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Patterns of distribution of the hermit crab *Loxopagurus loxochelis* (Moreira, 1901) (Decapoda, Diogenidae) in two coastal areas of southern Brazil

Patrones de distribución del cangrejo ermitaño *Loxopagurus loxochelis* (Moreira, 1901) (Decapoda, Diogenidae) en dos áreas de la costa sudeste de Brasil

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Resumen.- El presente estudio determinó el patrón de distribución del cangrejo ermitaño *Loxopagurus loxochelis* por medio una comparación de la captura, profundidad y factores ambientales en dos bahías separadas (Caraguatatuba y Ubatuba) del estado de São Paulo, Brasil. También se evaluó la influencia de parámetros medioambientales sobre la distribución de machos, hembras y hembras ovígeras. Los cangrejos se recolectaron mensualmente en las dos áreas de estudio, durante un año (julio de 2002 a junio de 2003), en siete profundidades, entre 5 y 35 m. Se registraron los factores abióticos: salinidad (psu) y temperatura (°C) en la superficie así como en el fondo, contenido de materia orgánica (%) y composición del sedimento (%). Se recolectó un total de 366 cangrejos en Caraguatatuba y 126 en Ubatuba. La mayor frecuencia de individos se obtuvo a una profundidad de 20 m en Caraguatatuba durante el invierno (julio) y a una profundidad de 25 m en Ubatuba durante el verano (enero). Las mayores frecuencias se registraron en áreas con salinidades entre 34 y 36 psu en el fondo, temperaturas entre 18 y 24°C también en el fondo y sustratos con bajos porcentajes de materia orgánica, grava y lodo, así como con altas proporciones de arena. No se encontró correlación significativa entre la frecuencia total de organismos y los factores medioambientales analizados en ninguna de las dos regiones. Estos resultados sugieren que algún otro factor ambiental o interacción biótica podría ser responsable de los patrones de distribución de *L. loxochelis* en las regiones estudiadas, consideradas zonas limítrofes de la distribución norte del cangrejo ermitaño.

Palabras clave: Crustacea, factores medioambientales, análisis cladístico, abundancia

Abstract.- The present study determined the distribution pattern of the hermit crab *Loxopagurus loxochelis* by a comparison of catch, depth and environmental factors at two separate bays (Caraguatatuba and Ubatuba) of São Paulo State, Brazil. The influence of these parameters on the distribution of males, non-ovigerous females and ovigerous females was also evaluated. Crabs were collected monthly, over a period of one year (from July/2002 to June/2003), in seven depths, from 5 to 35 m. Abiotic factors were monitored as follows: superficial and bottom salinity (psu), superficial and bottom temperature (°C), organic matter content (%) and sediment composition (%). In total, 366 hermit crabs were sampled in Caraguatatuba and 126 in Ubatuba. The highest frequency of occurrence was verified at 20 m during winter (July) in Caraguatatuba and 25 m during summer (January) in Ubatuba. The highest occurrences were recorded in the regions with bottom salinities ranging from 34 to 36 psu, bottom temperatures from 18 to 24°C and, low percentages of organic matter, gravel and mud; and large proportion of sand in the substrate. There was no significant correlation between the total frequency of organisms and the environmental factors analyzed in both regions. This evidence suggests that other variables as biotic interactions can influence the pattern of distribution of *L. loxochelis* in the analyzed region, which is considered the limit of the northern distribution of this species.

Keywords: Crustacea, environmental factors, clustering analysis, abundance

Introduction

The presence of a species in a certain habitat depends on many conditions. Any condition that exceeds the tolerance limits is called a limiting condition or limiting factor. This concept is not restricted to physical factors, since the biological inter-relationships are also important to the abundance and distribution of the organisms in nature (Odum 2001).

There is consensus among researchers that sea benthic species have their distribution and abundance limited by depth, temperature, texture of the sediment, amount of organic matter, salinity, beyond the intra and inter-specific relationships, and these environmental factors can act isolated or jointly (Abele 1974, Meireles *et al.* 2006).

The interactions between organisms and abiotic features determine models of temporal and spatial distribution. The concept of 'pattern' implies the repetition of a fact, which usually occurs on natural systems, and this repetition is not identical every time, although is similar. The existence of a repetition means that there is the possibility of a prediction on the distributional patterns (Melo 1985).

Some structural parameters of a community, such as density, biomass, richness and specific diversity, vary on a spatial and temporal scale along the continental platform considering the depth. This variation is the result of interactions among several physical and biological processes, which act in different ways providing distinct conditions to the benthic communities (Soares-Gomes *et al.* 2002). Due to such variation, it is necessary a continuous study of the benthic population structure.

Temperature is the main feature that controls the distribution and activity of marine animals, acting as a limiting factor in the reproduction, growth and distribution of organisms (Soares-Gomes & Figueiredo 2002). Therefore, rarely a species is homogeneously distributed in its occurrence area, because displacements may occur according to the environmental conditions or even due to different demands, during several life phases (Mantelatto *et al.* 1995).

One of the variables considered of extreme importance in the distribution of marine benthic crustaceans is the sediment texture (Abele 1974). According to Negreiros-Fransozo *et al.* (1997) and Fransozo *et al.* (1998) the sediment texture and the amount of organic matter were the factors that mostly influenced the distribution and maintenance of anomurans' populations in shallow waters of northern coast of São Paulo State. In the case of benthic animals, the type of substrate represents the main selective factor that determines the life habit and adaptations of these organisms (Pérès 1961).

Hermit crabs are an important, abundant and very successful marine macrozoobenthic organisms, encompassing representatives that inhabit the infralittoral to deep zones, distributed worldwide (Lancaster 1988). There are 48 hermit crab species described for Brazilian waters (Ayres-Peres & Mantelatto 2008), however, there are a few studies related to distributional pattern in a continued and systematic form emphasizing the abiotic factors influencing those patterns (Rieger & D'Incao 1991, Negreiros-Fransozo *et al.* 1997, Fransozo *et al.* 1998, Bertini & Fransozo 1999, Fernandes-Góes 2000, Branco *et al.* 2002, Bertini *et al.* 2004, Mantelatto *et al.* 2004, Meireles 2006 and Meireles *et al.* 2006).

Considering this promising scenario for ecological studies, we evaluated the distribution pattern of the hermit crab *Loxopagurus loxochelis* (Moreira, 1901) by a comparison of catch, depth and environmental factors at two separate bays of the northern São Paulo coast (Caraguatatuba and Ubatuba). With these findings, we verified the hypothesis that the species has a distribution pattern influenced by depth, demonstrating a preference by areas with low temperature as it was previously postulated in other regions.

Material and methods

Hermit crabs were collected monthly from July 2002 to June 2003, from a shrimp boat equipped with two double-rigged trawling nets (length 11 m, mouth 4.5 m, body mesh diameter 25 mm, cod-end mesh diameter 15 mm). Collections were made once during each month at the seven isobaths (5, 10, 15, 20, 25, 30 and 35 m). Each of seven transects (sites of sampling) (about 1.5 km each) was trawled for a 30 min period, sampling a total area of about 18000 m^2 in both Caraguatatuba (23º36'09" to 23º40'12" S and 45º07'16" to 45º25'35" W) and Ubatuba (23º26'08" to 23º31'57" S and 44º55'28" to 45º03'18" W) regions, northern coast of São Paulo State, Brazil (Fig. 1). According to Castro-Filho *et al.* (1987) these regions are affected by three important water masses, are the South Atlantic Central Water (SACW), Coastal Water (CW), and Tropical Water (TW).

This bathymetric methodology was previously tested and applied during the long-term project on Marine Biodiversity of Coast of São Paulo (BIOTA-FAPESP), aiming to collect macro fauna of decapods in different and representative depths (Meireles *et al.* 2006). After collection, the hermit crabs were frozen. In the laboratory, animals were counted and removed from shells, and the sex was checked (based in the gonopores position). The hermit crabs were measured for cephalothoracic shield length (CSL-mm). All animals were preserved in 80% ethyl alcohol and were deposited in the Crustacean Collection of the Department of Biology, Faculty of Philosophy, Sciences and Letters of Ribeirão Preto, University of São Paulo (CCDB/FFCLRP/USP) under numbers 1485 to 1514.

For seasonal analysis, months were grouped: spring (September, October and November), summer, (December, January and February), autumn (March, April and May) and winter (June, July and August).

Abiotic samples and protocols of analysis followed Mantelatto & Fransozo (1999). An eco-bathymeter coupled with a GPS (Global Positioning System-Garmin®) was used to record depth (m) at sampling sites. In each depth, sediment and water were collected for analysis of the environmental factors (three replications, beginning,

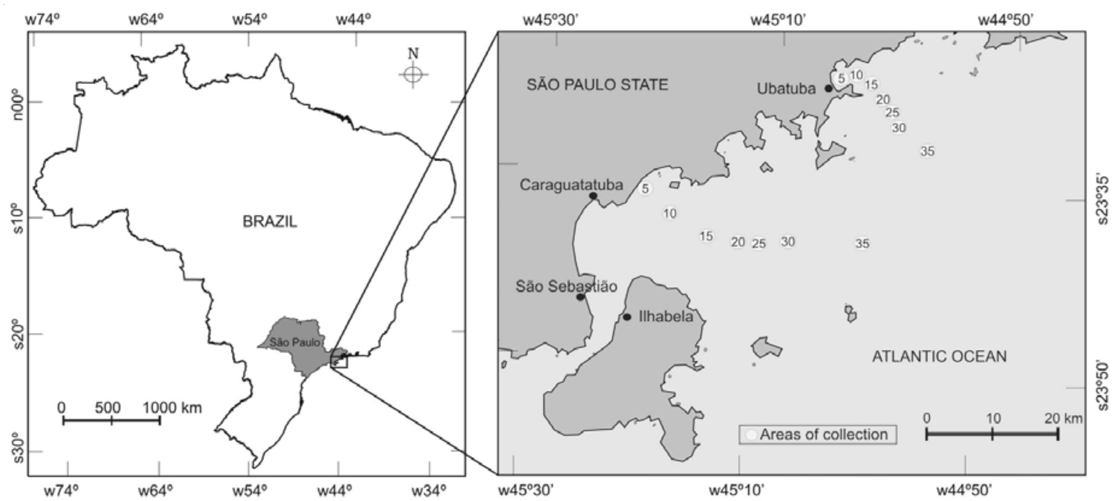

Figure 1

Areas of sampling of *Loxopagurus loxochelis*, northern coast of São Paulo State, Brazil

Las áreas de muestreo de *Loxopagurus loxochelis*, costa norte del Estado de São Paulo, Brasil

middle and end of each transect). Water was collected with a Nansen bottle to register bottom temperature (°C) and salinity (psu). In addition, surface water was collected to register temperature and salinity. Sediment was sampled with a van Veen grab. To separate the different grain size fractions the humid procedure was used; the first stage constituted in separating the silt + clay fraction from the other fractions. Following, two samples of 100 g were separated from sediment, which were washed in a bolter with mesh of 0.063 mm, allowing the passage of silt + clay. After that, the remaining particles were dried in an oven at 70°C for 24 h and subjected to the technique of the distinguishing sieved, by means of six bolters of different meshes (2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm and 0.063 mm), used orderly decreasing. The six different resultant weights of the sieved were grouped in three categories: gravel, sand and mud. The amount of organic matter was obtained by means of weight free from ashes, expressed in percentage. The results of the abiotic factors were organized into classes, to correlate them with the abundance of the hermit crab.

Regressions were used to evaluate the existence of correlation between the number of individuals and each environmental factor (depth, temperature, salinity, organic matter and sediment texture). The environmental parameters cited above were compared by ANOVA (Zar 1996) in relation to depths and season. The significant level was set at 0.05 in all statistical analyses.

Cluster Analyses (Euclidian Distance was used as a measure of dissimilarity to the data analyzed and Unweighted-Pair Group Averaging as link method) were applied with bottom salinity, bottom temperature, amount of organic matter, and sand of the substrate in relation to the depths of the two regions. This analysis carried in Statistica 6.0, was used to verify possible groups in the two different areas; with this result, we checked similarities among sampling sites in each region and within regions and then we determined if there was any relation with the animals distribution.

To detect the existence of patterns within the abiotic factors, sample point ordination was performed using Principal Component Analysis (PCA), with bottom salinity, bottom temperature, amount of organic matter, and sand of the substrate, to reduce the influence of the variation of the different measurement units of variables, the values were $\log_{10}(x+1)$ transformed by means.

Groups of interest frequencies (males, non-ovigerous females, ovigerous females, and juveniles = animals with CSL< 4 mm, according to Ayres-Peres & Mantelatto 2008) were evaluated in relation to depth, month, and season. The Pearson Linear Correlation was applied to determine the relationship among each abiotic factor analyzed, the total animal frequency and the groups of interest (Zar 1996).

The Mantel test, with 5,000 permutations (Sokal 1979, Smouse *et al.* 1986, Manly 1990), was applied to verify the correlation among various abiotic factors (bottom salinity, bottom temperature, organic matter of the substrate, and percentage of sand in the sediment); the other variables were not used to reduce the effect of autocorrelation among the factors and the total frequency of *L. loxochelis* in the two areas, both in function to depth, as well as to the sampled months. The data were $\log_{10}$ (x+1) transformed. This is a non-parametric procedure based on the randomization that generates statistics in significant levels to correlate distances and matrices without specific distribution supposition of probability (Cesaroni *et al.* 1997). The Mantel test works based on permutation and the association between two matrices that can be tested by the 'Z' distribution and then to establish the statistical significance of the matrix correlation (Sokal 1979, Smouse *et al.* 1986, Manly 1990, Cesaroni *et al.* 1997, Bispo 2002). The Mantel test was undertaken on the statistical program NTSYS 2.1 (Rohlf 2000).

Results

Distribution of *Loxopagurus loxochelis*

During the study, 492 hermit crabs were captured: 366 in Caraguatatuba and 126 in Ubatuba. The percentage of the groups of interest occurred similarly in both areas; in Caraguatatuba, 222 males (60.7%), 114 non-ovigerous females (31.1%), and 30 ovigerous females (8.2%), and in Ubatuba, 81 males (64.3%), 38 non-ovigerous females (30.1%), and only seven ovigerous females (5.6%).

The largest number of individuals were collected between depths from 20 to 25 m (more than 80% of the captured animals in the two areas), and at 35 m no hermit crab was collected in either Caraguatatuba or Ubatuba (Table 1). Young individuals were distributed, predominately, at 20 and 25 m. The highest occurrence of ovigerous females was at 20 m in Caraguatatuba, being incipient to the number of the same collection in Ubatuba. Both young individuals and ovigerous females were more numerous on July 2002 in Caraguatatuba and Ubatuba.

Loxopagurus loxochelis presented a large occurrence in July 2002, January 2003, and March 2003, in Caraguatatuba for all of the groups of interest. In Ubatuba, the highest occurrence was in July 2002, January 2003, and June 2003 (Table 1).

In relation to the seasons, there were more animals during the winter in Caraguatatuba, and in summer and winter (respectively) in Ubatuba. Young individuals were more frequent in winter (75.7% of the total) from Caraguatatuba, and in summer from Ubatuba (50% of the total). Ovigerous females were also more frequent in winter in Caraguatatuba.

There was no significant correlation ($r = 0.21$; $P > 0.05$) within the occurrence frequency of all hermit crabs, as well as for males, non-ovigerous females and ovigerous females, with the abiotic factors analyzed individually, for both locations.

Table 1

Abundance of *L. loxochelis* in relation to the depths (5 to 35 m) and months, in Caraguatatuba (CAR) and Ubatuba (UBA) Bays, from July/2002 to June/2003

Abundancia de *L. loxochelis* en relación con las profundidades (5 a 35 m) y meses estudiados en las bahías de Caraguatatuba (CAR) y Ubatuba (UBA) entre julio 2002 y junio 2003

Month	**DEPTHS**														**TOTAL**	
	05		10		15		20		25		30		35			
	CAR	UBA	CAR	UBA	CAR	UBA	CAR	UBA	CAR	UBA	CAR	UBA	CAR	UBA	CAR	UBA
July	01	-	23	-	08	-	154	13	17	05	01	-	-	-	204	18
August	04	-	-	-	-	-	-	-	04	01	02	-	-	-	10	01
September	-	-	01	-	-	-	07	-	-	-	-	-	-	-	08	-
October	-	-	-	-	01	-	-	02	-	01	-	-	-	-	01	03
November	-	-	-	-	-	-	-	04	-	08	-	-	-	-	-	12
December	-	-	-	-	02	01	01	09	02	02	-	-	-	-	05	12
January	11	-	-	01	03	-	29	35	08	04	-	-	-	-	51	40
February	-	-	-	-	-	01	06	02	-	-	03	-	-	-	09	03
March	-	-	01	-	-	-	03	06	39	-	-	-	-	-	43	06
April	-	-	01	-	01	02	10	01	01	-	-	-	-	-	13	03
May	-	-	04	02	-	-	02	07	-	-	01	-	-	-	07	09
June	07	-	03	-	04	-	-	19	01	-	-	-	-	-	15	19
Total	23	-	33	03	19	04	212	98	72	21	07	-	-	-	366	126

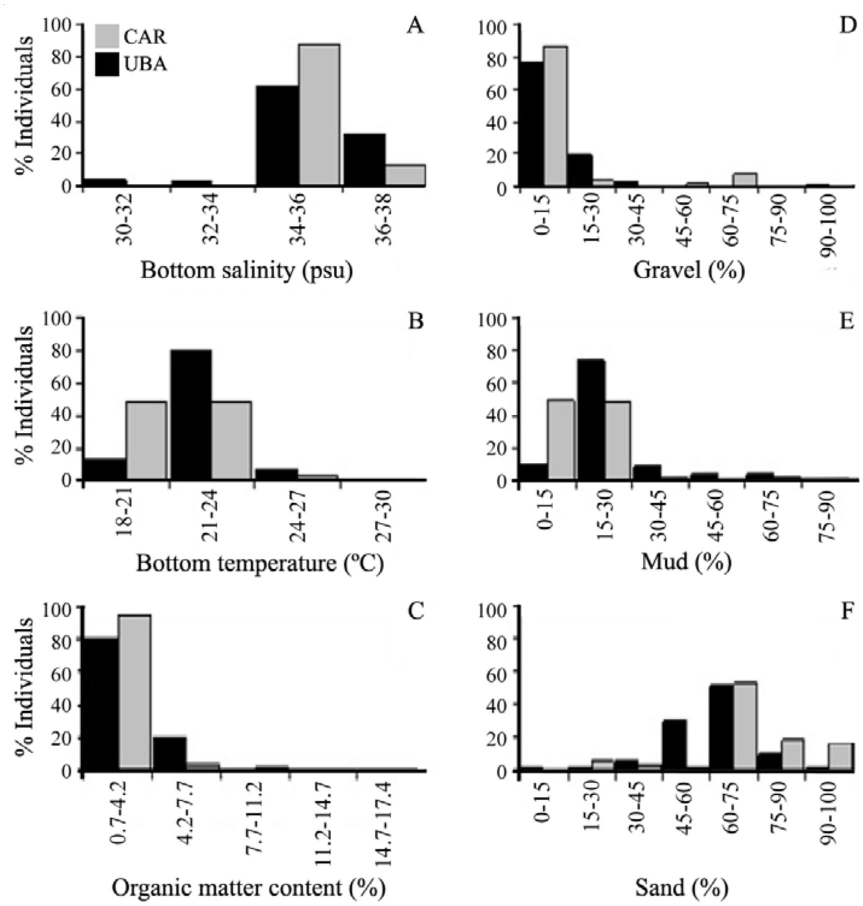

Figure 2

Distribution of the occurrence frequency of *L. loxochelis* in relation to abiotic factor classes analyzed in Caraguatatuba (CAR) and Ubatuba Bays (UBA), during the period of July/2002 to June/2003. A) Bottom Salinity (psu), B) Bottom Temperature (°C), C) Amount of Organic Matter (%), D) Gravel (%), E) Mud (%) and F) Sand (%)

Distribución de la frecuencia de ocurrencia de *L. loxochelis* en relación con los factores abióticos analizados (rangos) en las bahías de Caraguatatuba (CAR) y Ubatuba (UBA) durante el período comprendido entre Julio 2002 y Junio 2003. A) Salinidad de fondo (psu), B) Temperatura de fondo (ºC), C) Cantidad de materia orgánica (%), D) Grava (%), E) Lodo (%) y F) Arena (%)

Using the Mantel's test, significant differences were not found when the total hermit crab frequency was evaluated in relation to the various abiotic features in the different depths and sampled months.

Even though a significant correlation was not detected, evident patterns were observed associated with the individuals' occurrence in amplitude classes of the abiotic factors. There were more hermit crabs in both regions, when the bottom salinity varied from 34-36 psu (Fig. 2A). Higher animal frequencies were found when the bottom temperature was low and when about 90% of the samples were collected between 18-24°C (Fig. 2B).

In relation to organic matter (OM), practically all the animals were collected from locations with the lowest quantities of OM (0.7-4.2%) (Fig. 2C). The sediment composition analysis showed a large percentage of *L. loxochelis*, in both regions, in depths with small gravel proportions (0-20%) and mud (0-40%) in the sediment (Fig. 2D and E, respectively) and large sand proportions (60-100% in the sediment) (Fig. 2F). The PCA analysis confirms a higher hermit crab occurrence in areas with higher bottom salinity, more sand proportions, and less organic matter (Figs. 3 and 4).

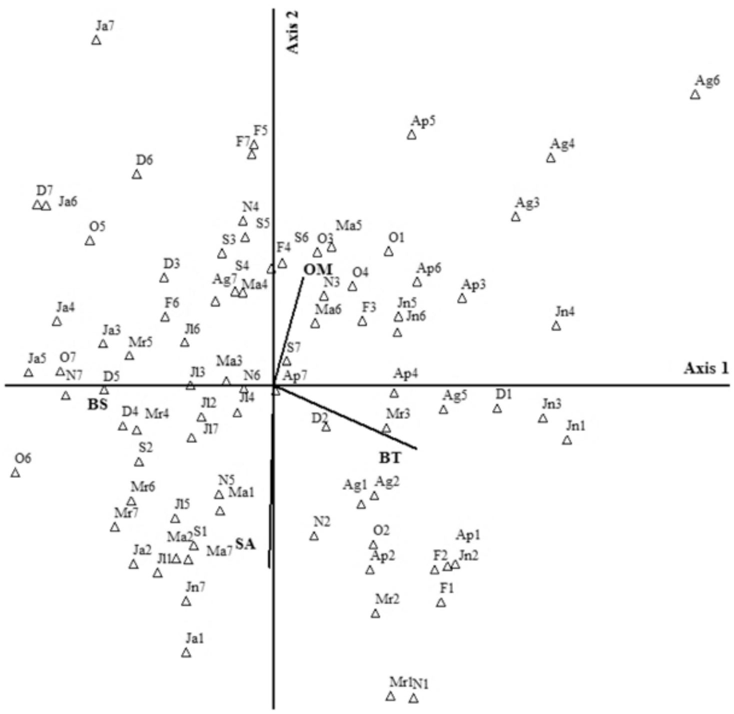

Figure 3

Dispersion diagram of 84 sample units on the axes 1 and 2, obtained by Principal Component Analysis (PCA) in Caraguatatuba. The numbers refer to the transects (1–5 m, 2–10m, 3-15 m, 4-20 m, 5-25 m, 6-30 m and 7-35 m), BS = Bottom salinity, BT = Bottom temperature, OM = Organic matter and SA = Sand. Letters correspond to the sampled months, i.e., from (Jl) July/2002 to (Jn) June/2003

Diagrama de dispersión de las 84 unidades de muestreo sobre los ejes 1 y 2 obtenido por Análisis de Componentes Principales (PCA) en Caraguatatuba. Los números hacen referencia a las transecciones (1-5 m, 2-10m, 3-15 m, 4-20 m, 5-25 m, 6-30 m and 7-35 m), BS: Salinidad de fondo, BT: Temperatura de fondo, OM: Materia orgánica y SA: Arena. Las letras corresponden a los meses, i.e. desde (Jl) julio/2002 al (Jn) junio/2003

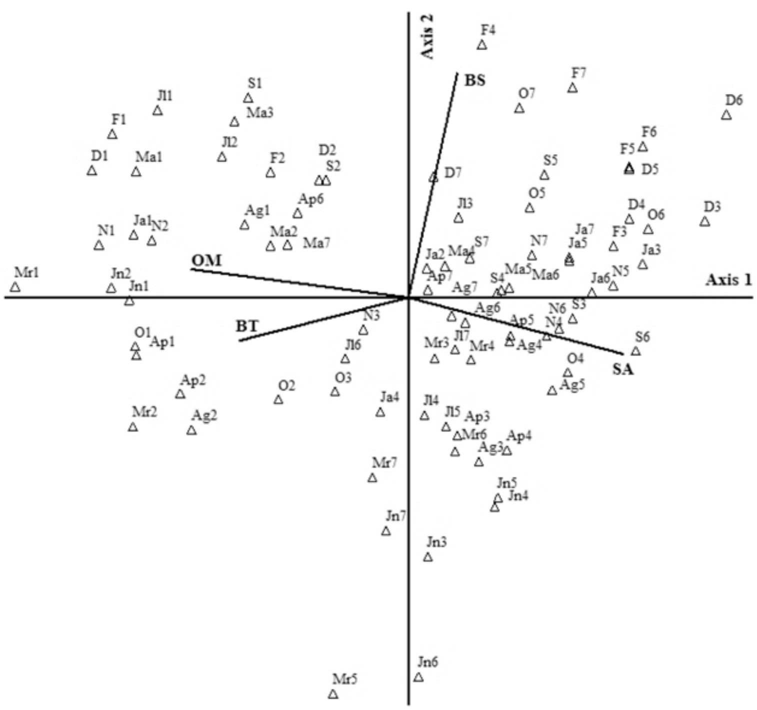

Figure 4

Dispersion diagram of 84 sample units on the axes 1 and 2, obtained by Principal Component Analysis (PCA) in Ubatuba. The numbers refer to the transects (1-5 m, 2-10 m, 3-15 m, 4-20 m, 5-25 m, 6-30 m and 7-35 m), BS = Bottom salinity, BT = Bottom temperature, OM = Organic matter and SA = Sand. Letters correspond to the sampled months, i.e., from (Jl) July/2002 to (Jn) June/2003

Diagrama de dispersión de las 84 unidades de muestreo sobre los ejes 1 y 2 obtenido por Análisis de Componentes Principales (PCA) en Ubatuba. Los números hacen referencia a las transecciones (1-5 m, 2-10 m, 3-15 m, 4-20 m, 5-25 m, 6-30 m and 7-35 m), BS: Salinidad de fondo, BT: Temperatura de fondo, OM: Materia orgánica y SA: Arena. Las letras corresponden a los meses, i.e. desde (Jl) julio/2002 al (Jn) junio/2003

Environmental factors

The mean sampling period temperature and salinity were 23.86 ± 2.56°C and 34.43 ± 1.39 psu in Caraguatatuba, respectively; and 23.86 ± 2.92°C and 34.67 ± 1.09 psu in Ubatuba, respectively. As the amount of organic matter, the average was 3.86 ± 2.29% in Caraguatatuba and 5.22 ± 4.61% in Ubatuba (Tables 2 and 3).

Table 2

Mean seasonal values (average of the seven transects in relation to the months which compose each season) and standard deviation of the environmental factors values in the Caraguatatuba (CAR) and Ubatuba (UBA) Bays, from July/2002 to June/2003

Valores medios estacionales (promedios de las 7 transecciones en relación con los meses del año que componen cada estación) y desvío estándar de los valores de factores ambientales en las bahías de Caraguatatuba (CAR) y Ubatuba (UBA) entre julio 2002 y junio 2003

Season	Area	Superficial Salinity (psu)	Bottom Salinity (psu)	Superficial Temperature (°C)	Bottom Temperature (°C)	Organic Matter (%)
Winter	CAR	32.8 ± 2.09^{a}	33.5 ± 1.88^{a}	22.9 ± 0.70^{a}	22.9 ± 0.81	3.9 ± 2.19^{a}
	UBA	$34.2 \pm 0.92^{A*}$	34.3 ± 1.07	23.3 ± 0.62	22.8 ± 0.68	5.2 ± 1.34^{A}
Autumn	CAR	34.9 ± 0.46^{b}	35.4 ± 0.64^{b}	25.9 ± 2.53^{b}	24.2 ± 1.93	4.2 ± 1.71^{a}
	UBA	34.0 ± 1.40^{AB}	34.9 ± 1.00^{A}	26.4 ± 2.72^{A}	24.5 ± 1.51	5.4 ± 2.50^{A}
Spring	CAR	34.1 ± 0.88^{c}	35.0 ± 0.78^{c}	24.6 ± 2.90^{a}	22.2 ± 1.52^{a}	3.8 ± 0.84^{a}
	UBA	34.3 ± 0.31^{AB}	35.2 ± 0.56^{A}	24.7 ± 4.28^{AB}	21.7 ± 1.64	5.5 ± 1.89^{A}
Summer	CAR	34.7 ± 0.50^{d}	35.1 ± 0.70^{bd}	26.9 ± 0.68^{b}	21.5 ± 1.29^{a}	3.6 ± 2.25^{a}
	UBA	34.7 ± 0.62^{C}	35.8 ± 0.78	26.6 ± 1.81^{AB}	20.8 ± 1.65	4.8 ± 1.00^{A}

*the values with at least one same letter, for the same abiotic factor, did not differ statistically, $P > 0.05$; ANOVA on Ranks; small letters to represent Caraguatatuba and capital letters Ubatuba

Table 3

Mean values reported for depths and registering transects and standard deviation of the analyzed environmental factors in the Caraguatatuba (CAR) and Ubatuba (UBA) Bays, from July/2002 to June/2003

Valores medios y desvío estándar de los factores ambientales analizados en las profundidades y transecciones registrados en las bahías de Caraguatatuba (CAR) y Ubatuba (UBA) desde julio/2002 a junio/2003

Transects (m)	Local	Bottom Salinity (psu)	Bottom Temperature (°C)	Organic Matter (%)
05	CAR	34.2 ± 1.27^{a}	24.5 ± 2.38^{a}	2.3 ± 1.29^{a}
	UBA	34.9 ± 0.63^{A}	24.6 ± 2.29^{A}	11.4 ± 1.89^{A}
10	CAR	34.4 ± 1.13^{a}	23.8 ± 2.16^{ab}	2.3 ± 0.70^{ab}
	UBA	34.6 ± 0.83^{A}	23.3 ± 2.07^{A}	12.1 ± 3.15^{A}
15	CAR	34.7 ± 1.57^{b}	22.9 ± 2.33^{bc}	5.0 ± 1.82^{c}
	UBA	35.1 ± 0.94^{AB}	22.3 ± 2.33^{Ab}	3.6 ± 2.92^{B}
20	CAR	34.9 ± 1.48^{bc}	22.1 ± 1.70^{cd}	6.1 ± 2.68^{cd}
	UBA	34.2 ± 0.88^{AB}	22.2 ± 2.24^{AB}	2.4 ± 1.44^{BC}
25	CAR	35.2 ± 1.30^{bcd}	21.9 ± 1.64^{cde}	4.5 ± 2.22^{cde}
	UBA	35.2 ± 1.33^{B}	21.8 ± 2.38^{ABC}	1.8 ± 0.88^{CE}
30	CAR	34.8 ± 1.73^{bcde}	21.8 ± 1.66^{cdf}	3.7 ± 1.88^{bcef}
	UBA	35.2 ± 1.42^{AB}	21.4 ± 2.10^{BCE}	2.2 ± 0.89^{BF}
35	CAR	35.3 ± 1.00^{bcde}	21.0 ± 1.57^{ef}	3.1 ± 2.23^{abef}
	UBA	35.2 ± 1.23^{AB}	21.6 ± 1.87^{BCE}	3.1 ± 1.30^{BCF}

*the values with at least one same letter, for the same abiotic factor, did not differ statistically, $P > 0.05$; ANOVA on Ranks; small letters to represent Caraguatatuba and capital letters Ubatuba

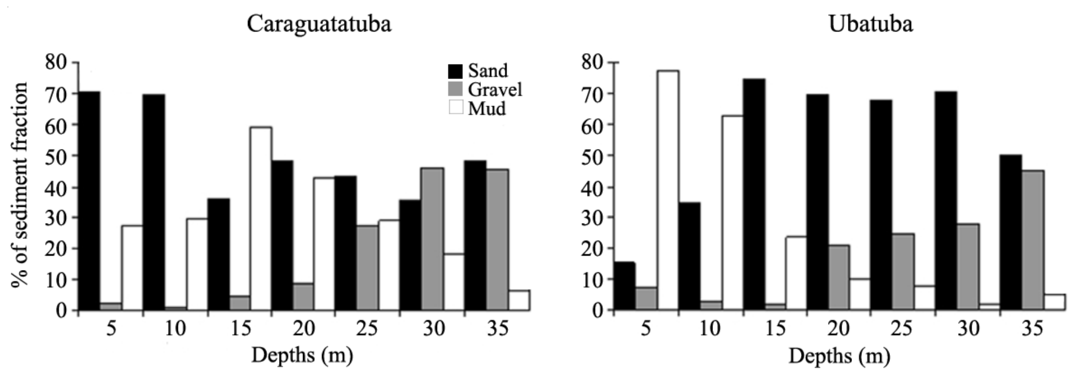

Figure 5

Sediment fraction percentage (Sand, Gravel and Mud) in relation to depths (m), sampled in Caraguatatuba and Ubatuba Bays, during the period from July/2002 to June/2003

Porcentaje de la fracción del sedimento (arena, grava, lodo) en relación con la profundidad (m) de muestreo en las bahías de Caraguatatuba y Ubatuba, durante el período comprendido entre julio 2002 y junio 2003

Sand and mud predominated in the shallower depths, and a greater percentage of gravel was observed beginning at 25 m. In Caraguatatuba there was a greater occurrence of sand, while in Ubatuba, mud predominated (Fig. 5).

The largest and significant (r>0.70) coefficients of the Pearson Linear Correlation were obtained in Caraguatatuba, between the bottom salinity and the surface (r = 0.74); in Ubatuba, among the depth and organic matter content (r = - 0.72), organic matter content and mud (r = 0.91), sand and mud (r = - 0.72), and depth and mud (r = - 0.82).

From the group analysis of depths in both areas of study, the only group that remained isolated was that at 20 m in Ubatuba (Fig. 6).

In the Principal Component Analysis (PCA), the two first axes presented 58.7% of the cumulated variance, in the four original variables analyzed (Table 4). PC1, in Caraguatatuba, explained 29.8% of the total data variation, the principal component of this axis were bottom salinity and bottom temperature, while PC2 explained 28.9% and their principal definers were amount of organic matter and sand (Fig. 3). The shallower depths (5-10 m) were related to high temperatures and low salinities, besides large quantity of sand. However, in Ubatuba, the two first axes presented 78.4% of the cumulated variance, in four original variables (Table 4). PC1 explained 50.8% of the total variation, where sand and organic matter were the principal component of this axis, where both were inversely proportional; and PC2, explained 27.6% of the variation, with bottom salinity being its principal component (Fig. 4), presenting the shallower depths (5-10 m) related to a high amount of organic matter.

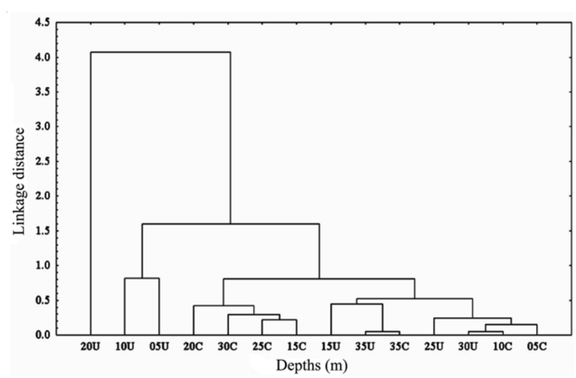

Figure 6

Clustering dendrogram (UPGA - Euclidian Distance) of the sampled transects of Caraguatatuba (C) and Ubatuba (U) Bays, during the period from July/2002 to June/2003, in relation to the following abiotic factors: bottom salinity (psu), bottom temperature (°C), amount of organic matter (%) and sand in the substrate (%)

Dendrograma (UPGA - Distancia Euclídea) de las transecciones estudiadas en las bahías de Caraguatatuba (C) y Ubatuba (U) durante el período comprendido entre julio 2002 y junio 2003, en relación con los siguientes factores abióticos: salinidad de fondo (psu), temperatura de fondo (ºC), cantidad de materia orgánica (%) y arena en el sustrato(%)

Table 4

Summarized results of Principal Components Analysis (PCA) of the relationship between environmental variables (Bottom salinity - BS, Bottom temperature - BT, amount of Organic Matter – OM and Sand in the substrate - SA) in the Caraguatatuba (CAR) and Ubatuba (UBA) Bays, from July/2002 to June/2003. Eigenvalues, percentages of variance and cumulative percentages explained for the four first axes

Recopilación de los resultados del Análisis de Componentes Principales (PCA) de la relación entre variables ambientales (salinidad de fondo - BS, temperatura de fondo - BT, cantidad de materia orgánica - MO y arena en el sustrato - SA) en las bahías de Caraguatatuba (CAR) y Ubatuba (UBA), desde julio 2002 a junio 2003. Eigenvalues, porcentaje de varianza y porcentaje acumulativo explicado por los cuatro primeros ejes

Axis	Eigenvalues		% of Variance		Cumulative % of Variance	
	CAR	UBA	CAR	UBA	CAR	UBA
1	1.192	2.030	29.803	50.758	29.803	50.758
2	1.158	1.105	28.940	27.614	58.743	78.372
3	0.902	0.575	22.541	14.368	81.284	92.741
4	0.749	0.290	18.716	7.259	100.000	100.000

Eigenvectors

	BT		BS		OM		SA	
	CAR	UBA	CAR	UBA	CAR	UBA	CAR	UBA
1	0.6247	-0.5092	-0.7173	0.2734	0.2851	-0.5782	-0.1184	0.5759
2	-0.4237	-0.3526	-0.0317	0.7950	0.5500	0.2852	-0.7190	-0.4029
3	-0.1790	0.7435	-0.3859	0.4780	-0.7738	-0.4661	-0.4694	-0.0374
4	-0.6311	-0.2521	-0.5793	-0.2544	0.1324	-0.6059	0.4986	-0.7104

Discussion

Environmental factors

The environmental parameters analyzed in the studied areas were very close to those observed by Mantelatto & Fransozo (1999) at the Ubatuba Bay. The northern region of São Paulo is highly influenced by the action of different marine currents, with diversified characteristics. Caraguatatuba is more protected than Ubatuba, due to the geographic position of São Sebastião Island, which makes a true physical defense to impacts from the open ocean (Pires-Vanin *et al.* 1993).

In both studied regions, salinity was inversely proportional to temperature and directly proportional to depth, while temperature was inversely proportional to depth. A similar pattern of relation between abiotic factors was confirmed by Bertini *et al.* (2004) in the Ubatuba region and by Meireles *et al.* (2006) in Caraguatatuba. In the shallower depths, which are consequently closer to the beach, there was a larger influence of freshwater coming from river discharge, so further from the coast, it gets deeper and the influence is reduced. As well as, the deeper the water column, the lower the solar radiation penetration promoting lower temperatures in these regions, facts confirmed by PCA.

The substrate organic matter content was much lower than that observed by Mantelatto & Fransozo (1999) in the Ubatuba Bay; this is probably because samples of the mentioned study were performed in different sites from the present study. The regions studied by Mantelatto & Fransozo (1999) ranged from 3.1 to 16.6 m depth. Regarding the sediment, a zoning was observed in the fraction distribution, in the shallower regions (5 and 10 m), where sand predominated in Caraguatatuba, and mud in Ubatuba. Starting at 25 m, in Caraguatatuba, there was a dominance of gravel, while in Ubatuba, from 15 to 25 m, there was a greater percentage of sand. According to Barros *et al.* (1997), in the Caraguatatuba region, the thicker material is concentrated close to the coastal region and as the depth increases, a decrease in the granulometry of the sediment occurs.

The cluster analysis corroborates the general similarities between both bays in terms of abiotic characteristics with almost complete separation of the studied depths in both areas. Only the depth of 30 m from Ubatuba was grouped with those of 5 and 10 m from Caraguatatuba. In addition, there was a clear separation between shallower depths (5 and 10 m) and the deeper ones. It is known that the coastal regions suffer a greater influence through river drainage and anthropogenic action. Particularly in the shallowest regions these alterations can cause sufficient modifications that are able to separate these transects from the others. These factors can lead to an increase in the quantity of organic matter and salinity, as well as a reduction in dissolved oxygen in the water. These results were confirmed with the principal components analysis, with a zoning of the different depths in relation to abiotic factors, the shallowest depths (5 to 15 m), with higher temperatures, and lower bottom salinity.

Distribution of *Loxopagurus loxochelis*

Most of the previous studies on distributional aspects of anomuran species were carried out in shallow water areas (until 15-20 m deep) and only in one region of the northern coast of São Paulo (i.e., Ubatuba). We break with this tradition during the development of this research, as part of a mega project on Marine Biodiversity of the São Paulo coast (BIOTA/FAPESP), working in different areas that were never sampled, as Caraguatatuba and extend our sampling until 35-45 m. We found that temperature is one of the factors that most strongly affects the distribution of this southern hermit crab species *L. loxochelis*. However, we believe that the combination with other factors such as substrate, deep, coexistent species, is also important in its distribution.

The highest frequency of occurrence of *L. loxochelis* was between 20 and 25 m. Fransozo *et al.* (1998) state that this species is the most abundant in bottom areas, which are not affected by freshwater drainage. Bertini *et al.* (2004) obtained the same result in their study with *L. loxochelis*, with more than 95% of the animals collected in these depths.

In Caraguatatuba, *L. loxochelis* was most frequent during the winter, and in Ubatuba, during the summer. Vernberg (1983) postulated that exists a direct relation between the water temperature variation and the metabolic pattern of crustaceans, so, in lower temperatures a decrease in the metabolic activities of these animals can be noted. In Ubatuba, the highest number of individuals was obtained in the summer, in accordance with the study by Mantelatto & Fransozo (2000), a fact due to the entrance and intensity of SACW during this period, bringing cold waters from the south.

The decrease in the number of individuals of *L. loxochelis* during spring probably is associated with the SACW arrival into the region, causing a temperature decrease and characterizing a decrease in the capture of hermit crabs, which might be a consequence of the individuals' migration to different deeper areas not sampled here, as previously observed for the coexistent species *Pagurus exilis* (Benedict, 1892) by Meireles *et al.* (2006).

Loxopagurus loxochelis can be considered a species preferring low temperature waters. Probably, this species migrates to areas of lower temperature, which would have made difficult the sampling during the present study. We cannot discard the possibility that these animals occur at great depths, since Rieger & D'Incao (1991) already observed *L. loxochelis* occurring in up to 50 m deep on the southmost region of Brazil (Rio Grande do Sul State).

In addition, *L. loxochelis* presented a large occurrence in areas with high salinity and low temperature. The same was observed by Bertini & Fransozo (1999), while studying *Petrochirus diogenes* (Linnaeus, 1798) in Ubatuba Bay, and by Bertini *et al.* (2004) and Mantelatto *et al.* (2004) with *L. loxochelis* also in Ubatuba. The hermit crab *P. exilis*, which is a species with distributional pattern similar to that of *L. loxochelis*, also presented this pattern in Caraguatatuba (Meireles *et al.* 2006). Low salinity could negatively affect the embryos (Giménez & Anger 2001), so females could actively migrate to high salinity areas when they are ovigerous.

Regarding the organic matter on the substrate, *L. loxochelis* occupied areas with low percentages of this component; fact also reported by Fransozo *et al.* (1998) for *L. loxochelis* and *Isocheles sawayai* Forest & de Saint Laurent 1968, in Ubatuba and by Meireles *et al.* (2006) for *P. exilis*, in Caraguatatuba. The amount of organic matter on the substrate also constitutes an important environmental factor for the organism's distribution, especially to those that use it as a food resource (Warner 1977). *Loxopagurus loxochelis* is a filtering animal (Fransozo *et al.* 1998, Mantelatto *et al.* 2004), which needs a great quantity of particles in suspension, that are provided during the coldest months (winter) by the change of marine currents in Ubatuba region (Castro-Filho *et al.* 1987). Consequently, this species should look for areas with high percentages of suspended organic matter in the water in detriment to the organic matter accumulated within the substrate particles.

Loxopagurus loxochelis was found in places with small percentage of gravel and mud, and high concentrations of sand. The nature of the substratum influences the frequency and ability of the hermit crabs in burying themselves, in a way, that they rarely choose another substrate that is not sand (Rebach 1974). This fact corroborates our observations in the present study, since *L. loxochelis*, a species which has the habit to bury itself (Mantelatto *et al.* 2004), was registered principally in locations with the highest percentage of sand.

Besides the interactions with the abiotic factors, the animals share the environment with other organisms from the benthic fauna. These inter-relations can interfere in the distribution of the specimens (Pardo *et al.* 2007). Particularly to the hermit crabs, the availability of shells in the environment can have a fundamental role in the population dynamic and distributional pattern (Meireles *et al.* 2003) although we did not evaluate the shell availability to the hermit crab community.

In Caraguatatuba and Ubatuba, other species of hermit crabs occur and present spatial distributional patterns of shell usage similar to those observed for *L. loxochelis*, such as *Dardanus insignis* (de Saussure 1858) (Fernandes-Góes 1997, 2000, Meireles 2006), *P. diogenes* (Bertini & Fransozo 1999, 2000), and *P. exilis* (Meireles *et al.* 2006, Terossi *et al.* 2006). This scenario, associated with our experience of working in these areas during the last 15 years, makes us able to infer that the distribution of *L. loxochelis* at 30 m in Caraguatatuba and 25 m in Ubatuba, was also influenced by the presence and abundance of other coexistent hermit crabs.

We believe that temperature and depth have a major role on the population distribution and reproduction dynamics of this species (Rieger & D'Incao 1991, Bertini *et al.* 2004), as it was mentioned by Meireles *et al.* (2006), studying *P. exilis* also in Caraguatatuba where those authors observed that the distribution of this hermit crab is closely related with depths between 15 and 35 m and temperatures between 22 and 24°C.

According to Melo (1985), the species alters the limits of its bathymetrical distribution, depending on the abiotic conditions present in the different regions where it lives. In Table 5, we showed the information on the occurrence and distribution of *L. loxochelis* in different areas. In the state of Rio Grande do Sul, the species has a distribution until 50 m, while in Argentina its greatest frequency is from 4 to 15 m (Scelzo, pers. comm.). With these data, it can be concluded that *L. loxochelis* changes its limits of distribution in the different areas, possibly in relation to the environmental factors that provide a better adaptation for each population at different environment conditions.

In agreement with Mantelatto *et al.* (2004), an important hypothesis that should be considered is the geographic distribution of the species. *Loxopagurus loxochelis* has Mar del Plata, Argentina as its southern distribution limit, and the Bahia State coast, northeastern Brazil as its northern one (Scelzo & Boschi 1973, Melo 1999). However, the distribution to the north was considered an accidental occurrence by Mantelatto *et al.* (2004), because few individuals were obtained in one sample in Bahia State and there is a sample gap of these animals from other region since this species is frequently found from southern Brazilian coast to Argentina, where the water temperature is usually lower almost all of the year, in comparison with the Brazilian southeastern region. The occurrence of *L. loxochelis* in the Ubatuba region represents the final limit of the northern distribution of the species and it can be considered the true north limit, as Mantelatto *et al.* (2004) mentioned earlier.

Further studies comparing in details aspects of population and abiotic and biotic interactions from different biogeographically separated areas, are needed and will undoubtedly contribute to further resolution and understanding of the distributional variability in near-shore hermit crabs.

In this study, we evidenced that several environmental factors act together to create the distribution pattern of *L. loxochelis*. Probably, the factors of greatest importance are the lower temperatures, deeper areas s and a predominant sandy substrate which corroborates the

Table 5

Synopsis on the distribution and occurrence of *Loxopagurus loxochelis*

Sinopsis de la distribución y ocurrencia de *Loxopagurus loxochelis*

Local	Occurrence (m)	Reference
Bahia, Brazil	-	Moreira (1901)*
Uruguay	18 – 30 m	Forest & Saint Laurent (1967)
Mar del Plata, Argentina	Coastal to 30 m	Scelzo & Boschi (1973)
Rio Grande, Brazil	Between 08 – 30 m	Hebling & Rieger (1986)
Rio Grande, Brazil	Until 50 m[1]	Rieger & D'Incao (1991)
Ubatuba, Brazil	4.4 – 13.0 m	Negreiros-Fransozo *et al.* (1997)
Ubatuba, Brazil	2.5 – 18.5 m	Fransozo *et al.* (1998)
Ubatuba, Brazil	01 – 30 m	Melo (1999)
Ubatuba, Brazil	05 – 20 m	Fernandes-Góes (2000)
Ubatuba, Brazil	05 – 35 m[2]	Bertini *et al.* (2004)
Ubatuba, Brazil	3.1 – 16.6 m (medium depth)[3]	Mantelatto *et al.* (2004)
Caraguatatuba, Brazil	05 – 30 m[4]	Present work
Ubatuba, Brazil	10 – 25 m[4]	Present work

* Original description of *L. loxochelis*; [1] young and adults; [2] Collections were made between 05 and 40 m, continuous reproduction, with ovigerous females in all stations, but the months had not been cited; [3] Collections are made only at this depths; [4] Collections made from the 05 to 35 m depth

hypothesis raised. Future studies evaluating the biological interactions (competition for shells, feeding, competition with other animals, predation) will enable a better understanding of those factors interfering on the distribution of *L. loxochelis.*

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Literature cited

Abele LG. 1974. Species diversity of decapod crustaceans in marine habitats. Ecology 55(1): 156-161.

Ayres-Peres L & FL Mantelatto. **2008**. Análise comparativa da estrutura populacional do ermitão endêmico do Altântico Ocidental *Loxopagurus loxochelis* (Decapoda, Anomura) em duas regiões do Estado de São Paulo, Brasil. Iheringia, Série Zoologia 98(1): 28-35.

Barros CE, ICS Corrêa, R Baitelli & ARD Elias. 1997. Aspectos sedimentares da enseada de Caraguatatuba, litoral do Estado de São Paulo. Anais da Academia Brasileira de Ciências 69(1): 19-36.

Bertini G & A Fransozo. 1999. Spatial and seasonal distribution of *Petrochirus diogenes* (Anomura, Diogenidae) in the Ubatuba Bay, São Paulo, Brazil. Iheringia, Série Zoologia 86: 145-150.

Bertini G & A Fransozo. 2000. Patterns of shell utilization in *Petrochirus diogenes* (Decapoda, Anomura, Diogenidae) in the Ubatuba Region, São Paulo, Brazil. Journal of Crustacean Biology 20(3): 468-473.

Bertini G, A Fransozo & AA Braga. 2004. Ecological distribution and reproductive period of the hermit crab *Loxopagurus loxochelis* (Anomura, Diogenidae) on the northern coast of São Paulo State, Brazil. Journal of Natural History 38(18): 2331-2344.

Bispo PC. 2002. Estudo de comunidades de Ephemeroptera, Plecoptera e Trichoptera (EPT) em riachos do Parque Estadual Intervales, Serra de Paranapiacaba, Sul do Estado de São Paulo. Doctoral Thesis. IB/USP, São Paulo. 120 pp.

Branco JO, A Turra & FX Souto. 2002. Population biology and growth of the hermit crab *Dardanus insignis* at Armação do Itapocoroy, southern Brazil. Journal of the Marine Biological Association of the United Kingdom 82(4): 597-603.

Castro-Filho BM, LB Miranda & SY Miyao. 1987. Condições hidrográficas na Plataforma Continental ao largo de Ubatuba: variações sazonais e em média escala. Boletim do Instituto Oceanográfico 35(2): 135-151.

Cesaroni D, P Matarazzo, G Allegrucci & V Sbordoni. 1997. Comparing patterns of geographic variation in cave crickets by combining geostatistic methods and Mantel tests. Journal of Biogeography 24(4): 419-431.

Fernandes-Góes LC. 1997. Distribuição e biologia populacional de *Dardanus insignis* (Saussure, 1858) (Crustacea, Decapoda, Anomura) na região de Ubatuba, SP. Master Dissertation, Instituto de Biociências, Universidade Estadual Paulista, Botucatu, São Paulo, 150 pp.

Fernandes-Góes LC. 2000. Diversidade e bioecologia das comunidades de anomuros (Crustacea, Decapoda) do substrato não consolidado da região de Ubatuba, SP. Doctoral Thesis. Instituto de Biociências, Universidade Estadual Paulista, Botucatu, São Paulo, 133 pp.

Forest J & M Saint-Laurent. 1967. Campagne de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961-1962). 6. Crustacés Décapodes: Pagurides. Annales de l'Institut Oceanographique de Monaco 45: 47-169.

Fransozo A, FL Mantelatto, G Bertini, LC Fernandes-Góes & JM Martinelli. 1998. Distribution and assemblages of anomuran crustaceans in Ubatuba Bay, north coast of São Paulo State, Brazil. Acta Biológica Venezuelica 18(4): 17-25.

Giménez JL & K Anger. 2001. Relationships among salinity, egg size, embryonic development, and larval biomass in the estuarine crab *Chasmagnathus granulata* Dana, 1851. Journal of Experimental Marine Biology and Ecology 260: 241-257.

Hebling NJ & PJ Rieger. 1986. Os ermitões (Crustacea, Decapoda: Paguridae e Diogenidae), do litoral do Rio Grande do Sul, Brasil. Atlântica 8: 63-77.

Lancaster I. 1988. *Pagurus bernhardus* (L.) – an introduction to the natural history of hermit crabs. Field Studies 7(1): 189-238.

Manly BFJ. 1990. Multivariate statistical methods: a primer, 159 pp. Chapman and Hall, London.

Mantelatto FL & A Fransozo. 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo State, Brazil. Revista Brasileira de Biologia 59(1): 23-31.

Mantelatto FL & A Fransozo. 2000. Brachyuran community in Ubatuba Bay, northern coast of São Paulo State, Brazil. Journal of Shellfish Research 19(2): 701-709.

Mantelatto FL, A Fransozo & ML Negreiros-Fransozo. 1995. Distribuição do caranguejo *Hepatus pudibundus* (Herbest, 1795) (Crustacea, Decapoda, Brachyura) na Enseada Fortaleza, Ubatuba (SP), Brasil. Boletim do Instituto Oceanográfico 43(1): 51-61.

Mantelatto FL, JM Martinelli & A Fransozo. 2004. Temporal-spatial distribution of the hermit crab *Loxopagurus loxochelis* (Decapoda, Anomura, Diogenidae) from Ubatuba Bay, São Paulo State, Brazil. Revista de Biologia Tropical 52(1): 47-55.

Meireles AL. 2006. Estudo comparativo da distribuição espaço-temporal, da estrutura populacional e da relação de simbiose entre o ermitão *Dardanus insignis* (de Saussure, 1858) (Anomura, Diogenidae) e o porcelanídeo *Porcellana sayana* (Leach, 1820) (Anomura, Porcellanidae) no litoral norte paulista. Doctoral Thesis em Biologia Comparada, Departamento de Biologia da Facultade de Filosofia, Ciencias e Letras de Ribeirão Preto, Universidade de São Paulo, São Paulo, 313 pp.

Meireles AL, R Biagi & FL Mantelatto. 2003. Gastropod shell availability as a potential resource for the hermit crab infralittoral fauna of Anchieta Island (SP), Brazil. Nauplius 11(2): 99-105.

Meireles AL, M Terossi, R Biagi & FL Mantelatto. 2006. Spatial and seasonal distribution of the hermit crab *Pagurus exilis* (Benedict, 1892) (Decapoda: Paguridae) in the southwestern coast of Brazil. Revista de Biología Marina y Oceanografía 41(1): 87-95.

Melo GAS. 1985. Taxonomia e padrões distribucionais e ecológicos dos Brachyura (Crustacea: Decapoda) do litoral sudeste do Brasil. Doctoral Thesis em Ciências Biologicas (Zoologia), Intituto de Biociências, Universidade de São Paulo, São Paulo, 215 pp.

Melo GAS. 1999. Manual de identificação dos Crustacea Decapoda do litoral brasileiro: Anomura, Thalassinidea, Palinuridea e Astacidea, 551 pp. Plêiade Editora, São Paulo.

Moreira C. 1901. Contribuições para o conhecimento da fauna brasileira: Crustáceos do Brasil. Archivos do Museu Nacional do Rio de Janeiro 11: 1-173.

Negreiros-Fransozo ML, A Fransozo, FL Mantelatto, MAA Pinheiro & S Santos. 1997. Anomuran species (Crustacea, Decapoda) and their ecological distribution at Fortaleza Bay sublittoral, Ubatuba, São Paulo, Brazil. Iheringia, Série Zoologia 83: 187-194.

Odum EP. 2001. Fundamentos de Ecologia, 929 pp. Fundação Calouste Gulbenkian, Lisboa.

Pardo LM, Piraud F, Mantelatto FL & FP Ojeda. 2007. Ontogenetic pattern of resource use by the tiny hermit crab *Pagurus villosus* (Paguridae) from the temperate Chilean coast. Journal Experimental Marine Biology and Ecology 353(1): 68-79.

Pérès JM. 1961. Océanographie Biologique et Biologie Marine: I la Vie Benthique, 541 pp. Presses Universitaires de France, Paris.

Pires-Vanin AMS, CL Rossi-Wongtschowski, E Aidar, H Mesquita, LSH Soares, M Katsuragawa & Y Matsuura. 1993. Estrutura e função do ecossistema de plataforma continental do Atlântico Sul brasileiro: síntese dos resultados. Publicação Especial do Instituto Oceanográfico (10): 217-231.

Rebach S. 1974. Burying behavior in relation to substrate and temperature in the hermit crab, *Pagurus longicarpus*. Ecology 55(1): 195-198.

Rieger PJ & F D'Incao. 1991. Distribuição de larvas de *Loxopagurus loxochelis* (Decapoda, Diogenidae) na região adjacente à Barra de Rio Grande, RS. Nerítica 6(1-2): 93-106.

Rohlf FJ. 2000. NTSYS 2.1: Numerical Taxonomy and Multivariate Analysis System. Exeter Software, New York.

Scelzo MA & EE Boschi. 1973. Aportes al conocimiento de la distribución geográfica de los crustáceos decápodos Anomura del Atlántico Sudoccidental, frente a las costas Argentinas. V Congreso Latinoamericano de Zoología 1: 204-216.

Smouse PE, JC Long & RR Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Systematic Zoology 35(4): 627-632.

Soares-Gomes A & AG Figueiredo. 2002. O ambiente marinho. In: Pereira RC & A Soares-Gomes (Org). Biologia Marinha, pp. 1-33. Interciência, Rio de Janeiro.

Soares-Gomes A, PC Paiva & PYG Sumida. 2002. Bentos de sedimentos não consolidados. In: Pereira RC & A Soares-Gomes (Org.). Biologia Marinha, pp. 127-146. Interciência, Rio de Janeiro.

Sokal RR. 1979. Testing statistical significance of geographic variation patterns. Systematic Zoology 28(2): 227-232.

Terossi M, DLA Espósito, AL Meireles, R Biagi & FL Mantelatto. 2006. Pattern of shell occupation by the hermit crab *Pagurus exilis* (Anomura, Paguridae) in northern Coast of Sao Paulo State, Brazil. Journal of Natural History 40(1-2): 77-87.

Vernberg FJ. 1983. Respiratory adaptations. In: Vernberg FJ & WB Vernberg (eds), The Biology of Crustacea 8: 1-42. Academic Press, New York.

Warner GF. 1977. The biology of crabs, 202 pp. Van Nostrand Reinhold Company, New York.

Zar JH. 1996. Biostatistical analysis, 907 pp. Prentice-Hall, Englewood Cliffs.

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