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# Growth, mortality, and reproduction of *Tagelus plebeius* (Bivalvia: Solecurtidae) in Southeast Brazil

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**Abstract** *Tagelus plebeius* (Lightfoot, 1786) is a stout razor clam that is economically exploited in several countries, including several local fisheries along the Brazilian coast. Despite its wide distribution and economic importance, there are few studies that have examined the population biology of this species. This study aimed to improve the current knowledge about the biology of *T. plebeius* by investigating its growth and mortality on a subtropical sandy beach in Southeast Brazil over a 1-year

period. In addition, the reproduction of *T. plebeius* was analyzed through qualitative and quantitative histological analyses during the last 7 months of the study. The parameters of the von Bertalanffy growth function were estimated to be  $L_{\infty} = 74.14$  mm,  $K = 0.52$  year<sup>-1</sup>,  $C = 0.47$ , and  $WP = 0.94$ . The instantaneous mortality rate ( $Z$ ) was 2.16 year<sup>-1</sup>, and the life span was 2.58 years. We confirmed variations ( $H = 651.35$ ;  $P < 0.05$ ) in the shell length over the months of the study, and the recruitment was higher—but still low—in summer. Four cohorts were observed in the distribution of shell length frequencies. The sex ratio of the population was 1:1 during the study period, and a synchronism in gonadal development and spawning was found between males and females. The high mortality ( $Z$ ) and low recruitment rates can be interpreted as reflecting that the population of *T. plebeius* is under a low restoration process and could be an indication that this species has an endangered status in the study area.

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## Introduction

Artisanal marine invertebrate fisheries on sandy shores have critical socioeconomic and ecological implications, mainly in developing countries. These small-scale fisheries represent a source of food for subsistence, generate important direct income to the community of fishermen, and in some cases, provide high revenues to the country (Defeo 2003). Nonetheless, they may also represent a source of impact on exploited species, reducing—or even depleting—species density and biomass (Ferns et al. 2000; Fagundes et al. 2004) and strongly affecting their

functional roles in marine ecosystems (Dayton et al. 1995; Gutiérrez et al. 2004; Anderson et al. 2011).

Since 1950, global invertebrate catch numbers have increased sixfold (Anderson et al. 2011), yet this exponential growth was not supported by management or regulations based on solid scientific knowledge (Defeo 2003). Population studies, which provide information about distribution, abundance, growth, and reproduction, are essential to achieve sustainable development of fisheries and to secure the long-term use of these resources (Metaxatos 2004; Calderon-Aguilera et al. 2010). However, exploited species are rarely monitored in independent research surveys to assess population trends (Anderson et al. 2011).

The suspension-feeding stout razor clam *Tagelus plebeius* is distributed along the coast of the Americas, from North Carolina (34°N, USA) to the San Matias Gulf (41°S, Argentina) (Rios 1994). This species is commonly used as a fishery resource in the majority of its occurrence area (Chile, Argentina, and Brazil); recently, an increasing commercialization of this species has been recorded (Gutiérrez et al. 2004). Despite its wide distribution and economic importance, there is a great lack of knowledge about the population biology of *T. plebeius*. To date, the population studies focusing on this species have been restricted to those conducted by Holland and Dean (1977a,

b) in the USA, by Clédon et al. (2004) in Argentina, and by Viégas (1982), Abrahão and Amaral (1999), Abrahão et al. (2010), and Ceuta and Boehs (2012) in Brazil.

The increasing exploitation of *T. plebeius*, together with the low number of studies of its biology, is expected to result in negative impacts on these populations (Gutiérrez et al. 2004; Beasley et al. 2005). Aiming to enhance the knowledge about *T. plebeius*, we analyzed its population biology over the course of 1 year on a subtropical sandy beach in Southeast Brazil. During the last 7 months of the study, we combined population dynamics analysis with reproductive analysis, an approach that was performed for the first time for this species.

## Materials and methods

### Study area

This study was conducted at Camaroeiro Beach (23°S, 45°W), an intermediate beach (Farinaccio and Tessler 2006; Amaral and Denadai 2011) located on the northern portion of Caraguatatuba Bay, State of São Paulo, Brazil (Fig. 1). Camaroeiro Beach is approximately 300 m long and 50 m wide and is composed of moderate to poorly sorted fine sand, with intermediate calcareous content

**Fig. 1** Map of the location of Camaroeiro Beach on the northern portion of Caraguatatuba Bay, State of São Paulo, Brazil



(1.51–6.04 %) and low organic matter content (0.28–0.99 %) (Amaral and Denadai 2011).

### Sampling procedures

Sampling was performed at spring low tide at monthly intervals from March 2006 through February 2007. Once the individuals bury themselves deeply in the sediment (50 cm), a great effort is involved in sampling, frequently precluding population studies. To achieve the minimum number of individuals necessary for analysis, we chose to apply a standard procedure used to sample razor clams (Gutiérrez and Iribarne 2003; Vásquez et al. 2006; Abrahão et al. 2010; Ceuta and Boehs 2012; Farias and Rocha-Barreira 2012) instead of using the most common methods used in macrofaunal studies (e.g., transects and/or random stratification). This approach consisted of (1) identifying the area of greatest abundance of *T. plebeius* (the upper level of the intertidal region of Camaroeiro Beach); (2) establishing a sector in this area (a 450 m<sup>2</sup> sector—30 m long and 15 m wide); and (3) excavating the sand in all locations where *T. plebeius* marks could be observed inside the sector. By following this procedure, approximately thirty replicates were collected in each month, which allowed us to achieve the minimum number of individuals necessary to perform growth and mortality analyses. However, the lack of randomization prevented us from performing abundance tests. In addition to biological sample collection, the salinity of the interstitial water was measured in situ with a Goldberg T/C portable refractometer (Mod. 10419<sup>®</sup>), and daily sea temperature data were obtained from the Marine Biology Center of the University of São Paulo (CEBIMar), which is located 40 km from Camaroeiro Beach.

### Population dynamics analysis

The shell length of all sampled *T. plebeius* individuals was measured with a digital caliper to the nearest 0.01 mm and used in the growth analysis. The data were modeled using the von Bertalanffy growth function modified for seasonality (VBGF: García-Berthou et al. 2012):

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

where  $L_t$  is the shell length (mm) at time  $t$ ;  $L_\infty$  is the theoretical maximum shell length (mm) attained by the species;  $K$  (year<sup>-1</sup>) is the curvature parameter;  $C$  is a constant for the amplitude of the seasonal growth oscillation;  $t_0$  is the age at length zero; and  $t_s$  is the initial point of seasonal oscillation in relation with  $t_0$  (Gayaniilo and Sparre

2005). The winter point (WP), i.e., the period of growth reduction, expressed as a decimal fraction of the year, was obtained through the equation  $WP = t_s + 0.5$  (Gayaniilo and Sparre 2005).

Two different methods were used to calculate the VBG parameters:

1. Modal progression analysis (MPA) [the NORMSEF routine of the FISAT II statistical program (Gayaniilo and Sparre 2005)], which consists of (a) separate shell length-frequency distributions using the NORMSEF routine; (b) assignment of absolute ages for the respective cohorts (lengths) and generation of the age-length relationship; and (c) the use of the age-length results to fit the von Bertalanffy growth curve modified for seasonal oscillation in growth by nonlinear least squares (Gómez and Defeo 1999; Defeo et al. 2001).
2. Length-frequency distribution analysis (LFDA), which was performed using the electronic length frequency analysis (ELEFAN I) routine of the FISAT II program. This routine generates a growth curve from the “best fit” to the length-frequency data and calculates the VBGF parameters. The different sub-routines of ELEFAN (K-scan, response surface analysis, and automatic search) were used to identify the VBGF that best fit the monthly length-frequency data using the  $Rn$  value as a criterion of fit (Petracco et al. 2003; Defeo and Martínez 2003; Herrmann et al. 2009).

The results from both methods were compared and evaluated, and the shell growth and mortality rates were modeled using the most appropriate parameters (Chatz Nikolaou and Richardson 2008).

The growth index  $\phi' = 2 \log_{10}(L_\infty) + \log_{10}K$  (Pauly and Munro 1984; Defeo et al. 1992) was employed as a measure of overall growth performance.

The theoretical life span ( $t_{max}$ ) was estimated based on the inverse of the von Bertalanffy growth equation, considering the maximum shell length as 95 % of the asymptotic length (Herrmann et al. 2011):

$$t_{max} = \frac{[\ln L_{95\%} - \ln(L_\infty - L_{95\%})]}{K}$$

The total mortality rate  $Z$  was estimated from the overall size-frequency distribution and the VBGF parameters based on a size-converted catch curve (Pauly 1984a, b; Lomovasky et al. 2002):

$$\frac{N_i}{\Delta t_i} = N_0 e^{-Zt_i}$$

where  $N_i$  is the number of individuals in size class  $i$ ,  $\Delta t_i$  is the time required to grow through this size class, and  $t_i$  is

the relative age in the midsize of class *i*. Total mortality *Z* is computed using the linear regression:

$$\ln\left(\frac{N_i}{\Delta t_i}\right) = a + bt_i; \quad Z = -b$$

The relative level of predation pressure was determined according to Brey and Gage (1997) and Lomovasky et al. (2002) from the relationship between the mortality rate *Z* and growth constant *K* using the index:

$$\Delta_{Z/K} = \log\left(\frac{Z_{\text{measured}}}{Z_{\text{predicted}}}\right); \quad -\infty \leq \Delta_{Z/K} \leq +\infty$$

Negative values indicate exploitation below the empirically determined average level and positive values above the empirically determined average level in benthic populations. *Z*<sub>predicted</sub> is derived from the empirical relation:

$$\log(Z_{\text{predicted}}) = 0.339 + 1.037 \times \log(K)$$

Temporal variations in mean size were assessed with a nonparametric Kruskal–Wallis test because the Kolmogorov–Smirnov test showed that the data were not normally distributed.

### Reproductive biology analysis

From November 2006 through May 2007, the twenty largest individuals (all larger than 40 mm in shell length) were selected for reproductive analysis. Their soft parts were removed from the shell, fixed in Bouin’s fluid for 24 h, and then preserved in 70 % ethanol. A cross-sectional block containing the gonad was dissected from each clam, dehydrated in an ethanol gradient (80, 95, and 100 %), cleared in xylene, and embedded in paraffin. Sections (5–7 μm thick) were stained in Harris’s hematoxylin and counter-stained in eosin (Humanson 1979). The slides were examined under 80×, 160×, and 320× magnifications to determine the sex and stage of reproductive development. The gametogenic stages were defined according to the predominance of specific cells (males: spermatogonia, spermatocytes, spermatids, and spermatozooids; females: oogonia, pre-vitellogenic oocytes, vitellogenic oocytes, and mature oocytes), a strategy modified from Gaspar and Monteiro (1998) and Morsan and Kroeck (2005). For each female, the diameter of the first 40 oocytes with an evident nucleus and nucleolus was measured to verify differences in the mean oocyte area during the study period. The oocyte diameter (*d*) was considered as the mean of four different measurements passing through the center of each oocyte (Corte et al. 2013), and the area of each oocyte was calculated as a circle ( $\pi(d/2)^2$ ). A Kruskal–Wallis test was applied to assess whether the average oocyte areas were different among months.

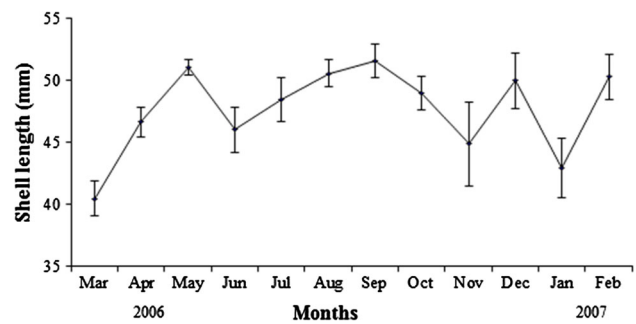
## Results

### Abiotic parameters

The interstitial salinity ranged from 16.6 in January 2007 to 28.6 in November 2006, and the sea water temperature ranged between 22.17 °C (±0.88) in September 2006 and 26.18 °C (±0.82) in March 2006.

### Population dynamics

The mean shell length of *T. plebeius* at Camaroeiro Beach during the study period was 47.2 mm (±10.79 mm) and varied throughout the months (*H* = 651.357; *P* < 0.05),

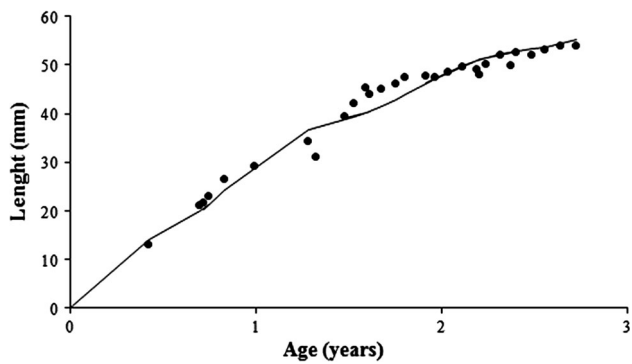


**Fig. 2** Variation in the mean shell length (mm) from March 2006 to February 2007. Bars above and under each dark quadrate indicate the standard error of the mean

**Table 1** Growth parameters estimated by NORMSEP plus nonlinear least squares fit of the von Bertalanffy function, and by ELEFAN routine

MPA			LFDA	
NORMSEP			ELEFAN	
Parameter	Mean (±SD)	<i>P</i>	Parameter	
<i>L</i> <sub>∞</sub> (mm)	74.14 (4.01)	<0.001	<i>L</i> <sub>∞</sub> (mm)	74.6
<i>K</i> (year <sup>-1</sup> )	0.52 (0.05)	<0.001	<i>K</i> (year <sup>-1</sup> )	0.4
<i>C</i>	0.47 (0.15)	0.003	<i>C</i>	0.4
WP	0.94 (0.09)	<0.001	WP	0.8
<i>r</i>	0.99		<i>Rn</i>	0.298
<i>ϕ</i> '	3.46		<i>ϕ</i> '	3.35
<i>t</i> <sub>max</sub> (year)	2.58		<i>t</i> <sub>max</sub> (year)	3.28
<i>Z</i> (year)	2.16		<i>Z</i> (year)	1.85
$\Delta_{Z/K}$	0.29		$\Delta_{Z/K}$	0.34
Smallest (mm)	4.98			
Largest (mm)	65.14			

*L*<sub>∞</sub> asymptotic length, *K* curvature parameter, *C* constant for the amplitude of seasonal oscillation of growth, *WP* point of lowest growth rate in the year, *r* correlation coefficient, *ϕ*' standard growth index (Pauly and Munro 1984), *t*<sub>max</sub> life span, *Z* mortality rate,  $\Delta_{Z/K}$  predation pressure, *SD* standard deviation

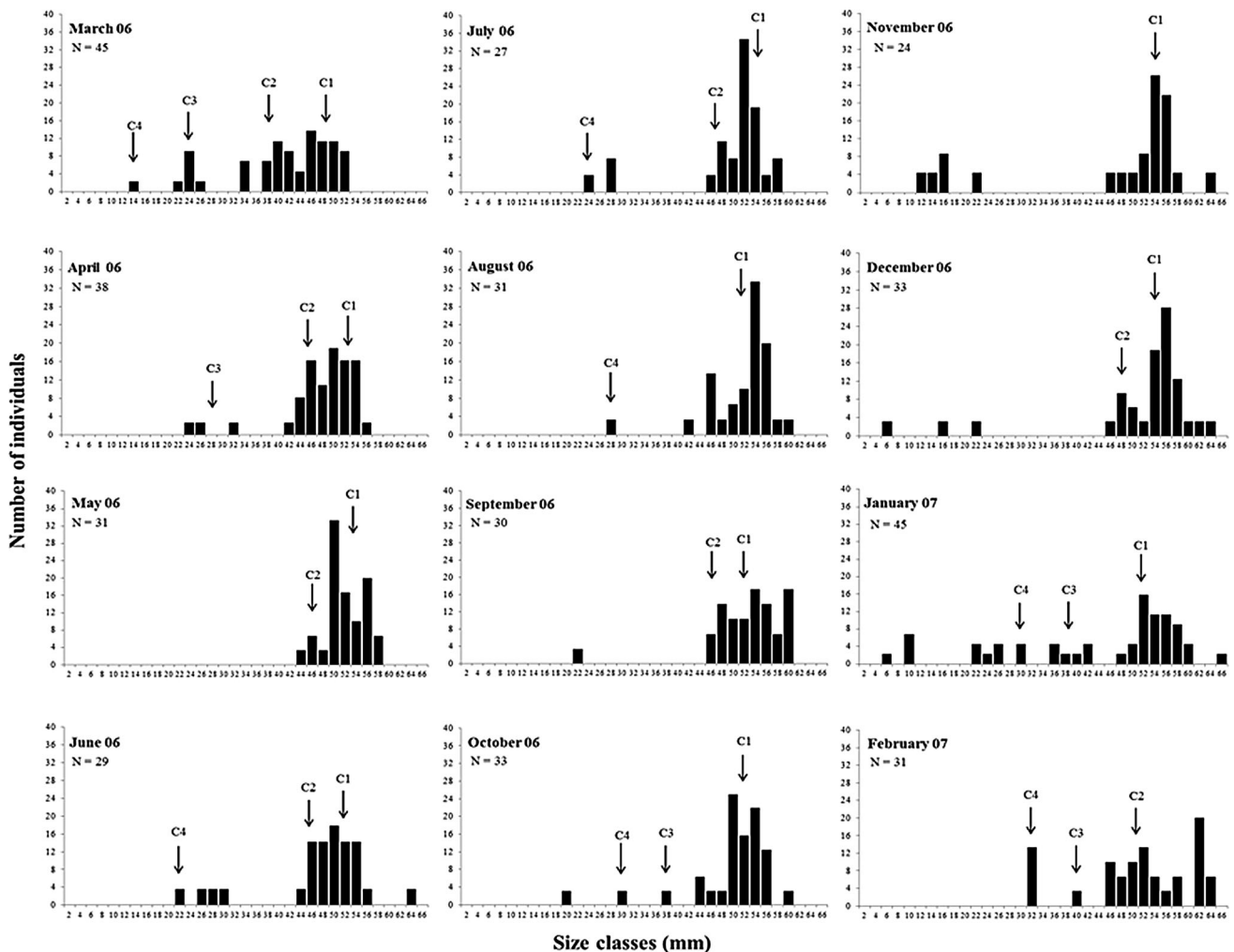


**Fig. 3** Average growth estimated for the population. The dots represent the mean size of each cohort at the specific relative age (year). The line represents the expected growth according to the seasonal version of the VBG equation observed for the population

lower mean in March 2006 ( $40.44 \pm 9.71$ ) (Fig. 2). The smallest individual (4.98 mm) was recorded in December 2006 and the largest (65.14 mm) in January 2007.

Similar growth parameters for the population of *T. plebeius* at Camaroeiro Beach were recorded when using MPA and LFDA methods (Table 1), which strengthens our findings and demonstrates the accuracy of our growth estimates. However, according to Chatzinikolaou and Richardson (2008), the MPA is a more appropriate method for analyzing data from relatively non-mobile populations due to large variations in annual recruitment. Therefore, we used the MPA results to discuss the *T. plebeius* population dynamics at Camaroeiro Beach.

The asymptotic size ( $L_{\infty}$ ) estimated by MPA was approximately 74 mm, with a moderate growth rate



**Fig. 4** Relative frequency (%) of shell length classes (mm) and population cohort distribution (C1, C2, C3, and C4) from March 2006 to February 2007

with a higher mean in May 2006 ( $51.03 \pm 3.54$ ) and a ( $K = 0.5 \text{ year}^{-1}$ ). The individuals grew relatively rapidly

in their first years, and parameter  $C$  (degree of seasonal variation) indicated a moderate oscillation in growth (Fig. 3). The value of WP (the point of lowest growth rate during the year,  $WP = t_s + 0.5$ ) showed growth reduction at the end of the year. The positive values of the  $\Delta_{Z/K}$  parameter indicated exploitation above the empirically determined average level of *T. plebeius*. Four cohorts were observed and tracked during the study period (C1, C2, C3, and C4) (Fig. 4).

### Reproductive biology

A total of 131 individuals were analyzed, and the sex ratio of the population was 1:1 ( $\chi^2 = 0.37$ ;  $P = 0.54$ ). No hermaphrodite individuals or sex reversals were observed during the study period.

After the histological analysis, five gametogenic stages were established for females (early active gametogenesis, late active gametogenesis, ripe, spawning, and spent) and three for males (gametogenesis, ripe, and spawning) (Table 2; Figs. 5, 6).

Females in the early active gametogenesis stage were observed in small percentages in November 2006 and mainly in February and March 2007 (Fig. 7a). The late active gametogenesis stage was identified in November 2006 and March and April 2007, with a peak in the latter month. Females in the ripe stage were observed in late spring and summer (November 2006–February 2007) and in autumn (May 2007). Individuals in the spawning stage were

observed in the same period as the ripe stage, from November 2006 to February 2007, with a peak in December 2006 and January 2007 and another in May 2007. Females in the spent stage were observed in small percentages from January to April 2007, after the spawning peak in summer.

Males in the gametogenesis stage were observed at almost all times throughout the study period, with a peak in February and March 2007 (Fig. 7b). The ripe stage was observed in late spring and summer, from November 2006 to January 2007, and in autumn, from April to May 2007. Individuals in the spawning stage were observed from November 2006 to January 2007 and also in May 2007. The gametogenic stages of the males and females were synchronized over the period of study.

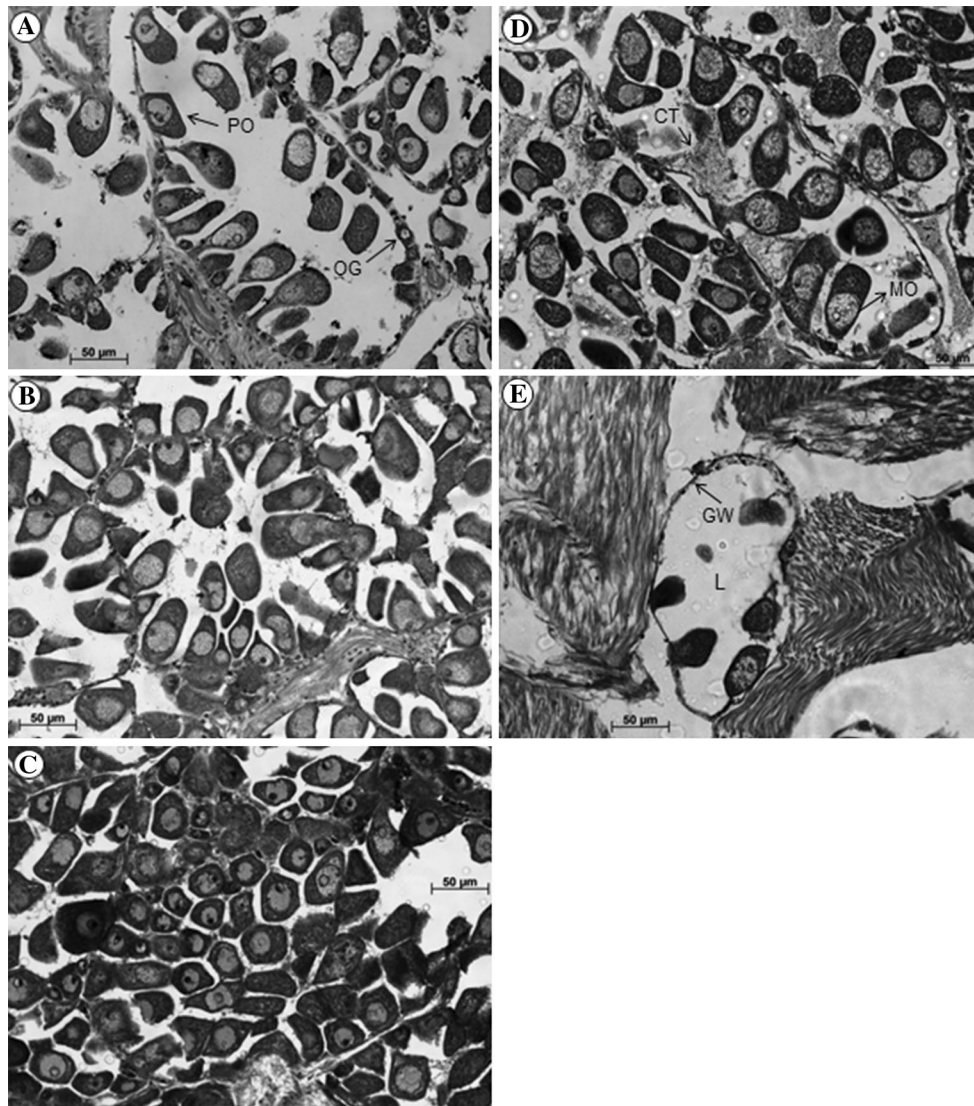
The quantitative histological analyses corroborate the qualitative findings, and lower values of the mean oocyte area were recorded from February to May 2007 ( $H = 96.66$ ;  $P < 0.001$ ), when a higher number of females in gametogenesis was observed (Fig. 8).

### Discussion

The VBG parameters estimated for the *T. plebeius* population from Camaroeiro Beach were higher or intermediate when compared to the results from previous studies. The growth curve constructed using MPA predicted an asymptotic size ( $L_\infty$ ) of 74.14 mm and a growth rate ( $K$ ) of  $0.52 \text{ year}^{-1}$ . This asymptotic size is larger than the

**Table 2** Description of the gametogenic stages of females and males

Stage	Brief description of gonad	Figures
<b>Female</b>		
Early gametogenesis	The connective tissue is abundant, the size of the follicles is small, and the initial stage of gametogenesis is present. Oocytes lie at the periphery of the gonadal walls and are attached to the basal membrane by a stalk	5a
Late gametogenesis	The size of the follicles increased and the initial stage of gametogenesis is still present, but restricted to the periphery of the follicles. Most mature oocytes are free in the lumina while some are still attached to the basal membrane by a thin stalk	5b
Ripe	The connective tissue has been reduced by the enlargement of the follicles by ripe gametes. The mature oocytes take polygonal shape due to packing. A decrease in the percentage of oogonia and pre-vitellogenic oocytes attached to the wall was also seen	5c
Spawning	Gametes are being released and empty spaces were observed in the follicular lumina	5d
Spent	The follicle lies empty with occasional residual oocytes present	5e
<b>Male</b>		
Gametogenesis	The connective tissue is abundant, and the size of the follicles is small. Spermatocytes proliferate toward the lumina, and rows of germinal cells in phases of maturation (spermatogonias, spermatocytes, and spermatids) form a germinal layer near the gonadal wall	6a
Ripe	The connective tissue has been reduced by the enlargement of the follicles by ripe gametes. Lumina is packed with ripe spermatozoa.	6b
Spawning	Follicles showed a radial arrangement of the spermatozoa as they are being released	6c

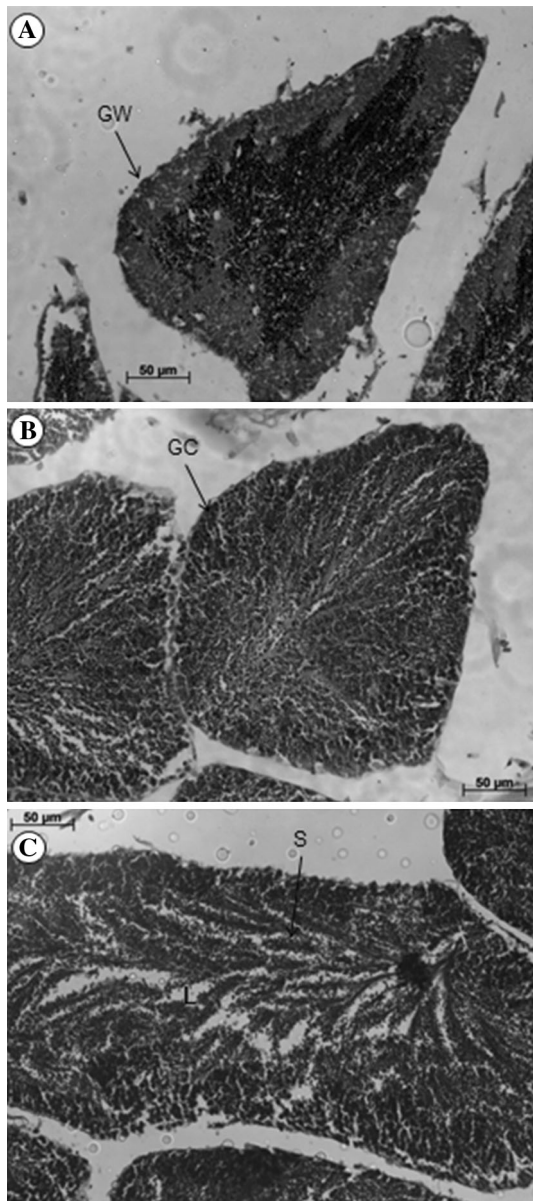


**Fig. 5** Female gonads in different stages of maturation. **a** Early gametogenesis, **b** late gametogenesis, **c** ripe, **d** spawning, **e** spent. *CT* connective tissue, *GW* gonadal wall, *MO* mature oocyte, *L* lumina, *OG* oogonia, *PO*, pre-vitellogenic oocyte

values estimated by Holland and Dean (1977b: 65 mm at 33°S), Viégas (1982: 51.73 mm at 9°S), and Abrahão et al. (2010: 67.01 mm at 23°S) but is lower than the maximum length recorded for the species (90 mm: Holland and Dean 1977a, b) (Table 3). The value of  $K$  ( $0.52 \text{ year}^{-1}$ ) was intermediate compared with those estimated by Abrahão et al. (2010:  $1.73 \text{ year}^{-1}$ ) and Viégas (1982:  $0.25$  and  $0.08 \text{ year}^{-1}$ ) for *T. plebeius* and by Urban (1996:  $0.232 \text{ year}^{-1}$  at 36°S) for *Tagelus dombeii* (Lamarck, 1818) (Table 3). The growth index (the overall measure of growth performance) of *T. plebeius* at Camaroeiro Beach (3.46) was also intermediate when compared to the value of 3.89 estimated by Abrahão et al. (2010) and 3.26 estimated for *T. dombeii* (Urban 1996) (Table 3).

Several studies have related differences in growth parameters of sandy beach species to environmental characteristics such as temperature (Defeo and Cardoso 2002) and sediment features (Henderson and Richardson 1994; Grant and Daborn 1994; Lomovasky et al. 2006). According to the latitudinal gradient hypothesis (LGH)—an extension of Bergmann's rule proposed by Defeo and Cardoso (2002)—there is a positive relationship between body size and latitude, and species inhabiting tropical and subtropical zones would present a higher growth rate and lower asymptotic size than temperate species due to the increase in metabolic rate at higher temperatures. Despite the widely accepted influence of temperature on growth of marine bivalves, our results differed from those recorded by Abrahão et al. (2010), which analyzed the growth





**Fig. 6** Male gonads in different stages of maturation. **a** Gametogenesis, **b** ripe, **c** Spawning. *GW* gonadal wall, *GC* germinal cells, *L* lumin, *S* spermatozoa

patterns of *T. plebeius* in an area at the same latitude with similar temperatures. In this sense, it is possible that other environmental factors may override the influence of temperature on the growth rate and asymptotic size of *T. plebeius*.

The salinity fluctuations observed in the study area represent another factor that does not appear to strongly affect the population biology of *T. plebeius* at Camaroeiro Beach. The range of interstitial salinity recorded for Camaroeiro Beach (16.6–28.6) is lower than that registered by Abrahão and Amaral (1999) (12–30) at Enseada Beach (Southeast Brazil) and by Farias and Rocha-Barreira (2012)

(5–40) in the Ceará River estuary (Northeast Brazil), who observed no influence of salinity on the population parameters of *T. plebeius*. These results confirm the euryhalinity of *T. plebeius* and suggest that this factor does not exert a major control over the population biology of this species in most of its occurrence area.

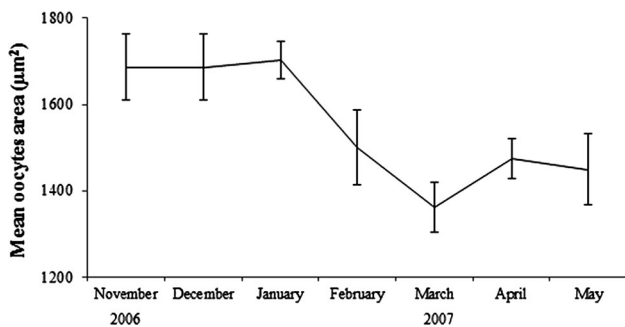
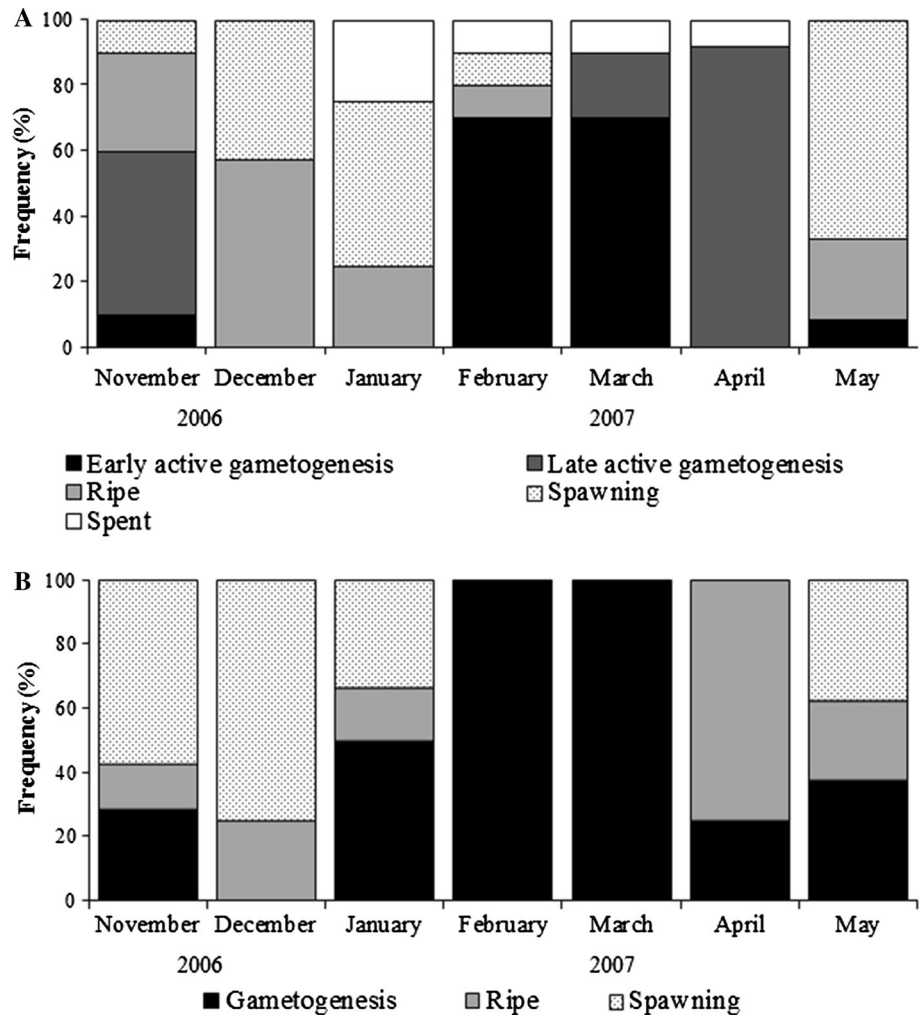
Fine sediments and high organic matter content are commonly viewed as indications of higher environmental stability and food availability, conditions that may enhance the growth and body size of suspension-feeding clams (Bayne and Worrall 1980; Grant and Daborn 1994). Comparing the results observed at Camaroeiro Beach with those of Abrahão et al. (2010), the growth index (the overall measure of growth) was higher in the latter study area, which presented finer sand and a higher organic matter content. Although not conclusive, these results may reinforce the influence of sediment characteristics and organic matter content on *T. plebeius* growth.

The smallest *T. plebeius* registered at Camaroeiro was 4.98 mm, suggesting that individuals smaller than this length either were not present in the population or were not collected. Although our sampling design may have a degree of size selectivity (larger individuals produce larger marks and could be more easily captured), we strongly attempted to avoid sampling bias by searching for all marks, and both small and large animals were collected at all times of the year. As observed in the present study, Holland and Dean (1977a) and Abrahão et al. (2010) also recorded few juveniles in their study areas. This low number of small individuals may be caused by (1) separate nursery sites for settlement; from these nursery habitats, juveniles then migrate and recruit into the main population sites and/or (2) a higher selective pressure on the juveniles. To test the first hypothesis, we sampled different areas in the intertidal and subtidal zones of Camaroeiro Beach and did not find a nursery site. However, more sampling is needed to properly test this hypothesis.

A higher selective pressure on juveniles may explain (at least in part) the low number of those individuals in *T. plebeius* populations. According to Verween et al. (2007), this stage of the invertebrate life history pattern is the most sensitive to abiotic parameters and age-specific predation pressure by birds, gastropods, and fishes. Larger bivalves tend to bury deeper, reducing their risk of predation, whereas young individuals remain near the surface of the substrate due to their short siphons (Hines et al. 1990; Lin and Hines 1994). This behavior results in a higher predation risk and increased rates of natural mortality over smaller individuals, as observed for *T. plebeius* in South Carolina, USA (Holland and Dean 1977b) and *T. dombeii* in Chile (Lardies et al. 2001).

The population of *T. plebeius* at Camaroeiro Beach was composed of four cohorts that were tracked during the entire study period. Similarly, Abrahão et al. (2010) found

**Fig. 7** Relative frequency (%) of the gametogenic stages in each month for both females (a) and males (b) from November 2006 to May 2007



**Fig. 8** Variation in the mean oocytes area (µm<sup>2</sup>) from November 2006 to May 2007

three cohorts in Southeast Brazil. The occurrence of several different generations occurring at the same time is most likely due to the short life span of the species in the study area (approximately 2.58 years). An even shorter life span for *T. plebeius* was observed by Abrahão et al. (2010)—populations ranging from 1.58 to 2.25 years (Table 3);

however, other studies suggest a long-lived pattern for razor clams. A life span of 19 years was reported for *Ensis siliqua* (Linnaeus, 1758) in Ireland (Fahy and Gafnney 2001), and Barón et al. (2004) suggested a 14–16 year age for *E. macha* (Molina, 1782) in Argentina, as based on the growth marks in its shell. The low longevities registered for *T. plebeius* along the Brazilian coast may be related to interspecific differences but also to a high mortality rate at lower latitudes, which could be explained by a combination of increasing metabolism at higher temperatures and insufficient food availability (Defeo and Cardoso 2004). Strengthening this hypothesis, the mortality rate observed for *T. plebeius* at Camaroeiro Beach (2.16 year<sup>-1</sup>) is slightly lower than that reported by Abrahão et al. (2010: 3.12) at a similar latitude (Table 3), but is much higher than the values reported for other bivalves inhabiting colder areas, such as *Protothaca thaca* (Molina, 1782) (0.47 year<sup>-1</sup> at 36°S, Urban and Campos 1994), *Callista chione* (Linnaeus, 1758) (0.27 year<sup>-1</sup> at 38°S, Metaxatos 2004), and *Eurhomalea exalbida* (Dillwyn, 1817)

**Table 3** Latitudinal variation in growth parameters and reproductive events of *T. plebeius* and *T. dombeii*

Species	$L_{\infty}$ (mm)	$K$ (year <sup>-1</sup> )	$Z$ (year <sup>-1</sup> )	Life span (year)	$\phi'$	Recruitment	Spawning	Lat.	Source
<i>T. plebeius</i>	65	–	–	–	–	–	–	33°20'	Holland and Dean (1977b)
<i>T. plebeius</i>	58.88	0.08	–	–	–	–	–	9°40'	Viégas (1982)
<i>T. plebeius</i>	51.73	0.25	–	–	–	–	–	9°40'	Viégas (1982)
<i>T. dombeii</i>	88.5	0.23	0.84	–	3.26	–	–	36°00'	Urban (1996)
<i>T. plebeius</i>	–	–	–	–	–	W–Spr	S	37°40'	Clédon et al. (2004)
<i>T. plebeius</i>	67.01	1.73	3.12	1.58–2.25	3.89	–	–	23°43'	Abrahão et al. (2010)
<i>T. plebeius</i>	–	–	–	–	–	W–Spr	W–Spr	14°16'	Ceuta and Boehs (2012)
<i>T. plebeius</i>	74.14	0.52	2.16	2.58	3.46	W–Spr	S	23°37'	Current study

$L_{\infty}$  asymptotic length,  $K$  curvature parameter,  $Z$  mortality rate,  $\phi'$  standard growth index, W–Spr winter–spring, S summer

(0.14 year<sup>-1</sup> at 54°S, Lomovasky et al. 2002). Another factor that may be influencing the mortality rate of the *T. plebeius* population is the predation pressure over this species. The positive values of the  $\Delta_{Z/K}$  parameter confirm the high level of predation (by natural predators or by anthropic action) at Camaroeiro Beach and highlight the importance of research surveys to assess population trends and stock assessments for *T. plebeius* in this area.

The relative amplitude of seasonal oscillations in growth rate,  $C = 0.47$ , indicated a moderately seasonal variation in growth. Growth was slowest at the winter point (WP) of 0.94 year units, equivalent to the summer (~mid-December). Histological analyses showed that during the 7 months analyzed in this study, the more intense period of gametogenesis in *T. plebeius* at Camaroeiro Beach occurred in summer months (January–March) right after the WP (Fig. 7). In this sense, the recorded WP may be related to a higher reproductive investment, with energy being transferred from somatic growth to the production of gametes.

Despite the reduced number of studies that analyzed the reproductive biology of *T. plebeius*, different reproduction patterns seem to occur for this species over the range of its distribution. A continuous gametogenic cycle, with both females and males undergoing gametogenesis and spawning throughout the year, was recorded in a tropical estuary in northeastern Brazil (14°S, Ceuta and Boehs 2012), whereas two spawning peaks, one in summer (between December and January) and the other in winter (June and July), were evidenced in northern Argentina (37°S, Clédon et al. 2004). At Camaroeiro Beach, a spawning peak was recorded in summer (between November 2006 and January 2007). After spawning, gonad recovery was immediate and most individuals were at maximum maturation and spawning in late autumn (May 2007). These results suggest a biannual gametogenic cycle for *T. plebeius* at Camaroeiro, a similar pattern to that recorded in northern Argentina (Clédon et al. 2004) and also observed in several populations of bivalves from subtropical and temperate areas, such as *Donax trunculus* (Tirado & Salas 1998, Gaspar

et al. 1999), *Protothaca antiqua* (Borzzone, 1989), and the razor clams *T. dombeii* (Avellanal et al. 2002) and *Ensis mancha* (Avellanal et al. 2002, Barón et al. 2004). However, as we have only seven months of histological analyses for the individuals from Camaroeiro, further studies with a greater period of sample are necessary to better elucidate the reproductive pattern of *T. plebeius* in this area.

The monthly variation in the mean oocyte area of *T. plebeius* corroborated our qualitative histological analyses, and a lower mean oocyte area was related to the gametogenesis stage due to the high quantity of developing (small) gametes. Conversely, when the ripe stage occurred, the mean oocyte area showed high values due to the presence of mature gametes. The equal sex ratio observed in this study is in agreement with observations by Clédon et al. (2004) and Ceuta and Boehs (2012) in other occurrence areas.

Although we did not analyze the annual somatic production ( $P$ ), annual mean biomass ( $B$ ), and turnover rate ( $P/B$ ), several reasonable extrapolations about these parameters can be developed. The low recruitment rate observed at Camaroeiro Beach generates a size structure composed mainly of adult clams, which have a high mean body mass ( $B$ ) but a low growth rate ( $K$ ). As smaller individuals are responsible for a considerable percentage of the population production (Robertson 1979; Urban and Campos 1994), the turnover rate ( $P/B$ ) is strongly influenced by the size structure of the population (Benke and Huryn 2006); therefore, the  $P/B$  ratio should be low in populations composed of larger individuals, as in the population at Camaroeiro. This fact leads to a low restoration of the population of *T. plebeius*, and together with the low recruitment and high mortality rate ( $Z$ ), could be an indication that the population of *T. plebeius* at Camaroeiro Beach is endangered.

This study provides baseline knowledge on *T. plebeius* that we expect to be useful for avoiding negative impacts to this species. Although this information is relevant to

support fishing activity, it is only a snapshot of *T. plebeius* population biology, and further studies on the range of this species distribution are required to better understand its population dynamics. It is necessary to improve our knowledge on the population biology of exploited species to develop correct management plans to prevent further uncontrolled exploitation and/or to achieve a more sustainable development of invertebrate fisheries (Botsford et al. 1997; Castilla and Defeo 2001; Anderson et al. 2011).

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