ORIGINAL ARTICLE

Population dynamics of two suspension-feeding bivalves on a sheltered beach in southeastern Brazil

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Abstract The population biology and secondary production of the bivalves *Anomalocardia brasiliana* (Gmelin, 1791) and *Diplodonta punctata* (Say, 1822) were studied on a sheltered beach on the southeast coast of Brazil (Flexeiras Beach) between December 2006 and February 2009. Six transects were established perpendicular to the shoreline. Along each transect, sampling units (SUs) were extracted every 3 m, with a 0.04 m² metal sampler and to a depth of 25 cm, from the base of the boulder wall until 9 m below the waterline during low tide. The abundances of *A. brasiliana* and *D. punctata* were inversely correlated over time. The populations differed in several aspects: (1) *A. brasiliana* occupied mainly the upper levels, whereas *D. punctata* occupied the lower level of the beach; (2) total abundance, growth rate, and production were higher for *A. brasiliana*; and (3) mortality and turnover rate were higher for *D. punctata*. The differences in growth, mortality, and production parameters may be associated with a difference in the species' abilities to exploit resources.

Keywords Growth · Mortality · Secondary production · *Anomalocardia brasiliana* · *Diplodonta punctata* · Sepetiba Bay

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Introduction

Knowledge of the ecology of sandy beach macrofauna along the exposed-sheltered gradient is clearly uneven worldwide. Several studies have focused on community ecology and population dynamics of macrofauna from exposed beaches (Defeo and McLachlan 2005, 2011), while sheltered beaches have been a historically neglected area of sandy-beach ecology (Cardoso et al. 2011). Surprisingly, few studies have analyzed population parameters of sheltered beach macrofauna (Denadai et al. 2004; Abrahão et al. 2010), even though these environments support a high diversity of species (Dexter 1992).

Mollusks are important components of the sheltered beach macrofauna, show different life styles (epifaunal and infaunal) and feeding habits (suspension-, deposit feeders, scavengers, and predators), and consequently play a key role in macrofauna ecology (Jaramillo et al. 2007). Among mollusks, bivalves usually dominate the macrofauna biomass on sheltered beaches (McLachlan and Brown 2006), affecting the vertical distribution and stability of the sediments (Hall 1994), the nutrient fluxes from the sediment to the water column (Michaud et al. 2006), and the oxygen availability (Michaud et al. 2005) by means of their burrowing habit.

Many species of bivalves coexist on sheltered beaches, including the suspension-feeding bivalves *Anomalocardia brasiliana* (Veneridae) and *Diplodonta punctata* (Ungulinidae) (Cardoso et al. 2011). *A. brasiliana* has a wide geographical distribution, from the West Indies to Uruguay (Rios 1994). This species is commonly found in the intertidal beaches, estuaries, and salt marshes, and it is considered eurythermal and euryhaline (Shaeffer-Novelli 1976), being adapted to live at low concentrations of dissolved oxygen and in the presence of hydrogen sulfide

(Hiroki [1977]). This species is exploited by commercial and recreational harvesters on the Brazilian coast because of its high abundance and protein value (Arruda-Soares et al. [1982]). Previous studies have addressed its demography and growth (Monti et al. [1991]); embryonic, larval and post-larval development (Mouëza et al. [1999]); functional morphology (Narchi [1972]); osmotic regulation (Leonel et al. [1983]); and depuration effects on trace metals (Wallner-Kersanach et al. [1994]). Already *Diplodonta punctata* has a distribution from North Carolina to Chile, where it is found in sandy and muddy bottoms (Rios [1994]). There is only a study about biological aspects of *D. punctata* (Domaneschi [1979]).

In the present study, we analyzed the population biology of the two bivalves *Anomalocardia brasiliana* and *Diplodonta punctata* in a sheltered beach located in southeastern Brazil. Like other suspension-feeding intertidal invertebrates, *A. brasiliana* and *D. punctata* constitute a major link in the energy flow between producers and higher trophic levels (DeLancey [1989]), beyond their key role in recycling nutrients through their excretions (Bergamino et al. [2011]). Thus, knowledge of the spatial distribution and life-history traits, the ecological relationship with other suspension feeders, and the contribution of these species to the productivity of the macrofaunal community is fundamental for an understanding and proper management of the studied sheltered beach ecosystem. We evaluated (1) the spatial and temporal distribution of the two bivalve species and (2) their population parameters and secondary production.

Materials and methods

Study site and sampling

Flexeiras Beach is a sheltered beach located in the inner Sepetiba Bay, southeastern Brazil (22°56'S, 43°53'W). The beach is about 350 m long and about 30 m wide, and has a microtidal regime with a mean tidal range of 1.5 m.

Samples were taken monthly in the intertidal zone between December 2006 and February 2009. They were taken along six transects perpendicular to the shoreline. Along each transect, sampling units (SUs) were extracted during low tide every 3 m, with a 0.04-m² metal sampler, and to a depth of 25 cm, from the boulder wall until 9 m below the waterline (during low-tide spring level). Each sample was sieved through a 0.5-mm mesh, and the retained material was taken to the laboratory.

Sediment samples for particle-size analysis were collected with a 3.5-cm diameter corer to a depth of 15 cm at lower, middle, and upper strata of two transects. Samples were oven-dried at 70°C and passed through a series of

sieves (−2.5 to 4.0 phi) in order of size, to determine the mean grain size (Folk and Ward 1957).

Laboratory procedures

The collected biological material was sorted and preserved in 10% formalin. *Anomalocardia brasiliana* and *Diplodonta punctata* individuals were measured with a vernier caliper along the greatest valve length, and the individuals of each species were grouped into 1-mm (*A. brasiliana*) and 0.5-mm (*D. punctata*) size classes. All soft parts of the individuals were removed and dried at 70°C until constant weight, weighed, ashed in a muffle furnace for 4 h at 600°C, and re-weighed.

Data analysis

t Test was used to compare the monthly abundances of *A. brasiliana* and *D. punctata*. A multi-factorial nested ANOVA was used to test significant differences in abundance in space (strata factor with three levels) and time (year with two levels; season with four levels; and month with twelve levels) for *A. brasiliana* and *D. punctata*, using months nested in seasons. One-way ANOVA was performed to compare the spatial variability of mean grain size. Tukey's honest significant difference (HSD) test was used a posteriori to assess significant differences. Normality and homogeneity of variance was assessed using the Cochran test, and where necessary, data were appropriately transformed. When variances were to be significantly heterogeneous even after transformation, untransformed data were analyzed and a significance level of 0.01 was adopted (Underwood [1981]). Relationship between *A. brasiliana* and *D. punctata* densities were modeled by linear and nonlinear fitting, and the best explained relationship was selected based on R^2.

Population parameters

Growth

For growth analysis, the ELEFAN (electronic frequency analysis) routine of the FISAT package (FAO ICLARM Stock Assessment Tools) was used. This approach assumes that growth is described by the von Bertalanffy growth function modified for seasonality (Gayanilo et al. [1996]) as:

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

where L_t is length (mm) at time t; L_∞ is the theoretical maximum length attained by the species; K is the curvature parameter; C is a constant for the amplitude of oscillation in seasonal growth; t_o is the theoretical age at zero length;

and WP is the winter point (i.e., period of growth reduction, expressed as a decimal fraction of the year). The growth index phi prime (Φ'), defined as: $\Phi' = 2\log_{10}(L_\infty) + \log_{10}K$ (Pauly and Munro 1984), was used to measure growth performance. This criterion was chosen because the negative correlation between K and L_∞ (Pauly and Munro 1984) invalidates comparisons based on individual parameters. Life span (t_{max}) was estimated by growth parameters of VBGF and on the basis of the length representing the 99th percentile of the population, $L_{99\%}$ (Sparre et al. 1989).

Mortality

The instantaneous mortality rate (Z) was calculated for each species by the single negative exponential model and by the length-converted catch curve method (Pauly et al. 1995) of 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 is the regression intercept; Z is the unbiased mortality estimated in a module, and t is the estimated age in each cohort (Pauly et al. 1995). The annual mortality rate (A) was obtained through the expression: $A = 1 - e^{-Z}$, according to Ricker (1975). An ANCOVA discriminated by species was used to compare instantaneous mortality, with age as the covariate.

Secondary production

The relationship between length and ash-free dry mass (AFDM) was estimated by the power function:

$$W = aL^b$$

where W is the mean monthly AFDM per length class (g); L is the length of the size class (mm); and a and b are constants. To compare the length–weight function between species, an ANCOVA was performed with length as covariate. Data were linearized (log-transformed) to fulfill ANCOVA assumptions.

Production was estimated by the weight-specific growth rate method. In these calculations, it is necessary to measure growth or mortality rates as a function of size and season and to sum the values throughout the year for each length class (Crisp 1984). Production was given by the equation:

$$P = \Sigma\Sigma f_i G_i w_i \Delta t$$

where f is the mean number of individuals of this length class existing in the population during the time interval Δt; G_i is the specific growth rate in weight of length class i; and w_i is the mean weight of the length class. G_i can be obtained by:

$$G_i = bK[L_\infty/L_i) - 1]$$

where b is the exponent of the length–weight relationship; K and L_∞ are VBGF parameters; and L_i is the mean length in length class i. Annual mean biomass was calculated as:

$$B = \Sigma\Sigma f_i w_i \Delta t.$$

Results

Physical characterization

The mean grain size ranged from 0.25 mm (medium sand) to 1.30 mm (very coarse sand). One-way ANOVA indicated significant differences of mean grain size among strata ($F = 4.57$; $df = 2/159$; $P < 0.05$), and Tukey test detected differences only in upper strata ($P < 0.05$).

Population structure

A total of 8,887 individuals of *Anomalocardia brasiliana* and 4,482 of *Diplodonta punctata* were measured during the field survey. The mean monthly abundance of *A. brasiliana* (289.40 ind m^{-2}) was significantly higher than that of *D. punctata* (77.96 ind m^{-2}) ($T = 11.30$; $df = 322$; $P < 0.001$). Nested ANOVA indicated significant differences between years for *A. brasiliana* ($F = 18.22$; $df = 1/255$; $P \ll 0.01$). Abundance was significantly higher for the first year than the second one (Tukey's HSD; $P < 0.05$). For *D. punctata*, nested ANOVA indicated significant differences among seasons ($F = 4.38$; $df = 3/255$; $P < 0.01$). Abundance was significantly higher in winter than others seasons (Tukey's HSD; $P < 0.05$) (Table 1). The high standard errors in monthly abundance of species suggest a clumped distribution of individuals (Fig. 1).

Anomalocardia brasiliana abundance was inversely correlated with that of *Diplodonta punctata* over time (exponential model; $R^2 = 0.1372$) (Fig. 2). The highest abundances were observed in the middle and lower strata for *A. brasiliana* and *D. punctata*, respectively ($F_{A.\ brasiliana} = 38.41$; $df = 2/255$; $P \ll 0.01$; $F_{D.\ Punctata} = 93.07$; $df = 2/255$; $P \ll 0.01$) (Table 1; Fig. 3).
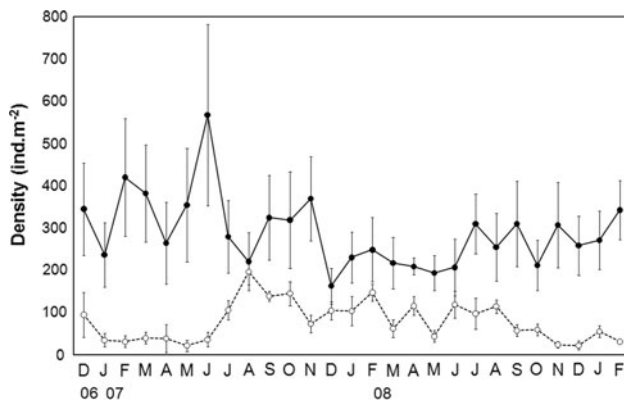
Growth

The lengths of the smallest individuals were 2.52 (June 2008) and 2.82 mm (December 2008) and of the largest ones 36.57 (September 2008) and 19.24 mm (July 2007) for *A. brasiliana* and *D. punctata*, respectively. L_∞ and K varied between the species, resulting in a different growth performance index (Φ') (Fig. 4). Parameter C (degree of seasonal variation) was higher in *A. brasiliana*

Table 1 Multi-factorial nested ANOVA defined by space (strata) and time (year, season, and month)

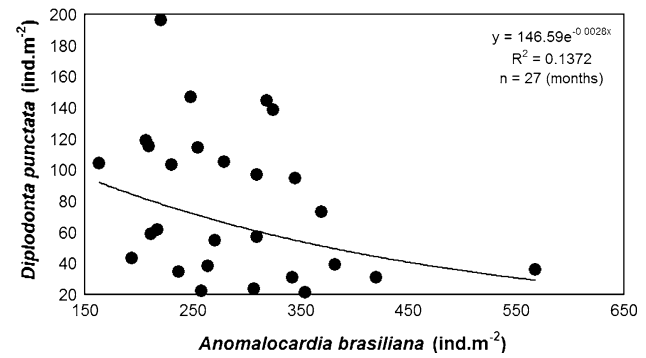| Factor	df	SS	F ratio	P value
Anomalocardia brasiliana				
Strata	2	10,681,189	38.4116	**0.000000**
Year	1	2,533,761	18.2238	**0.000028**
Season	3	235,827	0.5654	0.638301
Month (Season)	8	1,812,599	1.6296	0.116649
Residual	255	35,454,176		
Diplodonta punctata				
Strata	2	6,422,402	93.0675	**0.000000**
Year	1	66	0.0019	0.965266
Season	3	453,322	4.3794	**0.005005**
Month (Season)	8	479,530	1.7372	0.090203
Residual	255	8,798,518		

Significant terms of interest ($\alpha = 0.01$) are highlighted in bold

Fig. 1 Mean monthly density (ind m^{-2} ± SE) of *Anomalocardia brasiliana* (*black circles*) and *Diplodonta punctata* (*white circles*) at Flexeiras Beach

Fig. 2 Exponential model between *A. brasiliana* and *D. punctata* abundances (ind m^{-2}) at Flexeiras Beach
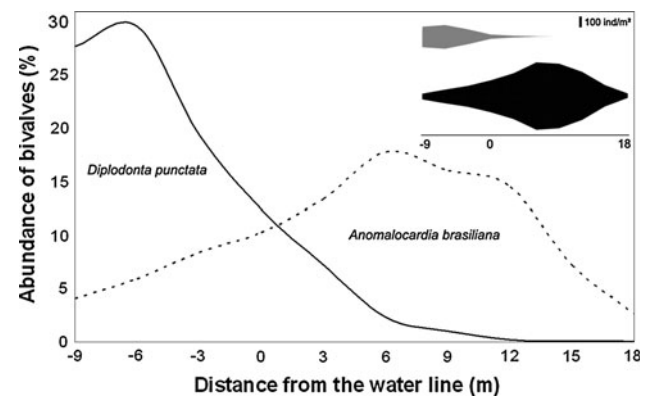
Fig. 3 Across-shore spatial distribution of abundance (%) of *Anomalocardia brasiliana* and *Diplodonta punctata*. The zero value on the horizontal axis represents the waterline, and the *negative* and *positive* values indicate a downshore and an upshore direction, respectively. The zonation of the bivalves is shown in the upper section of the plot (*A. brasiliana*: black diagram, and *D. punctata*: gray one)

than *D. punctata*, although both indicated a moderate oscillation in growth. Values of *WP* (point of lowest growth rate during the year) were close for the two bivalves, indicating lowest growth at the end of April and mid-February for *A. brasiliana* and *D. punctata*, respectively. The life span (t_{max}) of *A. brasiliana* was longer (2.64 years) than that of *D. punctata* (1.63 years) (Table 2).

Mortality

The mortality rate of *D. punctata* (3.53 year^{-1}) was significantly higher than that of *A. brasiliana* (3.17 year^{-1}) ($F = 57.81$; $df = 1/36$; $P < 0.001$) (Fig. 5). The annual finite mortality rates (*A*) were 0.96 and 0.97 year^{-1} for *A. brasiliana* and *D. punctata*, respectively (Table 3).

Secondary productivity

The regression equation between ash-free dry mass and length classes for the bivalve populations were expressed as: $W_{A.\ brasiliana} = (8 \times 10^{-6})L^{2.95}$ ($n = 221$; $r = 0.98$; $P < 0.001$) and $W_{D.\ punctata} = (4 \times 10^{-6})L^{3.03}$ ($n = 186$; $r = 0.97$; $P < 0.001$). These data did not satisfy the ANCOVA assumptions (homogeneity of slopes and homogeneity of variances). The turnover rates (*P/B*) were 1.27 and 1.82 year^{-1} for *A. brasiliana* and *D. punctata*, respectively (Table 4).

Discussion

The populations of two studied bivalves differed in several population parameters. *A. brasiliana* showed higher abundance, growth rate, and production than *D. punctata*. In contrast, *D. punctata* showed higher mortality and turnover
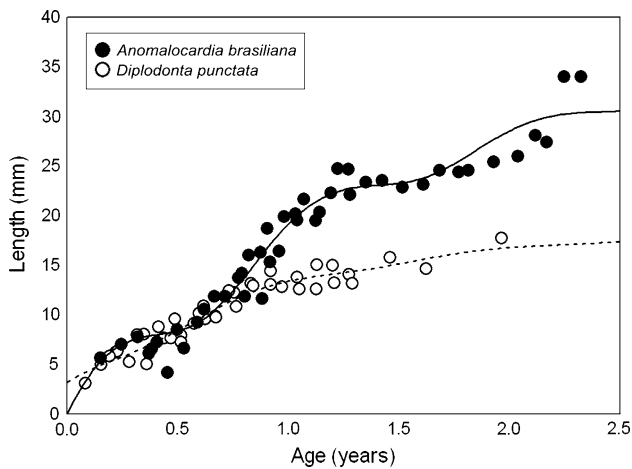
Fig. 4 Growth curves estimated for *Anomalocardia brasiliana* and *Diplodonta punctata* populations
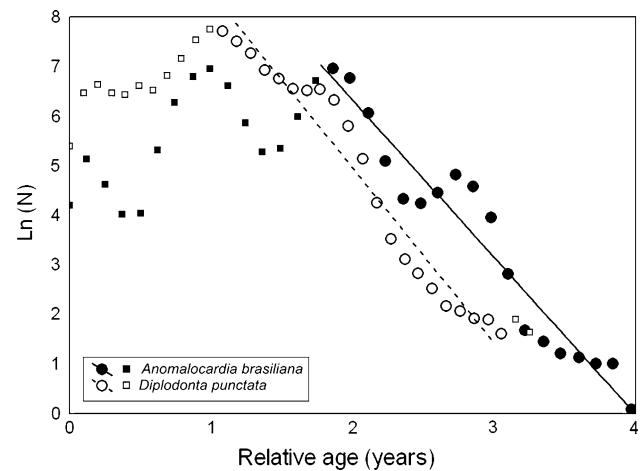

Fig. 5 Length-converted catch curves of *Anomalocardia brasiliana* and *Diplodonta punctata*. *Points* represented by *squares* were not used for fitting the linear regression

Table 2 Growth parameters estimated by nonlinear least squares fit of the von Bertalanffy function of *Anomalocardia brasiliana* and *Diplodonta punctata* populations

Parameter	*Anomalocardia brasiliana*		*Diplodonta punctata*	
	Mean (±SE)	*P*	Mean (± SE)	*P*
L_∞ (mm)	37.62 (±3.70)	0.000	18.48 (±2.55)	0.000
K (year^{-1})	0.71 (±0.15)	0.000	1.10 (±0.43)	0.016
C	0.85 (±0.17)	0.000	0.39 (±0.19)	0.048
WP	0.41 (±0.03)	0.000	0.20 (±0.11)	0.076
T_0 (year)	0.01 (±0.04)	0.767	−0.16 (±0.12)	0.177
R	0.98		0.96	
Φ'	3.00		2.58	
Smallest (mm)	2.52		2.82	
Largest (mm)	36.57		19.24	
t_{max} (year)	2.64		1.63	

L_∞ asymptotic length; K curvature parameter; C constant for the amplitude of seasonal oscillation of growth; WP point of lowest growth rate in the year; T_0 theoretical age at length 0; r correlation coefficient; Φ' standard growth index (Pauly and Munro 1984); t_{max} life span

rate than *A. brasiliana*. Beyond differences in population parameters, these species showed a spatial and temporal segregation (Figs. 2, 3). In relation to temporal segregation, the negative correlation between the abundance of the species over time suggests that the abundance peaks of *A. brasiliana* coincide with periods of low abundance of *D. punctata*. All these differences could be caused by: (1) physiological process (*A. brasiliana* has a high ecological valence, see introduction); (2) environmental characteristics (desiccation, grain size); and/or (3) interaction between species (competition for space and food).

The bivalves showed a clear spatial segregation, with *Anomalocardia brasiliana* dominating the middle strata

and *Diplodonta punctata* the lower strata of the beach (Fig. 3). This segregation could be associated with grain size; however, the middle and lower strata did not show statistically significant differences. So, others hypothesis are necessary to explain the spatial segregation of the bivalves.

The lower growth rate of *A. brasiliana* in relation to *D. punctata* can be related to a greater investment of energy in soft-part and shell production, since *A. brasiliana* individuals have more biomass and the shells are harder than in individuals of *D. punctata*. Furthermore, the largest theoretical maximum length was influenced, since L_∞ and K are inversely related. Therefore, there are other physiological and behavioral processes and plasticity in life-history traits (Brown 1996) that may explain the slower growth in *A. brasiliana*. The growth rate in both bivalves showed moderate seasonal variation, with the lowest growth rate (*WP*) occurring in autumn and summer for *A. brasiliana* and *D. punctata*, respectively. The decrease in growth rate during the autumn for *A. brasiliana* can be explained by the breeding season. Narchi (1976) and Boehs (2000), studying gametogenesis in two *A. brasiliana* populations, observed intense spawning periods during autumn and spring, although both populations had a continuous gametogenic cycle. These results concorded with the decrease in the growth rate during autumn, when energy is transferred from somatic growth to the production of gametes (Moura et al. 2008). The decrease in growth rate of *D. punctata* can be explained by the same process, since in subtropical regions, the summer period is more favorable for reproduction. A recent study on the reproductive cycle of the venerid *Callista chione* from the southwestern Portuguese coast detected three spawning peaks: January–March (winter), April–May (spring), and August–October

Table 3 Mortality estimates (Z) of *Anomalocardia brasiliana* and *Diplodonta punctata* populations and associated statistics (ANCOVA)

Parameter	*Anomalocardia brasiliana*		*Diplodonta punctata*	
	Mean (±SD)	P	Mean (±SD)	P
G	12.66 (±0.62)	0.000	12.02 (±0.37)	0.000
Z	3.17 (±0.21)	0.000	3.53 (±0.17)	0.000
R^2	0.94		0.96	
N	18		21	
ANCOVA $F_{1,36} = 57.81$; $P < 0.001$				

ANCOVA homogeneity of slopes: $F_{1,35} = 0.185$; $P = 0.182$. Homogeneity of variances: $F_{1,37} = 0.167$; $P = 0.685$

G regression intercept; R^2 determination coefficient; *n* number of points)

Table 4 Secondary production (P), biomass (B), and turnover rates (P/B) of *Anomalocardia brasiliana* and *Diplodonta punctata* populations

Parameter	*Anomalocardia brasiliana*	*Diplodonta punctata*
P (g AFDM m^{-2} $year^{-1}$)	11.60	0.79
B (g AFDM m^{-2})	9.14	0.43
P/B ($year^{-1}$)	1.27	1.82

(summer); the population has no resting period and a new gametogenic cycle began in early November, immediately after these spawning episodes (Moura et al. 2008). According to these authors, the energy reserves are probably directed toward the recuperation of gonads, inducing a phase of slow growth in *C. chione*. Other studies have found similar seasonal growth patterns (Gaspar et al. 1999, 2004).

The higher mortality of *D. punctata* compared to *A. brasiliana* can be associated with the different zones occupied by the species and by differences the shell fragility (*D. punctata* has a thinner shell than *A. brasiliana*). Surprisingly, infaunal species that live submerged, as *D. punctata,* can be subject to greater predation pressure (by benthivorous fishes or crustaceans) than species that are exposed during low tide. Lee (1996) observed that the infaunal bivalve *Tapes philippinarum* suffered from higher predation pressure than *Anomalocardia squamosa*, associating this difference to the thinner shell of the former species. The annual mortality rates observed for *A. brasiliana* in the present study are higher than the mortality of 0.76 $year^{-1}$ found at 23° S (Salvador 2001), as well as than the values reported for other venerids: 0.47 $year^{-1}$ for *Protothaca thaca* at 36° S (Urban and Campos 1994), 0.27 $year^{-1}$ for *Callista chione* at 38° N (Metaxatos 2004), and 0.14 $year^{-1}$ for *Eurhomalea exalbida* at 54° S (Lomovasky et al. 2002). These differences may be related

to latitude, because tropical regions show higher mortality rates compared to temperate regions (Ansell et al. 1978). According to Defeo and Cardoso (2004), the high mortality rate in subtropical beaches could be explained by a combination of rising metabolism at increasing temperature and insufficient food availability.

The higher production of *A. brasiliana* compared to *D. punctata* may be associated with the greater abundance of the venerid species. Because of the species' high abundance, the production of *A. brasiliana* accounts for a high percentage of the overall production of the local macrofaunal community. Among mollusks, *A. brasiliana* and the gastropod *Cerithium atratum* comprise more than 80% of all individuals in the macrofaunal community (Cardoso et al. 2011). On the other hand, the *P/B* ratio calculated for *D. punctata* was higher than for *A. brasiliana*, a difference which possibly relates to the former species' lower individual body mass (Brey and Clarke 1993; Tumbiolo and Downing 1994) and longevity (Waters 1977; Robertson 1979). According to Robertson (1979), populations that show a high *P/B* ratio consist of small individuals with a rapid growth rate and short life expectancy, while low *P/B* values are associated with large individuals showing slow growth rate and long life expectancy.

We can conclude that the negative correlation between the abundance of these two bivalves over time suggest a potential competition for resources. Franke and Janke (1998) noted that suspension-feeders that co-occur naturally in marine environments are able to establish inter- and intraspecific competition relationships for food resources. The differences in growth, mortality, and production parameters can be associated with differences in the ability to exploit resources. Peterson and Black (1993), comparing suspension-feeders in different biogeographical regions, observed some reduction in growth at lower latitudes, probably resulting from increased competition for food. Furthermore, this study has contributed to our knowledge of the biology of an important fishery resource (*A. brasiliana*) and has produced additional information for future shell fishery management. Finally, the study has provided some knowledge on *D. punctata*, a species that belongs to a taxonomic group (family Ungulunidae) for which population studies were heretofore lacking.

Future research will focus on species with the same feeding habit (e.g., the suspension-feeders *A. brasiliana* and *D. punctata*), developing experimental approaches both in the field and the laboratory to estimate interactions between macrofauna species, measuring the degree of interactions and possible consequences for population dynamics.

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