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TESE DE DOUTORADO

DINÂMICA POPULACIONAL DE CRUSTÁCEOS DECÁPODOS EM UMA ÁREA DE PROTEÇÃO AMBIENTAL DO SUDESTE DO BRASIL

Camila Hipolito Bernardo

Orientador: Prof.Dr. Adilson Fransozo

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CAMILA HIPOLITO BERNARDO

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Tese apresentada ao programa de pós-graduação em Ciências Biológicas: Zoologia, do Instituto de Biociências, Universidade Estadual Paulista (UNESP), Campus de Botucatu, como parte dos requisitos para a obtenção do título de Doutora em Ciências Biológicas – Área de Concentração: Zoologia.

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EPÍGRAFE

“A tarefa não é tanto ver aquilo que ninguém viu, mas pensar
o que ninguém ainda pensou sobre aquilo que todo mundo vê”
(Arthur Schopenhauer)

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CONSIDERAÇÕES INICIAIS

CONSEIDERAÇÕES INICIAIS

Esta tese foi elabora em quarto capítulos, os capítulos contam com coletas de 3 grandes projetos desenvolvidos pelo NEBECC. Os projetos realizados na Enseada da Fortaleza, comparação entre 20 anos (1988/1989 - 2008/2009), Enseada de Ubatuba (1995/1996) e região de Ubatuba no ano 2000. As espécies escolhidas para o desenvolvimento desta tese foram um siri *Achelous spinimanus* LATREILLE 1819, os caranguejos *Persephona lichtensteinii* Leach, 1817, *P. mediterranea* Herbst, 1794 e *P. punctata* Linnaeus, 1758 e o camarão *Litopenaeus schmitti* (Burkenroad, 1936).

A escolha de 3 grandes projetos e das espécies foi realizada para que houvesse uma abordagem ampla dos projetos realizados pelo NEBECC associado ao conhecimento de grupos distintos de Crustaceos, com representantes de siri, caranguejo e camarão.

Os dois primeiros capítulos foram relacionados as coletas realizadas na região de Ubatuba de janeiro a dezembro do ano 2000. Foram realizados arrastos em 8 profundidades, dos 5 aos 40 metros. A espécie destes dois capítulos, *Achelous spinimanus* pertence a ordem Decapoda, infraordem Brachyura e família Portunidae. É um siri comumente capturado como *bycatch* da pesca de arrasto direcionada a camarões de interesse comercial.

O primeiro capítulo abordou a distribuição dos grupos demográficos deste siri, tendo em vista que a distribuição diferencial já havia sido encontrada para outras espécies de siris como *Callinectes ornatus* ORDWAy 1863 (Andrade *et al*., 2014), *Callinectes danae* SMITH 1869 (Barreto *et al*., 2006 and Antunes *et al*., 2015) e *Arenaeus cribrarius* (LAMARck 1818) (Silva *et al*., 2018).

O segundo capítulos abordou aspectos relacionados a reprodução e estrutura populacional do *A. spinimanus,* sendo estes de suma importante para elaboração de medidias mitigadoras dos impacto causado pela pesca de arrasto.

O terceiro capítulo foi realiado com a coleta realizada em oito estações amostrais na Enseada de Ubatuba, de setembro de 1995 a agosto de 1996. O trabalho analisou a sobreposição de nicho de 3 espécies do gênero *Persephona*. E testou a hipótese de existência de *Phylogenetic signal.*

O último capítulo foi elabora com dados do projeto de 20 anos realizado na Enseada da Fortaleza. As coletas foram realizadas em sete transectos de novembro de 1988 a outubro de 1989 e repetidas de novembro de 2008 a outubro de 2009.

A espécie utilizada foi o camarão economicamente exploraro *L schmitti,* conhecido popularmente por camarão branco. Bernardo et al., (2018) mostraram que a Enseada da Fortaleza sofreu grandes modificações apos 20 anos, sendo a principal delas a sedimentação com o acumulo de silte e argila. Tendo em vista que *L. schmitti* é mais abundânte neste tipo de sedimento (Bochini et al., 2014 e Barioto et al., 2017), testamos a hipótese de que após 20 anos apesar dos impactos causados pelaa pesca de arrasto, haveria aumentado a quantidade de *L. schmitti* na Enseada da Fortelza.

REFERÊNCIAS

Andrade, L.S.; Bertini, G.; Fransozo, V.; Teixeira, G.M.; Barros-Alves, S.P.; Fransozo, A. 2014. Differential occupation of habitat as a reproductive strategy of the blue crab *Callinectes ornatus* Ordway, 1863 (Crustacea: Decapoda). *Marine Biodi- versity,* **44**: 27-36. http://10.1016/j.csr.2014.12.005

Antunes, M.; Fransozo, V.; Bertini, G.; Teixeira, G.M.; Fransozo, A. 2015. Abundance and distribution of the swimming crab *Callinectes danae* Smith, 1869 (Crustacea, Decapoda, Portunidae) in the Ubatuba region, southeastern Brazil. *Marine Biology Research,* **11**: 920-932. https://doi.org/10.1080/17451000.2015.1044998

Barreto, A.V.; Batista-Leite, L.M.A.; Aguiar, M.C.A. 2006. Maturidade sexual das fêmeas de *Callinectes danae* (Crustacea, Decapoda, Portunidae), nos estuários dos rios Botafogo e Carrapicho, Itamaracá, PE, Brasil. *Iheringia,* **96**(2): 141–146. https://doi. org/10.1590/s0073-47212006000200003

Silva, T.E.; Andrade, L.S.; Fransozo, V.; Freire, F.A.M.; Fransozo, A. 2018. Population parameters and distribution of *Arenaeus cribrarius* (Crustacea, Portunoidea), in southeastern brazilian coast. *Boletim do Instituto de Pesca*, **44**(1): 1-9. https://doi. org/10.20950/1678-2305.2018.187

Bernardo, C. H., Sancinetti, G. S., Taddei, F. G., Hiroki, K. A. N., de Almeida, A. C., & Fransozo, A. (2018). Abundance and spatio-temporal distribution of two Southwest Atlantic endemic shrimps: changes after 20 years. *Biologia*, *73*(6), 589-598.

Bochini, G. L., Fransozo, A., Castilho, A. L., Hirose, G. L., & Costa, R. C. (2014). Temporal and spatial distribution of the commercial shrimp *Litopenaeus schmitti* (Dendrobranchiata: Penaeidae) in the south-eastern Brazilian coast. *Journal of the Marine Biological Association of the United Kingdom*, *94*(5), 1001-1008.

Branco, J. O. 2005. Biologia e Pesca do camarão Sete-Barbas *Xiphopenaeus kroyeri* (Heller) (Crustacea, Penaeidae), na armação do Itapocory, Penha Santa Catarina, Brasil. Revista Brasileira de Zoologia, 22: 1050-1062.

CAPÍTULO 1

Environmental factors modulating the bathymetric distribution of the demographic groups of *Achelous spinimanus* (Crustacea)

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RESEARCH ARTICLE

Environmental factors modulating the bathymetric distribution of the demographic groups of *Achelous spinimanus* (Crustacea)

Camila Hipolito Bernardo[1], Veronica Pereira Bernardes[1],
Aline Nonato de Sousa[1], Gabriel Fellipe Barros Rodrigues[1],
Thiago Elias da Silva[1], Adilson Fransozo[1]

1 *Group of Study on Crustacea Biology, Ecology and Culture (NEBECC), Department of Zoology, São Paulo State University (UNESP), Institute of Biosciences, Botucatu, State of São Paulo, Brazil*

Corresponding author: *Camila H. Bernardo* (camila.hipolito@unesp.br)

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Abstract

The spatio-temporal distribution of *Achelous spinimanus* demographic groups (juveniles, and adult males and females) and its relation with environmental factors was analyzed in the region of Ubatuba, southeastern Brazil. We performed the samplings from January to December 2000, at eight sites of different depths. A total of 402 specimens of *A. spinimanus* was captured. The lowest abundance of all demographic groups occurred in summer, while in winter and spring the abundance of adults was very high. Spatially, juveniles were found at 5 to 35m of depth, while adults at 15 to 40m, but were more abundant at 25m. The low abundance of all demographic groups during summer is probably due to the arrival of the South Atlantic Central Water in the region, which decreased the water temperature and salinity. These changes caused the migration of *A. spinimanus* to more sheltered places of the bay, possibly due to more favorable environmental conditions. The high abundance of the demographic groups at 25m of depth was due to its more heterogeneous sediment, and to avoid competition with other species more abundant in shallower areas. Therefore, the factors that modulate the distribution of *A. spinimanus* may differ depending on the ontogenetic phase.

Keywords

Seasonal migration, SACW, ecological niche, interspecific relations

PENSOFT.

Introduction

The distribution of marine decapod crustaceans is generally linked to the depth gradient, and determined by one or a set of environmental factors (sediment texture, organic matter content, bottom salinity and temperature) and biotic factors (Mantelatto *et al.*, 1995; Fantucci *et al.*, 2009). In addition, Guillory *et al.* (2001) and Andrade *et al.* (2014) showed that habitat selection by individuals depends on the specific physiological needs of each life cycle phase. However, understanding the distribution patterns of benthic populations is difficult due to the extension of the marine environment and the complex interactions between species and environmental factors (Shirley *et al.*, 1990). Therefore, studies in small areas, such as coves and bays, can help to understand the interactions between these invertebrates and the environmental factors (Braga *et al.*, 2007).

The northern coast of the State of São Paulo has a high number of bays due to its proximity to the hills of Serra do Mar (Mahiques, 1995). This conformation allowed the formation of microhabitats that favor the development and establishment of the marine biota (Negreiros-Fransozo *et al.*, 1991). However, due to the presence of a rich biota, the Ubatuba region is intensely exploited by trawl fisheries targeting shrimps of commercial interest. Trawling is considered predatory and disturbs the benthic communities (Mantelatto *et al.*, 2016).

The swimming crab *Achelous spinimanus* (LATREILLE 1819) is part of the trawling bycatch fauna in Ubatuba (Fransozo et al., 2016; Mantelatto et al., 2016; Bertini et al., 2010ab). This species is considered an important element in the food chain, influencing the dynamics and organization of this environment (Bertini and Fransozo, 2004; Mantelatto and Fransozo, 1999). In addition, *A. spinimanus* reaches an appropriate size and its flavor is suitable for consumption, which makes it a fishing resource (Santos *et al.*, 1995, Andrade *et al.*, 2017). This swimming crab is distributed in the Western Atlantic, occurring from New Jersey (USA) to the State of Rio Grande do Sul (Brazil), where it is captured from the tidal zone to a depth of 90 m (Melo, 1996).

Achelous spinimanus has already been studied by other researchers. For instance, in the Ubatuba region (SP) Santos *et al.* (1994, 2000), Lima *et al.* (2014) and Sousa *et al.* (2018) studied its ecological distribution, and Santos and Negreiros-Fransozo (1999) its reproductive cycle. Branco and Lunardon-Branco (2002) reported its trophic ecology in Armação do Itapocoroy, Penha (SC). Ripoli *et al.* (2007) studied its population dynamics in a coastal stretch of Frade Island in Vitória (ES). De Carli *et al.* (2016) reported its fecundity and morphometry on the coast of São Paulo, and Andrade *et al.* (2017) reported its reproductive and population traits in Macaé (RJ). Despite all these studies with *A. spinimanus*, nothing is known about the spatio-temporal distribution of its demographic groups. A differential spatio-temporal distribution for demographic groups has been reported for other swimming crabs such as *Callinectes ornatus* ORDWAy 1863 (Andrade *et al.*, 2014), *Callinectes danae* SMITH 1869 (Barreto *et al.*, 2006 and Antunes *et al.*, 2015) and *Arenaeus cribrarius* (LAMARck 1818) (Silva *et al.*, 2018). In view of that, we believe that *A. spinimanus* also shows this pattern. Thus, this study analyzed the distribution of *A. spinimanus* demographic groups in relation to depth, months, and environmental factors (bottom temperature and salinity, phi and organic matter) in the Ubatuba region, from January to December 2000. With this information we will expand the knowledge on the biology of *A. spinimanus*, and help to develop more precise management strategies. These strategies are needed since Ubatuba is under intense exploitation by artisanal shrimp fisheries and *A. spinimanus* is commonly caught as a bycatch.

Methods

Study area

The region of Ubatuba, in the northern coast of the state of São Paulo, southeastern Brazil, is a region of faunistic transition between tropical and subtropical regions, and thus an important area for research on crustaceans (Mantelatto *et al.*, 2004 and Boschi, 2000). According to Pires (1992), Ubatuba is strongly influenced by three water masses: South Atlantic Central Water (SACW), with low temperature and salinity; Tropical Water (TW), with high temperature and salinity; and Coastal Water (CW), with high temperature and low salinity.

Data collect

Swimming crabs were collected monthly in the Ubatuba region with a fishing boat equipped with two double rig nets, in the period from January to December 2000. A total of eight depths (5, 10, 15, 20, 25, 30, 35 and 40 m) were delimited and monthly trawled over a 30-min period (about 2 km each) covering a sampling area of about 18.000 m^2 (Figure 1). An ecobathymeter coupled with a GPS was used to record depth at sampling sites. In each depth, samples of the substratum and water from the bottom were monthly collected for analysis of environmental factors. Water was collected with a Nansen bottle in order to obtain the temperature and the salinity. Surface water was sampled also for the temperature. The temperature (°C) was measured with a mercury thermometer and salinity (ppt) using an optical refractometer.

Sediment samples were obtained with a Van Veen grab (0.025 m^2) to analyze sediment grain size composition and organic matter content. Sediment samples were transported to the laboratory and oven-dried at 70°C for 48 h. For the analysis of grain size composition, two subsamples of 50 g were treated with 250 mL of NaOH solution (0.2 mol/L) and stirred for 5 min to release silt and clay particles. Next, the subsamples were rinsed on a 0.063 mm sieve. Grain size composition fol-

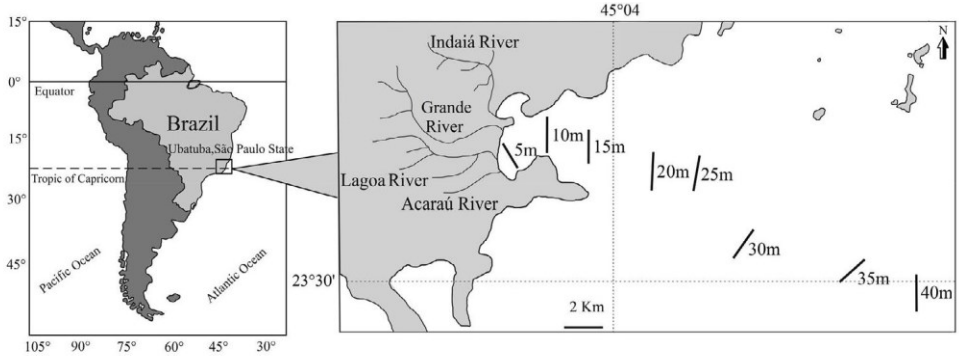

Figure 1. Location of the study region, indicating the depths sampled.

lowed the Wentworth (1922) American standard, for which sediments were sieved at: 2 mm (for gravel retention); 2.0-1.0 mm (very coarse sand); 1.0-0.5 mm (coarse sand); 0.5-0.25 mm (medium sand); 0.25-0.125 mm (fine sand) and 0.125-0.063 mm (very fine sand). Smaller particles were classified as silt and clay.

The three most quantitative important sediment grain size fractions were defined according to Magliocca and Kutner (1965): Class A – sediments in which gravel (G), very coarse sand (VCS), coarse sand (CS), and medium sand (MS) account for more than 70% of the sample weight. In Class B, fine sand (FS) and very fine sand (VFS) constitute more than 70% by of the sample weight. In Class C, more than 70% of the sediments are silt and clay (S+C). *Phi* values were calculated using the formula *phi* = – $\log_2$d, where d = grain diameter (mm), in which the following scale was obtained: -2 = *phi* < -1 (G); -1 = *phi* < 0 (VCS); 0 = *phi* < 1 (CS); 1 = *phi* < 2 (MS); 2 = *phi* < 3 (FS); 3 = *phi* < 4 (VFS); and *phi* ≥ 4 (S+C). From these scales, measures of central tendency were calculated in order to determine the most frequent grain size fraction in the sediment. These values were calculated from data extracted from cumulative curves of sediment frequency distribution. The values corresponding to the 16th, 50th and 84th percentiles were used to determine the mean diameter (md) using the formula md = *phi*16 + *phi*50 + *phi*84/3 (Suguio, 1973). These three categories were further combined to form nine different groups: PA = (MS + CS + VCS + G)>70%; PAB = prevalence of A over B (FS + VFS); PAC = prevalence of A over C (S + 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. Finally, organic matter content of sediment was estimated as the difference between initial and final ash-free dry weights of two subsamples (10 g each) incinerated in porcelain crucibles at 500°C for 3 h.

Laboratory procedures

The individuals were identified according to Melo (1996), separated by sex by abdominal morphology (triangular - males, rounded - females) and the number of pleopods (2 pairs - male, 4 pairs - female). Individuals with the sealed abdomen were considered immature (IM), and those with the unsealed abdomen were considered adult. The individuals were separated into demographic groups: juveniles (immature males + immature females), adult males and adult females.

Data analysis

The normality and homoscedasticity were tested by the Shapiro Wilk and Levene tests, respectively. The environmental variables and the abundance of the demographic groups were compared between the depths and the months sampled, using the Kruskal-Wallis statistical test, complemented by Dunn's multiple comparison test (Zar, 1996). The Mann-Whitney test was performed between the surface and bottom temperatures in the months and depths. A Redundancy Analysis (RDA) was used in order to detect possible relationships between the abundance of the demographic groups and the environmental factors (bottom temperature and salinity, phi and organic matter) (Oksanen *et al.*, 2013). The variables were considered biologically significant according to Rakocinski *et al*. (1996) (i.e. ≥ ± 0.4).

Two correspondence analyzes (CA) were made with the demographic groups mentioned above: one with the different depths and another with the months. The observed associations of both variables (abundance group and bathymetric distribution) and (abundance group and months) were summarized by the frequency of each cell in the table and then placed in a geometric dimensional space. The statistical significance of the values and proportion was evaluated using the chi-square test ($\chi 2$), with simulated p-value (based on 2000 permutations) (Nenadic and Greenacre, 2007).

Results

Mean bottom temperature was 23.6 ± 2.3°C, ranging from 16.6 to 23.7°C, with a significant difference between months ($H = 39.8$ and $p < 0.05$) and between depths ($H = 28.7$ and $p < 0.05$) (Figure 2a and Table 1). Mean surface temperature was 23.5 ± 2.7°C, ranging from 18.8 to 23.5°C, and it was significantly different between months ($H = 88.6$ and $p < 0.05$). A thermocline was observed from January to April (Figure 2a and Table 1) and at depths above 15 m (Figure 2b and Table 1). Mean salinity was 34.6 ± 2.1, ranging from 30 to 40. The highest salinity was recorded in June (Figure 3a), whilst the lowest occurred in May and September (Figure 3a and Table 1) ($H = 62.1$ and $p < 0.05$) and ($H = 47.0$ and $p < 0.05$), respectively. The sediment at depths of 5–15 m had high phi values, characterizing a very fine sediment, and also the highest organic matter content. At 20 m of depth and below, phi values decreased, indicating a more heterogeneous sediment, and the organic matter decreased too (Figure 4).

A total of 402 specimens of *A. spinimanus* was collected, 28 juveniles, 105 adult males, and 269 adult females. Only juveniles were found at the shallowest sites (5–10

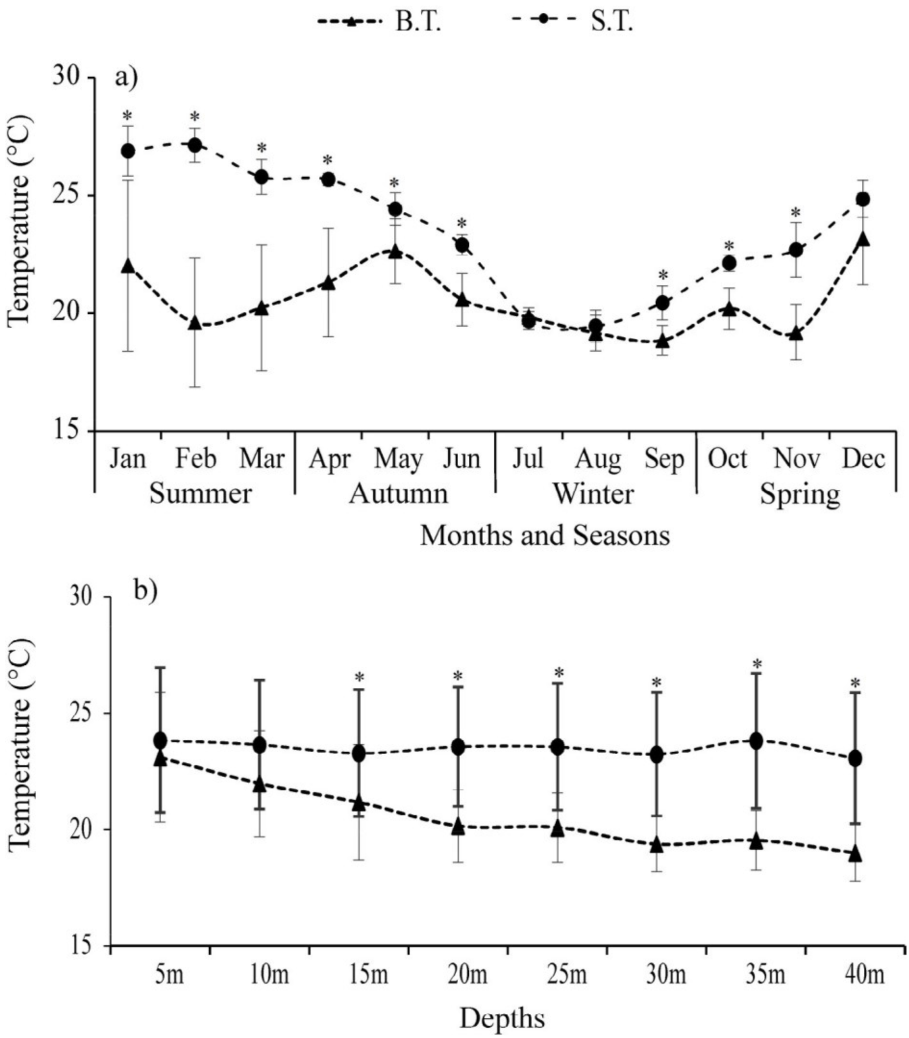

Figure 2. Mean and standard deviation of the bottom (B.T.) and surface (S.T.) temperatures sampled monthly (a) and depth (b) in the year 2000. * Mann-Whitney test, $p < 0.05$.

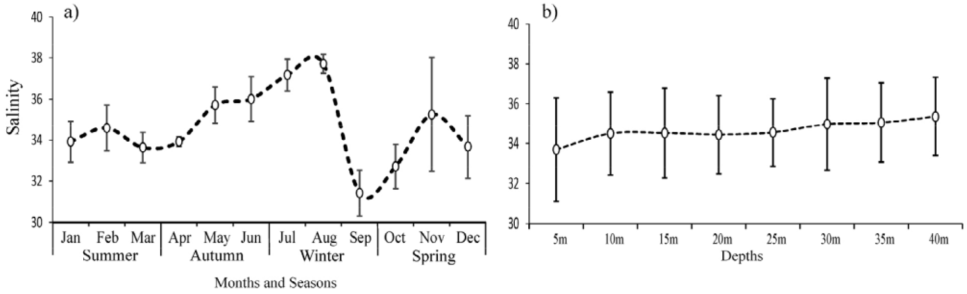

Figure 3. Mean and standard deviation of the bottom salinity sampled monthly (a) and by depth (b) in the year 2000.

Table 1. Mean and standard deviation (±SD) of bottom temperature (BT), surface temperature (ST) and bottom salinity (BS), recorded months and depths. Dunn test result; equal letters have no statistical difference (p>0.05).

Months	BT ± SD	Dunn	ST ± SD	Dunn	BS ± SD	Dunn
Jan	22.02 ±3.62	ab	26.89±1.06	ab	33.91±1.00	abcdf
Feb	19.60±2.73	a	27.14±0.72	a	34.58±1.12	abcfg
Mar	20.22±2.66	a	25.79±0.74	abc	33.62±0.74	bcd
Apr	21.31±2.29	ab	25.68±0.25	abc	33.91±0.23	abcd
May	22.62±1.37	b	24.42±0.69	bce	35.70±0.88	aefg
Jun	20.58±1.10	ab	22.89±0.42	cef	36.00±1.08	efg
Jul	19.83±0.38	ab	19.68±0.38	d	37.16±0.77	eg
Aug	19.16±0.80	a	19.45±0.66	d	37.70±0.45	e
Sep	18.85±0.63	a	20.43±0.71	df	31.41±1.10	d
Oct	20.18±0.88	ab	22.12±0.35	def	32.70±1.07	cd
Nov	19.18±1.16	a	22.68±1.16	def	35.25±2.76	abfg
Dec	23.15±1.93	b	24.85±0.79	abce	33.66±1.53	abcdf
Depths	**BT ± SD**	**Dunn**	**ST ± SD**	**Dunn**	**BS ± SD**	**Dunn**
5m	23.11±2.78	b	23.84±3.10	p>0.05	33.69±2.58	p>0.05
10m	21.98±2.27	ab	23.65±2.76		34.50±2.08	
15m	21.18±2.47	abc	23.29±2.72		34.52±2.24	
20m	20.16±1.54	abc	23.56±2.56		34.44±1.95	
25m	20.09±1.48	ac	23.56±2.72		34.55±1.69	
30m	19.39±1.18	c	23.24±2.64		34.97±2.31	
35m	19.55±1.27	c	23.81±2.89		35.05±1.98	
40m	19.01±1.22	c	23.06±2.80		35.36±1.96	

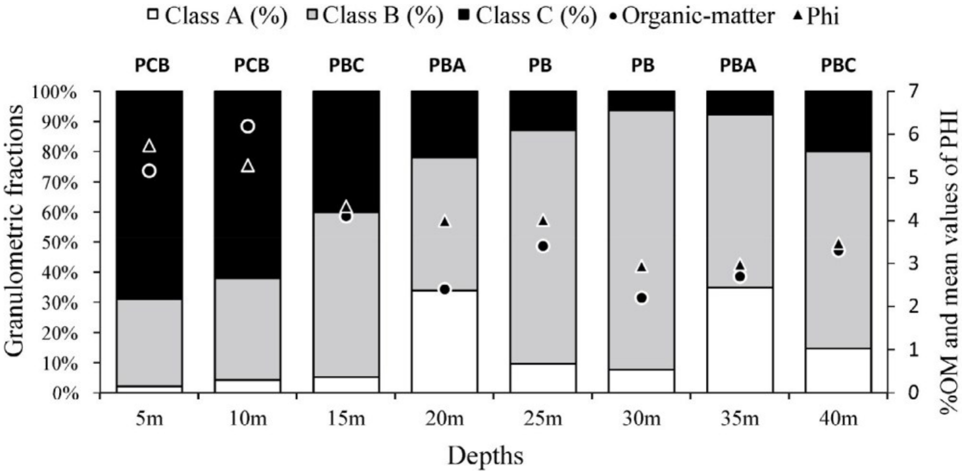

Figure 4. Percentages of granulometric classes and mean values of organic matter in the depths sampled at Ubatuba. A: Class A (gravel, very coarse sand, coarse and medium). B: Class B (fine and very fine sand). C: Class C (silt + clay).

m), while adults of both sexes were more abundant at 20–25 m of depth (Figure 5). The abundance of juveniles was not correlated with any depth (Figure 6a). Temporally, the lowest abundance of all demographic groups occurred in summer, while in winter and spring the abundance of adults was very high (Figure 5 and Figure 6b).

The RDA indicated, in axis 1 (67.55%), a positive correlation between juveniles and bottom temperature, phi, and organic matter, and a negative correlation with salinity. Adults, however, were negatively correlated with bottom temperature, phi, and organic matter, and positively with bottom salinity (Figure 7).

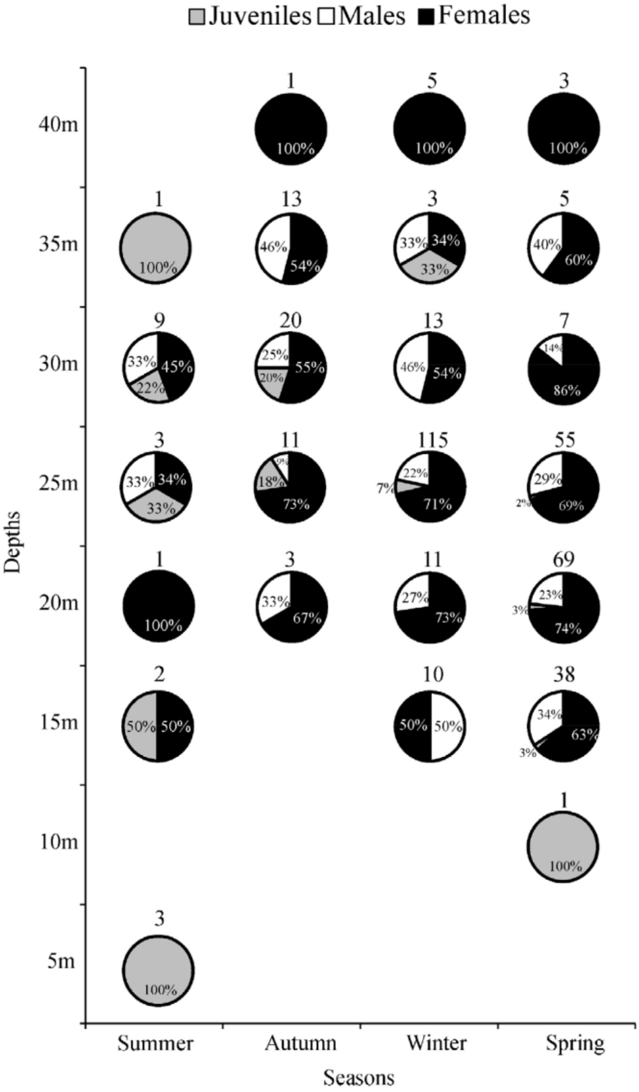

Figure 5. Distribution of demographic groups (juveniles, adult males and adult females) of *Achelous spinimanus* in the seasons and depths sampled. The number under the circle represents the total collected at the depth and season of the year.

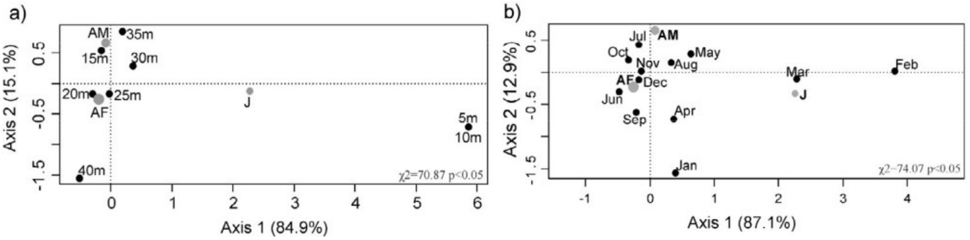

Figure 6. Correspondence Analysis of the abundance of demographic groups (AF = adult females, AM = adult males, J = juveniles) of *Achelous spinimanus* by depths (A) and months (B).

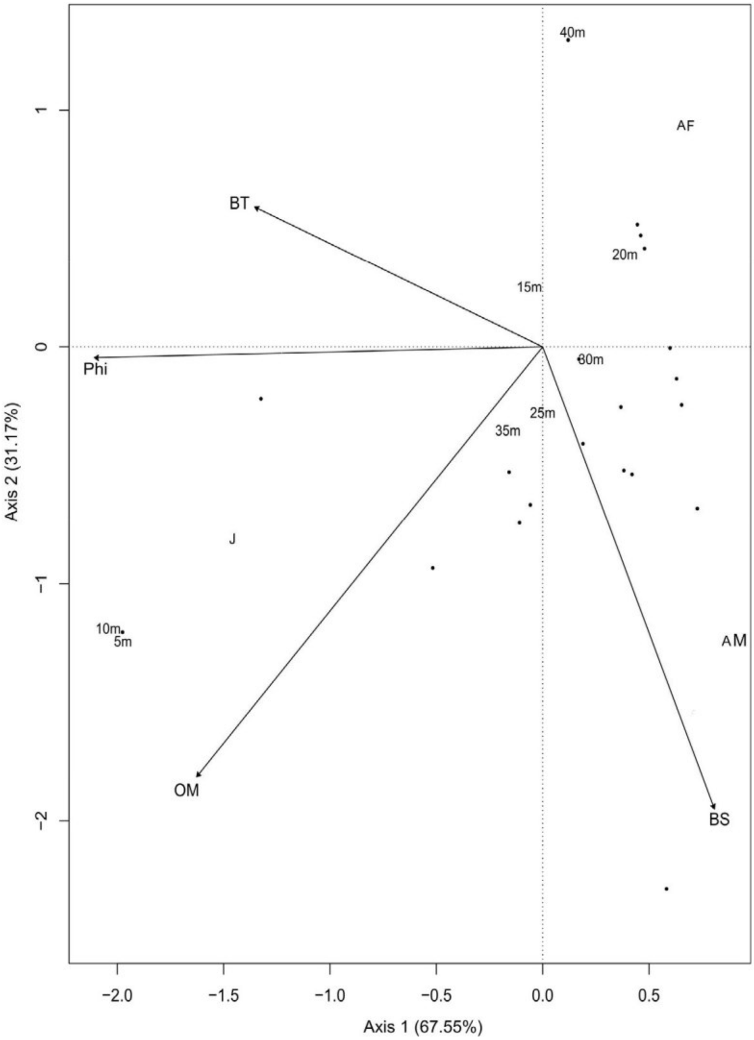

Figure 7. Redundancy Analysis (RDA) between the demographic groups of *Achelous spinimanus* (legend in figure 6) and the environmental variables (BT= bottom temperature; BS= bottom salinity; Phi; OM= organic matter).

Discussion

Our results showed that juveniles and adults of *A. spinimanus* were distributed differentially between depths and months. In Ubatuba, sediment characteristics change according to depth. Due to this change, plus other environmental factors and interspecific interactions, various benthic species of this region are distributed and adapted to certain depth ranges (Bertini and Fransozo, 2004b). The variation in sediment texture and water temperature and salinity are explained by the hydrodynamic regime of Ubatuba, as indicated by our results (Mahiques *et al.*, 1998). The interior area of the bay (5–15 m of depth) is composed of fine sediments with a high amount of silt + clay. This occurs due to the bay's low hydrodynamism, which favors the deposition of fine sediments (Mahiques *et al.*, 1998). On the other hand, sites with depths of 20 m and below are situated offshore, in a region without physical obstacles and strongly influenced by currents. There, the sediment texture is more heterogeneous and fine/very fine sand predominates, and the amount of organic matter is lower (Bertini *et al.*, 2003). In studies by Santos *et al.* (1994), Bertini and Fransozo (2004b) and Mantelatto *et al.* (2016), the swimming crab *A. spinimanus* was more abundant where the substrate was more heterogeneous. This fact explains its higher abundance, in this study, in regions over 20 m of depth. According to Williams (1984), crabs choose sites where their respiratory capacity is not impaired, and by the presence of sites of easier burial. Substrates composed only of very fine sediment, with a high amount of silt + clay, reduce the capacity to pump water to the gills. Thus, some crab species prefer more heterogeneous substrates.

The RDA showed that water temperature seems to modulate the temporal distribution of *A. spinimanus* demographic groups. The temporal variation of water temperature observed in this study may be related to the seasonal influence of the SACW, since a thermal amplitude occurred from January to March, i.e., when the region is under its influence. This thermocline has already been described by Pires (1992), Bertini *et al.* (2001) and Hiroki *et al.* (2011) along the northern coast of São Paulo. The SACW arrives in the region of Ubatuba, coming from deeper regions. It reaches up to 15 meters in late spring and early summer, causing changes in temperature and salinity, and increasing the primary productivity (Odebrecht and Castello, 2001; Lopes *et al.*, 2006).

The changes caused by the arrival of the SACW seem to trigger a seasonal migration of adults to regions where environmental conditions were more favorable to their establishment. Mantelatto *et al.* (2016) found a higher abundance of *A. spinimanus* in spring and summer in sheltered locations of Ubatuba, where there was little influence of this water mass. This seasonal migration helps to explain the low abundance of adults in the first semester of sampling. As of July (winter), when the region was no longer under SACW influence, the abundance of adult *A. spinimanus* increased at all sampling sites, especially at 20–25 m of depth, probably due to the adults' return from the sheltered areas of the bay. However, juveniles were distributed in several depths, including the shallower areas. Thus, the SACW had less influence on this group and also caused a direct relationship between the abundance of juveniles and the high bottom temperatures of these places.

In addition to the influence of temperature, the RDA indicated that adult abundance was positively correlated to salinity, whereas juvenile abundance was negatively correlated to salinity. Thus, juveniles had a wider distribution and occurred from deeper to shallower areas. The shallow areas have a greater variation in salinity due to freshwater supply from the continent. Adult males and females were more abundant in deeper areas where there was little variation in salinity. Thus, adults of both sexes were related to greater depths in the CA, the males at 15 m and the females at 20–25 m. This result suggests that at this development stage both sexes have practically the same environmental requirements.

Another factor that seems to modulate the presence of juveniles in shallower areas is the sediment's high organic matter content. According to Hines *et al.* (1987), the high number of juveniles at shallower depths may be related to the greater availability of shelter and food. A higher abundance of juveniles at lower depths was also observed by Santos *et al.* (1995) with *A. spinimanus*, Heck *et al.* (2001) with *Callinectes sapidus* RATHBUN 1896, Andrade *et al.* (2014) with *C. ornatus* and Antunes *et al.* (2015) with *C. danae*.

The distribution of all demographic groups of this species seems to be modulated not only by environmental factors, but also by interspecific interactions. According to Bertini and Fransozo (2004b) the swimming crabs *A. cribrarius*, *C. danae*, and *C. ornatus* are very abundant in the depths of 5–15 m (inside the bay). Moreover, *C. danae* and *C. ornatus* show agonistic behavior and territorialism, which hinders the establishment of other species (Andrade *et al.*, 2014, Antunes *et al.*, 2015). Thus, adults of *A. spinimanus* may have settled mainly outside the bay (at 20 m of depth and below) to avoid competition with these species.

To conclude, this study showed that, as reported for *C. ornatus* (Andrade *et al.*, 2014) and *C. danae* (Barreto *et al.*, 2006 and Antunes *et al.*, 2015), juveniles and adults of *A. spinimanus* were distributed differently between depths and months, corroborating our hypothesis. Juveniles were widely distributed, from shallower areas 5 m deep to areas 35 m deep, and were more abundant in summer, whereas adults were more abundant at greater depths (20–25 m), in winter and spring.

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References

ALMEIDA, A.C.; BAEZA, J.A.; FRANSOZO, V.; CASTILHO, A.L.; FRANSOZO, A. 2012. Reproductive biology and recruitment of *Xiphopenaeus kroyeri* in a marine protected area in the Western Atlantic: implications for resource management. *Aquatic Biology,* **17**(1): 57-69. https://doi.org/10.3354/ab00462

ANDRADE, L.S.; COSTA, R.C.D.; CASTILHO, A.L.; FRAMESCHI, I.F.; SANCINETTI, G.S.; FRANSOZO, A. 2017 Reproductive and population traits of the swimming crab *Achelous spinimanus* (Crustacea: Decapoda) in an upwelling region in southeastern Brazil. *Nauplius,* **25**: 1-11. http://dx.doi.org/10.1590/2358-2936e2017004

ANDRADE, L.S.; BERTINI, G.; FRANSOZO, V.; TEIXEIRA, G.M.; BARROS-ALVES, S.P.; FRANSOZO, A. 2014. Differential occupation of habitat as a reproductive strategy of the blue crab *Callinectes ornatus* Ordway, 1863 (Crustacea: Decapoda). *Marine Biodiversity,* **44**: 27-36. http://10.1016/j.csr.2014.12.005

ANTUNES, M.; FRANSOZO, V.;BERTINI, G.; TEIXEIRA, G.M.; FRANSOZO, A. 2015. Abundance and distribution of the swimming crab *Callinectes danae* Smith, 1869 (Crustacea, Decapoda, Portunidae) in the Ubatuba region, southeastern Brazil. *Marine Biology Research,* **11**: 920-932. https://doi.org/10.1080/17451000.2015.1044998

BARRETO, A.V.; BATISTA-LEITE, L.M.A.; AGUIAR, M.C.A. 2006. Maturidade sexual das fêmeas de *Callinectes danae* (Crustacea, Decapoda, Portunidae), nos estuários dos rios Botafogo e Carrapicho, Itamaracá, PE, Brasil. *Iheringia,* **96**(2): 141–146. https://doi.org/10.1590/s0073-47212006000200003

BERTINI, G.; FRANSOZO, A. 2004a. Biodiversity of brachyuran crabs (Crustacea: Decapoda) from non-consolidated sublittoral bottom on the northern coast of São Paulo State, Brazil. *Biodiversity and Conservation,* **13**: 2185–2207. https://doi.org/10.1023/B:BIOC.0000047900.96123.34

BERTINI, G.; FRANSOZO, A. 2004b. Bathymetric distribution of brachyuran crab (Crustacea, Decapoda) communities on coastal soft bottoms off southeastern Brazil. *Marine Ecology Progress Series,* **279**: 193–200. https://doi.org/10.3354/meps279193

BERTINI, G.; FRANSOZO, A.; BRAGA, A.A. 2003. 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. https://doi.org/10.1080/00222930310001625905

BERTINI, G.; FRANSOZO, A.; COSTA, R.C. 2001. Ecological distribution of three species of *Persephona* (Brachyura: Leucosiidae) in the Ubatuba region, Sao Paulo, Brazil. *Nauplius,* **9**(1): 31-42.

BERTINI, G.; FRANSOZO, A.; NEGREIROS-FRANSOZO, M.L. 2010. Brachyuran soft-bottom assemblage from marine shallow waters in the southeastern Brazilian littoral. *Marine Biodiversity,* **40:** 277-291. https://doi.org/10.1007/s12526-010-0049-9

BOSCHI, E.E. 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. *Revista de Investigación and Desarrollo Pesquero,* **13**: 7-136.

BRAGA, A.A.; FRANSOZO, A.; BERTINI, G.; FUMIS, P.B. 2007. Bathymetric distribution and recruitment of the spider crab *Libinia spinosa* H. Milne Edwards 1834 in the

Ubatuba and Caraguatatuba regions, northern coast of São Paulo, Brazil (Crustacea, Brachyura, Majoidea, Pisidae). *Senckenbergiana biológica,* **87**: 7–16.

BRANCO, J.O.; LUNARDON-BRANCO, M.J. 2002. Ecologia trófica de *Portunus spinimanus* Latreille, 1819, na Armação do Itacoporoy, Penha, Santa Catarina. *Revista Brasileira de Zoologia,* **19**:723-729. https://doi.org/10.1590/s0101-81752002000300009

DE-CARLI, B.P.; SEVERINO-RODRIGUES, E.; ROTUNDO, M.M.; MUSIELLO-FERNANDES, J.; ANCONA, M.C. 2016. Fecundidade e morfometria de *Achelous spinimanus* (Latreille, 1819) (Brachyura, Portunidae) capturado no litoral do estado de São Paulo, Brasil. *Boletim do Instituto de Pesca,* **40**(4): 487-495.

FANTUCCI, M.Z.; BIAGI, R.; MEIRELES, A.L.; MANTELATTO, F.L.M. 2009. Influence of biological and environmental factors on the spatial and temporal distribution of the hermit crab *Isocheles sawayai* Forest & Saint-Laurent, 1968 (Anomura, Diogenidae). *Nauplius,* **17**(1): 37–47.

FRANSOZO, A.; SOUZA, A.N.; RODRIGUES, G.F.B; TELLES, J.N.; FRANSOZO, V.; NEGREIROS-FRANSOZO, M.L. 2016. Crustáceos decápodes capturados na pesca do camarão-sete-barbas no sublitoral não consolidado do litoral norte do estado de São Paulo, Brasil. *Boletim do Instituto de Pesca,* **42**(2): 369– 386. https://doi.org/10.20950/1678-2305.2016v42n2p369

GUILLORY, V.A.; MCMILLEN-JACKSON, A.L.; HARTMAN, L.; PERRY, H.; FLOYD, T.; WAGNER, T.G.; GRAHAM, G. 2001. *Armadilhas de remoção de caranguejo azul e programas de remoção de armadilhas.* **Publicação da Comissão das Pescas Marinhas dos Estados do Golfo**. Mississippi, Ocean Springs, p.13.

HECK, JR. K.L.; COEN, L.D.; MORGAN, S.G. 2001. Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: Results from the north-central Gulf of Mexico. *Marine Ecology Progress Series,* **222**: 163–176. https://doi.org/10.3354/meps222163

HINES, A.H.; LIPCIUS, R.N.; HADDON, A.M. 1987. Population dynamics and habitat partitioning by size, sex and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Marine Ecology Progress Series,* **36**: 55–64. https://doi.org/10.3354/meps036055

HIROKI, K.A.N.; FRANSOZO, A.; COSTA, R.C.; CASTILHO, A.L.; SHIMIZU, R.M.; ALMEIDA, A.C.A.; FURLAN, M. 2011. Bathymetric distribution of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) (Decapoda, Penaeidae) in two locations off the southeastern Brazilian coast. *Marine Biology Research,* **7:** 176-185. https://doi.org/10.1080/17451000.2010.489614

LIMA, P.A.; ANDRADE, L.S.; ALENCAR, C.E.R.D.; PEREIRA, R.T.; TEIXEIRA, G.M.; FRANSOZO, A. 2014. Two species of swimming crabs of the genus *Achelous* (Crustacea, Brachyura): environmental requirements determining the niche. *Hydrobiologia,* **727**: 197-207. https://doi.org/10.1007/s10750-014-1803-y

LOPES, R.M.; KATSURAGAWA, M.; DIAS, J.F.; MONTÚ, M.A.; MUELBERT, J.H.; GORRI, C.; BRANDINI, P.F. 2006. Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. *Scientia Marina,* **70**(2): 189–202. https://doi.org/10.3989/scimar 2006.70n2189

MAGLIOCCA, A.; KUTNER, A.S. 1965 Sedimentos de fundo da Enseada do Flamengo, Ubatuba, SP. *Contribuições do Instituto Oceanográfico,* **198**: 1–15.

MAHIQUES, M.M. 1995. Dinâmica sedimentar atual nas enseadas da região de Ubatuba, Estado de São Paulo. *Boletim do Instituto Oceanográfico,* **43**: 111–122. https://doi.org/10.1590/s0373-55241995000200003

MAHIQUES, M.M.; TESSLER, M.G.; FURTADO, V.V. 1998. Characterization of energy gradient in enclosed bays of Ubatuba region, South-eastern Brazil. *Estuarine, Coastal and Shelf Science,* **47**: 431–446. https://doi.org/10.1006/ecss.1998.0368

MANTELATTO, F.L.M.; FRANSOZO, A.; NEGREIROS-FRANSOZO, M.L. 1995. Distribuição do caranguejo *Hepatus pudibundus* (Herbst, 1785) (Crustacea, Decapoda, Brachyura) na Enseada da Fortaleza, Ubatuba, SP, Brasil. *Boletim do Instituto Oceanográfico,* **43**(1): 51–61. https://doi.org/10.1590/s0373-55241995000100005

MANTELATTO, F.L.M.; FRANSOZO, A. 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo State, Brazil. *Revista Brasileira de Biologia,* **59:** 23-31. https://doi.org/10.1590/s0034-71081999000100004

MANTELATTO, F.L.M.; BIAGI, R.; FARIA, F.C.R.; MEIRELES, A.L.; MELO, G.A.S. 2004. Checklist on brachyuran fauna (Decapoda) from infralittoral rocky/sandy bottom of Anchieta Island, São Paulo State, Brazil. *Nauplius,* **12**(2): 135-142.

MANTELATTO, F.L.; BERNARDO, C.H.; SILVA, T.E.; BERNARDES, V.P.; COBO, V.J.; FRANSOZO, A. 2016. Composição e distribuição de crustáceos decápodos associados à pesca do camarão-sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862) no litoral norte do estado de São Paulo. *Boletim do Instituto de Pesca,* **42**(2): 307-326. https://10.20950/1678-2305.2016v42n2p307

MELO, G.A.S. 1996. *Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro.* São Paulo, Plêiade/FAPESP, 604 p.

NEGREIROS-FRANSOZO, M.L.; FRANSOZO, A.; PINHEIRO, M.A.A.; MENTELATTO, F.L.M.; SANTOS, S. 1991. Caracterização física e química da Enseada de Fortaleza, Ubatuba, P. *Revista Brasileira de Geociências,* **2**(2): 114-120. https://doi.org/10.25249/0375-7536.1991114120

NENADIC, O.; GREENACRE, M. 2007. Correspondence Analysis in R, with two- and three-dimensional graphics: The ca package. *Journal of statistical software.* **20**: 163–170. https://doi.org/10.18637/jss.v020.i03

ODEBRECHT, C.; CASTELLO, J.P. 2001. The convergence ecosystem in the southwest Atlantic. In Coastal marine ecosystems of Latin America. *Springer Berlin Heidelberg,* 147-165. https://doi.org/10.1007/978-3-662-04482-7_12

OKSANEN, J.; BLANCHET, F.G.; KINDT, R.; LEGENDRE, P.; MINCHIN, P.R.; O'HARA, R.B.; SIMPSON, G.L.; SOLYMOS, P.; HENRY, M.; STEVENS, H.; WAGNER, H. 2013. Vegan: Community Ecology Package. R package version 2.0-7. http://CRAN.R-project.org/package=vegan

PIRES, A.M.S. 1992. Structure and dynamics of benthic megafauna on the continental-shelf offshore of Ubatuba, southeastern Brazil. *Marine Ecology Progress,* **86**: 63–76. https://doi.org/10.3354/meps086063

RIPOLI, L.V.; FERNANDES, J.M.; ROSA, D.D.M.; ARAUJO, C.C.V. 2007. Dinâmica populacional de *Portunus spinimanus* Latreille, 1819 (Crustacea, Portunidae) em um trecho litorâneo da Ilha do Frade, Vitória-ES. *Boletim do Instituto de Pesca,* **33**(2): 205-212.

SANTOS, S. 2000. Influência dos fatores ambientais na abundância de *Portunus spinimanus* Latreille, 1819 (Crustacea, Brachyura, Portunidae) na enseada da Fortaleza, Ubatuba, SP. *Ciência e Natura,* **22**: 129-144. https://doi.org/10.5902/2179460x27115

SANTOS, S; NEGREIROS-FRANSOZO, M.L. 1999 Reproductive cycle of the swimming crab *Portunus spinimanus* Latreille, 1819 (Crustacea, Decapoda, Brachyura) from Uba- tuba, São Paulo, Brazil. *Revista brasileira de Zooogia, Curitiba,* **16**(4): 1183-1193. https:// doi.org/10.1590/s0101-81751999000400025

SANTOS, S.; NEGREIROS-FRANSOZO, M.L.; FRANSOZO, A. 1995. Morphometric relationships and maturation in *Portunus spinmanus* Latreille, 1819 (Crustacea, Brachyura, Portunidae). Brazilian *Journal of Biology,* **55**(4): 545-553.

SANTOS, S.; NEGREIROS-FRANSOZO, M.L.; FRANSOZO, A. 1994. The distribution of swimming crab *Portunus spinimanus* Latreille, 1819 (Crustacea, Brachyura, Portuni- dae) in Fortaleza Bay, Ubatuba, SP, Brazil. *Atlântica,* **16**: 125-141.

SHIRLEY, M.A.; HINES, A.H.; WOLCOTT, T.G. 1990. Adaptive significance of habitat se- lection by molting adult blue crabs *Callinectes sapidus* (Rathbun) within a subestuary of central Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology,* **140**: 107-119. https://doi.org/10.1016/0022-0981(90)90085-q

SILVA, T.E.; ANDRADE, L.S.; FRANSOZO, V.; FREIRE, F.A.M.; FRANSOZO, A. 2018. Population parameters and distribution of *Arenaeus cribrarius* (Crustacea, Portunoidea), in southeastern brazilian coast. *Boletim do Instituto de Pesca,* **44**(1): 1-9. https://doi.org/10.20950/1678-2305.2018.187

SOUSA, A.N.; BERTINI, G.; TADDEI F.G.; COSTA, R.C.; SILVA T.E.; FRANSOZO A. 2018. Modulating factors of the abundance and distribution of *Achelous spinimanus* (Latreille, 1819) (Decapoda, Portunoidea), a fishery resource, in Southeastern Brazil. *PeerJ,* **6**: e5720 https://doi.org/10.7717/peerj.5720

WENTWORTH, C.K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology,* **30**: 377–392. https://doi.org/10.1086/622910

WILLIAMS, A.B. 1984 *Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida.* Smithsonian Institution Press, Washington, D.C. 550 p.

ZAR, J.H. 1996. *Biostatistical Analysis.* Fourth edition. Upper Saddle River, New Jersey, Prentice-Hall. 663 p.

CAPÍTULO 2

Reproduction and population structure of *Achelous spinimanus* (Crustacea: Portunoidea) in the northern coast of São Paulo, Brazil, and influence of environmental factors

Biologia
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ORIGINAL ARTICLE

Reproduction and population structure of *Achelous spinimanus* (Crustacea: Portunoidea) in the northern coast of São Paulo, Brazil, and influence of environmental factors

Camila Hipolito Bernardo[1] & Veronica Pereira Bernardes[1] & Thiago Elias da Silva[1] & Aline Nonato de Sousa[1] & Fabiano Gazzi Taddei[2] & Adilson Fransozo[1]

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Abstract

We studied the reproduction and population structure of a population of *Achelous spinimanus* in the region of Ubatuba, Brazil. We collected them monthly, in 2000, in eight sites of different depths (5 to 40 m). The size at the onset of sexual maturity was estimated by the carapace width and the population structure was analyzed based on the size frequency distribution. In total, we collected 402 individuals: 28 juveniles, 105 males and 269 females. In 2000, *A. spinimanus* reproduced continuously and had a single peak in September–October. This timing contrasts with what has been observed in other populations and may be a local strategy to decrease the interspecific competition with other swimming crabs. The individuals of *A. spinimanus* from Ubatuba in 2000 were smaller (16.8–93.5 mm) than those from Fortaleza Bay (near Ubatuba) in 1988–1989 (19.0–97.3 mm). We suggest that intense trawling pressure may have contributed to a reduction in the size of individuals.

Keywords “Siri-candeia” · Ubatuba · Bycatch · Reproductive females

Introduction

The Portunidae swimming crab *Achelous spinimanus* (Latreille, 1819) is a predator of several invertebrates and plays an important role in the trophic chain of marine ecosystems (Branco and Verani 1997). Besides being commonly caught as a bycatch of shrimp fisheries (Mantelatto et al. 2016), it is also a species of increasing commercial interest and considered as a food resource in coastal regions of Brazil (Branco et al. 2002; Sousa et al. 2018; Bernardo et al. 2019) and other countries (FAO-Globefish 2013). *Achelous spinimanus* has a wide latitudinal distribution and occurs from the United States (New Jersey) to the south of Brazil (Rio Grande do Sul) (Melo 1996). The high tolerance of this species to different environmental conditions favors a wide latitudinal distribution and it is also reflected in its reproductive characteristics (Camp et al. 1977; Santos and Negreiros-Fransozo 1999; Andrade et al. 2017).

The reproductive period of species of Brachyura has been studied through the monthly observation of females with developed gonads or ovigerous (Batoy et al. 1987; Reigada and Negreiros-Fransozo 1999; Andrade et al. 2015a). Two types of reproduction are common in Brachyura: seasonal — when the reproduction is restricted to a few months of favorable environmental conditions, and continuous — when individuals reproduce throughout the entire year (Sastry 1983). In the latter case, peaks with higher reproductive intensity may occur (Bertini et al. 2010; Antunes et al. 2015; Andrade et al. 2015b).

The analyses of population structure and size at the onset of sexual maturity are as important as the determination of the reproductive period. The analysis of population structure can lead to a better understanding of the processes influencing inter- and intraspecific interactions in space and time and help

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* Camila Hipolito Bernardo
caah.hipolito05@gmail.com

[1] Group of Studies on Biology, Ecology and Culture of Crustaceans (NEBECC), Department of Zoology, Biosciences Institute, Universidade Estadual Paulista, UNESP, Botucatu, São Paulo, Brazil

[2] Amazon Crustacean Studies Laboratory (LECAM), Parintins Center for Advanced Studies (CESP/UEA), Universidade do Estado do Amazonas, Estrada Odovaldo Novo, Km 1, Parintins, Amazonas 69151–470, Brazil

to assess whether a population is vulnerable to natural or man-made events (Ricklefs and Miller 1999). The size at the onset of sexual maturity can help to determine the reproductive capacity of a species (Hines et al. 1987; Hartnoll and Gould 1988), and it can be estimated by observing the external morphology, size, and stage of gonadal development (Reigada and Negreiros-Fransozo 1999).

Altogether, these parameters (population structure, size at the onset of sexual maturity, and reproductive period) serve as a baseline for the establishment of protection measures. Such measures are necessary to ensure that this potential fishing resource is exploited rationally, thus preventing an imbalance in the benthic community and its local extinction (Negreiros-Fransozo and Fransozo 1995; Almeida et al. 2011). This study analyzed these three parameters in an *A. spinimanus* population from Ubatuba, Brazil, in 2000.

Material and methods

Study area

The region of Ubatuba, in the northern coast of São Paulo, is characterized by an irregular topography that creates several sites favorable for the establishment and development of marine benthos (Mahiques 1995). According to Pires (1992) the region is strongly influenced by three water masses: South Atlantic Central Water (SACW: temperature < 18 °C; salinity <36), Tropical Water (TW: temperature > 20 °C; salinity >36), and Coastal Water (CW: temperature > 20 °C; salinity <36).

Sampling

The samplings were carried out in the central part of Ubatuba Bay and extended to the open sea. The swimming crabs were collected with a fishing boat equipped with two double rig nets. Eight sites of increasing depth (5, 10, 15, 20, 25, 30, 35 and 40 m) were visited monthly, from January to December 2000. They were trawled for 30 min (about 2 km each), covering a sampling area of ∿18.000 m^2 (Fig. 1). An ecobathymeter coupled with a GPS was used to record the depth. Sediment and bottom water samples from each site were also collected monthly to evaluate the environmental factors. Water was collected with a Nansen bottle, bottom and surface temperature (°C) were measured with a mercury thermometer, and salinity (ppt) with an optical refractometer. Sediment samples were taken with a Van Veen grab (0.025 m^2) and used to analyze the grain size composition and organic matter content.

Laboratory procedures

All individuals were identified according to Melo (1996) and separated by sex based on the abdominal morphology (triangular in males; rounded in females) and the number of pleopods (2 pairs in males; 4 pairs in females). The carapace width (CW), excluding lateral spines, was measured using a caliper (0.01 mm).

The stage of external morphological maturation was analyzed according to Haefner (1990). Juveniles and adults were differentiated based on the shape and adhesion of the abdomen to the thoracic sternite: individuals with the abdomen sealed by the occlusion knob in the thoracic sternites were considered as juveniles (IM). The presence of ovigerous females (OF) was recorded. Lastly, the gonads of males and females were assigned to three development stages, based on procedures modified from Santos and Negreiros-Fransozo (1999): rudimentary (RU), developing (ED), and developed (DE).

Sediment samples were transported to the laboratory and oven-dried at 70 °C for 48 h. To analyze the grain size composition, two subsamples of 50 g were treated with 250 mL of

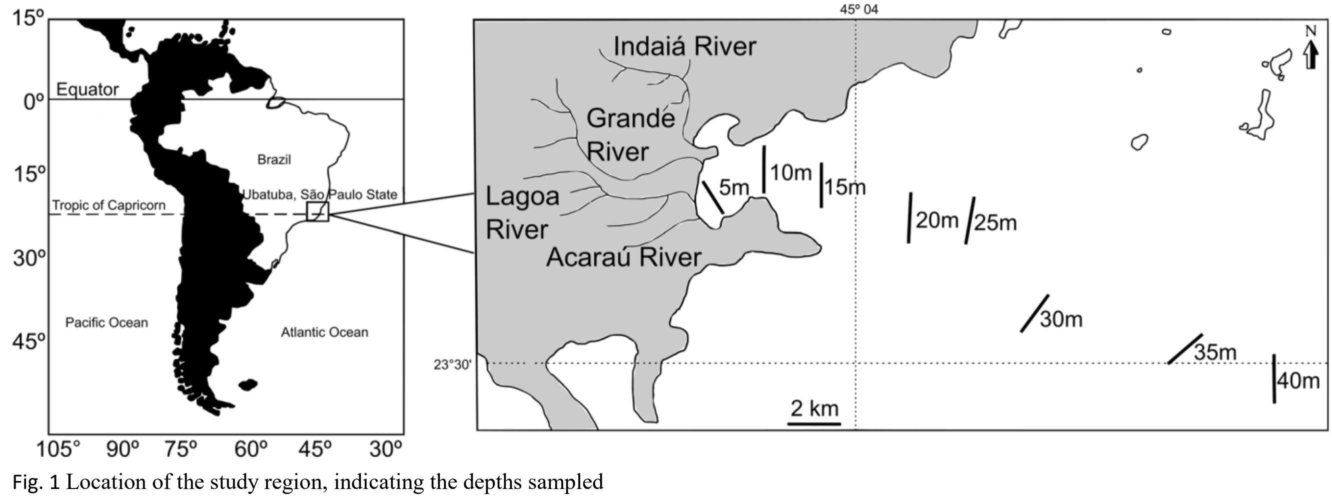

Fig. 1 Location of the study region, indicating the depths sampled

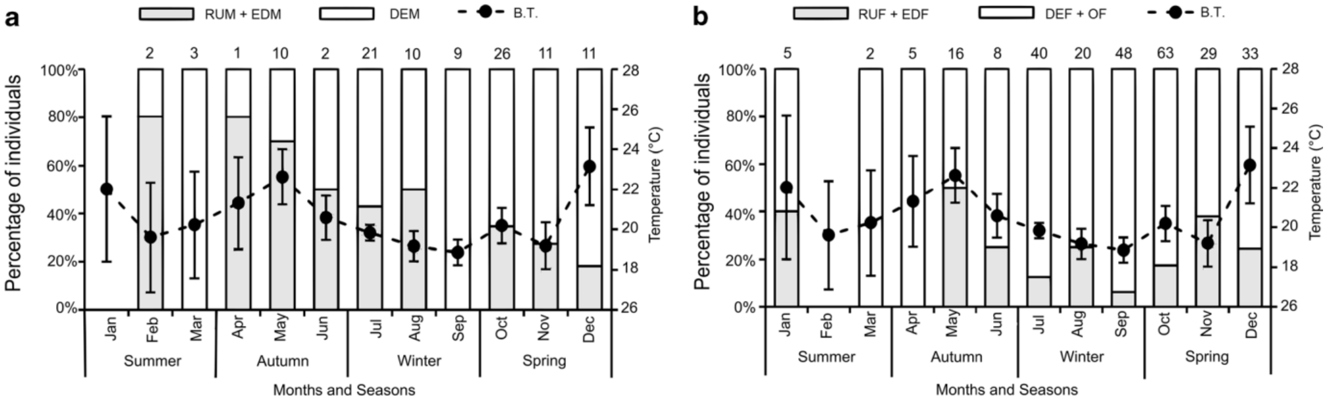

Fig. 2 *Achelous spinimanus*. Temporal distribution of males (a) and females (b) in relation to gonadal development Mean and standard deviation of bottom temperature (BT). RUM = rudimentary males; EDM = developing males; DEM = developed males; RUF = rudimentary females; EDF = developing females; DEF = developed females; OF = ovigerous females

NaOH solution (0.2 mol L^{-1}) and stirred for 5 min to release silt and clay particles. Then, the subsamples were rinsed in a 0.063 mm mesh sieve. The determination of grain size composition followed the categories of the Wentworth (1922) American Standard: gravel (G) = ≥2 mm; very coarse sand (VCS) = 2.0–1.0 mm; coarse sand (CS) = 1.0–0.5 mm; medium sand (MS) = 0.5–0.25 mm; fine sand (FS) = 0.25–0.125 mm; very fine sand (VFS) = 0.125–0.063 mm. Smaller particles were classified as silt and clay. *Phi* values were calculated using the formula *phi* = − log2d, where d = grain diameter (mm). Based on the *phi* values, the following scale was obtained: −2 = *phi* < −1 (G); −1 = *phi* < 0 (VCS); 0 = *phi* < 1 (CS); 1 = *phi* < 2 (MS); 2 = *phi* < 3 (FS); 3 = *phi* < 4 (VFS); and *phi* ≥ 4 (S + C). Measures of central tendency were used to determine the most frequent grain size fraction in the sediments. These values were calculated from the cumulative curves of sediment frequency distribution. The values corresponding to the 16th, 50th and 84th percentiles were used to determine the mean diameter (md) using the formula md = (*phi*16 + *phi*50 + *phi*84)/3 (Suguio 1973). Finally, the sediment organic matter content was estimated as the difference between the initial and final ash-free dry weight of two subsamples (10 g each), after incineration in porcelain crucibles at 500 °C for 3 h.

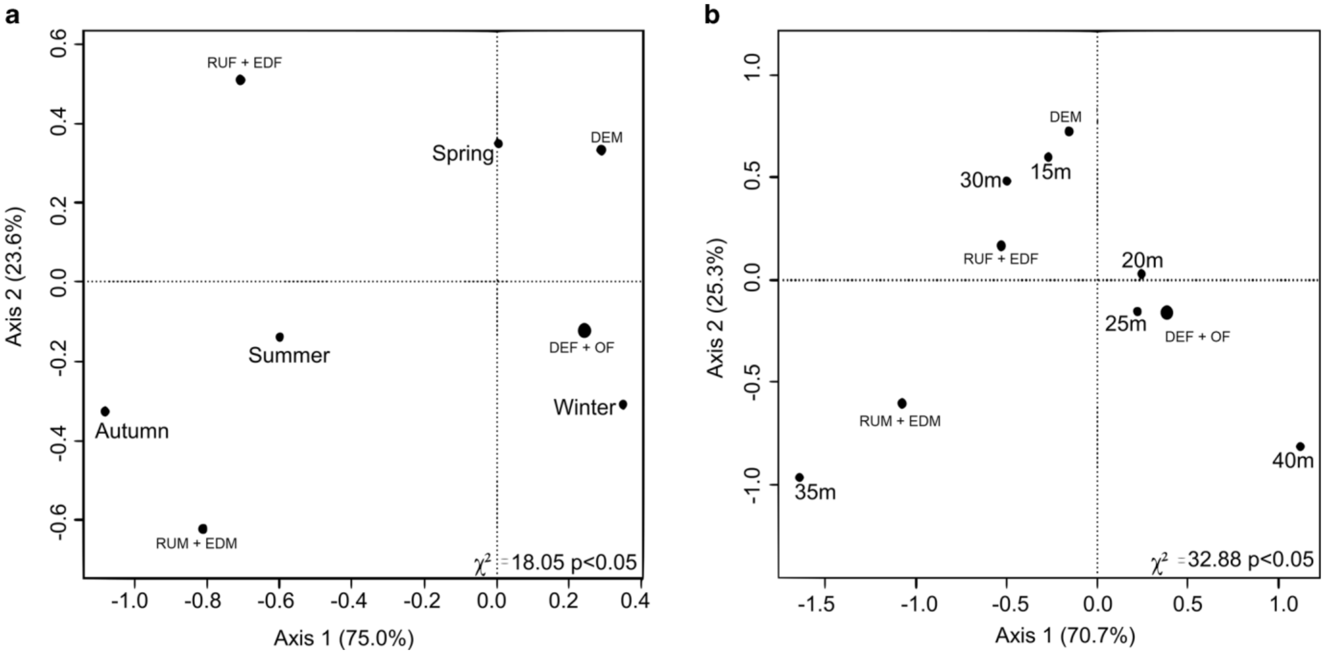

Fig. 3 *Achelous spinimanus*. Correspondence Analysis of the abundance of demographic groups by seasons (a) and depths (b). RUM = rudimentary males; EDM = developing males; DEM = developed males; RUF = rudimentary females; EDF = developing females; DEF = developed females; OF = ovigerous females)

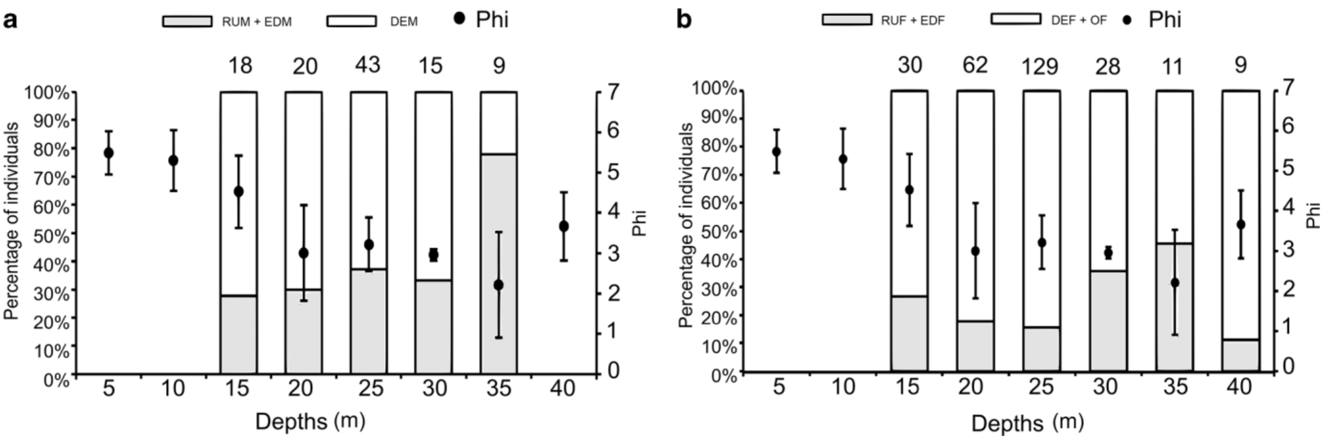

Fig. 4 *Achelous spinimanus*. Spatial distribution of males (a) and females (b) in relation to gonadal development. RUM = rudimentary males; EDM = developing males; DEM = developed males; RUF = rudimentary females; EDF = developing females; DEF = developed females; OF = ovigerous females. Mean and standard deviation of Phi

Data analysis

The normality and homoscedasticity were tested by the Shapiro Wilk and Levene tests, respectively. The Mann-Whitney test was performed between the surface and bottom temperatures in the months. The reproductive period was determined based on the presence of reproductive females (i. e. ovigerous or with developed gonads) (Reigada and Negreiros-Fransozo 1999). To investigate the abundance patterns, two Correspondence Analysis were employed: one relating the abundance of the different demographic groups to depth, and another relating it with the months. The observed associations (abundance vs. depth and abundance vs. months) were summarized in a contingency table and plotted in a bi-dimensional space. The statistical significance was evaluated using the Chi-square test (χ^2) with simulated *p*-values (based on 2000 permutations) (Nenadic and Greenacre 2007).

A Redundancy Analysis (RDA) was used to investigate the relationship between the environmental variables (bottom temperature and salinity, phi, and organic matter) and the abundance of reproductive females (OF = ovigerous females + DEF = developed females), non-reproductive females (RUF = rudimentary females + EDF = developing females), and males (RUM = rudimentary males + EDM = developing males; DEM = developed males). The RDA produces final coordination scores that summarize the linear relationship between explanatory and response variables. In this study, only environmental variables above 0.4 and below −0.4 were considered biologically significant (Rakocinski et al. 1996). The RDA was done using the package "*vegan*" (Oksanen et al. 2013) for R (Team 2016).

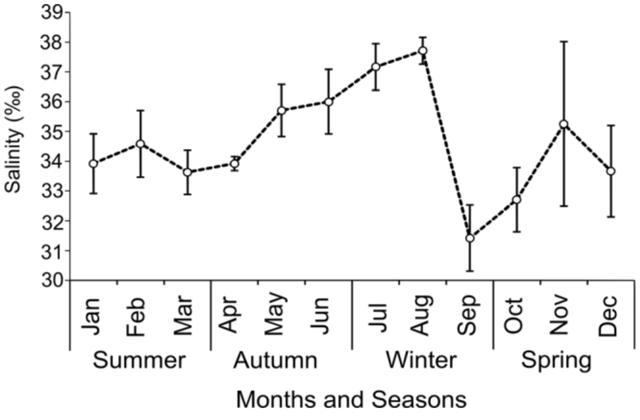

Fig. 5 Mean and standard deviation of bottom salinity, recorded in the region of Ubatuba per month

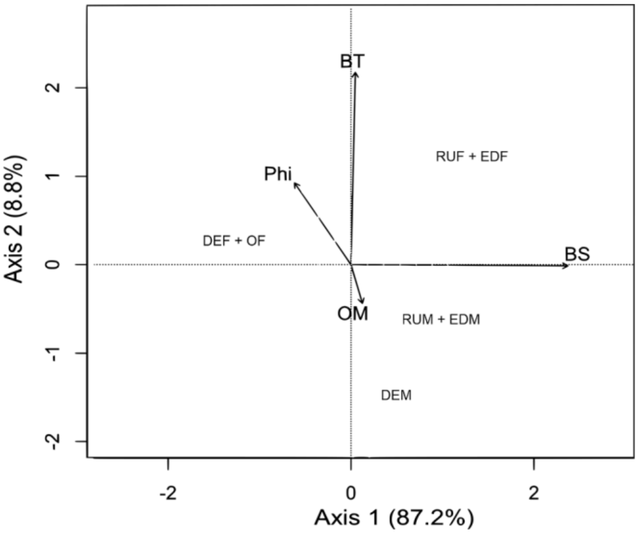

Fig. 6 Redundancy Analysis (RDA) between demographic groups of *Achelous spinimanus* and environmental variables. RUM = rudimentary males; EDM = developing males; DEM = developed males; RUF = rudimentary females; EDF = developing females; DEF = developed females; OF = ovigerous females; BT = bottom temperature; BS = bottom salinity; OM = organic matter; Phi

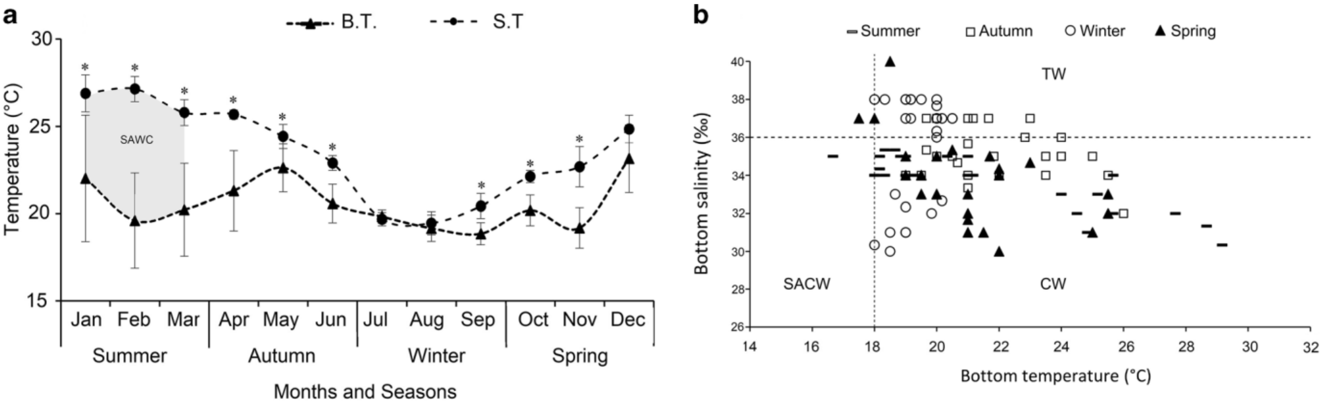

Fig. 7 a Mean and standard deviation of bottom temperature (B.T.) and surface temperature (S.T.), recorded in the region of Ubatuba per month. * Mann-Whitney test, $p < 0.05$. b Diagram showing the seasonal variation of water temperature and salinity from January 2000 to December 2000, at Ubatuba region, São Paulo State littoral, southeastern coast of Brazil. CW = Coastal Water;. TW = Tropical Water;. SACW = South Atlantic Central Water

To determine the size at the onset of sexual maturity, the swimming crabs were separated in juveniles and adults. Males and females were analyzed separately. The size where 50% of the individuals reached sexual maturity (CW50) was estimated by the relative frequency of adults (%) in each size class, adjusted to a sigmoid curve, based on the equation: $y\ ¼\ \frac{1}{1þe^{-rðCW-CW50Þ}}$ where y is the estimated proportion of mature males/females, and r is the slope of the logistic curve. The equation was adjusted by the least-squares method (Vazzoler 1996).

To represent the population structure, size classes were stablished using the method of Sturges (1926). The average size Kruskal Wallis test, followed by a post-hoc Dunn test (Zar 2010). The Binomial test (Wilson and Hardy 2002) was used to verify if the proportion of males and females in each size class differed.

Results

Our data were not normally distributed (Shapiro Wilk test, $p < 0.05$) or homoscedastic (Levene's test, $p < 0.05$). A total of 402 individuals were collected: 28 juveniles, 105 males, and 269 females. Adult males were found year-round, except in January (Fig. 2a). According to the Correspondence Analysis, the abundance of DEM was associated with spring, and RUM + EDM were associated with autumn (Fig. 3a). Reproductive females (34 DEF and 180 OF) were found in all months except February (Fig. 2b). The CA indicated a correlation between RUF + EDF and spring, and between reproductive females and winter (Fig. 3a). All adult demographic groups were absent in the sites 5–10 m deep, and the highest abundance of males and females was recorded at 20–25 m. At these depths the phi values were the lowest and the sediment was more heterogeneous (Fig. 4a, b). Only reproductive females were found in the deepest site (40 m) (Fig. 4b). The CA correlated the abundance of reproductive females to depths of 20, 25 and 40 m (Fig. 3b). The months with the highest abundance of reproductive females had low mean bottom temperatures: 18.8 in September (± 0.6 °C), and 20.2 in October (± 0.9 °C) (Fig. 2b). Bottom salinity varied through the year ($H = 69.66$, $p < 0.05$); the lowest salinity was recorded in September (31.4 ± 1.1 ‰) and the highest in August (37.7 ± 0.5 ‰) (Fig. 5). The RDA indicated, in axis 1 (87.2%), that RUM, EDM, DEM and RUF, EDF were positively related to organic matter, temperature and bottom salinity and negatively to phi. On the contrary, reproductive females were negatively correlated to organic matter, bottom temperature and salinity, and positively to phi (Fig. 6). Intrusion of water from the SACW can be seen in the region during the summer. This feature is indicated by the thermocline formed in the months of January, February and March (Fig. 7a), its existence was confirmed by the relationship of salinity and seawater temperature (Fig. 7b).

Table 1 *Achelous spinimanus*. Median, minimum, maximum size of demographic groups

Demographic groups	Minimum	Maximum	Median ± SD	Dunn test
Juveniles	16.8	47.7	35.4 ± 7.5	a
Adults males	43.0	84.7	66.7 ± 9.3	b
Adults females	43.5	93.5	65.5 ± 10.0	b
Ovigerous females	48.0	85.0	66.2 ± 7.7	b

SD = standard deviation. Equal letters do not present statistical difference (Dunn test; $p > 0.05$)

The individual size ranged from 16.80 to 93.50 mm. The mean juvenile size differed significantly from the other groups ($H = 85.21$ and $p < 0.05$). Males (72.00 ± 10.2 mm) were larger than females (66.7 ± 9.3 mm). The size of adult females ranged from 43.5 to 93.5 mm and the adult male size ranged

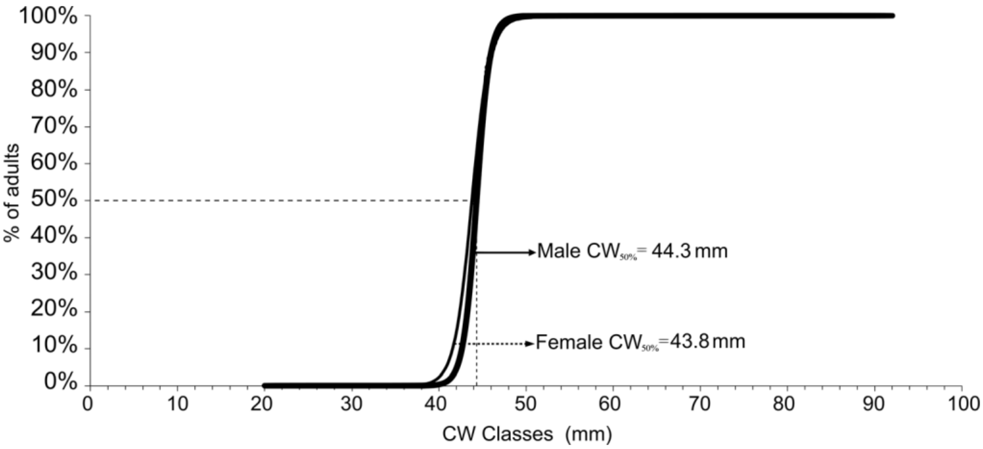

Fig. 8 *Achelous spinimanus*. Sexual maturity (based on gonadal development) for males and females, in the region of Ubatuba in the year 2000

from 43.0 to 84.7 mm (Table 1). The estimated size at the onset of sexual maturity of females and males was 43.7 mm and 44.3 mm, respectively (Fig. 8).

Juveniles occupied the first four size classes. Adult males were found mainly in the last classes, while adult and ovigerous females predominated in the intermediate classes. The highest frequency of adult and males and females and ovigerous females in the last size classes occurred in July–December and at depths of 20–25 m (Figs. 9 and 10). The sex ratio was significantly skewed towards females only in the size class 48–72 mm, but overall more females were observed in all size classes (Fig. 11).

Discussion

In this study, *A. spinimanus* reproduced continuously, confirming the findings of Santos and Negreiros-Fransozo (1999) in Ubatuba and those of Branco et al. (2002) in the south of Brazil. A continuous reproduction was also reported in other portunids such as *Callinectes danae* (Smith, 1869) and *Arenaeus cribrarius* (Lamarck, 1818) (Costa and Negreiros-Fransozo 1998; Pinheiro and Fransozo 2002). In this mode of reproduction, the individuals breed asynchronously, i. e., while one part of the population is breeding another is growing or going through gonad maturation (Pinheiro and Fransozo 1998; Andrade et al. 2014). However, intraspecific variation may take place, especially when a species is distributed across a wide latitudinal range (Santos and Negreiros-Fransozo 1999). For instance, the populations of *A. spinimanus* in the Northern Hemisphere (Florida, North Carolina and Virgin Islands in the United States) have a seasonal reproduction. Ovigerous females occur in a few months of the year, when the environmental conditions (mainly temperature) are more favorable (Dudley and Judy 1971; Camp et al. 1977; Olsen et al. 1978). This intraspecific variation can be explained by environmental or anthropogenic factors that can affect the metabolism, exert a selective pressure that alters the population structure and reproductive cycle, and influence growth, reproductive success, and behavior (Sastry 1983).

In our study, the reproductive peak of *A. spinimanus* occurred between the end of winter (September) and early spring (October), which differs from most species of Portunidae that usually breed when the SACW arrives. The SACW arrives seasonally in Ubatuba between late spring and early summer, forming a thermocline. This water mass induces a nutrient enrichment off the coast, favors primary production and increases the food availability for the planktonic larvae (Odebrecht and Castello 2001; Lopes et al. 2006). According to Bertini and Fransozo (2004), there is a high abundance of portunids in Ubatuba, e. g. *A. cribrarius, Callinectes ornatus* (Ordway, 1863), and *C. danae*. *Arenaeus cribrarius* reproduces seasonally, synchronized with the arrival of SACW (Andrade et al. 2013), while *C. ornatus* and *C. danae* reproduce continuously but have peaks synchronized with the SACW as well (Costa and Negreiros-Fransozo 1998). The highest reproductive intensity of *A. cribrarius* also occurs in summer (Pinheiro and Terceiro 2000). The fact *A. spinimanus* differs from these species regarding the timing of the reproductive peak may indicate a strategy to reduce the competition of their larvae for food, since in September–October fewer species are reproducing.

According to Santos et al. (2000), the reproduction of a population is influenced by a combination of biotic (such as predation, social structure, and competition) and physico-chemical factors. The positive correlation between the abundance of reproductive females and phi values indicates that this group prefers sites with higher food availability. Sediments with higher phi values have a higher organic matter content, which means a higher food availability for all demographic groups, and especially for ovigerous females. Furthermore, according to Santos and Negreiros-Fransozo (1999), tropical species with continuous reproduction may have peaks of intensive reproduction determined by several environmental factors. Indeed, in this study, the abundance of reproductive females was negatively correlated with bottom

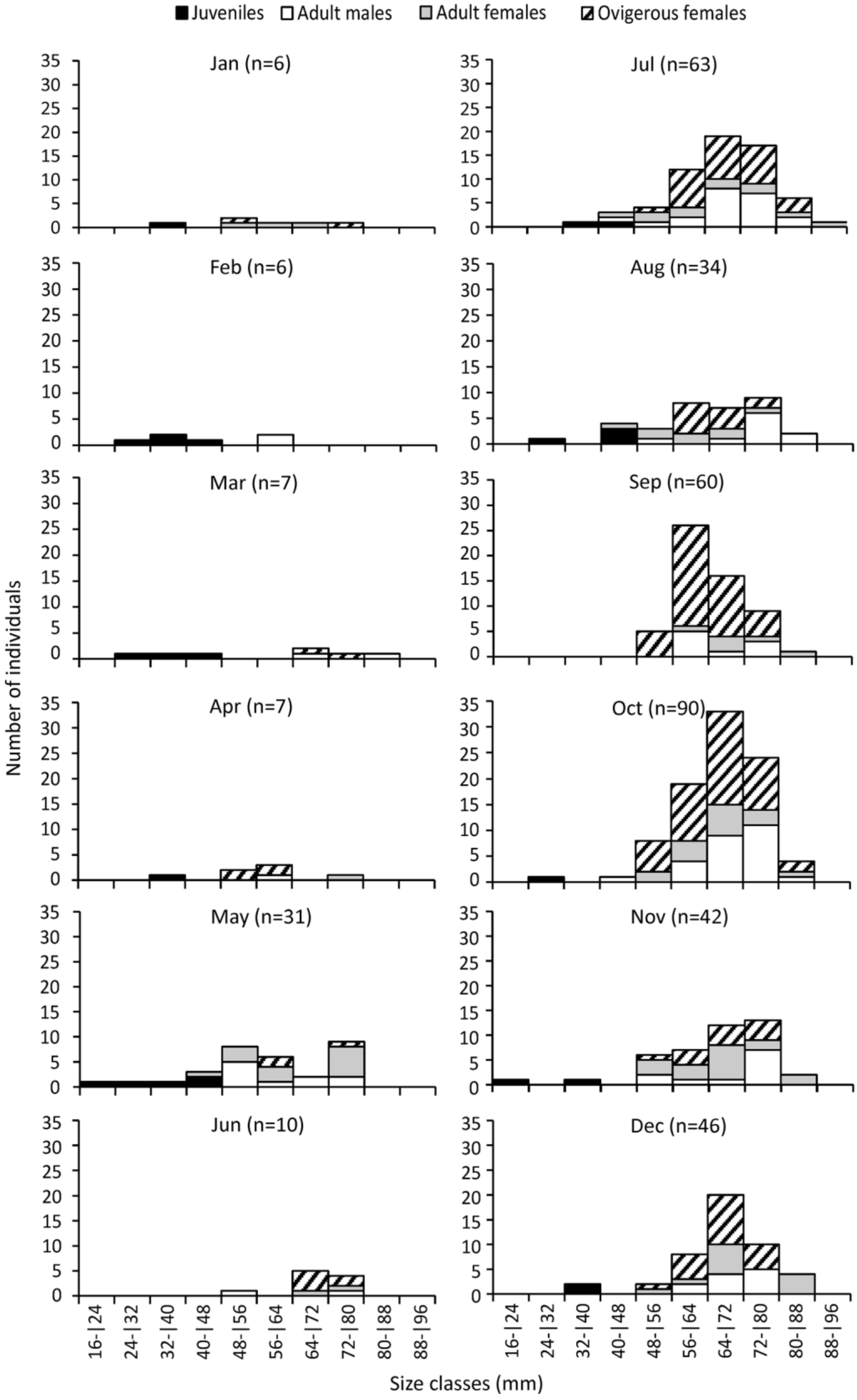

Fig. 9 *Achelous spinimanus*. Distribution in size classes of demographic groups by months sampled in the region of Ubatuba in the year 2000. Juveniles = IM (males and females); Adult males = RUM + EDM; DEM; Adult females = RUF + EDF + DEF

salinity and temperature, and, in September–October were recorded the highest abundance of reproductive females and the lowest bottom temperature and salinity.

Andrade et al. (2014, 2017) suggested that changes in water temperature, as well as in salinity, photoperiod, and food supply may cause changes in the reproductive

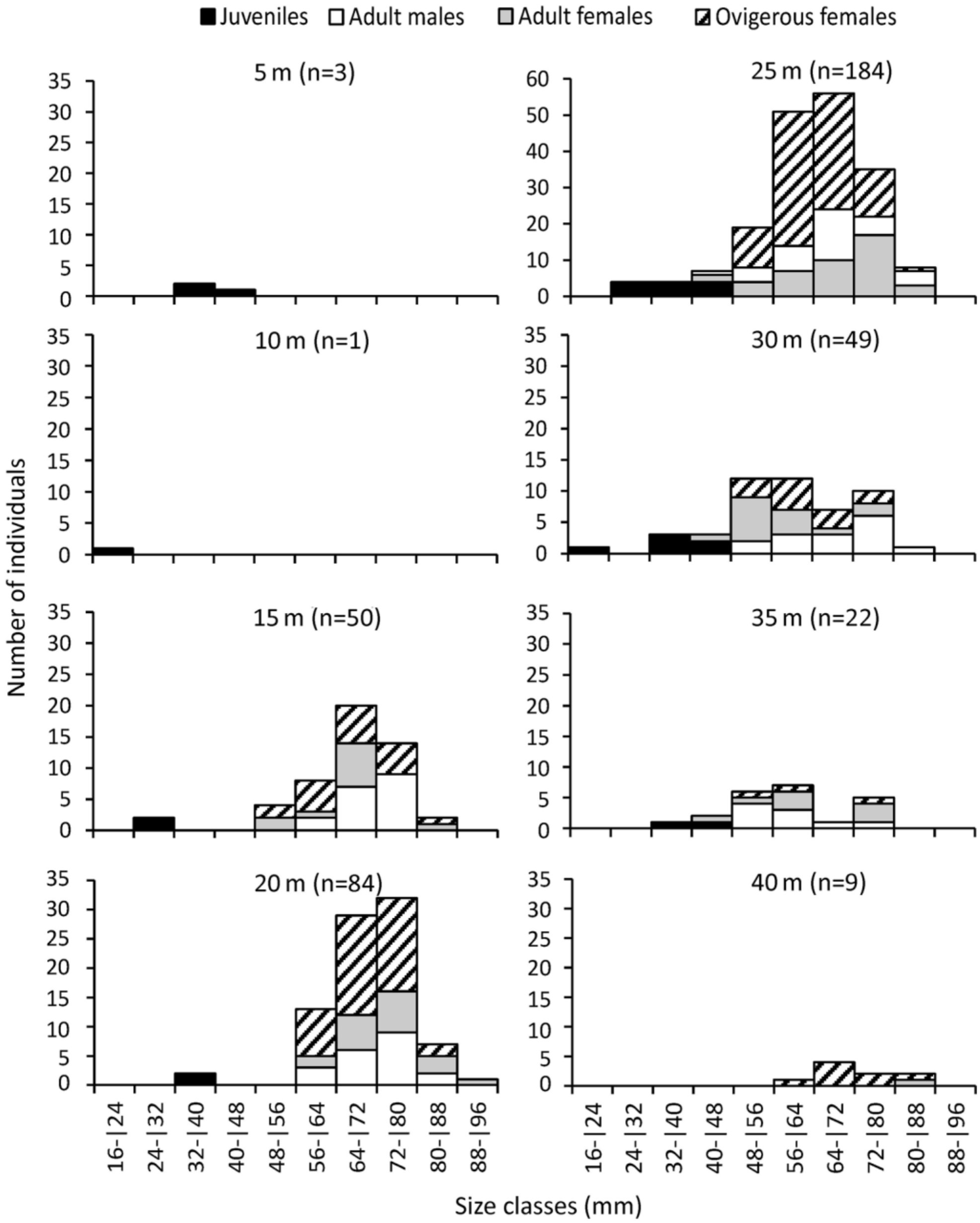

Fig. 10 *Achelous spinimanus*. Distribution in size classes of demographic groups by depth sampled in the region of Ubatuba in the year 2000. Juveniles = IM (males and females); Adult males = RUM + EDM; DEM; Adult females = RUF + EDF + DEF

patterns of decapods. Indeed, after sampling *A. spinimanus* in Fortaleza Bay (near Ubatuba) for two years, Santos and Negreiros-Fransozo (1999) showed that the timing of the reproductive peaks changed from year to year. These changes may indicate adaptations to fluctuations in the environmental factors that modulate the reproduction. The timing of the reproductive peak of *A. spinimanus* may be influenced by a combination of environmental factors associated with its ecological adaptations. Its continuous reproduction with peaks before the SACW possibly minimizes the larval competition with other species for food. Moreover, reproductive females were the only demographic group caught at higher depths, which indicates a strategy to maximize larval dispersion in an environment with less physiological stress, since the environmental conditions are more stable in deeper regions (Abelló et al. 1988; Pires 1992; Andrade et al. 2014).

Another reproductive aspect analyzed in this study was the sexual maturity based on body size and gonadal maturation. This information is fundamental for the conservation of the species, since it can be used to manage stocks and determine the minimum size for capture (Andrade et al. 2013). The individuals of *A. spinimanus* from Ubatuba in 2000 were smaller (16.8–93.5 mm) than those from ay (near Ubatuba) sampled by Santos et al. (1995) in 1988–1989 (19.0–97.3 mm). Keunecke et al. (2012) suggested that an intense trawling pressure may reduce the individual size and, consequently, the size

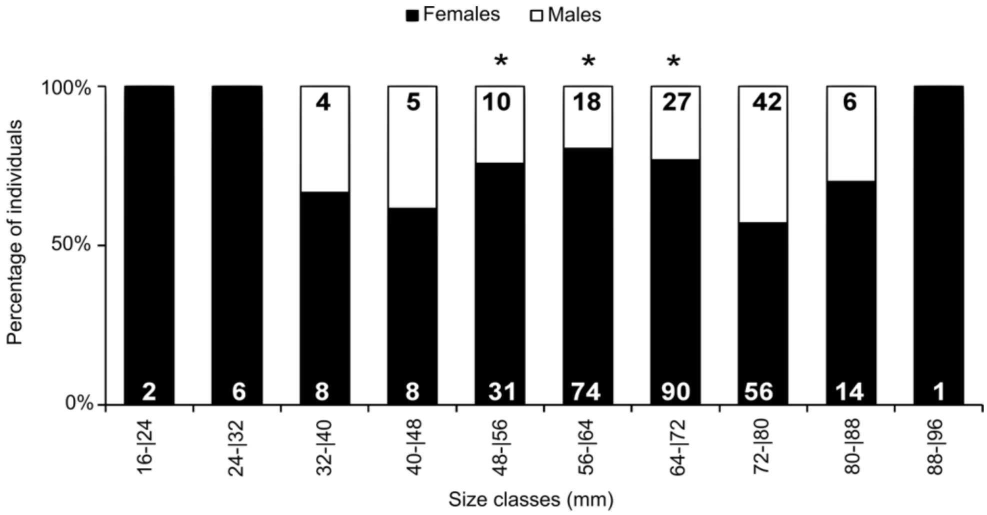

Fig. 11 *Achelous spinimanus*. Percentage and number of males and females in size classes (* Binomial test, $p < 0.05$)

at the onset of sexual maturity. Thus, the decrease in size might have been a consequence of 11 years of intense fishing activity in the region. It's important to emphasize that the decrease in size may have a detrimental effect, since this can affect fertility, reduce reproductive potential, and in the long run, reduce the population size.

Our results corroborate the observation of Branco and Masunari (1992) that, in general, portunid males are larger than females. Females allocate most of their energy to egg production and maturation, which reduces the energy directed to growth. Males, on the other hand, allocate their energy to growth, since size is an important adaptation for the copula (Lira et al. 2012). Larger males can grab and hold the females more effectively and maximize their success during fights with other males (Mantelatto and Fransozo 1999).

Our results concerning the sex ratio — differing from 1:1 and skewed towards females — corroborate Branco et al. (2002) and Santos et al. (1995). According to Wenner (1972), the 1:1 sex ratio is an exception rather than a rule among marine crustaceans. Females were present and more abundant than males in all size classes. However, in the first size classes the sex ratio was more balanced, supporting the observation that, upon hatching, the sex ratio tends to be close to 1:1 (Leigh 1970). After hatching, factors such as migration and differential mortality, longevity, and growth rate may affect this proportion (Wenner 1972).

Our results indicate that the reproductive peak of *A. spinimanus* is modulated by environmental and biotic factors. In addition, the overall individual size in 2000 was smaller than in previous years (Santos et al. 1995), and this might have been a consequence of the intense trawling activity in the region. Our results provide important information about *A. spinimanus* in Ubatuba that can support initiatives aiming at stablishing a controlled and sustainable fishery. These will help the preservation of economically important species as well as the bycatch fauna, which are fundamental components of the trophic webs and of the structure of benthic habitats.

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Compliance with ethical standards

Ethical approval All sampling in this study was conducted in compliance with current applicable state and federal laws.

Conflict of interest The authors declare that they have no conflict of interest.

References

Abelló P, Valladares FJ, Castellón A (1988) Analysis of the structure of decapod crustacean assemblages off the Catalan coast (north-West Mediterranean). Mar Biol 98:39–49. https://doi.org/10.1007/BF00392657

Almeida AC, Fransozo V, Teixeira GM, Furlan M, Hiroki KAN, Fransozo A (2011) Population structure and reproductive period of whitebelly prawn *Nematopalaemon schmitti* (Holthuis 1950) (Decapoda: Caridea: Palaemonidae) on the southeastern coast of Brazil. Invertebr Reprod Dev 55(1):30–39. https://doi.org/10.1080/07924259.2010.548641

Andrade LS, Fransozo V, Bertini G, Negreiros-Fransozo ML, López-Greco LS (2013) Reproductive plasticity in the speckled crab *Arenaeus cribrarius* (Decapoda, Brachyura, Portunidae) associated with a population decline. J Coast Res 31(3):645–652. https://doi.org/10.2112/OASTRES-D-13-00066.1

Andrade LS, Bertini G, Fransozo V, Teixeira GM, Barros-Alves SP, Fransozo A (2014) Differential occupation of habitat as a reproductive strategy of the blue crab *Callinectes ornatus* Ordway, 1968 (Crustacea: Decapoda). Mar Biodivers 44(1):27–36. https://doi.org/10.1007/s12526-013-0179-y

Andrade LS, Frameschi IF, Castilho AL, Costa RC, Fransozo A (2015a) Can the pattern of juvenile recruitment and population structure of the speckled swimming crab *Arenaeus cribrarius* (Decapoda: Brachyura) be determined by geographical variations? Mar Ecol 36(4):950–958. https://doi.org/10.1111/maec.12188

Andrade LS, Antunes M, Lima PA, Furlan M, Frameschi IF, Fransozo A (2015b) Reproductive features of the swimming crab *Callinectes danae* (Crustacea, Portunoidea) on the subtropical coast of Brazil: a sampling outside the estuary. Braz J Biol 75(3):692–702. https://doi.org/10.1590/1519-6984.21513

Andrade LS, Costa RCD, Castilho AL, Frameschi IF, Sancinetti GS, Fransozo A (2017) Reproductive and population traits of the swimming crab *Achelous spinimanus* (Crustacea: Decapoda) in an upwelling region in southeastern Brazil. Nauplius 25:1–11. https://doi.org/10.1590/2358-2936e2017004

Antunes M, Fransozo V, Leão Castilho A, José Cobo V, Teixeira GM, Fransozo A (2015) Assessment of reproductive capacity in females of *Callinectes danae* Smith, 1869 (Brachyura, Portunoidea) during a period of high reproductive activity. Invertebr Reprod Dev 59(1):9–16. https://doi.org/10.1080/07924259.2014.973971

Batoy CB, Sarmago JF, Pilapil BC (1987) Breeding season, sexual maturity and fecundity of the blue crab, *Portunus pelagicus* (L.) in selected coastal waters in Leyte and vicinity, Philippines. Annals of Tropical Research 9(3):157–177

Bernardo CH, Bernardes VP, Sousa AN, Rodrigues GFB, Silva TE, Fransozo A (2019) Environmental factors modulating the bathymetric distribution of the demographic groups of *Achelous spinimanus* (Crustacea). Neotrop Biol Conserv 14:13–28. https://doi.org/10.3897/neotropical.14.e34829

Bertini G, Fransozo A (2004) Biodiversity of brachyuran crabs (Crustacea: Decapoda) from non-consolidated sublittoral bottom on the northern coast of São Paulo state, Brazil. Biodivers Conserv 13:2185–2207. https://doi.org/10.1023/B:BIOC.0000047900.96123.34

Bertini G, Teixeira GM, Fransozo V, Fransozo A (2010) Reproductive period and size at the onset of sexual maturity of mottled purse crab, *Persephona mediterranea* (Herbst, 1794) (Brachyura, Leucosioidea) on the southeastern Brazilian coast. Invertebr Reprod Dev 54(1):7–17. https://doi.org/10.1080/07924259.2010.9652311

Branco JO, Masunari S (1992) Crescimento de *Callinectes danae* Smith (Decapoda, Portunidae) da Lagoa da Conceição, Florianópolis, Santa Catarina, Brasil. Rev Bras Zool 9(1/2):53–66

Branco JO, Verani JR (1997) Dinâmica da alimentação natural de *Callinectes danae* Smith (Decapoda, Portunidae) na Lagoa da Conceição, Florianópolis, Santa Catarina, Brasil. Rev Bras Zool 14(4):1003–1018

Branco JO, Lunardon-Branco MJ, Souto FX (2002) Population structure of *Portunus spinimanus* Latreille (Crustacea, Portunidae) in the Armação do Itapocoroy, Penha, Santa Catarina, Brazil. Rev Bras Zool 19(3):731 – 738. https://doi.org/10.1590/S0101-81752002000300010

Camp DK, Whiting NH, Martin RE (1977) Nearshore marine ecology at Hutchinson Island, Florida: 1971-1974. V. Arthropods. Florida Mar Res Publication 25:1–63

Costa TM, Negreiros-Fransozo ML (1998) The reproductive cycle of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) in the Ubatuba region, Brazil. Crustaceana 71(6):615–627. https://doi.org/10.1163/156854098X00617

Dudley DL, Judy MH (1971) Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort inlet, North Carolina. NOAA Tec Rep 637:1–10

Fao-Globefish (2013) Crab commodity update. Copenhagen, GLOBEFISH databank

Haefner PA Jr (1990) Morphometry and size at maturity of *Callinectes ornatus* (Brachyura, Portunidae) in Bermuda. Bull Mar Sci 46(2): 274–286

Hartnoll RG, Gould P (1988) Brachyuran life history strategies and the optimization of egg production. Sym Zool Soc 59:1–9

Hines AH, Lipcius RN, Haddon AM (1987) Population dynamics and habitat partitioning by size, sex and molt stage of blue crabs *Callinectes sapidus* in a subestuary of Central Chesapeake Bay. Mar Ecol Prog Ser 36:55–64. https://doi.org/10.3354/meps036055

Keunecke KA, D'Incao F, Verani JR, Vianna M (2012) Reproductive strategies of two sympatric swimming crabs *Callinectes danae* and *Callinectes ornatus* (Crustacea: Portunidae) in an estuarine system, South-Eastern Brazil. J Mar Biol Assoc U K 92(2):343–347. https://doi.org/10.1017/S0025315411000397

Leigh EG Jr (1970) Sex ratio and differential mortality between the sexes. Am Nat 104(936):205–210

Lira JJ, Calado T, Araújo MS (2012) Condition factor of *Goniopsis cruentata* (Crustacea, Brachyura, Grapsidae) from Mundaú/Manguaba estuarine complex, Alagoas, Brazil. Iheringia Ser Zool 102(3):285–291. https://doi.org/10.1590/S0073-47212012005000001

Lopes RM, Katsuragawa M, Dias JF, Montú MA, Muelbert JH, Gorri C, Brandini PF (2006) Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. Sci Mar 70(2):189–202

Mahiques MM (1995) Dinâmica sedimentar atual nas enseadas da região de Ubatuba, Estado de São Paulo. Bol Inst Oceanogr 43(2):111–122

Mantelatto FLM, Fransozo A (1999) Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo state, Brazil. Rev Bras Biol 59(1):23–31

Mantelatto FL, Bernardo CH, Silva TE, Bernardes VP, Cobo VJ, Fransozo A (2016) Composicao e distribuicao de crustaceos decapodos associados a pesca do camarao-sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862) no litoral norte do estado de Sao Paulo. Bol Inst Pesca 42(2):307–326. https://doi.org/10.20950/1678-2305.2016v42n2p307

Melo GAS (1996) Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. São Paulo, Plêiade, pp 1–604

Negreiros-Fransozo ML, Fransozo A (1995) On the distribution of *Callinectes ornatus* Ordway, 1863 and *Callinectes danae* Smith, 1869 (Brachyura, Portunidae) in the Fortaleza bay, Ubatuba, Brazil. Iheringia Ser Zool 79:13–25

Nenadic O, Greenacre M (2007) Correspondence analysis in R, with two- and three-dimensional graphics: the ca package. J Stat Softw 20: 163–170. https://doi.org/10.18637/jss.v020.i03

Odebrecht C, Castello JP (2001) The convergence ecosystem in the Southwest Atlantic. In: Seeliger U, Kjerfve B (eds) Coastal marine ecosystems of Latin America, ecological studies. Springer, Berlin, pp 147–166

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2013) Vegan: community ecology package. R package version 2.0–7. http://CRAN.R-project.org/package=vegan

Olsen DA, Demmann AE, La Place JA (1978) *Portunus spinimanus* Latreille, a portunid crab whit resource potential in the US Virgin Islands. Mar Fish Rev 40(7):12–14

Pinheiro MAA, Fransozo A (1998) Sexual maturity of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Decapoda, Brachyura, Portunidae), in the Ubatuba littoral, São Paulo state, Brazil. Crustaceana 71(4):434–452

Pinheiro MAA, Fransozo A (2002) Reproduction of the speckled swimming crab *Arenaeus cribrarius* (Brachyura: Portunidae) on the

Brazilian coast near 23 30′ S. J Crustacean Biol 22(2):416–428. https://doi.org/10.1163/20021975-99990249

Pinheiro MAA, Terceiro OSL (2000) Fecundity and reproductive output of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Brachyura, Portunidae). Crustaceana 73(9):1121–1137

Pires AMS (1992) Structure and dynamics of benthic megafauna on the continental-shelf offshore of Ubatuba, southeastern Brazil. Mar Ecol Prog Ser 86:63–76

Rakocinski CF, Lyczkowski-Shultz J, Richardson SL (1996) Ichthyoplankton assemblage structure in Mississippi sound as revealed by canonical correspondence analysis. Estuar Coast Shelf Sci 43:237–257. https://doi.org/10.1006/ecss.1996.0067

Reigada ALD, Negreiros-Fransozo ML (1999) Maturidade sexual em *Hepatus pudibundus* (Decapoda, Brachyura, Calappidae). Iheringia Ser Zool 86:159–164

Ricklefs RE, Miller GL (1999) Ecology. WH Fr. and C, New York, pp 1–898

Santos S, Negreiros-Fransozo ML (1999) Reproductive cycle of the swimming crab *Portunus spinimanus* Latreille, 1819 (Crustacea, Decapoda, Brachyura) from Ubatuba, São Paulo, Brazil. Rev Bras Zool 16(4):1183–1193. https://doi.org/10.1590/S0101-81751999000400025

Santos S, Negreiros-Fransozo ML, Fransozo A (1995) Estructura poblacional de *Portunus spinimanus* Latreille, 1819 (Crustacea, Brachyura, Portunidae) en la Ensenada de la Fortaleza, Ubatuba (SP), Brasil. Rev Investig Mar 16(1–3):37–43

Santos S, Rieger PJ, Vieira RRR, Barutot RA (2000) Composição e distribuição dos Crustacea (Decapoda) na Lagoa do Peixe, Rio Grande do Sul, Brasil. Rev Bras Zool 17(1):213–223. https://doi.org/10.1590/S0101-81752000000100018

Sastry AN (1983) Ecological aspects of reproduction. In: Bliss DE (ed) The biology of Crustacea: environmental adaptations. Academic, New York, pp 179–270

Sousa AN, Bertini G, Taddei FG, Costa RC, Silva TE, Fransozo A (2018) Modulating factors of the abundance and distribution of *Achelous spinimanus* (Latreille, 1819) (Decapoda, Portunoidea), a fishery resource, in Southeastern Brazil. PeerJ 6:e5720. https://doi.org/10.7717/peerj.5720

Sturges HA (1926) The choice of a class interval. J Am Stat Assoc 21(153):65–66

Suguio K (1973) Introducão à Sedimentologia, Edgard Blucher: EDUSP

Team RC (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Vazzoler AEAM (1996) Biologia da reprodução de peixes teleósteos: teoria e práctica. EDUEM/SBI, São Paulo, Maringa, pp 1–169

Wenner AM (1972) Sex ratio as a function of size in marine Crustacea. Am Nat 106(949):321–350

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30(5):377–392

Wilson K, Hardy IC (2002) Statistical analysis of sex ratios: an introduction. In: Hardy IC (ed) Sex ratios: concepts and research methods. Cambridge University Press, New York, pp 48–92

Zar JH (2010) Biostatistical analysis, 5th edn. Prentice-Hall, Upper Saddle River, New Jersey

CAPÍTULO 3

Pattern of niche overlap between three species of the genus *Persephona* (Crustacea, Decapoda Leucosidae) in southeastern Brazil

Pattern of niche overlap between three species of the genus *Persephona* (Crustacea, Decapoda, Leucosidae) in southeastern Brazil

Camila Hipolito Bernardo[1]; Veronica Pereira Bernardes[1]; Aline Nonato de Sousa[1]; Fabiano Gazzi Taddei[1,2]; Gustavo Monteiro Teixeira[1,3]; Fernando Luis Mantelatto[4]; Adilson Fransozo[1]

[1] Group of Studies on Biology, Ecology and Culture of Crustaceans (NEBECC), Department of Zoology, Biosciences Institute, Universidade Estadual Paulista, UNESP, Botucatu, São Paulo, Brazil

[2] Amazon Crustacean Studies Laboratory (LECAM), Parintins Center for Advanced Studies (CESP/UEA), Universidade do Estado do Amazonas, Estrada Odovaldo Novo, Km 1, Parintins, Amazonas 69151–470, Brazil

[3] Universidade Estadual de Londrina (UEL), Campus Universitário. Rodovia Celso Garcia Cid, Km 380, s/n Londrina, Paraná, Brasil

[4] Laboratório de Bioecologia e Sistemática de Crustáceos (LBSC), Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP). Universidade de São Paulo (USP), 14040-901, Ribeirão Preto, SP, Brasil

ABSTRACT

The objective of this study was to investigate the niche overlap between three species of the genus *Persephona*, as well as to test the hypothesis of Phylogenetic signal existence between them. Monthly (September / 1995 to August / 1996), collections were performed in 8 sampling stations in Ubatuba Bay, Brazil. A Redundancy Analysis was performed to verify the influences of these environmental factors (temperature and bottom salinity and sediment classes) on the abundance of the 3 congeners species. Width and niche overlap measurements were estimated using the Levins method. 128 *P. mediterranea*, 356 *P. punctata* and 34 *P. lichtensteinii* were sampled. In station I (mouth of the bay) 82% of the abundance of *P. mediterranea* was obtained, where the sediment is composed predominantly of fine and very fine sand, with a low percentage of silt and clay (5.5%). This species presented the smallest niche amplitude (1.43) and little overlap with the other 2 congeners. The amplitude of the spatial niche of *P. punctata* was 3.06 and that of *P. lichtensteinii* was 2.36, both were sampled in places with a higher amount of silt and clay, and showed a high percentage of niche overlap (92.3%). In comparison with other studies, we suggest that the supernumerary occurrence of *P. punctata* in Ubatuba may be a consequence of the greater plasticity of this species in relation to water temperature. *Persephona lichtensteinii*, seems to be more adapted to warmer temperatures, being more abundant in regions of lower latitudes. Our results contradict the hypothesis of the existence of Phylogenetic signal, given the lesser ecological similarity between *P. mediterranea* and *P. punctata*, which are phylogenetically closer.

Keywords: Phylogenetic signal; congeners; sediment; SACW; heatmap

INTRODUCTION

The ecological niche can be interpreted as a hypervolume or multidimensional space, where its dimensions are represented by the resources and environmental characteristics that make possible the existence of a species (Hutchinson, 1957; Colwell and Rangel, 2009). Therefore, it involves the set of abiotic conditions, resources and interactions to which it is subject, and which define its function in the environment (Cornell, 2012). The width or breadth of a niche refers to space, within a given dimension of the niche, where the species can be found and where it is capable of exploring it sustainably. The niche amplitude can be measured by spatial aspect (habitat, substrate) and temporal aspect (periods of the year and times) (Colwell and Futuyma, 1971; Abrams, 1980).

Each species is inserted in an ecological community in a particular way, with its own levels of tolerance to different environmental factors, intra and interspecific interactions (Miller and Spoolman, 2009) and with this, they play an important role in structuring that community (Ventura et al., 2000). Sympatric species of crustaceans have similar environmental requirements, therefore, they can use the same biological resources in the same area (Bertini and Fransozo, 2004; Keunecke et al., 2012).

Some researchers report the existence of competition in habitat sharing, particularly in species that have similar niches, this fact can generate niche overlap, which was defined by Cornell (2012) as the partial or total sharing by two or more species of resources or other ecological factors (predators, foraging space, sediment type). Historically, it has been postulated that competition is more intense between taxonomically related species (Elton and Miller, 1954). In addition to the interactions and competitions for resources, variations in the abundance and distribution of the species of benthic crustaceans, both in time and space, are also related to environmental characteristics such as temperature, salinity, organic matter content and size of the sediment grain (Abele, 1974; Carvalho et al., 2010). Understanding these variations is a fundamental part of interpreting the species distribution pattern.

The region of Ubatuba has a great wealth of species of Brachyura, with that, there are bays that shelter many congeneric species, as: *Achelous spinimanus* Latreille, 1819 and *Achelous spinicarpus* (Stimpson, 1871), *Callinectes danae* Smith, 1869 and *Callinectes ornatus* Ordway, 1863, *Libinia spinosa* (Guérrin, 1832) and *Libinia ferreirae* Brito Capello, 1871 (Mantelatto & Fransozo 2000; Mantelatto et al 2016; Fransozo et al 2016). However, studies that assess the peculiarities of environmental exploration that allow the coexistence of morphologically similar species (Mantelatto et al., 2016; Fransozo et al., 2016) and phylogenetically close ones are rare.

The target species in this study are sympatric: *Persephona lichtensteinii* Leach, 1817, *P. mediterranea* Herbst, 1794 and *P. punctata* Linnaeus, 1758. The three species are commonly caught as fauna accompanying fishing directed to commercially exploited shrimp (Branco and Fracasso, 2004; Mantelatto et al., 2016) and although they have no economic interest, they play essential ecological roles within the marine trophic chain (Almeida et al., 2013). They are considered generalists and feed mainly on polychaetes in the infauna (Petti et al., 1996; Bellwood, 2002).

On the north coast of São Paulo, investigations related to niche overlap have already occurred, such as the study by Pinheiro et al. (1997) and Lima et al. (2014) with Portunídeos. Expanding the knowledge related to these crabs, this study investigated the occurrence of these three species of the genus *Persephona*, in view of the environmental parameters, as well as the amplitude and niche overlap between them. For this, it was taken into account: (a) variations in the abundance of the three species of the genus *Persephona* over different sampling stations, (b) temporal variations in their abundance, (c) environmental variables that can affect their distributions, (d) niche spatial width and (e) niche overlap.

MATERIAL AND METHODS

Study area

The Ubatuba Bay (23 ° 26'S and 45 ° 02'W) is located on the north coast of the State of São Paulo, Brazil. Currently, it is part of a Marine APA of the North Coast (Marine Environmental Protection Area of the North Coast: Sector Cunhambebe, proclamation n °: 53,525, by the Ministry of the Environment - October 8, 2008), instituted with the objective of prioritizing the conservation, such as the sustainable use of the region's marine resources. Artisanal fishing of shrimp of commercial interest is allowed and carried out inside and outside the bay throughout the year, with interruption only in the closed period, from March 1 to May 31 (Normative Instruction IBAMA nº189 / 2008).

Collect of the data

The specimens of genus *Persephona* were identified to species level (Melo 1996; Magalhães et al. 2016). Details on the sampling methodology can be found in Mantelatto & Fransozo (1999, 2000). The collections were carried out monthly from September / 1995 to August / 1996, using a fishing boat equipped with a double-rig bottom trawl, in eight permanent sampling stations, established within the Ubatuba Bay (Figure 1). Each station was sampled for 1 km in length, with a duration of 20 min, making collections in each of them for three consecutive days (14th to the 16th day of each month). An ecobathymeter coupled with a GPS was used to record depth at sampling station. At each sampling station, samples of sediment, bottom water were collected, before trawling, for analysis of environmental factors. Water was collected with a Nansen bottle for obtain the temperature and the salinity. Measurements with the ad of a mercury thermometer (ºC) and salinity and an optical refractometer (‰), respectively.

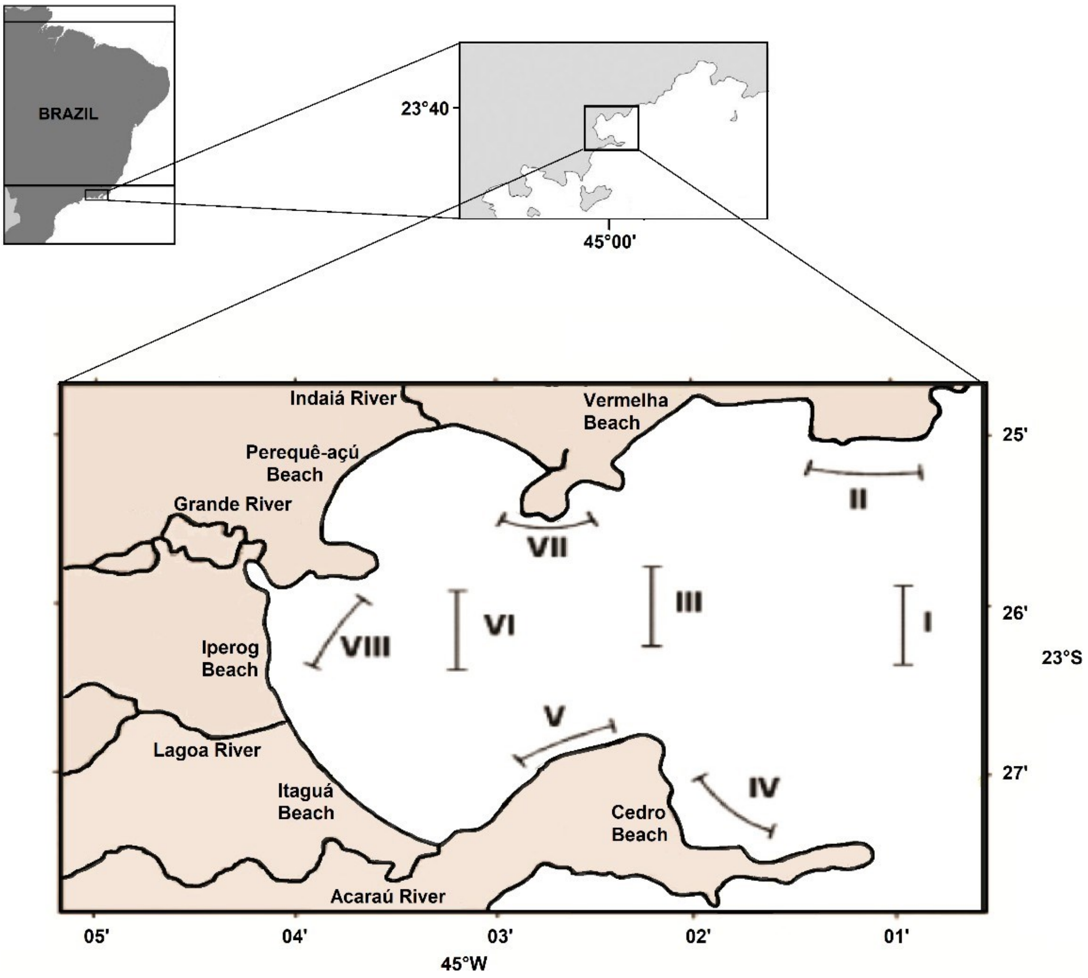

Figure 1. Map of the study region showing Ubatuba Bay with the sampling stations.

The methodology used to measure the texture and organic-matter content of the sediment was similar to that described by Hakanson and Jansson (1983) and Tucker (1988). Sediment samples were obtained collected at each transect with a Van Veen grab (0.063 m^2) for sediment grain size composition and organic matter content determination. Samples were transported to the laboratory and oven-dried at 70 °C for 72 h. For the analysis of grain size composition, two subsamples of 50 g were treated with 250 ml of NaOH solution (0.2 mol l^{-1}) and stirred for 5 min to release silt and clay particles. The subsamples were then rinsed on a 0.063 mm sieve. Grain sizes were classified according to Wentworth (1922) scale: sediments sieved at >2 mm (gravel), 1.0 – 2.0 mm (very coarse sand), 0.5 – 1.0 mm (coarse sand), 0.25 – 0.5 mm (medium sand), 0.125 – 0.25 mm (fine sand), 0.125 – 0.063 mm (very fine sand), and smaller particles classified as silt and clay.

The three most quantitatively important sediments were defined according to Magliocca and Kutner (1965): class A corresponds to sediments in which medium sand (MS), coarse sand (CS), very coarse sand (VCS) and gravel (G); in class B, fine sand (FS) and very fine sand (VFS) and class C with silt and clay (S+C). From these three categories, groups were established according to the combination of granulometric fractions in several proportions: PA = (MS + CS + VCS + G) > 70%; PAB = prevalence of A over B (FS + VFS); PAC = prevalence of A over C (S + 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. For organic matter content determination, we put 10g subsamples in porcelain containers, previously individually identified and weighed. Incinerated in an oven (500ºC for 3 hours) and weighed again. The difference between the initial and final weigh indicated the organic matter content of each sample, which was expresses as proportion of the initial weight.

Data analysis

Foi realizada uma análise exploratória de dados, seguindo as premissas indicadas por Zuur et al. (2010). A Redundancy Analysis (RDA) was used to investigate the relationship between abundance of three species and environmental variables. The RDA produces a final coordination score that summarizes the linear relationship between explanatory and response variables (Jongman et al. 1995). A RDA analyzes were performed using R (R Development Core Team 2016; Zar 2010). We used the "vegan" package (Oksanen et al. 2012) for the RDA and the adjustment of the environmental vectors (ENVIFIT). For all tests, we adopted the significance level of 0.05. Bottom temperature and salinity were compared between sampling station and season using the Friedman test ($\alpha = 0.05$) (Zar 2010).

According to Krebs (1989) the amplitude of the spatial niche can be measured by the distribution of individuals of a species within a set of resources. In the present study, for spatial niche amplitude, it was considered that each of the eight areas where collections were made (artificial sampling units) had environmental differences (different resources; ex: water temperature and salinity, sediment texture and matter content organic) and this determined whether the animals were present or not in these places. Such data served for the elaboration of a resource matrix, where the species are arranged in rows and the resources in columns (Colwell and Futuyma 1971).

From it, the amplitude of the niche of each species was calculated using the standardized Levins measure (B_A) (Krebs 1989) as follows: $B_A = \frac{B-1}{n-1}$ where $B = \frac{1}{\Sigma pj2}$ Levins measure (niche amplitude); ($pj = \frac{Nj}{y}$) proportion of individuals using the "j" resource; (Nj) number of individuals found using the "j" resource; ($y = \Sigma Nj$) total number of individuals sampled; (n) total number of resources. The niche overlap was calculated according to the formula: $Pjk = [\Sigma$ (minimum pij, pik)]. 100 where: (Pjk) percentage of overlap between the niche of species "j" and "k"; (pij, pik) proportion of resource "i" in relation to the total resources used by species "j" and species "k"; (n) total number of resources (Krebs 1989). The analyzes were performed using R (R Development Core Team 2016; Zar 2010). We used the "spaa" package (Zhang 2016).

Finally, hierarchical dendograms of the total abundance of each species and the median value of each abiotic variable per transect were plotted using the function "Heatmap" (package ComplexHeatmap), as described by Kassambara (2017). This technique uses a graphic representation of these values in which all data is standardized and certain colors indicate higher and lower values regardless of the initial data. In these analyzes, only variables that showed differences in temporal or spatial comparisons were used.

RESULTS

Environmental variables

The sediment presented different granulometric compositions in each sample station. The stations with the most heterogeneous sediment were IV and V, which had a large number of classes A and B. These two sample stations have a thicker sediment, since class A is composed of biodetritic fragments (Figure 2). While stations III, VI and VIII were the most homogeneous, where all particle sizes are well represented (Figure 2).

The bottom water temperature (BT) showed a significant difference between the sampling stations (Fr = 55.96; Df = 7; $p < 0.05$) (Figure 3A) and seasons (Fr = 21.60; Df = 3; $p < 0.05$) (Figure 3B). The lowest values of background temperature were sampled at sampling stations I (22.55 ± 2.89 ° C) and II (23.40 ± 2.85 ° C) (Figure 3A) and in winter (20.97 ± 1.88 ° C) and in spring (22.80 ± 0.62 ºC) (Figure 3B).

The bottom water salinity showed its lowest value in the sample station VIII (32.78 ± 1.56) and the highest in I (33.73 ± 1.56) and III (33.40 ± 1.81). This difference was statistically significant (Fr = 19.58; Df = 7; $p < 0.05$) (Figure 4A). Temporally, the lowest salinity value was recorded in spring (31.40 ± 1.40) and the highest in winter (34.40 ± 0.46) (Figure 4B), this difference was statistically significant (Fr = 22.20; Df = 3; $p < 0.05$).

Spatio-temporal distribution in relation to environmental variables

A total of 128 specimens of *Persephona mediterranea*, 356 of *P. punctata* and 34 of *P. lichtensteinii* were sampled. The species *P. mediterranea* was more abundant in sampling station I, which has a large amount of fine and very fine sand (class B), with a low percentage of silt and clay. *Persephona punctata* was more sampled in seasons IV, V and VI, showing a wider distribution, tolerating greater variations in the percentage of class C sediment. *Persephona lichtensteinii* was found mainly in season VI, whose sediment is composed of large percentages of silt and clay (Table I).

The results of the RDA on axis 1 (89.9%) showed a directly proportional correlation between *P. lichtensteinii* and *P. punctata* and class C of the sediment and bottom temperature and inversely proportional with class B and the bottom salinity. For *P. mediterranea* there was a directly proportional correlation with class B and the bottom salinity and inversely proportional with class C of the sediment and bottom temperature (Figure 5).

Based on the heatmap created in the spatial comparison (Figure 6), we can verify the formation of 4 groups of associations between abiotic factors and species abundance in each season. In the first group, it is characterized by the lowest abundance of all analyzed species, comprising seasons II, III, VII and VIII. The second group can already observe substantial amounts of *P. punctata* in seasons V and IV, being evidenced by locations with low amounts of sediment type C and B. The third group is marked by only transect I, with higher values being presented at this point. BS and B, as well as low BT and C, and the presence of the highest abundance of *P. mediterranea*. The fourth group is formed by the transect VI, where it presents the co-occurrence of two species (*P. punctata* and *P. lichtensteinii*), and is characterized by higher values of BT and C. We also see that the abundance of *P. punctata* and *P.lichtensteinii* are more similar, being later grouped with *P. mediterranea*.

Based on the heatmap created in the spatial comparison (Figure 6), we can verify the formation of 4 groups of associations between abiotic factors and species abundance in each season. In the first group, it is characterized by the lowest abundance of all analyzed species, comprising seasons II, III, VII and VIII. The second group can already observe substantial amounts of *P. punctata* in seasons V and IV, being evidenced by locations with low amounts of sediment type C and B. The third group is marked by only transect I, with higher values being presented at this point. BS and B, as well as low BT and C, and the presence of the highest abundance of *P. mediterranea*. The fourth group is formed by the transect VI, where it presents the co-occurrence of two species (*P. punctata* and *P. lichtensteinii*), and is characterized by higher values of BT and C. We also see that the abundance of *P. punctata* and *P.lichtensteinii* are more similar, being later grouped with *P. mediterranea*.

Temporally there is a clear division, being winter with spring and summer with autumn grouped. We can verify that the three species co-occur during the winter and spring, however it is possible to verify a different grouping in terms of abundance, in which *P. mediterranea* is closer to *P. lichtensteinii*, both being more collected in spring, a season that was characterized by temperature and low salinity. While *P. punctata* appears separate, with a greater number of specimens found in winter, the season had high salinity and lower temperature characteristics than in spring (Figure 7).

Niche breadth and overlap

The spatial niche of largest breadth was *P. punctata* (3.06) followed by *P. lichtensteinii* (2.36) and *P. mediterranea* (1.43) (Table I). The lowest percentage of niche overlap occurred between *P. mediterranea* and *P. lichtensteinii* (2.10%), while the highest overlap was found between *P. punctata* and *P. lichtensteinii* (92.3%) (Table II).

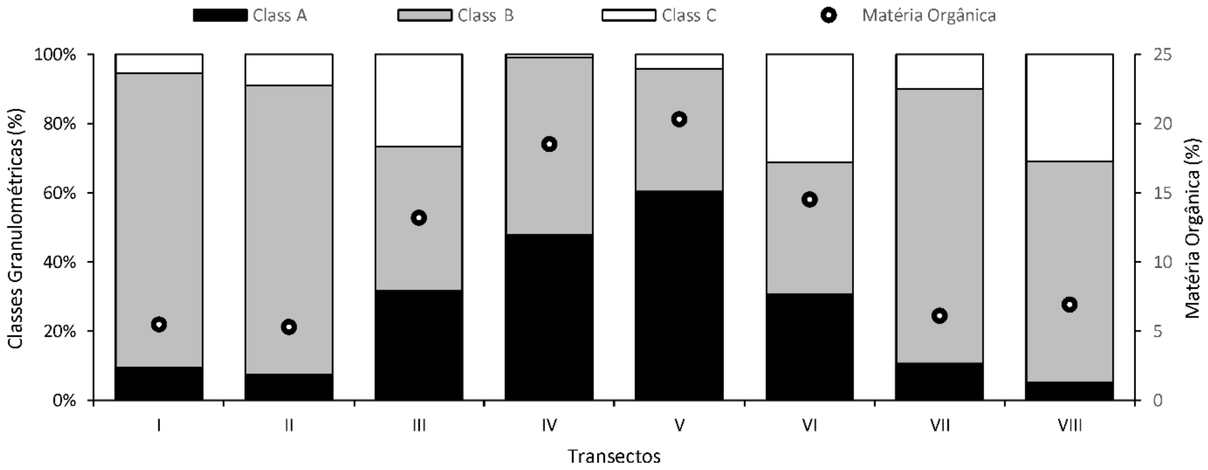

Figure 2. Percentages of the granulometric classes at each sampling station in Ubatuba Bay. A. class A (gravel, very coarse sand, coarse and medium); B. Class B (fine and very fine sand); C class C (silt and clay).

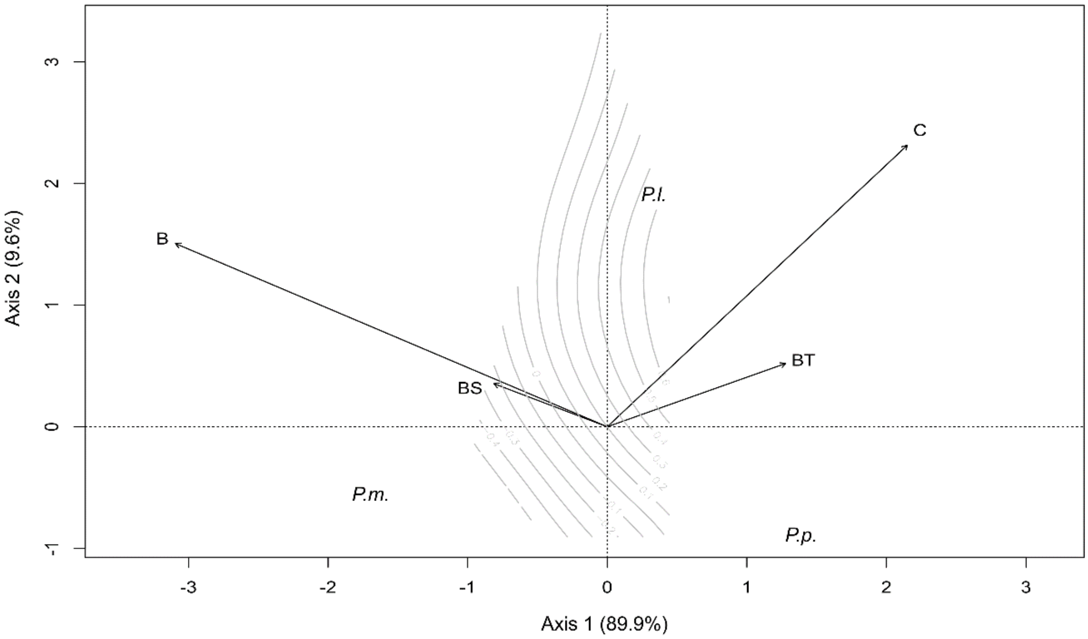

Figure 3. Redundancy analysis (RDA) of the abundance matrix of *P. punctata* (*P.p.*), *P. editerranea* (*P.m.*) and *P. lichtensteinii* (*P.l.*) and the matrix of environmental data considered significant at $p < 0.05$ (BS = bottom salinity; BT = bottom temperature, B = class B; C = class C) sampled in the study carried out in the Ubatuba Bay. See Material and methods for details.

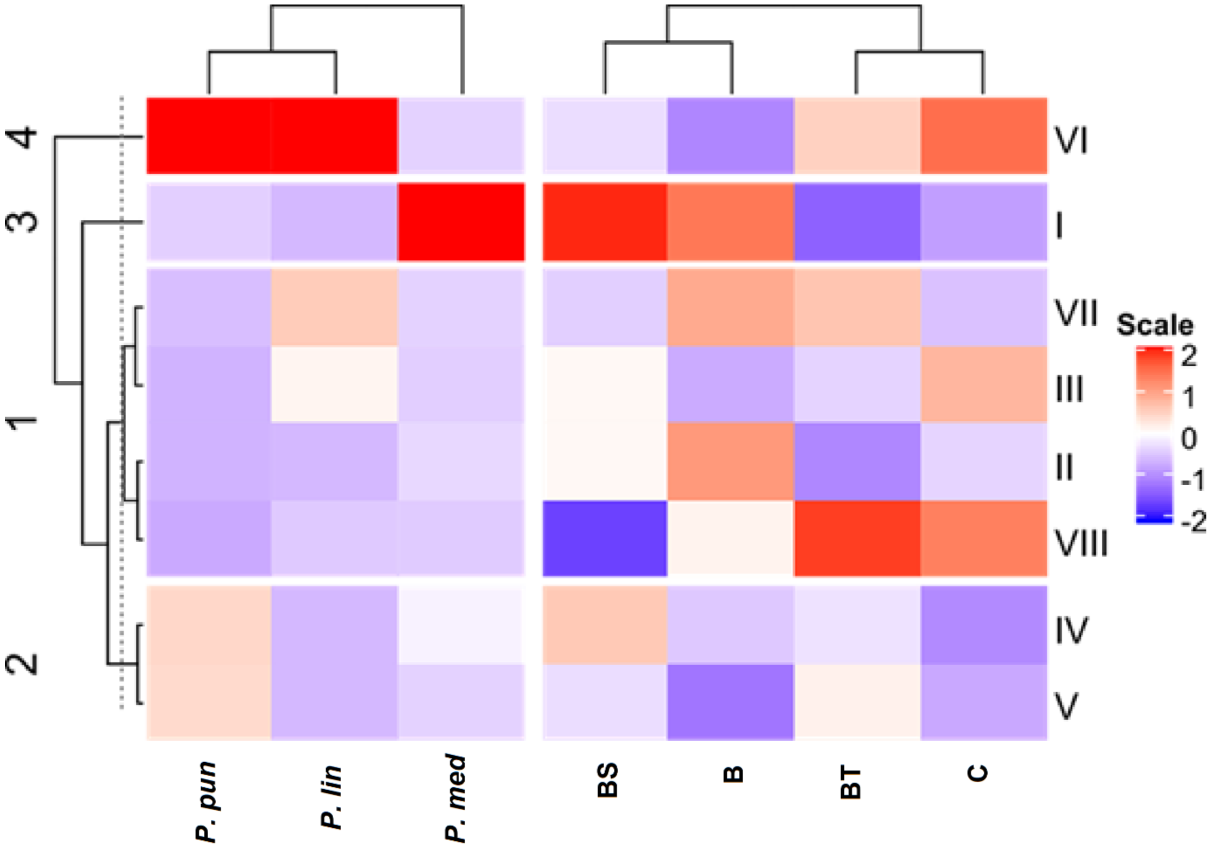

Figure 4. Hierarchical clustering heatmap of the total abundance of 3 species of crabs of the genus Persephona and abiotic variables per transect sampled in the Ubatuba Bay. Caption: P. pun = Persephona punctata; P. lic = Persephona lichtensteinii; P. med = Persephona mediterranea; BS = Bottom Salinity; BT = Bottom Temperature; B = class B; C = class C; numbers in the left margin indicate the groups formed by transect (figures in the right margin).

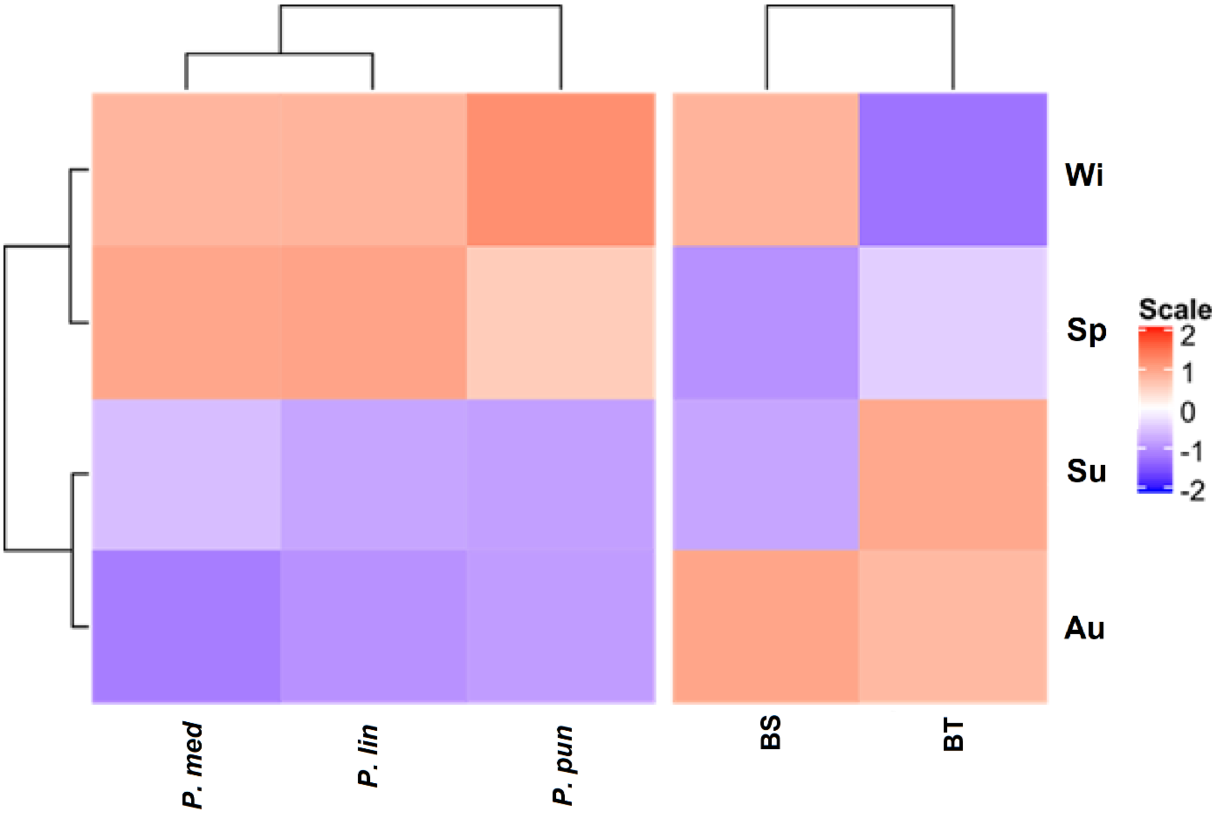

Figure 7. Hierarchical clustering heatmap of the total abundance of 3 species of crabs of the genus Persephona and abiotic variables per season sampled in the Ubatuba Bay. Caption: P. pun = Persephona punctata; P. lic = Persephona lichtensteinii; P. med = Persephona mediterranea; BS = Bottom Salinity; BT = Bottom Temperature; letters on the right margin indicate the seasons (Wi = Winter; Sp = Springer; Su = Summer; Au = Autumn).

Table I. Abundance and percentage of individuals per sampling station and season. (B_A = Amplitude of the spatial niche of each species).

Species		**Sampling stations**								**B_A**
		I	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	
P. punctata	N	20	5	5	70	68	177	11	-	3.06
	%	5.6	1.4	1.4	19.7	19.1	49.7	3.1	-	
P. meriterranea	N	105	4	1	12	2	2	2	-	1.43
	%	82.0	3.1	0.8	9.4	1.6	1.6	1.6	-	
P. lichtensteinii	N	-	-	5	-	-	20	8	1	2.36
	%	-	-	14.7	-	-	58.8	23.5	2.94	

		Seasons				
		Spring	**Summer**	**Autumn**	**Winter**	**Total**
P. punctata	N	130	26	24	176	356
	%	36.5	7.3	6.7	49.4	
P. meriterranea	N	50	21	10	47	128
	%	39.1	16.4	7.8	36.7	
P. lichtensteinii	N	14	4	3	13	34
	%	41.2	11.8	8.8	38.2	

Table II. Percentage of overlap between the niches of three species of *Persephona* collected in the eight sampling stations of the Ubatuba Bay, São Paulo, from September / 1995 to August / 1996.

	Spatial niche overlap	
Species	***P. punctata***	***P. mediterranea***
P. mediterranea	23.3%	-
P. lichtensteinii	92.3%	2.1%

DISCUSSION

The sediment texture, possibly, is the main modulating factor of the spatial distribution of the 3 congeners species. The greatest abundance of *P. mediterranea* occurred in the deepest areas of this bay, where the sediment is composed mainly of fine and very fine sand. This distribution pattern was reported by Bertini et al. (2001; 2010). This species is generally more abundant in regions between 15 and 25 meters (Bertini and Fransozo, 2004). This evidence was corroborated by our results, since 82% of the abundance of *P. mediterranea* was sampled in season I (deeper). With this restricted distribution profile largely on a single bay location made *P. mediterranea* had the smallest spatial amplitude and niche overlap when compared to the other two species studied

Persephona punctata was shown to be the species with the greatest plasticity in terms of variations in sediment and environmental conditions such as water temperature and salinity. This fact is evidenced by having been registered in a larger number of the sampled stations. This greater capacity to inhabit several habitats, possibly, is due to its greater abundance and, consequently, it has a greater spatial niche amplitude among the three congeners. *Persephona lichtensteinii* was sampled in stations that had sediment with high values of silt and clay, however, among the 3 species of the genus, this was the least abundant. Its low abundance in Ubatuba / SP was generally related to the idea that this location would be its southern limit of geographic distribution, in the state of São Paulo (Melo 1996). However, in a recent study, Branco et al. (2015) found *P. lichtensteinii* in the state of Santa Catarina, expanding the geographical distribution to the south.

Observing the spatial distribution of the 3 species of the genus *Persephona* in the Ubatuba Bay, it is possible to infer that the low abundance of *P. lichtensteinii* may be due to the overlapping of the environmental requirements of this species with *P. punctata*, a fact supported by 92.3% of spatial overlap between both. As a result, only one of the two species would have a greater number of individuals, and could be considered more apt to this environment and with greater reproductive success, a fact that would provide a significant advantage in interspecific competition. A detailed experimental study involving competition for space between them could help to improve the understanding of the relationship of spatial occupation between species.

According to Wiens and Graham, 2005, species are expected to inhabit environments that bear some resemblance to those of their close relatives, thus, to a certain extent, niches are conserved. However, few sister species can share identical niches, limiting this supposed niche conservation (Wiens and Graham, 2005). The data obtained by Carvalho et al. (2010) in Ilhéus (Northeast Brazil), reinforce our results from the Heatmap, in which they show that the water temperature has a particular influence on the abundance of *P. punctata* and *P. lichtensteinii*. In Ilhéus, located at latitude 14º 47'S, as it is closer to the equator, it has higher temperatures, thereby Carvalho et al. (2010) sampled 183 of *P. lichtensteinii* and 58 of *P. punctata*, while in our study carried out at 23º 26'S, we obtained inverse proportions with 356 of *P. punctata* and 34 of *P. lichtensteinii*. We suggest that *P. lichtensteinii* seems to be more adapted to higher temperatures while *P. punctata* is more abundant at intermediate temperatures.

Regarding the temporal distribution, the three species were more abundant in spring and winter. According to Pereira et al. (2014), this difference in the abundance of crabs associated with the seasons is due to the influence of temperature variations on the biology of these organisms and the availability of food. It is known that, in late spring and early summer, the region of Ubatuba suffers seasonal influence from the South Atlantic Central Waters (SACW), which reaches the region and causes a decrease in the temperature and salinity of the deepest waters (above 15 meters) and promote an enrichment of the water column by the development of phytoplankton and zooplankton (Pires-Vanin et al. 1993).

In the winter with the retraction of the SACW and the frequent passages of cold fronts, the bottom water becomes increasingly cold and the bottom is upturned and subject to the intense resuspension of the sediments. This resuspension triggers a trophic cascade, causing an increase in the availability of food and consequently an increase in the abundance of some species (Pires-Vanin et al. 1993). The representatives of the superfamily Leucosiidae are known to remain buried in the sediment and capture polychaetes in the infauna, thus, the grain size and the availability of food can contribute to the delimitation of the patterns of spatial and temporal distribution (Petti et al., 1996; Bellwood, 2002).

The temporal heatmap showed a cluster between *Persephona mediterranea* and *P. lichtensteinii*, which were more abundant in the spring. Although the arrival of SACW in spring causes a reduction in the bottom temperature, when we compare the temperature of this season with winter, those obtained in winter are lower. As we have seen, low temperatures seem to limit the abundance of *P. lichtensteinii*. In winter, the most abundant species was *P. punctata* which, as we have already seen, is more adapted to lower temperatures, which were recorded this season. Bertini et al (2010) analyzed the ecological distribution of the three species of *Persephona* and also found this pattern of distribution in relation to the seasons, with greater abundance of *P. mediterranea* and *P. lichtensteinii* in spring and *P. punctata* in winter.

In view of the ecological distribution patterns observed for the three congeners, in which *P. punctata* spatially was more like *P. lichtensteinii* and temporally *P. mediterranea* was more similar to *P. lichtensteiniii*. We can say that our results contradict the hypothesis of the existence of Phylogenetic signal, since *P. mediterranea* and *P. punctata*, which are phylogenetically closer, showed to have less ecological similarity.

Although the Phylogenetic signal was not observed in our study, it has already been detected in several other studies, such as ecophysiological characteristics among European plants (Prizing et al. 2001), ecological determinants in the occupation of the lake by sunfish (Helmus et al. 2007), climatic niche among neotropical hilid frogs (Wiens et al 2008), among others.

For crustaceans, studies with this focus are still scarce, we can mention some such as Murphy and Austin et al. (2004), with the phylogenetic relationships of the freshwater shrimp genus *Macrobrachium* (Crustacea: Decapoda), Pons et al. (2014) with the investigation of the phylogenetic signal in *Metacrangonyctidae* (Crustacea, Amphipoda) and Van-Der-Wal et al. (2019) with studies on the phylogeny of *Squilloidea* (Crustacea, Malacostraca).

With this, our study brings important aspects and still little addressed on phylogenetic relationships and ecological distribution of 3 Persephona. In addition to contributing to the understanding of the niche overlap between three congeners. In which *P. punctata* and *P. litchensteinii* showed many similarities in the spatial distribution, being found in places with a large amount of silt and clay, mainly in the shallow regions of the bay. Such condition results in a high percentage of niche overlap, in which its occurrence seems to be limited by the water temperature. *Persephona mediterranea* showed the lowest amplitude and the lowest percentages of niche overlap. This is probably due to the fact that *P. mediterranea* was sampled in deeper stations of the bay, where the sediment was composed mainly of fine and very fine sand. Temporally, water temperature and food availability seem to modulate the abundance peaks of the three species of *Persephona*, which were more abundant in spring and winter.

REFERÊNCIAS

Abele, LG, 1974. Species diversity of decapod crustaceans in marine habitats. Ecology 55: 156–161.

Abrams, P. (1980). Some comments on measuring niche overlap. Ecology, 61(1), 44-49.

Almeida, AC, Hiyodo, C, Cobo, VJ, Bertini, G, Fransozo, V, Teixeira, GM, 2013. Relative growth, sexual maturity, and breeding season of three species of the genus *Persephona* (Decapoda: Brachyura: Leucosiidae): a comparative study. Journal of the Marine Biological Association of the United Kingdom, 93(6): 1581-1591.

Bellwood, O, 2002. The occurrence, mechanisms and significance of burying behavior in crabs (Crustacea: Brachyura). J. Nat. Hist., 36(10): 1223-1238.

Bertini, G, Fransozo, A, 2004. Bathymetric distribution of brachyuran crab (Crustacea, Decapoda) communities on coastal soft bottoms off southeastern Brazil. Marine Ecology Progress Series, 279, 193-200.

Bertini, G., Fransozo, A. & Costa, R.C., 2001. Ecological distribution of three species of *Persephona* (Brachyura: Leucosiidae) in the Ubatuba region, São Paulo, Brazil. Nauplius 9(1): 31-42.

Bertini, G., Teixeira, G. M., Fransozo, V., Fransozo, A. 2010. Reproductive period and size at the onset of sexual maturity of mottled purse crab, *Persephona mediterranea* (Herbst, 1794) (Brachyura, Leucosioidea) on the southeastern Brazilian coast. *Invertebrate Reproduction & Development*, *54*(1), 7-17.

Blomberg, S. P., & Garland Jr, T. (2002). Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, *15*(6), 899-910.

Branco, J.O., Freitas Júnior, F.; Christoffersen, M.L. 2015 Bycatch fauna of seabob shrimp trawl fisheries from Santa Catarina State, southern Brazil. Biota Neotropica, 15(2): 1-14

Branco, JO, Fracasso, HAA, 2004. Ocorrência e abundância da carcinofauna acompanhante na pesca do camarão sete-barbas, *Xiphopenaeus kroyeri* Heller (Crustacea, Decapoda), na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. Revista Brasileira de Zoologia, 21(2): 295–301.

Cain, M. L., Damman, H., & Muir, A. (1998). Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs*, *68*(3), 325-347.

Carvalho, FL, Carvalho, EAS, Couto, ECG, 2010. Comparative analysis of the distribution and morphological sexual maturity of *Persephona lichtensteinii* and *P. punctata* (Brachyura, Leucosiidae) in Ilhéus, BA, Brazil. Nauplius 18: 109–115.

Chhapgar, B. F. 1955. On the life history of Philyra globosa (Fabricius) (Decapoda, Brachyura).— Records of the Indian Museum 53: 87–92

Colwell, R. K., & Rangel, T. F. (2009). Hutchinson's duality: the once and future niche. Proceedings of the National Academy of Sciences, 106(Supplement 2), 19651-19658 Colwell, RK, Futuyma, DJ, 1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

Cornell, H, 2012. Niche Overlap. In: A. Hastings & L. J. Gross (eds) Encyclopedia of Theoretical Ecology, University of California Press 489-497.

De Léo, FC, Pires-Vanin, AMS, 2006. Benthic megafauna communities under the influence of the South Atlantic Central Water intrusion onto the Brazilian SE shelf: a comparison between an upwelling and a non-upwelling ecosystem. Journal of Marine Systems 60: 268–284.

Elton, CS, Miller, RS, 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. Journal of Ecology 42: 460–496.

Fransozo A, De Sousa AN, Rodrigues GFB, Telles JN, Fransozo V, Negreiros-Fransozo ML, 2016. Crustáceos decápodes capturados na pesca do camarão-sete-barbas no sublitoral não consolidado do litoral norte do Estado de São Paulo, Brasil. Bol Inst Pesca 42(2): 369–386.

Hakanson L, Jansson M, 1983. Principles of lake sedimentology. Germany: Springer-Verlag. Hutchinson, GE. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology. 22: 415-42

Jongman, E. (1995). *Data analysis in community and landscape ecology*. Cambridge university press.

Kassambara, A. 2017. Pratical Guide to Cluster Analysis in R: Unsupervised Learning Machine. Vol. 1. STHDA.

Keunecke KA, D'Incao F, Verani JR, Vianna M. 2012. Reproductive strategies of two sympatric swimming crabs *Callinectes danae* and *Callinectes ornatus* (Crustacea: Portunidae) in an estuarine system, south-eastern Brazil. J Mar Biol Assoc U. K 92(1):343–347.

Krebs, CJ, 1989. Ecological methodology. New York, Harper & Row Publishers, 645p.

Helmus, M.R., Savage, K., Diebel, M.W., Maxted, J.T. & Ives, A.R. (2007). Separating the determinants of phylogenetic community structure. Ecol. Lett., 10, 917–925.

Lima, PA, Andrade, LS, Alencar, CE, Pereira, RT, Teixeira, G, Fransozo, A, 2014. Two species of swimming crabs of the genus *Achelous* (Crustacea, Brachyura): environmental requirements determining the niche. *Hydrobiologia, 727*, 197-207.

Magalhães, T., Robles, R., Felder, D. L., & Mantelatto, F. L. (2016). Integrative taxonomic study of the purse crab genus Persephona Leach, 1817 (Brachyura: Leucosiidae): combining morphology and molecular data. *PloS ONE*, *11*(4), e0152627.

Magliocca A, Kutner AS, 1965. Sedimentos de fundo da Enseada do Flamengo, Ubatuba, SP.

Contrib Avulsas Inst Oceanogr 198:1–15

Mantelatto FL, Bernardo CH, Silva TE, Bernardes VP, Cobo VJ, Fransozo A (2016) Composição e distribuição de crustáceos decápodes associados à pesca do camarão-sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862) no litoral norte do estado de São Paulo. Bol Inst Pesca 42(2):307–326.

Melo, GAS, 1996. Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. Editora Plêiade, São Paulo.

Miller, GT, Spoolman, SE. "Each Species Plays a Unique Role in Its Ecosystem," in *Essentials of Ecology*, 5th ed. (Belmont: Cengage Learning, 2009), 91.

Murphy, N. P., & Austin, C. M. (2005). Phylogenetic relationships of the globally distributed freshwater prawn genus Macrobrachium (Crustacea: Decapoda: Palaemonidae): biogeography, taxonomy and the convergent evolution of abbreviated larval development. *Zoologica Scripta*, *34*(2), 187-197.

Oksanen JF, Blanchet G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H 2012. Vegan: Community Ecology Package. R package version 2.0-5. http://CRAN.Rproject.org/package=vegan

Pereira, RT, Teixeira, GM, Bertini, G, Lima, PAD, Alencar, CE, Fransozo, V, 2014. 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. *Latin American Journal of Aquatic Research*, 307-321.

Petti, MAV, Nonato, EF, Paiva, PC, 1996. Trophic relationships between polychaetes and brachyuran crabs on the southeastern Brazilian coast. Rev. Bras. Oceanogr., 44(1): 61-67.

Pinheiro, MAA, Fransozo, A, Negreiros-Fransozo, ML, 1997. Dimensionamento e sobreposição de nichos dos portunídeos (Decapoda, Brachyura), na enseada da Fortaleza, Ubatuba, São Paulo, Brasil. Revista Brasileira de Zoologia 14: 371–378.

Pires-Vanin, AMS, Rossi-Wongtschowski, CLDB, Aidar, E, Mesquita, HDS, Soares, L SH, Katsuragawa, M, Matsuura, Y, 1993. Estrutura e função do ecossistema de plataforma continental do Atlântico Sul brasileiro: síntese dos resultados. *Publicação Especial do Instituto Oceanográfico*, 10, 217-231.

Pons, J., Bauzà-Ribot, M. M., Jaume, D., & Juan, C. (2014). Next-generation sequencing, phylogenetic signal and comparative mitogenomic analyses in Metacrangonyctidae (Amphipoda: Crustacea). *BMC genomics*, *15*(1), 566.

Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2001). The niche of higher plants: evidence for phylogenetic conservatism. Proc. R. Soc. Lond. B, 268, 2383–2389.

Quintana, R. 1984. Observations on the early post-larval stages of *Leucosia craniolaris* (L., 1758)

(Brachyura: Leucosiidae).—Report of Usa Marine Biological Institute, Kochi University 6: 7–21

R Core Team. 2016. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Salman, S. D. 1982. Observations on the larvae of North European crabs of the genus *Ebalia*

Terada, M. 1979. On the zoeal development of five species of the subfamily Iliinae and Leucosiinae (family Leucosiidae).—Researches on Crustacea 9: 27–42

Tucker , M, 1988. Techniques in sedimentology. Boston (MA): Blackwell Scientific Publications. Ventura, CRR, Grillo, MCG, Fernandes, FC, 2000. Feeding niche breadth and feeding niche overlap of paxillosid starfishes (Echinodermata: Asteroidea) from a midshelf upwelling region, Cabo Frio, Brazil. Echinoderms 227-233.

Van Der Wal, C., Ahyong, S. T., Ho, S. Y., Lins, L. S., & Lo, N. (2019). Combining morphological and molecular data resolves the phylogeny of Squilloidea (Crustacea: Malacostraca). *Invertebrate Systematics*, *33*(1), 89-100.

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377–392.

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.*, *36*, 519-539

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006). Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. Am. Nat., 168, 579–596.

Zar, JH, 2010. Biostatistical analysis. Upper Saddle River (NJ): Prentice Hall

Zhang, J. 2016. spaa: SPecies Association Analysis. R package version 0.2.2. https://CRAN.R-project.org/package=spaa.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, *1*(1), 3-14.

CAPÍTULO 4

Long-term changes in the abundance and spatio-temporal distribution of *Litopenaeus schmitti* Burkenroad, 1936 (Crustacea, Decapoda, Penaeoidea): a potential fishing resource

Long-term changes in the abundance and spatio-temporal distribution of *Litopenaeus schmitti* Burkenroad, 1936 (Crustacea, Decapoda, Penaeoidea): a potential fishing resource

Abstract

The white shrimp *Litopenaeus schmitti* is exploited economically along the Brazilian coast. Commercial exploitation associated with long-term intense anthropic activity in coastal cities can impact the abundance of animals targeted for fishing. In this respect, this study compared the abundance and distribution of *L. schmitti* against environmental factors, in two distinct periods, separated by a long term (20 years). The specimens and environmental variables (temperature and bottom salinity, Phi and rainfall) were collected monthly at Fortaleza Bay in 7 sampling stations in the first period (November / 1988 to October / 1989) and in the second period (November / 2008 to October / 2009). Sampling was carried out with a shrimp fishing boat equipped with a double-rig type net. In total, 52 individuals were obtained in P1 and 520 in P2 (U = 2296.0; p <0.05). The greater abundance of *L. schmitti* in P2 can be explained by the association with the greater rainfall volume and the increase in the proportions of silt and clay at all sampling stations. Although sedimentation may be due to some anthropic impacts, the results indicate how certain species can benefit, to the detriment of others, with long-term environmental changes.

Key words: El niño, La niña, sedimentation, rain, white shrimp, penaeoidea

Introduction

The Ubatuba region has been exploited for many years by artisanal trawling (Instituto de Pesca de São Paulo). The rampant increase in tourism and the population density of urban areas is proportional to the search for fishing resources. As a result of the growth, there is evidence of a decline in stocks of shrimp of the species *Farfantepenaeus brasiliensis* (Latreille, 1817), F. paulensis (Pérez-Farfante, 1967), and *Litopenaeus schmitti* (Burkenroad, 1936) according to Valentini et al. (1991) and Avila-da-Silva et al. (2018). Between 1967 and 2016, there was a decrease in the relative abundance of *F. brasiliensis, F. paulensis* and *L. schmitti* stocks in the Southeast / South regions (Neto & Dornelles, 1996 and Avila-da-Silva et al. 2018).

Litopenaeus schmitti (Burkenroad, 1936), target species of this study, is one of the main fishing resources in Southeast / South Brazil, mainly due to the high commercialization value, as they reach large sizes (Costa et al., 2005, Barioto et al., 2017). Popularly known as white shrimp, *L. schmitti* is found up to 30 meters in depth, but occurs in greater numbers between 18 and 25 meters. This species has a geographic distribution with a northern limit in the Antilles (23 ° 30 'N) and a southern limit in the Lagoa dos Patos estuary, Rio Grande do Sul, Brazil (29 ° 45' S), being restricted to the Western Atlantic.

The elaboration of monitoring and conservation strategies, in order to minimize the impacts of fishing on fish stocks, require knowledge about the spatio-temporal distribution of species. The content of organic matter and the texture of the substrate, in addition to variations in salinity and temperature of the bottom water, can be considered the main modulating factors in the distribution of the shrimps (Fransozo et al., 2004; Costa et al., 2007; Castilho et al., 2008; Bernardo et al., 2018). El Niño events as well as the variation in rainfall have been correlated with the variation in the abundance of *L. schmitti* (Santos et al., 2008; Capparelli et al., 2011). However, comparative studies in the same place over a wider range of time are rare and extremely important for efficient monitoring to take place in the conservation and sustainable use of the fishing resource.

Considering changes that occurred over 20 years in Fortaleza Bay, caused both by natural factors and by anthropogenic activities (Bernardo et al., 2018), the increase in silt + clay in all the transects of the Bay is highlighted. According to Bochini et al. (2014) and Barioto et al. (2017), such sediment favors the abundance of *L. schmitti*. Thus, although anthropic impacts have caused changes in the Fortaleza Bay, an increase in the number of individuals of the *L. schmitti* shrimp is expected. Therefore, this study aimed to compare the abundance and spatial-temporal distribution of the shrimp *L. schmitti*, regarding environmental factors (water temperature and salinity, sediment texture and rainfall) in Fortaleza Bay, north coast of the State of São Paulo, Brazil.

Material and methods

Study area

The Ubatuba region, located on the northern coast of São Paulo State has several bays with typical characteristics of semi confined environments (Mahiques, 1995). This study took place in one of these bays, Fortaleza (23°29′30”S 45°06′30”W), a Marine Protection Area (Sector Cunhambebe; Decree No. 53525, October 08, 2008). Commercial fishery is not allowed in the Bay, whereas only subsistence fishing by the traditional communities and/or amateur fishing are allowed (Figure 1). In such bay, near the sampling station IV, there are two rivers, Escuro e Comprido, which supply fresh water, sediment and organic matter (Negreiros-Fransozo *et al.,* 1991).

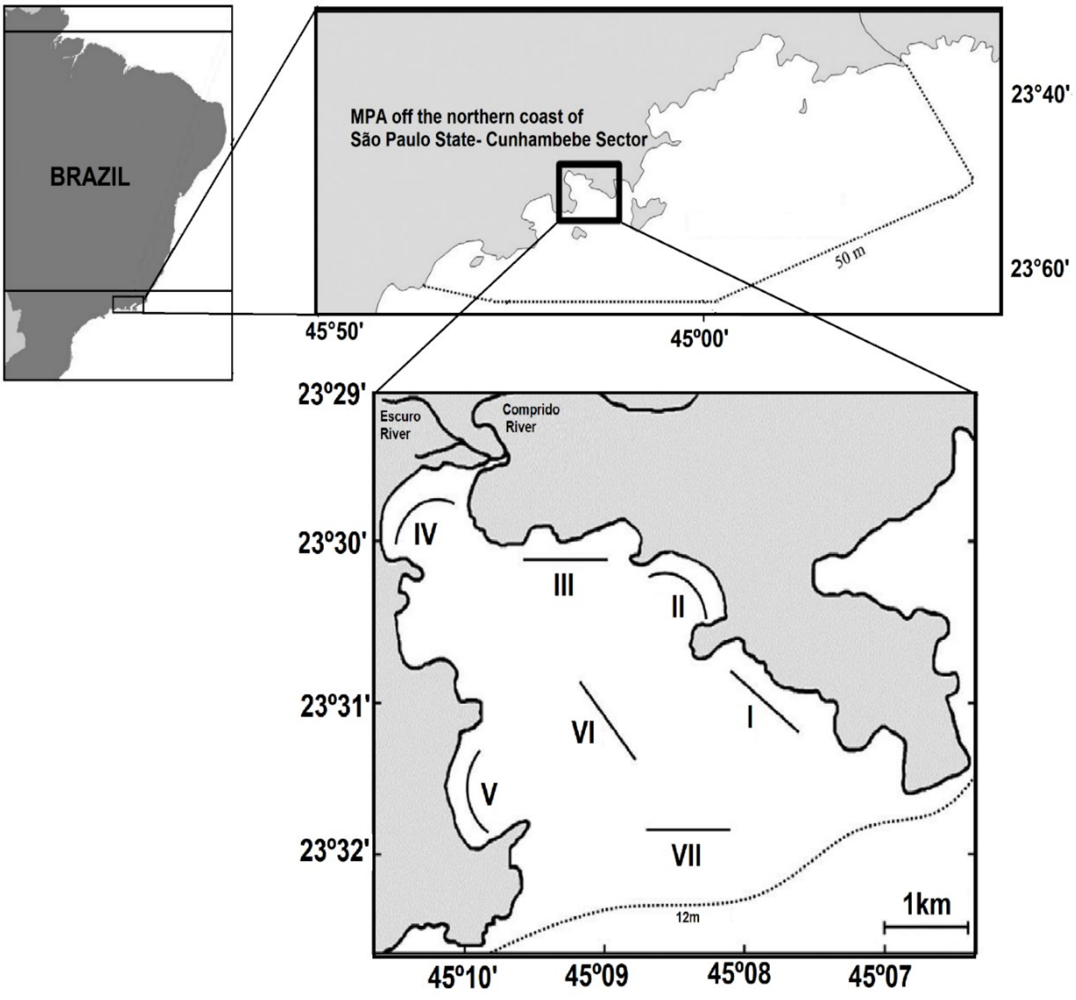

Figure 1. Map of the study region showing the Marine Protection Area (MPA) (Sector Cunhambebe) and the Fortaleza Bay with the sampling stations.

The region is influenced by three masses of water: Coastal Water (CW: temperature > 20 °C, salinity <36), Tropical Water (TW: temperature > 20 °C, salinity >36) and South Atlantic Central Water (SACW: temperature < 18 °C, salinity< 36) (Castro-Filho *et al*., 1987; Odebrecht and Castello 2001). During late spring and early summer (November– January) in Ubatuba, the SACW enters in to the lower layer of the continental shelf forming a thermocline at depths greater than 10 m. During winter (June, July and August), the SACW retracts towards the platform break and is replaced by CW. As a result, there is no stratification in the interior of the continental shelf in winter (Pires, 1992; Pires-Vanin and Matsuura, 1993). In Ubatuba, the sediment is mainly composed of fine, very fine sand and silt + clay due to the low hydrodynamics inside the bays, and between the bays and the adjacent continental shelf (Mahiques *et al*., 1998).

Biological sampling

We performed the samplings (shrimps and environmental factors) monthly for an entire year and repeated the sampling 20 years later. The first sampling took place from November 1988 to October 1989 (P1) and the second from November 2008 to October 2009 (P2). The sampling procedures, where the same in both periods. The fishing boat was equipped with a double-rig net with a length of 7.5 m, 2 m aperture, 15 mm internodes in the panning, and 10 mm in the bagger.

We carried out seven sampling stations inside the bay, each 1 km each, totalizing an area of 4 km^2 by trawl, approximately (Fig. 1). At the end of each trawl, we sorted and counted the shrimps. After that, we transported them into labelled bags to the laboratory, inside a thermal box. The identification of the shrimps were accomplished according to Perez Farfante (1969). The individuals were separated according to sex (presence of petasma in males and thellycum in females). The shrimps were measured with regard to cephalothorax length (CL) with a precision caliper (0.01 mm). The shrimps were separated into three demographic categories: juveniles, adult males and adult females.

Sampling of environmental factors

We obtained the environmental factors (water bottom temperature, water bottom salinity and sediment) at each sampling station. Bottom water samples were obtained with a Nansen bottle. Water temperature and salinity were measured with a mercury thermometer (accuracy: 0.5 °C) and an optical rephractometer (accuracy: 0.5), respectively. We used a Van Veen trap (0.025 m^2) to collect sediment samples, which were transported to the laboratory and oven-dried at 70 °C for 48 h. To analyze the grain-size composition, two subsamples of 50 g each were treated with 250 ml NaOH (0.2 mol L−1) and shaken for 5 min to separate the silt + clay from the particles, and rinsed over a 0.063 mm sieve.

Grain-size composition followed the Wentworth (1922) American standard: sediments were sieved at 2mm (for gravel retention), 2.0–1.0 mm (very coarse sand), 1.0–0.5 mm (coarse sand), 0.5–0.25 mm (medium sand), 0.25–0.125 mm (fine sand), and 0.125–0.063 mm (very fine sand). Smaller particles were classified as silt + clay. The three most important sediment grain-size fractions were defined according to Magliocca and Kutner (1965): Class A - sediments in which gravel (G), very coarse sand (VCS), coarse sand (CS), and medium sand (MS) account for more than 70% of the sample weight; Class B - fine sand (FS) and very fine sand (VFS). Os dados de precipitação foram obtidos no primeiro período em www.hidrologia.daee.sp.gov.br e no segundo período em www.ciiagro.org.br.

Data analysis

The premises of homoscedasticity (Levene test) and normality (Shapiro-Wilk test) were tested. Differences in the abundance of *L. schmitti* were analyzed separately by sampling station, month using a Friedman test ($\alpha = 0.05$). We used the Mann-Whitney test to compare the abundance of species and the environmental variables (bottom salinity and temperature of water and depth) between periods. We used the T test to compare the rainfall between periods. A Generalized Linear Model (GLM) was used to investigate the relationship between shrimp abundance and environmental variables (bottom temperature and salinity, rainfall and phi). All analyzes were performed using the R software.

Results

In the first period of sampling, we obtained 52 specimens, and in the second, 520 with statistical significant differences in their abundance (U= 2296.0; $p < 0.05$). In both periods we sampled invidids from all demographic groups (juveniles, male and female adults) (Table 1). Spatially, the highest abundances of *L. schmitti* were seen in stations I and IV, in both periods with no significant differences between station (For P1, Friedman test = 1,7589; $p > 0.05$ and P2 Friedman test = 4,8839; $p > 0.05$). We observed an increase for mud (silt and clay) in the stations with the highest abundance of *L. schmitti* (I and IV) in the second period. Thus, this was directly proportional to the abundance of individuals (Figure 2 and Table 2).

Overall, the sediment grain-size decreased as the classes B and C increased in all sampling stations, compared to the first period, indicating a deposition of finer sediments in the bay (Figures 2 and 3). The mean depth in Fortaleza Bay in the first period was 8.9 ± 3.0 m, decreasing to 7.9 ± 1.9 m in the second period (U = 2804.5; $p < 0.05$). During both periods, station IV had the lowest depth and station VII, the highest (Figure 4).

In P1 there were no significant differences in abundance between months (Friedman test = 17,835; $p > 0.05$) (Figure 5). However, in the second period, July was significantly different of November, December, January, February and March (Friedman test= 79,8516; $p < 0.05$) (Figure 5). Seasonally, in the P1, the lowest temperatures were recorded in December, January, and July (22.4 °C, 22.2 °C, and 21.0 °C, respectively). In the P2, the lowest temperatures occurred in December (19.7 ± 1.6 °C) and July (21.0 °C). From February until April, temperature means were higher than 26 °C in both periods. The Mann-Whitney indicated a significant difference in mean temperature between the two periods ($p < 0.05$) in December, January, February, April, May, September, and October (Figure 5). In the P1, the mean bottom temperature was 23.5 °C ± 2.5 and in the P2, 23.5 °C ± 2.1 (U = 3273.0; $p > 0.05$).

In the first period, from May to August, it was verified mean salinities above 35, while in the second one, in the same months, salinity was close to 33. Bottom salinity differed between the two periods in every month except for January, March, September, and October (Mann-

Whitney test, $p > 0.05$) (Figure 6). The overall mean bottom salinity did not vary much between the two study periods, with a mean of 34.4 ± 1.4 in first period and 34.2 ± 1.6 in the second period ($U = 3119.0$; $p > 0.05$).

Rainfall was highest during the P2, with a yearly average of 223.41 ± 107.92 mm and with November, January, March, April and October experiencing rainfall of above 250 mm. The P1 had an average rainfall of 135.72 ± 85.82 mm and precipitation above 250 mm only during the month of March. This difference was statistically significant (T test= -2,2031; $p < 0.05$) (Figure 7). The GLM results indicated an inversely proportional correlation between shrimps' abundance and bottom temperature and salinity, rainfall, and a directly proportional correlation with phi. Most factors were significant, except the bottom temperature (Table 3).

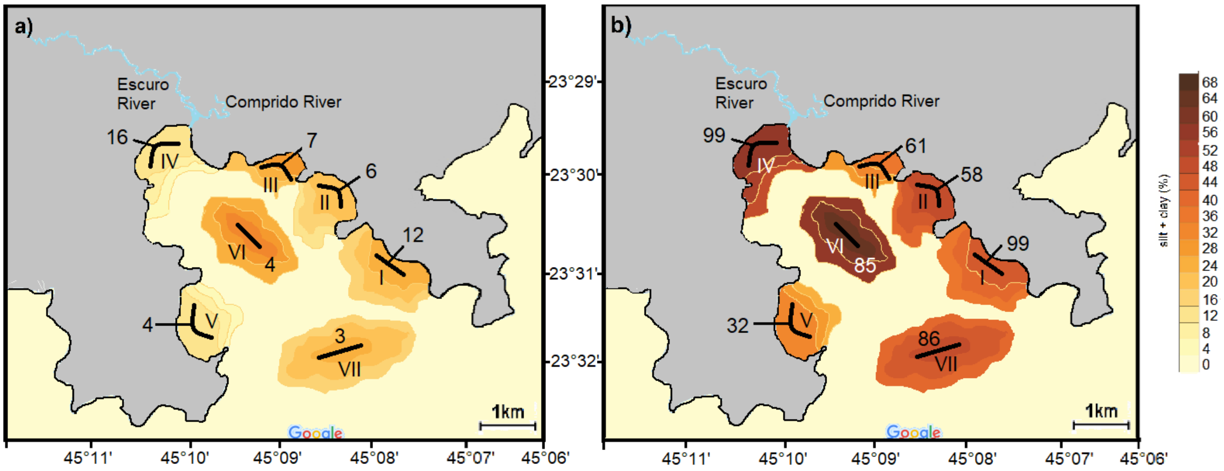

Figura 2. *Litopenaeus schmitti* (Burkenroad, 1936). Spatial abundance of white shrimp and spatial variations in the proportions of silt and clay. a) first period; b) second period.

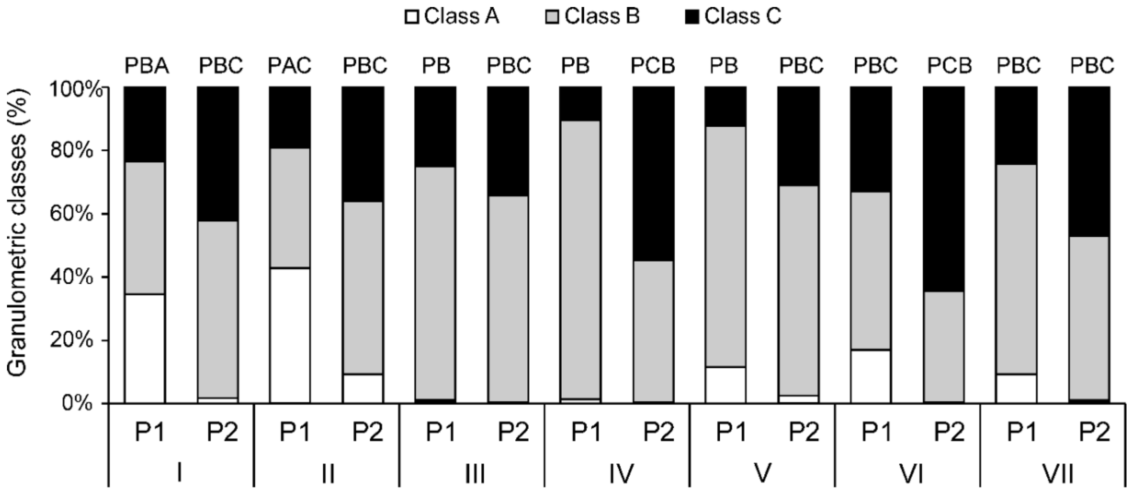

Figure 3. Percentages of the granulometric classes at each sampling station in the two study periods. (P1 = from November 1988 to October 1989 and P2 = from November 2008 to October 2009). A. class A (gravel, very coarse sand, coarse and medium); B. Class B (fine and very fine sand); C. class C (silt and clay); (PBA = predominance of B over A; PBC = predominance of B over C; PAC = predominance of A over C; PB = predominance of B; PCB = predominance of C over B)

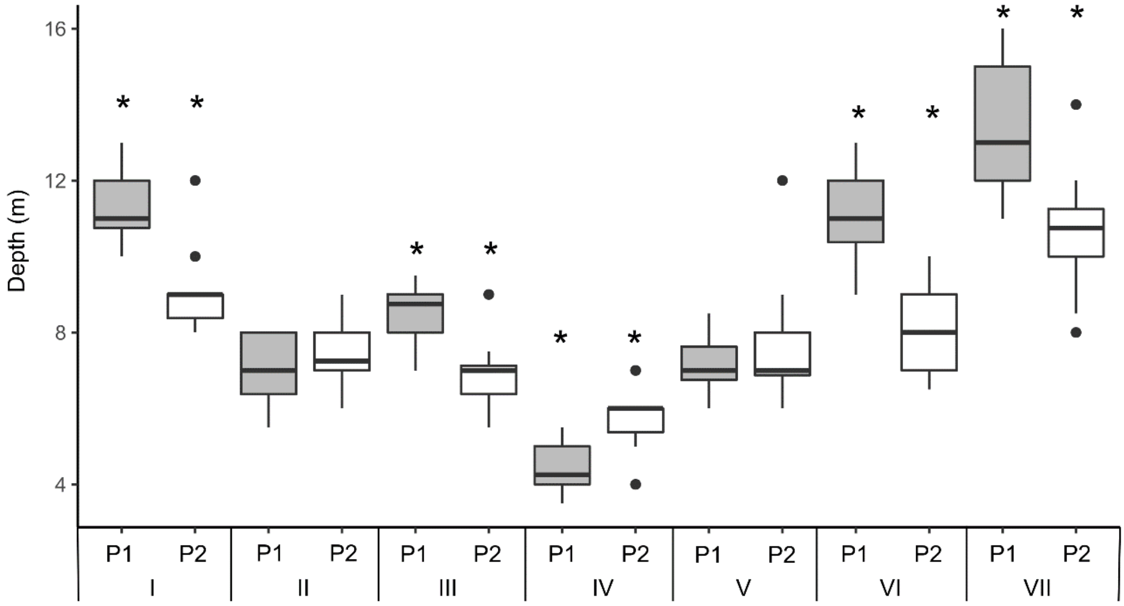

Figure 4. Boxplot of depth, recorded at the sampling stations in the two study periods (P1 = from November 1988 to October 1989 and P2 = from November 2008 to October 2009) (*Mann-Whitney test, $p < 0.05$)

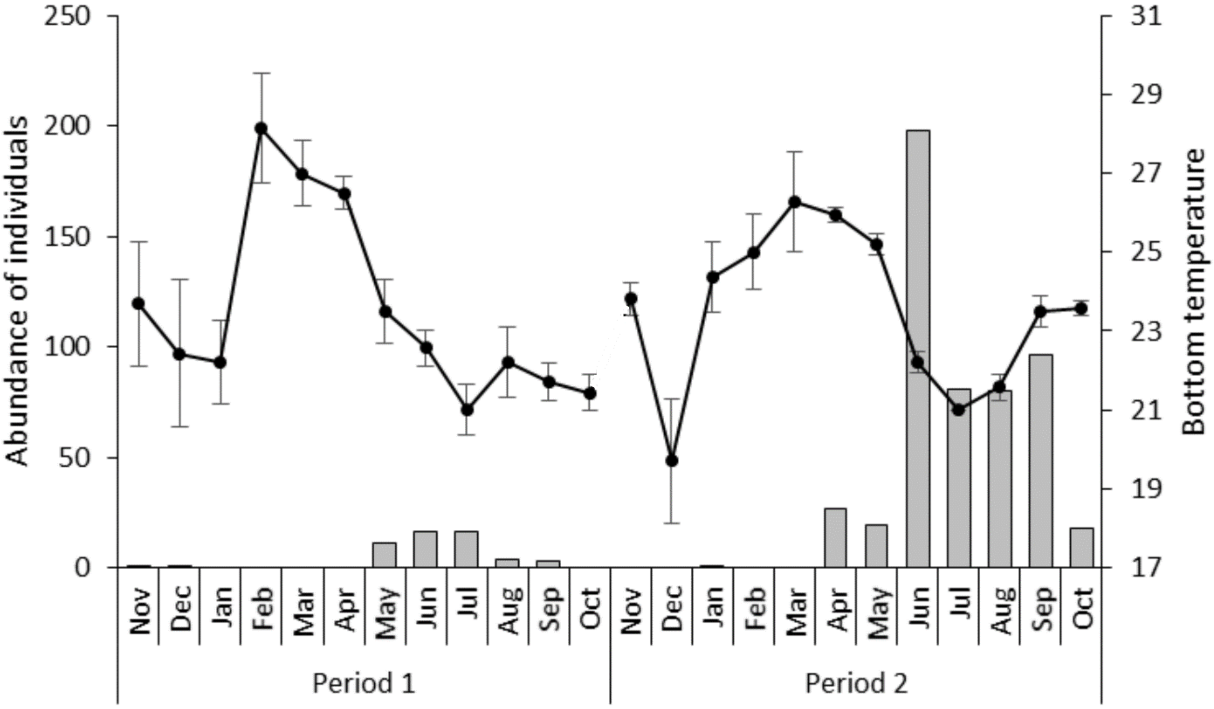

Figure 5. *Litopenaeus schmitti* (Burkenroad, 1936). Abundance of shrimps and rainfall in both sampling periods. (Period 1 = from November 1988 to October 1989 and Period 2 = from November 2008 to October 2009)

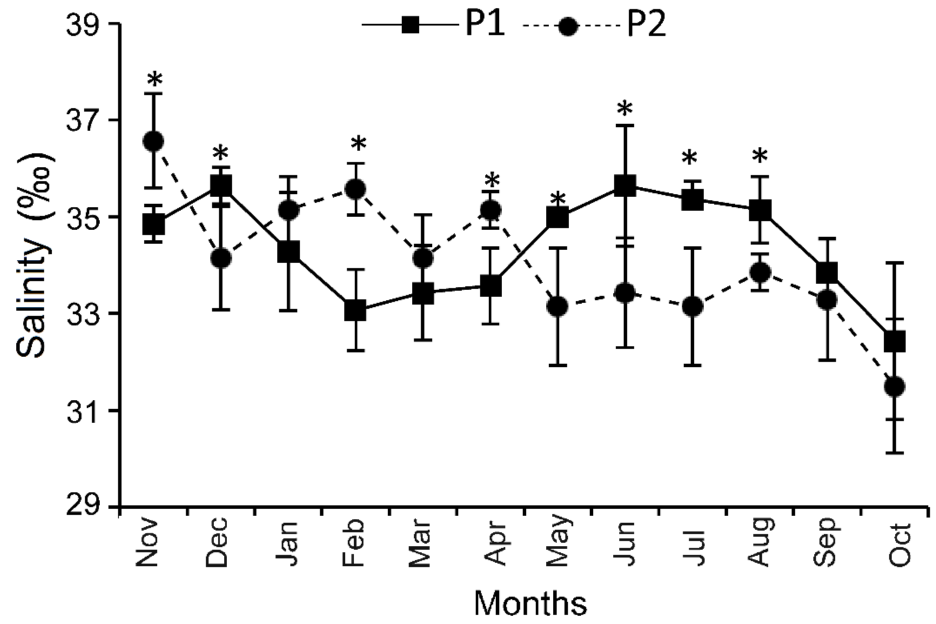

Figure 6. Mean and standard deviation of bottom salinity, recorded in the two study sampling periods per month (P1 = from November 1988 to October 1989 and P2 = from November 2008 to October 2009) (* Mann-Whitney test, $p < 0.05$)

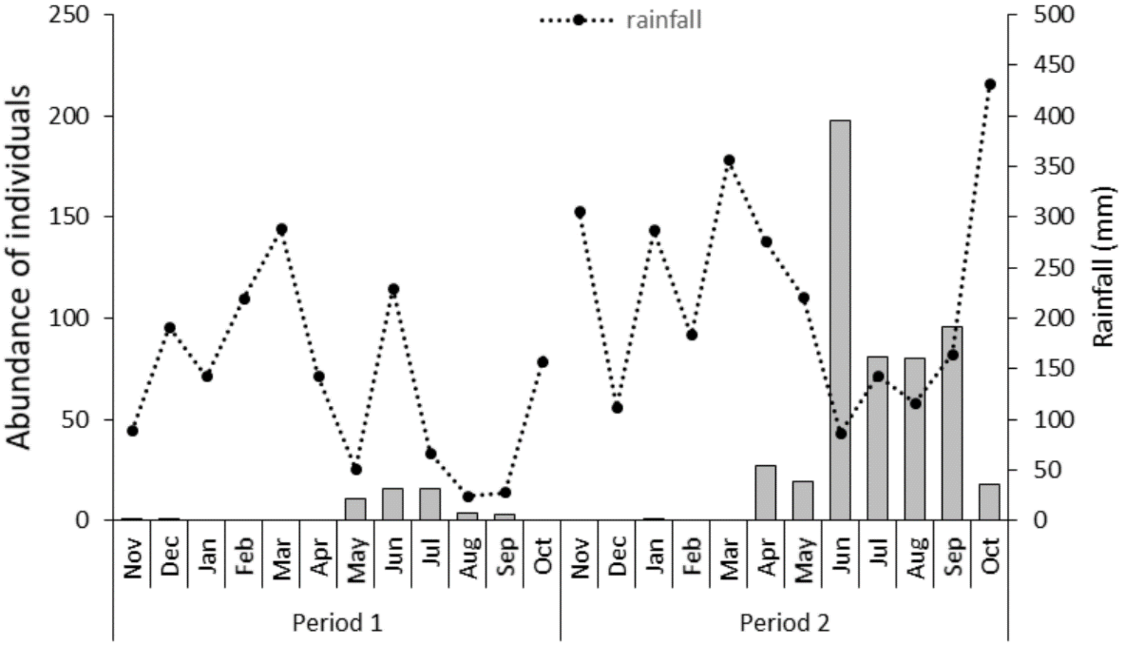

Figure 7. *Litopenaeus schmitti* (Burkenroad, 1936). Abundance of shrimps and rainfall in both sampling periods. (Period 1 = from November 1988 to October 1989 and Period 2 = from November 2008 to October 2009)

Table 1. Abundance of demographic groups, during the two sampling periods (P1 = from November 1988 to October 1989 and P2 = from November 2008 to October 2009) in the Fortaleza Bay. (N= Number of individuals).

Demographic groups	N		Max - Min		Mean ± SD	
	P1	P2	P1	P2	P1	P2
Juveniles	5	16	18.0-21.6	19.4-24.8	19.7±1.5	22.8±1.7
Males	23	290	26.7-38.2	24.0-39.7	33.0±2.8	30.3±2.7
Females	24	214	25.3-48.6	25.0-46.9	33.4±5.7	33.3±4.3
Total	52	520	18.0-48.6	19.4-46.9	31.9±5.9	31.3±4.0

Table 2. Grouping of grain size fractions (groups), percentage of silt and clay (% mud) and abundance of individuals at each sampling station, during the two sampling periods (First period = from November 1988 to October 1989 and Second period = from November 2008 to October 2009) in the Fortaleza Bay. (N= Number of individuals)

	Period 1				Period 2			
Sampling Stations	Groups	Phi	% Mud	*L. schmitti*	Groups	Phi	% Mud	*L. schmitti*
I	PBA	3.25 ± 1.41	23.44	12	PBC	4.75 ± 0.48	42.00	99
II	PAC	2.54 ± 1.24	19.22	6	PBC	4.28 ± 1.00	36.00	58
III	PB	3.97 ± 0.42	25.11	7	PBC	4.45 ± 0.50	34.00	61
IV	PB	3.54 ± 0.16	10.37	16	PCB	5.09 ± 0.35	55.00	99
V	PB	2.97 ± 0.18	12.32	4	PBC	4.37 ± 0.25	31.00	32
VI	PBC	3.97 ± 0.52	32.79	4	PCB	5.42 ± 0.56	64.00	85
VII	PBC	3.82 ± 0.37	24.23	3	PBC	4.90 ± 0.61	47.00	86

Table 3. *Litopenaeus schmitti* (Burkenroad, 1936). Result of the analysis of the Generalized Linear Model (GLM) with the environmental variables and abundance of individuals in Fortaleza Bay. * statistically significant values (p <0.05).

	estimate	standard error	z value	p value
Intercept	8.3018	1.4278	8.8140	<0.05*
Bottom temperature	-0.0652	0.0372	-1.7500	>0.05
Bottom salinity	-0.1995	0.0346	-5.7510	<0.05*
Phi	0.6273	0.0537	11.6720	<0.05*
Rainfall	-0.0054	0.0006	-8.8960	<0.05*

Discussion

After 20 years, some changes were observed in the Ubatuba region. The urban growth rise from 47000 (1988/1989) to 75000 (2008/2009) inhabitants (IBGE), consequently, causing the increase in the search for fishing resources (Instituto de Pesca de São Paulo). According to Muehe (2006) and Katsanevakis et al. (2011), urbanization, tourism and intense exploitation of natural resources are among the main anthropic causes of sedimentation in the marine environment. The hypothesis of this study was confirmed considering that, after 20 years, there was an increase in the abundance of *L. schmitti* at Fortaleza Bay.

It was possible to observe in the present study, a significant reduction in the depth of all sampling stations in the second period and an increase in the percentage of silt + clay sediment. It is known that benthic animals have their distribution closely related to substrate conditions (Fransozo et al., 2004; Pantaleão et al,. 2016). Shrimps of the genus *Farfantepenaeus* are more abundant in places with heterogeneous sediment, which is composed marjoritly by class A (Costa et al., 2016; Sousa et al., 2019). Shrimps of the species *Artemesia longinaris* Spence Bate, 1888 are more abundant in places with composite sediment with a higher percentage of fine and very fine sand (Class B) (Costa et al., 2005; Bernardo et al., 2018). On the other hand, species such as *Xiphopenaeus kroyeri* (Heller, 1982) and *L. schmitti* are more often found in places with a high percentage of silt + clay (class C), which were studied by Costa et al. (2007) and Bochini et al. (2014), respectively.

In view of these distribution patterns related to sediment, the increase in silt + clay in all sampled stations of the Fortaleza Bay seems to have interfered in a particular way in the abundance of each species. For *A. longinaris*, the increase in class C in the sediment may have been one of the causes of the reduction in abundance, after 20 years, at this same bay (Bernardo et al., 2018). In 1988/1989 the same authors sampled a total of 3088 specimens, which were reduced to 1252 in 2008/2009, with the increase in class C in the sediment. On the other hand, showing a behavior similar to *L. schmitti*, Almeida et al. (2012) noted an increase in the abundance of *X. kroyeri* in Fortaleza Bay, where 13298 individuals were registered in the first period and 44029 in the second.

Therefore, we suggest that the increase in sedimentation that occurred in Fortaleza Bay, in the interval of 20 years, may have contributed to the increase in the abundance of *L. schmitti*. This sedimentation may have been caused by anthropic factors, such as increased urbanization in the city of Ubatuba, in addition to the construction of a new bridge over the Escuro and Comprido rivers, close to the IV sampling station (Bernardo et al., 2018).

In addition, south of Fortaleza Bay, is the São Sebastião channel, which has a port with an average annual handling of 5,000 ships (PORTO SÃO SEBASTIÃO). Due to this intense activity, Furtado et al. (1998) and Barcelos & Furtado (2018), reported a process of sedimentation in the channel. To enable the passage of ships, there is the dredging of the same. During this process, a resuspension of a large amount of fine sediment occurs, which can be transported by currents to regions further north, as is the case of Fortaleza Bay.

Natural factors, such as movement of currents, may also have contributed to the deposition of fine sediment in Fortaleza Bay. According to Gyllencreutz et al. (2010) and Mahiques et al. (2010), the Brazil Current (BC), flows to the south, and the Brazilian Coastal Current (BCC) flows to the north, with the confluence of these two main current systems occurring near latitude 24 ° S and this influences sediment transport along the southeastern Brazilian platform. In addition, during intense El Niño-Oscilação Sul (ENOS) and La Niña-Oscilação do Sul (LNOS) events, the fine sediment particles deposited in the Rio da Prata are resuspended and carried along the southeastern coast of Brazil by the BCC. In the period of 20 years, we had El Niño-Oscilação Sul events in the years 1991-1993, 1992-1993, 2002-2003, 2006 and 2009 and La Niña-Oscilação do Sul events in 1988-1989, 1998-2000 and 2007-2008 (www.cptec.inpe.br).

The ENOS and LNOS events are currently considered the main sources of short-term climate variability in the world, leading to droughts and floods worldwide (Silva, 2001). In Brazil, ENOS is characterized mainly by being associated with intense rain in the south and southeast, and with droughts in the north and northeast (Silva, 2001). The pluviometric results prove this condition, because in the first period the phenomenon of LNOS occurred and there was a low rainfall volume (135 ± 85.82 mm); while in the second period there was ENOS and a high volume of rainfall (223 ± 107.92 mm). Several authors have related the abundance peaks of *L. schmitti* to the rains in the regions where the studies were carried out (Chagas-Soares et al., 1995; Santos et al .. 2008; Capparelli et al., 2011).

It is known that *L. schmitti* has a type II life cycle, that is, the post-larvae enter the estuaries and remain in that environment until they reach the juvenile or sub-adult phase, and then return to the ocean areas (Dall et al ., nineteen ninety). More intense rains make individuals return to inlets (Santos et al., 2008; Capparelli et al., 2011). The results obtained here also show this pattern, with peaks of abundance in months following the intense rains. In the first period, more shrimps were collected in the months of May to July, possibly due to the rains from January to April; while in the second, the intense rains occurred from June to September, probably due to the rains from January to May.

The spatial distribution of *L. schmitti*, in both periods, occurred in great abundance in station IV. This factor reinforces its condition of the type II life cycle, since in this place there are the mouth of two rivers, which are used by *L. schmitti* to complete its life cycle. This same pattern was observed by Simões et al. (2017) and Barioto et al. (2017) for *L. schmitti*. This result is also confirmed by the GLM result, with an inversely proportional correlation between the abundance of *L. schmitti* and the bottom salinity. In station IV, there is a low salinity and a high abundance of shrimp. Additionally, this station has a high percentage of silt + clay, which favors the greater abundance of *L. schmitti*, as previously reported by Costa et al. (2004, 2007) and Bochini et al. (2014). This type of sediment can facilitate the burial of these shrimp, since grains with a larger diameter are more difficult to be turned, so that the shrimp spends a greater amount of time and energy (Ameeri and Cruz, 1998). Furthermore, according to these authors, when the shrimp is buried, it uses less energy and is protected against its potential predators.

We conclude that, after 20 years, the sedimentation mainly composed of silt + clay that occurred in Fortaleza Bay, associated with the ENOS event, with greater rainfall in the second period may have contributed to the significant increase in the abundance of *L. schmitti*. The temporal distribution of *L. schmitti* seems to be modulated, mainly, by the rains; while, spatially, by the composition of the substrate associated with sites, which contribute to complete its life cycle. These results suggest that, although anthropic impacts have increased sedimentation in coastal areas and may be harmful to the ecosystem as a whole, they may favor certain species, as observed for *X. kroyeri* by Almeida et al. (2012) and in the present study for *L. schmitti*. We suggest that studies with more recent samples can be carried out aiming at a broader comparison, particularly, to verify the impacts of the implementation of the APA, in 2008.

However, the present investigation shows that, in addition to the possible changes caused by APA, external factors generate important changes in this bay and this fact must be taken into account in future studies.

References

Almeida AC, Baeza JA, Fransozo V, Castilho AL, Fransozo A (2012) Reproductive biology and recruitment of *Xiphopenaeus kroyeri* in a marine protected area in the western Atlantic: implications for resource management. Aquat Biol 17(1):57–69. https://doi.org/10.3354/ab00462

Ameeri A.A. and Cruz E.M. (1998) Effect of sand substrate on growth and survival of *Penaeus semisulcatus* de Haan juveniles. Journal of Aquaculture in the Tropics 13, 239–244.

Ávila-da-Silva, A. O., Carneiro, M. H., Mendonça, J. T., Bastos, G. C. C., Miranda, L. V., Ribeiro, W. D. R., & Santos, S. D. (2011). Produção pesqueira marinha e estuarina do Estado de São Paulo: dezembro de 2010. *Inf. Pesqueiro de São Paulo*, *5*, 1-4.

Barioto, J. G., Stanski, G., Grabowski, R. C., Costa, R. C., & Castilho, A. L. (2017). Ecological distribution of *Penaeus schmitti* (Dendrobranchiata: Penaeidae) juveniles and adults on the southern coast of São Paulo state, Brazil. *Marine Biology Research*, *13*(6), 693-703.

Barcellos, R. L., & Furtado, V. V. (2006). Organic matter contents and modern sedimentation at São Sebastião Channel, São Paulo State, south-eastern Brazil. *Journal of Coastal Research*, 1073-1077.

Bernardo, C. H., Sancinetti, G. S., Taddei, F. G., Hiroki, K. A. N., de Almeida, A. C., & Fransozo, A. (2018). Abundance and spatio-temporal distribution of two Southwest Atlantic endemic shrimps: changes after 20 years. *Biologia*, *73*(6), 589-598.

Bochini, G. L., Fransozo, A., Castilho, A. L., Hirose, G. L., & Costa, R. C. (2014). Temporal and spatial distribution of the commercial shrimp *Litopenaeus schmitti* (Dendrobranchiata: Penaeidae) in the south-eastern Brazilian coast. *Journal of the Marine Biological Association of the United Kingdom*, *94*(5), 1001-1008.

Branco, J. O. 2005. Biologia e Pesca do camarão Sete-Barbas *Xiphopenaeus kroyeri* (Heller) (Crustacea, Penaeidae), na armação do Itapocoroy, Penha Santa Catarina, Brasil. Revista

Brasileira de Zoologia, 22: 1050-1062.

Capparelli M.V., Kasten P., Castilho A.L. and Costa R.C. (2012) Ecological distribution of the shrimp *Litopenaeus schmitti* (Burkenroad, 1936) (Decapoda, Penaeoidea) in Ubatuba Bay, São Paulo, Brazil. Invertebrate Reproduction and Development 56, 173–179.

Castilho AL, Pie MR, Fransozo A, Pinheiro AP, Costa RC (2008) The relationship between environmental variation and species abundance in shrimp community (Crustacea: Decapoda: Penaeoidea) in south-eastern Brazil. J Mar Biol Assoc UK 88(01):119–123. https:// doi.org/10.1017/S0025315408000313

Castro-Filho BM, Miranda LB, Miyao SY (1987) Condições hidrográficas na plataforma continental ao largo de Ubatuba: Variações sazonais e em média escala. Boletim do Instituto Oceanografico 35(2):135–151

Chagas-Soares F., Pereira O.M. and Santos E.P. (1995) Contribuição ao ciclo biológico de *Penaeus schmitti* Burkenroad, 1936, *Penaeus brasiliensis,* Latreille, 1817 e *Penaeus paulensis* Perez-Farfante, 1967, na região lagunar-estuarina de Cananéia, São Paulo, Brasil. Boletim do Instituto de Pesca, São Paulo 22, 49–59.

Coleção Meio Ambiente. Série Estudos - Pesca 20. IBAMA, Brasília, 165p.

Costa RC, Fransozo A, Freire FA, Castilho AL (2007) Abundance and ecological distribution of the Sete-Barbas shrimp *Xiphopenaeus kroyeri* (Heller, 1862) (Decapoda, Penaeoidea) in three bays of the Ubatuba region, southeastern Brazil. Gulf Caribb Res 19(1):33–41. https://doi.org/10.18785/gcr.1901.04

Costa RC, Fransozo A,Melo GAS, Freire FAM(2003) An illustrated key for Dendrobranchiata shrimps from the northern coast of São Paulo, Brazil. Biota Neotropica 3:1–12. https://doi.org/10.1590/S1676-06032003000100011

Costa, R. C.; Fransozo, A. & Negreiros-Fransozo, M. L. 2005. Ecology of the rock shrimp *Sicyonia dorsalis* Kingsley, 1878 (Crustácea: Sicyoniidae) in a subtropical region of Brazil.

Gulf and Caribbean Research, Ocean Springs, 17(1): 49-56.

D’Incao, F. 1995. Taxonomia, Padrões distribucionais e ecológicos dos Dendrobranchiata (Crustacea: Decapoda) do litoral brasileiro. (Tese de Doutorado) – Curitiba, Universidade Federal do Paraná. 365f.

Dias Neto, J. & Dornelles, L. C. C. 1996. Diagnóstico da Pesca Marítima do Brasil. Edições IBAMA/MMA, 163p.

Fransozo A, Costa RC, Castilho AL, Mantelatto FL (2004) Ecological distribution of the shrimp Camarão Serrinha *Artemesia longinaris* (Decapoda, Penaeidea) in Fortaleza Bay, Ubatuba, Brazil, in relation to abiotic factors. Rev Invest Des Pesq 16:45–53

Furlan M, Castilho AL, Fernandes-Goes LC, Fransozo V, Bertini G, Costa RC (2013) Effect of environmental factors on the abundance of decapod crustaceans from soft bottoms off southeastern Brazil. An Acad Brasil Ciênc 85(4):1345–1356. https://doi.org/10.1590/0001-3765201394812

Furtado, V. V., Bonetti Filho, J., Rodrigues, M., & Barcellos, R. L. (1998). Aspectos da sedimentação no Canal de São Sebastião. *Relat. téc. inst. oceanogr.,(43)*, 15-31.

Gyllencreutz R, Mahiques MM, Alves DVP, Wainer IKC (2010) Mid- to late-Holocene paleoceanographic changes on the southeastern Brazilian shelf based on grain size records. The Holocene 20(6): 863–875. https://doi.org/10.1177/0959683610365936

Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2002) Modification of marine habitats by trawling activities: prognosis and solutions. Fish Fish 3:114–136. https://doi.org/10.1046/j.1467-2979.2002.00079.x

Katsanevakis S, Stelzenmüller V, South A, Sørensen TK, Jones PJS (2011) Ecosystem-based marine spatial management: review of concepts, policies, tools, and critical issues. Ocean Coast Manag 54: 807–820. https://doi.org/10.1016/j.ocecoaman.2011.09.002

Magliocca A, Kutner AS (1965) Sedimentos de fundo da Enseada do Flamengo, Ubatuba, SP.

Contrib Avulsas Inst Oceanogr 198:1–15

Mahiques MM(1995) Dinâmica sedimentar atual nas enseadas da região de Ubatuba, Estado de São Paulo. Boletim do Instituto Oceanografico 43(2):111–122

Mahiques MM, Sousa SHM, Furtado VV, Tessler MG, Toledo FAL (2010) The southern Brazilian shelf: general characteristics, quaternary evolution and sediment distribution. Braz J Oceanogr 58(special issue PGGM):25–34. https://doi.org/10.1590/S1679-87592010000600004

Mahiques MM, Tessler MG, Furtado VV (1998) Characterization of energy gradient in enclosed bays of Ubatuba region, south-eastern Brazil. Estuar Coast Shelf Sci 47:431–446. https://doi.org/10.1006/ecss.1998.0368

Muehe D (2006) Erosion in the Brazilian coastal zone: an overview. J Coast Res 39:43–48

Negreiros-Fransozo ML, Fransozo A, Pinheiro MA, Mantelatto FL, Santos S (1991) Caracterização física e química da Enseada da Fortaleza, Ubatuba, SP. Rev Bras Geoc 21(2):114–120

Neto, J. D. & DornelleS, L. D. C. 1996. Diagnóstico da Pesca Marítima do Brasil. Ibama, Coleção Meio Ambiente – Série Estudos da Pesca, Brasília

Neto, J. D. 1991. Pesca de camarões na costa norte do Brasil. Atlântica, 13: 21-28.

Odebrecht C, Castello JP (2001) The convergence ecosystem in the Southwest Atlantic. pp 147–166 *In*: Seeliger U, Kjerfve B (eds) Coastal marine ecosystems of Latin America, ecological studies. Springer, Berlin.

Pantaleão, J. A. F., Carvalho-Batista, A., Fransozo, A., & da Costa, R. C. (2016). The influence of upwelling on the diversity and distribution of marine shrimp (Penaeoidea and Caridea) in two tropical coastal areas of southeastern Brazil. Hydrobiologia, 763(1), 381-395.

Perez Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*. Fishery Bulletin, 67:

461- 591.

Pires AMS (1992) Structure and dynamics of benthic megafauna on the continental shelf offshore of Ubatuba, southeastern Brazil.Mar Ecol Prog Ser 86:63-76

Pires-Vanin AMS, Matsuura Y (1993) Estrutura e função do ecossistema de plataforma continental da região de Ubatuba, Estado de São Paulo: uma introdução. Bol Inst Oceanogr 10:1–8

Santos, J. L. D., Severino-Rodrigues, E., & Vaz-dos-Santos, A. M. (2008). Population structure of the white-shrimp *Litopenaeus schmitti* in the estuarine and marine regions of the Baixada Santista, São Paulo, Brazil. *Boletim do Instituto de Pesca*, *34*(3), 375-389.

Santos, J. L.; Severino-RodrigueS E. & Vaz-dos-Santos, A. M. 2008. Estrutura populacional do camarão-branco *Litopenaeus schmitti* nas regiões estuarina e marinha da Baixada Santista, São Paulo, Brasil. Boletim do Instituto de Pesca, São Paulo, 34(3): 375-389

Silva J.F. (2001) El Niño, O fenômeno climático do século. Brasilia: Thesaurus Editora, 135 pp.

Simões S.M., Costa R.C., Fransozo A. and Castilho A.L. (2010) Diel variation on the abundance and size of seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) (Crustacea, Penaeoidea) in Ubatuba region, Southeastern of Brazil. Anais da Academia Brasileira de Ciências 82, 369–378.

Simões, S. M., Heckler, G. S., & Costa, R. C. (2017). Reproductive period and recruitment of Penaeoidea shrimp on the southeastern Brazilian coast: implications for the closed season. *Crustaceana*, *90*(7-10), 1177-1192.

Valentini, H.; D'Incao, F.; Rodrigues, F. L.; Neto, J. E. R. & Rahn, E. 1991. Análise da pesca do camarão-rosa, *Penaeus brasiliensis* e *Penaeus paulensis*, nas regiões Sudeste e Sul do Brasil. Atlântica, Rio Grande, 13: 143-157.

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377–392.

CONSIDERAÇÕES FINAIS

CONSEIDERAÇÕES FINAIS

No primeiro capítulo pudemos observar a distribuição diferencial dos grupos demográficos do siri *A. spinimanus*, com os indivíduos jovens apresentando uma distribuição mais ampla em relação aos adultos de ambos os sexos. A maior abundancia de todos os grupos ocorreu nos 20 e 25 metros e se deve, principalmente, ao tipo de sedimento que é mais heterogêneo. Observamos também uma baixa abundância de todos os grupos demográficos durante o verão, sabe-se que sazonalmente há a chegada de uma massa de água chamada ACAS (Água Central do Atlântico Sul) na região durante esse período. Essa massa tem por característica possuir baixas temperatura e salinidade. Acredita-se que a chegada desta massa, faça com que o *A. spinimanus* migre sazonalmente para regiões mais protegidas da enseada.

No segundo capítulos observamos que o siri *A. spinimanus,* possui reporduçaõ contínua, com picos reprodutivos antes da chegada da ACAS. Sabe-se que muitas espécies se reproduzem com a chegada da ACAS. Como por exemplo. *A. cribrarius, Callinectes ornatus* (Ordway, 1863) e *C. danae*. *Arenaeus cribrarius* (Andrade et al. 2013, Costa e Negreiros-Fransozo 1998). O fato do *A. spinimanus* possuir picos antes disso, pode ser uma estratégia para evitar competição por alimentos das suas larvas. Além disso, observamos uma redução no tamanho da largura da carapaça de *A. spinimanus,* sendo possivelmente cauda pela intensa atividade de pesca de arrasto que existe na região.

No terceiro capítulo observaos uma alta sobreposição de nicho espacial entre as espécie *P. punctata* e *Persephona lichtensteinii*, e baixa sobreposição de ambas com *P. mediterranea.* Com isso, rejeitamos nossa hipotese de existencia de *Phylogenetic signal,* tendo em vista que *P. mediterranea* é grupo irmão de *P. punctata,* portanto, esperava-se maior sobreposição entre elas.

No último capítulo observamos que a sedimentação ocorrida na Enseada da Fortaleza, de fato favoreceu a abundância de *L. schmitti*, após 20 anos houve um aumento de 10 vezes. (1º período - 52 indivíduos; 2º período – 520 indivíduos). Além da sedimentação, o evento de ENOS com maior volume pluviométrico no segundo período podem ter contribuído para o aumento da abundância de *L. schmitti*.

A elaboração destes quatro capítulos, possibilitou o conhecimento mais amplo da região de Ubatuba em vários períodos distintos, pois esta tese abrangeu varios projetos realizados pelo NEBECC. Além disso, as espécies escolhidas possuiam características distintas por pertencer a diferentes grupos dentro da Classe Crustacea na Ordem Decapoda. Tal fato, permitiu agregar mais conhecimento e proporcionou uma tese mais abrangente.

REFERÊNCIAS

Andrade LS, Fransozo V, Bertini G, Negreiros-Fransozo ML, López- Greco LS (2013) Reproductive plasticity in the speckled crab Arenaeus cribrarius (Decapoda, Brachyura, Portunidae) associated with a population decline. J Coast Res 31(3):645–652. https://doi. org/10.2112/OASTRES-D-13-00066.1

Costa TM, Negreiros-Fransozo ML (1998) The reproductive cycle of Callinectes danae Smith, 1869 (Decapoda, Portunidae) in the Ubatuba region, Brazil. Crustaceana 71(6):615–627. https://doi. org/10.1163/156854098X00617

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