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## Research Article

# Environmental factors influencing the distribution of three species within the genus *Persephona* Leach, 1817 (Crustacea, Decapoda, Leucosiidae) in two regions on the northern coast of São Paulo State, Brazil

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**ABSTRACT.** Patterns of spatio-temporal distribution of Brachyura are determined by the interaction among life history traits, inter and intraspecific relationships, as well as by the variation of abiotic factors. This study aimed to characterize patterns of spatio-temporal distribution of *Persephona lichtensteinii*, *Persephona mediterranea* and *Persephona punctata* in two regions of the northern coast of São Paulo State, southeastern region of Brazil. Collections were done monthly from July 2001 to June 2003 in Caraguatatuba and Ubatuba, using a shrimp fishery boat equipped with double-rig nets. The patterns of species distribution were tested by means of redundancy analysis (RDA) and generalized linear mixed models (GLMM) in relation to the recorded environmental factors (BT: bottom temperature, BS: bottom salinity, OM: organic matter and granulometry (Phi)). The most influent environmental factor over the species distribution was the Phi, and the ascendant order of influence was *P. lichtensteinii*, *P. punctata* and *P. mediterranea*. The greater abundance of *P. mediterranea* showed a conservative pattern of distribution for the genus in the sampled region. The greater occurrence of *P. punctata* and *P. lichtensteinii*, in distinct transects than those occupied by *P. mediterranea*, seems to be a strategy to avoid competition among congeneric species, which is related to the substratum specificity.

**Keywords:** Brachyura, *Persephona lichtensteinii*, *Persephona mediterranea*, *Persephona punctata*, ecological distribution, sediment, Brazil.

## Factores ambientales que influyen en la distribución de tres especies del género *Persephona* Leach, 1817 (Crustacea, Decapoda, Leucosiidae) en dos regiones de la costa norte del estado de São Paulo, Brasil

**RESUMEN.** Los patrones de distribución espacial-temporal de los Brachyura son determinados por la interacción entre aspectos de la historia de vida, relaciones inter e intraespecíficas, así como por las variaciones de los factores abióticos. El objetivo de este estudio fue caracterizar los patrones de distribución espacio-temporal de *Persephona lichtensteinii*, *Persephona mediterranea* y *Persephona punctata* en dos regiones de la costa norte del estado de São Paulo, Brasil. Se realizaron muestreos mensuales, de julio de 2001 a junio de 2003 en las regiones de Caraguatatuba y Ubatuba, utilizando un barco camaronero equipado con redes de arrastre de tipo "double-rig". Los patrones de distribución de las especies fueron testeados por medio de un análisis de redundancia (RDA) y de modelos lineales generalizados mixtos (GLMM) por su asociación con los factores ambientales registrados (TF: temperatura de fondo, SF: salinidad de fondo, MO: materia orgánica y Phi). El factor ambiental más influyente sobre distribución de las especies fue el tamaño medio de

grano (Phi). Siendo el grado de orden de influencia ascendente a partir de *P. lichtensteinii*, *P. punctata* y *P. mediterranea*. La mayor abundancia de *P. mediterranea* sobre *P. punctata* y *P. lichtensteinii* mostró un patrón de distribución conservativo de género para la región muestreada. Esta variación de abundancia puede estar relacionada con el límite de distribución de las especies. La mayor presencia de *P. punctata* y *P. lichtensteinii* en puntos distintos de los ocupados por *P. mediterranea* parece ser una estrategia para evitar la competencia entre especies congénicas, relacionada con la especificidad del sustrato.

**Palabras clave:** Brachyura, *Persephona lichtensteinii*, *Persephona mediterranea*, *Persephona punctata*, distribución ecológica, sedimento, Brazil.

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## INTRODUCTION

Aspects of life history traits and intra and interspecific interactions may be related to the distribution of different species of Brachyura. Furthermore, several physical and chemical characteristics of the environment and available resources may influence the distribution of brachyuran crab communities, leading to broad or restricted distributions (Carvalho *et al.*, 2010; Hiroki *et al.*, 2011).

*Persephona lichtensteinii* Leach, 1817, *P. mediterranea* Herbst, 1794 and *P. punctata* Linnaeus, 1758 are widely distributed in the Western Atlantic benthic zones, in substrates composed by mud, sand, shells, calcareous algae and corals. In Brazil, *P. mediterranea* and *P. punctata* have a wider distribution compared to *P. lichtensteinii*. The first is distributed from Amapá to Rio Grande do Sul States, while *P. lichtensteinii* is distributed from Amapá to São Paulo (Melo, 1996).

There are few studies on the biology of leucosiid species, including *P. lichtensteinii*, *P. mediterranea* and *P. punctata*. The early larval development of *P. mediterranea* was described by Negreiros-Fransozo *et al.* (1989). The spatial and temporal distribution of *Persephona* spp., reproductive period and the sexual maturity of *P. mediterranea* were reported by Bertini *et al.* (2001, 2010) in Ubatuba region. A comparative analysis of the distribution and sexual maturity of *P. lichtensteinii* and *P. punctata* in Ilhéus, Bahia State, was performed by Carvalho *et al.* (2010). The relative growth, sexual maturity, and breeding season of three species of the genus *Persephona* were compared by Almeida *et al.* (2013) in Ubatuba bay.

Crabs of the genus *Persephona* are commonly caught as bycatch fauna of marine shrimp fisheries in trawls (Branco & Fracasso, 2004), although they are not commercially exploited. *P. lichtensteinii*, *P. mediterranea* and *P. punctata* might play an essential ecological role within the trophic web of benthic environments in which they are inserted (Almeida *et al.*, 2013), the study of the species is fundamental to

understand the species population dynamics and evaluate possible impacts of trawl fisheries on the communities of Brachyura, and thus establish mitigation activities for the species conservation. These actions are necessary, especially in areas such as southeastern coast of Brazil, where marine ecosystems are affected by intense and uncontrolled expansion of tourism (Mantelatto *et al.*, 1995), which provides higher fishery exploration in order to feed the demand of organisms that serve as food to the human population.

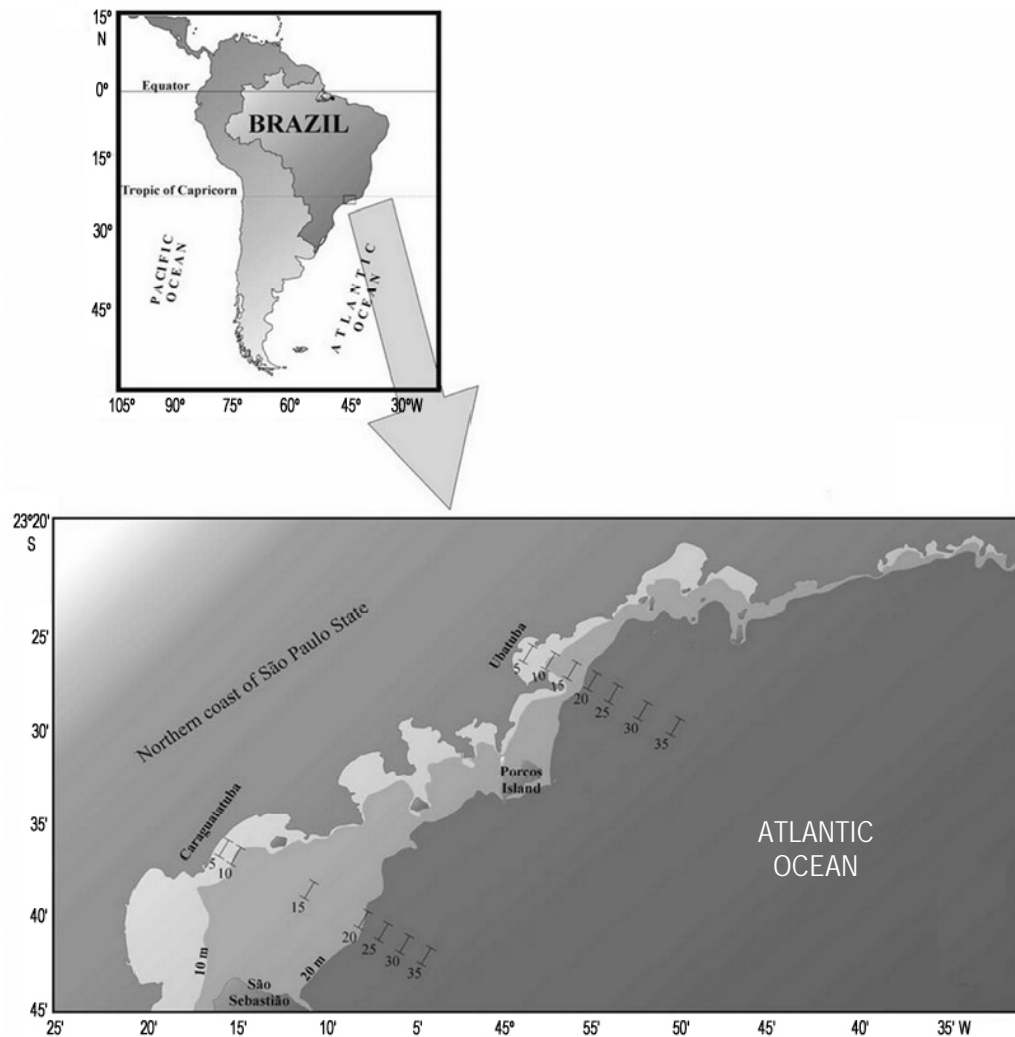
The aim of the present study was to characterize the spatio-temporal distribution patterns of three species of the genus *Persephona* in Ubatuba and Caraguatatuba, on the southeastern Brazilian coast. These patterns of distribution were correlated with the main environmental factors and bathymetry.

## MATERIALS AND METHODS

### Sampling and data collection

Crabs were monthly collected from July 2001 to June 2003 in Ubatuba (UBA) and Caraguatatuba (CA) regions on the northern coast of São Paulo State (UBA = (23°26'27"S, 45°03'18"W); CA = (23°36'09"S, 45°20'25"W) (Fig. 1). In each region, seven transects were sampled, located at mean depths of 5, 10, 15, 20, 25, 30 and 35 m (Table 1). A shrimp fishery boat equipped with double-rig nets (mesh size 20 mm, 15 mm in the cod end) was used for trawling. Transects were trawled during 30 min, covering 18,000 m<sup>2</sup>. Captured specimens were labeled and stored frozen until analysis. In laboratory, the crabs were identified according to Melo (1996).

The main differential on northern coast of São Paulo (São Paulo Bight; Zembruiski, 1979) is its geomorphological aspect, historically related to the presence of the ledge of Serra do Mar, thus forming an extremely irregular littoral with many bays with peculiar internal relief (Ab'Saber, 1955; Mahiques *et al.*, 2004), with semi-confined characteristics, sugges-



**Figure 1.** Study area. Locality of Ubatuba and Caraguatatuba regions, northern littoral of São Paulo State, Brazil, indicating the transects of collection.

**Table 1.** Geographic coordinates of each transects in the studied regions in the period from July 2001 to June 2003.

Transects (m)	Ubatuba		Caraguatatuba	
	Latitude	Longitude	Latitude	Longitude
5	23°26'27"S	45°03'18"W	23°36'09"S	45°20'25"W
10	23°26'08"S	45°02'11"W	23°36'47"S	45°25'35"W
15	23°26'49"S	45°00'41"W	23°39'52"S	45°14'23"W
20	23°28'03"S	44°59'39"W	23°40'07"S	45°11'41"W
25	23°28'51"S	44°58'55"W	23°40'12"S	45°09'50"W
30	23°30'14"S	44°58'06"W	23°42'04"S	45°07'16"W
35	23°31'57"S	44°55'28"W	23°43'07"S	45°00'42"W

ting a restrict interchange of water and sedimentary material between the coastal region and shallow continental shelf (Mahiques, 1995).

At each transect salinity and temperature (bottom: BS, BT and surface water: SS, ST), depth, organic matter content (OM%), and mean grain-size (Phi)

were measured. Bottom water was sampled using a Nansen bottle. Salinity (SU) was measured with an Atago S/1000 optic refractometer and temperature (°C) using a thermometer attached to the bottle. An ecobathymeter coupled with GPS (Global Positioning System) was used to record depth (m) at transects. Sediment samples were collected seasonally with a 0.06 m<sup>2</sup> Van Veen grab. In the laboratory, the sediment was dried at 70°C during 72 h in an oven. Two 50 g subsamples were separated, treated with 250 mL of a 0.2 N NaOH solution, and stirred for 5 min to release silt and clay particles. Subsamples were then sieved on a 0.063 mm mesh in order to analyze the grain size composition. Sediments were sieved and the cumulative particle size curves were plotted using the Phi scale (see details in Tucker, 1988).

The organic matter content (%) was obtained by ash weighting: three aliquots, each one containing 10 g, were placed in porcelain crucibles and incinerated for 3 h at 500°C. Samples were then re-weighted (Mantelatto & Fransozo, 1999).

The sediment texture was represented graphically by histogram using the three most important granulometric classes, as in Magliocca & Kutner (1965). Granulometric class A corresponds to sediments in which mean sand (MS), coarse sand (CS), very coarse sand (VCS), and gravel ( $G > 0.25$  mm) account for more than 70% by weight. In class B, fine sand (FS) and very fine sand (VFS) make up more than 70% by weight of sediment samples. More than 70% of sediments in class C are silt and clay (S + C). These three categories were further combined to form different groups: PA = (MS + CS + VCS + G) > 70%; PAB = prevalence of A over B; PAC = prevalence of A over C; PB (FS + VFS) > 70%; PBA = prevalence of B over A; PBC = prevalence of B over C; PC (S + C) > 70%; PCA = prevalence of C over A; PCB = prevalence of C over B.

### Statistical analysis

Initially, data were tested in relation to the univariate and multivariate normality, through Shapiro-Wilk test (Shapiro & Wilk, 1965) and symmetry and multivariate kurtosis tests (Mardia, 1970; 1980) (with modifications proposed by Doornik & Hansen, 2008 - omnibus test), respectively. In order to test the homogeneity of variances the Levene test was used (Levene, 1960). In addition, Box's M test (Anderson, 1958) was performed to evaluate the equivalence (multivariate homogeneity) among covariance matrices with permutations of Monte Carlo for the significance value of the test. A correlation matrix of environmental variables Depth, BT, ST, BS, SS, OM and Phi was created to observe the existence of

collinearity among them. The Spearman correlation was preferred for this matrix because it disregards linear relations among variables. High collinearity was considered for modular correlation values higher than 0.7. Environmental variables that presented collinearity were removed from the following analysis. Data was complementary evaluated by the Variance Inflation Factor (VIF). Collinearity was considered for values higher than 10 for VIF.

To verify the influence of environmental factors on the species abundance, a principal component analysis (PCA) was conducted followed by a redundancy analysis (RDA) and Generalized Linear Model (GLM) for each *Persephona* species. Initially PCA was performed with the aim to investigate and determine which environmental variables were capable to explain data variation, considering as significant those loadings higher than 0.7 and the main components that assigned for a cumulative variance from 70%. Environmental variables that satisfied such previous evaluation were separated for a posterior RDA used to assess the relation of abundance of *P. lichtensteinii*, *P. mediterranea* and *P. punctata* and environmental factors on each analyzed transect. In addition, environmental vectors were fitted on RDA through the function "envfit", a routine that traces the maximum correlation of environmental variables with data from an ordination. The evaluation of vectors value significance occurred by permutations ( $n = 999$ ) using the goodness of fit of the square correlation coefficient ( $r^2$ ). According to Oksanen *et al.* (2012) for environmental variables this is defined as  $r^2 = 1 - (SSw / SSt^{-1})$ , being SSw the sum of squares within the group and SSt the sum of total squares.

Generalized Linear Models (GLM) was used to model each studied species by environmental factors. Independent variables were those abiotic variables indicated by the fit of environmental vectors on RDA and categorical variables (region and season), using the distribution of Poisson with function logarithmic-type. For the categorical variable Region, the "CA" level (region of Caraguatatuba) was fixed because the highest abundance of species was verified in this region. For the categorical variable Season, the winter level was fixed also because of the greater amount of individuals found in this season.

Due to the great number of zeros recorded in the abundance of each species (dependent variables), a Generalized Linear Mixed-Models Zero-Inflated was chosen. When executing such models, data were treated in two ways, the first one grouped all data in which there were abundance values and performed a GLM Poisson (Count part), and in the second data were transformed in presence/absence followed by a

GLM Binomial (Occurrence part), it means, in mixed models the influence of independent variables on the variation of abundance and occurrence were evaluated (Zuur *et al.*, 2009) for the *Persephona* species:

$Y \sim \text{Count part} \mid \text{Occurrence part. Equal to:}$

$Y \sim X_1 + X_2 + X_3 + X_4 + X_i \mid X_1 + X_2 + X_3 + X_4 + X_i$

where Y is the dependent variable (species of *Persephona*),  $X_i$  the independent variables (categorical or quantitative).

The occurrence of over dispersion ( $\phi$ ) of data was tested through the likelihood ratio (L/R), which was applied with the same data of each species between a GLMM Zero-Inflated by Poisson distribution (GLMM ZIP) and a GLMM Zero-Inflated by Negative Binomial distribution (GLMM ZINB), indicating overdispersion through the significant difference ( $P < 0.05$ ) between the models. Overdispersion of data refers to the ratio of residual deviation in function of degrees of freedom, surpassing the unitary equality ( $\phi \neq 1$ ), it means, when the obtained values of variance are significant higher than the mean.

Only reduced models of GLMM were considered for the better interpretation among *Persephona* species. In addition, the reduced models were developed by manual technique of variable removed step by step. All adopted proceedings for GLMM were based on Zuur *et al.* (2009).

All statistical analyses were made using the software R (R Development Core Team, 2013), considering  $\alpha = 0.05$  (Zar, 1999). The following packages were used: “vegan” (RDA, envifit, Oksanen *et al.*, 2012), ‘pscl’ (GLMM Zero-Inflated, Jackman, 2012), ‘lme4’ (Likelihood Ratio Test, Zeileis & Hothorn, 2002).

## RESULTS

Salinity presented the more homogeneous values in Ubatuba, ranging from 32 to 37. In Caraguatatuba values ranging from 30 to 37 were observed, constant values were observed during the first year and in autumn such values decreased. In the second year the lowest values were observed in winter. Among the transects, the lowest salinity values were found in shallower waters (5 and 10 m) in both regions.

Considering the bottom temperature, the lowest mean values were recorded in October and November (spring) of the first year in both regions. However, the highest mean values occurred in February (summer) of the first year in Ubatuba, and in April (autumn) of the second year in Caraguatatuba. In both sampled regions the decrease of temperature was directly related to the increase of depth of transects. In greater depths it was

possible to observe a decrease of bottom temperature during spring and summer in the two regions, but variations of bottom temperature were more pronounced in Ubatuba (Fig. 2).

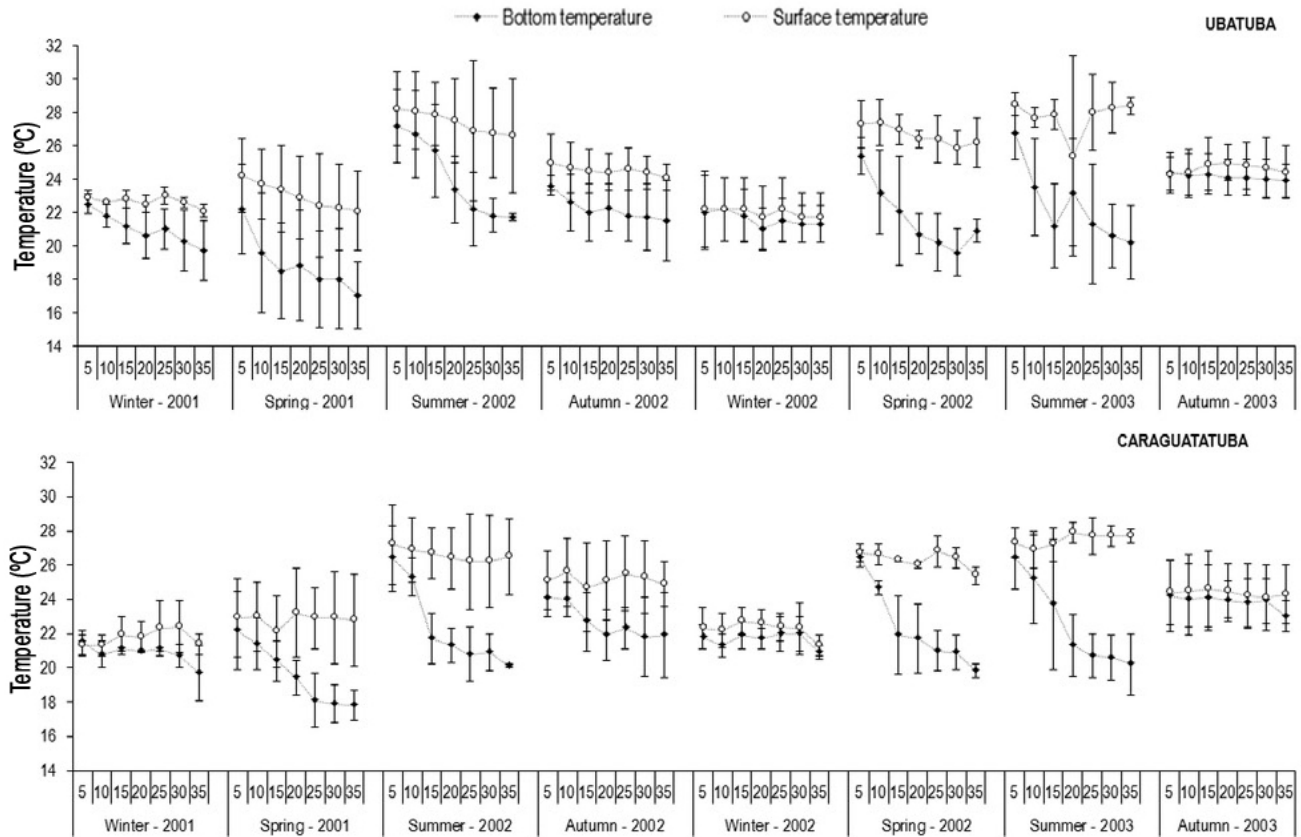
Variations in the proportion of granulometric classes of the sediment mean values of Phi and the organic matter content are represented in Figure 3. In the region of Ubatuba a predominance of class C was observed in shallower transects, 5 and 10 m, and of classes A and B in deeper transects, 30 and 35 m. In the same region the tendency of reduction of Phi and percentage of organic matter are higher as depth increases. In Caraguatatuba the class C predominated in intermediate transects, mainly in 15 and 20 m, and the lowest values of Phi and percentage of organic matter tended to be located in shallower and deeper transects, it means, those with predominance of larger granulometric sediments.

Overall, 1492 individuals were collected. In Ubatuba, 433 *P. mediterranea*, 47 *P. punctata* and 18 *P. lichtensteinii* were recorded, while in Caraguatatuba 814 *P. mediterranea*, 140 *P. punctata* and 40 *P. lichtensteinii* were captured (Fig. 4, Table 2).

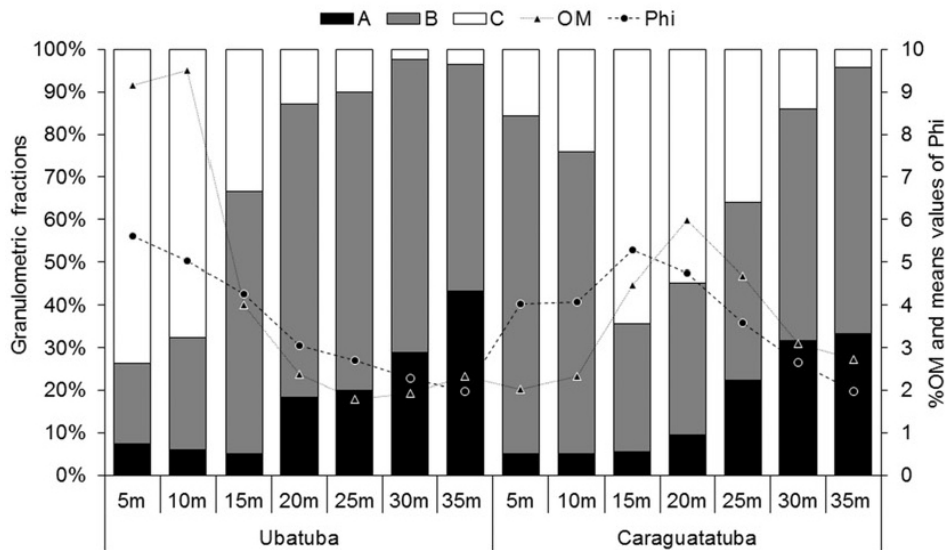
The crab *P. mediterranea* was collected in greater abundance in winter months and in lower amounts in spring months (Fig. 5). In the region of Ubatuba peaks were observed in July of both years and the lowest number of individuals was recorded in the months with lower bottom temperatures. In Caraguatatuba peaks of abundance were observed in July and January of the first year and in September, January and May of the second year. The greater abundance of *P. punctata* was recorded in winter months (Fig. 5), both in Ubatuba and Caraguatatuba. The crab *P. lichtensteinii* was captured predominantly in autumn and winter months in the two regions (Fig. 5), coinciding with higher bottom temperatures.

The crab *P. mediterranea* was more abundant in intermediate transects, it showed greater abundance in 15 m and 20 m in Ubatuba and 15-30 m in Caraguatatuba. The lowest abundance was recorded in both regions in shallower transects. To *P. punctata*, the higher abundance was recorded in 5 m in Ubatuba, while in Caraguatatuba the greater abundance was in 15 and 20 m. The crab *P. lichtensteinii* was collected only in 5-15 m in Ubatuba, while in Caraguatatuba this species was more abundant in 25 and 30 m (Fig. 6).

None of the environmental variables reached the Spearman correlation limit established in 0.7 and the VIF limit by 10. On the PCA, the main components PC1, PC2 and PC3 accumulated 85.55% of data variation (Table 3). According to the PCA, the regions



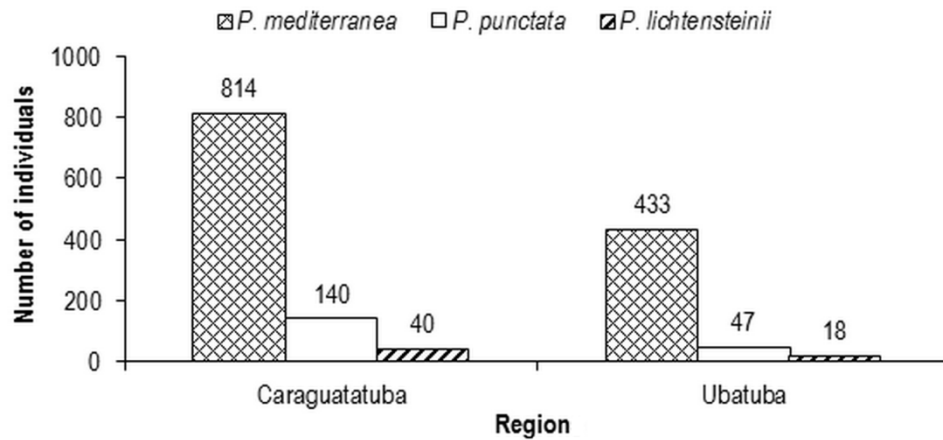
**Figure 2.** Variations in the means of bottom and surface temperatures ( $\pm$  standard deviation) by transects, during the sampling period (July 2001 to June 2003).



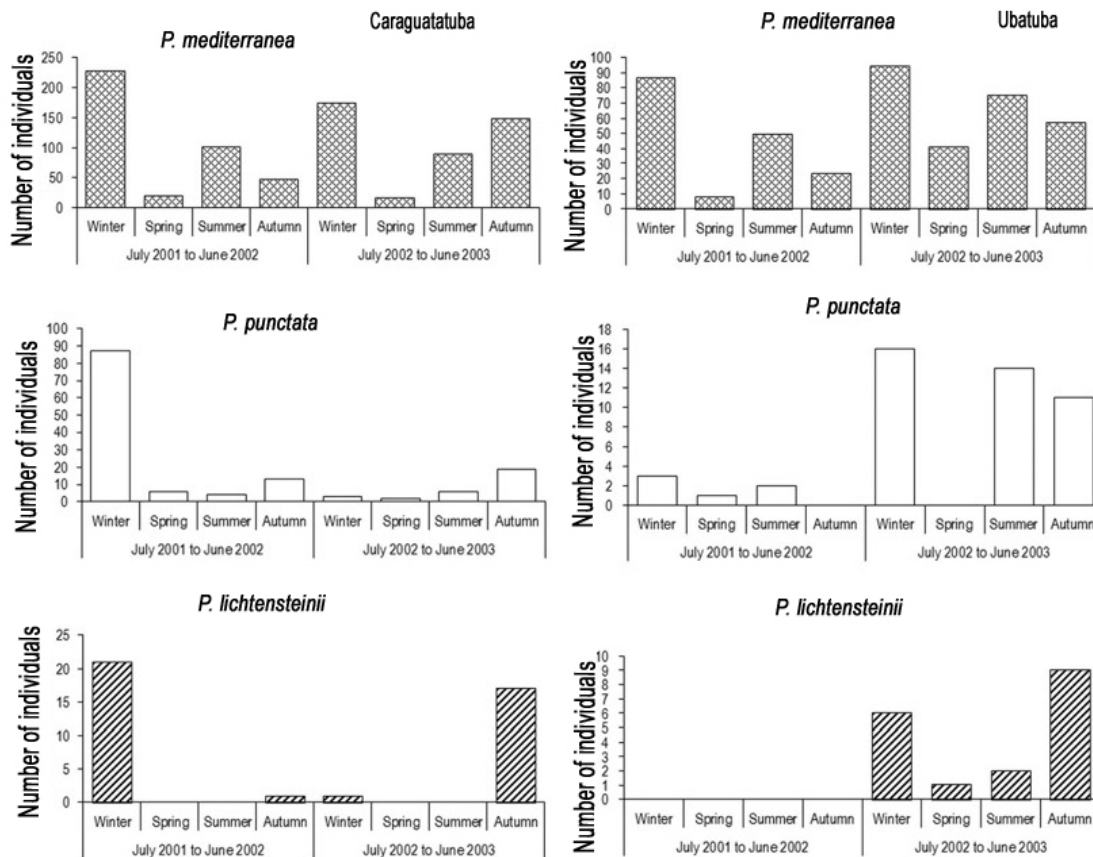
**Figure 3.** Proportions of grain size classes, central tendency of bottom sediments (Phi), and mean organic matter content (%) for each transect. See Material and Methods for granulometric class classifications.

of UBA and CA were homogeneous in space and time as evidenced when observing the scores of main components 1 and 2. For better observing spatio-temporal patterns, the scores of main components 1

and 2 were plotted separately for each region (Ubatuba and Caraguatatuba) (Fig. 7). Thus, all environmental variables were used for the association of *Persephona* species in the following analysis.



**Figure 4.** Abundance of species of the genus *Persephona* in Ubatuba and Caraguatatuba regions, northern littoral of São Paulo State, Brazil.



**Figure 5.** Seasonal distribution of species of the genus *Persephona* in Caraguatatuba and Ubatuba regions, northern littoral of São Paulo State, Brazil.

The abundance of species associated to environmental factors (BT, OM, Phi, BS) of both sampled regions evidenced by means of RDA that the most influent environmental factor over the distribution of the three studied species was sediment granulometry (Phi,  $r^2 = 0.5549$ ,  $P = 0.0091$ ) (Fig. 8), being the ascendant order of influence *P. lichtensteinii*, *P. punctata* and *P. mediterranea*.

In Ubatuba the greater abundance was recorded in shallower transects, where finer sediments predominate, while in Caraguatatuba the distribution of individuals were more homogenous, with greater abundance in transects of 25 and 30 m, in which values of Phi were intermediate. In Ubatuba Phi values ranged from 3.1 to 4.0 and in Caraguatatuba they varied from 2.1 to 6.0 (Fig. 8).



**Table 2.** Monthly collections of *Persephona* species in each region (1<sup>st</sup> = July 2001 to June 2002; 2<sup>nd</sup> = July 2002 to June 2003), and total for each season, in the northern littoral of São Paulo State, Brazil. UBA: Ubatuba, CA: Caraguatatuba.

Month	<i>Persephona mediterranea</i>						<i>Persephona punctata</i>						<i>Persephona lichtensteinii</i>					
	UBA		CA		Total		UBA		CA		Total		UBA		CA		Total	
	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>	1 <sup>st</sup>	2 <sup>nd</sup>
July	66	65	125	58	191	123	2	9	7	1	9	10	0	1	9	1	9	2
August	18	9	95	46	113	55	1	2	78	2	79	4	0	4	12	0	12	4
September	2	20	6	70	8	90	0	5	2	0	2	5	0	1	0	0	0	1
October	3	10	16	10	19	20	1	0	6	1	7	1	0	0	0	0	0	0
November	3	8	0	2	3	10	0	0	0	0	0	0	0	0	0	0	0	0
December	2	23	2	3	4	26	0	0	0	1	0	1	0	1	0	0	0	1
January	27	32	100	68	127	100	0	1	4	4	4	5	0	0	0	0	0	0
February	22	7	0	4	22	11	2	9	0	0	2	9	0	2	0	0	0	2
March	0	36	0	16	0	52	0	4	0	2	0	6	0	0	0	0	0	0
April	0	30	0	42	0	72	0	1	0	5	0	6	0	1	0	1	0	2
May	5	22	15	65	20	87	0	10	0	3	0	13	0	6	0	7	0	13
June	18	5	30	41	48	46	0	0	13	11	13	11	0	2	1	9	1	11
Total	166	267	389	425	555	692	6	41	110	30	116	71	0	18	22	18	22	36
						1247						187						58

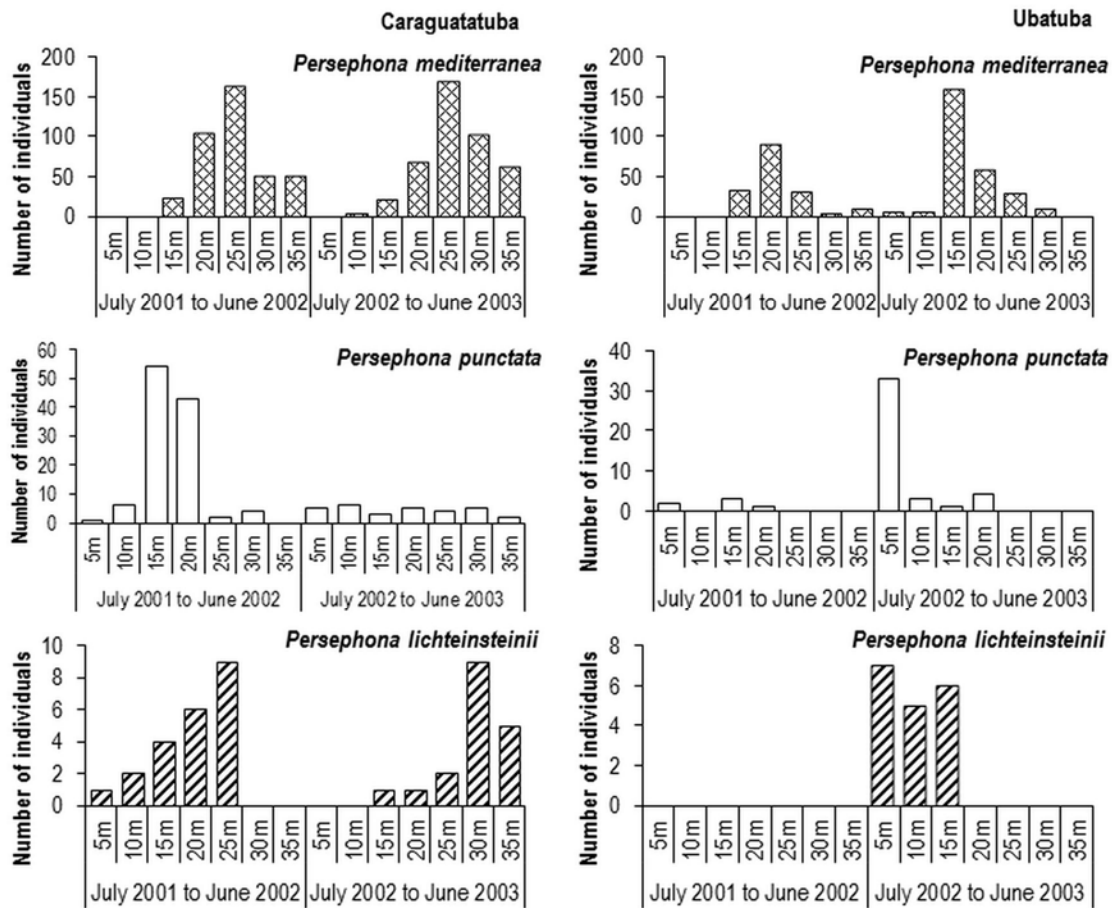
The occurrence of overdispersion on GLMM ZIP (Table 4) attested the use of GLMM ZINB (Zuur *et al.*, 2009) for each species. Results of GLMM ZINB corroborated those indicated by RDA, showing that Phi influences more the abundance of *P. mediterranea* (Table 5) and *P. punctata* (Table 6). However, GLMM ZINB results for *P. lichtensteinii* (Table 7) were not significant for any evaluated factor, both for counting and occurrence data. This is evident in Figure 8 in which *P. lichtensteinii* is very next to the origin in the RDA plot.

## DISCUSSION

Environmental factors may influence the distribution of marine organisms, defining the occupation in wide areas or restricting their distribution. In general it was observed more individuals of *P. mediterranea*, followed by *P. punctata* and *P. lichtensteinii*, respectively. The same relation of abundance was observed by Bertini *et al.* (2001) and Almeida *et al.* (2013). This difference may be associated with the limits of the species distribution. Considering the low abundance of *P. lichtensteinii* when compared to the other species, we suppose that it occurs due to this species limits of distribution that were related for São Paulo State by Melo (1996) and involves restrict environmental conditions related to this region on the Brazilian coast.

The Northern coast of São Paulo presents a characteristic composition of water masses with seasonal intrusion of a cold and saline water mass, South Atlantic Central Water, thus forming a thermocline (Castro-Filho *et al.*, 1987) that has decisive role on the distribution of several Brachyura species (Franzoso *et al.*, 1992; Pinheiro *et al.*, 1996; Léo & Pires-Vanin, 2006). Thus, with extreme environmental conditions acting over the physiology and biology of the animal, its abundance is reduced in neighboring regions of its distribution.

In a comparative study of the distribution of *P. lichtensteinii* and *P. punctata* in Ilhéus, northeastern coast of Brazil, Carvalho *et al.* (2010) verified a predominance of *P. lichtensteinii*, contrasting with the abundance pattern observed for the genus in southern and southeastern Brazil. However, in a six-year study (1996-2002) on the occurrence and abundance of accompanying crustaceans of the Atlantic seabob fishery (*Xiphopenaeus kroyeri*) in Armação do Itapocoroy, Penha, Santa Catarina State, Branco & Fracasso (2004) recorded the presence of 53 individuals of *P. lichtensteinii* between 2001 and 2002. This allows us to suggest that through the two years the species increased its limits of distribution



**Figure 6.** Principal Component Analysis (PCA) for the two sampling regions. A: Caraguatatuba, B: Ubatuba. The acronyms represent the seasons (S: summer, A: autumn, W: winter, SP: spring) of each region (CA: Caraguatatuba and UBA: Ubatuba).

**Table 3.** Principal Component Analysis (PCA) of collections of *Persephona* species in two regions of the northern littoral of São Paulo State, Brazil.

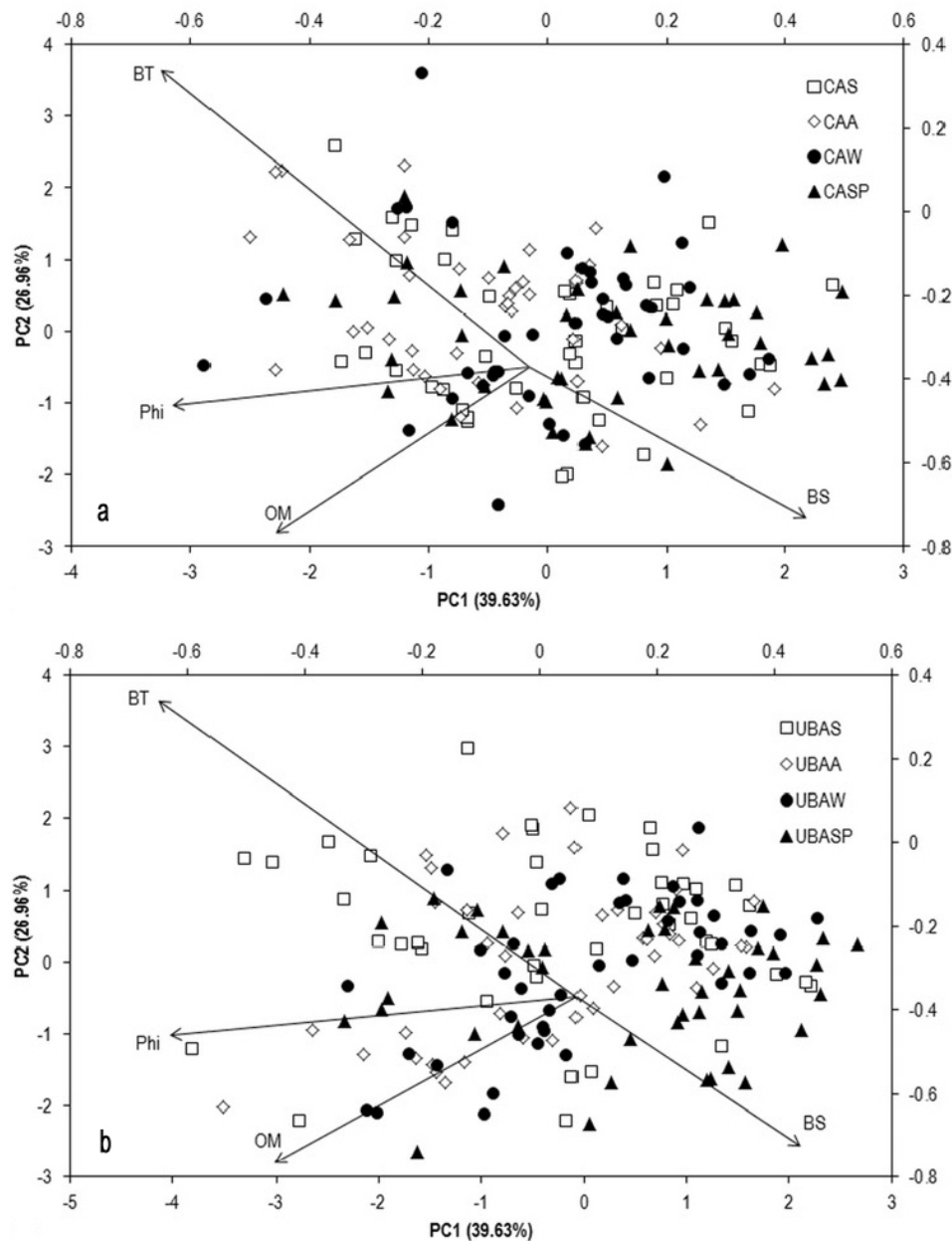
	PC1	PC2	PC3	PC4
Standard deviation	1.259	1.0384	0.8709	0.7605
Proportion of variance (%)	0.3963	0.2696	0.1896	0.1446
Cumulative proportion (%)	0.3963	0.6658	0.8554	1

because there was the improvement of this species records (Branco & Fracasso, 2004), not following the pattern proposed by Melo (1996). Nevertheless, the species presented lower abundance when compared to the other species of the genus, thus keeping the distribution pattern known for the genus.

Individuals of the three species were captured in different transects. This highlights that the distribution patterns of *P. mediterranea*, *P. punctata* and *P. lichteinsteinii* are influenced by environmental factors acting together, and it is not possible to comprehend them analyzing only transects depth.

The greater abundance of *P. mediterranea* was recorded in the transects of 15 and 20 m, what is in accordance with results obtained by Pires (1992) and Bertini *et al.* (2001, 2010). These transects were similar in relation to Phi and OM values, which were composed predominantly by thin sediments, granulometric class C (silt and clay). Meanwhile, *P. punctata* and *P. lichteinsteinii* were captured in greater amounts in shallower transects, corroborating the results obtained by Fransozo *et al.* (1992), Negreiros-Fransozo *et al.* (1992, 1999), Mantelatto & Fransozo (2000) and Bertini *et al.* (2001).

When comparing the abundance of species in relation to temporal variables, it can be observed that species were collected in greater amounts in autumn and winter months. Such difference in the abundance of crabs associated with the seasons is due to the influence of temperature variations in the biology of these organisms. It was noted that the lower abundance was recorded in spring and summer months, both under the influence of SACW (South

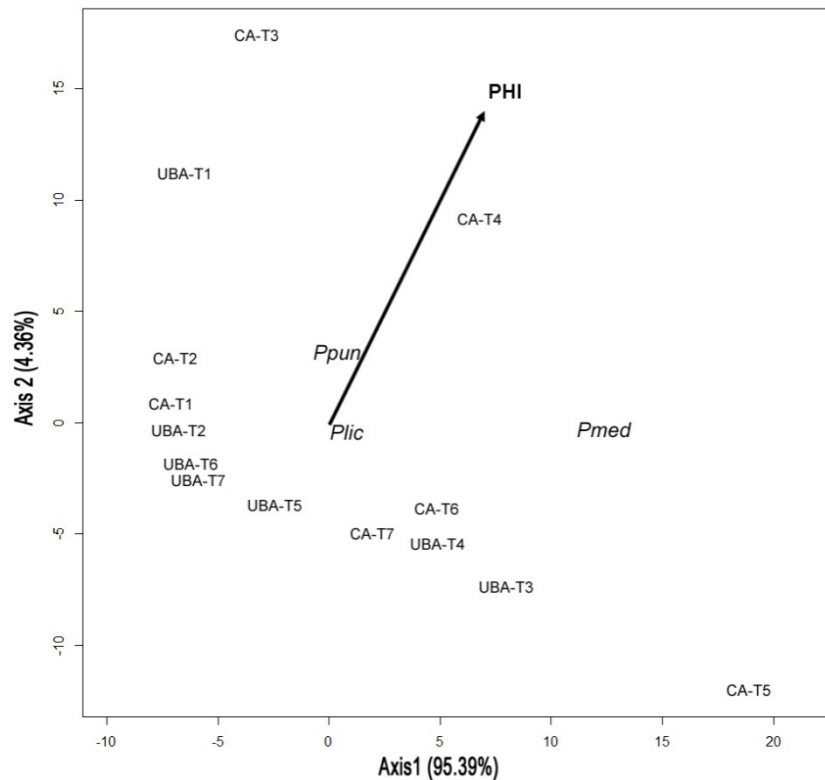


**Figure 7.** Redundancy analysis (RDA) for three species of the genus *Persephona* in the regions of Caraguatatuba and Ubatuba. The acronyms represent the transects (T1 to T7) of each region (CA and UBA). Only significant environmental variables were represented, according to 'envfit'.

Atlantic Central Water). This suggests the preference of such organisms by regions that present water with higher temperatures. The ecological distribution of such species corroborates results obtained by Bertini *et al.* (2001) only for *P. lichtensteinii*, being this species more abundant in winter months. The same author collected *P. mediterranea* and *P. punctata* in greater amounts during spring months, differing from the results here presented. In a study performed on the coast of Ilhéus, Bahia, the greater abundance of *P.*

*lichtensteinii* and *P. punctata* was recorded in autumn months (Carvalho *et al.*, 2010).

When comparing patterns of spatiotemporal distribution of the three species, a differential distribution was observed. These variations may indicate a strategy to avoid competition among congeneric species, and it may be related to the substratum specificity and to the organic matter associated with it, or the environmental characteristics that vary among seasons.



**Figure 8.** Variation in abundance of the genus *Persephona* per transect in Caraguatatuba and Ubatuba regions, northern littoral of São Paulo State, Brazil.

**Table 4.** Likelihood ratio test between model 1 (GLMM ZINB) and model 2 (ZIP) to data overdispersion for each studied species of the genus *Persephona*. Global models used:  $Y \sim \text{Bay} * \text{Season} + \text{BS} + \text{BT} + \text{OM} + \text{Phi} \mid \text{Bay} * \text{Season} + \text{BS} + \text{BT} + \text{OM} + \text{Phi}$ . Y: Dependent variable (*Persephona* species data), Bay\*Season: Interaction between Bay vs Season, df: degrees of freedom, LogLik: log likelihood value,  $\chi^2$ : Chi-Square,  $P(>\chi^2)$ : P-value, \*\*\*: significance value.

		df	LogLik	df	$\chi^2$	$P(>\chi^2)$
<i>Persephona mediterranea</i>	Model 1	24	-999.53			
	Model 2	25	-560.18	1	878.7	<2.2e-16***
<i>Persephona punctata</i>	Model 1	18	-243.38			
	Model 2	19	-192.81	1	101.14	<2.2e-16***
<i>Persephona lichtensteinii</i>	Model 1	18	-109.12			
	Model 2	19	-94.078	1	30.081	0.00000004144***

The greater influence of sediment (Phi) on limiting the distribution of crabs of the genus *Persephona* may be associated with their life habit, which is to bury itself and capture polychaetes from infauna, its main food item (Petti *et al.*, 1996; Bellwood, 2002). The *Persephona* crabs were more abundant in thin sediment, which facilitates its burying habit. The preference for thinner sediment can also be related to the search for food. When there is more organic matter available it is verified an increase in the number of organisms that feed of it (*e.g.*, polychaetes). Since these organisms are prey to *Persephona*, according to

the food availability, the crabs tend to increase. The same association with food availability was verified for the brachyuran *Callinectes ornatus* (Mantelatto, 2000). Although the three species presented differential spatial distribution with the bathymetry, all of them occupying areas with fine sediment mainly composed by silt clay, as verified by Fransozo *et al.* (1992), Negreiros-Fransozo *et al.* (1999) and Bertini *et al.* (2001). The relation between OM and Phi and its influence on the distribution was also verified for other decapods, such as *Portunus spinimanus* Latreille, 1819, *Hepatus pudibundus* Herbst, 1785 and *Petrochirus*

**Table 5.** GLMM ZINB for *Persephona mediterranea* in two regions of the northern littoral of São Paulo State, Brazil. (Significant codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1).

Count model	Estimate	Std. Error	z value	P (> z )
(Intercept)	2.3432	0.6071	3.86	0.000113***
Bay UBA	-0.8282	0.5161	-1.605	0.108553
Spring	-1.0751	0.6447	-1.668	0.095384
Summer	0.3052	0.5429	0.562	0.573955
Winter	1.1486	0.5354	2.145	0.031921*
Phi	-0.2213	0.1331	-1.663	0.096402
Bay UBA: Spring	1.1741	0.8861	1.325	0.185131
Bay UBA: Summer	0.6768	0.8191	0.826	0.408684
Bay UBA: Winter	-0.4492	0.7674	-0.585	0.558314
Log (theta)	-1.4338	0.2057	-6.97	0.00000000000318***

Binomial model	Estimate	Std. Error	z value	P (> z )
(Intercept)	-13.7772	1537.4	-0.009	0.99285
Bay UBA	13.6362	1537.4	0.009	0.99292
Spring	15.3052	1537.4	0.01	0.99206
Summer	15.0413	1537.4	0.01	0.99219
Winter	14.5195	1537.4	0.009	0.99246
Phi	-0.5684	0.2181	-2.606	0.00915**
Bay UBA: Spring	-13.44	1537.4	-0.009	0.99302
Bay UBA: Summer	-13.1885	1537.4	-0.009	0.99316
Bay UBA: Winter	-15.1665	1537.4	-0.01	0.99213

**Table 6.** GLMM ZINB for *Persephona punctata* in two regions of the northern littoral of São Paulo State, Brazil. (Significant codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1).

Count model	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	-3.1345	0.9858	-3.18	0.00147**
Bay UBA	1.3477	1.1839	1.138	0.25496
Spring	-0.3074	0.9891	-0.311	0.75594
Summer	-0.856	0.5493	-1.558	0.11914
Winter	1.2183	0.6084	2.002	0.04525*
Phi	0.6361	0.2086	3.05	0.00229**
Bay UBA: Spring	-3.7282	2.2748	-1.639	0.10123
Bay UBA: Summer	-0.6308	1.6312	-0.387	0.69899
Bay UBA: Winter	-2.8956	1.4624	-1.98	0.0477*
Log (theta)	-1.0293	0.3182	-3.235	0.00122**

Binomial model	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	-13.6488	1668.66	-0.008	0.9935
Bay UBA	18.6024	1668.66	0.011	0.9911
Spring	18.4933	1668.66	0.011	0.9912
Summer	-4.5893	60074	0	0.9999
Winter	16.3526	1668.66	0.01	0.9922
Phi	-0.8366	0.3687	-2.269	0.0233*
Bay UBA: Spring	-19.4697	1668.66	-0.012	0.9907
Bay UBA: Summer	3.6221	60074	0	1
Bay UBA: Winter	-19.4756	1668.66	-0.012	0.9907

**Table 7.** GLMM ZINB for *Persephona lichtensteinii* in two regions of the northern littoral of São Paulo State, Brazil. (Significant codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1).

Count model	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	-1.59329	1.31019	-1.216	0.22396
Bay UBA	-0.44209	0.50554	-0.874	0.38186
Spring	-0.43149	1.55664	-0.277	0.78163
Summer	0.55715	1.47988	0.376	0.70656
Winter	0.03439	0.44604	0.077	0.93855
Phi	0.24376	0.27145	0.898	0.3692
Log (theta)	-1.05752	0.3424	-3.089	0.00201 **

Binomial model	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	338.183	326.598	1.035	0.3
Bay UBA	68.085	90.02	0.756	0.449
Spring	383.504	348.673	1.1	0.271
Summer	297.597	309.694	0.961	0.337
Winter	-11.482	72.647	-0.158	0.874
Phi	-111.476	102.548	-1.087	0.277
Bay UBA: Spring	-162.62	154.133	-1.055	0.291
Bay UBA: Summer	-43.526	3177.59	-0.014	0.989
Bay UBA: Winter	-9.629	156.234	-0.062	0.951

*diogenes* Linnaeus, 1758, by Santos *et al.* (1994), Mantelatto *et al.* (1995) and Bertini & Fransozo (1999), respectively.

Environmental factors act together influencing the distribution of the three species of the genus *Persephona*. It is possible that biotic relations act over the distribution patterns of *P. mediterranea*, *P. punctata* and *P. lichtensteinii*, thus altering them. Thereby, we suggest that studies regarding intra- and inter-specific interactions of such crabs must be developed in order to obtain information that help in the comprehension of the observed patterns of distribution. Furthermore, more studies related to the food habits of *Persephona* species must be done in order to understand if sediment characteristics influence the distribution of such organisms and their preys.

The present study represent a gain of information about patterns of bathymetric distribution of three species of the genus *Persephona* on the southeastern Brazilian continental shelf, once the knowledge regarding such patterns were limited to the transects of 20 m in three bays of Ubatuba region (Bertini *et al.*, 2001). Results here presented allows the improvement of information related to bathymetry because of the greater capture effort (5 to 35 m) and also to the comparison of two regions considered distinct regarding their oceanographic characteristics (Ubatuba and Caraguatatuba).

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