

Differences in the secondary production of *Emerita brasiliensis* (Decapoda: Hippidae) on two sandy beaches in Rio de Janeiro State, Brazil

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Abstract

The present study evaluated the differences in the secondary production of *Emerita brasiliensis* on two different types of beaches. Sampling was carried out monthly at Jaconé and Massambaba beaches in the state of Rio de Janeiro, Brazil, from June 2007 through May 2008. Jaconé Beach is predominantly reflective, with medium to coarse sand (0.87 mm), a steep slope, and a narrow surf zone. Massambaba Beach has an intermediate morphodynamic, with fine sand (0.43 mm), a gentle slope, and a wide surf zone. Population parameters were estimated such as growth rate and longevity. The secondary production was calculated by the weight-specific growth-rate method. The growth rate and longevity (K) was higher at Massambaba Beach 1.95 for males and 2.26 for females. The peak of production occurred in the smallest length classes (3 to 8 mm), where the highest abundances were also observed at both beaches. The secondary production (g AFDW m⁻² y⁻¹), and P/B ratio (y⁻¹) of *E. brasiliensis* population at Massambaba (P = 193.74g AFDW m⁻² y⁻¹; B = 33.26g AFDW m⁻²; P/B = 5.82 y⁻¹) were higher than at Jaconé Beach (P = 96.8g AFDW m⁻² y⁻¹; B = 41.74g AFDW m⁻²; P/B = 2.31 y⁻¹). Comparisons of the results suggest that beaches with gentler slopes and finer sand have higher community production, owing to the filter-feeders in the intertidal zone.

Key words: secondary production, *Emerita brasiliensis*, sandy beaches.

Introduction

Sandy beaches are highly dynamic transitional systems that constantly adjust to fluctuations in local energy levels. The wave energy not only determines the morphodynamic of the beach, but also controls the matter and energy flow of this ecosystem (Gianuca, 1983; McLachlan and Romer, 1990; McLachlan *et al.*, 1993; Defeo and Gomez, 2005). The degree of exposure to waves, and the morphology of the beaches are determining factors for the richness, diversity, and trophic structure of their biological communities (Brown and McLachlan, 1990; Defeo *et al.*, 1992a; Dexter, 1992; McLachlan, 1990, 1996; McLachlan *et al.*, 1993; McLachlan and Jaramillo, 1995). Therefore, community structure is strongly correlated with the different morphodynamic types of

beaches, and consequently with the swash climate (McLachlan *et al.*, 1993; Gomez and Defeo, 1999; Defeo *et al.*, 2001; Defeo and Gomez, 2005; Defeo and McLachlan, 2005). Recent studies show that allochthonous inputs of wrack to beaches plays an important role as habitat and food source for the macrofauna inhabiting exposed sandy beaches (Dungan *et al.*, 2000; Colombini and Chelazzi, 2003; Lastra *et al.*, 2008; Olabarria *et al.*, 2009).

In these very dynamic coastal ecosystems, the filter-feeders are a significant link between the water column and the sediment, playing an important role in energy flow (Dame, 1976; Wildish and Kristmanson, 1997; Jaramillo and Lastra, 2001; Thompson and Schafferner, 2001). The relative importance of the suspension-feeders in an ecosystem depends, in part, on the population dynamics of each species (Thompson and Schafferner, 2001).

Among the filter-feeders of reflective and dissipative beaches, crustaceans of the genus *Emerita* Scopoli, 1777 are very common along the coasts of North and South America (McLachlan, 1983; Dungan *et al.*, 1991, 1994; Dungan and Hubbard, 1996; Veloso and Cardoso, 2001; Defeo and Cardoso, 2002; Veloso *et al.*, 2003a,b). The majority of species in this genus show wide geographic variation, which has stimulated studies on the influence of latitude on population parameters such as growth rate, fecundity, and breeding season (Jaramillo *et al.*, 2001; Defeo and Cardoso, 2002, 2004; Defeo and Alava, 2005).

Emerita brasiliensis Schmitt, 1935 is one of the most common and abundant macrofaunal species of beaches on the south and southeast coast of Brazil and the coast of Uruguay (Efford, 1970; Defeo *et al.*, 1992b; Veloso *et al.*, 1997; Peluffo, 1998; Veloso and Cardoso, 1999, 2001). Variations in population dynamics of this species have been analyzed according to the beach morphodynamic type (Dungan and Hubbard, 1996; Contreras *et al.*, 2003; Jaramillo *et al.*, 2000; Defeo *et al.*, 2001; Veloso and Cardoso, 2001; Cardoso *et al.*, 2003). These studies have shown that population on dissipative beaches show higher growth rates, fecundity, and biomass, although their abundance is similar among the different beach types.

In spite of the significant role of *E. brasiliensis* as trophic intermediates between primary producers and higher level organisms (like birds and fish) very little information is available on secondary production (Veloso and Cardoso, 1999; Defeo *et al.*, 2001; Cardoso *et al.*, 2003; Veloso *et al.*, 2003a). Production is an important measure to understand the role of a population within a community, and is related to important population components such as density, biomass, growth rate, and reproduction (Benke, 1993, 1996). The productivity of a population varies temporally as a consequence of changes in the density and structure of the population (such as during recruitment periods). The importance of the secondary production of macroinfauna has been little investigated, as well as the variation of this production according to the beach morphodynamic type (Waters, 1977; Warwick, 1980; Wilson, 1999; Thompson and Schaffner, 2001; Gillet and Torresani, 2003; Baeta *et al.*, 2005).

For the most part, studies of secondary production of beach macrofauna are limited to estimating the production of one species in one beach

morphodynamic type. In Brazil, studies of secondary production of the macroinfauna of sandy beaches are also few, in spite of the great extent of these ecosystems. The first studies treating secondary production on exposed beaches were carried out by Gianuca (1985). Later, Santos (1994) estimated the secondary production of the polychaete *Scolecopsis gaucha* in southeastern Brazil. Significant studies at Atami beach, coast of Paraná, reported the secondary production of the ghost shrimp *Callinectes major* (Souza *et al.*, 1998), and the polychaetes *Scolecopsis squamata* (Souza and Borzone, 2000) and *Euzonus furciferus* (Souza and Borzone, 2007). On the coast of Rio de Janeiro, Cardoso and Veloso (1996) estimated the secondary production of the amphipod *Pseudorchestoidea brasiliensis*. The same authors in 2003 studied the secondary production of the bivalve *Donax hanleyanus* at Restinga da Marambaia, and Caetano *et al.* (2003) assessed the secondary production of the gastropod *Ollivancillaria vesica vesica*. Veloso *et al.* (2003a) estimated the secondary production for the three most abundant crustacean species at Prainha beach *Emerita brasiliensis*, *Pseudorchestoidea brasiliensis* and *Excirologa brasiliensis*. In 2006, Caetano *et al.* studied the production of the isopod *Excirologa brasiliensis* on beaches with different morphodynamic aspects. These investigators did not observe significant differences in the density of individuals between the different morphodynamic types of beaches; however, in all cases, the months with higher secondary production were related to the entry of juveniles into the ecosystem.

Specifically, this study analyzes the influence of the density and population structure of *Emerita brasiliensis* on secondary production on two beaches with different morphodynamic characteristics and compares the secondary production of this species with estimates available in the literature.

Material and Methods

Geomorphological Variables

Sampling was carried out monthly from June 2007 through May 2008, during low tide. The pole method of Emery (1961) was used to estimate the slope of each transect. The degree of exposure of the beach was calculated according to McLachlan (1980), and Dean's parameter: $\Omega = Hb/(Ws^*T)$

(Wright and Short, 1984) was used to calculate the morphodynamic state of the beach, where: H_b is the wave height (cm), W_s is the sedimentation velocity (cm/s), and T is the wave period (s). The width and period of the swash zone were measured with the aid of a chronometer and tape measure. For the granulometric analysis, sediment samples were taken with a PVC tube 3.5 cm in diameter, to a depth of 10 cm in the sublittoral zone. The sieving method was used, according to Suguio (1973), with sieves at intervals of 0.5 phi according to the Wentworth scale.

Sampling, Laboratory Procedures, and Statistical Analyses

Six transects (each 10 m long) were delineated, extending from above the drift line to below the swash line, and four strata parallel to the waterline were sampled, according to a stratified random design, defined as: 1) upper intertidal, located near the drift line; 2) middle intertidal and lower intertidal, between the drift line and the waterline; 3) upper sublittoral; and 4) sublittoral, where the sand is permanently saturated with water. From each stratum, one replicate was randomly taken with a 0.04 m² quadrat sampler to a depth of 25 cm. The sediment was washed through a 0.71 mm sieve, and the material retained was taken to the laboratory, where the organisms were sorted by species, counted, and fixed in 5% formaldehyde. Student's T-test (Zar, 1996) was used to test the difference in values of biomass and production between the beaches.

Growth and Longevity

To carry out growth analysis, the monthly length-frequency distributions discriminated by sex were used according to procedures suggested by Gómez and Defeo (1999) and Defeo *et al.* (2001). The procedure suggested by these authors consists of: (1) separate normally distributed components of length-frequency distributions through the NORMSEP routine of the FISAT (FAO-ICLARM Stock Assessment Tools) program (Gayaniilo *et al.*, 1996); (2) assign absolute ages to respective cohorts (lengths) and build an age-length key; (3) using the resulting age-length key for each sex and beach to fit the von Bertalanffy

growth function for seasonality (VBGF: Gayaniilo *et al.*, 1996) by non-linear least squares:

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

where L_t is length at time t (mm); L_{∞} is the theoretical maximum length attained by the species; K is the curvature parameter; C accounts for the intensity of seasonal growth oscillations; t_0 is 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 longevity and the population parameters were estimated according to Cardoso and Veloso (1996).

Secondary Production

The secondary production was estimated by the weight-specific growth rate method (Crisp, 1984) and is given by the equation: $P = \sum f_i * G_i * w_i * \Delta t$, where f_i is the mean number of individuals of this size class existing in the population during the period Δt , G_i is the weight specific growth rate of size class i , w_i the mean weight of the size class, and Δt is the interval of time between the sampling. G_i can be obtained by $G_i = b * K * [(L_{\infty} - L_i)/L_i]$, where b is the exponent of the length-weight relationship; K e L_{∞} are VBGF parameters, L_{∞} is the theoretical maximum length attained by the species; K is the curvature parameter and L_i is the mean length in length class i .

Results

The beaches of Jaconé (22°56'08.79"S; 42°37'04.8"W) and Massambaba (22°57'02.25"S; 42°06'29.8"W) are located on the north coast of the state of Rio de Janeiro. These beaches have distinct physical characteristics. Jaconé Beach is characterized by a reflective morphodynamic state, with coarse sand, a narrow surf zone, a mean beach width of 38 m, and a medium-steep slope. Massambaba Beach shows predominantly intermediate characteristics, with fine sand, a wide surf zone, a mean beach width of 63 m, and a gentle slope (Table I). The physical parameters show significant differences in the swash ($t = 2.906$; $p = 0.0008$), slope ($t = 5.914$; $p = 0.0004$), and grain size ($t = 12.118$; $p = 0.0002$). The values for

Table I. Physical characteristics of Jaconé and Massambaba beaches. Data are expressed as mean \pm standard deviation.

Physical variables	Jaconé	Massambaba
Mean grain size (mm)	0.87	0.43
	0.12	0.15
Swash period (sec)	8.30	11.5
	3.70	0.72
Wave period (sec)	14.90	11
	4.20	3.26
Wave height (m)	1.28	0.65
	0.70	0.06
Dean's parameter	0.73	2.08
	0.33	0.2
Intertidal slope (1/m)	10.50	14.9
	0.60	1.66

wave height did not differ significantly between the beaches ($t = 0.4532$; $p = 0.6545$).

The density of *Emerita brasiliensis* did not differ significantly between the beaches ($t = 0.5991$, $p = 0.5447$). The mean abundance was higher at Massambaba (mean \pm standard deviation: 3478.73 ± 993.66 ind.m⁻²) compared to Jaconé (2039.52 ± 822.21 ind.m⁻²). However, the unpaired T test indicated significant differences in the biomass of *E. brasiliensis* between the beaches ($t = 3.792$ and $p < 0.001$), with higher values observed at Jaconé (Figs. 1 and 2). At Jaconé, the density showed a peak during spring, whereas the maximum value for biomass was observed in April (austral late summer). At Massambaba Beach, the highest values of density were recorded in October and March, and the peak of biomass occurred in January.

Juvenile individuals of *E. brasiliensis* reached their greatest abundance 2 to 3 months after the maximum occurrence of reproductive females. Massambaba Beach showed two periods of juveniles, the first in the spring months (September through November) and the second at the end of summer (March/April). Jaconé Beach showed a maximum abundance of juveniles in October (Fig. 3).

The peak of production occurred in the smallest length classes (3 to 7 mm), where the highest abundances were also observed. On Massambaba Beach, the length classes between 3 and 10 mm showed the highest abundance.

The growth parameters were significant for males and females on both beaches (Table II). The growth rate (K) was higher for males and females at Massambaba Beach. The longevity (t_{\max}) corre-

Table II. Von Bertalanffy growth parameters: L_{∞} (mm); K; C; WP (winter point); Rn; T_{\max} (meses) estimated for *Emerita brasiliensis* during the sampling period.

	Jaconé				Massambaba			
	Males	p	Females	p	Males	p	Females	p
L_{∞}	15.03	0.000	22.86	0.000	14.175	0.000	23.04	0.000
K	1.70	0.001	1.53	0.001	1.95	0.000	2.26	0.000
C	0.58	0.023	0.45	0.021	0.81	0.001	0.72	0.000
WP	0.55	0.002	0.63	0.001	0.45	0.000	0.68	0.001
T_{\max}	19		20		21		23	

Table III. Secondary production (g AFDW m⁻² year⁻¹), mean biomass (g AFDW m⁻²), and turnover rates (yr⁻¹) values for *Emerita brasiliensis* on two sandy beaches. P (production), B (biomass).

dados atuais	P	B	P/B
Jaconé	96.80	41.74	2.31
Massambaba	193.74	33.26	5.82

sponding to these estimates was 19 for males and 20 for females at Jaconé and 21 for males and 23 for females at Massambaba.

The unpaired T test indicated significant statistical differences between the secondary production at Jaconé and Massambaba ($t = 2.582$ and $p = 0.017$). The highest rate was recorded for March at Massambaba (Fig. 5). Jaconé showed an increased rate in October.

A higher mean biomass was observed at Jaconé; however, the turnover rate (P/B) was higher for Massambaba (Table III).

Discussion

The increase in richness, abundance, and biomass at the community level from reflective to dissipative beaches is accepted as a paradigm for the ecosystems of exposed sandy beaches (McLachlan, 1990; McLachlan *et al.*, 1981, 1993, 1996; Defeo *et al.*, 1992b; Jaramillo and McLachlan, 1993; Borzone *et al.*, 1996; Ricciardi and Bourget, 1999; Defeo *et al.*, 2001; Defeo and McLachlan, 2005). Nevertheless, for populations, the pattern of abundance is not as clear. Many studies have found no clear correlation between density and population parameters with beach morphodynamics. The abundance of *Emerita analoga*, for example, was very similar among different beach morphodynamic types, and some studies have found much higher values for intermediate beaches compared to dissipative beaches (Dugan *et al.*, 1994; Dugan

et al., 2000; Jaramillo and Lastra, 2001; Contreras *et al.*, 2003). Species of the supralittoral, such as the amphipod *Atlantorchestoidea brasiliensis*, show an increase in the abundance of juveniles, ovigerous females and body size toward reflective beaches (Gomez and Defeo, 1999). A study of 15 exposed beaches on the coast of Rio de Janeiro by Veloso

et al. (2003b) showed higher densities of *Emerita brasiliensis* at both dissipative and reflective beaches (granulometry 0.2 to 1.19 mm). Cardoso *et al.* (2003), comparing the population dynamics of *E. brasiliensis* for two years between the intermediate Restinga da Marambaia beach and the reflective Grumari Beach on the shore of Rio de Janeiro,

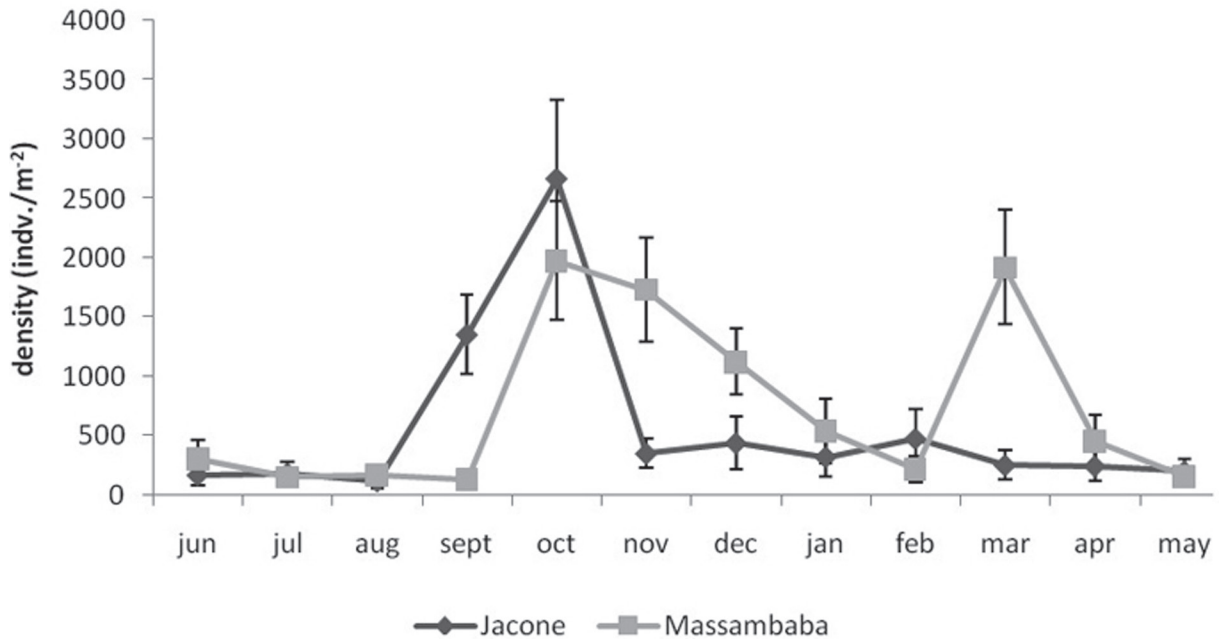


Figure 1. Monthly variations in mean density of *Emerita brasiliensis* from June 2007 through May 2008, at Jaconé and Massambaba beaches (density, \pm SD).

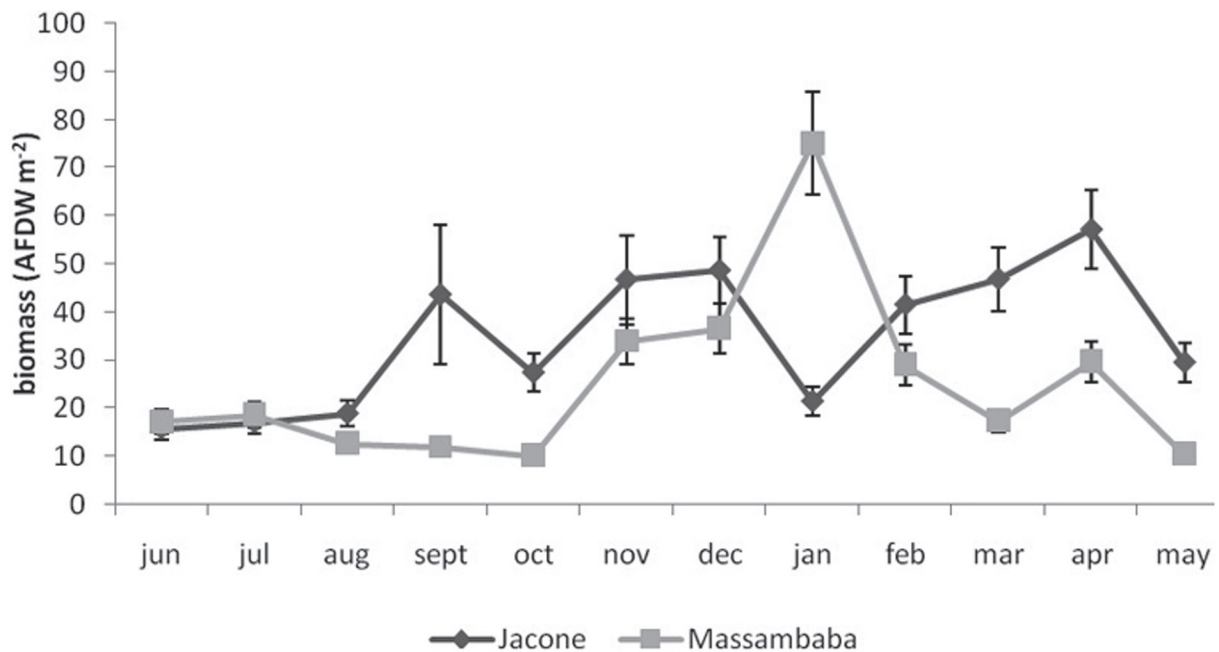


Figure 2. Monthly variations in mean biomass \pm SD (g AFDW m⁻²) of *Emerita brasiliensis* estimated at Jaconé and Massambaba beaches.

found no significant differences in density. These authors related the variations in density to the entrance of juveniles into the population. Our data confirm the results found in the literature, with no significant differences in the density between the two beaches studied. The peaks in density coincided with high abundances of juveniles.

Different investigators have concluded that the variability in the density of populations of invertebrates in beaches and other coastal ecosystems is more closely related to reproductive events or to success in recruitment than to differences in morphodynamic factors (Seitz and Schaffner, 1995; Veloso *et al.*, 1995; Thompson and Schaffner,

2001; Defeo and Cardoso, 2002; Caetano *et al.*, 2006). Defeo and McLachlan (2005) suggested that the age/size structure of a population is a good index of the degree of retention of larvae and of the possibility that they will return to the parent population. These researches showed that populations with good representation of all age/length classes are the result of successive recruitments, and occur principally in dissipative beaches. In contrast, high variability in abundance, with a narrow period of reproduction and recruitment, has been found on reflective beaches. Thus, success in larval recruitment depends on the circulation system of the surf zone and on the beach face for the return of the

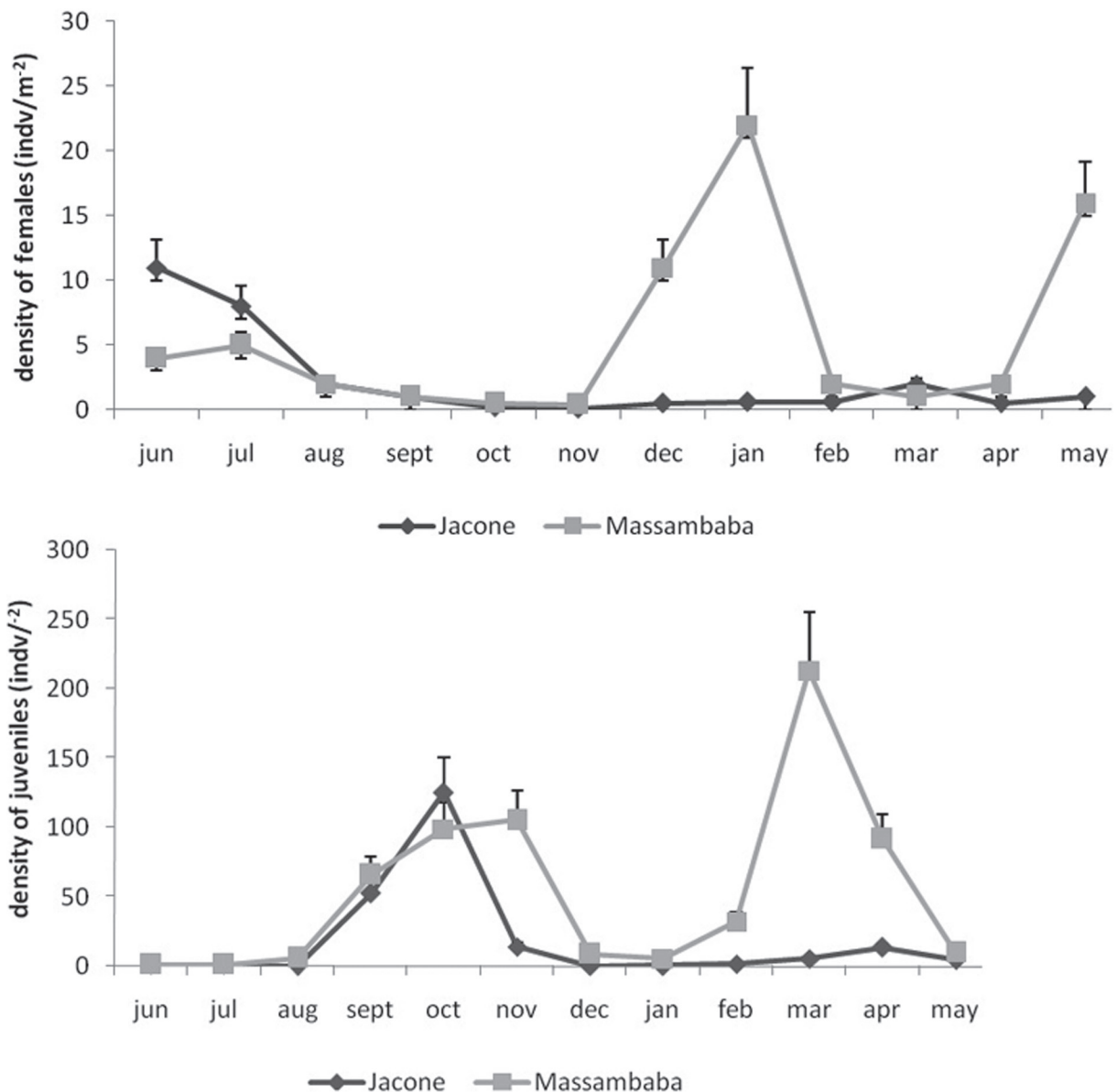


Figure 3. Temporal variation in the abundance of ovigerous females and juveniles of *Emerita brasiliensis* at Jacone and Massambaba beaches (density, \pm SD).

larva. The conditions of reflective beaches, such as the short swash period, severe wave climate, and steep profile reduce recruitment success. This paper confirms the pattern suggested by Defeo and McLachlan (2005) where the population density of *E. brasiliensis* at Massambaba Beach varied less among months, with higher frequencies of all length classes and a higher proportion of juveniles

during the year compared to Jaconé Beach. Veloso and Valentin (1993), analyzing the distribution of larvae of *Emerita*, showed that these can be found at great distances from the coast, and that they depend on the circulation of the surf zone for recruitment success. According to these investigators, the last larval stage was most abundant near the beach face, whereas the other larval stages were found far

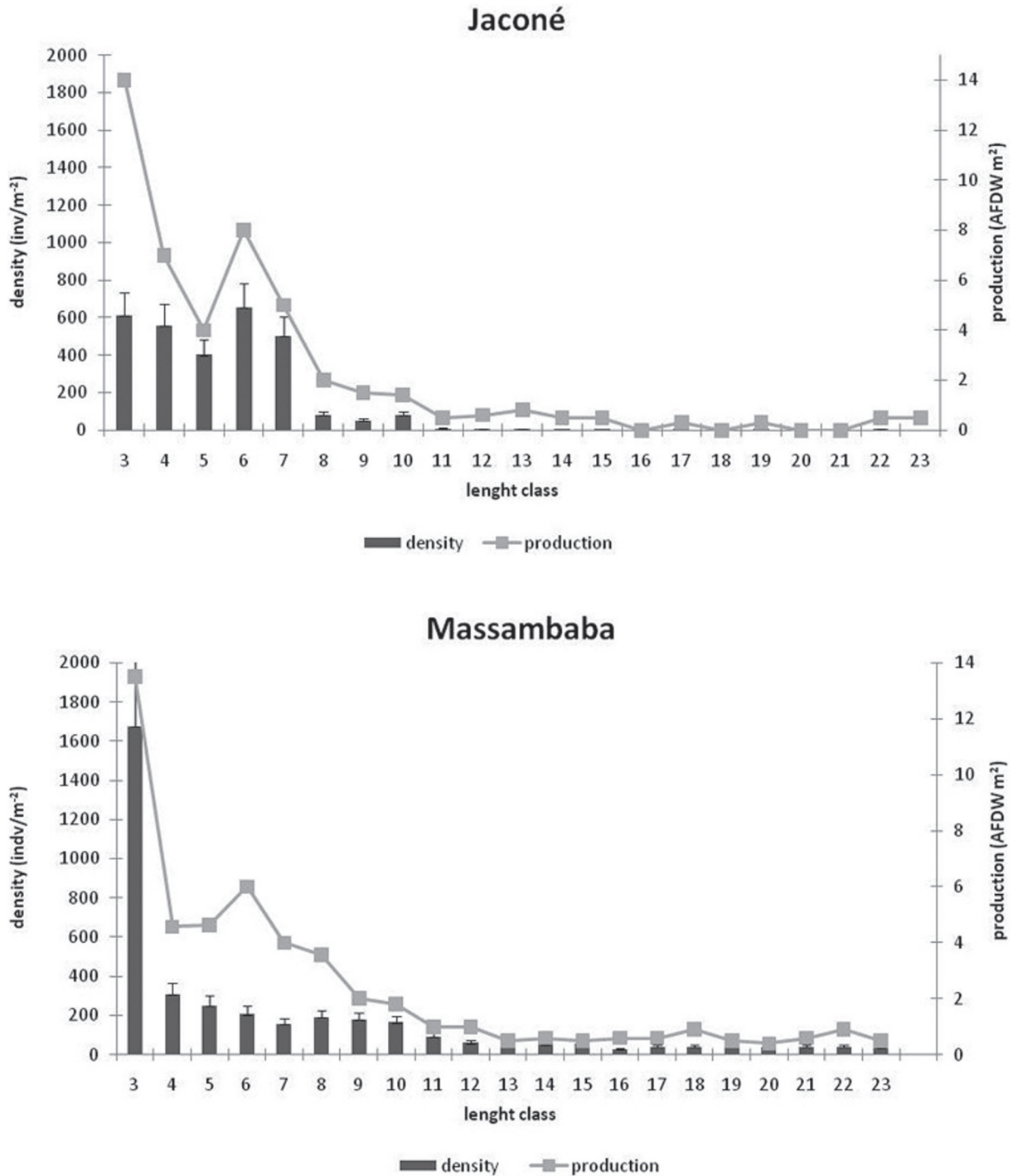


Figure 4. Density and production in relation to mean length, for *Emerita brasiliensis* at Jaconé and Massambaba beaches.

from the surf zone. Nevertheless, data on the abundance of larvae, recruitment, and circulation patterns of the surf zone are not obtained in the majority of studies, making it difficult to understand the population dynamics at a particular beach.

The availability of food has also been indicated as one of the factors determining population abundance (McLachlan, 1990; Dugan *et al.*, 1994). The material deposited above the drift line is more closely correlated with the species of the upper midlittoral and supralittoral (Colombini and Chelazzi, 2003; Dugan *et al.*, 2000), whereas the phytoplankton and phytobenthos production is more important for the species of the surf and swash zones. Dissipative beaches appear to be favorable for filter-feeders because of the longer water residence time and consequently higher phytoplankton primary production (Defeo and McLachlan, 2005; Defeo *et al.*, 2001). Nevertheless, Margem *et al.* (2003) found similar values of production of phytoplankton and phytobenthos for Grumari (reflective) and Marambaia (intermediate) beaches on the coast of Rio de Janeiro. Cardoso *et al.* (2003), studying the same beaches, found significant differences in the biomass and population structure of *E. brasiliensis*, and attributed these differences to distinct recruitment patterns, since they found no differences in primary production. Primary production assumes greater importance, however, when we compare beaches at different latitudes. Beaches of the same morphodynamic type located in areas of high primary pro-

duction show higher macrofaunal abundance and biomass compared to tropical areas with low primary production (Defeo and McLachlan, 2005).

Population parameters such as growth rate, fecundity, and mortality also showed no direct correlation with the morphodynamics. Defeo and Cardoso (2002) found a higher growth rate for males of *E. brasiliensis* on the reflective beach, whereas the females grew more rapidly on the dissipative beach. Conteras *et al.* (2003) found significant differences among beaches only for the growth of females. Many factors can influence population parameters, such as environmental variables (temperature, salinity), quality and quantity of food, and density-dependent factors (Defeo *et al.*, 2001; Cardoso *et al.*, 2003; Defeo and McLachlan, 2005). Certainly, these factors do not act in isolation: the type and intensity of the interactions must vary locally, influencing the population parameters. To identify and quantify all the factors that affect these parameters is no easy task, since it requires different methodologies.

Variations in secondary production are directly related to density, biomass, and the proportions of the different size classes (Highsmith and Coyle, 1991; Cardoso *et al.*, 2003; Veloso *et al.*, 2003a). Consequently, secondary production will vary spatially and temporally. Temporal variations have been related to the greater densities of juveniles, which decreased the values of biomass but increased the values of production (Defeo *et al.*, 2001; Cardoso *et al.*, 2003; Veloso *et al.*, 2003a).

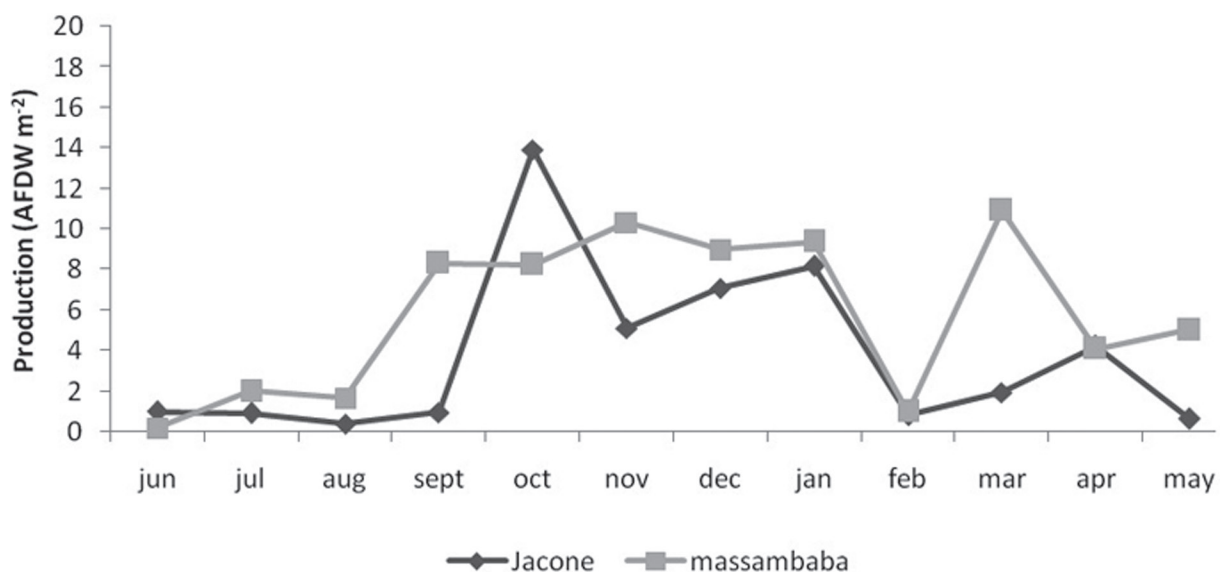


Figure 5. Monthly variations in secondary production (g AFDW m⁻²y⁻¹) of *Emerita brasiliensis* estimated at Jacone and Massambaba beaches.

Comparing the estimated values for production of *E. brasiliensis* among the beaches of the Rio de Janeiro coast (Table IV), it is apparent that the dissipative beaches show higher production than the reflective beaches.

The milder conditions of dissipative beaches, with a wide surf zone, less action of the waves on the beach face, longer water residence time in the swash zone and a more constant profile, appear to favor primary production in the surf zone, reproductive events, recruitment success, and survival of recruits, and principally the filter-feeders (Gianuca, 1985; Defeo *et al.*, 2001; Cardoso *et al.*, 2003; Veloso *et al.*, 2003a).

A good parameter to compare the productivity among different species and populations is the turnover rate (P/B) (Ansell *et al.*, 1978). This rate is essentially a record of the mean value of the rate of increase in biomass of all the individuals of a population (Benke, 1996). *Emerita brasiliensis* showed turnover rates between 1.15 and 2.82 for the beaches studied on the Rio de Janeiro coast. These rates were similar to those found by Gianuca (1985) for Rio Grande do Sul (33°S) (P/B = 7.3 yr⁻¹). The turnover rate is a parameter related to the size and age structure of a population, as well as other parameters such as predation and fishing that select certain size classes. Long-lived organisms with large numbers in the smaller size classes tend to show high P/B values (Zaika, 1973; Robertson, 1979; Thompson and Schaffner, 2001; Veloso *et al.*, 2003a). Thus, although the values for production on dissipative beaches are higher than for reflective beaches, the latter tend to show a similar or higher P/B, due to the lower biomass values.

In summary, the secondary production of a beach, although it is not directly related to the morphodynamic factors, is certainly indirectly influenced by the beach type. Factors such as primary production, input of dissolved and particulate organic matter, distribution of larvae, recruitment, and mortality rate are influenced by the hydrodynamic conditions of beaches. On a broad scale, in addition to local morphodynamic characteristics, latitudinal factors must be important, since they are related to the temperature and primary production of the coastal region.

The majority of studies (Defeo and Cardoso, 2002; Cardoso *et al.*, 2003; Caetano *et al.*, 2006) compare only two morphodynamic states and lack information on the local coastal circulation pat-

Table IV. Values of secondary production (g AFDW m⁻² yr⁻¹), mean biomass (g AFDW m⁻²), and turnover rates (yr⁻¹) for *Emerita brasiliensis* on Rio de Janeiro sandy beaches. P (production), B (biomass).

		P	B	P/B
Jaconé	reflective	96.8	41.74	2.31
Massambaba	intermediate	193.74	33.26	5.82
Grumari**	reflective	106.81	27.44	3.89
Restinga**	intermediate/dissipative	217.86	39	5.59
Prainha*	reflective	150.95	23.09	6.54

*data: Veloso *et al.*, 2003a

** unpublished data

terns. The effort expended in sampling and in the laboratory to estimate the secondary production certainly limits the number of beaches studied. Nevertheless, it is necessary to amass more information in order to determine patterns in production on exposed sandy beaches.

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