

ORIGINAL ARTICLE

Population biology and secondary production of the harvested clam *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae) in Southeastern Brazil

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Keywords

Population dynamic; sandy-beaches; Veneridae.

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Accepted: 3 December 2013

doi: 10.1111/maec.12137

Abstract

The population structure, growth and production of the trigonal clam *Tivela mactroides* were investigated by monthly sampling between January 2003 and October 2004 in two areas (southern and northern) of the intertidal and subtidal zones of Caraguatatuba Bay, Southeastern Brazil. Intertidal sampling was carried out in each area along eight transects perpendicular to the shoreline. In the subtidal zone of both areas, one 50-m dredging was performed along five sampling stations arranged on three transects perpendicular to the coast. The intertidal abundance of *T. mactroides* was higher in the southern (more dissipative conditions) than in the northern area. High abundances occurred in February–March 2004 in the south and in September 2004 in the north. The size structure showed that younger individuals dominated in the sublittoral, indicating that recruitment occurs in this zone, followed by the migration of these individuals to the intertidal, where they complete their life cycle. *Tivela mactroides* showed continuous reproduction, with 26 cohorts detected in the study period. The lower estimates for the growth index ($\phi' = 3.22$), mortality rate ($Z = 2.10 \text{ year}^{-1}$) and turnover rate ($P/B = 1.21 \text{ year}^{-1}$), and conversely the longer life span (2.5 years) of *T. mactroides* in Caraguatatuba Bay (24°S) compared with Venezuelan populations (10°N) suggests a latitudinal pattern of these life-history traits. The high production of *T. mactroides* in Caraguatatuba Bay was due to continuous recruitment and rapid and continuous growth, and demonstrates the importance of *T. mactroides* as a biological resource for many marine species and for the local residents.

Introduction

Marine living resources are subject to different kinds of impacts, from overexploitation to habitat degradation, which are intensified in coastal areas. In particular, sandy-beach macrofauna are faced with environmental alterations resulting from global and local changes, and the intensification of recreational, artisanal, and commercial fisheries that has followed improved access to shorelines (Brown & McLachlan 2002; Schlacher *et al.* 2007;

Defeo *et al.* 2009). One example of organisms subjected to such environmental and anthropic pressures are the commercially important bivalves of sandy beaches (McLachlan *et al.* 1996). The trigonal clam *Tivela mactroides* is an important representative of this group and has a wide distribution, occurring from Venezuela to Brazil (Pará to Santa Catarina State) and the West Indies (Rios 1994). This suspension feeder inhabits the intertidal and subtidal zones of sandy beaches and is often the dominant macrofaunal component in these environments

(Narchi 1972; Tata & Prieto 1991; McLachlan *et al.* 1996; Denadai *et al.* 2005; Herrera & Bone 2011). According to McLachlan *et al.* (1996), *T. mactroides* is abundant near river mouths, where organic matter and terrigenous particles accumulate, and is widely consumed by humans and marine organisms, including several commercially important fish species (Mendoza & Marcano 2000; Arrieche & Prieto 2006). Given the ecological and socioeconomic importance of this kind of resource, management efforts are needed.

Several populations of *T. mactroides* have been studied on Venezuelan sandy beaches, where this species is extensively harvested (McLachlan *et al.* 1996; Mendoza & Marcano 2000). These studies addressed the distribution, reproductive aspects, population dynamics, and production of this clam (Etchevers 1976; Prieto 1980; Tata & Prieto 1991; Menzoza & Marcano 2000; Arrieche & Prieto 2006) and found that *T. mactroides* populations generally show high density and biomass and rapid growth on these tropical beaches.

Caraguatatuba Bay, situated in Southeastern Brazil, is subject to impacts from oil and gas facilities, harbor expansion, fisheries regulations, and rapid population increases. In this region, *T. mactroides* is used as food and a source of income by local fishermen, and is also an important food for different marine species. This clam inhabits the intertidal and subtidal zones up to a depth of 5 m, with the smallest individuals occupying the subtidal zone and the largest ones the intertidal zone (Denadai *et al.* 2005). This kind of distribution was observed by McLachlan *et al.* (1996) for other sandy-beach bivalves of economic importance. These authors hypothesized that such populations generally have long reproductive periods, early reproduction, high growth rates, and considerable fluctuations in density associated with recruitment and/or mortality events, a characterization that should be formally tested. Since population parameters may vary in relation to latitude and beach morphodynamics (Defeo & McLachlan 2005), best management practices should be based on evaluations of the local population parameters, to provide for the sustainable use of these marine resources.

Studies on the population biology and secondary production of harvested sandy-beach species are generally lacking (McLachlan *et al.* 1996; Petracco *et al.* 2012a, 2013). This is particularly true for *T. mactroides*, since studies on this species are generally restricted to beaches on the Venezuelan coast, and there is little information regarding the ecology of this species over its wide range along the Brazilian coast (Denadai *et al.* 2005; Turra *et al.* 2013). This lack of information prevents macroecological studies, thus limiting the knowledge and management of sandy-beach resources. This study analyzed the popula-

tion biology of *T. mactroides* in Caraguatatuba Bay, including spatio-temporal variations in abundance, growth and mortality parameters, and secondary production. Moreover, different from most existing studies, this population of *T. mactroides* was evaluated considering both its intertidal and subtidal distribution, which provided important information on its ecology.

Material and Methods

Study area

The coastline of Caraguatatuba Bay (23°37' to 23°44' S and 45°24' to 45°26' W) is about 16 km long and includes several sandy beaches (Enseada, Flecheiras, Porto Novo, Romance, Palmeiras, Pan-Brasil, Indaiá, Centro and Camaroeiros; Fig. 1). Enseada is a very wide tidal flat. In the southern part of the bay, Flecheiras, Porto Novo, Romance, Palmeiras and Pan-Brasil beaches have flat and regular slopes, with well-sorted fine sand. In the northern part, Indaiá, Centro and Camaroeiros beaches have a steeper slope in the upper intertidal zone and a flat tidal terrace in the lower levels, which is only apparent at low tide. The sand of these beaches is also fine, but poorly sorted.

A previous study on the spatial distribution of *Tivela mactroides* in this area (Denadai *et al.* 2005) revealed higher densities on Porto Novo and Centro beaches. Therefore, two linear areas with 2 km each, homogeneous but distinct from each other, were selected for this study (Fig. 1). The first southern area extended from Porto Novo to Palmeiras; and the northern area from Indaiá to Centro beaches.

Physical characterization

The northern and southern study areas were compared with respect to some physical characteristics. To characterize these areas, mean values of wave heights, number of wave breaks, wave periods, surf-swash zone width, and current speed were recorded monthly using the methodology suggested by Perillo & Piccolo (1987). The beach total elevation, mean elevation, and standard deviation of elevation were also recorded. All these variables were measured monthly at a fixed point in the center of each study area during spring low-tide periods. These observations were made simultaneously in the two areas from February 2003 through October 2004.

The wave height of 30 consecutive waves was measured, but only the height of the 10 highest waves was included in the calculation of the monthly mean. The mean number of wave breaks, calculated based on the counts of successive wave breaks from the beginning of

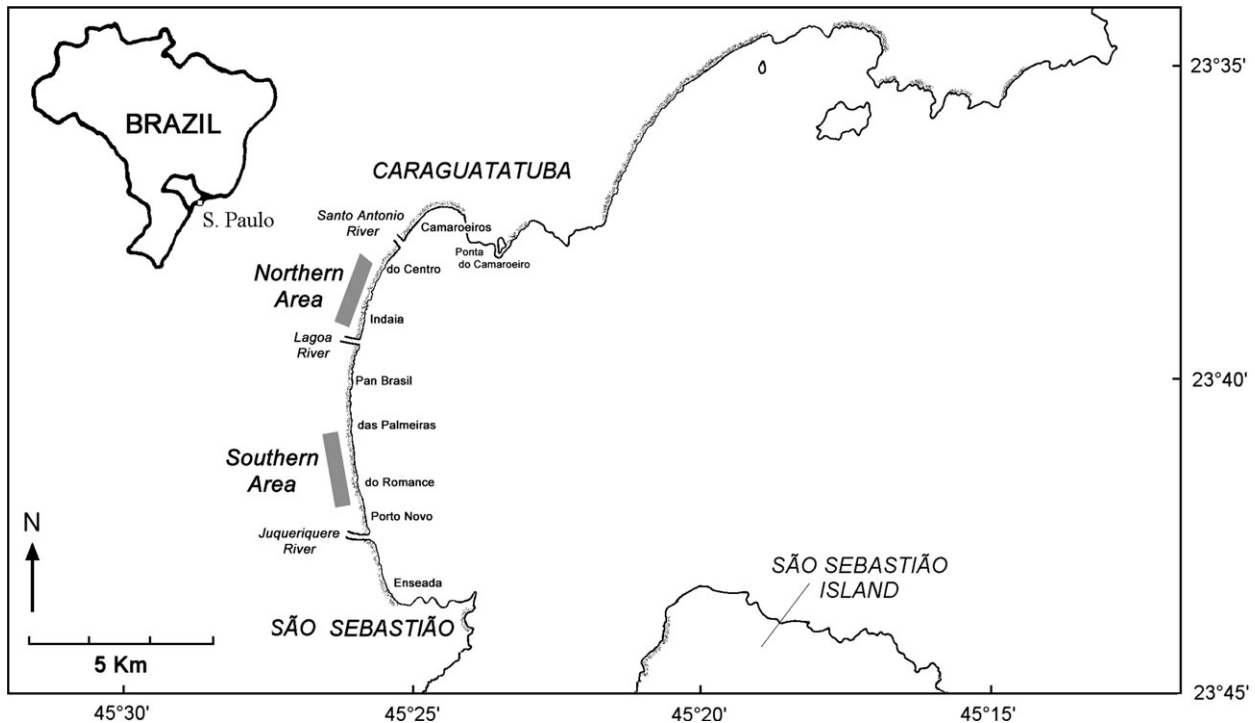


Fig. 1. Caraguatatuba Bay, showing the northern and southern study areas.

the surf zone until the swash zone, was based on 10 replicates. At that time, the width of the surf/swash zones was estimated visually in meters. The mean wave period was evaluated considering three replicate counts of the time taken for 11 waves to cross a fixed point. The mean current speed was also calculated based on three replicates, considering the alongshore movement of a yellow wood square ($20 \times 20 \times 2$ cm), measured in the middle of the surf zone for 1 min by an observer located in the dry-sand zone. This distance was then divided by 60 s to obtain the current speed in $\text{m}\cdot\text{s}^{-1}$.

The beach profile was evaluated using Emery rulers, in 8-m intervals from the upper edge of the supralittoral zone (vegetation in the southern and berm in the northern area) to mean low water (MLW, 0.0 m). Thirteen intervals were used in the southern (104 m) and seven in the northern (56 m) area. The total beach height, mean elevation and standard deviation of elevation were then calculated. Total beach height was the vertical distance between the highest part of the beach (vegetation or berm) and MLW. The mean elevation was obtained by averaging all the elevation values recorded (13 in the southern and seven in the northern area). The standard deviation (SD) of elevation was calculated based on these values, to represent the degree of heterogeneity in beach slope, *i.e.* if the profile is more (smaller values of SD) or less (larger SD) homogeneous.

Three samples were taken in each area, 78 m below the vegetation line in the southern and 28 m below the berm in the northern, to characterize the sediment. These heights were selected because they represented the center of the area occupied by *T. mactroides* in the intertidal zone (Denadai *et al.* 2005). The mean grain size and the sorting coefficient of the sediment were then analyzed (Suguio 1973). This method consisted in weighing dry sand grains according to the Wentworth scale in phi units [$\phi = -\log_2$ (mean grain diameter in mm)]. The mean values of the environmental variables were compared between the study areas through a paired *t*-test (Zar 1999), using monthly samples as replicates.

Population sampling

Clams were sampled monthly from January 2003 through October 2004 in the intertidal and subtidal zones. In the intertidal, eight transects were randomly sorted in each study area (southern and northern) from 200 possibilities, *i.e.* the linear 2000 m area divided into 10-m intervals. Each transect was positioned with a GPS, and the distance from the southern limit of each area was recorded. Sample squares of 0.5×0.5 m (0.25 m^2) were dug to a depth of about 10 cm at regular intervals in the cross-shore distribution of *T. mactroides* (see Denadai *et al.* 2005). Eight squares were sampled at 8-m intervals

(56 m) in the southern area, and seven squares were sampled at 6-m intervals (36 m) in the northern one. Thus, a total of 64 squares (8 squares × 8 transects) were sampled monthly in the southern and 56 (7 × 8) in the northern area, totaling 120 squares per month, or 30 m².

In the subtidal zone, semi-quantitative sampling was performed using three randomly sorted transects in each study area. The sorting procedure was similar to that used in the intertidal zone. The positions of each transect were previously stored in a GPS at the mean low-water line. Then, using a fishing boat, the points representing 400, 800, 1200, 1600 and 2000 m from MLW were located perpendicular to the coast. One 50-m dredging was performed at each distance, using a rectangular dredge (70 × 25 cm) with 3.0 mm internal mesh size, totaling 15 dredgings per month per area (3 transects × 5 depths). The sediment was washed with seawater over a 3.0-mm-mesh sieve, using buckets. Clams were collected, counted and measured for total length (in mm). Almost all the individuals of *T. mactroides*, from both intertidal and subtidal, were returned alive to the sea after the measurements.

Abundance

The number of individuals in the intertidal was estimated per strip transect (IST, see Defeo & Rueda 2002) and calculated by linear interpolation as follows:

$$IST_r = \frac{\sum_{i=1}^n q_i}{n_r} w_r$$

where q is the mean density (ind. m⁻²); n is the number of samples from transect r (eight in the southern and seven in the northern area); and w is the width of transect r that corresponds to the across-shore distribution of *Tivela mactroides* as verified after pilot evaluations (56 m in the southern and 36 in the northern area). The abundance in the subtidal was expressed as the mean number of individuals from each 50-m dredging. Two-way ANOVAs were employed to test the null hypothesis that the abundance of *T. mactroides* in the intertidal and in subtidal zones was not influenced by areas (northern and southern) or sampling months.

Intertidal across-shore distribution

Graphs showing the number of individuals in each sampling level per month per area were constructed to illustrate the differences in the across-shore distribution of *Tivela mactroides* between the areas, and also the variations during the study period.

Growth

Monthly length–frequency distributions obtained from all individuals sampled (intertidal and subtidal individuals pooled) were used to estimate growth parameters of the *Tivela mactroides* population. The ELEFAN I (electronic length frequency analysis) routine of the FISAT II package (FAO-ICLARM Stock Assessment Tools) was employed to perform the growth analysis. This approach assumes that growth is described by the von Bertalanffy growth function (VBGF) modified for seasonality (Pauly & Gaschutz 1979):

$$L_t = L_\infty \left[1 - e^{-K(t-t_0) - (CK/2\pi)[\sin 2\pi(t-WP+0.5) - \sin 2\pi(t_0-WP+0.5)]} \right]$$

where L_t is the length (mm) at age ‘ t ’; L_∞ is the asymptotic length; K is the growth rate or the von Bertalanffy curve parameter; t_0 is the age when the length is zero, and was estimated as 0.06 years, considering the time between hatching of larvae and recruitment of *T. mactroides* (Severejn *et al.* 2000); C is the seasonal growth oscillation constant; t_s is the initial point of seasonal oscillation in relation to $t = 0$ ($t_s = WP - 0.5$), and WP (winter-point) is the period in which the growth is minimum (expressed in year fraction). The combination of the growth parameters generates an adjustment index termed R_n , which varies from 0 to 1 and represents the exponential form of the ratio ESP/ASP:

$$R_n = 10^{(ESP/ASP)/10}$$

where ESP is the ‘explained sum of peaks’ in the curve generated by the model, and ASP is the ‘available sum of peaks’ in the frequency distribution. The growth parameters (seeds) were varied until the best adjustment was reached, *i.e.* that which results in the highest R_n value. The growth index phi-prime (ϕ') was calculated to give the growth performance (Pauly & Munro 1984):

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

The longevity was estimated using the length representing the 99th percentile of the population (Sparre *et al.* 1989) and also considering the maximum length as 95% of the asymptotic length (King 1995). A modal progression analysis was also performed, using the length–frequency distribution according to the method of Bhattacharya (1967). This enabled the separation of the modal components into distinct cohorts. The length-converted catch curve was employed to estimate the instantaneous mortality rate (Z) by the decrease in numbers of the individuals in the different age classes (Pauly 1983). For these analyses, all individuals sampled (intertidal and subtidal individuals pooled) were used.

Secondary production

Annual somatic production (P) was estimated by the mass-specific growth rate method (Crisp 1984; Brey 2001) from the length–frequency distribution obtained from all intertidal pooled samples, the length–mass relationship, and the von Bertalanffy growth function parameters. The annual production is given by: $P = \sum N_i \cdot M_i \cdot G_i$, where N_i is the annual mean number of individuals in length class i , M_i is the mean individual mass in length class i , which is calculated from the mean length in length-class i , and G_i is the mass-specific growth rate in length-class i , obtained through the equation: $G_i = b \cdot K \cdot [(L_\infty/L_i) - 1]$, where b is the exponent of the length–mass relationship ($AFDM_{(g)} = 0.00003 \text{Length}_{(mm)}^{2.675}$; Turra *et al.* 2013), K and L_∞ are von Bertalanffy growth function parameters, and L_i is the mean length in length-class i . The P/B ratio was calculated as the ratio between the annual production (P) and the annual mean biomass (B). Since the production and P/B ratios are strongly influenced by the population size structure (Benke & Huryn 2006), and the subtidal samples were semi-quantitative, these population parameters were estimated only for the intertidal zone.

Results

Physical characterization

The mean wave height, the mean wave period, and the current speed were similar between the areas (Table 1). The mean values of the number of wave breaks and the

width of the surf-swash zone were higher in the southern area, which shows dissipative characteristics, than in the northern area, which is more reflective. The current speed did not show a clear seasonal pattern but was equivalent between the study areas.

The mean sand-grain diameter and sorting coefficients had opposite patterns in the two areas. The sand was coarser and poorly sorted in the northern area, and finer and better sorted in the southern area. The sand type varied from fine to very fine in the northern area, and was exclusively very fine in the southern. The total slope, the mean slope, and its standard deviation were significantly different between the study sites, always being higher in the northern than in the southern area. These values reflect the morphological differences between the areas. In the northern area, the total elevation was higher, and the mean elevation and standard deviation indicated a steeper and discontinuous slope, in contrast to the gentler, even slope of the southern area (Table 1).

Abundance

The mean abundance of *Tivela mactroides* in the intertidal was 431.73 ± 93.40 ind. m^{-2} and 867.44 ± 83.58 ind. m^{-2} (\pm SE) in the northern and southern areas, respectively. The abundance varied widely during the study period ($F = 464.28$; $df = 18$; $P < 0.001$) and between areas ($F = 52.22$; $df = 1$; $P < 0.001$). There was interaction between areas and months ($F = 3.64$; $df = 18$; $P < 0.001$), indicating that temporal variation in clam abundance was independent of the study areas. In general, the clams were more abundant in the southern than the northern area (Fig. 2a). In the beginning of the sampling period, the abundance in the southern area was relatively high, decreasing after February 2003 and remaining low until July 2003. In September, many young individuals appeared in the intertidal population (see below), increasing the abundance of individuals in the southern area. The abundance remained high until June 2004, with a slight decrease in January 2004. From July to October 2004, the density in the southern area was relatively low. In the northern area, the abundance was low in the first 7 months of sampling, increasing in the spring–summer period (September 2003 to February 2004) and decreasing in March 2004. From April to June 2004 the density remained low, increasing from July on and reaching a very high peak in September. In October the abundance of *T. mactroides* in the northern area was again low.

In the subtidal, the mean abundance varied among months ($F = 13.28$; $df = 19$; $P < 0.00001$) but not between areas ($F = 0.18$; $df = 19$; $P > 0.05$). There was interaction between areas and months ($F = 13.28$;

Table 1. Paired *t*-test comparison of the mean values of the environmental variables between the southern and northern areas in Caraguatatuba Bay.

	Mean \pm SD South	Mean \pm SD North	P
Wave height (cm)	43.46 \pm 13.56	44.64 \pm 13.99	0.634
Break number	5.16 \pm 3.11	4.16 \pm 2.71	0.015
Wave period (s)	63.88 \pm 12.24	63.78 \pm 11.09	0.970
Current velocity ($m \cdot s^{-1}$)	0.05 \pm 0.04	0.06 \pm 0.04	0.517
Mean grain size (phi)	3.70 \pm 0.07	3.08 \pm 0.38	<0.001
Sorting coefficient (phi)	0.25 \pm 0.07	0.97 \pm 0.30	<0.001
Surf-swash width (m)	197.35 \pm 144.53	121.59 \pm 71.50	<0.01
Total elevation (cm)	171.36 \pm 14.72	256.08 \pm 20.33	<0.001
Slope (mean – cm)	13.66 \pm 1.23	19.10 \pm 1.02	<0.001
Slope (standard deviation – cm)	5.57 \pm 0.78	21.53 \pm 2.25	<0.001

Significant differences are highlighted in bold.

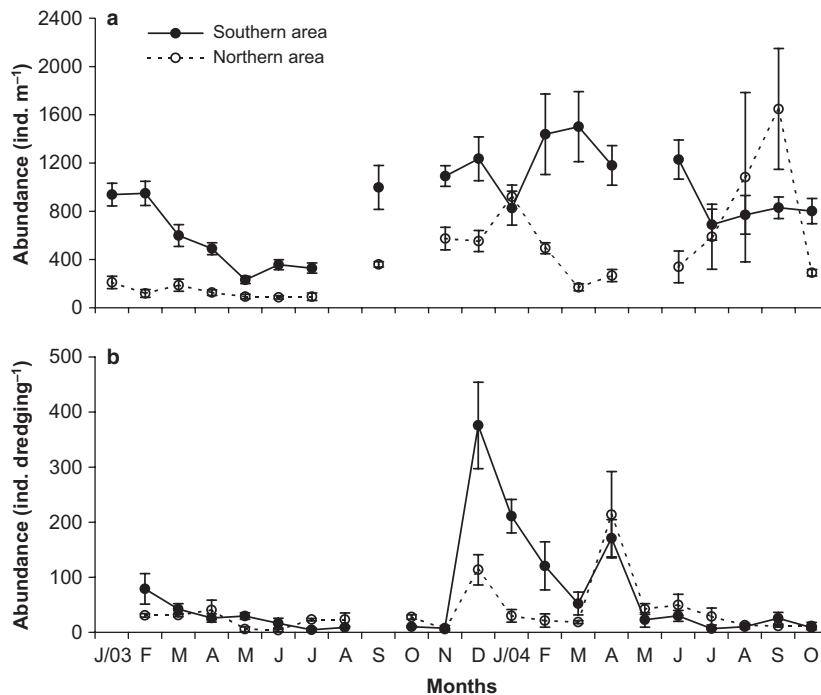


Fig. 2. *Tivela mactroides*. (a) Variation in intertidal abundance ($\bar{x} \pm SE$) of the ind. m^{-1} (individuals per strip transect) and (b) variation in subtidal abundance ($\bar{x} \pm SE$) of the individuals/50 m dredging in the two study areas. Missing data result from the impossibility of sampling in the intertidal zone in August and October 2003 and May 2004, and in the subtidal in January and September 2003.

df = 19; $P < 0.001$), with peaks of abundance in December 2003 and April 2004 in the two areas (Fig. 2b). The high standard errors in months with high abundances suggest a clumped distribution of *T. mactroides* individuals (Fig. 2a,b).

Intertidal across-shore distribution

In the southern area, from January to July 2003 only a few individuals were observed in the entire intertidal strip, mainly in the lower levels (0–24 m) (Fig. 3a). From September 2003 to April 2004, the number of individuals decreased gradually from the lower to higher levels, and from June to October 2004, higher numbers of individuals were observed in the middle levels.

In the northern area, the few individuals that occurred from January to July 2003 were equally distributed through the intertidal. From September 2003 to March 2004, the individuals exhibited a slight tendency to occupy the lower levels. From June to October 2004, the highest number of individuals occurred mainly in the middle levels (12–24 m) (Fig. 3b).

This pattern of intertidal distribution observed in both areas may be related to the sizes of individuals during the study period (Fig. 4). In the January–July 2003 period, the intertidal population was dominated by larger individuals, which occupied the entire intertidal area equally. In September 2003, the entry of young individuals into the intertidal zone led to a dominance of individual

numbers in the lower level, mainly in the southern area. This condition persisted until March–April 2004. From July to October 2004, a bimodal distribution in the size of individuals caused a peak of larger individuals in the middle levels, mainly in the northern area, and a peak of smaller clams in the lower levels.

Growth and secondary production

The histograms for the shell length-class frequencies during the study period show the growth dynamics of the individuals, and also the spatial differences between the subtidal and intertidal zones (Fig. 4). In the subtidal, a cohort of smaller individuals was evident from the beginning of the sampling period (January 2003) until November, when they reached the size of 14–18 mm. In the same period, individuals of this same size appeared in the intertidal zone, suggesting a migration to the shallower levels. The subtidal received a large number of recruits (individuals 2–6 mm long) in August 2003 and a much larger number in December 2003. This cohort from December dominated the subtidal population, showing continuous growth until the end of the sampling period in October, when they had reached a size of 12–18 mm. A non-significant recruitment event occurred in August 2004, and a bimodal size-class distribution persisted until October 2004.

In the intertidal, the main cohort in the first months of sampling was composed of larger individuals (larger

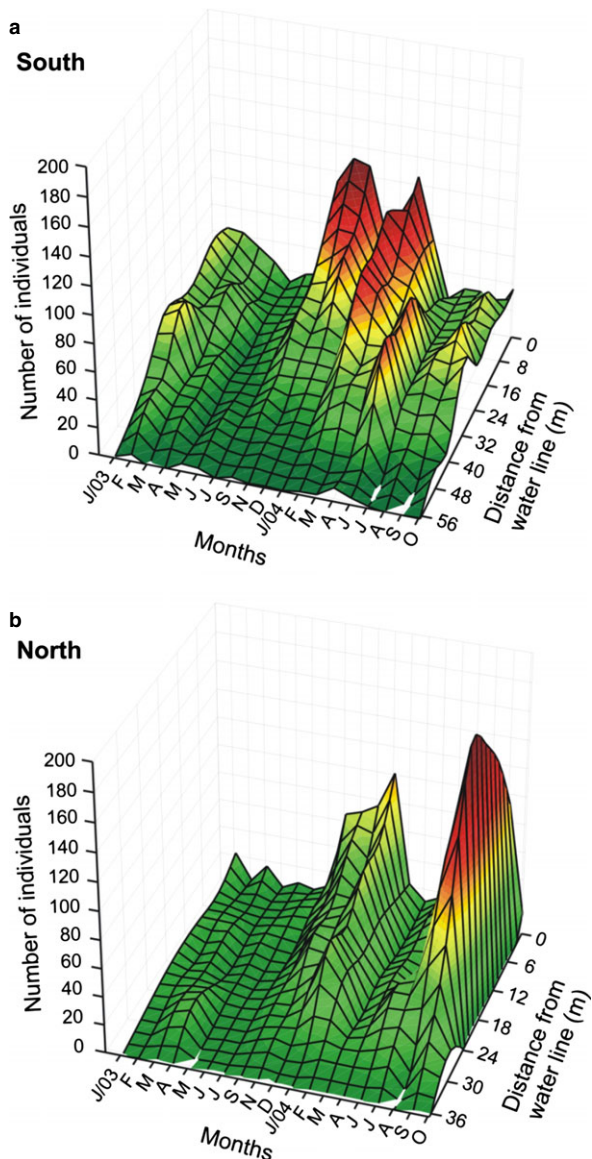


Fig. 3. *Tivela mactroides*. Spatial distribution of the individuals in the intertidal levels during the study period in the (a) southern and (b) northern areas.

than 26 mm). In May 2003, smaller individuals that were not recruits (size between 6 and 12 mm) appeared in the population. These individuals probably migrated from the subtidal zone. The same occurred in September 2003 and July 2004. The frequent arrival of migrating individuals from the subtidal to the intertidal led to a polymodal distribution of the size classes of the individuals in this beach strip.

No seasonal oscillation in individual growth was observed in this population. The estimated values for the VBGF were: $L_{\infty} = 40.9$, $k = 1.0$, $C = 0.0$, $R_n = 0.159$. The growth index (ϕ') was 3.22. Longevity was estimated as

1.92 and 3.05 years, considering the length representing the 99th percentile of the population and 95% of the asymptotic length, respectively. This indicated a life span of 2.5 years. The Bhattacharya (1967) progression analysis indicated the existence of 26 cohorts during the study period (Fig. 5). These cohorts are evidence of the continuous recruitment events in this population. The modes detected are not easily perceived in the histograms in Fig. 5, and were only determined by the progression analysis. These estimated curves show that growth was continuous and rapid.

The length-converted catch curve indicated four mortality events in the population; the first three were adjacent and concentrated in the first year of life of the clams (Fig. 6, Table 2). The first event was the most intense and involved newly recruited individuals (<5 months, <15 mm in shell length). The second event represented the mortality in individuals from 2 to 7 months old (7–18 mm) and was less intense. The third event did not markedly reduce the number of individuals and was concentrated in individuals from 6.5 months to 1 year (17–24 mm); and the last event, more intense than the third, involved individuals older than 1.5 years (larger than 30 mm). The estimated mortality for the entire population (Z) was 2.10 year^{-1} .

The mean annual biomass values in the southern and northern areas and for all individuals in the intertidal zone combined were estimated, respectively, as $182.33 (\pm 22.59)$, $72.74 (\pm 14.37)$ and $123.15 (\pm 12.75) \text{ g AFDM} \cdot \text{m}^{-1}$, and the annual production was estimated as 188.32 , 110.97 and $148.56 \text{ g AFDM} \cdot \text{m}^{-1} \cdot \text{year}^{-1}$, respectively. Individuals with lengths from 25 to 33 mm and from 17 to 25 mm were responsible for most of the estimated production for the southern (68%) and northern (55%) areas, respectively. For all intertidal individuals combined, clams with lengths between 25 and 32 mm contributed most to the production (50%), despite a significant contribution of individuals measuring 17–24 mm (32%). The P/B ratio was higher in the northern area (1.53 year^{-1}) than in the southern area (1.03 year^{-1}); for both areas the ratio was 1.21 year^{-1} (Fig. 7a–c).

Discussion

The main environmental factors affecting the spatial distribution and abundance of *Tivela mactroides* in Caraguatubá Bay seem to be structural, such as the grain diameter and slope. The number of wave breaks and the width of the surf-swash zone, which differed significantly between the areas, agree with the structural differences between the areas; the southern area is intermediate to dissipative, and the northern is reflective, with a dissipative terrace at low tide (*sensu* Short 1996). The clams

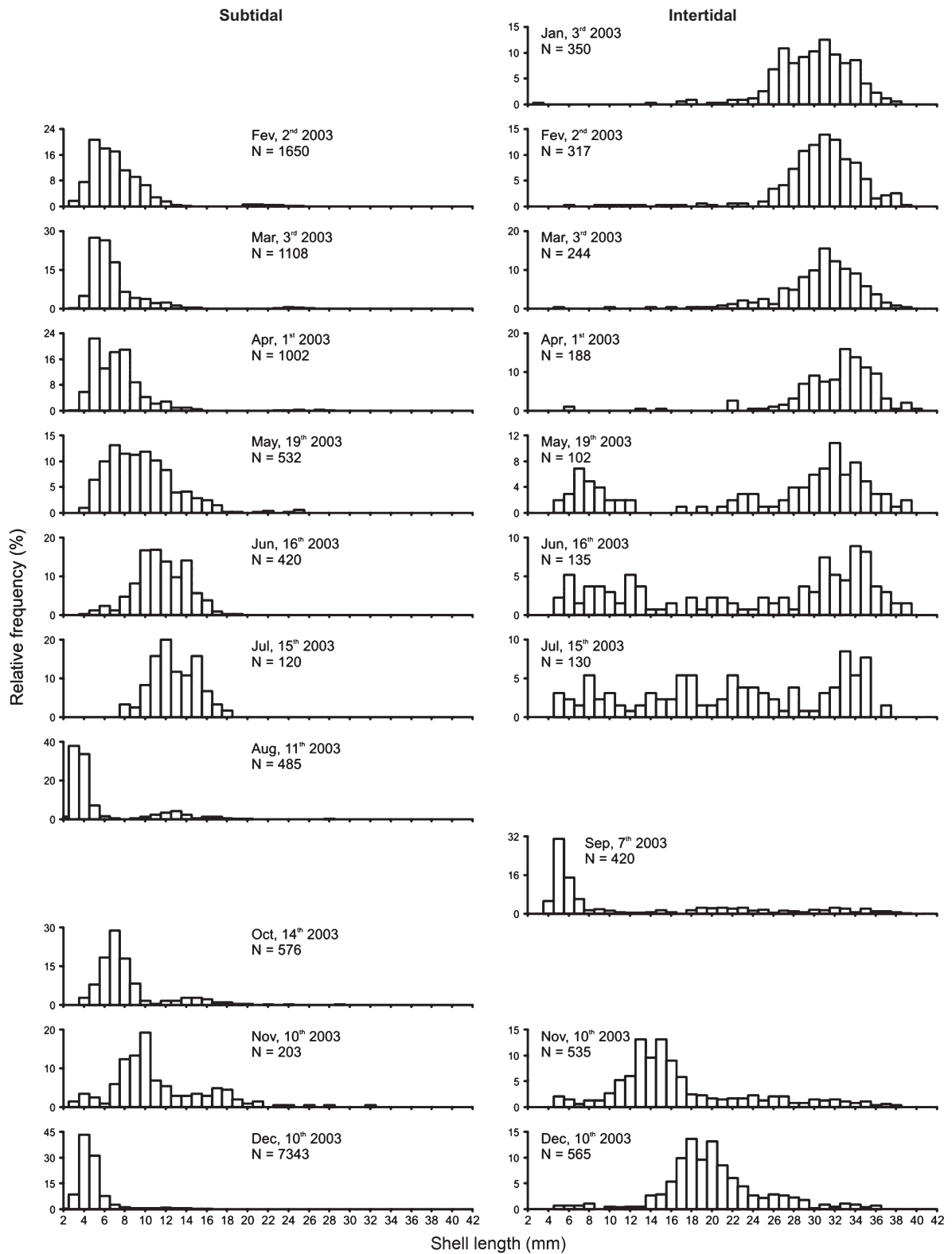


Fig. 4. *Tivela mactroides*. Frequency distribution of shell length classes on each sampling date. Missing data result from the impossibility of sampling in the intertidal zone in August and October 2003 and May 2004, and in the subtidal in January and September 2003. The data presented correspond to the middle sampling period.

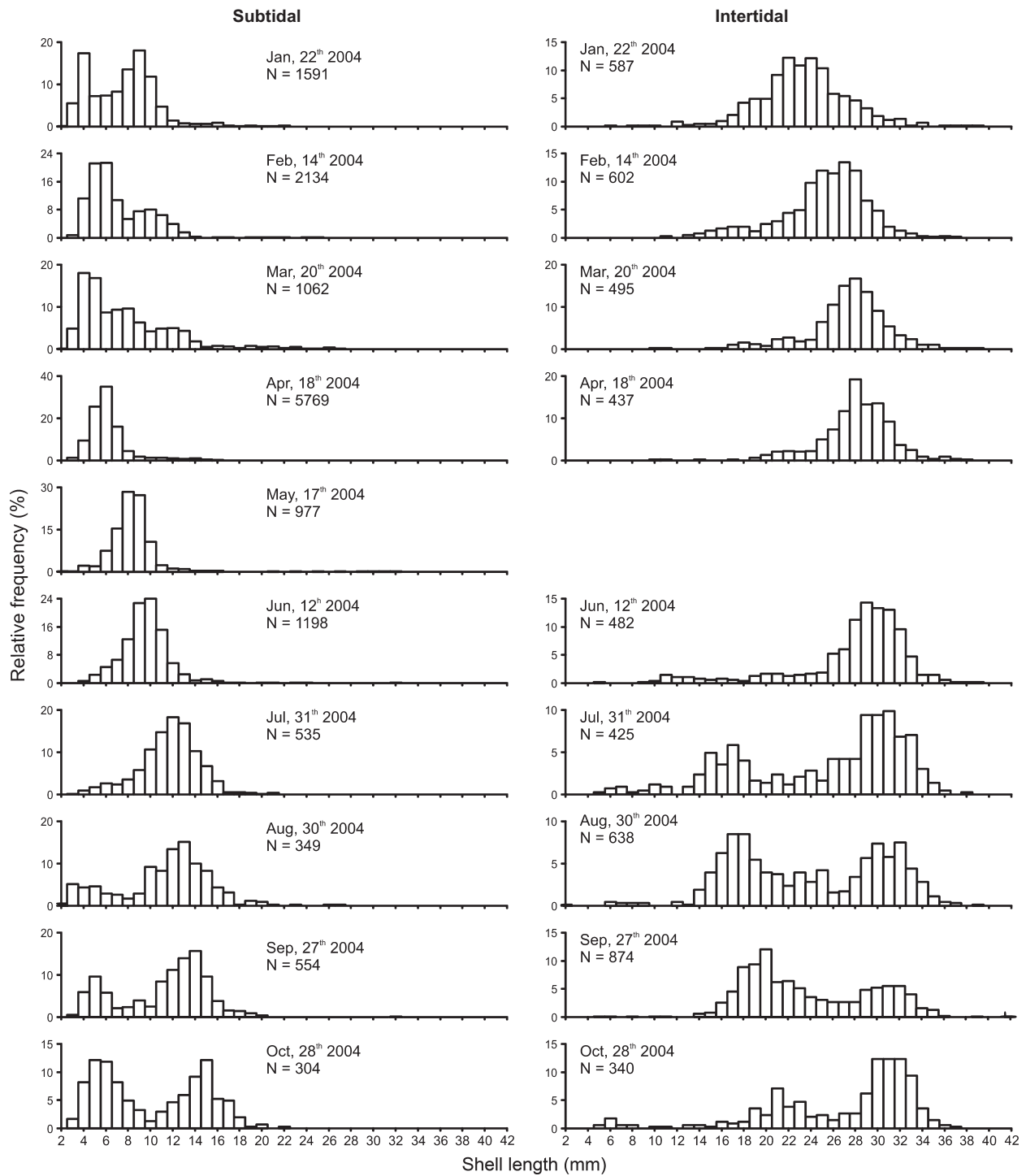


Fig. 4. Continued.

were present in higher densities in the southern area, where the sediment was finer and the slope gentler. The rivers that flow into the bay, although not specifically considered here, are presumed to play an important role in affecting the abundance of this species (McLachlan

et al. 1996; Denadai *et al.* 2005). The southern area is influenced by the Juqueriquerê River (Fig. 1), the largest in this bay. The Lagoa River also affects the southern area, due to the southward along-shore currents. The large amounts of suspended organic material in this area

Fig. 5. *Tivela mactroides*. Modal progression analysis based on the shell length-class frequency distribution, according to the method of Bhattacharya (1967).

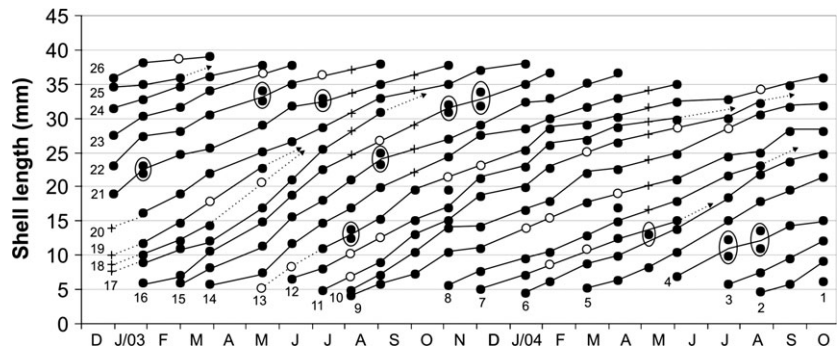


Table 2. Estimates of mortality (Z : year⁻¹) based on the length-converted catch curve (see Fig. 6 for plot).

Fitted models	Points	n	Equation	r ²	Z
1	4–7	4	$y = 16.053 - 14.491x$	0.992	14.491
2	8–14	7	$y = 14.205 - 6.588x$	0.992	6.588
3	17–23	7	$y = 11.581 - 1.561x$	0.941	1.561
4	32–36	5	$y = 15.922 - 3.634x$	0.997	3.634
Total	4–36	33	$y = 12.675 - 2.101x$	0.810	2.101

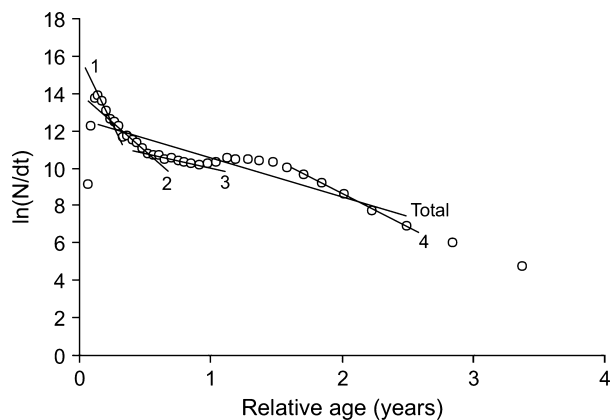


Fig. 6. *Tivela mactroides*. Length-converted catch curve used to estimate the mortality of four successive age classes (1–4) and of the total populations. (The regression equations and estimated r^2 and Z values are given in Table 2.)

are highly important for the maintenance and growth of the individuals from this population. This same condition explains the relatively large number of individuals obtained on the last transect of the northern area in July, August and September 2004. These transects were located generally close to the Santo Antonio River. These observations agree with those of McLachlan *et al.* (1996), who noted that the presence of a freshwater discharge is, together with the sand-grain diameter and beach slope, an important factor structuring *T. mactroides* populations. This discharge is also responsible for the structural

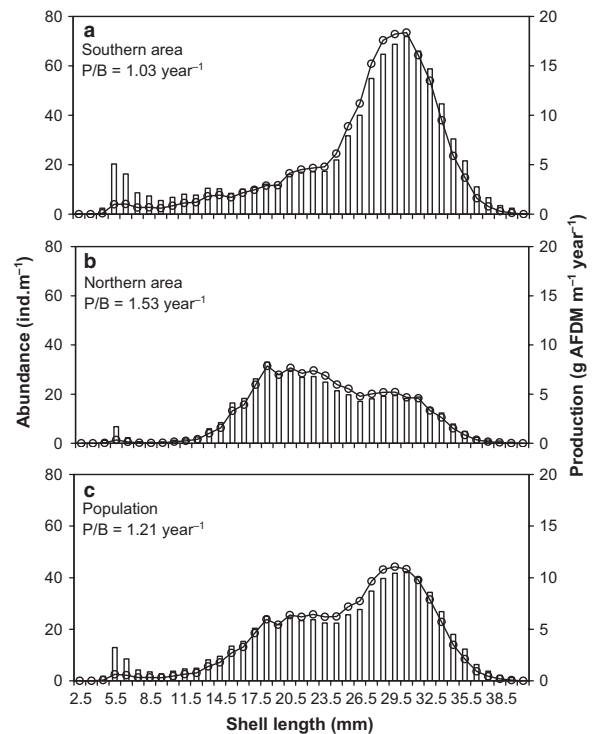


Fig. 7. *Tivela mactroides*. Distribution of abundance (bars) and production (open circles) for different length classes in (a) southern area, (b) northern area, and (c) all intertidal individuals.

characteristics (grain diameter and slope) in the southern area, due to the large contribution of fine terrigenous particles in the area of the Juqueriquerê River.

On a temporal scale, the abundance in the intertidal zone is mainly controlled by the arrival of migratory individuals from the subtidal; the settlement of larvae and recruits in the intertidal population is negligible because these events occur mainly in the subtidal (about 5 m deep; Denadai *et al.* 2005). Therefore, a higher abundance was also expected in the southern subtidal area. The lack of a difference in subtidal abundance between the areas may be due to (i) the southward current in

Caraguatatuba Bay (Souza 1997) and (ii) the gentler slope in the southern area. Both factors would facilitate the migration of individuals from the subtidal to the intertidal zones in the southern area. The higher abundance of smaller individuals (<15 mm) in the southern intertidal supports this idea (Fig. 4). However, the estimates of subtidal abundance should be viewed with caution because of the semi-quantitative sampling used in this zone.

The mean density in the intertidal of Caraguatatuba Bay (14 ind. m⁻²) is much lower than densities observed in some sandy beaches in Venezuela: Playa Caicara, 53 ind. m⁻² (Arrieche & Prieto 2006); Playa Guíria, 485 ind. m⁻² (Tata & Prieto 1991); Higuero sandy beaches, 3250 ind. m⁻² (Herrera & Bone 2011) and La Guardia, 12,000 ind. m⁻² (Etchevers 1976). However, the density is higher than in the São Sebastião Channel (0.12–0.16 ind. m⁻²) in Southeastern Brazil (Arruda & Amaral 2003). The density of *T. mactroides* tends to oscillate over unknown time intervals. In 2007–2008 on the same sandy beach, Turra *et al.* (2013) found a density 150 times higher than that estimated in this study. According to those authors, successive recruitments in the subtidal with subsequent migration to the intertidal led to this notable increase in density within a short time period (about 30 months).

The zonation of individuals in the intertidal seems to be strongly influenced by the size of the clams. In general, the smaller clams occurred in the lower intertidal levels. This is evidence of the migration of individuals from the subtidal to the intertidal zone during their life span (Denadai *et al.* 2005). The reasons for this migration are still unknown, but the intertidal seems to be more favorable for the survival of this species (McLachlan *et al.* 1996). The spatial segregation according to size allows the smaller individuals to inhabit a more stable environment (subtidal zone) and may also minimize the risk of passive filtration of the larvae by the adults in the intertidal zone. In the data obtained here, a likely explanation for the high abundance in the lower intertidal levels in the period from September 2003 to March–April 2004 is the arrival of small individuals (4–8 mm) in the intertidal in this period (see Figs 3 and 4).

The individual growth of *T. mactroides* in Caraguatatuba Bay was continuous, indicating the absence of limiting factors such as temperature and food. The regional temperatures and also the dry–wet seasons vary little and are not sufficient to alter the metabolic rates of the clams, a factor that may control growth (Vakily 1992). In addition, the river discharges provide unlimited food due to the constant arrival of suspended organic material. Denadai *et al.* (2005) found higher abundances of *T. mactroides* in areas under the influence of the rivers, indicating

the success of this suspension-feeding mollusk close to the river mouth, as also observed by McLachlan *et al.* (1996). Other conditions in Caraguatatuba Bay contribute to nutrient enrichment, such as the intense wastewater runoff from the seaside residences, the residues from artisanal fishing, and the rainy climate conditions. The constant recruitment events (about eight per year) may also be favored by the non-limiting food resource and stable temperatures, allowing rapid gonad development (M.R. Denadai, unpublished data) and the survival of planktonic larvae and of just-established individuals.

These favorable conditions allow rapid recovery of the stock of this *T. mactroides* population, despite the considerable mortality rate estimated. The higher mortality affects mainly the just-established individuals, as is the natural tendency for marine populations; and also the larger ones (shell length larger than 30 mm). In the case of the larger individuals, two main factors may be reducing the stock: (i) harvesting by local people and tourists, and (ii) density-dependent mass mortality events (Turra *et al.* 2013). The medium-sized individuals, as well as the smaller ones, are also consumed by a variety of predators, such as sea-stars (*Astropecten marginatus* and *Luidia senegalensis*), swimming-crabs (*Callinectes danae*) and some fishes (*Trachinotus carolinus*, *Cathorops spixii*, *Paralonchurus brasiliensis*, *Aspistor luniscutis* and *Genidens genidens*) (M.R. Denadai unpublished data).

Although available information on the population dynamics of *T. mactroides* is limited, some trends could be observed by comparing the life-history traits of different populations of this species. The higher growth performance (ϕ') for *T. mactroides* on tropical beaches than in the subtropical population of Caraguatatuba Bay is in agreement with the positive relationship between ϕ' and temperature observed for bivalve populations (Vakily 1992; Herrmann *et al.* 2009) (Table 3). The higher mortality on the tropical beaches can also be attributed to the increased metabolic rate at high temperatures, which is reflected in the increase in the parameter K (Moreau 1987). Thus, the longer life span estimated for the subtropical population of *T. mactroides* is expected, since life span increases from tropical to subtropical beaches due to the lower mortality in the latter (Defeo & McLachlan 2005). These differences in life-history traits between the subtropical and tropical populations of *T. mactroides* are in agreement with the latitudinal pattern observed for many species of macrofauna of sandy beaches, such as the bivalves *Donax hanleyanus* (Cardoso & Veloso 2003; Herrmann *et al.* 2009) and *Mesodesma mactroides* (Herrmann *et al.* 2011), and the crustaceans *Emerita brasiliensis* (Defeo & Cardoso 2002), *Excrolana brasiliensis* (Cardoso & Defeo 2004) and *E. armata* (Petracco *et al.* 2010, 2012b).

Table 3. Growth parameters of the von Bertalanffy growth function [L_{∞} (mm) and K (year^{-1})], growth index phi prime (ϕ'), instantaneous mortality rate (Z , year^{-1}) and life span (LS, years) of *Tivela mactroides* populations at different latitudes.

L_{∞}	K	ϕ'	Z	LS	Latitude	Source
39.10	1.80	3.44	3.60		10°05'N	Mendonza & Marcato (2000)
44.32	1.98	3.59	2.41	1.50	10°10'N	Arrieche & Prieto (2006)
			2.88	1.50	10°40'N	Tata & Prieto (1991)
31.80	1.70	3.24	1.98	1.50	10°40'N	Prieto (1987)
40.90	1.00	3.22	2.10	2.50	23°40'S	This study

The higher production in the southern than in the northern intertidal area can be attributed to the high abundance of larger individuals (26–30 mm), which were responsible for most of the production in the former area (42%) and for the intertidal zone as a whole (33%). This higher production in the southern area implies that more food is available for the clams, since production is an estimate of the intensity of the utilization of a food source (Benke, 1996). The production of *T. mactroides* in Caraguatatuba Bay was much lower than production rates estimated for this species in Venezuela (Tata & Prieto 1991), and closer to those estimated in Southeastern Brazil for another venerid, *Anomalocardia brasiliana* (Salvador 2001; Corte 2011; Mattos & Cardoso 2012) (Table 4). However, the production of *T. mactroides* was higher than the median of the estimates obtained for sandy-beach bivalves (Petracco *et al.* 2012a, 2013). Furthermore, the broad distribution of *T. mactroides* across- and along-shore in Caraguatatuba Bay, including the subtidal zone, suggests that the overall production of this bivalve in the bay is high.

The lower P/B ratio of this subtropical population than the tropical population at Guiria Beach, Venezuela, is expected, and follows the latitudinal pattern observed for

other bivalve species (Cardoso & Veloso 2003; Herrmann *et al.* 2009; Petracco *et al.* 2013). However, the P/B ratio of the subtropical population is probably underestimated, since the smaller individuals that live in the subtidal were not included in the calculation of production, because of the semi-quantitative sampling in the subtidal. When these smaller individuals were included, the P/B ratio was estimated at *c.* 2.30 year^{-1} , which seems a more realistic estimate considering the relationship of Allen (1971: $Z = P/B$). This P/B ratio is generally higher than most estimates calculated for other venerid populations (Table 4) as well as for sandy-beach bivalve populations as a whole (Petracco *et al.* 2012a, 2013). The high production and P/B ratio of *T. mactroides* in Caraguatatuba Bay were due to the continuous entry of recruits in the population and the rapid and continuous growth of the clams. These high values make *T. mactroides* an important item in the food web of the beach-surf zone ecosystem and a vital resource for local people, and reinforce the idea that the stock is able to recover rapidly.

In summary, *T. mactroides* shows continuous reproduction, a short life span (2.5 years), and rapid and continuous growth in Caraguatatuba Bay. The higher abundance and production in the southern intertidal area was associated with the more dissipative conditions (gentler slope, finer sand, and wider surf zone) and the presence of a relatively large river. The high production and turnover rate of *T. mactroides* demonstrated the importance of this population as a biological resource for many marine species and for the local people. Despite the limited information about *T. mactroides*, the life-history traits of populations of this species seem to follow a latitudinal pattern. Further studies on the range of distribution of *T. mactroides* should be performed to elucidate aspects of macroecology of this important bivalve of sandy beaches.

Acknowledgements

This work was partially financed by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) within the Biota/FAPESP – The Biodiversity Virtual Institute Program (www.biota.org.br). We also thank FAPESP for the ‘Programa Jovem Pesquisador em Centro Emergente’

Table 4. Annual production (P: g AFDM·m⁻²·year⁻¹), mean biomass (B: g AFDM·m⁻²), turnover ratio (P/B: year⁻¹) of venerid clams at different latitudes (Lat).

Species	P	B	P/B	Lat	Source
<i>Anomalocardia brasiliana</i>	11.60	9.14	1.27	22°56'S	Mattos & Cardoso (2012)
<i>Anomalocardia brasiliana</i>	5.45	1.96	2.78	23°37'S	Corte (2011)
<i>Tivela mactroides</i>	3.23	2.68	1.2–2.3	23°40'S	This study
<i>Anomalocardia brasiliana</i>	1.47	0.79	1.85	23°45'S	Salvador (2001)
<i>Anomalocardia brasiliana</i>	0.59	0.66	0.89	23°45'S	Corte (2011)
<i>Tivela mactroides</i>	136.64	67.68	2.20	10°40'N	Tata & Prieto (1991)

grant offered to M.R.D. (Proc. No. 05/60041-6 and 06/57575-1). Thanks also to Centro Universitário Módulo for the logistical resources and to Dr. Janet W. Reid, who revised the English text.

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