J.J. Beukema. 1997. Loss of body mass in winter in three intertidal bivalve species: an experimental and


