



Latitudinal patterns in abundance and life-history traits of the mole crab *Emerita brasiliensis* on South American sandy beaches

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ABSTRACT

Demographic and life-history attributes of the mole crab *Emerita brasiliensis* were analysed along 2700 km of the Atlantic coast of South America, including sandy beaches at the southernmost limit (Uruguay) and at the core of its geographical range (Brazil). Population features varied markedly within this range and exhibited systematic geographical patterns of variation. Abundance significantly increased from temperate to subtropical beaches, and the same held true for the asymptotic weight of males. Conversely, length at maturity and asymptotic weight of females increased from subtropical to temperate beaches, being inversely related to sea water temperature. Macroecological patterns in abundance and body weight showed the first large-scale evidence of scaling of population density to body size for a sandy beach population. Mortality rates (both sexes) followed a nonlinear increase from low-density temperate beaches to high-density subtropical beaches. The effect of habitat quality and availability could explain discontinuities in the species distribution within its range, and also differential responses in life-history attributes at a local scale. Asymmetries and converse latitudinal trends between sexes suggest that there is not a single general factor determining large-scale patterns in life-history traits of this species. Our results reinforce the view that density-dependent and environmental factors operating together regulate sandy beach populations. The need to develop macroecological studies in sandy beach ecology is highlighted, as knowledge acquired from local to large spatial scales throws light on population structure and regulation mechanisms.

Keywords

Crustacea, Anomura, Hippidae, macroecology, population dynamics, sandy beaches, South America.

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INTRODUCTION

Global patterns of species richness in sandy beaches have been tightly related to physical variables such as sediment type, wave height, tide range, and beach slope. Research effort has been largely directed at describing the relationship between species richness or abundance and beach morphodynamics, defined in terms of a subtle combination of grain size, wave period and height (Short, 1996). Worldwide data compilation and analysis showed an increase in community descriptors from reflective to dissipative microtidal beaches (McLachlan, 1990, 2001; Defeo *et al.*, 1992a; Jaramillo & McLachlan, 1993). Latitudinal variations at a community level have also been documented (Dexter, 1992; McLachlan *et al.*, 1993; Ricciardi & Bourget, 1999; Soares, 2003).

Surprisingly, few studies have sought to document life-history

variations exhibited by sandy beach populations across the geographical range of a species, as well as potential explanations of the underlying mechanisms. In particular, there are few studies that investigate how sandy beach species respond to geographical environmental variations in demographic terms, i.e. whether life-history characteristics undergo latitudinal changes. This is of great importance in sandy beach ecology, where major challenges are to explain fluctuations in abundance at large spatio-temporal scales, and to disentangle the relative importance of density-dependent and density-independent factors (Defeo *et al.*, 1997; Lima *et al.*, 2000; Schoeman & Richardson, 2002; Cardoso & Veloso, 2003). Such information has the potential to yield insights into the factors that determine the internal abundance structure of the geographical ranges of the species (Brewer & Gaston, 2003).

The mole crab *Emerita brasiliensis* (Crustacea: Anomura: Hippidae) is a short-lived intertidal species found in microtidal Atlantic sandy beaches of South America (Efford, 1976; Tam *et al.*, 1996), mainly from 34°36' S (Uruguay) to 23°00' S (Brazil). The species is also found in very low densities in northern Brazil (E. Guerreiro, pers. com.) and Venezuela (Penchaszadeh, 1983), co-occurring with the congeneric *Emerita portoricensis*. Recently, a macroscale analysis (Defeo & Cardoso, 2002) showed large-scale variations in some life-history traits of the mole crab, namely: (1) a shift from continuous to seasonal reproductive and recruitment events from subtropical to temperate beaches; (2) an increase of ovigerous females, fecundity at size, individual size and relative representation of females from subtropical to temperate beaches; and (3) a decrease in mortality rates towards temperate beaches. In this paper, we extend our previous study by documenting large-scale variations in other key population variables, notably abundance, size at maturity, body weight and seasonal growth rates of the mole crab in a 12°-latitude range between the southernmost extreme limit (35° S: Uruguay) and the core of its occurrence in Brazil (23° S). We also examine the effect of water temperature on life-history attributes. Large-scale patterns in abundance and body weight are employed to scale population density to body size.

METHODS

We collated information coming from sandy beaches along the Atlantic coast of South America, between Brazil (22°56' S) and Uruguay (34°36' S) (Table 1). The lack of information from Rio de Janeiro northwards precluded the integration of the full geographical distribution range. Following Defeo & Cardoso (2002), and unless stated otherwise, we only included studies with monthly samples taken for at least one full year. Our database used in the previous paper was enriched by unpublished or

recently published data (Table 1). Additional information on sampling design and beach characterization is provided by Defeo & Rueda (2002) and Defeo & Cardoso (2002).

Large-scale variations in abundance were assessed in terms of density (ind m⁻²) because most data extracted from the literature were expressed in this unit. Data were analysed for the entire population and by population component (female, male and megalops). When abundance was available as numbers per linear meter of beach or strip transect (*IST*, ind m⁻¹; Brazeiro & Defeo, 1996), conversion to density estimates was obtained by dividing *IST* values by the corresponding mole crab distribution width in each beach. Density and mean body wet weight for the whole population were used to scale body size to density. Ordinary least squares fitting of log body size on log population density included estimates from snapshot samplings in Brazilian beaches (Table 1).

The proportion of ovigerous females in each size class, recorded during the reproductive season, was available for the beaches Grumari, Restinga, Urca (Brazil) and Barra del Chuy (Uruguay). Data were used to model the maturity–size relationship through the logistic maturity model

$$O_L = \frac{\beta}{1 + e^{(\alpha_1 - \alpha_2 L)}} \quad (1)$$

where O_L is the fraction of ovigerous females in each size L and α_1 , α_2 and β are parameters. An additional end point with a 0.0 value was included at the lower end of the distribution (Trippel & Harvey, 1991). The nonlinear fitting procedure using the quasi-Newton algorithm included a penalty function by which β was constrained to values ≤ 1 . The mean size at maturity ($L_{50\%}$) for each beach was obtained by:

$$L_{50\%} = -\frac{\alpha_1}{\alpha_2} \quad (2)$$

Table 1 Sources of data used for assessing macroscale patterns in life-history traits of *E. brasiliensis*. Abbreviations for each beach are subsequently used in the figures. Asterisks denote beaches included only for modelling the relationships between density and temperature (*) and between density and body weight (**). Beaches denoted with ** were added subsequent to our previous research (Defeo & Cardoso, 2002). Beaches from 22° S to 24° S were categorized as 'subtropical', whereas the 'temperate' beaches analysed were located south to 30° S

Beach	Latitude South	Morphodynamics	Exposure	Data sources used in this paper
Jaconé (J)**	22°56'	Reflective	Exposed	Veloso <i>et al.</i> (2003)
Urca (U)	22°57'	Intermediate	Semi-exposed	Veloso & Cardoso (1999)
Itaipu (It)**	22°58'	Reflective	Semi-exposed	Veloso <i>et al.</i> (2003)
Itaipuaçu (Ip)**	22°58'	Reflective	Exposed	Veloso <i>et al.</i> (2003)
Massambaba (M)**	22°58'	Intermediate	Exposed	Veloso <i>et al.</i> (2003)
Prainha (P)	23°02'	Reflective	Exposed	Petracco (2000), Petracco <i>et al.</i> (2003)
Grumari (G)	23°03'	Reflective	Exposed	Cardoso <i>et al.</i> (2003)
Restinga da				
Marambaia (R)	23°03'	Intermediate	Exposed	Cardoso <i>et al.</i> (2003)
Barra da Tijuca (T)**	23°10'	Intermediate	Exposed	Veloso <i>et al.</i> (2003)
Cidreira (C)*	30°11'	Dissipative	Exposed	Silveira (1997)
Barra del Chuy (B)	33°45'	Dissipative	Exposed	Defeo <i>et al.</i> (1992a, 2001), Brazeiro & Defeo (1996), Defeo (unpublished)
Polonio (Po)*	34°23'	Intermediate	Exposed	Peluffo (1998)
Arachania (A)	34°36'	Reflective	Exposed	Defeo <i>et al.</i> (2001)

with α_1 and α_2 defined in Equation 1. The logistic maturity models fitted were compared through the nonlinear analysis of the residual sum of squares (ARSS: Chen *et al.*, 1992).

We analysed the annual population structure discriminated by sex in three subtropical (Grumari, Prainha and Restinga da Marambaia) and two temperate (Arachania and Barra del Chuy) beaches, for which information was fully available. We identified and separated normal components in length frequency distributions (LFDs: grouped by 1 mm CL) using the Bhattacharya method and a separation index > 2 as criterion to separate contiguous normal components (Gayaniilo & Pauly, 1997). Growth and natural mortality (M) estimates of *Emerita brasiliensis*, discriminated by sex, were available from Defeo & Cardoso (2002). We enlarged our database to include estimates of *Emerita brasiliensis* from Barra del Chuy (Uruguay) during 2-year consecutive sampling in 1988–89 (Defeo, unpublished). We also reassessed our database to fit the generalized von Bertalanffy growth function (VBGF: Gayaniilo & Pauly, 1997), which comprises the asymptotic length (L_∞), the curvature parameter (K), the amplitude of the seasonal growth oscillation (C), and the winter point (WP), expressed as a decimal fraction of the year where growth is slowest. Additional estimates of the t_0 parameter of the VBGF were used to convert relative to absolute ages. The L_∞ estimate for each beach and sex was converted to asymptotic weight W_∞ using the carapace length–ash-free dry weight (CL–AFDW) relationship $AFDW = a \cdot CL^b$, where a and b are parameters. Then, AFDW estimates were transformed to wet weight estimates following Ricciardi & Bourget (1998), in order to document W_∞ in this standard unit. Growth parameters K and W_∞ discriminated by sex were employed to calculate the growth index $P = \log_{10} K + \log_{10} W_\infty$, which provides a direct indication of growth performance (Longhurst & Pauly, 1987). Both variables were plotted in an ‘auximetric grid’, defined as a double logarithmic plot of the parameters W_∞ and K (Moreau, 1987), which graphically represents differences between beaches and sexes by means of their growth parameters. Between-sex differences in P index were analysed by ANOVA. M estimates discriminated by sex were used to depict concurrent large-scale variations with total mole crab density.

Latitudinal gradients in life-history characteristics were defined using mean annual surf-water temperature rather than latitude, in order to adjust for temporal variations when considering different sampling events at the same location. Temperature was measured during sampling time at the surf zone, and mean annual values were obtained for each locality as the average of individual estimates. The relationship between population variables and water temperature was modelled by linear or nonlinear fitting procedures, which are more appropriate than multiple comparison procedures through discrete categorization (e.g. ANOVAs) of continuous variables (e.g. temperature, latitude) to depict large-scale patterns (see e.g. Ricciardi & Bourget, 1999; Sagarin & Gaines, 2002a). When available, data for each beach coming from different years were included as separate entities to perform statistical analyses. To minimize the potential confounding effect derived from multiple sampling on a single beach, we first determined whether the within-beach variation

added comparable variation, or if it would make any difference if the analysis were done on a beach basis only. Thus, a lack-of-fit model was used to determine whether beach-to-beach variation differed from within-beach variation, fitting the regression and using ‘beaches’ as a class variable. Then we tested for differences between within-beach variation and between-beach variation. When the F test provided P values > 0.05 , this indicated no differences between both components of variation, thus allowing us to use all data for regression analysis. Conversely, when P values derived from F tests < 0.05 , we used the ‘beach to beach variation’, i.e. we averaged over the beaches and reran the regression. In all the cases analysed in this paper, both approaches (i.e. using raw and average data) gave almost identical results. For this reason, and in order to explicitly account for the within-beach variation, we used raw data for model fitting.

RESULTS

Density (D) of the mole crab *E. brasiliensis* significantly increased from temperate to subtropical beaches according to the potential function $D = a \cdot T^b$, where T is the mean annual temperature of the surf zone (Fig. 1). This model explained ($0.46 < r^2 < 0.67$; $P < 0.001$) large-scale patterns for the whole population and also for all population components (Table 2), providing the highest coefficient of determination r^2 when compared with other models. Analysis of covariance (ANCOVA), using population component as categorical variable, showed homogeneity of slopes ($F_{2,51} = 1.51$; $P = 0.23$) and significantly more abundance of megalops than males and females (main effect $F_{2,53} = 7.24$; $P < 0.002$: Table 2), as denoted by the multiple comparison performed by Tukey’s HSD test ($P < 0.01$).

Mole crab densities and body sizes ranged over more than two orders of magnitude. The lowest mean individual wet weight estimated for Urca (0.02 g; 22°57’ S) was 139 times lower than that at Barra da Tijuca (2.78 g; 23°10’ S). Densities ranged from 3275 ind m⁻² in Restinga to 7 ind m⁻² in Barra da Tijuca, and varied as a power function of body weight. An inverse relationship ($r = -0.72$; $P < 0.001$) between log population density and log body size was found, according to the model (Fig. 2):

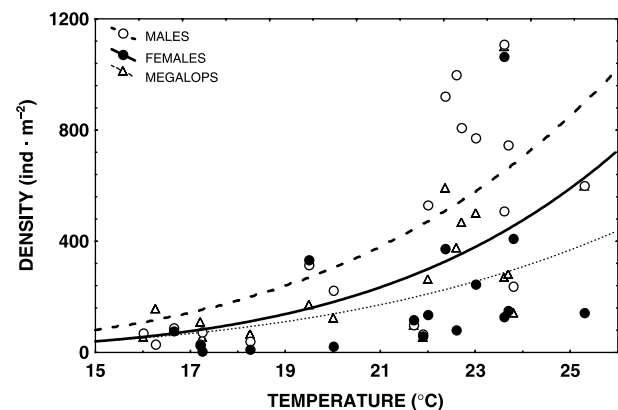


Figure 1 Relationship between surf water temperature and density (ind m⁻²) for females, males and megalops of *E. brasiliensis*.

Table 2 Parameter estimates and associated statistics of the linearized potential model $\ln D = \ln a + b \cdot \ln T$ that relates density of *E. brasiliensis* and mean annual temperature of the surf zone. Standard errors are in parenthesis. ANCOVA results (log-transformed data) are also shown, including tests of homogeneity of slopes and differences in density for a same temperature (main effect) between population components

	Total	Females	Males	Megalops
$\ln a$	11.40 (2.95)**	-7.95 (3.12)**	-15.66 (3.61)***	-18.80 (6.58)**
b	5.84 (0.97)***	4.36 (1.03)***	6.96 (1.19)***	7.65 (2.16)**
r^2	0.667***	0.498***	0.655***	0.456**

ANCOVA. Homogeneity of slopes: $F_{2,53} = 1.51$; $P = 0.232$. Main effect: $F_{2,53} = 7.24$; $P = 0.002$. ** $P < 0.01$; *** $P < 0.001$.

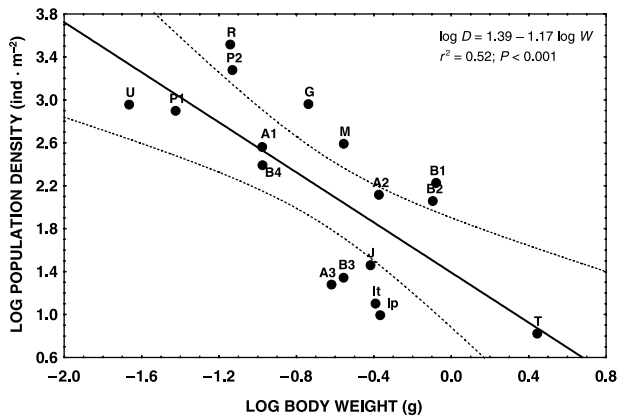


Figure 2 Linear regression of population density (D) on body size (W), both expressed as logarithms. Points represent mean annual density (whole population) and individual body weight estimates of *E. brasiliensis* for each beach. Abbreviations beside each point refer to the corresponding beaches as in Table 1. Associated numbers refer to different years analysed for the same beach.

$$\log D = 1.39 - 1.17 \cdot \log W \quad (3)$$

The progression from immaturity to maturation showed a successive increase in the proportion of mature females with size, and thus the maturity-size relationship was successfully explained by the sigmoid function (Eq. 1) for the four populations analysed (Table 3). Females were 100% mature in the oldest length classes, which was reflected in the asymptote $\beta \sim 1$ for all beaches. The individual size of ovigerous females consistently increased towards the temperate Barra del Chuy, both for the smallest and largest CL (Table 3). A smooth transition to maturity was observed at Urca, whereas the sigmoid function was clearly steeper at Barra del Chuy (Fig. 3), suggesting a more abrupt transition to maturity. Thus, the logistic maturity curve significantly differed between populations ($ARSS: F_{9,31} = 266.08$; $P < 0.01$), and the length at maturity $L_{50\%}$ was higher at Barra del Chuy than in the three subtropical Brazilian beaches (Fig. 3, Table 3). The local effect of beach exposure was noticeable: for roughly the same latitude, the semiexposed Urca had a smoother logistic curve than the exposed Grumari and Restinga da Marambaia, as well as the smallest ovigerous sizes and $L_{50\%}$ (Table 3).

The population structure presented latitudinal differences (Fig. 4). The LFDs of females (monthly samples pooled) revealed

Table 3 Parameters of the maturity function (Eq. 1) and size at maturity $L_{50\%}$ (Eq. 2) of *E. brasiliensis*, estimated from nonlinear regression for selected beaches. Smallest and largest (CL, in mm) ovigerous females are also presented. All fitted functions were highly significant ($P < 0.001$)

	Urca	Grumari	Restinga da Marambaia	Barra del Chuy
β	0.98	1.00	1.00	1.00
α_1	12.10	571.41	12.95	36.67
α_2	0.83	31.71	0.71	2.01
$L_{50\%}$ (mm)	14.66	18.02	18.16	18.22
r^2	0.99	0.94	0.99	0.99
Smallest CL	10	15	12	18
Largest CL	23	24	25	27

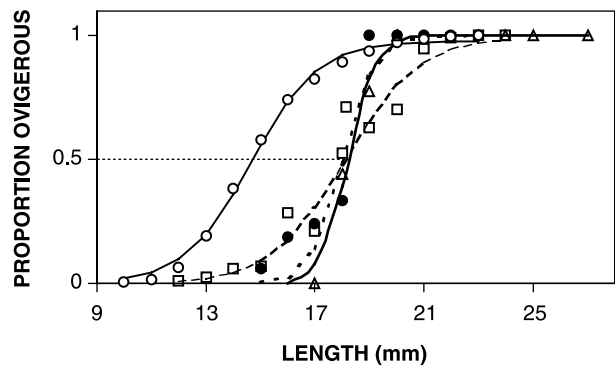


Figure 3 Maturity functions of *E. brasiliensis* for Urca (—○—, 22°57' S), Restinga da Marambaia (—□—, 23°03' S), Grumari (—●—, 23°03' S) and Barra del Chuy (—△—, 33°45' S), fitted by nonlinear regression. Statistical results are given in Table 3. The horizontal line represents a proportion of 0.5 of ovigerous females.

three modal classes for the five beaches analysed. However, the third mode was consistently higher in temperate beaches, notably at Barra del Chuy, suggesting higher growth rates and individual sizes than in subtropical ones (Table 4). The LFDs at the subtropical Prainha and Restinga da Marambaia presented a low relative representation of organisms > 8 mm CL and a virtual disappearance of sizes > 22 mm CL (Fig. 4). The strongest modal peaks at CL < 5 mm generated asymmetric and platikurtic LFDs, with two weak modes close to 12 mm CL and 20 mm CL

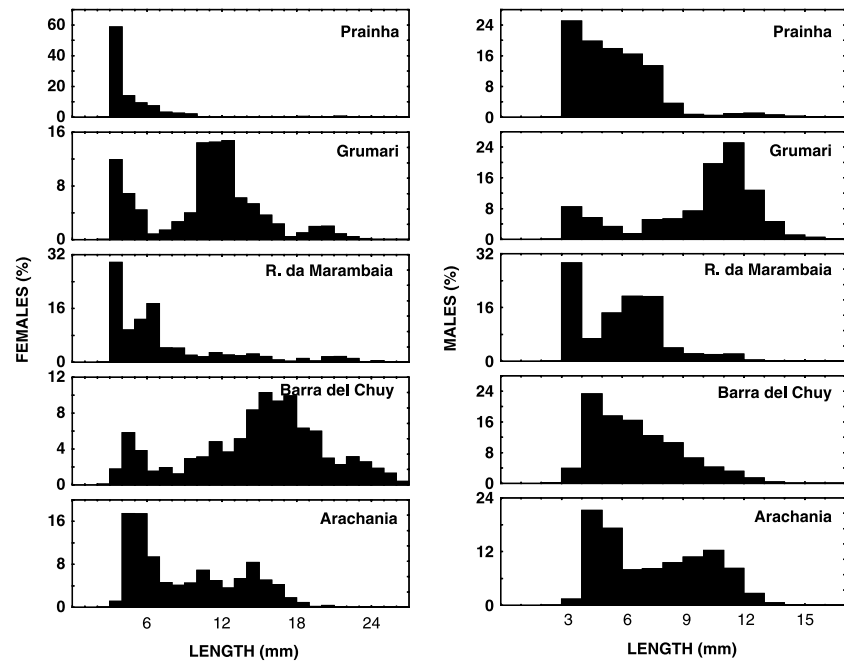


Figure 4 Length frequency distributions of *E. brasiliensis* discriminated by sex in five sandy beaches of the Atlantic coast of South America. Note the different scales in the X and Y axes.

Table 4 Annual modal values (\pm SD) derived from the LFD analysis of mole crabs discriminated by sex (mm CL) in three subtropical and two temperate sandy beaches of the Atlantic coast of South America

	Subtropical beaches			Temperate beaches	
	Prainha	Grumari	Restinga da Marambaia	Barra del Chuy	Arachania
<i>Females</i>					
1st mode	3.00 (0.84)	3.15 (1.42)	1.68 (2.69)	5.03 (0.87)	5.82 (0.96)
2nd mode	14.50 (0.50)	12.37 (1.92)	12.50 (2.18)	15.38 (3.40)	12.07 (2.60)
3rd mode	20.00 (1.58)	20.33 (1.42)	20.84 (0.96)	24.06 (1.25)	22.27 (2.32)
<i>Males</i>					
1st mode	3.98 (2.00)	2.79 (1.97)	6.32 (1.17)	4.92 (0.78)	5.33 (0.76)
2nd mode	12.43 (1.32)	11.37 (1.27)	10.43 (1.48)	10.23 (1.52)	10.22 (1.32)

(Table 4). Conversely, female crabs at temperate beaches exhibited three well-differentiated modes, the third one at sizes larger than 22 mm CL (Table 4). LFDs of male mole crabs showed the reverse trend, i.e. they were larger in subtropical than in temperate beaches (Fig. 4). In Grumari, the bimodal structure was noticeable, especially the mode (\pm SD) at 11.37 ± 1.27 mm CL, whereas even though males at temperate beaches showed the same bimodal structure, the strongest peak was detected close to 5 mm CL and the second, weak one, at sizes smaller than those estimated for subtropical beaches (Table 4).

Growth curves of *E. brasiliensis* from different latitudes were quite distinct. Mole crabs from the temperate beaches Arachania and Barra del Chuy showed intense intra-annual growth oscillations ($C = 1$), stopping growth in winter ($WP = 0.60$). Conversely, the subtropical beaches presented continuous (e.g. $C = 0$ in Urca) or quasi-continuous (e.g. $C = 0.3$ in Prainha) growth throughout the year (Fig. 5), and a period of minimal growth between late autumn and early spring ($0.30 < WP < 0.85$). The growth parameters K and W_{∞} showed clear geographical

patterns. In females, K was positively ($r = 0.85$; $P < 0.0002$) and W_{∞} inversely correlated ($r = -0.75$; $P < 0.001$) with water temperature. More than 5 g difference in W_{∞} was found between the latitudinal extremes (6.7 g at Barra del Chuy and 1.3 g at Urca). Conversely, males showed a positive correlation between W_{∞} and water temperature ($r = 0.54$; $P < 0.04$; Fig. 6a), whereas K was not correlated with the latter.

The auximetric grid clearly separated between-sex trends in growth performance, generating two distinct nonoverlapping clusters of W_{∞} - K combinations (Fig. 6b). The P index was significantly higher for females than males (ANOVA $F_{1,30} = 155.92$; $P < 0.001$). Regression analysis showed that geographical trends were not statistically significant; however, a clear local effect of beach exposure was depicted (Fig. 6b): both females and males at the three exposed subtropical beaches Prainha, Restinga da Marambaia and Grumari had higher P index than in the semi-exposed Urca. The effect of intra-annual growth variability was observed for Urca: male summer cohorts (U2, U5 and U9) had higher K -values than the other ones. The temperate dissipative

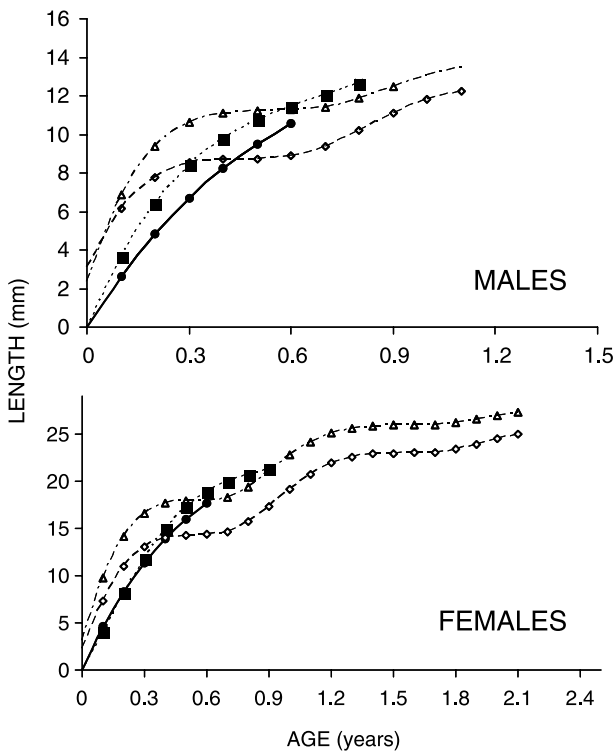


Figure 5 Seasonal growth curves of *E. brasiliensis* fitted for both sexes by the nonlinear generalized VBGF for Urca (●) and Prainha (■) (subtropical beaches) and Arachania (△) and Barra del Chuy (◇) (temperate beaches).

Barra del Chuy showed the highest growth rates for females and the lowest ones in males (Fig. 6b).

Natural mortality (M) estimates were related with large-scale variations in density. For both sexes, M increased asymptotically with total density of mole crabs (D) according to the nonlinear model (Fig. 7):

$$M = M_{\infty}(1 - e^{-bD}) \quad (4)$$

where M_{∞} is the asymptotic mortality and b measures how fast the species approaches M_{∞} . The model ($r^2 = 0.29$ and 0.31 for females and males, respectively) and parameters M_{∞} and b were statistically significant ($P < 0.01$). M_{∞} was 10.81 yr^{-1} for females and 9.53 yr^{-1} for males, resulting from extremely high mortalities in subtropical beaches that were on average 2.55 (males) and 2.79 (females) times higher than in temperate ones (Fig. 7). Parameter b was 0.0059 for both sexes, indicating an identical curvature of the function. This relationship suggests an upper ceiling in M at subtropical beaches despite different exposure regimes, even though M tended to be higher in the semi-exposed Urca than in the exposed Prainha, Restinga da Marambaia and Grumari (Fig. 7).

DISCUSSION

Most life history and demographic traits of *Emerita brasiliensis* markedly varied throughout 2700 km of its distribution range.

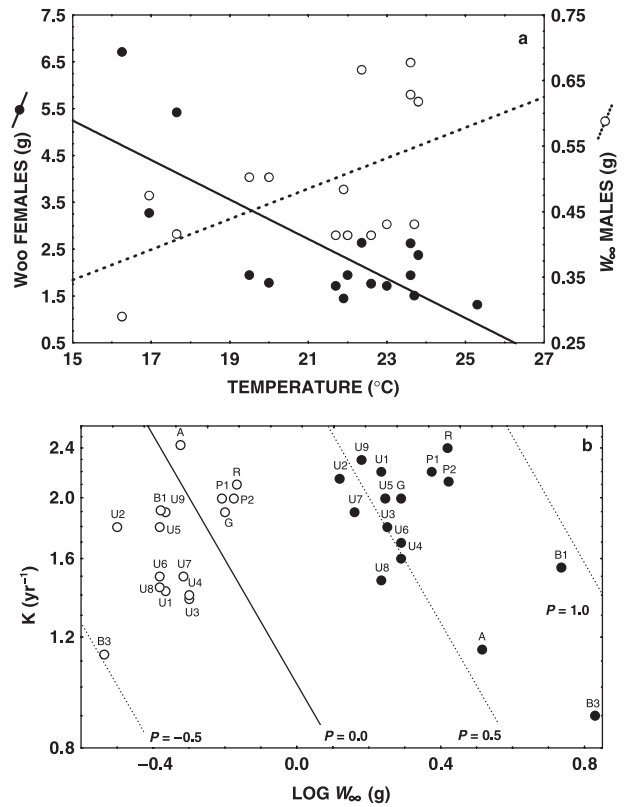


Figure 6 (a) Linear regression between water temperature of the surf zone and asymptotic weight W_{∞} of *E. brasiliensis*; and (b) auximetric grid representing latitudinal variations in the log-log relationship between W_{∞} and the curvature parameter K of the VBGF. (●) females (○) males. Dashed lines connecting P values indicate the same growth performance. Abbreviations beside each point refer to the corresponding beaches as in Table 1. Associated numbers refer to different cohorts analysed for the same beach.

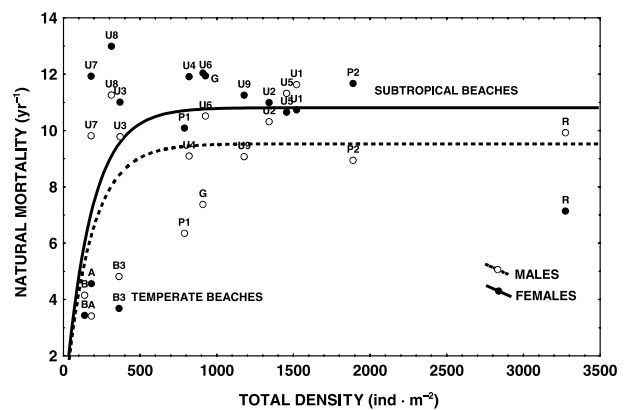


Figure 7 Asymptotic model (Eq. 4) relating total density of *E. brasiliensis* and natural mortality for females (●) and males (○). Abbreviations beside each point refer to the corresponding beaches as in Table 1. Associated numbers refer to different cohorts analysed for the same beach.

Clear macroecological patterns derived from beach-specific intensive studies (at least one year of monthly sampling) provided support to well-known latitudinal trends and ecogeographical rules that predict that animals at high latitudes have larger body sizes and life spans, and lower mortality rates than at low latitudes (Mayr, 1956; Atkinson & Sibly, 1997). However, these patterns remained valid mainly for female mole crabs, as discussed below.

Density of *Emerita brasiliensis* did not vary randomly across its main geographical range, but exponentially increased from temperate to subtropical beaches. The very low densities documented in northern Brazil (Cardoso, unpublished) and Venezuela (Penchaszadeh, 1983) suggests that high-density beaches of mole crabs clustered together in subtropical latitudes could be close to the central region of the range. It has been suggested that abundance does not necessarily vary smoothly from the central region to range boundaries (Sagarin & Gaines, 2002a), because of spatial variations in habitat quality (Caddy, 1989; Maurer & Taper, 2002). The limited evidence available mentioned above suggests that mole crab abundance declines sharply from subtropical to tropical beaches, thus determining a skewed, large-scale unimodal distribution pattern within the range. Our northern limit of coverage was close to Cabo Frio (23° S), which separates the Warm-temperate Biogeographical Province from the Tropical South-western Atlantic Province (Sullivan & Bustamante, 1999). Drastic changes in coastal physiognomy also occur northwards: beaches are attenuated and interspersed with mangrove stands, estuaries and extensive coral reef formations. Exposed beaches, which constitute the suitable habitat for *E. brasiliensis*, almost disappear between Cabo Frio and Venezuela, where sheltered, pocket beaches, prevail (Defeo & de Alava, 2004). These beaches are unsuitable for *E. brasiliensis*. We hypothesize that macroscale variations in coastal physiognomy ultimately interact with large-scale environmental variables (e.g. temperature) to determine asymmetries in species distribution. However, the severely under-sampled northern range precluded the evaluation of the 'abundant centre' hypothesis (*sensu* Sagarin & Gaines, 2002b), suggesting that more information is needed to depict the species distribution pattern within the range, as well as the trends in life-history patterns in that portion of the range.

The highest densities documented for subtropical reflective beaches go against worldwide trends that show highest macrofauna abundance invariably occurring in dissipative microtidal beaches (McLachlan, 2001; but see Gómez & Defeo, 1999; Defeo & Martínez, 2003). Moreover, sandy beaches located in the south (Barra del Chuy and Arachania) had similar density and mortality figures, despite the different morphodynamics (see also Defeo *et al.*, 2001). In turn, density was dramatically lower (orders of magnitude) than in subtropical reflective beaches. This should not have to be expected if the morphodynamic criterion should be of relevance in explaining large-scale variations in abundance. Moreover, the negative relationship found between population density and the indirect measure of available energy, elsewhere described by dissipateness of beaches (Brown & McLachlan, 1990; McLachlan, 1990), is inconsistent with the idea of a simple limitation by energy. Thus, morphodynamics could not be

invoked to explain the large scale trends in abundance documented here, and could be ascribed to other factors operating at larger spatial scales (e.g. temperature). The effect of morphodynamics should only be envisaged on a local scale (i.e. for a same latitude), as demonstrated by Defeo & Cardoso (2002), Defeo & Martínez (2003) and Cardoso *et al.* (2003). Between-beach variability on a local scale could reflect species responses to concurrent variations in ecosystem quality. In this setting, higher growth and size-at-maturity and lower mortality rates in dissipative beaches have been attributed to the usually high food availability documented in temperate dissipative beaches.

We provide the first large-scale evidence of an inverse relationship between density and body size for a sandy beach population. Body size explained a significant amount of variation in population density at a large spatial scale. The only previous study that addressed the question of scaling body size to density in sandy beaches found a positive relationship between both variables (Dugan *et al.*, 1995). Our results go against this finding, but are in agreement with those reported for rocky intertidal (Marquet *et al.*, 1990, 1995) and terrestrial (e.g. Currie & Fritz, 1993; Blackburn & Gaston, 2001; Marquet, 2002) communities. Differences between results may be related to the temporal and spatial scales addressed, as well as the hierarchical levels employed for hypothesis testing: Dugan *et al.* (1995) performed a snapshot sampling of the macrofauna community of a single beach, whereas we focused on a single species at a macroscale, with most data coming from intensive annual studies. The mole crab is dominant in terms of biomass in sandy beach communities, and thus fluctuations in scaling could be attributed to intraspecific rather than to interspecific effects.

Marked large-scale differences in population structure and dynamics were detected between sexes. Females from temperate beaches had three age groups, larger sizes and asymptotic parameters (W_{∞}), became sexually mature at larger sizes and had lower K values than in subtropical beaches. Conversely, males showed shorter life expectancy (two main age groups) and higher individual sizes and asymptotic growth parameters towards subtropical beaches. This trend goes against the well-known inverse relationship between individual size and temperature reported for marine and terrestrial species (Kinne, 1970; Atkinson, 1994; Atkinson & Sibly, 1997). A range of mechanisms could explain between-sex differences in large-scale patterns, notably density-dependence. Populations peripherally located at the south of the range could be subject to more intense intraspecific competition (Maurer & Taper, 2002). In this setting, Defeo & Cardoso (2002) showed a relative dominance of large females at temperate beaches situated at the edge of the range, concurrently with smaller male sizes. For the same beaches, Lercari & Defeo (1999) showed a significant inverse relationship between male growth rates and female abundance, defining smaller males as subordinate intraspecific competitors for food (see also Defeo *et al.*, 2001). Conversely, high-density, centrally located subtropical populations, in theory less constrained by intraspecific competition (Maurer & Taper, 2002), had higher sizes, abundance and relative representation of males than in temperate beaches (Defeo & Cardoso, 2002). Asymmetric intraspecific competition is now considered a

critical regulating process in sandy beach populations (Defeo & de Alava, 1995; Defeo, 1996, 1998; Lima *et al.*, 2000).

Mole crabs showed maximum intra-annual growth oscillation in temperate beaches ($C = 1$), shifting to almost continuous growth in subtropical ones ($C < 0.5$). The marked growth oscillation in temperate populations, already observed for several beach species in the South-western Atlantic Ocean, has been ascribed to seasonal variations in temperature (de Alava & Defeo, 1991; Defeo *et al.*, 1992b; Gómez & Defeo, 1999; Defeo & Martínez, 2003). The period where growth is slowest (WP) did not show significant large-scale trends, with minimum growth consistently detected close to the winter season, concurrently with lowest temperatures. The effect of temperature was also inferred from large-scale variations in mortality. High mortality rates and low life span in high-density subtropical beaches could be explained by a combination of rising metabolism at increasing temperatures and insufficient food availability. The continuous reproductive season all year round in subtropical populations (Defeo & Cardoso, 2002) could compensate for the higher mortality.

In summary, we showed that *E. brasiliensis* is subject to marked variation in its life history across latitudinal gradients, adapting through plasticity to the local environment. Patterns in female mole crabs adhered to predictions of ecogeographical rules and could be explained by processes occurring at macro (i.e. latitudinal variations of temperature) and local (i.e. major efficiency of food conversion in dissipative beaches) spatial scales. Conversely, the increasing sizes, relative representation and growth rates of males from temperate to subtropical beaches suggest that large-scale patterns of males are affected by other factors besides limitations on growth at increasing temperatures. The patterns found at a macroscale were critical for hypothesizing about the relative importance of factors regulating local populations and reinforce the view that sandy beach populations are controlled by biotic and abiotic factors operating together.

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