

Natural drivers of distribution of ghost crabs *Ocypode quadrata* and the implications of estimates from burrows

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ABSTRACT: Ghost crabs are important sandy beach dwellers whose bioindicator potential depends on a broader understanding of the relationship between environmental and biological parameters. We analyzed variations in ghost crab populations both directly (abundance, size, and sex ratio) and indirectly (burrow occupation rate and size differences between crabs and burrows) in relation to their across-shore distribution and their relationship with beach features. Nine pristine areas with distinct morphodynamics and wave exposure levels were sampled quarterly over 1 yr. Across-shore variability was recorded with larger crab sizes, lower occupation rates, and proportionally more females landwards. Storm surge period was a determining factor with respect to ghost crab populations, causing individuals to contract their distribution landwards and increases in burrow occupation rate and mean crab size estimates. Beach features influenced population parameters, with crab density and mean size tending to increase towards smaller grain sizes and with steeper slopes in the crab's range of occurrence favoring crab abundance. Burrow occupation rate differed according to slope and crab density. Our results revealed an intrinsic variability of ghost crab populations over time and among and within beaches that may be a source of bias in environmental studies. Therefore, these phenomena should be considered in the design of monitoring strategies and impact assessment protocols. This study also emphasizes the need for a cautionary approach in data interpretation of crab number and size based on burrow estimates.

KEY WORDS: Morphodynamics · Wave exposure · Abundance · Size · Indicator species · Monitoring

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INTRODUCTION

Pattern recognition is central to ecology as the repetition of events allows scientists to make important predictions in time and space (MacArthur 1972). In sandy beach ecology, beach morphodynamics is an essential element driving such patterns. According to the habitat harshness hypothesis, intertidal biota benefits from gentler slopes and finer sand grains due to greater water retention and larger amounts of organic matter. Consequently, higher species richness, diversity, and biomass are observed towards dissipative conditions (Celentano & Defeo 2006, Delgado & Defeo

2007). Backshore individuals, in contrast, have an opposite trend because steeper slopes and less compact, coarser sediment on reflective beaches would offer shelter for organisms, mainly burrowing crustaceans that are not directly exposed to wave action, as proposed by the hypothesis of habitat safety (Defeo & Martínez 2003, Defeo & Gómez 2005). However, knowledge of supralittoral species biology is scarcer compared to that of intertidal organisms. Many important anthropogenic stressors on sandy beaches are concentrated in this area, especially due to its recreational use as well as to vegetation removal, shore armoring, bulldozing and nourishment, mechanical

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cleaning, and excessive trampling (Brown & McLachlan 2002, Defeo et al. 2009). Further knowledge on the effect of such activities on supralittoral organisms is required to allow impact assessment and proper management of human activities on sandy beaches.

This also applies to the ecology of one of the most conspicuous organisms on sandy beach backshores around the globe, the ghost crab, a common name given to individuals belonging to species of the subfamily Ocypodinae, type genus *Ocypode*. These individuals build and maintain burrows across sandy beaches in the tropics and subtropics around the world (Sakai & Türkay 2013). Ecological research on *Ocypode* has increased since the late 1980s, and from then on several investigations on the distribution pattern of the different species have been carried out. Quijón et al. (2001), for example, did not find a direct relationship between beach morphodynamics and density of *Ocypode gaudichaudii*; Lucrezi (2015) recorded higher densities on more dissipative beaches, considering the burrows of 3 different species combined (*O. ceratophthalma*, *O. madagascariensis*, and *O. ryderii*); Turra et al. (2005) observed lower densities of *O. quadrata* associated with very fine and poorly to moderately sorted grains in low-energy tide-dominated beaches. Despite these records, the relationship between abundance and basic environmental parameters, such as grain size, well known for small-sized beach crustaceans, has not been widely recognized for *Ocypode* species (Defeo & Martínez 2003, Celentano & Defeo 2006, Defeo & McLachlan 2011). This has hindered predictions of abundance and size based on beach features, and complicated impact assessment and monitoring programs.

The lack of patterns recognized for these species may have several explanations. First, their interactions with the environment, including resistance to desiccation, might be very different from those of intertidal species as well as from those of smaller semi-terrestrial crustaceans. Second, variations in some population aspects between beaches may be due to greater anthropogenic impacts in the backshore than in the intertidal, rather than due to natural sandy beach features, blurring eventual patterns. Finally, difficulties in directly assessing individuals due to their burrowing behavior may also be a source of bias. The majority of studies on ghost crabs have compared populations from different periods or areas using indirect measures, i.e. burrow number or size. Therefore, to some extent, the lack of patterns may derive from differences in the relationship between these 2 distinct study subjects: burrows and individuals. In spite of that, the use of indirect measures is

actually one of the greatest advantages in using these species as an environmental indicator because assessing burrows is easier, faster, and less disruptive than directly assessing individuals (Barros 2001, Neves & Bemvenuti 2006, Schlacher et al. 2016).

The occupation rate of these burrows (or, in other words, how indirect and direct measures relate to each other) has only been assessed recently (Pombo & Turra 2013, Silva & Calado 2013). The method of counting burrows considering occupation signs (Wolcott 1978), broadly used to guide the decision of whether burrows should be considered in ghost crab assessments, has proved to be prone to relevant biases, especially regarding comparisons among areas (Pombo & Turra 2013). Many studies of the effects of anthropogenic activities on ghost crab populations have been carried out recently using burrow counts (Barros 2001, Neves & Bemvenuti 2006, Hobbs et al. 2008, Jonah et al. 2015); therefore, understanding the potential divergence between conclusions derived from data on individuals and burrows, including responses to natural environmental features, becomes essential.

Ocypode quadrata is the only ghost crab species that occurs throughout the Atlantic coast of the Americas, inhabiting several beach types. Here, we selected 9 different pristine beaches, sampled on 4 dates over 1 yr, so as to take account of the variability of natural environmental factors. Basic population parameters, namely abundance, size, and sex ratio, were directly assessed by collecting crabs. Because one of our underlying objectives was to analyze how information obtained through individuals and burrows differed from each other, we assessed both occupation rate of burrows and estimates of individual size based on burrows. Thus, the first general objective was to analyze how these variables were distributed across the shore, considering the different beaches and dates sampled; the second general objective was to assess the relationships between population parameters, measured using direct and indirect methods, and physical beach features. Our results led to a broad understanding of the spatial distribution of *O. quadrata* and highlighted the difference in patterns revealed by burrows and by individuals.

MATERIALS AND METHODS

Study areas

Nine pristine, low-use beaches were chosen to single out the influence of natural factors on the population parameters assessed. These beaches were dis-

tributed along the São Paulo coast, southeastern Brazil ($24^{\circ}30'60''\text{S}$, $47^{\circ}10'40''\text{W}$ and $23^{\circ}21'15''\text{S}$, $44^{\circ}55'60''\text{W}$), comprising approximately 350 km of coastline with a great variety of sandy beach types. Beaches were also selected to ensure a wide gradient of abiotic factors concerning morphodynamics and degree of exposure to waves in a balanced design (Fig. 1). To support our choices of study sites, we referred to a previous geological study on morphodynamic characterization of local beaches (Rocha 2008), while visual field assessments and satellite images were used for a preliminary beach exposure assessment. For organization purposes, the study beaches were categorized by morphodynamic states (dissipative [D], intermediate [I], and reflective [R]) and by degree of exposure within each group (low [+], intermediate [++], high [+++]), as follows: Costa (D+), Arpoador (D++), and Una (D+++); Justa (I+), Brava (I++), and Felix (I+++); Figueira (R+), Puruba (R++), and Prumirim (R+++). To support this general characterization, the granulometry, slope in the range of occurrence of *Ocypode* individuals, and exposure to waves were systematically assessed on each beach, as described below.

Sampling procedures and environmental characterization

To assess environmental and biological parameters in a 1 yr cycle, each beach was sampled once on the central dates of each season throughout 2012 (i.e. February, May, August, and November/December 2012). All sampling procedures complied with the license from the federal environmental agency (Ministério do Meio Ambiente [MMA] – Instituto Chico Mendes de Conservação da Biodiversidade [ICMBio] No. 31629-1; acronyms for Ministry of the Environment – Chico Mendes Biodiversity Conservation Institute).

For each beach, a visually homogeneous along-shore section of ~200 m was selected to avoid the eventual influence of adjacent rivers, headlands, or any other possible source of disruption. In each sampling event, three 2 m wide transects were randomly placed within the section, laid perpendicular to the water line, and assessed from the first burrow seawards to the last observed burrow landwards, includ-

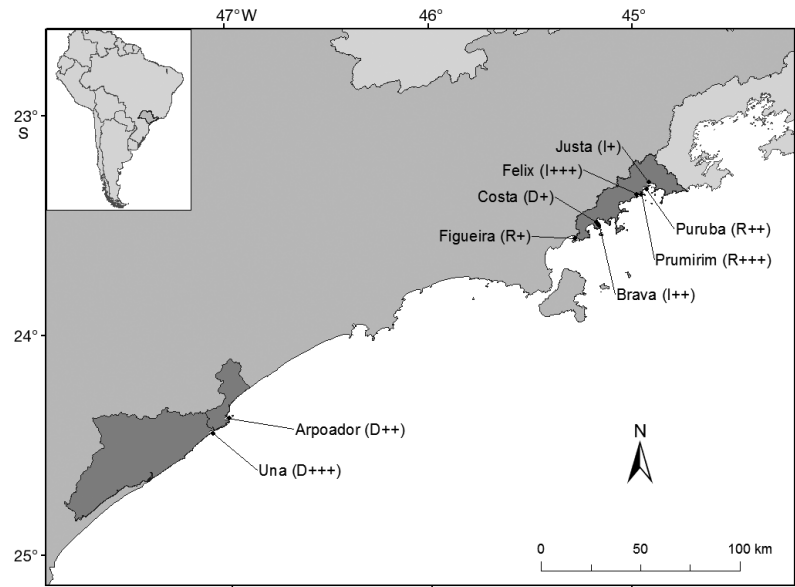


Fig. 1. The State of São Paulo coast, southeastern Brazil: the dark gray regions (municipalities) encompass all 9 beaches studied. Beaches were selected by morphodynamic states (dissipative: D, intermediate: I, and reflective: R) and by degree of exposure (low: +, intermediate: ++, high: +++) within each group

ing those inside the vegetation or coastal dunes. Transects were divided into 2 m sequential quadrats, i.e. each with an area of 4 m², so that their number varied according to beach width.

The number of burrows and individuals were counted in each quadrat, regardless of any sign of occupation, because the absence of these signs is not an accurate indication of absence of crabs (Pombo & Turra 2013). Burrow diameter was measured at the bottom of the funnel-shaped portion of burrows (upper portion) to reduce bias derived from sediment deformation on the sediment surface. Burrows were then excavated to search for crabs, with the help of a flexible steel cable to locate and guide excavation to the bottom of the burrow (Pombo & Turra 2013). During excavation, probing around helped to detect occasional extensions or side branches in the burrows. All captured crabs were counted, had their width, length, and height measured (cm), and were sexed.

The environmental factors assessed were slope in the range of occurrence, mean grain diameter, grain sorting coefficient, wave height, wave period, and length of the living area, each assessed as follows: The slope, calculated as the traditional 'rise over run', i.e. the tangent of the angle opposite to the leg of 1 transect, was measured at each quadrat across the range of occurrence, in order to characterize the profile of the area inhabited by the crabs. The range of occurrence of individuals per transect was the across-shore length (m) from the first to the last burrow recorded.

Sediment was collected for each transect in the supralittoral (backshore), upper midlittoral, and lower midlittoral for grain size analyses. Mean grain size and its standard deviation (sorting coefficient), in phi units, were obtained following the screening procedure described by Day (1965).

To quantify exposure levels in each sampling, a numerical model was applied to propagate waves onshore according to the nearshore morphology. The numerical model applied was Delft3D (open source version of Deltares WAVE module), which simulates the propagation and transformation of wind-generated waves as they move over varying bottom morphologies (Holthuijsen et al. 1994). Offshore boundary conditions representing the dominant wave climate (significant wave height and corresponding wave period) were defined for each sampling month based on the information extracted from the global wave generation model WaveWatch III (NCEP/NOAA; Tolman 2002), at a point close to shelf break. After running the model for each period, wave data were extracted in front of the sampled beaches (at depths of about 3 to 4 m). Two main wave parameters were considered: wave height (H), in meters, and wave period (T), in seconds. Wave exposure of a beach is a key physical feature that affects biota. For ghost crabs, wave energy may affect not only crab population but also the relative amount of burrows (occupation rate) because the higher the exposure, the higher the wave's potential for closing burrows. The first parameter, H , is strongly influenced by wave transformation due to coastline geography, i.e. it better represents beach exposure. The second parameter, T , is more affected by offshore boundary conditions, i.e. it better represents the overall temporal variation in wave climate than H . These wave parameters were defined for every 6 h in 2012; the mean value between the sampling day and the day immediately after the previous sampling date was used to characterize the period so that no occurrence of extreme events would be disregarded.

The range of occurrence of individuals per transect was the length (m) from the first burrow to the last one recorded. The largest range of occurrence on each beach was considered as the local (potential) length of the living area and used in subsequent density calculations.

Preliminary assessments

A common question in abundance assessments of *Ocypode quadrata* is whether tide height might

influence results. Our field work was very time consuming, and it was not possible to limit it to a specific tidal height. Therefore, tidal influence was assessed by correlating the ranges of occurrence of *O. quadrata* to the tidal height of each transect in each sampling event (beach and period, all noted down during our samplings). All beach datasets showed normal distribution patterns, which allowed for Pearson's correlation tests. No significant correlation was recorded for any beach (Costa $r = -0.27$, $p = 0.43$; Arpoador $r = -0.29$, $p = 0.37$; Una $r = -0.22$, $p = 0.49$; Justa $r = 0.23$, $p = 0.47$; Brava $r = 0.27$, $p = 0.46$; Felix $r = -0.16$, $p = 0.62$; Figueira $r = 0.47$, $p = 0.12$; Puruba $r = 0.11$, $p = 0.73$; Prumirim $r = -0.57$, $p = 0.05$). On Prumirim, a marginally significant result was identified, but its correlation coefficient was also low. Therefore, the influence of tides was considered of no relevance in the validation of further results.

The behavior of 2 units of abundance was primarily investigated: the number of occurrences per strip transect (IST; Defeo & Rueda 2002), and density (ind. m^{-2}). IST is usually preferred for comparisons within an area because calculating ghost crab density for distinct periods is more challenging and, therefore, more subject to biases. However, density is an important descriptor in comparisons among beaches. Here, to calculate density, the area of the transect with the largest range of occurrence (potential length of the living area) was fixed as a common denominator for all transects within a given beach. This approach may be understood as a modification of the IST; it accounts for the effects of agglomeration, avoids skewing of results due to differences in width among beaches, and does not compromise comparisons over time within a beach (i.e. avoiding over- or underestimations resulting from temporal variations in across-shore aggregation). Both variables behaved very similarly in the exploratory analysis, but IST showed more noticeable correlations with the across-shore range of occurrence, as expected (Pearson's correlation tests of range of occurrence with $\text{IST}_{\text{burrows}}$ $r = 0.53$, $p < 0.001$; $\text{IST}_{\text{individuals}}$ $r = 0.51$, $p < 0.001$; $\text{density}_{\text{burrows}}$ $r = -0.29$, $p = 0.002$; $\text{density}_{\text{individuals}}$ $r = -0.22$, $p = 0.021$). Hence, density, the relative measure of abundance, was used when different beaches were compared.

The crab dimensions that showed better correlation with burrow diameter were width (Pearson's $r = 0.71$, $p < 0.01$, $n = 531$) and length ($r = 0.70$, $p < 0.01$, $n = 531$). Height did not have a strong correlation coefficient ($r = 0.09$, $p = 0.03$, $n = 531$). Width was chosen for further analyses because it is the most fre-

quently used crab measure in literature (Burggren & McMahon 1988).

Data analysis

The population parameters directly assessed from crabs were abundance, size, and sex ratio. For abundance and size, some related information from burrows were also assessed, namely, the occupation rate of burrows and an estimation of the size of individuals based on burrow size. These parameters were assessed regarding 2 spatial approaches that define our 2 general objectives: (1) Across-shore distribution; because this ghost crab uses the whole beach extension it is likely that there are differences within beaches. (2) Relationships with environmental features, which are useful to reveal broader distribution patterns among distinct areas.

Across-shore distribution

Our first objective was to identify across-shore distribution patterns, considering variations among sampling beaches and dates. This analysis was applied to abundance of individuals, occupation rate of burrows, size of individuals, and sex ratio. To address this first general objective, a factor was created denoting across-shore position. Quadrats within each transect were numbered according to their position in relation to the terrestrial fringe, i.e. the vegetation line. This line was defined as 0 (zero) for all transects. Seaward quadrats received sequentially lower values (negative), while landward quadrats were assigned higher values. These quadrat values were normalized, in order to make values equivalent for all beaches: the upper limit of distribution within each beach was considered as 1, and the lower was 0. Regression models (individually described below) were used to assess the variation in each population parameter as a function of position, considering different beaches and dates. A backward stepwise model selection was performed based on Akaike information criteria (AIC), starting with the most complex model; when AIC differences between models were <1 , model comparison based on log-likelihood ratio test (LRT; for GLM) or F -test (for LM) was used to support the decision (see the Supplement at www.int-res.com/articles/suppl/m565p131_supp.pdf). Final models were properly validated.

Post hoc tests were carried out whenever at least 1 of the 2 categorical factors (beach and/or date) was

significant. For simple main effects, a Tukey post hoc test was carried out (function *glht* in R library *multcomp*; Hothorn et al. 2008). Should there be any significant interactions (which in this case necessarily included at least 1 categorical variable: beach and/or date), contrasts were set (either to perform all possible pairwise comparisons for a categorical variable, e.g. beach, across all levels of another variable, e.g. date; or to compare the regression slopes if there was interaction between a categorical variable, e.g. beach, and a continuous variable, i.e. across-shore position) and tested using an F test, with p-value corrected using a Holm-Bonferroni method (function *testInteractions* in R library *phia*; de Rosario-Martinez 2015).

For the analysis of across-shore abundance of individuals, the gross number of individuals, IST, was modeled as a function of across-shore position and sampling dates, using a Poisson generalized linear model (GLM) with a logit-link function. This was performed individually for each beach because differences in abundance among beaches would blur across-shore distribution patterns (and density per quadrat would not be different because they all have the same area). All other parameters were modeled as a function of across-shore position, beach, and date using the appropriate model in each case, as follows: burrow occupation rate, the proportion of occupied burrows per quadrat, was modeled using a binomial GLM with a logit-link function (Zuur et al. 2009); for size, crab width (cm) was modeled using a linear regression; for sex ratio, the sexual proportion ($n \text{ male} / [n \text{ male} + n \text{ female}]$) per quadrat was modeled using a binomial GLM with a logit-link function (Wilson & Hardy 2002). Sex ratio was the variable with the lowest number of observations in this section and the only case with a significant 3-way interaction because some beaches did not have enough data to verify the across-shore sex ratio distribution during some periods. Therefore, to avoid confusing models due to the combination of a nominal variable with very few points, this model selection was restarted from the full 2-way interaction (all results are shown in the Supplement).

Relationship with environmental factors

The second general objective was to assess the relationship between each population parameter and physical beach attributes. This assessment was performed for density of individuals (ind. m^{-2}), occupation rate of burrows, and size estimate of indi-

viduals based on burrows (the latter is simply the relationship analysis of crab sizes including burrow size as a factor); this approach does not apply to sex ratio. For these models, we used mean transect values of response variables. Explanatory variables measured for each transect were the mean values of slope in the range of occurrence of crabs, mean grain size (ϕ), and grain sorting coefficient (ϕ). Because granulometry was assessed in 3 different beach strata and there was a naturally high collinearity among them, a correlation and scatterplots matrix was used to determine a suitable and common strata to be used in all further analysis. Explanatory variables measured for each sampling event (same beach and date) were wave height (H ; m) and wave period (T ; s). The explanatory variable calculated for each beach was length of the living area (m). Although the latter is not a physical feature per se, it is highly determined by beach length and has an important biological meaning. In summary, 12 values were plotted (4 seasons, 3 replicates) for each of the 9 beaches, totaling 108 values of each dependent variable. All parameters were here modeled using an ordinary linear regression model (LM). Similarly to the across-shore analysis, model selection was performed using a backward stepwise method, based on AIC, provided that when AIC differences between

models were ≤ 1 , a model comparison based on F -test was used to support the decision (see Supplement); final models were properly validated. However, because of the number of continuous explanatory variables here, a preliminary selection was performed, starting with a full additive model with no interactions. Significant factors were then assessed for interaction starting with the most complex model, and model selection and validation were repeated.

Regarding abundance, the parameter modeled was mean ghost crab density (ind. m^{-2} using a fixed range per beach). After model validation, the residuals from the linear model were assessed for spatial autocorrelation using Moran's I test (with the help of the *spdep* R library; Bivand et al. 2013, Bivand & Piras 2015) to assess to what extent it might explain the variance which was not explained by the model. For burrow occupation rate, in addition to the above-mentioned environmental factors, crab density was also included as an explanatory variable. Finally, for size, crab width was the dependent variable and burrow diameter was included as an explanatory variable, in order to describe the best linear model to estimate the size of individuals based both on burrow size and on environmental factors.

Proper models specifically applied for each population parameter are summarized in Table 1.

Table 1. Summary of objectives and respective methods regarding population parameters of *Ocypode quadrata* sampled on 9 pristine beaches, comprising different morphodynamic and wave exposure levels, on 4 dates from February to November/December 2012. Population parameters abundance, size, and sex ratio were directly assessed (from crabs) as well as the related burrow parameter, where applicable (occupation rate and relationship with crab size). Our 2 general objectives were to assess (1) across-shore distribution and (2) relationship with environmental factors. The corresponding tests for each combination of objective and population parameter are shown. Within each general objective, the common factors (Fc) accounted for by the models are shown. Extra (+) or non-used (–) factors are designated where appropriate using Fc 'name', below the respective method. IST: individual per strip transect; GLM: generalized linear model; LM: ordinary linear regression model

General objectives	Parameter	Method
1. Across-shore distribution (Fc: across-shore position, beach, date)	Crab abundance (IST; for each beach separately)	Poisson GLM – Fc beach
	Burrow occupation (Yes or No)	Binomial GLM
	Crab size (width; cm)	LM
	Sex ratio (proportion of males)	Binomial GLM
2. Relationship with environmental factors (Fc: slope in the range of occurrence, grain size, grain sorting coefficient, wave height, wave period, across-shore length of living area)	Crab abundance (ind. m^{-2} ; using fixed range per beach)	LM
	Burrow occupation rate (proportion of occupied burrows)	LM + Fc crab density
	Crab size (width; cm)	LM + Fc burrow size

RESULTS

Characterization of environmental factors

The length of the across-shore living area of *Ocy-pode quadrata* ranged from 10 to 60 m. The narrowest ranges of occurrences were observed on Costa and Justa beaches throughout the year, while the broadest ranges were observed on Una and Brava beaches (Fig. 2A). Variability within sampling events (i.e. among transects) was generally low, but noticeable differences were recorded over the sampling dates. The largest areas of occurrence were generally observed during summer (February), and the shortest ones were observed on the date in autumn (May).

Mean slope in the range of occurrence of crabs did not necessarily correspond to the whole beach slope (Fig. 2B), as previously characterized by Rocha (2008). Costa beach showed some of the steepest slopes across the area inhabited by individuals, probably because it is a dissipative tide-dominated beach. Arpoador, Una (previously classified as dissipative), and Brava (previously classified as intermediate) showed gentler slopes, followed by Felix beach (intermediate). Costa, Justa (intermediate), Figueira, Puruba, and Prumirim showed the steepest slopes across the areas inhabited by *Ocypode*. The mean upper midlittoral grain size (used in further analysis; Fig. 2C) of each beach followed the previous characterization of morphodynamics, i.e. phi values decreased from dissipative to reflective beaches. Among dissipative beaches, Costa had the highest mean grain sizes and sorting coefficients (phi units). With a few exceptions, mean phi values did not have high standard deviations within and between seasons, but dissipative beaches tended to show higher deviations during the summer (Fig. 2D). Wave height values (H) generally confirmed the visual choice of beaches according to their exposure (Fig. 2E). Wave period (T), which better reflects temporal variations, showed less intense (shorter period) wave energy during the summer, followed by spring, autumn, and winter (in ascending order), with similar values for all beaches (Fig. 2F).

Population parameters

Across-shore distribution

Abundance of crabs. Six of the 9 areas showed at least 1 significant predictor (Table 2). Only Justa and

Puruba showed no significant effects, while Prumirim only showed a significant effect for date. Across-shore distribution patterns among beaches were evident and similar, with higher concentration of individuals closer to the water on the date in summer (Table 2, ASP denotes the slope on the date in summer; all significant values were negative, which means higher abundance towards lower across-shore positions on these beaches) and a shift towards vegetation on other dates, mainly in autumn (Table 2, last 3 lines denote the slope on other dates compared to summer slope; all significant values were positive and tended to be higher in autumn and winter than in spring). The influence of across-shore position on abundance distribution and its shift over the dates was more evident on Brava and Félix. This same trend was also recorded on the dissipative beaches Arpoador and Una (higher abundance towards the waterline during summer and lower on other dates, mainly autumn); even Costa, the beach with the shortest range of occurrence, showed evidence of this trend, with marginally significant values. Regarding differences between dates, there were generally higher values on the date in summer, and the lowest coefficients were observed in the autumn (Table 2).

Burrow occupation rate. Higher values of occupation rate mean a closer correspondence between number of burrows and individuals, i.e. the higher this rate, the better that estimates based on burrows correspond to effective crab abundance. Across-shore analysis showed a significant influence of position (GLM; $\chi^2_1 = 16.83$, $p < 0.01$), beaches (GLM; $\chi^2_8 = 20.43$, $p < 0.01$), and sampling dates (GLM; $\chi^2_3 = 10.22$, $p = 0.02$), with no interaction between factors (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m565p131_supp.pdf for optimal model selection details). The effect of across-shore position was negative (slope $z = -4.05$, $p < 0.01$), meaning that occupation rate decreased landwards, while burrows closer to the waterline showed higher chances of housing a crab; this trend was observed on all dates and beaches (Fig. 3A: Across-shore position effect). The highest mean (± 1 SE) occupation rate was observed on Arpoador (0.57 ± 0.05 ind. burrow⁻¹), while a significantly lower occupation rate ($z = -4.13$; $p < 0.01$) was observed on Figueira, with a mean of 1 crab for each 4 burrows (0.25 ± 0.04). All other beaches showed intermediate values (Fig. 3C: Beach effect). Occupation rate was higher on dates corresponding to autumn, when cold front entries begin and storm surges are more frequent and intense (Fig. 3B). During the subsequent sampling

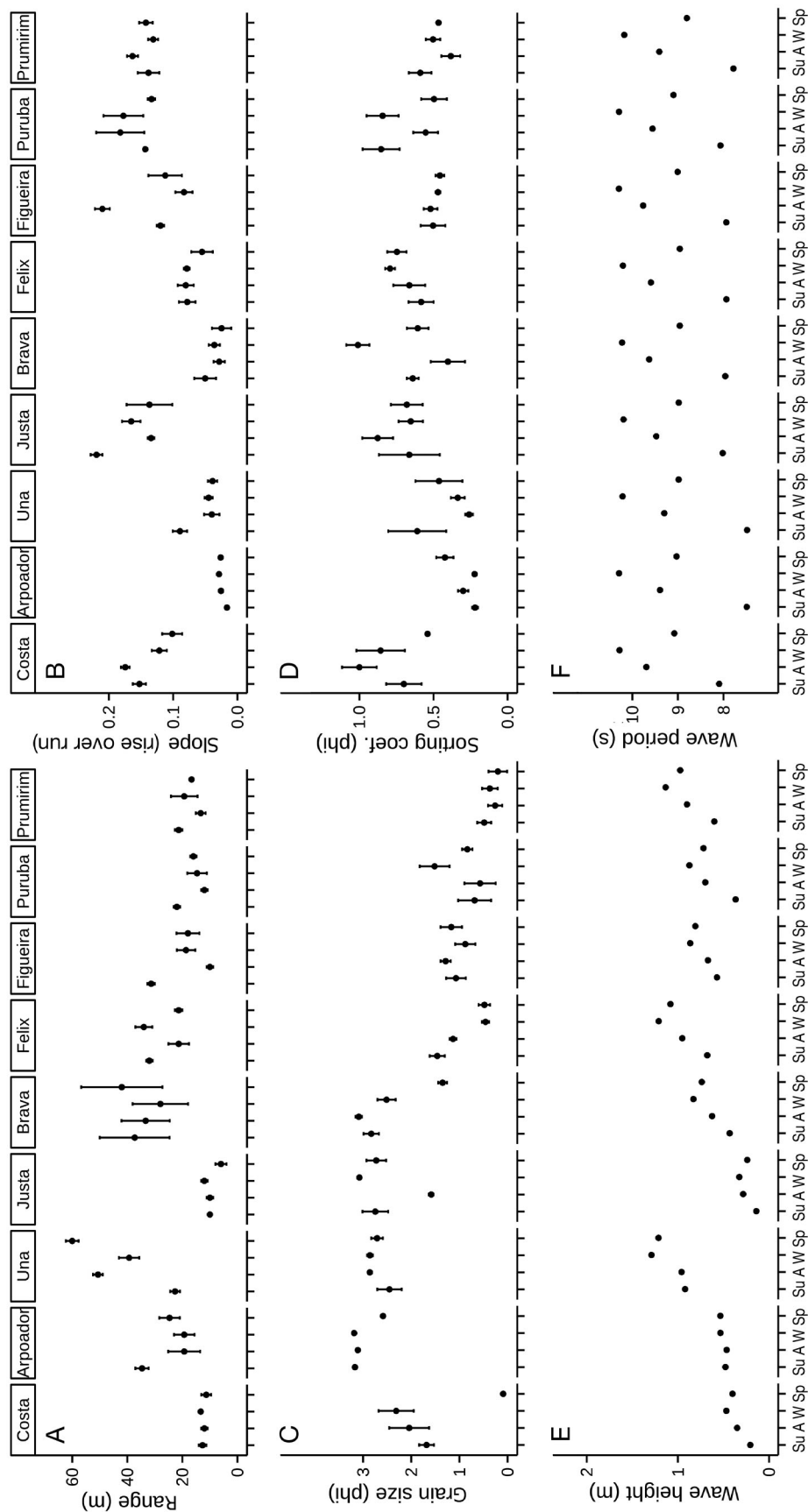


Fig. 2. Mean and standard error of (A) range of occurrence of *Ocyropsis quadrata* (m), (B) slope in the range of occurrence (rise over run), (C) upper midlittoral grain diameter (phi), and (D) sorting coefficient (phi) from 3 transects sampled quarterly from February to November/December 2012; each sampling date in the center of a season: Summer (Su), Autumn (A), Winter (W), and Spring (Sp). Study beaches comprise distinct morphodynamic states (dissipative [D], intermediate [I], and reflective [R]) and exposure degrees (low [+], intermediate [++], high [+++]), as follows: Costa (D++), Arpoador (D++), Una (D+++), Justa (I+), Brava (I+), Felix (I+++), Figueira (R+), Puruba (R++), and Prumirim (R+++). For (E) wave height (m) and (F) period (s), the simulation was performed for the entire area so that only one value was provided per sampling date within each beach

Table 2. Coefficients of the models (in logit units) of variation in abundance (individual per strip transect [IST]) of *Ocypode quadrata* according to across-shore position (ASP), sampling date (corresponding to central period of Summer, Autumn, Winter, and Spring; Summer was the baseline condition and is given as the intercept), and interaction between these terms (one per season). The values shown refer to the baseline condition (intercept) on each beach. Values were estimated using a Poisson generalized linear model with logit-link function for each beach. Cell shading denotes the following significance value intervals: light grey = $0.05 > p > 0.01$; dark grey = $p < 0.01$

Predictor	Beaches								
	Costa	Arpoador	Una	Justa	Brava	Félix	Figueira	Puruba	Prumirim
Intercept	1.12	0.04	0.28	-0.01	1.01	0.63	0.09	-0.70	-0.39
ASP	-1.36	-2.07	-2.24	0.38	-2.06	-3.12	-4.45	-0.06	-0.51
Autumn	-1.77	-6.80	-1.79	-0.86	-0.57	-2.49	-5.11	1.55	2.86
Winter	0.13	-3.51	-1.43	-1.01	-2.12	-2.10	-3.11	-2.07	-0.94
Spring	-1.28	-0.00	-0.62	0.16	-2.03	-3.50	-0.51	1.06	3.40
ASP*Autumn	2.56	9.88	3.35	1.17	0.36	5.65	10.45	-2.02	-5.09
ASP*Winter	-3.30	5.46	2.97	-0.24	2.04	3.47	6.28	2.69	0.49
ASP*Spring	1.43	1.55	1.11	-4.47	2.52	5.50	3.36	-2.04	-4.06

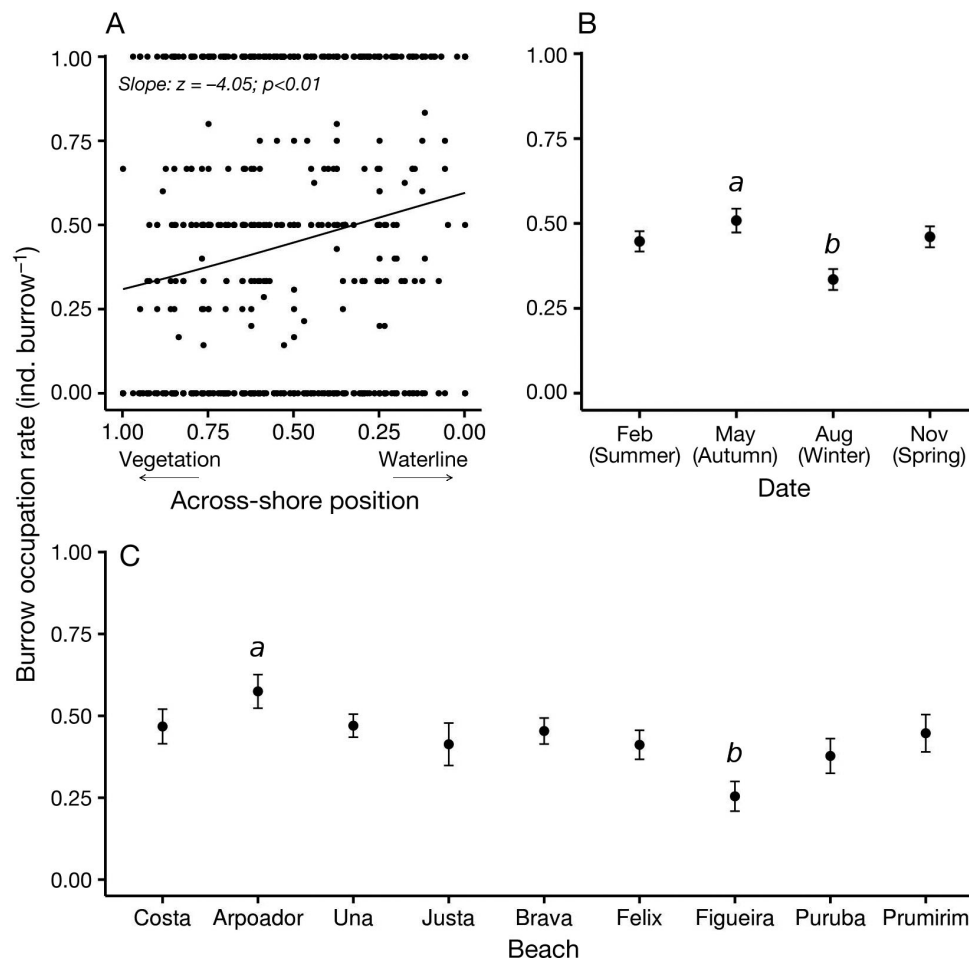


Fig. 3. Significant effects of the optimum model estimated using a stepwise-selected binomial generalized linear model for the burrow occupation rate (proportion of occupied burrows per quadrat) of *Ocypode quadrata*: simple effects of (A) across-shore normalized position, (B) sampling date, and (C) sampling beach. The model accounted for these 3 factors and their interaction. Sampling was carried out on 9 pristine beaches, comprising different morphodynamics and wave exposure levels, on 4 dates from February to November/December 2012. Italicized text or letters denote results of (A) z-test of the slope or (B, C) Tukey test; absence of letters denotes no significant differences from any other level

period, winter, it was significantly lower ($z = -3.10$; $p = 0.01$). The warmest sampling dates (summer and spring) showed intermediate values, which were not significantly different from any other (Fig. 3B: Date effect).

Size. The optimum model of across-shore distribution of crab sizes had 2 significant interactions (see Table S2 in the Supplement for optimal model selection details): Across-shore position*Beach and Beach*Date (LM; $F_{44,486} = 4.13$, $p < 0.01$ Adj- $r^2 = 0.21$). Regarding the first one (LM; interaction $F_{8,490} = 3.25$, $p < 0.01$), size segregation varied according to beach; whenever it was present, the trend always denoted larger sizes landwards (Fig. 4A: Across-shore position*Beach). The subsequent analysis of contrasts for Across-shore*Beach position formed 3 groups, where Figueira (with the steepest regression slope; Fig. 4A) significantly differed from Arpoador ($F_{1,486} = 11.25$, $p = 0.03$), Brava ($F_{1,486} = 13.59$, $p < 0.01$), and Costa ($F_{1,486} = 16.34$, $p < 0.01$). The latter also differed from Félix, which had the second steepest regression slope ($F_{1,486} = 11.66$, $p = 0.02$).

The interaction Beach*Date was also significant (LM; interaction $F_{24,482} = 2.17$, $p < 0.01$). The temporal trend was similar in most areas: increase in crab size from summer to autumn, the latter with the highest general values, and a sharp decrease in winter, followed by an increase in spring (Fig. 4B: Beach*Date effect). However, a few differences among beaches regarding this general trend led to a significant interaction. More specifically, the post hoc analysis of contrasts regarding dates (i.e. pairwise comparison of dates across beaches) showed that spring significantly differed among beaches in relation to summer ($F_{8,486} = 4.37$; $p < 0.01$) and marginally differed from autumn ($F_{8,486} = 2.47$; $p = 0.06$). In contrast, differences among beaches (across dates) were only due to Una beach, which was significantly different from Figueira ($F_{3,486} = 6.15$, $p = 0.01$) and marginally different from Félix ($F_{3,486} = 5.05$, $p = 0.06$).

Sex ratio. There was a significant segregation of individuals according to sex, which differed according to sampling dates, resulting in an optimum model with the interaction Across-beach position*Date (GLM; $\chi^2_3 = 319.70$; $p = 0.03$); beach effect was not significant (but see Table S3 in the Supplement for optimal model selection details), i.e. the trend was homogeneous across the study beaches (GLM; Beach effect $\chi^2_8 = 328.64$; $p = 0.55$). Therefore, summer samples showed the most intense sexual segregation on all study beaches (Fig. 5), with females concentrating landwards (summer slope $z = -3.16$; $p < 0.01$). This trend was similar during autumn, yet not significant

(autumn slope $z = -1.58$; $p = 0.11$). The number of females was higher during winter (significantly higher than summer values; $z = 2.93$; $p < 0.01$), and spatial segregation was not significant although it showed an opposite trend to the first 2 sampling dates (winter slope $z = 0.79$, $p = 0.43$; Fig. 5). On the subsequent sampling date, corresponding to spring, the trend shifted again to concentrate females landwards, although not significantly (spring slope $z = -0.27$; $p = 0.79$). The post hoc analysis of date slopes was only marginally significant between summer and winter ($\chi^2_1 = 6.27$; $p = 0.07$). The significance of Across-shore beach position*Date is ensured by the model selection process, but the latter result indicates that despite across-shore segregation, simple effects alone were important drivers of sex ratio: across-shore segregation was significant ($\chi^2_1 = 6.20$; $p = 0.01$) and negative in general (higher proportions of males towards the waterline), while summer had a significant higher proportion of males than winter ($z = -2.93$; $p = 0.01$); the winter sampling was the only one with a higher proportion of females.

Relationship with environmental factors

Abundance. The density of individuals was positively related to upper midlittoral grain diameter (in phi units; higher densities in finer sediments), wave period, slope in the range of occurrence, and sorting coefficient (in phi units; higher densities in more poorly selected sediments); the 2 latter factors interacted with each other (see Table S4 in the Supplement for optimum model selection details).

Results show that the smaller the grain size, the higher the density (Table 3a), i.e. a tendency to increase density towards dissipative conditions, according to this morphodynamic descriptor (grain size). However, the behavior of density also varied according to the interaction of slope and sorting coefficient: abundance of individuals increased towards poorly selected grains when the slope in the range of occurrence was steeper (Fig. 6A).

This feature is likely due to the influence of dissipative tide-dominated beaches. These beaches have smaller yet more poorly selected grains and steeper slopes in the range of occurrence of individuals (upper-midlittoral and supralittoral), and results indicate that this combination was favored by ghost crabs. Exposure to waves was not retained in the optimal density model (Table 3a), but it is possibly reflected in this combination of dissipative beaches with steeper back areas (sheltered). Moreover,

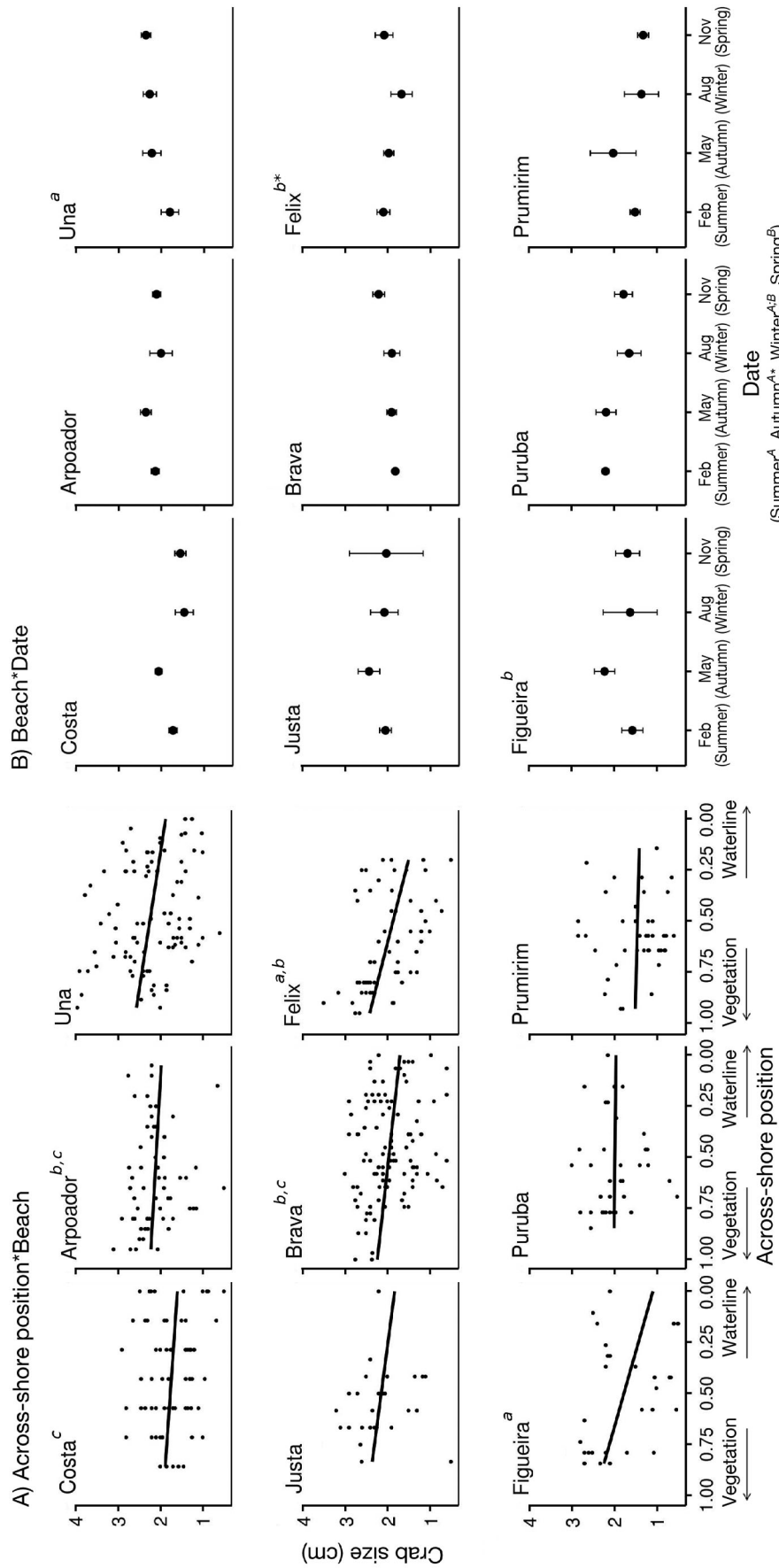


Fig. 4. Significant effects of the optimum model estimated by a stepwise-selected linear model for size of *Ocypode quadrata* (carapace width; cm): (A) Across-shore position*Beach and (B) Beach*Date. The model accounted for the factors across-shore normalized position, sampling beach, and sampling date. Sampling was carried out on 9 pristine beaches, comprising different morphodynamics and wave exposure levels, on 4 dates from February to November/December, 2012. The respective *a posteriori* tests of the interaction contrasts are denoted by italicized superscript letters; lowercase letters indicate pairwise comparisons between the factor Beach and (A) regression slope and (B) date; uppercase letters indicate pairwise comparisons of (B) dates across beach levels; * denotes marginal significance ($0.05 < p < 0.10$); absence of letters denotes no significant differences from any other level

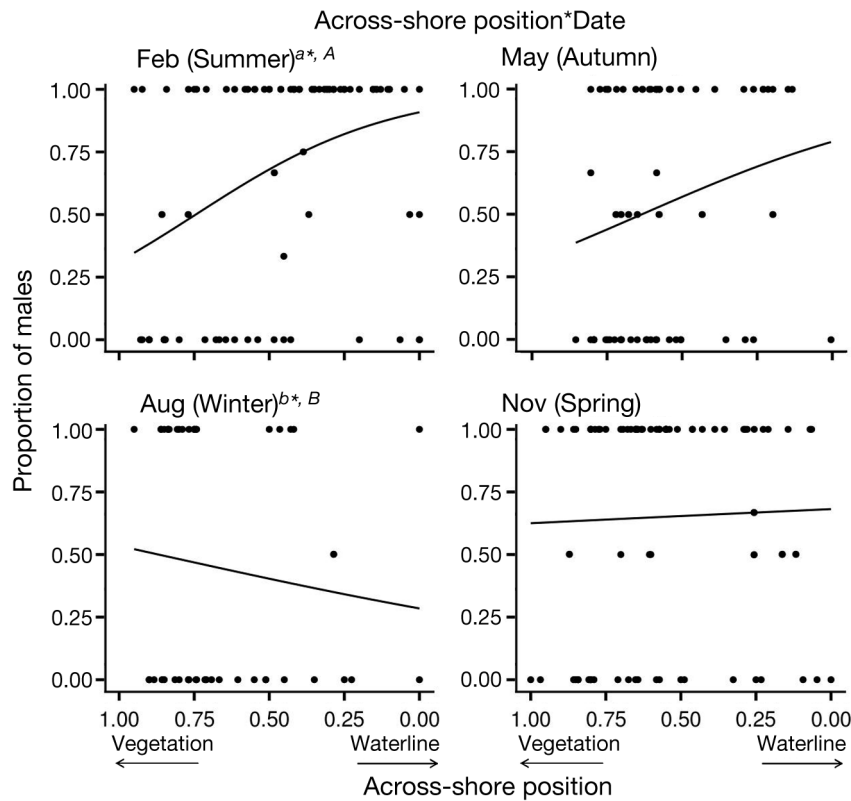


Fig. 5. Significant effect of the optimum model—the interaction Across-shore position*Date—estimated by a stepwise-selected binomial generalized linear model for the sexual proportion of males per quadrat (males/(males + females)) of *Ocypode quadrata*. The model accounted for the factors across-shore normalized position, sampling beach, and sampling date. Sampling was carried out on 9 pristine beaches, comprising different morphodynamics and wave exposure levels, on 4 dates from February to November/December 2012. Italicized superscript letters denote the *a posteriori* comparison between regression slopes (lowercase; lines) or dates (uppercase), with different letters indicating significant difference; *denotes marginal significance ($0.05 < p < 0.10$); absence of letters denotes no significant differences from any other level

wave period was negatively related to crab density, i.e. lower crab abundance occurred on dates with longer wave periods (higher energy). It is worth noting that wave period reflects temporal variations and was similar among areas, with higher values corresponding to winter and autumn. This corresponds, therefore, to the occurrence of lower densities on these dates. The spatial autocorrelation of residuals was not significant (Moran's $I = -0.06$; $z = -0.52$; $p = 0.70$).

Occupation rate. The regression for the relationship between environmental factors and crab density showed that occupation rate was significantly related to crab density and slope in the range of occurrence, both interacting with each other (Table 3b; see Table S5 in the Supplement for optimal model selection details). The higher the density of individuals, the higher the occupation rate, which means fewer burrows per individuals, and the effect of population density on burrow occupancy was less important on gentler slopes (Fig. 6B). Thus, the proportion of occupied burrows was influenced by temporal (date effect in the across-shore analysis), environmental (slope), and behavioral factors (changes according to density).

Table 3. Relationship between environmental factors and (a) density (ind. m^{-2}) ($F_{5,101} = 9.25$, $p < 0.01$, adjusted $r^2 = 0.28$), (b) burrow occupation rate (ind. burrow $^{-1}$) ($F_{3,101} = 21.59$, $p < 0.01$, Adj. $r^2 = 0.37$) and (c) crab size (cm) ($F_{2,334} = 276.7$, $p < 0.01$, Adj. $r^2 = 0.62$) of *Ocypode quadrata*: the significant coefficients estimated by stepwise-selected linear models, with the respective standard errors and t -values, are presented. The initial model included, as factors, the slope in the range of occurrence, grain size (ϕ), grain sorting coefficient (ϕ), wave height (m), wave period (s), and length of the living area (m). For (b) occupation rate, crab density (ind. m^{-2}) was included as a factor, and for (c) crab size, burrow diameter was included as a factor. Sampling was carried out on 9 pristine beaches, comprising different morphodynamics and wave exposure levels, on 4 dates from February to November/December 2012

Objective / Parameters	Parameter estimates		
	Coefficient	SE	t -value
(a) Density			
Grain size (ϕ)	0.03	0.01	2.64
Wave period (s)	-0.02	<0.01	-3.64
Slope*Grain sorting coefficient (ϕ)	1.44	0.65	2.21
(b) Occupation rate			
Intercept	0.40	0.05	8.13
Slope	-1.24	0.38	-3.17
Crab density (ind. m^{-2})	0.62	0.48	1.30
Crab density*slope	7.11	3.52	2.02
(c) Size of individuals			
Burrow diameter (cm)	0.75	0.03	22.83
Grain size (ϕ)	0.06	0.03	2.30

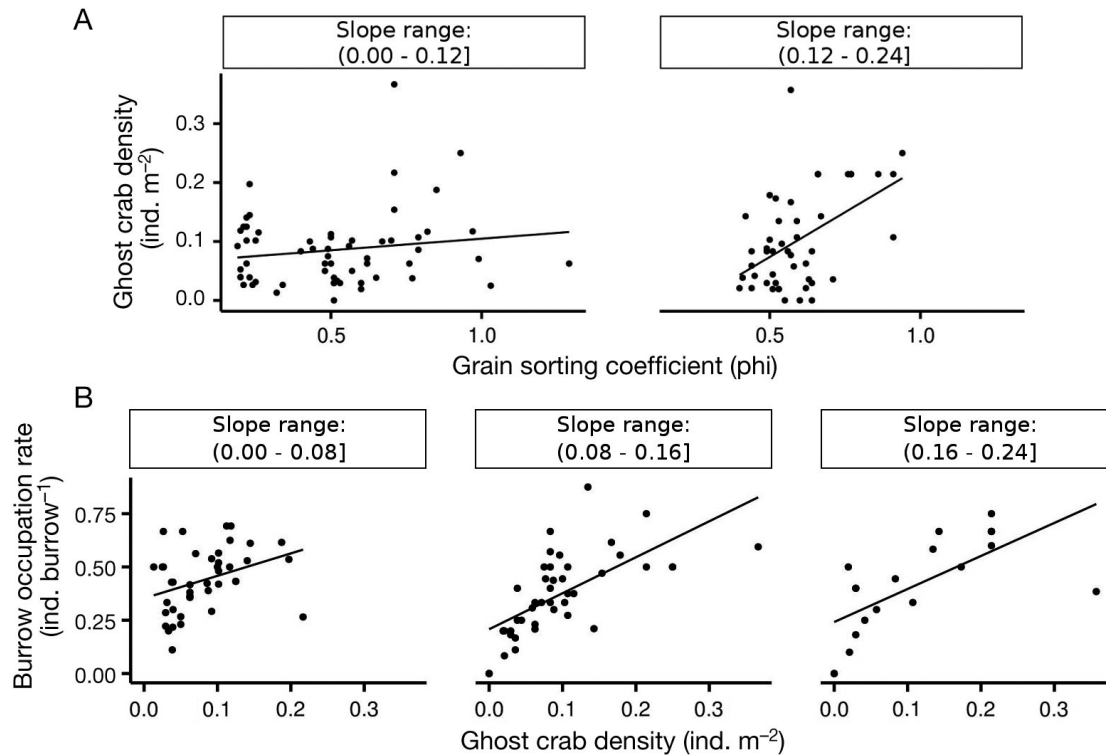


Fig. 6. Significant interaction effect of the optimum model estimated by backward stepwise-selected linear models for (A) the density of *Ocypode quadrata* (ind. m⁻²; per transect), the interaction slope*grain sorting coefficient (phi), and (B) the burrow occupation rate of *O. quadrata* (proportion of occupied burrows; per transect), the interaction 'slope*crab density'. Sampling was carried out on 9 pristine beaches, comprising different morphodynamics and wave exposure levels, on 4 dates from February to November/December 2012. Full optimum model coefficients are shown in Table 3a,b

Size. Crab width, estimated as a function of physical factors and burrow diameter, was mainly influenced by burrow size, as expected, and also by grain size and wave period (see Table S6 in the Supplement for optimal model selection details). No interactions between factors were significant. Mean crab size slightly increased towards finer grains (larger phi) and with wave period, which indicates that crabs were larger in more intense wave periods. An optimum model describing the size estimate of individuals based on burrows and environmental factors is summarized in Table 3c.

DISCUSSION

Several investigations of the distribution pattern of ghost crabs have been carried out recently (Quijón et al. 2001, Turra et al. 2005, Rosa & Borzone 2008, Hobbs et al. 2008, Branco et al. 2010, Lucrezi 2015), but a relationship between abundance and basic environmental parameters has not been solidly recognized, unlike many other beach species. Difficulties

in establishing patterns for ghost crabs may be partly due to assessments of population parameters based on burrows because most population studies on the species are carried out using the indirect method. The results regarding both across-shore distribution and relationship with environmental factors are hereinafter discussed considering population parameters assessed based on crabs, but also considering how these parameters were influenced by burrow counts.

One important spatial dimension for sandy beach organisms is the across-shore extension because it is the main direction in which changes in physical features occur. This is not different for ghost crabs because these individuals use the whole extension of the upper mid- and supralittoral, thus ranging from the waterline to dunes and vegetation. Some population parameters of ghost crabs are known to be spatially segregated across the shore, e.g. size (Alberto & Fontoura 1999, Turra et al. 2005). Here, other features such as abundance, sexual proportion, and occupation rate also differed across shore, with segregation intensity often varying according to beach and/or sampling date.

Regarding abundance, there was a higher general concentration of individuals in lower zones during summer, while the shift landward was more intense on the date in autumn. Moreover, sampling in autumn showed high mortality of individuals (lower abundances); such periods are associated with storm surges (Gan & Rao 1991), and this date defined important patterns here, observed both in across-beach distributions and in general spatio-temporal aspects, with similar temporal patterns regardless of beach type. Hobbs et al. (2008, p. 1457) also recorded high mortality rates during high-energy oceanographic events, stating that these autumn events 'essentially remove all of the ghost crabs'.

An important result referred to burrow occupation rate, primarily because it showed a positive trend toward uppermost areas, i.e. lower occupation rates in the upper beach levels than closer to the waterline. Due to the acknowledged and observed size segregation, with larger individuals concentrated landward, larger individuals are more prone to be overestimated by indirect methods. More protected burrows are probably rarely reached by the water and last longer because they are closer to or inside the vegetation and are thus more protected from collapsing due to wind and substrate instability. It is essential to consider this condition in population ecology studies and environmental quality inferences based on population structure. Moreover, sampling beaches and dates were also significant factors affecting general occupation rate values. The highest occupation rates during autumn were probably related to a natural reset of burrows during storm surge events and burrows newly built by crabs seeking shelter further back in backshore zones. In southeastern Brazil, where the study areas are situated, storm surges are more frequent and intense during autumn (higher frequencies of cyclogenesis; Gan & Rao 1991). Accordingly, we might hypothesize that after these harsh events, these backward burrows become gradually abandoned and, due to their location (which is more protected from collapsing), they had the smallest values of occupation rate on the subsequent sampling date, 3 mo later. Naturally, other important features such as crab density itself contribute to changes in occupation rate, as shown here. These features will be discussed further.

The size segregation results observed here were expected, with larger individuals tending to concentrate landwards. This known trend has already been described for burrows (Alberto & Fontoura 1999, Turra et al. 2005). Our results related this trend to individuals and showed that the intensity of size seg-

regation varied according to beach, although not to season. General spatial and temporal conditions observed here highlighted the importance of storm surges (threat) and dunes and vegetation (shelter) to the species. Other studies have argued that individuals migrate inland into dunes for protection and that it is essential to include individuals from these areas in population analyses (Alberto & Fontoura 1999, Barros 2001). The highest mean size values were also observed on the date in autumn. This may be partly due to the fact that smaller individuals are more threatened (and killed) during these periods because they occupy the beach zone closer to the waterline and their mobility to higher areas is thus more costly (Tullis & Andrus 2011).

Although storm surges are periods of high mortality, this may be an advantage for the purposes of impact assessments because it would account for those individuals that are able to survive harsh events, i.e. the most resilient strata of the population. The presence of ghost crabs on a given beach at a random moment does not necessarily mean that this is a viable population: it may also reflect a genetic 'sink', but not a 'source' population, meaning that an area may receive individuals that will not live long enough to reproduce and spread their genes (Dias 1996). Furthermore, during the periods after harsh environmental conditions, when the beaches showed their highest burrow occupation rates, abundance estimates based on burrows would be more accurate.

Sexual segregation results are especially important to population studies addressing reproduction. General sexual proportion and across-shore segregation differed between dates and were homogeneous across sampling beaches. Males tended to stay closer to the waterline on warmer dates, probably due to courtship display, since summer is an important reproductive period (Haley 1972, Negreiros-Fransozo et al. 2002). Our results contradict the findings of Corrêa et al. (2014), who found males concentrated closer to the vegetation line than females, whose number was very low. Another important factor is that their methodology was very different from that in this study, with active capture of crabs on the beach surface. Sex ratio also changed over the seasons. Higher relative numbers of captured females occurred in periods of higher recruitment of young individuals (winter). Branco et al. (2010) also observed differences in the sex ratio of *Ocypode quadrata* throughout 1 yr. A possible explanation is that females have higher rates of mortality during warmer periods. Consider, for instance, that hatching and settlement rates would not be higher for males

(although they might be for females) but that rates of mortality would be higher for females. These would be more fragile while incubating (jeopardized mobility) and would thus be exposed to a higher range of predators while spawning in the water.

Specifically considering abundance, density tended to increase towards dissipative conditions (finer grains), in contrast to other supralittoral crustaceans and in agreement with what has been observed for other ghost crab species (Lucrezi 2015). Furthermore, sorting coefficient was also relevant for steeper slopes in the range of occurrence of ghost crabs (backshore and higher zones). This result was especially evident for Costa beach; this dissipative tide-dominated beach tended to have higher values of sorting coefficient and a high density of individuals. These findings indicate that steeper slopes in the range of occurrence provide more shelter to individuals during extreme periods, while less compact sediment may favor digging efficiency and burrow stability. A different relationship was found for *O. gaudichaudii* (Quijón et al. 2001), a species found in the Central and South Pacific coast of America (including the Galapagos), which showed an indirect relationship between abundance and slope in the dry zone. Those authors also found a direct relationship between dry zone length and burrow density, while here the length of the range of occurrence did not affect density. It is important to highlight that, when different dates within a beach are compared, the great differences recorded for the ranges of occurrence across shore may have had an important and misleading effect on density analysis. For example, this range tended to be broader in periods of higher abundance and during reproductive period peaks, which occur mostly during warmer seasons (Negreiros-Fransozo et al. 2002), when males also tend to be closer to the waterline. Therefore, the approach of fixing the widest range of occurrence per beach (length of the living area) to calculate density is likely to eliminate this influential factor, enhancing the feasibility of comparisons among beaches without compromising differences over time.

Across-shore position and date (across-shore distribution) as well as slope in the range of occurrence and crab density (relationship with environmental factors) were the relevant drivers of occupation rate among beaches. Therefore, in addition to the effects physical features have on the occupation rate of *O. quadrata* burrows, the fact that crab density was also a significant driver of occupation rate suggests a behavioral element: when relatively larger areas are available (i.e. smaller densities), there are more bur-

rows per crab (i.e. lower occupation rate). Conversely, when density of individuals is higher, which means smaller relative areas and more or closer neighbors, the number of burrows per crab is lower (occupation rate is higher). This may be due to an intraspecific agonistic behavior displayed by ghost crabs (Hughes 1966, Schöne 1968). The indirect method is an important tool for the assessment of ghost crab populations and is most certainly essential for monitoring and management purposes, but its traditional use might hinder significant advances on the ecology of this group, and we must take into account that it is a potential source of biases.

The relationship between burrow size and size of individuals has already been estimated previously for the species (Alberto & Fontoura 1999, Turra et al. 2005, Branco et al. 2010, Oliveira et al. 2016). Mean burrow size was also demonstrated here to be an imperative driver for estimates of crab size (carapace width), with carapace width generally 0.75-fold the burrow size (intercept was not significantly different from zero). This did not depend on physical factors, such as grain size; however, it is worth noting that the bottom of the funnel-shaped portion of the burrow was measured in this study because the upper portion is more prone to deformation due to grain type and size and is thus more prone to biased crab size estimates. Mean crab size increased towards finer grain sizes, which also differed from the tendency showed by other small supralittoral crustaceans (Defeo & Martínez 2003, Defeo & Gómez 2005). Longer wave periods were also associated with an increase in mean crab size, reflecting the significantly larger size of crabs during samplings in autumn and their higher resistance to wave action. As the model was totally additive (i.e. with no interaction between factors), these factors may all be considered independent in providing inferences on mean crab size.

This information suggests a puzzling balance between sandy beach features and population parameters: finer grains, associated with dissipative conditions, were associated with higher densities (and ultimately with higher occupation rates), in contrast to other supralittoral crustaceans and to what was expected by the habitat safety hypothesis for such individuals (Defeo & Gómez 2005). Ghost crabs probably sense the environment much differently from other small, semi-terrestrial crustaceans inhabiting the supralittoral. One of the major differences is that *Ocypode* has planktonic larvae, while other supralittoral crustaceans undergo direct development. This feature is very important because larval settlement plays an important role in defining benthic

community, and larvae are influenced by substratum properties while they are still in the aquatic environment (Pawlik 1992). Hence, although dissipative conditions do not necessarily favor survival, they could play a more important role during settlement. Another particularity of this group is that its distribution in the supralittoral extends landwards; for insects sharing these characteristics, higher densities have also been found on dissipative beaches (Defeo & McLachlan 2011). Ghost crabs are also substantially larger than other supralittoral crustaceans, which may imply that the resistance offered by the sediment does not pose an important hindrance for these individuals. Conversely to the higher densities on dissipative beaches, steeper slopes in the species range of occurrence were also related to higher crab densities, attributed to favorable conditions in sheltered beaches. This feature, in turn, corroborated the hypothesis of habitat safety for this group (Defeo & McLachlan 2011). Therefore, although environmental drivers in the supralittoral may affect ghost crabs and other crustaceans differently in fundamental aspects, this pattern is much more related to safety.

In summary, across-beach distribution showed that individuals contracted their distribution landwards during harsh periods (e.g. storm surges), which emphasizes the importance of vegetated areas as a fundamental part of *O. quadrata* habitats. Crab density and mean size tended to increase towards smaller grain sizes; steeper slopes in the crab range of occurrence also favored their abundance. Burrow occupation rate differed according to several factors, including across-shore position, where higher proportions of empty burrows were surveyed landwards. This pattern urges special caution in population studies. The highest burrow occupation rates and higher mean crab sizes were associated with harsher wave conditions. Thus, for monitoring purposes, it is advisable to consider periods after high mortality events, because abandoning the indirect methodology in such cases is not a viable option. Checking and understanding these parameters is of utmost importance to refine the understanding of ghost crab populations and might ideally lead to the development of a framework for these studies from the standpoint of the ecological and management importance of this group.

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