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Ecological distribution of the hermit crab *Dardanus insignis* in shallow waters of the tropical-subtropical transition zone on the Brazilian coast

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Abstract *Dardanus insignis* is the most abundant hermit crab on sublittoral of soft bottoms along the southeastern coast of Brazil. It is among the Decapoda species that structure the macrobenthic community, from shallow regions to deeper areas up to 100 m. This study evaluated the distribution of *D. insignis* in a tropical-subtropical transition zone. In three bays (Ubatumirim, Ubatuba and Mar Virado), sampling was conducted monthly for two years, on four transects parallel to the coastline (at depths of 5, 10, 15, and 20 m), as well as one transect sheltered from wave action, and another in a more exposed area. Environmental variables were monitored in each sampling. The size fractions of coarse, medium and fine sand showed a positive correlation with the distribution of demographic groups on transects 15 and 20 m deep. On the other hand, the mean grain size (Phi) and silt+clay are negatively correlated with the distribution of the species. Adult males and females showed no environmental-specific relationship similar to the juveniles, and ovigerous females were negatively correlated by the bottom temperature. These results reveal that *D. insignis* is found in greater abundance on transects farther from the coastline, places that are less affected by the continual environmental oscillations in coastal regions and which, therefore, offer greater protection and stability for hermit crabs.

Keywords Distribution · Spatial variation · Environmental factors · Diogenidae

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Introduction

Studies on the distribution of marine organisms are essential to obtain information about coastal regions affected by human activity and contamination. Detailed studies of species with important roles in the dynamics of small areas may contribute to understanding the factors controlling their distributions (Mantelatto et al. 2004).

Shallow benthic habitats are structurally complex environments, where a large number of biological and environmental factors (such as inter- and intraspecific relationships or physical changes, respectively) determine habitat quality and generate different stress levels that determine population and community structure and dynamics (Pallas et al. 2006). In shallow marine coastal areas, the marine soft-bottom fauna is frequently composed of a large number of species with different patterns of distribution and temporal dynamics (Van Hoey et al. 2004). Coastal zones of southeastern Brazil are variable environments, directly subject to continental, atmospheric and oceanic influences. The instability of the coastal zone affects the benthic community, determining the patterns of distribution and density and the trophic relationships among the species (Santos and Pires-Vanin 2004).

As described by Boschi (2000), the southern and southeastern coast of Brazil is an area of hydrological and faunal transition, and consequently contains species of various origins in addition to the local endemics. This region harbors a mixture of faunas originating from tropical, subtropical and subantarctic regions (Sumida and Pires-Vanin 1997). Located along the northern coastline of the state of São Paulo, the Ubatuba region is an important area for crustacean research (Mantelatto and Fransozo 2000). The spatial and temporal distribution of a species results from aspects of the animal's biology such as the feeding mode, behavior and local characteristics (Negreiros-Fransozo et al. 1997; Sant'Anna et al. 2006).

Hermit crabs are an important part of intertidal benthic communities over much of the continental shelf (Fransozo and Mantelatto 1998). The red brocade hermit crab *Dardanus insignis* (Saussure 1858) occurs in almost all the western Atlantic, from North Carolina (USA) to Argentina. In Brazil, it is distributed from Rio de Janeiro to Rio Grande do Sul, over a wide depth gradient from 1.5 to 500 m (Melo 1999). It is the most abundant hermit crab of soft bottoms off southeastern Brazil (Fransozo et al. 2011, 2012; Furlan et al. 2013). *D. insignis* is classified as one of the species that structure the benthic megafauna, from shallow regions to depths greater than 100 m (Pires 1992; De Léo and Pires-Vanin 2006). The abundance of this species in relation to the number of coexisting species of hermit crabs in this area (Fransozo et al. 1998, 2008; Mantelatto and Garcia 2002) is puzzling. Several recent studies have described some features of *D. insignis*, including the post-embryonic development (Hebling and Mansur 1995), fecundity (Miranda et al. 2006), and population dynamics (Branco et al. 2002; Fernandes-Góes et al. 2005). However, the scarcity of studies on its distribution, as well as the spatio-temporal relationships to environmental variables, leaves a knowledge gap to be filled, the answers to which may reveal patterns that help us unravel the reasons for its great abundance along the southeastern Brazilian coast. To investigate the hypothesis that environmental stability is correlated with the abundance and the distribution pattern of *D. insignis*, this study investigated the spatial-temporal variation of the red brocade hermit crab in shallow water, as well the relationship among demographic groups and environmental variables.

Materials and methods

Study area

In this tropical/subtropical portion of the Brazilian coast, the "Serra do Mar" coastal range nears the Atlantic Ocean, enclosing a narrow coastal plain. The northern coast of São Paulo State is markedly sinuous, forming many embayments that have some typical features of semi-confined environments. The study area comprised the shallow waters of three bays (Ubatumirim, Ubatuba and Mar Virado) on this coast. Ubatumirim Bay faces southwest, with several small islands close to its mouth; Ubatuba Bay faces east and has a seaward constriction formed by rocky projections; and the seaward end of Mar Virado Bay faces southeast (Mahiques 1995).

Field collections

Hermit crabs were collected monthly during 1998 and 1999 in Ubatumirim, Ubatuba and Mar Virado bays. Six transects were established in each bay: at depths of 5, 10, 15, and 20 m (parallel to the beach line), as well as one transect in an area sheltered (She=7.5 m) from wave action, and another in a more exposed area (Exp=10 m) (Fig. 1). A shrimp-fishing boat equipped with double-rig nets (mesh size 20 mm and 15 mm at the cod end) was used for trawling. In each trawl, the nets were deployed for 2 km over a period of 30 min, covering an area of approximately 18,000 m^2.

Environmental variables

Monthly measurements for each transect, the bottom and surface water temperatures and bottom salinity were recorded using a mercury thermometer attached to a Nansen bottle and an optical refractometer. An ecobathymeter coupled with global positioning system (GPS) equipment was used to record depths in meters at the sampling sites. Sediment samples were collected in each season with a Van Veen grab sampler, sampling a bottom area of 0.06 m^2 to measure the organic matter content (%) and grain size of the sediment.

The sediment was dried at 70 °C for 72 h in an oven. The sediment organic matter content (%) was obtained through ash-weighing: 3 aliquots of 10 g each per station were placed in porcelain crucibles and incinerated for 3 h at 500 °C. The samples were then re-weighed to calculate the organic-matter content. The sediment remaining after analysis of the organic matter was re-dried and passed through a series of sieves with graduated mesh sizes, following the Wentworth (1922) scale. All the procedures for sediment analysis followed Håkanson and Jansson (1983) and Tucker (1988).

Laboratory procedures

After each trawl, all collected material was inspected, frozen, and transported to the laboratory, where the samples were kept until analysis. Hermit crabs were identified according to Melo (1999). All individuals of *D. insignis* were counted, manually removed from their shells, sexed based on the position of the gonopores (on the coxa of the third pair of pereiopods in

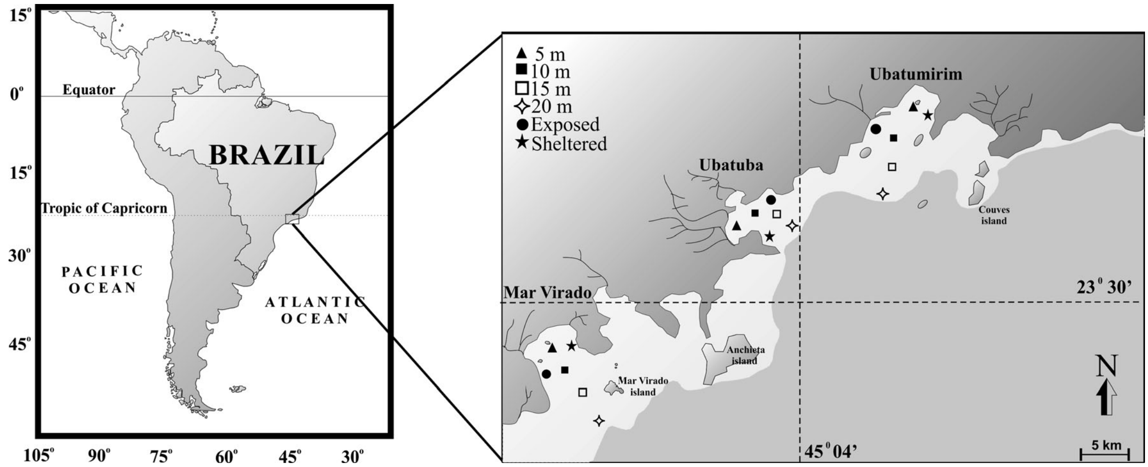

Fig. 1 Map showing the locations of Ubatumirim, Ubatuba and Mar Virado Bays and the sampling depths

females and fifth pereiopods in males), and had their cephalothoracic shield length (CSL) measured with a caliper (0.10 mm). Juveniles were classified based on size, shape and color of gonads observed under a stereomicroscope (gonad thin and translucent, undifferentiated for males and females) (Lancaster 1988).

Statistical analyses

Abundance data were evaluated for normality by the Shapiro-Wilk normality test (Shapiro and Wilk 1965). When not normal, the data were log-transformed (log x+1) and an analysis of variance (one-way ANOVA) was performed in order to assess the differences in abundance among seasons (temporal analysis) and among transects (spatial analysis). The length (CSL) of specimens in each demographic group of each bay was compared by one-way ANOVA. The Tukey multiple comparison test, at the 5-% probability level, was applied to identify differences among the sample means (Zar 1999). The differences in sex ratio were tested for significant divergence from the expected 1:1 ratio, by a binomial test (Wilson and Hardy 2002).

Data for the abundance of each demographic group in each bay and transect were organized in a two-factor contingency table to conduct a correspondence analysis (CA) for each of the demographic groups separately. During the CA, the associations of both types of variables (demographic group and spatial abundance) were summarized by the frequency of each table cell, and then positioned in a geometric dimensional space, since the positions of each line and column were consistent with the associations of the table (as performed by Frameschi et al. 2013, 2014). Statistical significance of the eigenvalues and proportion was assessed using the chi-squared test with a simulated *p*-value (based on 2000 randomizations) (Nenadic and Greenacre 2007).

A redundancy analysis (RDA) was used to detect possible relationships between fluctuations in the abundance of demographic groups and the environmental variables measured. We used the RDA and not the canonical correspondence analysis (CCA) for being the canonical version of the main component analysis (PCA), and used the direct algorithm (Anderson 1996; Peres-Neto et al. 2003; Peck 2010). RDA does not affect the choice of running the analysis in an array covariance or correlation, however, since it concerns selection of variables response using the adjusted coefficient of determination (Zar 1999; Dormann et al. 2007; Jones et al. 2008; Peres-Neto and Legendre 2010). Randomization tests (Monte Carlo test, 999 permutations), which provided *p*-values, were performed to check the validity of the PCA axis, and to check the linear relationship between response and explanatory matrices, and association between the first and second sets of sample unit ordination scores in RDA analyses (ter Braak 1986). *P*-values from these randomization tests indicate the confidence level of the predictions (Peck 2010). The multivariate analyses were run in PC-ORD (version 6, Mccune and Mefford 2011).

Results

Spatio-temporal variation

In 432 hauls made during 24 months, 3169 hermit crabs were caught, 2232 in the first year and 846 in the second year. In both periods, the abundance of D. *insignis* was higher in Ubatuba Bay (1st year=1319, 2nd year=357) compared with Ubatumirim Bay (1st year=557, 2nd year=283) and Mar Virado Bay (1st year=447, 2nd year=206). The abundance of hermit crabs was significantly different between the bays (df=2; F=14.42, $P<0.01$) and study periods (df=1; F=3.84, $P<0.01$). The highest abundance of *D. insignis* during 1998 occurred in winter (df=7; F=1.123, $P<0.01$). Temporal variation in the abundance of males and females followed the

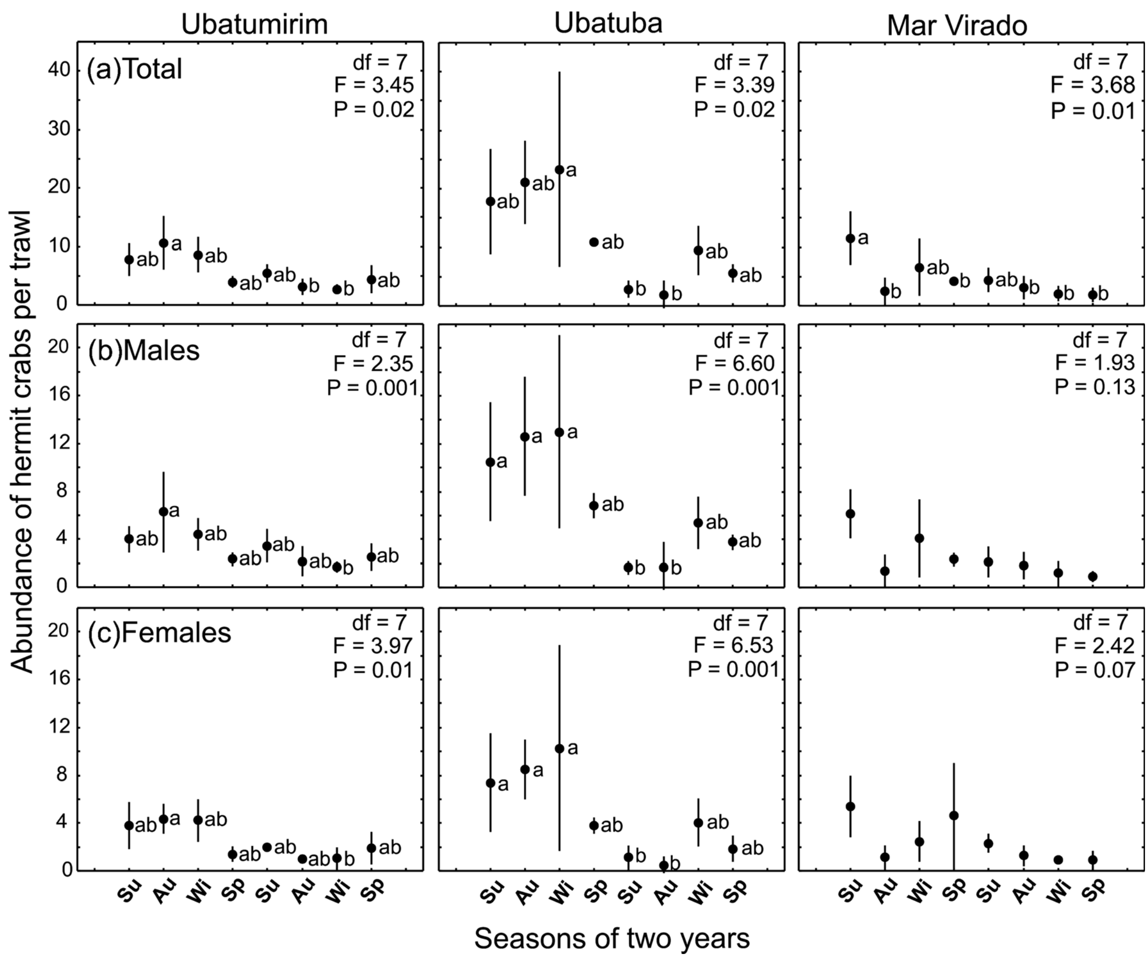

Fig. 2 Mean abundance (*point*) and standard deviation (*line*) of *Dardanus insignis* caught per trawl in each bay by season of the year. Values in each figure indicate results of the ANOVA test. Values with at least one letter in common after each point in the graph did not differ statistically (ANOVA; *a posteriori* Tukey test; $P<0.05$)

same pattern as the total abundance in each bay (Fig. 2). The sex ratio over time was skewed toward males in all three bays. Higher proportions of females were observed during the spring and summer (Table 1).

Hermit crabs were more abundant on the deeper transects, at 20 m and 15 m (df=17; $P<0.05$; Fig. 3), with the exception of the protected transects (She) and exposed (Exp) in Ubatuba Bay. Males and females occupied most transects in similar proportions, with rare exceptions (Table 2). The largest adult males were captured in UBA (Fig. 4). No difference was observed in the sizes of females and young between the bays. Females were significantly smaller than males in all the bays (Fig. 4).

Table 1 Number of *Dardanus insignis* hermit crabs caught and the sex ratio in each bay and season, on the northern coast of São Paulo State, Brazil. Numbers in bold indicate the significance of the sex ratio (df=1; $P<0.05$) and * means=presence of ovigerous females

		Ubatumirim			Ubatuba			Mar Virado		
		Males	Females	M:F	Males	Females	M:F	Males	Females	M:F
1998	Summer	72	68*	0.94	189	133*	**0.70**	111	97	0.87
	Autumn	113	78	**0.69**	227	153	**0.67**	25	21	0.84
	Winter	79	76*	0.96	234	186*	0.79	74	44	**0.59**
	Spring	42	29*	0.69	123	74*	**0.60**	42	33	0.79
1999	Summer	62	36	**0.58**	30	21	0.70	38	41	1.08
	Autumn	39	18	**0.46**	26	9	**0.35**	33	23	0.70
	Winter	30	19	0.63	97	73*	0.75	22	16	0.73
	Spring	45	34*	0.76	68	33*	**0.48**	17	16*	0.94

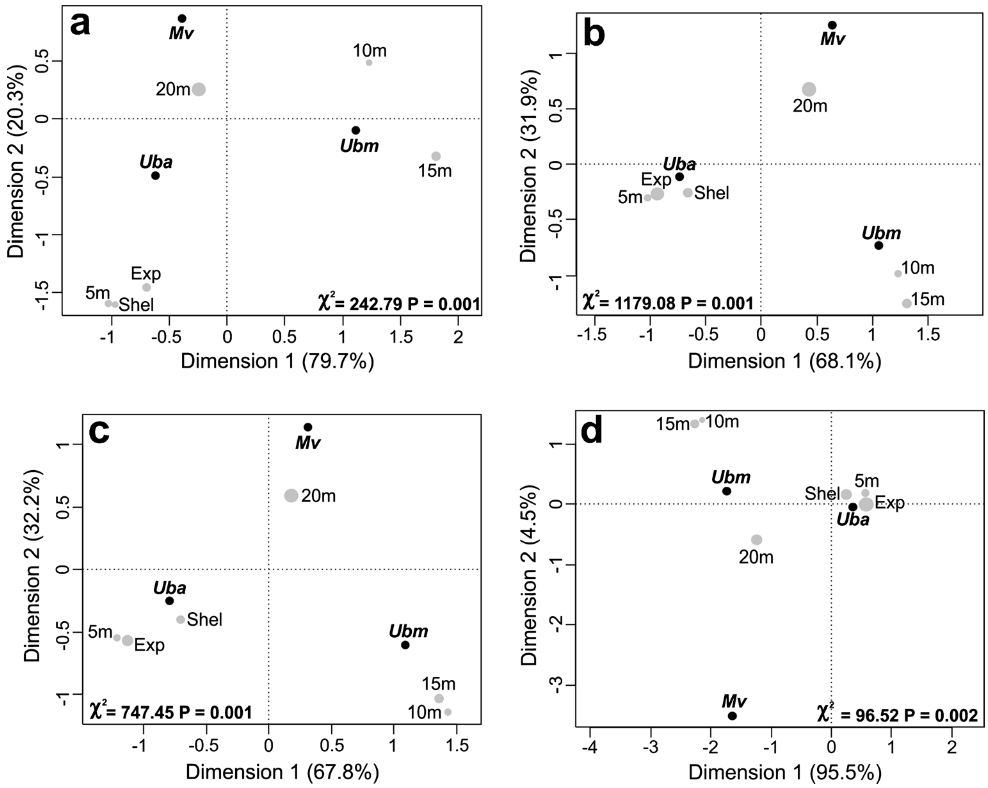

Fig. 3 Distribution of the abundance of *Dardanus insignis* on transects in three bays, indicating the differential distribution relative of each demographic groups. (**a**) Abundance of juveniles; (**b**) Abundance of adult males; (**c**) Abundance of adult females; (**d**) Abundance of ovigerous females. The values in each figure indicate the correspondence analysis (CA) results, and the statistical significance of the proportions for analysis performed for each group separately

Relationship between abundance and environmental variables

The RDA permutation test revealed that the observed eigenvalue for the first axis (RDA1) was significant, allowing us to reject the null hypothesis of no structure between the matrices, indicating that the patterns of association were identified (Table 3). This permutation also showed that the variation observed between the fitted scores and the scores on the space of the response variable was significant, and the first two axes accounted for 53.1 % of the RDA variation in demographic groups of *D. insignis* (Fig. 5). Correlations between environmental variables and the ordination axes showed that the coarse, medium and fine sand particle size fractions showed a positive correlation with the distribution of demographic

Table 2 Number of each demographic group of *Dardanus insignis* (M=males; F=females; OF=ovigerous females) and sex ratio (M:F) in each bay and on each transect, on the northern coast of São Paulo State, Brazil. Values with at least one letter in common on the line do not differ statistically ($P<0.05$; *a posteriori* Tukey test). n=total of individuals; *=(df=11; $P<0.05$)

	Transects	Ubatumirim					Ubatuba					Mar Virado				
		n	M	F	OF	M:F	n	M	F	OF	M:F	n	M	F	OF	M:F
1998	**20 m**	261 **a**	141 **a**	113 **a**	7	1:0.8	394 **b**	211 **b**	174 **b**	9	1:0.9	423 **a**	235 **a**	188 **a**	-	1:0.8*
	15 m	203 **a**	114 **b**	85 **b**	4	1:0.8	15 **c**	8 **b**	7 **bc**	-	1:0.8	7 **b**	4 **b**	3 **b**	-	1:0.7
	10 m	42 **bc**	15 **cd**	26 **b**	1	1:1.8	3 **c**	2 **b**	1 **bc**	-	1:0.5	3 **b**	2 **b**	1 **b**	-	1:0.5
	5 m		-	-	-	-	24 **c**	12 **b**	10 **bc**	2	1:1		-	-	-	-
	Exp	31 **bc**	24 **cd**	7 **b**	-	1:0.3*	876 **a**	537 **a**	258 **a**	81	1:0.6*	3 **b**	3 **b**	-	-	-
	She	20 **bc**	12 **cd**	5 **b**	3	1:0.7	7 **c**	3 **b**	4 **bc**	-	1:1.3	11 **b**	8 **b**	3 **b**	-	1:0.4
1999	**20 m**	108 **b**	60 **c**	37 **b**	11	1:0.8	102 **c**	58 **b**	42 **bc**	2	1:0.8	188 **b**	100 **b**	86 **b**	2	1:0.9
	15 m	142 **ab**	90 **c**	49 **b**	3	1:0.6*	18 **c**	13 **b**	5 **bc**	-	1:0.4	14 **b**	8 **b**	6 **b**	-	1:0.8
	10 m	9 **bc**	7 **cd**	2 **b**		1:0.3	2 **c**	1 **b**	1 **bc**	-	1:1	1 **b**	1 **b**	-	-	0
	5 m	1 **bc**	1 **cd**	-	-	0	15 **c**	8 **b**	5 **bc**	2	0		-	-	-	0
	Exp	8 **c**	7 **cd**	1 **b**	-	1:0.1*	4 **c**	-	4 **bc**	-	0		-	-	-	0
	She	15 **bc**	11 **cd**	3 **b**	1	1:0.4	216 **b**	141 **b**	45 **bc**	30	1:0.5*	3 **b**	1 **b**	2 **b**	-	1:2

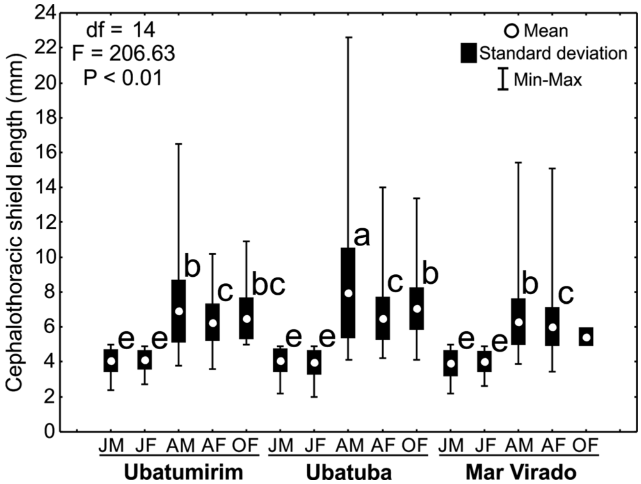

Fig. 4 Mean, standard deviation, and minimum (Min) and maximum (Max) size of cephalothorax shield length for demographic groups of *Dardanus insignis* in each bay. Values with at least one letter in common on the line did not differ statistically (ANOVA; *a posteriori* Tukey test; $P<0.05$)

groups. On the other hand, the mean grain size (Phi) and silt+clay had negative correlation with the distribution of the species (Fig. 5). According to the correlation values (Table 3), the latter variables were most important in explaining the variability in the distribution of demographic groups of *D. insignis*. Juveniles of both sexes were positively associated with the particle size fractions that affected axis 1 (see Table 3). Adult males and females showed no environmental-specific relationship similar to the juveniles, but did show a negative relationship with the mean grain size. The distribution of ovigerous females was negatively correlated with the bottom temperature.

Table 3 Summary results of redundancy analysis (RDA) for each demographic group of *Dardanus insignis* in a tropical-subtropical transition zone on the coast of Brazil. Values are correlations among the respective variables with ordination axes. Values in **bold** indicate the highest correlations

	Axes		*P* (Monte-Carlo permutation test)
	RDA1	RDA2	
Summary statistics of ordination axes			
Eigenvalue (total inertia=0.792)	0.275	0.146	0.005
Cumulative % variation explained	34.7	53.1	
Species-predictor correlation	0.727	0.556	0.005
Juvenile Males (JM)	**0.715**	−0.116	
Juvenile Females (JF)	**0.618**	−0.129	
Adult Males (AM)	**0.794**	−0.020	
Adult Females (AF)	**0.795**	0.071	
Ovigerous Females (OF)	**0.471**	0.261	
Bottom Temperature (BT)	**−0.481**	0.050	
Bottom Salinity (BS)	**0.038**	0.069	
% Organic Matter (OM)	−0.148	**−0.182**	
Mean grain size (Phi)	**−0.653**	0.059	
Biodetritus fragments (BDF)	**0.270**	−0.040	
Very coarse sand (VCS)	**0.476**	0.122	
Coarse sand (CS)	**0.740**	0.195	
Medium sand (MS)	**0.810**	0.156	
Fine sand (FS)	**0.668**	0.377	
Very fine sand (VFS)	−0.112	**0.132**	
Silt and clay (S+C)	**−0.544**	−0.401	

Discussion

The three bays differed with respect to environmental variables. The southeastern coast of Brazil is affected by three water masses (Coastal Water - CW, Tropical Water - TW, and South Atlantic Central Water - SACW) with different distribution patterns in summer and winter (Castro-Filho et al. 1987). These patterns are responsible for seasonal changes in temperature, salinity and nutrient concentration (Costa et al. 2000). According to Mahiques et al. (1998), the direction of the opening of each bay, and the presence of physical barriers make the physical characteristics act at different intensities throughout time and space. The sediment characteristics differed among the bays, reflecting changes in the predominance of the finer sediment fractions (very fine sand, silt and clay) from south to north. These changes result from more homogeneous hydrodynamics, because of the presence of physical barriers represented by the islands of São Sebastião and Mar Virado, reflecting the formation of an area of deposition of fine sediments, especially silt, in Mar Virado Bay, in relation to Ubatumirim (Pires-Vanin et al. 1993).

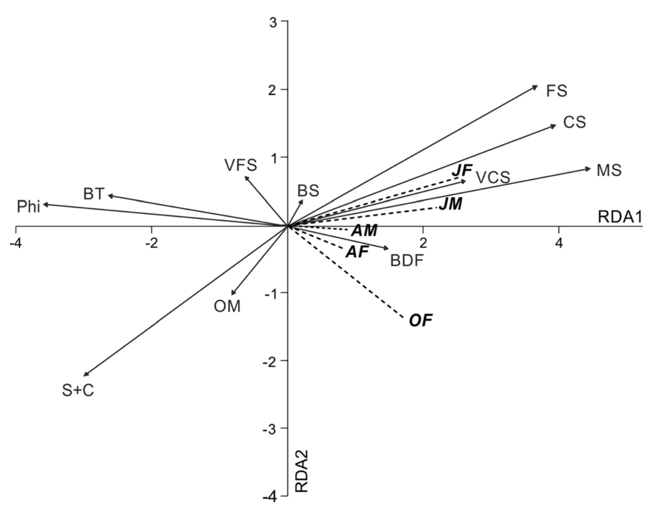

Fig. 5 Correlation biplot of the redundancy analysis (RDA) of variations in environmental variables (indicated by *solid arrows*) of demographic groups of *Dardanus insignis* (indicated by *broken arrows*). Refer to Table 3 for codes of each demographic group and environmental variables

The results also reveal alterations in the texture of the sediment according to depth, during the two study periods. According to Mahiques et al. (1998), the sediment of the inner parts of the bays is mainly composed of silt+clay, with higher organic-matter content, due to the local hydrodynamics that allow the deposition of fine sediments in these locations. Beginning at 15 and 20 m, the influence of the open sea is stronger, with no physical obstacle and little influence from the coast and land. This leads to more homogeneous sediment, with a predominance of coarse sediments and lower organic-matter content (Soares-Gomes and Pires-Vanin 2003).

According to Pires (1992), the diversity, occurrence and abundance of benthic macro-organisms are strongly related to the complexity of micro-environments. This relationship is determined by the composition of the substrate, which can be used as shelter, a feeding site and a nutritional resource (Abele 1974). The significant numbers of *D. insignis* on transect Exp of UBA (of 1998) can be explained by the high rates of deposition of sediment and organic matter originating from the continent. According to precipitation records, rainfall was especially intense between winter 1997 and winter 1998 (CIIAGRO 2013), causing a drastic change in the composition of the sediment from the nearest coastal regions, which can explain the high abundance of *D. insignis* in this transect in Ubatuba Bay during the autumn and winter of 1998. According to Posey et al. (1996), large amounts of rainfall altered the characteristics of the sediment, determining the presence/absence of benthic organisms, especially those which show a preference for firmer substrate.

The results obtained here allowed us to establish a relationship between the abundance of the hermit crab *D. insignis* and the medium and coarse sand fractions. This sediment characteristic seems to limit the distribution of this species to the transects farther than 15 m from shore. The sediment also seems to account for the differential occupation of young compared to adults. According to Hazlett (1981), the different stages of ontogenetic development in hermit crabs directly affect the differential occupation of space, especially when individuals are young or when they are ovigerous (Pardo et al. 2007).

Fransozo et al. (2008, 2012) suggested that species characteristic of unconsolidated substrate in the subtropical region of Brazil have higher diversity and richness during the summer, but species of decapods reach their highest abundance during the colder months of the year (autumn and winter). This pattern is consistent with the results obtained here for *D. insignis*, as well as those of Fernandes-Góes et al. (2005) and with the record of Branco et al. (2002) for the same species, respectively, for the bays of Ubatuba and Armação do Itapocoroy in southern Brazil. This higher abundance in the colder months may be due to seasonal reproduction, which, according to Miranda et al. (2006), occurs in the warmer months of the year (spring and summer). This breeding period coincides with the months of higher primary productivity, since the entrance of SACW in these seasons promotes nutrient enrichment in the region, increasing the available food for planktonic larvae (De Léo and Pires-Vanin 2006).

The population of *D. insignis* studied here showed temporal and spatial oscillations in the sex ratio, always in favor of males, which also reached larger sizes than females, demonstrating the characteristic sexual dimorphism of this hermit crab. Similar higher abundances and larger size of males compared to females were also reported by Branco et al. (2002) for a population of *D. insignis* on the southern coast of Brazil, as well as for other hermit crabs, including *Loxopagurus loxochelis* (Moreira, 1901) and *Petrochirus diogenes* (Linnaeus, 1758) studied by Bertini and Fransozo (1999) and Bertini et al. (2004), respectively. According to Gherardi (1991), an unequal sex ratio can be explained by several factors, including differential migration by demographic groups, ontogenetic development, growth, and mortality between the sexes. Hazlett (1981) stated that in hermit crabs, these factors are determined by an essential feature: gastropod shells. Also according to this author, sexual dimorphism favors a higher abundance of males, because they reach larger sizes. This statement can also be extended to *D. insignis*. Young (immature) specimens of this species do not show differences in growth, but as adults, males and females use energy in different ways, since upon reaching sexual maturity (Bertini et al. 2004). According to Abrams (1988), combined with the availability of the gastropods shells, three other factors can interfere at the sexual dimorphism of hermit crabs: (1) males of larger size have a greater chance of obtaining females for copulation as a function of intraspecific fights; (2) the difference in energy available for growth, with males growing faster as they do not spend energy in egg production, but use their full energy for structural metabolism; and (3) the larger reproductive effort belongs to the males due to their ability to fertilize more than one female. These factors can modulate directly the sex ratio and size of *D. insignis*.

Environmental temperature and salinity factors had little influence on the distribution of *D. insignis*, since the species was most abundant on transects with wider variations of temperature and salinity. Possibly the local variations are well within the tolerance limit of this species. The composition of the sediment appeared to be the most important environmental characteristic affecting the distribution of *D. insignis*. Thus, for species that have an exclusively benthic habit, such as hermit crabs, the type of substrate seems to be essential for their occurrence, which explains the high correlation of all demographic groups of *D. insignis* with the mean grain size (Phi) and the granulometric fractions. The nature of the substrate may influence not only the abundance and frequency of individuals, but also the ease of burying, especially during the molting process (Rebach 1974). The type of substrate also seems to coincide with habitats that harbor a wider diversity of gastropods (Dias et al. 2011), resulting in greater availability of shells. The abundance and richness of shells is a limiting factor for the distribution and abundance of populations of hermit crabs (Childress 1972; Bertini and Fransozo 2000; Meireles et al. 2003). Because of these factors, these species rarely choose a substrate other than that which is predominantly sand.

The decrease in numbers of hermit crabs during the year of 1999 can be explained by the process of migrating to deeper regions, since the sediment in the bays changed more during periods of heavy rainfall, making the sampling areas less favorable for the species. The great abundance of *D. insignis* in southeastern Brazil is not only attributed to its adaptation to environmental conditions predominant in the region of study, but also can be attributed to a large number of variables, including (1) the highest fertility rate of all species coexisting in the study region (Miranda et al. 2006), (2) robustness in shell occupation, using a wide diversity of gastropod species (Fransozo et al. 2008), and (3) good availability of shells, an indispensable resource for rapid growth of hermit crabs (Lancaster 1990). This study allowed us to add these variables: (4) the sediment found in the region is conducive to the establishment of this species, and (5) males are larger and more abundant than females, favoring intra- and interspecific competition for shells (Yoshino and Goshima 2002).

Thus, the present study reveals that occurrence of *D. insignis* in regions less than 15 meters deep was seasonal, caused by considerable environmental changes. The environmental stability on transects farther from the coastline is correlated with the continuous abundance and the distribution pattern of this species, since these places are less affected by the continual environmental oscillations and which, therefore, offer greater protection and stability for hermit crabs.

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