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Variation in the body growth parameters of the ghost crab *Ocypode quadrata* from morphodynamically distinct sandy beaches*

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ABSTRACT

Investigations of patterns of distribution of sandy beach macrofauna show that dissipative beaches tend to concentrate higher richness and biomass at the intertidal zone, as well as better fitness and larger sizes of a species, than reflective beaches. For supralittoral crustaceans, these trends are inverted, as predicted by the habitat safety hypothesis (HSH). For ghost-crabs, however, higher population abundance has been observed on dissipative beaches, but their life-history traits and the response to different beach morphologies were not well defined. Here, variation in crab size and growth was evaluated over a one year period using indirect measures from three low-impact beaches on the northern coast of São Paulo State, southeastern Brazil. These beaches represent the three basic types of morphodynamics: dissipative (Costa beach), intermediate (Felix beach) and reflective (Puruba beach). At each site, five 2m wide transects were randomly selected each month, and assessed across the crabs' entire area of occurrence. The fit of the von Bertalanffy body growth model was compared among sites. For all three beaches, a main mode due to the settlement of juveniles (mm) was identified in August and September. In the following summer, according to growth estimates, the settlement group would be approximately the same size as the main mode (mm) that was recorded during the previous summer. Specifically, the growth parameters estimated were: Costa (dissipative) $L\infty$= 46.36mm, K= 0.90year^{-1} and t0= -0.19; Félix (intermediate) $L\infty$= 57.95mm, K= 0.87year^{-1} and

RESUMO

Os padrões de distribuição da macrofauna de praias arenosas têm sido amplamente investigados, mostrando que o entre-marés de praias dissipativas tende a concentrar maiores valores de riqueza e biomassa, bem como indivíduos de maior sucesso reprodutivo e tamanho, do que praias reflexivas. Para crustáceos do supralitoral essa tendência é em geral oposta. Para o guaruçá, *Ocypode quadrata*, frequentemente o grupo mais conspícuo desses ambientes, são raras as investigações de dinâmica populacional e respostas a diferentes morfologias praiais. Aqui, a variação de tamanho e o crescimento corpóreo foram avaliados ao longo de um ano através do método indireto em três praias com reduzido impacto antrópico no Litoral Norte de São Paulo. Estas foram escolhidas de froma a representarem três tipos básicos de morfodinâmica: dissipativa (Costa), intermediária (Félix) e reflectiva (Puruba). Em cada praia, cinco transectos de 2m de largura foram aleatorizados mensalmente, e avaliados da primeira à última ocorrência de tocas. O ajuste do modelo de crescimento de von Bertalanffy foi comparada entre as áreas. Para as três praias uma moda principal, devido à entrada de juvenis (mm), foi identificada em agosto/setembro. Esses indivíduos atingiram no verão seguinte um tamanho correspondente à moda principal do verão anterior, e dentro daquela que foi dominante no período como um todo. Especificamente, os parâmetros de crescimento foram: Costa (dissipativa) $L\infty$ = 46,36 milímetros, K = 0,90 ano^{-1} e t0 = -0,19; Félix (intermediária) $L\infty$ = 57,95 milímetros, K = 0,87

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t0= -0.12; Puruba (reflective) L∞= 53.01mm, K= 1.11year^{-1} and t0= -0.07. The body growth adjustments were similar between Puruba and Felix, but distinct from Costa. Growth performance indexes ranged from 3.29 (Costa) to 3.46 (Félix) and 3.49 (Puruba), indicating both the homogeneity of this parameter among distinct beaches and close agreement between the intermediate and reflective beaches. This study suggests that variations in the development of ghost crabs concur with those observed for other supralittoral, crustaceans and the habitat safety hypothesis, with higher individual fitness for reflective beaches.

Descriptors: *Ocypode*, Sandy Beach, Morphodynamic, Body Growth, Longevity.

ano^{-1} e t0 = -0,12; Puruba (reflexiva) L∞ = 53,01 milímetros, K = 1,11 ano^{-1} e t0 = -0,07. Esses ajustes foram iguais estatisticamente entre Puruba e Felix, sendo ambos distintos da praia do Costa. Os índices de crescimento, phi-prima, variaram de 3,29 (Costa) a 3,49 (Puruba), enquanto na praia Félix esse valor foi 3,46, indicando homogeneidade deste parâmetro entre as praias, mas reforçando a maior semelhança a praia intermediária e reflexiva.

Descritores: *Ocypode*, Praia Arenosa, Morfodinâmica, Crescimento Corpóreo, Longevidade.

INTRODUCTION

Beach ecology has been researched with increasing frequency over the last few decades. Some theories concerning the influence of environmental factors on community and population dynamics are recurrently supported around the globe (MCLACHLAN et al. 1993; DEFEO; MCLACHLAN, 2011). Intertidal species richness, diversity and biomass have been shown to increase under more dissipative conditions, corresponding to a paradigm of sandy beach ecology known as the habitat harshness hypothesis (DEFEO; MARTÍNEZ, 2003). The steeper the slope, the coarser the grains, and therefore the lower the soil water content (SHORT, 1996). Therefore, dissipative conditions, particularly for exposed sandy beaches, allow greater accumulation of organic matter, which in turn favors higher abundance and size of individuals than for dissipative sandy beaches (CELENTANO; DEFEO, 2006; DEFEO; DELGADO, 2007). In contrast, for crustaceans species, especially for supralittoral species, an inverse of that trend has been demonstrated regarding population descriptors, which is called the habitat safety hypothesis (HSH; DEFEO; MARTÍNEZ, 2003; DEFEO; GÓMEZ, 2005). For these species, steeper slopes, narrower swash zones and even higher soil permeability are considered more favorable conditions.

Investigations of ghost crab populations, which occupy the upper intertidal and backshore zones of sandy beaches, have important peculiarities when compared to other macrofauna species; an outstanding one is that taking representative, random samples of the population directly can be very difficult. Capturing them outside of their burrows cannot be considered a precise random sample of the population, and to ensure their presence in the burrows may be very time consuming (POMBO; TURRA, 2013). Hence, most studies rely on burrow features, which are assumed to correspond in size and number to population features (FISHER; TEVESZ, 1979; ALBERTO; FONTOURA, 1999; BARROS, 2001; VALERO-PACHECO et al., 2007). The relationship between the size of the burrows and their occupant crabs have been supported, but abundance relationships are not similarly well defined, and comparisons of abundance of burrows over distinct areas might be particularly tricky (ALBERTO; FONTOURA, 1999; TURRA et al. 2005; POMBO; TURRA, 2013). Thus, although using burrows to assess ghost crab populations makes field studies more feasible, there are possible constraints that must be taken into account.

Ocypode quadrata is the only ghost crab species occurring along the eastern coast of the Americas. It is well documented that these populations are distributed over the entire upper extension of both oceanic and estuarine sandy beaches, from the upper intertidal zone up to the dunes and vegetation; a gradient of sizes of the individuals occurs, increasing towards the upper level of the beaches (ALBERTO; FONTOURA, 1999; TURRA et al., 2005; ROSA; BORZONE, 2008; BRANCO et al., 2010). Reproductive activity has been shown to exhibit peaks during warmer periods, but recruitment was observed throughout the year in Southeastern Brazil (HALEY, 1972; NEGREIROS-FRANSOZO et al., 2002). Body growth parameters are important descriptors in population ecology, specifically for species of management concern (SPARRE; VENEMA, 1998). Modal progression analysis is a powerful tool for this purpose once the assumption of development of a cohort is incorporated. This technique has already been applied to other crustacean groups (GOMEZ; DEFEO, 1999; TURRA; LEITE 2000; DEFEO; MARTÍNEZ, 2003) and was considered a feasible tool to assess *O. quadrata* body growth from burrows (OLIVEIRA et al., 2016).

Here, we defined *O. quadrata* life-history traits by assessing body growth parameters through the von Bertalanffy model parameterization on three distinct beaches. The selected beaches were low-use to exclude the influence of anthropogenic impacts, because environmental perturbations may alter population structure and even certain life-history parameters (BENTON; GRANT, 1999). Beach type, as well as human disturbance, may influence population life-history. Understanding how population parameters behave naturally among beaches with distinct morphodynamics is a central issue in sandy beach ecology. A relation between population features and beach dynamics is not supported for ghost crabs, unlike many other sandy beach species (DEFEO; MCLACHLAN, 2011). Whether differences in the fitness of individuals are apparent for morphodynamically distinct areas is crucial given that these species have been proposed as an indicator of environmental quality (BARROS, 2001; BLANKENSTEYN, 2006; LUCREZI et al., 2009). This study examined the influence of some physical factors on the ecological parameters of this potential indicator species.

MATERIAL AND METHODS

Study area and sampling

Three beaches were selected on the northern coast of São Paulo State, southeastern Brazil, in an attempt to represent the three basic types of morphodynamics: dissipative (Costa beach), intermediate (Felix beach) and reflective (Puruba beach). These designations were based on previous characterizations. These beaches were selected to avoid additional sources of variation, such as beach use.

From December 2011 to November 2012, each of these areas was sampled monthly, during daylight hours, to count and measure *O. quadrata* burrows. A homogeneous area, 200 m long, was defined on each beach; during every sampling procedure, five 2-m-wide transects were randomly laid out perpendicular to the shoreline.

In every 2 m of the transect (in 4 m² quadrats), burrows were assessed from the low intertidal zone to the vegetated area, until the uppermost burrow was recorded. A brief characterization of each area was performed. For that, seasonal samples of the midlittoral sediment were taken for granulometric assessments in three out of five transects. Grain size of the three basic beach strata (supra-, mid- and sublittoral) tend to be highly correlated, but the midlittoral is the zone that best represents a combination of beach dynamics and *O. quadrata* living area, so was chosen for granulometric assessments.

Following the methodology proposed by POMBO and TURRA (2013), all burrows deeper than 10 cm were considered regardless of direct signs of occupation. These burrows were identified using a steel semi-flexible cable; when necessary, burrows were excavated for verification. Closely separated burrows were checked for connectivity to ensure that these were not concurrent openings to a single burrow; if so, the shorter was discarded. Size measurements considered the smaller diameter of the bottom of the funnel-shaped portion of the burrow openings.

All measurement activities and collections complied with the permit from the appropriate federal environmental agency (Ministério do Meio Ambiente (MMA) – Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) No. 31629-1; in English: Ministry of the Environment – Chico Mendes Biodiversity Conservation Institute).

Data analysis

A general assessment of spatio-temporal size distribution was performed. The mean general size (independent from transect) was compared among areas and months using a factorial ANOVA, followed by the Tukey post-hoc test, once the required assumptions were properly met.

Transect data were gathered for each month and beach and then apportioned in 5 mm size classes. For each of these sets of samples, frequency distributions were decomposed using the NORMSEP method using FiSAT software (FAO, Rome) by identifying the main modes. Mean values, standard deviations and number of individuals were computed over curves within a month, with a restriction of not allowing superposition indexes under 2.00.

A settlement age for lowest size class was estimated based on DIAZ and COSTLOW (1972) and HALEY (1972) and used to build the age-size key. The values from this key were then applied to the von Bertalanffy body growth model, to estimate the asymptotic length ($L\infty$), growth constant (K) and age of length 0 (t0). For each study area the convergence of the parameters to the von Bertalanffy body growth model was performed using the nls function using the R software to determine weighted least squares estimates of the parameters of non-linear models (R CORE TEAM, 2014).

An analysis of the residual sum of squares (ARSS) was performed to assess if the three curves were coincident. In cases where this hypothesis was rejected, likelihood ratio pair wise tests were performed to assess what details differed (KIMURA, 1980; CHEN et al., 1992) using the vblrt function available in the fishmethods package from R (NELSON, 2014). Growth performances over areas were also compared based on a constant calculated from the values of L∞ and K (phi-prime performance index). This is calculated as logK + 2logL∞ and, because K and L∞ tend to be inversely proportional, this index remains equal for distinct values of K and L∞, representing a similar growth performance (MUNRO; PAULY, 1983).

RESULTS

At Costa beach, 904 burrows were identified and measured, from which 172 (19.02%) were excluded because of insufficient depth or double openings. For Felix beach, out of 836 burrows, 151 were excluded (18.06%); for Puruba beach, out of 606 burrows, 130 were not used (21.45%). In total, 1983 valid burrows were measured throughout the study period. The beach granulometry results were in agreement with previous characterizations, in which Costa is considered a dissipative beach (1.75 ± 0.57 phi), Félix an intermediate (1.37 ± 0.31 phi) and Puruba a reflective beach (1.11 ± 0.21 phi).

General patterns of size distribution were similar among beaches, tending to be unimodal with mode values of approximately 20 mm, slightly skewed towards larger sizes (Figure 1). It is possible, however, to observe a slight deviation from the main mode to the right towards reflective conditions, a pattern emphasized by the ANOVA of size among beaches (F=9.35, d.f.=2, p<0.01). The mean value of burrow diameter observed for Costa beach (21.01mm ± 7.75 SD) was significantly lower than either Félix (22.40mm ± 8.02 SD) or Puruba (22.84mm ± 7.78 SD) beaches, which did not differ significantly between each other.

Burrow size varied by month and this variation depended on the beach (beach*month F=3.82, d.f.=22, p<0.01), with means varying from 17.42 to 26.5 mm. The lowest means were observed in February, June and November for Costa beach and September for both Felix and Puruba, while the highest mean values occurred in February for both Félix and Puruba as well as April for Puruba. The results of the Tukey test for temporal differences were provided for each beach separately to facilitate the identification of common patterns over areas (Figure 2). From the histograms, we note that the months with the smallest size classes, which were common among beaches, were August and September (Figure 3). For Puruba, this condition lasted until October.

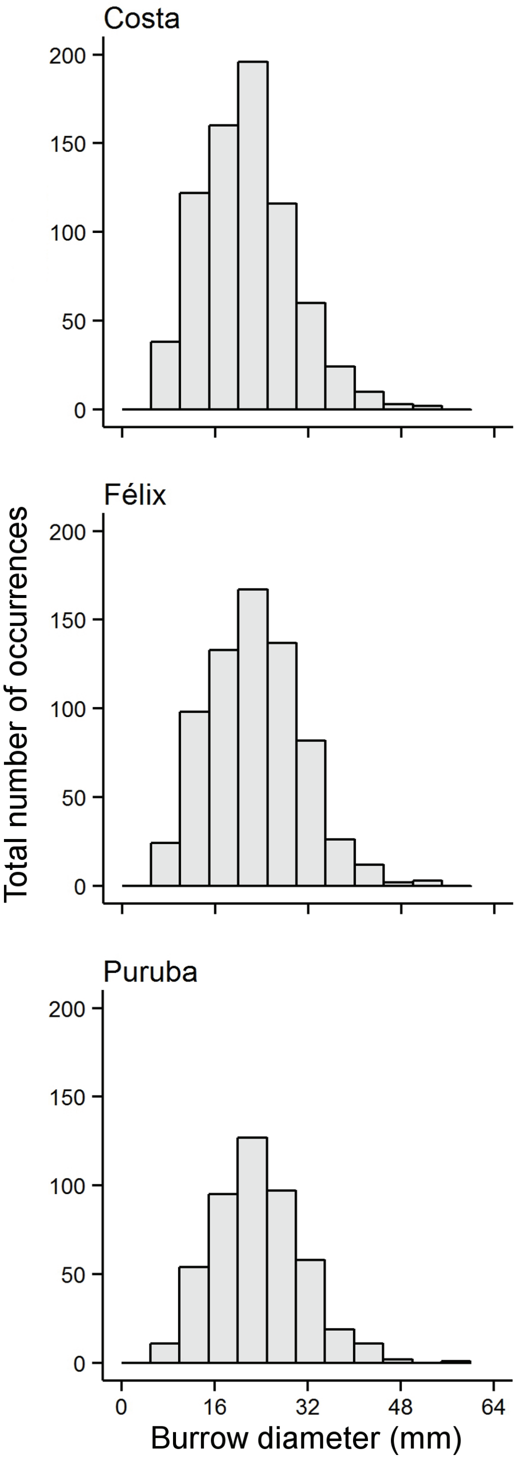

Figure 1. Diameter (mm) for class distribution of *Ocypode quadrata* burrows, sampled in three beaches with different morphodynamics (Costa-dissipative, Félix-intermediate and Puruba-reflective) from December/2011 to November/2012.

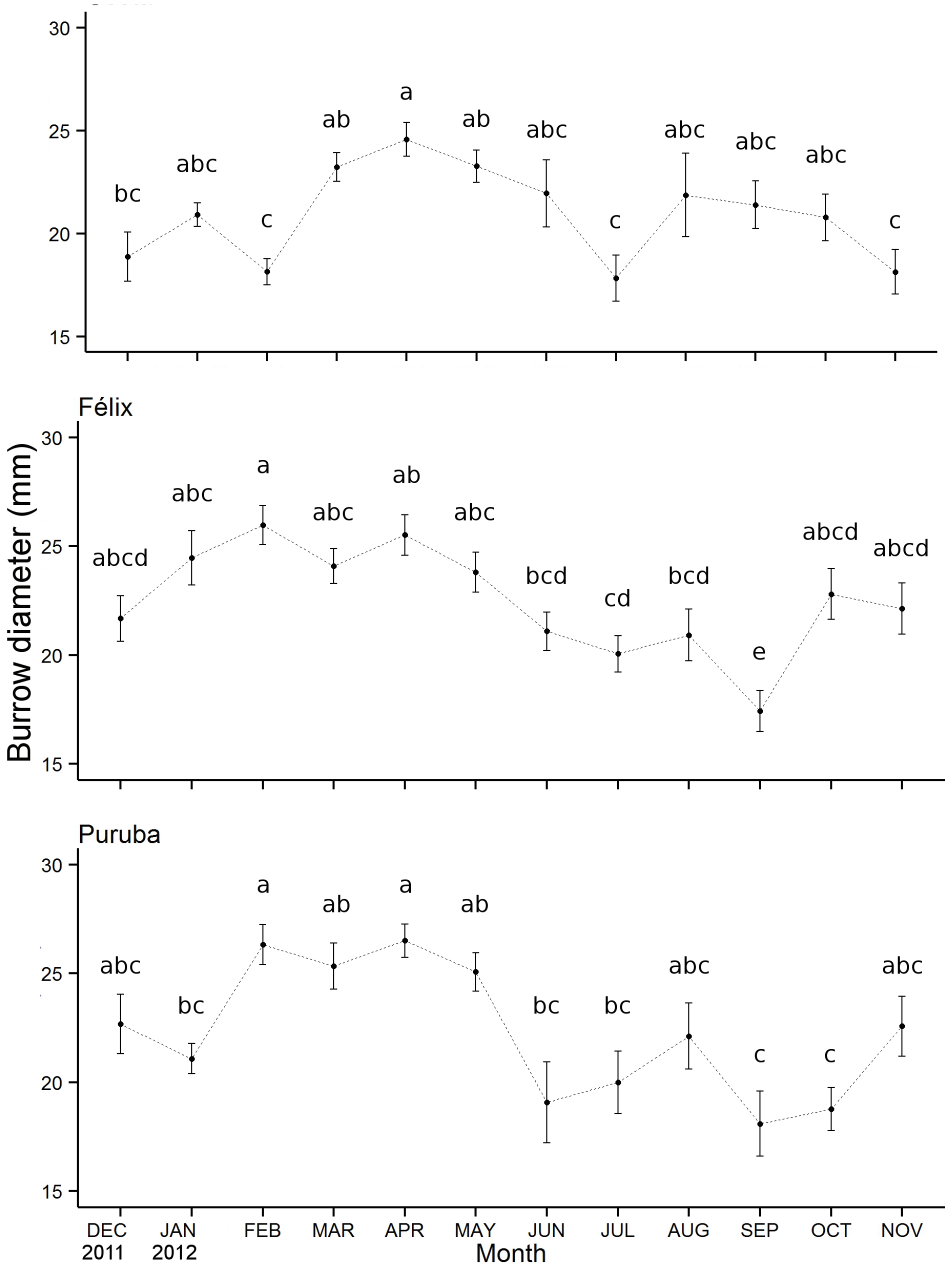

Figure 2. Temporal variation of the diameter (mm; mean ± standard error, n=5, α=0.05) of *Ocypode quadrata* burrows, sampled in three beaches with different morphodynamics (Costa-dissipative, Félix-intermediate and Puruba-reflective) from December/2011 to November/2012. Different letters denote significant differences among months by beach, using the Tukey test.

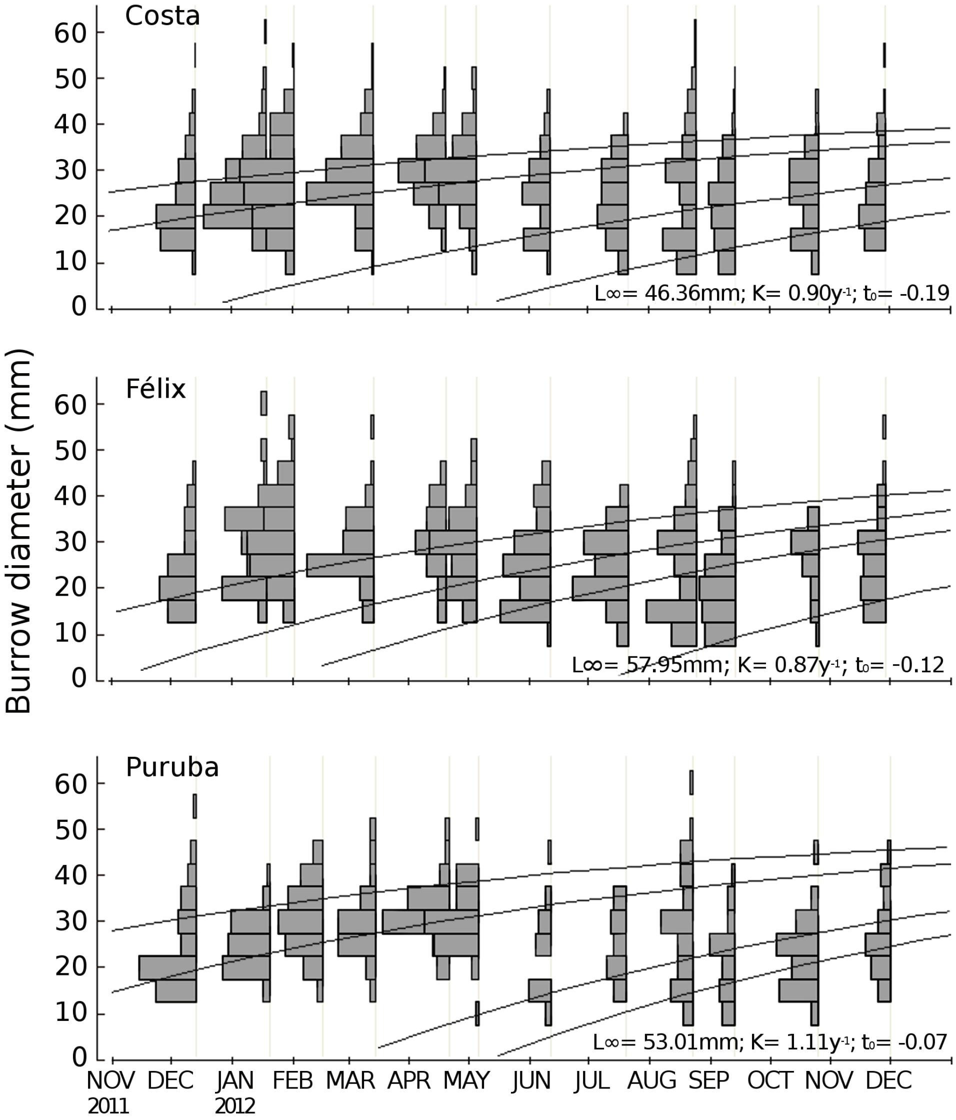

Figure 3. Monthly histograms with curves representing the estimated parameters of the von Bertalanffy growth model within the main identified modal progressions, of *Ocypode quadrata* burrows, sampled in three beaches with different morphodynamics (Costa-dissipative, Félix-intermediate and Puruba-reflective) from December/2011 to November/2012.

Values from the age-length key obtained from modal progression analysis converged to the von Bertalanffy body growth model, computing output values with biological meaning for the three parameters (assymptotic length - L∞, growth index - K, age at which the organisms would have had zero size. For the dissipative beach, Costa, the estimated value of L∞ was the lowest of the three areas, along with an intermediate value of K (46.36 mm and 0.90 yr^{-1} respectively; Table 1). Félix, the intermediate beach, had the largest L∞ and the lowest K (57.95 mm and 0.87yr^{-1}). Finally, Puruba, the reflective beach, showed an intermediate L∞ and the highest value of K (53.01 mm and 1.11 yr^{-1}). The parameters estimated, for each beach, are summarized in Table 1. The respective growth curves were included in the monthly histograms (Figure 3) for the main modal progressions identified. Residuals were tested for normal distribution and the results supported the analysis (Costa: W=0.843, p=0.034; Felix: W=0.868, p=0.177; Puruba: W=0.956, p=0.792).

Table 1. Values of the parameters from von Bertalanffy individual growth model adjusted from *Ocypode quadrata* burrows sampled from December 2011 through November 2012, in three different beaches in Southeastern Brazil. L∞=assymptotic length; K= growth parameter; t0 =theoretical point in time when the individual has zero length; Φ= growth performance index (phi-prime). Each parameter is followed by a respective estimative for each studied area, and its standard error when available (SE). r² values are presented for each fitted model.

	Costa			**Félix**			**Puruba**		
	Estimate	SE	r²	Estimate	SE	r²	Estimate	SE	r²
L∞ (mm)	46.36	16.12	0.99	57.95	69.76	0.96	53.01	26.90	0.98
K (y^{-1})	0.90	0.54		0.87	1.78		1.11	0.98	
t0 (year)	-0.19	0.08		-0.12	0.26		-0.07	0.9	
Φ	3.29	-	-	3.46	-	-	3.49	-	-

The ARSS test results pointed to significant differences among von Bertalanffy growth curves, indicating that individual fitness is not the same among the distinct populations (F=13.02; d.f.=6,15; p<0.01). Therefore, a common adjustment grouping data from the three beaches was not considered suitable. According to the likelihood ratio tests, used to make pairwise comparison of the beaches, Costa beach was the responsible for this result regarding overall parameters (Table 2). This means that the growth parameters of the individuals from Costa differed from each of the other beaches. Similarly, the phi-prime performance index calculated was lower for Costa beach (3.29), and very similar between Félix and Puruba beach (3.46 and 3.49,respectively). These results corroborate the ARSS/log-likelihood and show that the growth performance of Costa individuals was lower than of those from the other beaches.

Table 2. Matrix of results of the likelihood ratio tests comparing estimates of the von Bertalanffy body growth parameters of *Ocypode quadrata* among beaches (Costa, Félix and Puruba). Columns show the parameter compared between beaches and rows correspond to the respective test results.

Beaches		**Costa**				**Félix**			
		L∞	**K**	**t0**	**all**	**L∞**	**K**	**t0**	**all**
Félix	chi²	0.08	0.00	0.15	19.00	-			
	d.f.	1	1	1	3				
	p	0.77	1.00	0.70	<0.01				
Puruba	chi²	0.08	0.08	1.72	34.38	0.01	0.03	0.06	2.18
	d.f.	1	1	1	3	1	1	1	3
	p	0.77	0.77	0.19	<0.01	0.92	0.86	0.80	0.54

DISCUSSION

The patterns of size distribution of *O. quadrata* had both noticeable similarities and differences over the study areas. A positive skew in the general size structure (histograms) reflected the presence of oversized burrows at the three beaches. Because they correspond to individuals larger than those described in previous literature using direct measures (HALEY, 1969; ALBERTO; FONTOURA, 1999; NEGREIROS-FRANSOZO et al., 2002), the size of these burrows may have been distorted over time after abandonment. Examining the monthly histograms, it is interesting to note that all areas had higher numbers of these larger burrows, simultaneously, during August 2012. This coincides with the period shortly after the main cold fronts in the region. The previous months tended to have lower numbers of these burrows, mainly at Costa and Puruba beaches. During periods of intense cold fronts, the individuals retreat to back dunes and vegetation, followed by an increase in the frequency of abandoned burrows, which may remain after abandonment for several weeks (CAMPAGNOLI; POMBO; TURRA, submitted). All this corroborates the hypothesis that the largest burrows are abandoned and remain a certain period of time before collapsing completely, justifying the acceptance of L∞ values under the largest sampled burrows.

This common feature in August was reflected in larger mean size values in relation to the adjacent months, for all areas. According to both mean values and histograms, it is possible to observe that from June to September, soon after the main cold front period, the greatest entrance of young individuals was recorded for all areas. A similar recruitment peak was observed by OLIVEIRA et al. (2016; near 22ºS latitude), while BRANCO et al. (2010; near 26ºS latitude) observed an elevated number of recruits in July.

The size of these young individuals indicates that they had just settled; when combined with the lack of small-sized classes in previous samplings, this might indicate that individuals that settle shortly before or during the main storm surges are very unlikely to survive because they are very vulnerable to these extreme events. When conditions are milder, individuals are better able to survive and recruitment events are observed. Settlement and wind stress for a few days prior were positively correlated in other Brachyura (PAULA et al., 2001). If this trend also applies to ghost crabs, recruitment intensity after storm surge periods may be even more prominent.

According to the growth parameters, represented in the histogram growth curves, this main entrance would correspond in December 2012 to a size very similar to that recorded as the main mode in December 2011. Further, a noticeable modal progression could be identified from the December 2011 main mode, which could be followed until April/May. Therefore, although the species has been shown to reproduce during most of the year (HALEY, 1972; NEGREIROS-FRANSOZO et al., 2002), our data support the idea that there is a single main cohort within a year, derived from the entrance of recruits after cold fronts. The main peak in reproductive activity has been recorded during summer for the area (corresponding to December-February). However, ovigerous females are commonly recorded during Spring and Fall in addition to Winter (NEGREIROS-FRANSOZO et al., 2002). HALEY (1972) estimated 45 days from ovulation to hatching for ghost crabs, and DIAZ and COSTLOW (1972) recorded that a minimum of 34 days were required for individuals to reach the megalopal stage from hatching (under experimental conditions at 25ºC), totaling 79 days until the megalopal stage (the settlement stage). Experiments with a similar species, *Cyclograpsus cinereus*, demonstrate that development is slower at lower temperatures, while the survival rate is considerably increased (COSTLOW; FAGETTI, 1967). The information for the time expended as megalopa is not available because, according to the previous authors, the survival of individuals at this stage under artificial conditions is extremely low. Nevertheless, the experiments of COSTLOW and FAGETTI (1967) corroborate the view that during winter the survival rates of the larvae would be higher and the estimated period (79 days) of larval development, until the megalopa stage, would be longer. *Ocypode quadrata* was reported to reproduce continuously in the tropics, but typically in a summer and an autumn pulse in temperate areas (HALEY, 1972; NEGREIROS-FRANSOZO et al., 2002). Therefore, the highest settlement observed in August-September here would likely correspond to a reproductive peak period in autumn. To correspond to a peak of reproduction in summer over 6 months of larval development from fecundity to settlement, would be needed. This correspond to about 3.5 months as a megalopa compared to 79 days as previous larval stages, which seems unlikely given what is known for another Ocypodidade, for which the complete larval development has been observed; for *Ucides cordatus*, for example, the seven larval stages before megalopa summed about 160 days, and another 115 as megalopa (RODRIGUES; HEBLING, 1989). Developmental timing specifically in *Ocypode quadrata*, however, is poorly known (DIAZ; COSTLOW, 1972, HALEY, 1972) and should be assessed to better understand how reproduction peaks and recruitment are linked.

The predominance of low size modes was important to define the body-growth parameter estimation. Frequent records of higher size classes, obtained from indirect measures, should be considered with caution with respect to this species. First, the number of larger burrows in relation to the real population tend to be overestimated. Second, size deviations for the burrows in relation to the individuals are disproportionately higher for larger burrows (POMBO et al., 2017). Using cohort progression for smaller size classes, with burrows that are reset by the tide more frequently, would be an approach to more reliably estimate population parameters from indirect measures.

For the species as a whole, the present results suggest that the growth constant was approximately 1 year^{-1} for *Ocypode quadrata* populations in the region, with growth performance indexes between 3.30-3.50, slightly above that found (3.20) by OLIVEIRA et al. (2016) in the only study regarding growth parameters of the species. However, the study areas were morphodynamically distinct and such differences have been shown to affect population abundance and the mean size of individuals of other species (MCLACHLAN et al., 1993; DEFEO et al., 2001; DEFEO; DELGADO, 2007). For supralittoral species, this effect has been shown to be positive for more reflective beaches (DEFEO; MARTÍNEZ, 2003; DEFEO; GÓMEZ, 2005). For *Ocypode*, this relationship is not yet well established (DEFEO; MCLACHLAN, 2011), but from the present results, with respect to growth parameters and potential maximum sizes, individuals from reflective beaches seem to have advantages. The differences estimated, namely lower values for both growth parameter and asymptotic length for Costa beach, were not due to a lack of larger size classes in any of the areas. Rather, the modal progressions identified did not reach higher classes, particularly for Costa beach, for which the lowest asymptotic length was estimated. Therefore, if this population does not reach larger sizes as in the other areas, but has similar growth performances, there may be differential mortality among beaches, with lower longevity for this population. If so, it would be important to understand the reason. There is the alternative possibility that the asymptotic length for the other areas is overestimated. It has been observed that the size of burrows are larger with respect to individuals in coarser grained areas (POMBO et al., 2017), but there was no interaction between burrow size and grain size, i.e, this would not alter the slope of the curve through modes. Further efforts to understand such population dynamics are needed, given the importance of this crustacean group for beach management and conservation across the globe. This study suggests that the development of individuals may mirror that seen for other supralittoral crustaceans and therefore provide further evidence for the habitat safety hypothesis (DEFEO; MARTÍNEZ, 2003; DEFEO; GÓMEZ, 2005).

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