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**Composição e diversidade dos camarões marinhos
(Crustacea: Decapoda: Penaeoidea) e dinâmica
populacional de *Xiphopenaeus kroyeri* (Heller, 1862)
no litoral sudeste do Brasil**

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kroyeri* (Heller, 1862) no litoral sudeste do Brasil**

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“Tenho esperança de que um maior conhecimento do mar, que há milênios dá sabedoria ao homem, inspire mais uma vez os pensamentos e as ações daqueles que preservarão o equilíbrio da natureza e permitirão a conservação da própria vida.”

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Considerações iniciais

1. Considerações iniciais

A exploração de camarões constitui uma atividade de grande importância em todo o mundo, gerando elevados benefícios econômicos, especialmente para os países em desenvolvimento (Gillett, 2008). A captura média global de espécies marinhas representadas pelos crustáceos decápodos das infraordens Penaeidea e Caridea, aumentou consideravelmente durante as últimas seis décadas, com capturas variando de 580 480 toneladas na década de 1950, a 3 267 264 toneladas na década de 2000 (FAO, 2012). No Brasil, observou-se um crescimento gradual da captura média de camarões marinhos nos anos de 1950 a 1989, atingindo o pico máximo de produção na década de 1980 com, aproximadamente, 52 252 toneladas. Nas décadas de 1990 e 2000, um decréscimo de 26 e 9%, respectivamente, foi registrado, seguido de um acréscimo de 4% no ano de 2010, quando 38 374 toneladas de camarões foram obtidas (FAO, 2012).

Segundo D’Incao (1995), 61 espécies de camarões peneóideos foram registradas ao longo do litoral brasileiro. Entre estas espécies, os camarões-rosa *Farfantepenaeus brasiliensis* (Latreille, 1817), *F. paulensis* (Pérez Farfante, 1967), e *F. subtilis* (Pérez Farfante, 1967), o camarão-branco *Litopenaeus schimitti* (Burkenroad, 1936), e o camarão sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862), constituem os estoques mais rentáveis tanto para a pesca industrial quanto para a pesca artesanal de arrasto (Vasconcellos *et al.*, 2007, 2011; MPA, 2012). Em 2010 a captura destes camarões resultou em um total de 29 590 toneladas (MPA, 2012), o que correspondeu a 77% da captura de todas as espécies de camarões marinhos do litoral brasileiro (Penaeidea e Caridea) (FAO, 2012; MPA, 2012).

No litoral sudeste do Brasil, com exceção do camarão-rosa *F. subtilis*, todas as demais espécies são amplamente exploradas pela pesca de arrasto, seja ela artesanal ou comercial (Costa & Fransozo, 1999; D’Incao *et al.*, 2002; Costa *et al.*, 2007, 2008,

2011). No entanto, com o aumento da frota pesqueira e consequente redução dos desembarques destas espécies nos últimos anos, uma grande expansão na exploração de outros camarões peneóideos tem sido observada, como a exploração do camarão barbaruça *Artemesia longinaris* Bate, 1888 e do camarão-santana *Pleoticus muelleri* (Bate, 1888) (D’Incao *et al.*, 2002; Costa *et al.*, 2004, 2005; Fransozo *et al.*, 2004; Castilho *et al.*, 2007, 2012).

A pesca de arrasto constitui uma atividade extremamente prejudicial, causando sérios impactos diretos e indiretos, tanto para a estrutura dos ecossistemas costeiros e marinhos, quanto para a sociedade, que por sua vez é altamente dependente de inúmeros recursos oferecidos por estes ecossistemas. Segundo Kaiser *et al.* (2002), os impactos da pesca de arrasto sobre os ecossistemas incluem: mudanças nas relações presa-predador, levando a uma desestruturação na cadeia alimentar; variações nos padrões de abundância e distribuição das espécies; redução no tamanho corpóreo dos organismos, resultando em uma fauna dominada por indivíduos de pequeno tamanho; seleção genética em relação às diferentes variáveis ambientais e características reprodutivas (ex: maturidade sexual precoce); remoção de espécies não exploradas comercialmente (*bycatch*); redução da complexidade de habitats; ressuspensão de sedimentos superficiais e alteração da estrutura das comunidades bentônicas. Assim, em função da importância ecológica e econômica dos recursos pesqueiros, a compreensão dos impactos causados pela pesca de arrasto sobre a estrutura e função dos ecossistemas costeiros e marinhos torna-se essencial (Dayton *et al.*, 2002; Gillett, 2008). Contudo, além da extração constante e indiscriminada de tais recursos, a degradação do meio ambiente, acentuada principalmente pelo crescimento urbano e turismo, também pode estar exercendo forte influência, sobretudo devido à poluição e à perda de áreas costeiras e estuarinas, essenciais para que as espécies completem seu ciclo de vida.

Por outro lado, os rendimentos da pesca de arrasto também são fortemente influenciados por mudanças climáticas (Gillet, 2008). De acordo com Daw *et al.* (2009), tais mudanças climáticas também podem exercer vários impactos diretos e indiretos, com diversas implicações para a economia, assim como para as comunidades tradicionais de pescadores. A temperatura da superfície do mar (TSM) desempenha um papel fundamental na regulação do clima e da sua variabilidade (Deser *et al.*, 2010). Em geral, a variabilidade interanual do clima em todo o mundo tem sido investigada em conexão com os eventos El Niño Oscilação Sul (ENOS) (Trenberth, 1997). No Brasil, estes eventos estão geralmente associados às severas secas no nordeste, e enchentes no sul (Liu & Negrón Juárez, 2001; Hastenrath, 2006; Garcia *et al.*, 2004; Grimm, 2011). E, ao longo da plataforma sudeste do Brasil, os eventos ENOS, associados às condições locais oceanográficas, incrementam os padrões de produtividade primária, e consequentemente, aumentam as condições de sobrevivência larval das espécies presentes na região (Paes & Moraes, 2007).

Frente às diversas consequências do uso irracional dos recursos pesqueiros marinhos, associado à degradação do meio ambiente, e o quanto isso implica no funcionamento das comunidades como um todo, várias medidas têm sido implantadas a fim de contribuir para uma melhor gestão destes recursos a níveis sustentáveis de exploração (Palumbi, 2001; Amaral & Jablonski, 2005; Prates, 2007; McCay & Jones, 2011; Rice & Houston, 2011), assim como para a manutenção da capacidade de suporte dos ecossistemas marinhos para aquelas espécies extensivamente exploradas (Vasconcellos & Gasalla, 2001) e, consequente manutenção da biodiversidade (Palumbi, 2001; Amaral & Jablonski, 2005). Entre estas medidas, destacam-se a limitação do esforço de pesca via licenciamento e limitação da frota, caracterização e regulamentação dos aparelhos utilizados (equipamentos de pesca e suas restrições de

uso), criação de áreas de proteção ambiental, determinação de um tamanho mínimo para a captura das espécies-alvo, proibição da pesca (períodos de defeso), entre outras (Perez *et al.*, 2001; Amaral & Jablonski, 2005; Devaraj, 2010).

O camarão sete-barbas *X. kroyeri* distribui-se amplamente no Atlântico Ocidental, da Carolina do Norte (Estados Unidos) até Santa Catarina (Brasil), embora haja registros de sua ocorrência em Virgínia (Estados Unidos) e Rio Grande do Sul (Brasil) (Holthuis, 1980; D’Incao *et al.* 2002). Esta espécie apresenta um tamanho corpóreo relativamente grande, podendo atingir 100 mm de comprimento total, além de ser muito abundante em profundidades inferiores a 30 m (Holthuis, 1980; Branco, 2005; Costa *et al.* 2007), tornando-se objeto de uma atividade pesqueira de relevante valor comercial, desenvolvida principalmente nas regiões sudeste e sul do Brasil (D’Incao *et al.*, 2002; Costa *et al.*, 2007, 2011). Segundo Castro *et al.* (2005) e Costa *et al.* (2007, 2011), os indivíduos jovens de *X. kroyeri* não são dependentes dos pequenos estuários presentes ao longo do litoral norte do Estado de São Paulo, completando seu ciclo de vida em águas costeiras rasas. Assim, a espécie apresenta o ciclo de vida III e não II, como proposto por Dall *et al.* (1990). No ciclo de vida III, as espécies são totalmente restritas ao ambiente marinho, com migrações ocorrendo de regiões costeiras rasas para regiões mais distantes e profundas, onde a reprodução ocorre. Apesar das medidas de manejo tomadas para a manutenção e sustentabilidade dos estoques de *X. kroyeri* no litoral norte paulista, e das demais espécies mencionadas anteriormente, como o controle do número e tamanho das embarcações e malhas de rede, criação de áreas protegidas e fechamento temporário da pesca, os indivíduos jovens e adultos *X. kroyeri* continuam sendo extensivamente explorados pela pesca artesanal de arrasto, principalmente em função do tipo de ciclo de vida apresentado pela espécie. Consequentemente, devido à elevada captura de indivíduos de todas ou quase todas as

classes de tamanho e/ou idade pela pesca de arrasto exercida na região, os estoques de *X. kroyeri* encontram-se em um estado de sobre-exploração ou em ameaça de sobre-exploração (Instrução Normativa Nº 5, 21 de maio de 2004) (Vasconcellos *et al.*, 2007, 2011).

Deste modo, apesar dos inúmeros estudos desenvolvidos desde 1988 pelos pesquisadores do Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos (NEBECC) no litoral norte do Estado de São Paulo, enfocando principalmente a biologia e ecologia dos crustáceos decápodos, este é o primeiro estudo comparativo desenvolvido. O presente estudo foi conduzido na Enseada da Fortaleza, região de Ubatuba, situada uma recente Área de Proteção Ambiental (APA), durante dois períodos distintos; de novembro/1988 a outubro/1989, e de novembro/2008 a outubro/2009, o qual visou à obtenção de importantes informações sobre as mudanças na estrutura da comunidade dos camarões peneóideos em um intervalo de 20 anos, a fim de fornecer subsídios para a avaliação das variações espaço-temporais dos padrões de abundância e distribuição das espécies frente às mudanças de algumas variáveis ambientais, como temperatura e salinidade da água, granulometria e conteúdo orgânico do sedimento, assim como das medidas de gestão e manejo já adotadas, e para o estabelecimento de ações futuras, visando à utilização racional e consequente conservação da biodiversidade local e dos recursos pesqueiros. A presente tese foi constituída por quatro capítulos. No primeiro capítulo, a composição e diversidade dos camarões pertencentes à infraordem Penaeidea foram analisados. Os demais capítulos abordaram importantes tópicos relacionados à dinâmica populacional do camarão setebardas *X. kroyeri*, incluindo aspectos como variações espaço-temporais da abundância da espécie, estrutura populacional, dimorfismo sexual, razão sexual, reprodução e recrutamento juvenil.

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Capítulo I

Composition and diversity of the Penaeidea

community (Crustacea: Decapoda:

Dendrobranchiata) on the southeastern

coast of Brazil: did it change after 20 years?

Abstract

The structure of the Penaeidea community at Fortaleza Bay was analyzed over a range of 20 years. The abundance, species richness (S), indexes of dominance (D), diversity (H'), and evenness (J') were determined at spatial and temporal scales during two distinct study periods, from November 1988 to October 1989, and from November 2008 to October 2009, in seven permanent transects established within Fortaleza Bay. Also, correlations between the abundance of the penaeid shrimp species and the environmental variables, as bottom temperature and salinity, texture and organic matter content of the sediment, were assessed. The Penaeidea community was composed by one superfamily, three families, seven genera and ten species, including those target species (*Artemesia longinaris*, *Farfantepenaeus brasiliensis*, *F. paulensis*, *Litopenaeus schmitti*, *Xiphopenaeus kroyeri* and *Pleoticus muelleri*) and non-target species (*Rimapenaeus constrictus*, *Sicyonia dorsalis*, *S. laevigata* and *S. typica*). The species richness was maintained over a range of 20 years, but the number of individuals increased substantially during the second study period, mainly concerning the species *F. brasiliensis*, *L. schmitti*, *R. constrictus*, *X. kroyeri*, and *S. dorsalis*. The opposite was observed for *A. longinaris*, *F. paulensis*, and *P. muelleri*, in which the abundance decreased up 42%, 10% and 35%, respectively. Overall, *X. kroyeri* was the dominant species. Such dominance influenced considerably the diversity and evenness values, that increased when the lowest dominance values were recorded, as observed in transects I (period 1), II (period 1), V (period 2), VI (period 1), and VII (periods 1 and 2), and during months from November 1988 to January 1989, and July 1989, January 2009, March 2009, and from June 2009 to August 2009. Changes in the Penaeidea community at Fortaleza Bay could be also related to variations in the environmental variables analyzed. A remarkable sedimentation was observed between the first and the

second study periods, which might have been caused by natural phenomena and/or human activities. While the variations in the bottom temperature and salinity were related mainly to the hydrodynamics of water masses present in the Ubatuba region. The spatial and temporal patterns of penaeid shrimp abundance at Fortaleza Bay are in agreement with previous studies carried out in the study region, regarding their strong relationship with temperature, salinity and sediment characteristics. Along with the environmental variables, the management measures created and implemented along the southeastern coast of Brazil, e.g. fishing effort control and creation of Marine Protected Area, were essential in maintaining the Penaeidea community at Fortaleza Bay over a range of 20 years.

Keywords: Abundance; ecological indexes; environmental variables; Marine Protected Area; spatio-temporal variations

1. Introduction

Brazil has one of the highest marine biodiversity in the world (Couto et al., 2003), being primarily influenced by the physical and geological history of this ecosystem (Miloslavich et al., 2011). In general, tropical and subtropical characteristics dominate the entire Brazilian coastline, although regional phenomena define climatic and oceanographic conditions, leaving distinct impressions on the biodiversity (Amaral and Jablonski, 2005). Such biodiversity broadly promotes the provision of marine ecosystem functions, including those critical to human survival and well-being (Palumbi et al., 2009).

The greatest threats to marine and coastal biodiversity are the degradation and modification of habitats, depletion of resources as overexploitation for consumption and/or ornamentation, introduction of exotic species, and others (Amaral and Jablonski, 2005; Costello et al., 2010; Katsanevakis et al., 2011; Miloslavich et al., 2011; Rice and Garcia, 2011), which result in the biodiversity reduction at levels of ecosystems, genes and species (Katsanevakis et al., 2011). However, the habitat loss as a result of several factors, like coastal urbanization and fishery bottom trawling (Costello et al., 2010), is most serious, especially in coastal areas with a wide diversity of species and most vulnerable to human action (Amaral and Jablonski, 2005). The social, economic and urban growth encourage investments in infrastructure, transport, and industries but, instead of the fragility of the coastal ecosystem, new human activities are always under development, leading to changes in quality of such ecosystem (Pereira and Ebecken, 2009). Thus, a consistent management to sustain natural biodiversity – via conservation of species richness, genetic diversity, species composition, and habitat diversity – can assist to maintain the integrity and stability of this ecosystem (Palumbi et al., 2009).

Along with exploitation, habitat alteration and also pollution, climate change is reducing the abundance of several marine species, increasing the likelihood of local, and in some cases global, extinction (Harley et al., 2006). Costello et al. (2010) stated that climate change encompasses a range of environmental threats, as temperature change, sea-level rise, upwelling, and others, resulting in biodiversity variations. Conversely, how it will change in the future is difficult to predict because of the complexity of biodiversity, from genes to species to ecosystems (Costello et al., 2010). As climate change influences the structure and functioning of marine ecosystem and the use of coastal areas, a robust approach of future spatial planning that also takes cross-boundary development is extremely necessary (Katsanevakis et al., 2011).

Information on habitat types, as well as abundance and distribution patterns of the species and the factors that influence them, are considered methods for assessment of the condition and trends of biodiversity (UNEP, 2006). In addition, soft-sediment benthic communities are considered as potential ecological indicators to measure natural and/or anthropogenic disturbances, reflecting the stability of these communities with respect to their species richness and diversity (Lui et al., 2007). According to Dayton et al., (2002), marine fishing practices have both temporary and long-term effects on habitat, which can lead to impacts on species diversity, population size, and the ability of a population to replenish itself.

In the Ubatuba region, southeastern coast of Brazil, various studies have been carried out on species composition and diversity of decapod crustaceans inhabiting soft-bottom, as crabs (Mantelatto and Fransozo, 2000; Bertini and Fransozo, 2004; Braga et al., 2005; Bertini et al., 2004, 2010), hermit crabs (Fransozo et al., 2008, 2011), and shrimps (Nakagaki et al., 1995; Costa et al., 2000; Fransozo et al., 2002; Mortari and Negreiros-Fransozo, 2007), which have provided a basis for understanding of the

processes affecting the equilibrium of these communities, as well as the ecosystems (Bertini et al., 2004). This region has been severely impacted by many anthropogenic activities, as urbanization, tourism, and trawl fisheries targeting shrimp species as *Farfantepenaeus brasiliensis* (Latreille, 1817), *F. paulensis* (Pérez Farfante, 1967), *Litopenaeus schimitti* (Burkenroad, 1936), and *Xiphopenaeus kroyeri* (Heller, 1862). Possibly, such anthropogenic activities, associated with natural changes, are inducing degradation and loss of this coastal ecosystem, resulting in disturbance in the composition, distribution and abundance patterns of marine communities along the southeastern Brazilian coast. According to Sousa (1984), disturbance is both a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities and an agent of natural selection in the evolution of life histories of the organisms. Thus, the Ubatuba region offers a good opportunity for studying changes in this ecosystem, associated with anthropogenic activities and environmental conditions, with implications for the maintenance of diversity and stability at population, community, and ecosystem level.

The objective of the present study was to identify the spatial and temporal variations in the composition and diversity of the Penaeidea community over a range of 20 years. The investigation was conducted at Fortaleza Bay, located in a recent Marine Protected Area (MPA) on the northern coast of São Paulo State, during two study periods, from November 1988 to October 1989, and from November 2008 to October 2009. Also, the abundance and distribution patterns of the penaeid shrimp species were assessed in relation to changes in the environmental variables, as bottom temperature and salinity, texture and organic matter content of the sediment. This is the first comparative study conducted in the Ubatuba region, aiming information on changes in the Penaeidea community structure in such long interval period.

2. Material and Methods

2.1. Study site

Fortaleza Bay (23°29'30"S to 45°10'30"W) is located in the recently established MPA on the northern coast of São Paulo State (Área de Proteção Ambiental Marinha do Litoral Norte – Setor Cunhambebe; Proclamation No. 53 525, October 08, 2008) (Figure 1). The region is characterized by innumerable spurs of the Serra do Mar that form an extremely indented coastline (Ab'Saber, 1955). Exchange of water and sediment between the coastal area and the adjacent shelf is very limited (Mahiques, 1995). Thus, the sediment is composed mainly of fine and very fine sand and silt and clay given the low water movement (Mahiques et al., 1998). The northern coast of São Paulo State is affected by three water masses: 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; Nitrogen:Phosphorus – 16:1) (Castro-Filho et al., 1987; Odebrecht and Castello, 2001). During summer, the SACW penetrates into the bottom layer of the coastal area and forms a thermocline over the inner shelf located at depths of 10 to 15 m. During winter, the SACW retreats to the shelf break and is replaced by the CW. As a result, no stratification is present over the inner shelf during winter months (Pires, 1992; Pires-Vanin and Matsuura, 1993). Within Fortaleza Bay, 12 sandy beaches are flanked by rocky shores and, there is no considerable depth variation, depths range from 1 to 12 m. Two rivers, Escuro and Comprido, originating from the Atlantic coastal forest (Mata Atlântica), flow into the bay and support an important mangrove ecosystem.

2.2. Data collection

The present study comprised two distinct sampling periods: period 1, from November 1988 to October 1989; and period 2, from November 2008 to October 2009. The same methodology was employed in both study periods.

Shrimp samples were collected monthly during periods 1 and 2, using a fishing boat equipped with double-rig nets (7.5 m long; 2.0 m horizontal mouth opening; 15 mm and 10 mm mesh diameter at the body and cod end of the net, respectively). A total of 7 permanent transects were established within Fortaleza Bay (Figure 1). One haul per transect and month was made throughout the sampling periods. Each transect was trawled for 1 km (each haul lasted ~ 20 min) covering a total area of 4 km² transect⁻¹.

During trawling, bottom water samples were taken with a Nansen bottle in each of the different transects. Water temperature (°C) and salinity were measured with a mercury thermometer (accuracy = 0.5°C) and an optical refractometer (precision = 0.5), respectively. Depth (m) was recorded by a delimited cable connected in the Nansen bottle.

Sediment samples were obtained during each month at each transect with a Van Veen grab (0.025 m²) to analyze the grain size composition and organic matter content of the sediment. 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 followed 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 $\phi \geq 4$ (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). 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.

Shrimps collected during each sampling period were transported in cool box to the laboratory where they were identified to species level according to Pérez Farfante and Kensley (1997) and Costa et al. (2003).

2.3. Data analysis

A Principal Components Analysis (PCA) was conducted in the PAST software (version 2.15) (Hammer et al., 2001) using the environmental variables (depth, bottom temperature and salinity, texture and organic matter content of sediment) sampled during each period. The purpose of this analysis was to identify the maximum variance among the data set in relation to the transects and months. The environmental variables

were standardized by calculating *z-scores* (Lepš and Šmilauer, 2003). The principal components in which the total percentage (cumulative) of the data set variance accounted for 80% were selected. Within each selected principal component, the most relevant environmental variables were chosen by excluding those values whose loadings (eigenvectors) were intermediate of -1 and 1 and less than 0.7 (Jolliffe, 2002).

In order to investigate spatial and temporal changes in the Penaeidea community over a range of 20 years, the abundance, species richness (*S*), indexes of dominance (*D*) (Berger and Parker, 1970), diversity (*H'*) (Shannon, 1948), and evenness (*J'*) (Pielou, 1966) were analyzed by transects and months during each study period. Cluster analyses using Bray-Curtis index (Bray and Curtis, 1957) were performed to explore the similarity of species present in the Penaeidea community at Fortaleza Bay, and the similarities in the abundance data of penaeid shrimps among transects and months. Next, based on such Bray-Curtis similarity matrices of the transects and months, non-metric multidimensional scaling (MDS) analyses were performed between both study periods. MDS ordination plots are adequately represented by high dimensional data set with stress values < 0.1 (Clarke, 1993). The *D*, *H'* and *J'* indexes were computed using the BioDiversity Pro software (version 2.0) (McAleece et al., 1997), and the similarity analyses and MDS plots were performed in the PAST software (version 2.15) (Hammer et al., 2001).

Correlations between the environmental variables (bottom temperature and salinity, organic matter content of the sediment, and phi) and the species encountered at least 10% of the 84 hauls (seven hauls per month) made during each study period at Fortaleza Bay, were assessed using Multiple Regression (MR; $\alpha = 0.05$) in the software Statistica (version 8.0).

3. Results

3.1. Environmental variables

In general, most environmental variables showed maximum variance during study periods 1 and 2. The first three principal components of the PCA accounted up to 80% of the variability in the data set by transects (89%) and months (82%) (Table I). Spatially, the depth, bottom temperature and salinity, granulometric class A, and organic matter content were the most relevant environmental variables in the first principal component, and the granulometric class C in the second principal component (Table I, Figure 2a). Temporally, the granulometric classes A, B and C, bottom salinity and organic matter content, were the most relevant environmental variables in the first and second principal components (Table I, Figure 2b).

The average ($\pm$ standard deviation [SD]) depth at Fortaleza Bay over the entire study periods 1 and 2 was 8.9 ± 3.0 m, ranging from 3.5 to 16.0 m, and 7.9 ± 1.9 m, ranging from 4.0 to 14.0 m, respectively. In the period 1, there was a greater depth variation among sampled transects compared to the period 2, that was nearly homogeneous (Figure 3a). During both study periods, transects IV and VII were characterized by the lowest and highest average values of depth (Figure 3a).

The bottom temperature ranged from 20.0 to 29.5°C in the period 1, and from 18.0 to 27.5°C in the period 2. The average bottom temperature was similar between both study periods, 23.5°C, while the SD was slightly different, 2.5°C (period 1) and 2.1°C (period 2). The transects I and VII, located closely to the mouth of the Fortaleza Bay, showed the lowest average bottom temperature during both study periods (Figure 3b). Concerning the variation of it by month, there was a decrease from November 1988 to January 1989, an abrupt increase in February 1989, followed by a constant decrease up to July 1989 (Figure 4a). In the months from January 2009 to March 2009, the

bottom temperature increased in the bay followed by a decrease during the following months up to July 2009 (Figure 4a). In December 2008, it was recorded the lowest average bottom temperature ($19.7 \pm 1.6^{\circ}\text{C}$) obtained during over the study periods 1 and 2.

Average values of bottom salinity did not vary much among transects and months during both study periods (Figures 3c and 4b). Overall, it ranged from 30 to 38, and from 29 to 38, with an average of 34.4 ± 1.3 and 34.1 ± 1.6 recorded during study periods 1 and 2, respectively. The lowest average value of bottom salinity was obtained in transect IV (Figure 3c) due to the proximity of the mangrove ecosystem present at Fortaleza Bay (see Figure 1). The months from February 1989 to April 1989, October 1989, from May 2009 to July 2009, September 2009 and October 2009, showed the lowest average bottom salinity values (Figure 4b).

In general, the sediment at Fortaleza Bay was characterized as fine and very fine sand and silt and clay during both study periods; grains with a diameter smaller than 0.25 mm dominated the sediment samples ($> 90\%$) (Figures 3d and 4c). There was a drastic reduction in the sediment fraction corresponding to Class A in transects I, II, V, VI and VII during period 2 compared to the period 1 (Figure 3d). Such reduction was also observed among the months (Figure 4c). Consequently, there was an increase in the sediment fractions corresponding to Class B and C for both transects and months (Figures 3d and 4c). The average phi values obtained during periods 1 and 2 corresponded to 3.4 ± 0.9 and 4.8 ± 0.7 , ranging from 1.0 to 5.2 and from 2.0 to 6.3. As expected, the phi values increased during period 2 compared to the period 1 (Figures 3e and 4d). According to the phi scale, fine sand, very fine sand and silt and clay were the most frequent granulometric fractions in the sediment sampled by transects and months throughout periods 1 and 2 (Figures 3e and 4d). The average organic matter

content varied substantially among transects and months during both study periods (Figures 3e and 4d). The highest average value of organic matter content was obtained in transects II (period 1) and VI (period 2) (Figure 3e), and in September 1989, October 1989, April 2009 and June 2009 (Figure 4d).

3.2. *Penaeidea* community

In the present investigation, the *Penaeidea* community at Fortaleza Bay was represented by one superfamily, three families, seven genera and ten species (Table II). The Family Penaeidae was the most representative, contributing to six species of the total identified species (Table II).

Over a range of 20 years, there was a remarkable variation in the number of individuals of nearly all species recorded at Fortaleza Bay. From 168 hauls (84 hauls per period) performed, a total of 58 940 individuals were obtained; being that 16 829 and 42 111 individuals were collected during study periods 1 and 2, respectively. *Xiphopenaeus kroyeri* was the most abundant species and contributed to 79% (period 1) and 94% (period 2) of total shrimps sampled (Tables III, IV). Whereas *S. laevigata* had the lowest abundance; only one specimen was sampled during period 1 (Tables III, IV). The abundance of *F. brasiliensis*, *L. schmitti*, *R. constrictus*, *X. kroyeri*, *S. dorsalis*, and *S. typica* increased substantially in the study period 2, compared to the study period 1 (Tables III, IV). The opposite was observed for *A. longinaris*, *F. paulensis*, and *P. muelleri*, in which the abundance decreased up 42%, 10% and 35%, respectively (Tables III, IV).

Litopenaeus schmitti and *X. kroyeri* were caught in all transects during both study periods (Table III). The highest abundance of *A. longinaris* were recorded in transects I and VII (Table III). This last transect was also characterized by the highest

abundance of *S. dorsalis* and *P. muelleri* (Table III). During period 1, the species *F. brasiliensis* and *F. paulensis* were most abundant in transect II. During period 2, the highest abundance of *F. brasiliensis* was also recorded in transect II, while the most individuals of *F. paulensis* was caught at transect V (Table III). The transect II was also characterized by the highest abundance of *R. constrictus* and *S. typica* during period 2 (Table III).

Throughout study periods 1 and 2, the species *A. longinaris*, *S. dorsalis*, *S. typica* and *P. muelleri* were obtained during spring and summer months (summer: January–March; autumn: April–June; winter: July–September; spring: October–December), usually in December and January, whereas *L. schmitti* was most abundant from June to September, months of which correspond to fall and winter (Table IV). The species *F. brasiliensis* and *F. paulensis* were obtained generally among months corresponding to summer and fall during both study periods, mainly from March to June (Table IV). High number of individuals of *R. constrictus* was obtained only in November 1988 (spring), but from May 2009 to July 2009 (fall and winter) it was recorded the highest abundance of the species (Table IV). Finally, *X. kroyeri* was most abundant in April (fall) and from July to August (winter) during study period 1, while during study period 2, it was recorded the highest number of individuals in January and February (summer), and from April to June (winter) (Table IV).

The species richness (S) and the indexes of dominance (D), diversity (H') and evenness (J') obtained throughout study periods are represented in the figures 5 and 6. During both study periods the lowest S was recorded at transect IV (periods 1 and 2; $S = 3$) (Figure 5), and in the months of February 1989 ($S = 3$), April 2009 and September 2009 ($S = 4$) (Figure 6). The D index changed considerably over transects and months during study period 1, ranging from 0.65 to 0.97 spatially and from 0.57 to 1.00

temporally, whereas in the study period 2 it was practically homogeneous ($D \geq 0.83$) (Figures 5 and 6). Index variations of H' and J' followed a similar pattern among transects and months during both study periods (Figures 5 and 6). The highest values of H' and J' were recorded in transects II (period 1; $H' = 1.43$, $J' = 0.45$) and V (period 2; $H' = 1.00$, $J' = 0.32$) (Figure 5), and in January during both study periods (period 1; $H' = 1.14$, $J' = 0.49$; period 2; $H' = 0.72$, $J' = 0.24$) (Figure 6).

The abundance data of all species obtained at Fortaleza Bay showed 51% similarity (Bray-Curtis similarity analysis) between the study periods 1 and 2. During each study period, the Bray-Curtis similarity matrix allowed the classification of two main groups (A and B), which showed the lowest similarity values among the species. In the study period 1, the group A was formed only by the species *S. laevigata*, and the group B included the species *A. longinarius* and *X. kroyeri* (Figure 7a). In the study period 2, *X. kroyeri* and *A. longinarius* formed the groups A and B, respectively (Figure 7b). Other two groups including the species *F. brasiliensis* and *F. paulensis* (period 1) and *F. brasiliensis* and *R. constrictus* (period 2) were identified and showed 77% and 72% similarity, respectively (Figure 7a,b). Considering the abundance data of the Penaeidea community by transect, the Bray-Curtis similarity matrix evidenced that the transects II and V (group A) sampled during study period 1, and the transect V (group A) sampled during study period 2, had the lowest similarity values compared to the remaining transects (Figure 8a,b). Whereas the transects I and VI (period 1) and III and VI (period 2) showed the highest similarity values; with 86% and 97% similarity, respectively (Figure 8a,b). Monthly, two main groups were also formed during study periods 1 and 2, which comprehended the months from December 1988 to February 1989 and August 1989 (group A), and the months from January 2009 to February 2009

and May 2009 (group A), in relation to all other months sampled during study periods 1 and 2 (Figure 9a,b).

The MDS ordination plots performed between both study periods by transect and month are represented in the figure 10. Such MDS ordination plots based on Bray-Curtis similarity matrices using the abundance data of all species identified showed acceptable stress values (< 0.2). There were some clear groupings plotted by transects and months according to their similarity, with those closest together being generally more similar to one another than those that are farther apart, as observed for transects II and V (period 1), which showed the lowest abundance data, compared to transect IV (period 2) and to transects I, III and VI (period 2), that presented the highest abundance data obtained at Fortaleza Bay (Figure 10a). Also, the abundance data of the Penaeidea community were similar considering the months of December 2008, July 2009 and October 2009, even as the months of March 1989, May 1989, September 1989, October 1989 and August 2009, in which these groups presented the highest and lowest abundance data, respectively (Figure 10b). Despite the similar abundance data obtained during the months of January 1989 and April 1989 (about 1500 individuals obtained in each month), they were dissimilar since the abundance data of the species *A. longinarius* and *X. kroyeri* varied considerably between these months.

The MR used to test for correlations between environmental variables and species abundance explained different associations throughout the study periods 1 and 2 (MR, $p < 0.05$; Table V). Only the species *S. laevigata* and *S. typica* were excluded from the analysis because they were sampled less than 10% of the 168 hauls (84 hauls per study period) made in this investigation. Positive correlations were observed between the abundance of *A. longinarius*, bottom salinity and phi during study periods 1 and 2, respectively (MR, $p < 0.05$; Table V). For *F. brasiliensis* and *F. paulensis*

sediments characterized by thicker grains were most relevant for their occurrence during both study periods, as well as observed for *R. constrictus*, but only during study period 2 (MR, $p < 0.05$; Table V). The opposite was observed for *X. kroyeri*; the highest abundance of the species correlated positively with finer sediments (period 1). Interestingly, negative (period 1) and positive (period 2) correlations were also observed between the abundance of *X. kroyeri* and bottom temperature (MR, $p < 0.05$; Table V). At low bottom temperature and salinity, *L. schmitti* and *P. muelleri* had the greatest number of individuals collected during study period 2 (MR, $p < 0.05$; Table V). While the abundance of *S. dorsalis* correlated positively with bottom salinity during the same study period (MR, $p < 0.05$; Table V). Overall, bottom temperature and phi showed strong positive and negative correlations with almost all species (MR, $p < 0.05$; Table V).

Table I: Principal components analysis showing the parameters of the first three principal components (PC) of environmental variables analyzed by transect and month.

TRANSECT			
	PC-1	PC-2	PC-3
Eigenvalue	3.270	1.592	1.370
% variance	47	23	20
% cumulative variance	47	69	89
Depth	0.8*	0.0	-0.5
Bottom temperature	-0.7*	0.1	0.6
Bottom salinity	0.8*	0.2	-0.3
Class A	0.7*	0.5	0.5
Class B	-0.6	0.6	-0.5
Class C	0.1	-1.0*	0.0
Organic matter	0.8*	0.1	0.5
MONTH			
	PC-1	PC-2	PC-3
Eigenvalue	2.577	1.273	1.056
% variance	43	21	18
% cumulative variance	43	64	82
Bottom temperature	0.1	-0.1	0.9*
Bottom salinity	0.4	-0.7*	-0.4
Class A	0.8*	0.4	0.0
Class B	0.9*	-0.3	0.0
Class C	-1.0*	-0.1	0.0
Organic matter	0.1	0.8*	-0.2

* = eigenvector values ≥ 0.7

Table II: Penaeid species recorded throughout sampling period at Fortaleza Bay.

Infraorder Penaeidea Rafinesque, 1815
Superfamily Penaeoidea Rafinesque-Schmaltz, 1815
Family Penaeidae Rafinesque-Schmaltz, 1815
<i>Artemesia longinaris</i> Bate, 1888
<i>Farfantepenaeus brasiliensis</i> (Latreille, 1817)
<i>Farfantepenaeus paulensis</i> (Pérez Farfante, 1967)
<i>Litopenaeus schmitti</i> (Burkenroad, 1936)
<i>Rimapenaeus constrictus</i> (Stimpson, 1874)
<i>Xiphopenaeus kroyeri</i> (Heller, 1862)
Family Sicyoniidae Ortmann, 1898
<i>Sicyonia dorsalis</i> Kingsley, 1878
<i>Sicyonia laevigata</i> Stimpson, 1871
<i>Sicyonia typica</i> (Boeck, 1864)
Family Solenoceridae Wood-Mason, 1891
<i>Pleoticus muelleri</i> (Bate, 1888)

Table V: Results of the multiple linear regressions explaining changes in the abundance of penaeid shrimps in each study period (p = probability of significance; * $\alpha = 0.05$).

Environmental variables	PERIOD 1															
	<i>A. longinarius</i> t	<i>A. longinarius</i> p-level	<i>F. brasiliensis</i> t	<i>F. brasiliensis</i> p-level	<i>F. paulensis</i> t	<i>F. paulensis</i> p-level	<i>L. schmitti</i> t	<i>L. schmitti</i> p-level	<i>R. constrictus</i> t	<i>R. constrictus</i> p-level	<i>X. kroyeri</i> t	<i>X. kroyeri</i> p-level	<i>S. dorsalis</i> t	<i>S. dorsalis</i> p-level	<i>P. muelleri</i> t	<i>P. muelleri</i> p-level
Bottom temperature	-1.87	0.06	1.70	0.09	1.67	0.10	-1.29	0.20	-0.95	0.35	-2.38	0.02*	-1.22	0.23	-1.68	0.10
Bottom salinity	3.15	<0.01*	-0.83	0.41	-0.97	0.34	1.02	0.31	0.29	0.77	0.36	0.72	1.48	0.14	0.50	0.62
Organic matter	-0.14	0.89	0.92	0.36	0.98	0.33	-2.25	0.03*	0.01	0.99	-1.15	0.26	1.31	0.19	0.71	0.48
Phi	0.73	0.47	-2.98	<0.01*	-3.89	<0.01*	1.03	0.31	-0.19	0.85	3.41	<0.01*	-0.33	0.74	0.30	0.77
Environmental variables	PERIOD 2															
	<i>A. longinarius</i> t	<i>A. longinarius</i> p-level	<i>F. brasiliensis</i> t	<i>F. brasiliensis</i> p-level	<i>F. paulensis</i> t	<i>F. paulensis</i> p-level	<i>L. schmitti</i> t	<i>L. schmitti</i> p-level	<i>R. constrictus</i> t	<i>R. constrictus</i> p-level	<i>X. kroyeri</i> t	<i>X. kroyeri</i> p-level	<i>S. dorsalis</i> t	<i>S. dorsalis</i> p-level	<i>P. muelleri</i> t	<i>P. muelleri</i> p-level
Bottom temperature	-1.73	0.09	2.51	0.01*	2.16	0.03*	-2.39	0.02*	1.00	0.32	2.03	0.05*	-1.54	0.13	-2.50	0.01*
Bottom salinity	1.11	0.27	-1.57	0.12	-0.21	0.83	-2.50	0.01*	-0.63	0.53	-0.10	0.92	4.45	<0.01*	1.20	0.23
Organic matter	-2.93	<0.01*	1.66	0.10	1.50	0.14	0.84	0.40	1.85	0.07	0.17	0.87	-1.78	0.08	-1.76	0.08
Phi	2.04	0.04*	-5.22	<0.01*	-3.92	<0.01*	1.19	0.24	-4.18	<0.01*	1.18	0.24	0.21	0.83	0.61	0.54

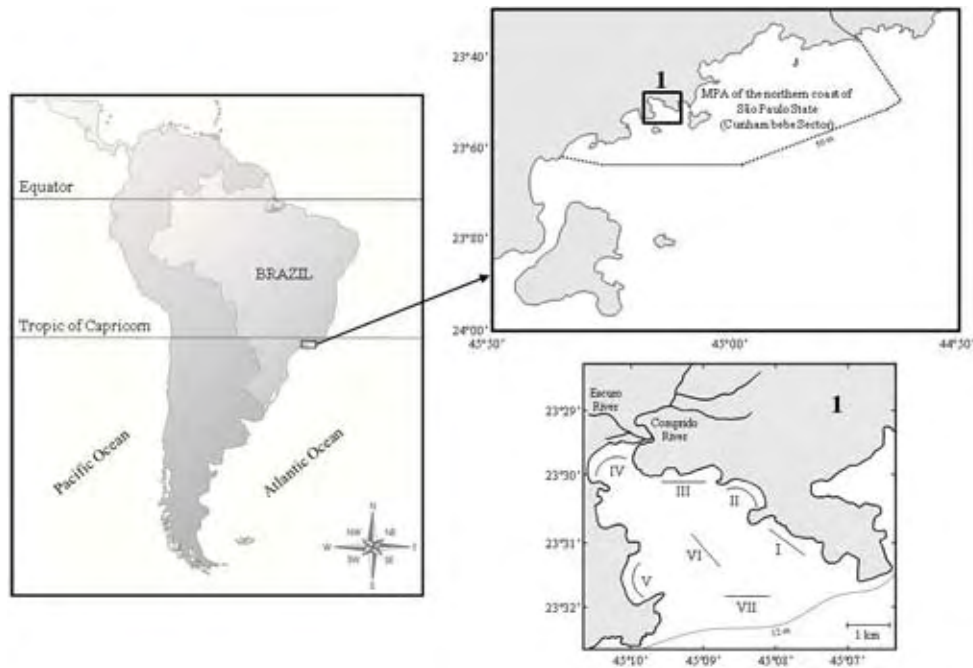


Figure 1: Map of the study region showing the Marine Protected Area (MPA – Cunhambebe Sector) and Fortaleza Bay with the sampling transects.

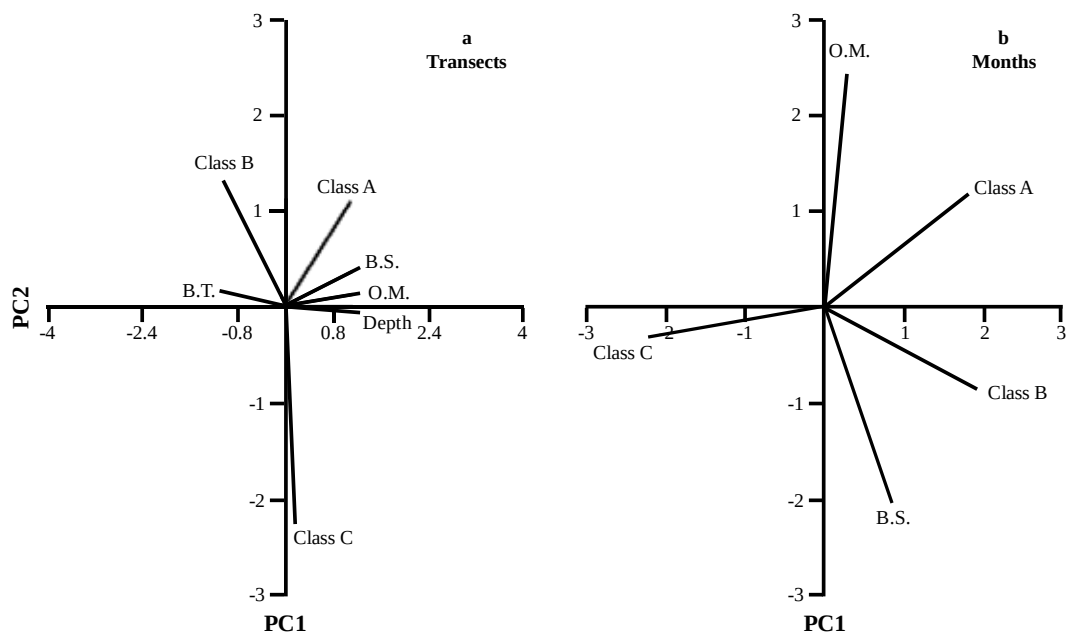


Figure 2: Principal component (PC) plots showing the environmental variables analyzed at Fortaleza Bay by transect (a) and month (b) (B.S. = bottom salinity; B.T. = bottom temperature; O.M = organic matter content).

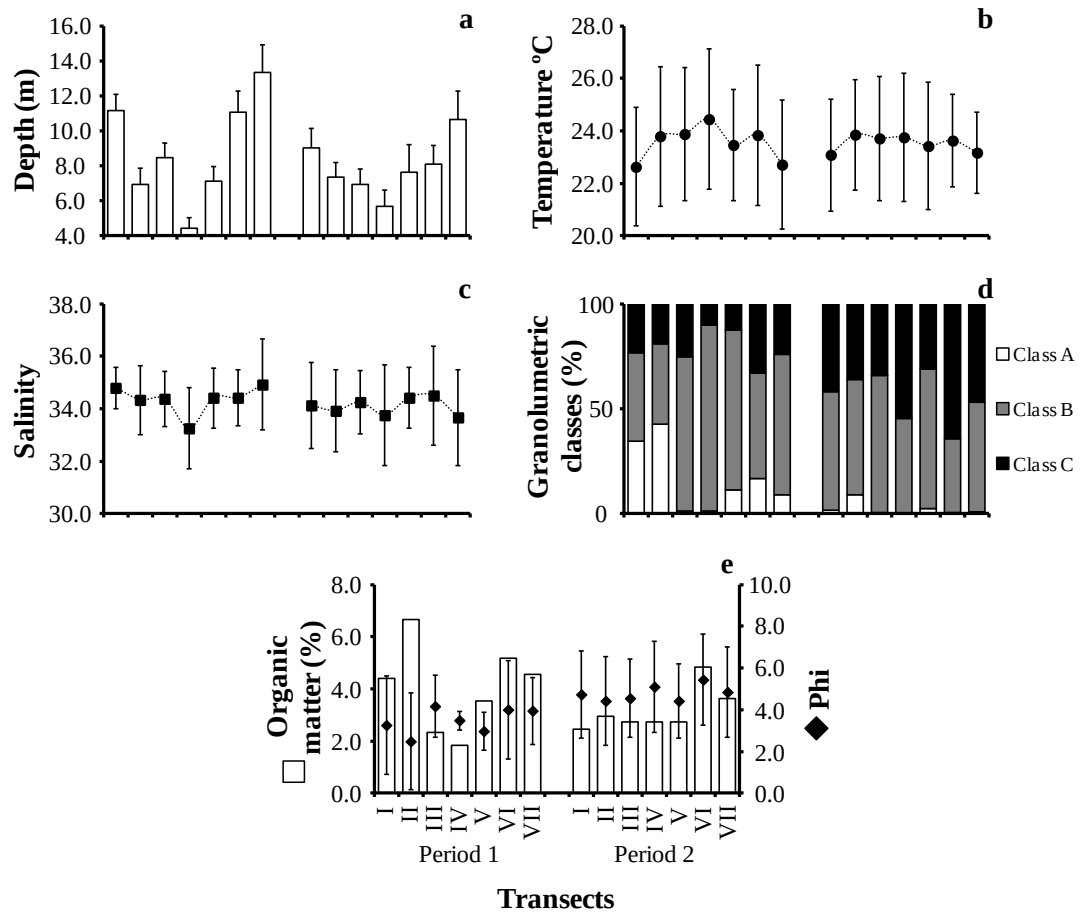


Figure 3: Spatial variations of the environmental variables at Fortaleza Bay during the sampling periods 1 and 2.

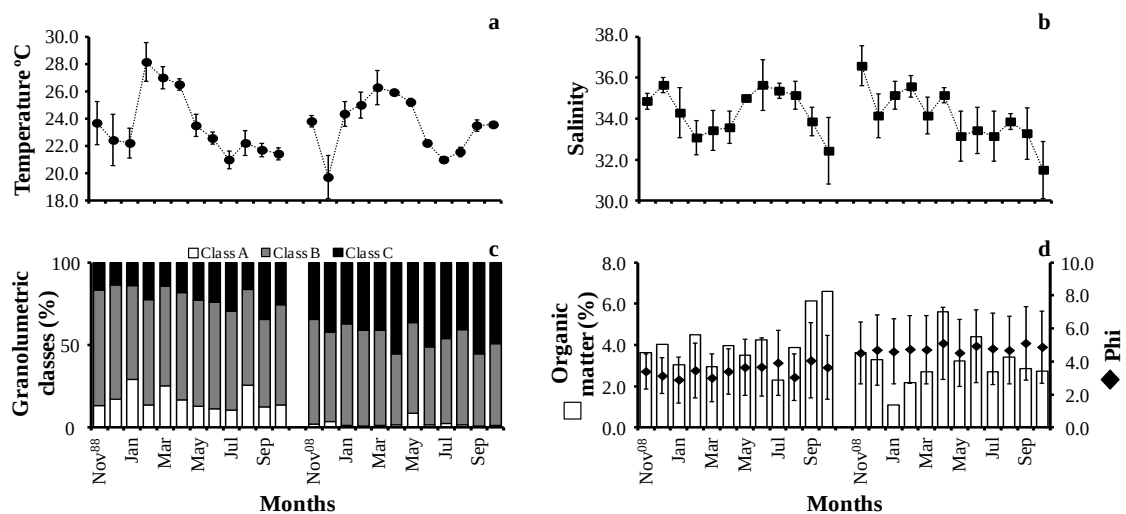


Figure 4: Monthly variations of the environmental variables at Fortaleza Bay during the sampling periods 1 and 2.

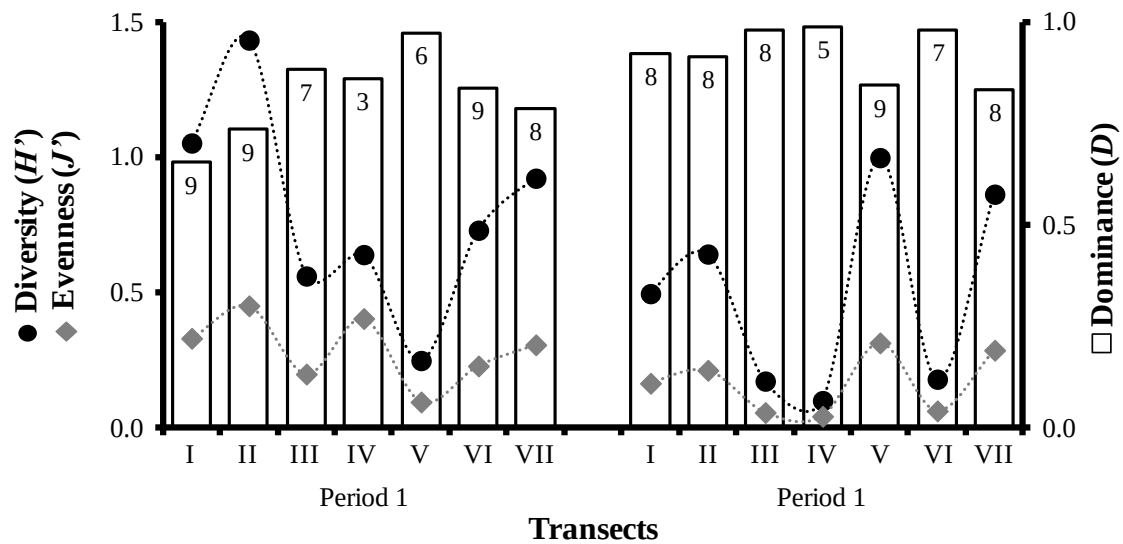


Figure 5: Spatial values of the dominance, diversity and evenness indexes obtained during the study periods 1 and 2. The numbers up correspond to the species richness.

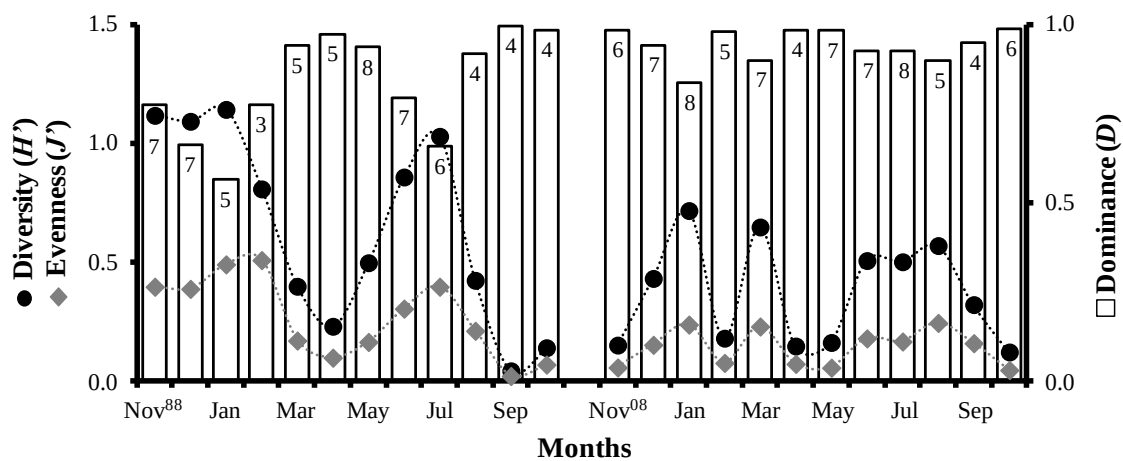


Figure 6: Monthly values of the dominance, diversity and evenness indexes obtained during the study periods 1 and 2. The numbers up correspond to the species richness.

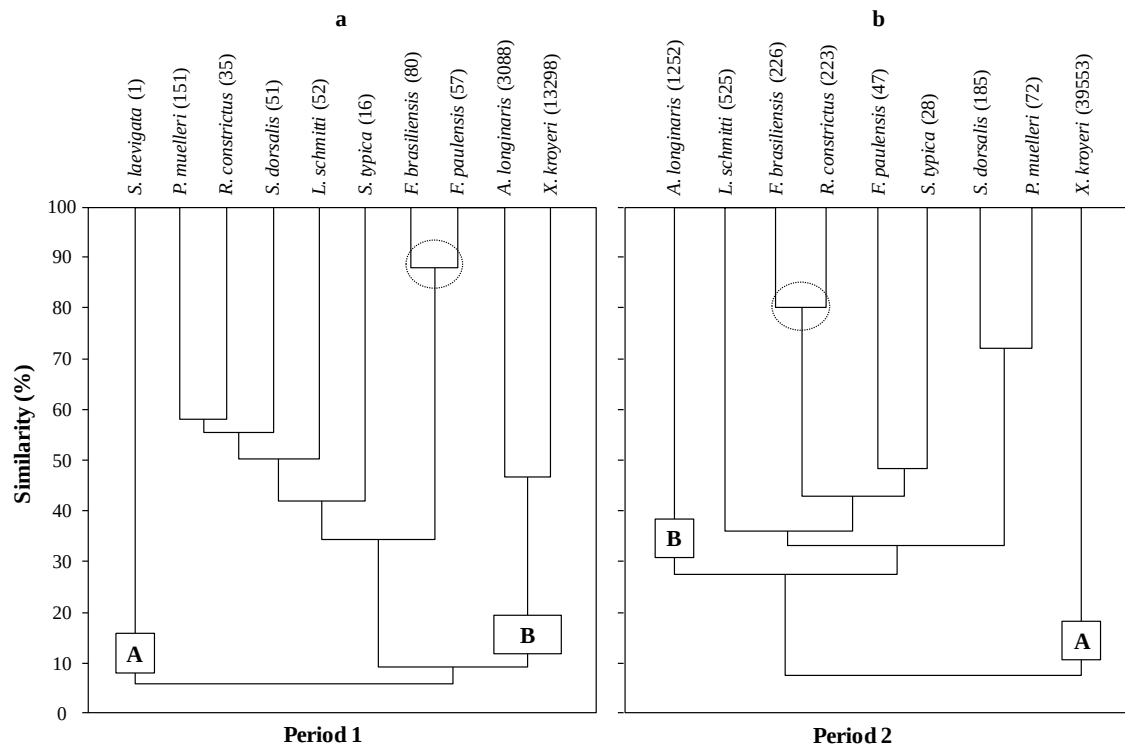


Figure 7: Dendrogram showing the similarity (Bray-Curtis) between the abundance of the species obtained at Fortaleza Bay during the study periods 1 and 2.

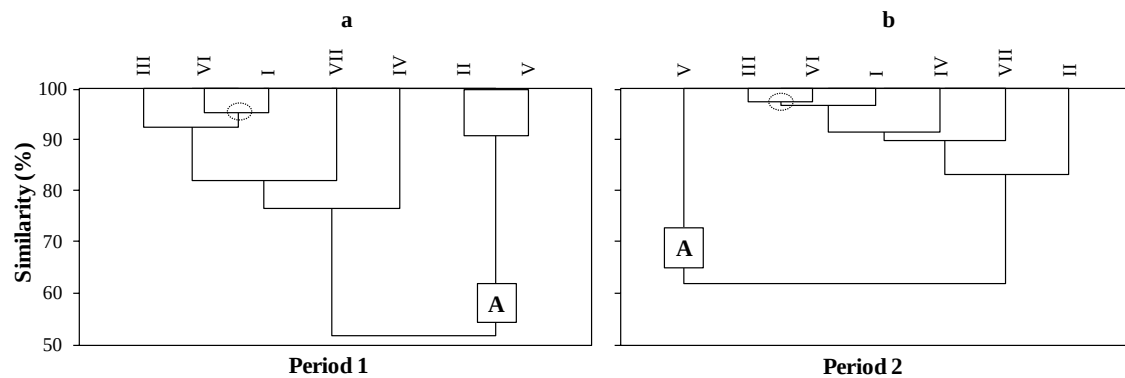


Figure 8: Dendrogram showing the similarity (Bray-Curtis) among the sampled transects at Fortaleza Bay during the study periods 1 and 2.

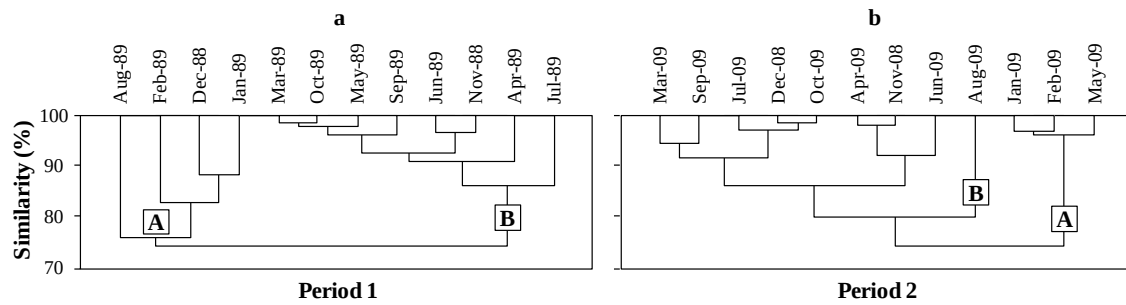


Figure 9: Dendrogram showing the similarity (Bray-Curtis) among the sampled months at Fortaleza Bay during the study periods 1 and 2.

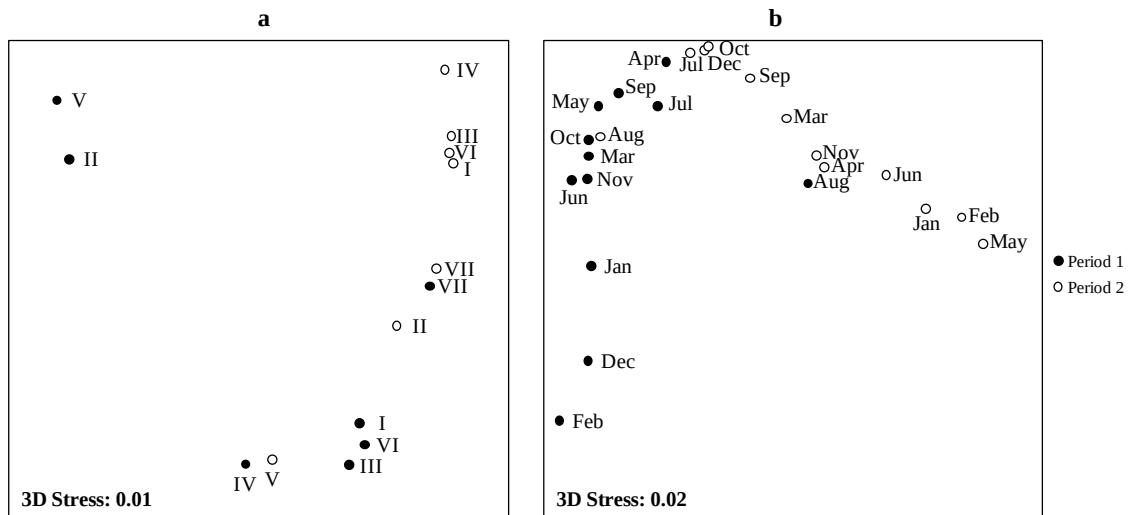


Figure 10: MDS plot for all sampled transects and months at Fortaleza Bay during the study periods 1 and 2.

4. Discussion

From 61 penaeid species occurring along the Brazilian coastline (D’Incao, 1995), a total of 10 species were recorded at Fortaleza Bay, on the northern coast of São Paulo State. Previous studies conducted in the study region have showed similar results, as observed by Nakagaki et al. (1995), Costa et al. (2000), and Fransozo et al. (2002). These authors identified a total of 8, 12 and 10 penaeid species, respectively. *Acetes americanus* Ortmann, 1893 and *S. parry* (Burkenroad, 1934) were recorded only for Costa et al. (2000). Interestingly, *A. americanus* is a pelagic shrimp, so the sampling of this species at Fortaleza Bay was not possible according to the type of fishing gear used during both study periods 1 and 2. In general, the species that make up the Penaeidea community along the coastal areas of the northern coast of São Paulo State are mostly the same, including target species (*A. longinaris*, *F. brasiliensis*, *F. paulensis*, *L. schmitti*, *X. kroyeri* and *P. muelleri*) and non-target species (*R. constrictus*, *S. dorsalis*, *S. laevigata* and *S. typica*).

According to Palumbi et al. (2009), species richness provides a reservoir of biological options that help to ensure that an ecosystem can respond to some level of perturbation without catastrophic failure. At Fortaleza Bay the species richness was maintained over a range of 20 years. Importantly, the number of individuals obtained between the study periods 1 and 2 increased substantially, mainly concerning the species *F. brasiliensis*, *L. schmitti*, *R. constrictus*, *X. kroyeri*, and *S. dorsalis*. Overall, *X. kroyeri* was the dominant species at spatial and temporal scales throughout the study periods 1 and 2. Such dominance influenced considerably the diversity and evenness values, that increased when the lowest dominance values were recorded, as observed in transects I (period 1), II (period 1), V (period 2), VI (period 1), and VII (periods 1 and 2), and during months from November 1988 to January 1989, and July 1989, January

2009, March 2009, and from June 2009 to August 2009. Also, the diversity and evenness values obtained by transect and month during study period 2 were slightly lower compared to the study period 1, probably due to the increase in the number of individuals of *X. kroyeri*. According to Pires (1992) and Pires-Vanin (2001), the presence of this species contributes strongly to the existence and maintenance of the benthic communities along the southeastern Brazilian coast, being considered as a key-species on complex interactions existing within these communities. In this way, it is acceptable that *X. kroyeri* had a dominant role in structuring the Penaeidea community at Fortaleza Bay.

Several authors have also pointed out that some environmental variables, as temperature, salinity and substrate type, play an important ecological role in structuring many communities of decapod crustacean (Pires, 1992; Pires-Vanin, 2001; Fransozo et al., 2002; Bertini and Fransozo, 2004; De Léo and Pires-Vanin, 2006; Lui et al., 2007; Castilho et al., 2008a; Fransozo et al., 2008; Muñoz et al., 2008; Juan and Cartes, 2011). In the present investigation, variations in the Penaeidea community at Fortaleza Bay can be related to changes in the environmental variables analyzed during both study periods. As observed, the first three axes of the PCA performed by transects and months displayed more than 80% of the variance in the data of bottom temperature and salinity, texture and organic matter content of the sediment. Consequently, such environmental variables were the most important factors accounting for changes in the species composition and its respective abundance.

Among the environmental variables analyzed at Fortaleza Bay, a remarkable sedimentation was observed between the first and the second study periods. The granulometric class corresponding to Class C increased considerably among transects sampled, resulting in a decrease of the granulometric class corresponding to Class A,

even as the depth. Such sedimentation might have been caused by natural phenomena, as local hydrodynamic conditions and El Niño/La Niña Southern Oscillation (ENSO/LNSO) events, and/or human activities, as urban growth. The interaction of several processes like wind, water masses circulation, tidal currents, and waves, occurring along the Southeastern Brazilian shelf, associated to the high discharge and resuspension of fine sediments from La Plata River during ENSO/LNSO events (Mahiques et al., 2002, 2010; Gyllencreutz et al., 2010), as well as the urbanization rates increase, with constructions of vacation homes installed around Fortaleza Bay, roads and bridges, mainly in permanent protected areas as mangrove and restinga forests (Muehe, 2006; Cunha-Lignon et al., 2009), can be considered as the major responsible for the great input of finer sediments within study region over a range of 20 years.

Habitat heterogeneity, considering the sediment complexity and consequent formation of microhabitats, support a higher diversity of organisms in soft bottom environments (Pires, 1992; Sumida and Pires-Vanin, 1997; Arasaki et al., 2004; Bertini and Fransozo, 2004; De Léo and Pires-Vanin, 2006; Muñoz et al., 2008). According to Miranda et al. (2005), closely related species are assumed to use similar habitat and resources, thus a loss of local heterogeneity may limit the number of niches available and thus decrease the level of taxonomic differences within communities. Conversely, higher resource and habitat diversity is supposed to promote higher taxonomic diversity levels in local communities because it would enhance the coexistence of weakly related species with contrasting ecological requirements. At Fortaleza Bay, the transects I, II, V, VI and VII showed high percentage of thicker sediment during study period 1 compared to the study period 2. As a result, such transects were characterized by high diversity and evenness values, as mentioned previously, except the transect V. Despite

the heterogeneous sediment presented by this latter transect, it showed the lowest diversity and evenness values among all other transects, and therefore the highest dominance value, which was related to the greatest abundance of *X. kroyeri*. The transects I, II, VI and VII also showed high species richness during study period 1, with occurrence of most penaeid shrimps. Concerning the study period 2, the transects II and V had a modest amount of thicker sediment compared to the other transects. Nevertheless, the transect II was also characterized by considerable silt and caly amount, which favored the greatest abundance of *X. kroyeri* (Costa et al. 2007, 2011, Simões et al. 2010, Freire et al. 2011), resulting again in a decrease of diversity and evenness values and increase of dominance index. Thus, the highest diversity and evenness values and species richness were recorded specifically at transect V, differing from the study period 1, when the opposite was observed. Interestingly, the transect VII also showed high diversity and evenness values. However, the sediment of this transect was composed only by granulometric classes corresponding to Classes B and C. Probably, other environmental variables, as bottom temperature and salinity, might have influenced on species composition and abundance data at transect VII – as the great occurrence of the species *A. longinaris* and *P. muelleri* – than the sediment type, resulting in changes of dominance, diversity and evenness indexes.

Changes in the bottom temperature and salinity also seemed to be very important in structuring the Penaeidea community at Fortaleza Bay, as well as in the benthic megafauna along the southeastern Brazilian coast (Pires, 1992; De Léo and Pires-Vanin, 2006). The interaction of the water masses CW, TW and SACW present in the study region result in notable changes in such environmental variables during months of summer and winter (Castro-Filho et al., 1987; Pires, 1992; Pires-Vanin and Matsuura, 1993). Despite the slight variations in the bottom temperature and salinity observed in

the present investigation, they followed a similar pattern, with the exception of the average value of bottom temperature recorded in December 2008 (19.7°C). In general, based on most average values of bottom temperature and salinity, the CW water mass (temperature > 20°C and salinity < 36) was constantly present at Fortaleza Bay during both study periods. Notwithstanding, the occurrence of *A. longinaris* and *P. muelleri*, observed mainly from November to January, might be associated to the intrusion of SACW into the continental shelf, since these species are considered as indicators of cold water (Costa et al., 2004, 2005a; Fransozo et al., 2004; Gavio and Boschi, 2004; Castilho et al., 2008a). Throughout study periods 1 and 2, the highest diversity and evenness values were obtained when both high and low average values of bottom temperature and salinity were recorded at Fortaleza Bay, as observed during the months from November 1988 to January 1989, and July 1989, January 2009, March 2009, and from June 2009 to August 2009. Concomitantly, fluctuations in the abundance of the dominant species, *X. kroyeri*, were also observed during these months. As a result, the other species (e.g. *A. longinaris* and *P. muelleri*) also took over the same months at Fortaleza Bay, probably because the lower competition rates by the same resources among the Penaeidea community during such months.

Besides the importance of some environmental variables in explaining the Penaeidea community structure at Fortaleza Bay, the creation and implementation of several measures aiming to promote the correct management of the ecological-economic resources present in coastal ecosystems to sustainable levels of exploitation (Palumbi, 2001; Amaral and Jablonski, 2005; Prates, 2007; Gillett, 2008; McCay and Jones, 2011; Rice and Houston, 2011), as well as the conservation of the biological diversity (Palumbi, 2001; Amaral and Jablonski, 2005), have been proposed in the last years. Coastal management in Brazil is conducted by a national plan legally enforced,

complemented by states and counties plans, and a coastal ecological-economic zoning (EEZ) limited to small portions of the coastal zone (Jablonski and Filet, 2008). The creation of the Anchieta Island State Park integrated into a conservation unit (Proclamation No. 9 629, March 29, 1977, and Federal Law No. 9 985, July 18, 2000), the implementation and regulation of the coastal EEZs (Proclamation No 5 300, December 07, 2004), and the recent establishment of the special management area at Mar Virado Island and the MPA of the northern coast of São Paulo State (Proclamation No. 53 525, October 08, 2008), reduced drastically the fishing boats operating around the study region in the course of 20 years, contributing significantly to the maintenance and preservation of biological diversity at Fortaleza Bay, even as to the stock enhancement of the most valuable species targeted by the industrial and artisanal fisheries on the southeastern Brazilian coast, including *F. brasiliensis*, *L. schmitti* and *X. kroyeri*.

The spatial and temporal patterns of penaeid shrimp abundance at Fortaleza Bay are in agreement with previous studies carried out in the study region, regarding their strong relationship with temperature, salinity and sediment characteristics. According to Castilho et al. (2008a), little is known about how changes in environmental variables translate into the abundance patterns at the level of the entire Penaeidea community on the southeastern coast of Brazil. However, this knowledge is fundamental, not only to understand the mechanisms underlying shrimp community dynamics, but also to effectively manage shrimp fishery resources (Castilho et al., 2008a). As noted before, the sedimentation occurred at Fortaleza Bay over a range of 20 years, was extremely favorable to the greatest abundance of those species that usually inhabit substrate composed mainly by fine and very fine sand and silt and clay, like *L. schmitti* (Capparelli et al., 2012), *R. constrictus* (Costa and Fransozo, 2004; Hiroki et al., 2011),

X. kroyeri (Costa et al. 2007, 2011, Simões et al. 2010, Freire et al. 2011), and *S. dorsalis* (Costa et al., 2005b; Castilho et al., 2008b). According to Dall et al. (1990), the preference of several penaeid shrimps by finer sediments are closely related to their burrowing behavior, which is facilitated in such sediment by reducing energy requirements for excavation. However, only the species *X. kroyeri* showed a positive correlation with finer sediments (phi values > 4) during study period 1, corroborating with several investigations (Costa et al. 2007, 2011, Simões et al. 2010, Freire et al. 2011) carried out along the study region. Interestingly, *R. constrictus* correlated negatively with such sediment type during study period 2. However, previous studies have stated that *R. constrictus* is mostly abundant in sediment composed by fine and very fine sand (Costa and Fransozo, 2004; Hiroki et al., 2011). Probably, the highest abundance of this species at transect II, which had an elevated percentage of thicker sediment compared to the other transects, might have influenced this result. But this transect was also characterized by considerable finer sediment amount, as well as the transects III (period 2), V (period 2), and VII (periods 1 and 2), which also showed high number of individuals.

The pink shrimps *F. brasiliensis* and *F. paulensis* also showed negative correlations with finer sediment throughout study periods 1 and 2. The greatest abundance of both species were obtained at transects II and V. However, variations in the abundance and distribution patterns of these species are generally related to seasonal changes in temperature and salinity (Pérez-Castañeda and Defeo, 2001, 2004; May-Kú and Ordóñez-López, 2006; Costa et al., 2008; Lüchmann et al., 2008; Freitas Jr et al., 2011), since these pink shrimps display different requirements throughout their life cycle, with migration of subadults occurring from estuaries and shallow coastal areas toward offshore waters, where the reproduction takes place (Garcia and Le Reste, 1986;

Dall et al., 1990; D’Incao, 1991; Pérez-Castañeda and Defeo, 2001, 2004). Besides the sediment texture, high bottom temperature also showed significant influence on abundance of *F. brasiliensis* and *F. paulensis* at Fortaleza Bay, but only during study period 2. From March 2009 to May 2009, months of which correspond to the late summer and early fall, it was recorded the highest abundance of both species. With respect to the remaining months, practically no individual was obtained. Such changes in temporal pattern of abundance and distribution of *F. brasiliensis* and *F. paulensis* can be associated to the migration of the species along the study region (Costa et al., 2008). Likewise, bottom temperature demonstrated to influence the abundance of *L. schmitti* during study period 2. A negative correlation was obtained between the abundance of the species and such environmental variable. Almost all individuals of *L. schmitti* were collected during fall and winter. As suggested for the pink shrimps *F. brasiliensis* and *F. paulensis*, seasonal changes in the abundance of *L. schmitti* can be also related to the migration processes. In the study conducted by Capparelli et al. (2012) at Ubatuba Bay, northern coast of São Paulo State, the entry of the postlarvae in the Indaiá estuary increased the number of juveniles present in this environment during late spring and summer (December–February). As a result, high catch of subadults and adults was observed after a few months. Thus, corroborating with Castilho et al. (2008a) and based on above all results, although the lack information regarding the age composition of *F. brasiliensis*, *F. paulensis* and *L. schmitti* populations in the present investigation, differential migrations during both study periods might be evidenced for the three species.

Significant negative and positive associations were obtained between *X. kroyeri* and bottom temperature throughout study periods 1 and 2, respectively. During period 1, the species was most abundant during the months corresponding to winter (42% of

the total specimens caught), when bottom temperature reached low mean value (21.6°C). During period 2, the highest abundance of *X. kroyeri* was obtained in summer and fall (36 and 35% of the total specimens caught, respectively), mainly in the months of January 2009, February 2009 and May 2009. Concomitantly, during these seasons the highest mean values of bottom temperature were recorded (25.2 and 24.5°C, respectively). In general, bottom temperature values below 21°C might be considered as a limiting factor for the occurrence of *X. kroyeri* along the southeastern Brazilian coast, as suggested before by Castro et al. (2005) and Costa et al. (2007).

Concerning *S. dorsalis*, a positive association between the abundance of the species and bottom salinity was found during study period 2. Such association can be related to the elevated number of individuals sampled from November 2008 to February 2009, when high average values of bottom salinity were recorded in the study region. Costa et al. (2005b), investigating the ecology of the same species in the bays on the northern coast of São Paulo State, verified an opposite association. However, these authors and also Castilho et al. (2008b), suggest that sediment composed by more than 70% of silt and clay seems to favor the occurrence and abundance of *S. dorsalis* than salinity. At Fortaleza Bay, the species was caught mainly in the transects II (period 2), V (period 2) and VII (periods 1 and 2), where the silt and clay amount varied from 31% to 65%. Herein, fine and very fine sand amount also provided favorable conditions to the settlement of *S. dorsalis*.

At lower bottom temperature, *A. longinaris* and *P. muelleri* showed the highest abundance in the present investigation. Although the relationships obtained between the abundance of *A. longinaris* and the sediment characteristic, as phi and organic matter content, also observed by several authors along the southeastern Brazilian coast (Costa et al., 2005a; Castilho et al., 2008a; Batista et al., 2011), the bottom temperature might

be considered as the most relevant environmental variable in affecting the abundance and distribution patterns of this species, even as *P. muelleri* (Costa et al., 2004, 2005a; Castilho et al., 2008a). Importantly, only the abundance of *P. muelleri* was negatively correlated with bottom temperature, while a positive correlation between the abundance of *A. longinaris* and salinity was observed. However, the highest number of these subantarctic shrimps was recorded at the deeper transects I and VII, which were located closely to the mouth of the Fortaleza Bay, and had the lowest average bottom temperature throughout study periods 1 and 2. Thus, such results confirm the importance of lower temperature in driving the abundance and distribution patterns of *A. longinaris* and *P. muelleri* at Fortaleza Bay.

Overall, the observed variations in the Penaeidea community and in the spatial and temporal patterns of species abundance at Fortaleza Bay could be influenced by at least two main external forcing factors: (1) environmental variable changes and (2) creation and implementation of management measures of natural resources. Throughout study periods 1 and 2, changes in the environmental variables analyzed at Fortaleza Bay drove fluctuations in the species richness, dominance, diversity and evenness indexes among transects and months. Importantly, the species composition and the dominant species (*X. kroyeri*) was maintained comparing the study periods 1 and 2. The management measures created, as the implementation and regulation of the coastal EEZs and the establishment of the MPA in the study region, were essential in maintaining the Penaeidea community at Fortaleza Bay over a range of 20 years. In addition, the sedimentation process observed between the first and second study periods favored the abundance increase of most penaeid shrimps species, including those valuable species targeted by the industrial and artisanal fisheries on the southeastern Brazilian coast, as *L. schmitti* and *X. kroyeri*. These findings demonstrated that the

composition, species richness and the abundance data of the Penaeidea community were influenced by spatial and temporal changes in the environmental variables, as well as due to the benefits resulting from the adopted management measures in the study region. However, monitoring studies along southeastern Brazilian coast are still necessary in an attempt to provide essential information on changes at spatial and temporal scales in the local biodiversity and consequent conservation.

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Capítulo II

*Ecology assessment of the commercially
exploited shrimp *Xiphopenaeus kroyeri*
(Decapoda: Penaeidea) in a Marine
Protected Area over a range of 20 years*

Abstract

The spatial and temporal patterns of abundance and distribution of *Xiphopenaeus kroyeri* and its relationship with several environmental variables were compared over a range of 20 years. The abiotic and biotic data set were obtained monthly during two distinct study periods; period 1, from November 1988 to October 1989; and period 2, from November 2008 to October 2009, in seven permanent transects established within Fortaleza Bay, on the southeastern coast of Brazil. A remarkable sedimentation was observed between the first and the second study periods, which might have been caused by natural phenomena and/or human activities. While the variations in the bottom temperature and salinity were related mainly to the hydrodynamics of water masses present in the Ubatuba region. The abundance of *X. kroyeri* increased considerably over a range of 20 years. A total of 13 298 and 39 553 specimens were obtained throughout the sampling periods 1 and 2, respectively. The total abundance of the species and the abundance of males and females differed spatially, while the abundance of juveniles differed seasonally, during each study period (ANOVA, $p < 0.05$). Overall, the highest abundance of the species was recorded in those transects which the sediment was composed mainly by fine and very fine sand and silt and clay. The presence of algae and plant floating near the marine floor at Fortaleza Bay also favored the occurrence and settlement of *X. kroyeri*. Interestingly, during period 1 the species was most abundant in winter, when bottom temperature reached low mean value (21.6°C). While during period 2, the highest abundance of *X. kroyeri* was obtained in summer and fall. Concomitantly, the highest mean values of bottom temperature were recorded during these seasons (25.2 and 24.5°C, respectively). So, the species appeared to be under influence of the water mass Costal Water, which shows high temperature ($> 20^{\circ}\text{C}$) and rich continental suspended material. The intense El Niño (1990-1993 and 1997-1998)

events recorded between the study periods 1 and 2, might have also contributed to the high abundance of *X. kroyeri* at Fortaleza Bay, by increasing the primary productivity and consequently boosting larval condition and/or survival of the species in the study region. Finally, the management measures created for the study region, in an attempt to control the fishing effort, probably contributed significantly to the stock enhancement of *X. kroyeri* in the study region, representing important tools for conservation, preservation and sustainable use of this important fishery resource available in the study region.

Keywords: Abundance; environmental variables; management measures; natural phenomena; spatio-temporal variations

1. Introduction

Marine and coastal ecosystems are ecologically and economically important due to the goods and services proportionate to the environment and human society, as the provision of shoreline protection, water quality maintenance, fishery resources, habitat, food, tourism, and other (Turner et al., 1998; UNEP, 2006; Katsanevakis et al., 2011). Despite the importance of these ecosystems, their degradation is intense and increasing worldwide (Pereira and Ebecken, 2009; UNEP, 2006; Barbier et al., 2008; Katsanevakis et al., 2011; Parravicini et al., 2012). Thus, pressures upon marine and coastal ecosystems call for a well planned approach of space managing use. However, fisheries and aquaculture, offshore wind farms, gas and oil industry, coastal defense systems, extraction of building materials, shipping, tourist industry, and the need for marine conservation, all compete for the same valuable space (Katsanevakis et al., 2011).

Shrimp fisheries are one of the most important activities in the world, generating substantial economic benefits, especially for many developing countries (Gillet, 2008), as observed for Latin American countries, in which the artisanal fishery represents a source of food for subsistence and employment, generating important direct incomes to traditional human communities (Castilla and Defeo, 2001). Along the Brazilian coastline, the development of artisanal fishery faces many challenges due to the lack of policies, strategies and concrete experiences that can support sustainable fisheries production, better organization and improvement of the livelihood of fishing communities. There has been a continuous worsening of the problems affecting the production of artisanal fishery owing to the depletion of fishery resources, environmental degradation of coastal areas, and ultimately to the ineffectiveness of governmental strategies in overcoming the obstacles that impede the sustained development of the artisanal fishing communities (Vasconcellos, et al. 2011).

On the environmental side, shrimp fisheries are strongly influenced by climatic drivers (Gillet, 2008). According to Daw et al. (2009), climate change is predicted to have a range of direct and indirect impacts on marine capture fisheries, with implications for fisheries-dependent economies, coastal communities and fishermen. The sea surface temperature (SST) plays a key role in regulating climate and its variability (Deser et al., 2010). In general, the interannual climate variability around the world has been studied in connection with the El Niño Southern Oscillation (ENSO) events (Trenberth, 1997). In Brazil, the ENSO-related climate anomalies are generally associated to severe droughts on the northeastern, and floods on the southern (see Liu and Negrón Juárez, 2001; Hastenrath, 2006; Kayano and Andreoli, 2006; Garcia et al., 2001, 2003, 2004; Grimm, 2003, 2011). Along the Southeastern Brazilian shelf, the ENSO events, associated with the local oceanographic conditions, increment the primary productivity patterns (Paes and Moraes, 2007). However, climate change impacts on fisheries have uneven effects on different geographic areas and, make future effects of climate change on fisheries is difficult to predict due to the variety of different impact mechanisms, complex interactions between social, ecological and economic systems, and the possibility of sudden and surprising changes (Daw et al., 2009).

On the northern, northeastern, southeastern and southern regions of the Brazil, that were described by Matsuura (1995) as the major marine fishing grounds, the pink shrimps *Farfantepenaeus brasiliensis* (Latreille, 1817), *F. paulensis* (Pérez Farfante, 1967), and *F. subtilis* (Pérez Farfante, 1967), the white shrimp *Litopenaeus schimitti* (Burkenroad, 1936), and the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862), are the most valuable species targeted by the industrial and artisanal fisheries (Vasconcellos et al., 2007, 2011; Ministry of Fisheries and Aquaculture, 2012). In 2010, the average catch of these shrimps resulted in a total of 29 590 tons (Ministry of Fisheries and

Aquaculture, 2012), corresponding to 77% of all species of marine shrimps caught along the Brazilian coastline (Penaeidea and Caridea) (FAO, 2012; Ministry of Fisheries and Aquaculture, 2012). Approximately 52% (15 276 tons) of this total corresponded to the capture of the seabob *X. kroyeri*. As a result, the stocks of the species have presented a continuous decrease in landings since the late 1980s (Valentini et al., 1991, D’Incao et al., 2002, IBAMA/CEPSUL, 2006, Vasconcellos et al., 2007).

In the Ubatuba region, southeastern coast of Brazil, where the average bottom temperature usually ranges from 21 to 25°C, and the sediment is composed mainly by fine and very fine sand and silt and clay, seems to favor the high abundance of *X. kroyeri* (Costa et al., 2007, 2011). According to the authors Castro et al. (2005) and Costa et al. (2007, 2011), juvenile individuals are not dependent on estuaries along Ubatuba region, completing their life cycle in shallow coastal areas. So, *X. kroyeri* displays the life cycle type III rather than type II as reported by Dall et al. (1990). In life cycle type III, the species are restricted to truly marine environments, with migrations occurring from shallow coastal areas toward offshore waters, where the reproduction takes place. Therefore, both juveniles and adults are largely caught by trawling activities, resulting in possible disturbances on population structure of *X. kroyeri* in the Ubatuba region. Thus, in an attempt to assess fluctuations in the total abundance and by demographic category of this commercially exploited shrimp over a range of 20 years, the variations of several environmental variables at spatial, and temporal scales and its relationship with the occurrence and settlement of the species were evaluated in a recently established Marine Protected Area (MPA), on the southeastern Brazilian coast. Also, possible influences of natural phenomena that occurred in the interval time between November 1988 to October 1989 and November 2008 to October 2009, were assessed in explaining the abundance and distribution patterns of *X. kroyeri*. As well as

the efficiency of management measures created for the study region, providing subsidies for the evaluation of the current management measures, and for the establishment of future actions in order to protect, ensure and discipline the rational use of this resource in the study region, promoting the sustainable development.

2. Material and Methods

2.1. Study site

Ubatuba region, northern coast of São Paulo State, is characterized by innumerable spurs of the Serra do Mar that form an extremely indented coastline (Ab'Saber, 1955). Exchange of water and sediment between the coastal area and the adjacent shelf is very limited (Mahiques, 1995). This region is affected by three water masses: Coastal Water (CW: temperature $> 20^{\circ}\text{C}$; salinity < 36), Tropical Water (TW: temperature $> 20^{\circ}\text{C}$; salinity > 36) and South Atlantic Central Water (SACW: temperature $< 18^{\circ}\text{C}$; salinity < 36 ; Nitrogen:Phosphorus – 16:1) (Castro-Filho et al., 1987; Odebrecht and Castello, 2001). During summer, the SACW penetrates into the bottom layer of the coastal area and forms a thermocline over the inner shelf located at depths of 10 to 15 m. During winter, the SACW retreats to the shelf break and is replaced by the CW. As a result, no stratification is present over the inner shelf during winter months (Pires, 1992; Pires-Vanin and Matsuura, 1993). The sediment is composed mainly of fine and very fine sand and silt and clay given the low water movement within the bay and between the bay and the adjacent continental shelf (Mahiques et al., 1998).

Fortaleza Bay ($23^{\circ}29'30''\text{S}$ to $45^{\circ}10'30''\text{W}$) is situated in Ubatuba region. Within this bay, 12 sandy beaches are flanked by rocky shores and, there is no considerable depth variation, it usually ranges from 1 to 12 m. Two rivers, Escuro and Comprido, originating from the Atlantic coastal forest (Mata Atlântica), flow into the Fortaleza Bay and support a diverse intertidal mangrove ecosystem. In 2008, the government of São Paulo State dictated the creation of the Marine Protected Area (MPA) along the northern coast, that consist of three sectors; Cunhambebe, Maembipe and Ypautiba (Área de Proteção Ambiental – APA Marinha do Litoral Norte;

Proclamation No. 53 525, October 08, 2008). Fortaleza Bay is included in the Cunhambebe Sector (Figure 1). Overall, in this MPA, fishing is only permitted if it is necessary for the subsistence of traditional human communities. Also, amateur sport fishing but not commercial fishing is allowed.

2.2. Sampling procedures of shrimps and environmental conditions

The present study comprised two distinct sampling periods: period 1, from November 1988 to October 1989; and period 2, from November 2008 to October 2009. The same methodology was used in both periods.

Shrimp samples were collected monthly during periods 1 and 2, using a fishing boat equipped with double-rig nets (7.5 m wide; 2.0 m mouth; 15 mm and 10 mm mesh diameter at the body and cod end of the net, respectively). A total of 7 permanent transects were established within the Fortaleza Bay (Figure 1). Each transect was trawled for 1 km (each trawl lasted ~ 20 min) covering a total area of 4 km² transect⁻¹.

During trawling, surface and bottom water samples were taken with a Nansen bottle in each of the different transects. Water temperature (°C) and salinity were measured with a mercury thermometer (accuracy = 0.5°C) and an optical refractometer (precision = 0.5), respectively. Depth (m) was recorded by a delimited cable connected in the Nansen bottle.

Sediment samples were obtained during each month at each transect with a Van Veen grab (0.025 m²) 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 followed 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 $\phi \geq 4$ (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). 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.

During period 2, considerable amounts of algae and plant fragments present in trawl samples were collected, sorted and its biomass (total wet weight, Kg) was recorded with a balance (precision = 0.0001 g).

Shrimps collected were transported in cool box to the laboratory where they were identified (according to Pérez Farfante and Kensley, 1997 and Costa et al., 2003),

counted and sexed (presence of petasma in males and thelycum in females). In large shrimp samples, logistic and time constraints did not permit sexing each collected individual. Thus, subsamples of 100 and 250 g were randomly separated during periods 1 and 2, respectively, from each sample for analysis. Next, shrimps were separated into three demographic categories: juveniles, adult males and females. During period 1, shrimps smaller than 13.7 mm carapace length were considered juveniles according to the size at which 50% of the population reached sexual maturity (see Fransozo et al., 2000). Whereas in the period 2, males and females were categorized as juveniles or adults based on macroscopic observations of secondary sexual characters (petasma and thelycum) and maturity stage of terminal ampoules (in males) and ovaries (in females) (see Almeida et al., in press).

2.3. Statistical analysis

A Principal Components Analysis (PCA) was conducted using the environmental variables (depth, bottom temperature and salinity, texture and organic matter content of sediment) sampled during each period in order to identify the maximum variation among this set of data in relation to the transects and months. The environmental variables were standardized by calculating the *z-scores*, since each variable usually has its own scale (Lepš and Šmilauer, 2003). The principal components in which the total percentage (cumulative) of data set variation accounted for 80% were selected. Within each selected principal component, the most relevant environmental variables were selected by excluding those values whose loadings (eigenvectors) were intermediate of -1 and 1 and less than 0.7 of the absolute value (Jolliffe, 2002).

Differences in the total abundance of *X. kroyeri* and by demographic categories were analyzed by transect and month during each period and between both periods

using analysis of variance (One-way and Factorial ANOVA, $\alpha = 0.05$), followed by a multiple comparison test (Tukey, $\alpha = 0.05$). The assumptions of homoscedasticity (Levene test) and normality (Shapiro-Wilks test) were tested, and the data were log₁₀-transformed prior to the analysis (Zar, 2010).

The association of depth, bottom temperature and salinity, and texture and organic matter content of the sediment with species abundance was assessed by multiple regression (MR) for each period ($\alpha = 0.05$). A Spearman correlation ($\alpha = 0.05$) was performed to test for a relationship between the abundance of *X. kroyeri* and the algae and plant fragments biomass obtained during period 2.

3. Results

In general, most environmental variables showed maximum variation in the data set during the study periods 1 and 2. The first three principal components of the PCA conducted by transect and month accounted for 89 and 82% of the variability in the data set, respectively (Table I). The PCA results by transect indicated that the depth, bottom temperature and salinity, sediment fraction corresponding to Class A, and organic matter content, were the most relevant environmental variables in the first principal component, and the sediment fraction corresponding to Class C in the second principal component (Table I). Analyzing the PCA results by month, the sediment fractions corresponding to Class A, B and C, the bottom salinity and organic matter content, and the bottom temperature were the most relevant environmental variables in the first, second and third principal components, respectively (Table I).

The average ($\pm$ standard deviation [SD]) depth at Fortaleza Bay over the entire study periods 1 and 2 was 8.9 ± 3.0 m, ranging from 3.5 to 16.0 m, and 7.9 ± 1.9 m, ranging from 4.0 to 14.0 m, respectively. In the period 1, there was a greater depth variation among sampled transects compared to the period 2, which was nearly homogeneous (Figure 2a). During both study periods, the transects IV and VII were characterized by the lowest and highest average values of depth, respectively (Figure 2a).

The bottom temperature ranged from 20.0 to 29.5°C in the period 1, and from 18.0 to 27.5°C in the period 2. The average bottom temperature was similar between the periods, 23.5°C, while the SD was slightly different, 2.5°C (period 1) and 2.1°C (period 2). The transects I and VII, located closely to the mouth of the Fortaleza Bay, showed the lowest average bottom temperature during both periods (Figure 2b). Concerning the variation of the bottom temperature by month, there was a decrease from November

1988 to January 1989, an abrupt increase in February 1989, followed by a constant decrease up to July 1989 (Figure 3a). In the months from January 2009 to March 2009, the bottom temperature increased in the bay followed by a decrease during the following months up to July 2009 (Figure 3a). In December 2008, it was recorded the lowest average bottom temperature ($19.7 \pm 1.6^{\circ}\text{C}$). The average monthly values of surface temperature in the period 1 were extracted from the manuscript of Negreiros-Fransozo et al. (1991). The overall average surface temperature was $24.5 \pm 2.6^{\circ}\text{C}$, ranging from 21.1 to 29.2°C . The highest average value of it was recorded in February 1989 (Figure 3a). The average surface temperature sampled during period 2 was a little higher than average bottom temperature, $24.7 \pm 2.3^{\circ}\text{C}$, and varied from 21.0 to 29.0°C . It followed a similar pattern of spatial and temporal variation to that reported for bottom temperature (Figures 2b and 3a).

Average values of bottom salinity did not vary much among transects and months during both study periods (Figures 2c and 3b). Overall, it ranged from 30 to 38, and from 29 to 38, with an average of 34.4 ± 1.3 and 34.1 ± 1.6 recorded during periods 1 and 2, respectively. The lowest average value of bottom salinity was registered in transect IV (Figure 2c) due to the proximity of the mangrove ecosystem in the Fortaleza Bay (see Figure 1). The months from February 1989 to April 1989, October 1989, from May 2009 to July 2009, September 2009 and October 2009, showed the lowest average bottom salinity values (Figure 3b). The average monthly values of surface salinity obtained during period 1, that were also extracted from manuscript of Negreiros-Fransozo et al. (1991), ranged from 29.4 to 35.2, with an overall average of 33.2 (Figure 3C). Surface salinity in the Fortaleza Bay increased and decreased during period 2 following a pattern similar to the bottom salinity registered in the transects and months (Figures 2c and 3b).

In general, the sediment at Fortaleza Bay was characterized as fine and very fine sand and silt and clay during both study periods; grains with a diameter smaller than 0.25 mm dominated the sediment samples (> 90%) (Figures 2d and 3c). There was a drastic reduction in the sediment fraction corresponding to Class A in transects I, II, V, VI and VII during period 2 compared to the period 1 (Figure 2d). Such reduction was also observed among the months (Figure 3c). Consequently, there was an increase in the sediment fractions corresponding to Class B and C for both transects and months (Figures 2d and 3c). Average phi values obtained during periods 1 and 2 were 3.4 ± 0.9 and 4.8 ± 0.7 , ranging from 1.0 to 5.2 and from 2.0 to 6.3. As expected, the phi values increased during period 2 compared to the period 1 (Figures 2d and 3c). According to the phi scale, fine sand, very fine sand and silt and clay were the most frequent granulometric fractions in the sediment sampled by transects and months throughout periods 1 and 2 (Figures 2d and 3c). The average organic matter content varied substantially among transects and months during both study periods (Figures 2d and 3c). The highest average value of organic matter content was obtained in transects II (period 1) and VI (period 2) (Figure 2d). In September 1989, October 1989, April 2009 and June 2009 were also registered the highest average value of organic matter content (Figure 3c).

During period 2, large amounts of algae and plant fragments were mainly observed in transects II, III and IV (Figure 4a). However, it showed considerable variation among the sampled months, with the highest average value obtained in November 2008 (Figure 4b).

3.2. Spatial and temporal variations in abundance of Xiphopenaeus kroyeri

A total of 13 298 and 39 553 specimens of *X. kroyeri* were captured from 168 trawls conducted throughout the sampling periods 1 (84 trawls) and 2 (84 trawls), respectively. The total abundance of juveniles, males and females adults corresponded to 524, 744 and 912 specimens analyzed during period 1, and to 1 949, 2 293 and 2 327 specimens analyzed during period 2, respectively.

The total, male and female abundance differed spatially, while the juvenile abundance differed seasonally, during each study period (ANOVA, $p < 0.05$; Table II). Although *X. kroyeri* was caught in all transects within Fortaleza Bay, the highest mean number of shrimp was obtained in transects VII and IV during periods 1 and 2, respectively (Figure 5a). The transect VII differed statistically from the transects II (Tukey, $p < 0.01$) and V (Tukey, $p < 0.01$), while transect IV differed statistically from the transect V (Tukey, $p < 0.01$) because the lowest mean number of shrimp sampled during both study periods (Figure 5a). Concerning the spatial distribution of the demographic categories of *X. kroyeri*, the juveniles were most abundant in transects III (period 2), IV (period 1) and VI (periods 1 and 2) (Figure 5b,c), although no significant difference in the abundance was detected (ANOVA, $p = 0.18$ [period 1], $p = 0.97$ [period 2]; Table II). Male abundance varied significantly among transects (ANOVA, $p < 0.01$ [periods 1 and 2]; Table II), and the transects I (period 2), III (period 1), VI (period 2), and VII (period 1) showed the greatest mean number of males caught throughout the study periods (Figure 5b,c), differing significantly from the transects II (period 1; Tukey, $p < 0.01$) and V (periods 1 and 2; Tukey, $p < 0.01$). The highest abundance of females occurred in transects VI and VII during both periods 1 and 2 (Figure 5b,c), which differed statistically only from the transect V (Tukey, $p < 0.05$ [period 1], $p < 0.01$ [period 2]).

Significant differences in the total abundance of *X. kroyeri* were not recorded among months (ANOVA, $p = 0.17$ [period 1], $p = 0.11$ [period 2]; Table II). However, abundance peaks were identified in March 1989 and April 1989, in July 1989 and August 1989, in January 2009 and February 2009, and in May 2009 (Figure 6a). The juvenile abundance varied among months (ANOVA, $p = 0.01$ [period 1], $p < 0.01$ [period 2]; Table II). In the period 1, the highest mean number of juveniles was obtained in December, January and March, that differed statistically from February (Tukey, $p < 0.05$), when the lowest abundance was observed (Figure 6b). The months of November and May were characterized by the highest juvenile abundance during period 2 (Figure 6c). In contrast, the lowest abundance of *X. kroyeri* juveniles occurred from July to October (Figure 6c). These months differed statistically from November and May (Tukey, $p < 0.05$). The seasonal variation of the male and female abundance followed the same pattern during periods 1 and 2, although it had no shown significant differences (ANOVA, $p > 0.05$; Table II). Increases in the abundance of both sexes were observed from February 1989 to July 1989 – with a decrease in the male abundance in June 1989 – from November 2008 to February 2009, and from May 2009 to July 2009 (Figure 6b,c).

Considering the interaction between the study periods 1 and 2, the total abundance of *X. kroyeri* varied spatially and seasonally (ANOVA, $p < 0.05$; Table II), while the distribution pattern of juveniles, males and females was maintained (Table II). As mentioned above, the transects II and V were characterized by the lowest mean number of shrimps captured during period 1 (Figure 5a). As a result, they differed from all transects sampled during period 2 (Tukey, $p < 0.05$), that had a high abundance of *X. kroyeri* (Figure 5a). Similar results were observed in relation to the spatial variation in the abundance of male and females (Figure 5b,c). In February 1989 it was recorded the

lowest mean number of shrimps, contrasting with the highest abundance of the species obtained during all period 2, from November 2008 to October 2009, except in August 2009 (Tukey, $p < 0.05$; Figure 6a). Additionally, the lowest abundance of juveniles was observed in February 1989 and June 1989, which differed statistically from almost all months sampled during period 2 (Tukey, $p < 0.05$; Figure 6b,c), except from August 2009 to October 2009, when the lowest abundance of juveniles was also observed (Figure 6b,c).

3.3. Environmental variables and the association with *Xiphopenaeus kroyeri*

There was significant relationship between abundance of *X. kroyeri* and the environmental variables sampled during periods 1 and 2 (MR, $p > 0.01$ [period 1], $p = 0.02$ [period 2]; Table III; Figure 7). The best environmental variables related to the variations in abundance of the species throughout the period 1 were depth, bottom temperature and salinity, sediment fractions corresponding to Class A, B and C, and organic matter content of the sediment (MR, $p > 0.05$; Table III; ; Figure 7). During period 2, bottom temperature and sediment fraction corresponding to Class A were significantly associated with the abundance of *X. kroyeri* (MR, $p > 0.05$; Table III; Figure 7). In addition, a positive correlation was observed between the abundance of the species and the algae and plant biomass during period 2 (Spearman correlation, $R_s = 0.4$, $t = 3.6$, $p < 0.01$; Figure 7). At spatial scales (transects), depth and sediment characteristic probably exerted considerable influence on the variation of *X. kroyeri* abundance. At temporal scales (months), temperature seemed to be the most important explanatory variable, reflecting significant influence on abundance of *X. kroyeri* at Fortaleza Bay.

Table I: Principal components analysis showing the parameters of the first three principal components (PC) of environmental variables analyzed by transect and month.

TRANSECT			
	PC-1	PC-2	PC-3
Eigenvalue	3.270	1.592	1.370
% variance	47	23	20
% cumulative variance	47	69	89
Depth	0.8*	0.0	-0.5
Bottom temperature	-0.7*	0.1	0.6
Bottom salinity	0.8*	0.2	-0.3
Class A	0.7*	0.5	0.5
Class B	-0.6	0.6	-0.5
Class C	0.1	-1.0*	0.0
Organic matter	0.8*	0.1	0.5
MONTH			
	PC-1	PC-2	PC-3
Eigenvalue	2.577	1.273	1.056
% variance	43	21	18
% cumulative variance	43	64	82
Bottom temperature	0.1	-0.1	0.9*
Bottom salinity	0.4	-0.7*	-0.4
Class A	0.8*	0.4	0.0
Class B	0.9*	-0.3	0.0
Class C	-1.0*	-0.1	0.0
Organic matter	0.1	0.8*	-0.2

* = eigenvector values ≥ 0.7

Table II: *Xiphopenaeus kroyeri*. Results of the variance analysis of total abundance and by demographic categories by transect and month during each period (One-way ANOVA), and between both periods (Factorial ANOVA) (P1 = study period from November 1988 to October 1989; P2 = study period from November 2008 to October 2009; N total = total abundance; DF = degrees of freedom; MS = mean square; F = MS factor/MS residual; p = probability of significance; * $\alpha = 0.05$).

Source of variation	DF	MS				F				P				
		N total	Juvenile	Male	Female	N total	Juvenile	Male	Female	N total	Juvenile	Male	Female	
P1	Transect	6	5.31	0.35	1.26	0.82	10.55	1.52	9.52	4.25	< 0.01*	0.18	< 0.01*	< 0.01*
	Month	11	1.16	0.50	0.23	0.39	1.44	2.54	1.06	1.80	0.17	0.01*	0.40	0.07
P2	Transect	6	1.48	0.05	0.37	0.12	7.26	0.21	5.82	2.50	< 0.01*	0.97	< 0.01*	0.03*
	Month	11	0.44	0.66	0.10	0.08	1.62	4.62	1.15	1.69	0.11	< 0.01*	0.34	0.09
P1 × P2	Transect	6	1.29	0.09	0.25	0.25	3.66	0.41	2.55	2.13	< 0.01*	0.87	0.02*	0.05*
	Month	11	1.11	0.46	0.19	0.15	2.06	2.69	1.31	1.12	0.03*	< 0.01*	0.23	0.35

Table III: Results of the multiple linear regressions explaining changes in the abundance of *Xiphopenaeus kroyeri* in each study period (P1 = study period from November 1988 to October 1989; P2 = study period from November 2008 to October 2009; p = probability of significance; * $\alpha = 0.05$).

Environmental variables	P1		P2	
	t	p-level	t	p-level
Depth	3.89	< 0.01*	1.25	0.21
Bottom temperature	-2.27	0.03*	2.00	0.05*
Bottom salinity	-1.06	0.29	-0.11	0.91
Class A	-2.06	0.04*	-3.06	0.00*
Class B	-2.59	0.01*	-1.41	0.16
Class C	1.99	0.05*	-1.10	0.27
Organic matter	-2.42	0.02*	0.09	0.93

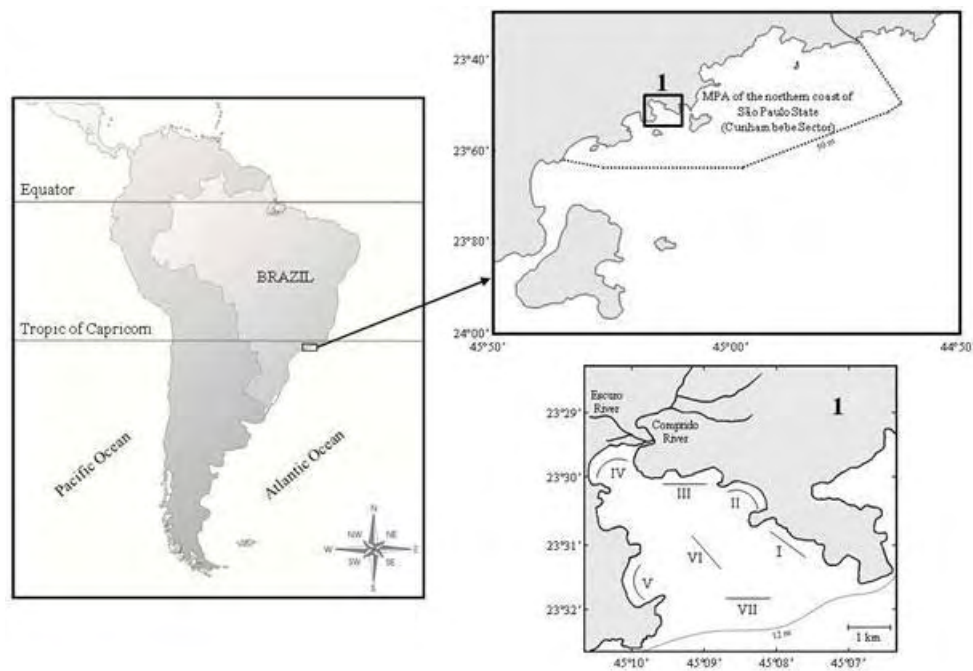


Figure 1: Map of the study region showing the Marine Protected Area (MPA – Cunhambebe Sector) and Fortaleza Bay with the sampling transects.

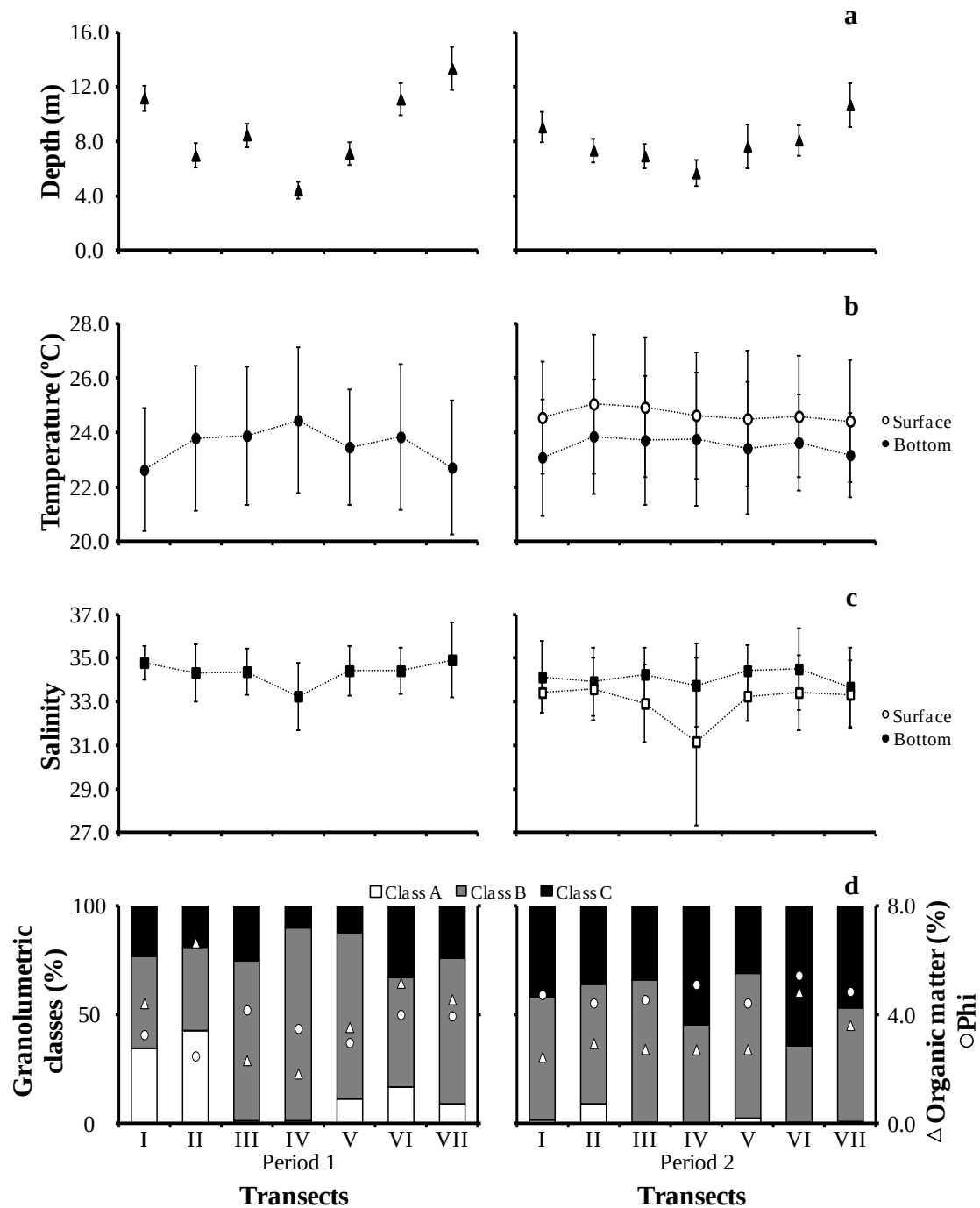


Figure 2: Spatial variations of the environmental variables at Fortaleza Bay during the sampling periods 1 and 2.

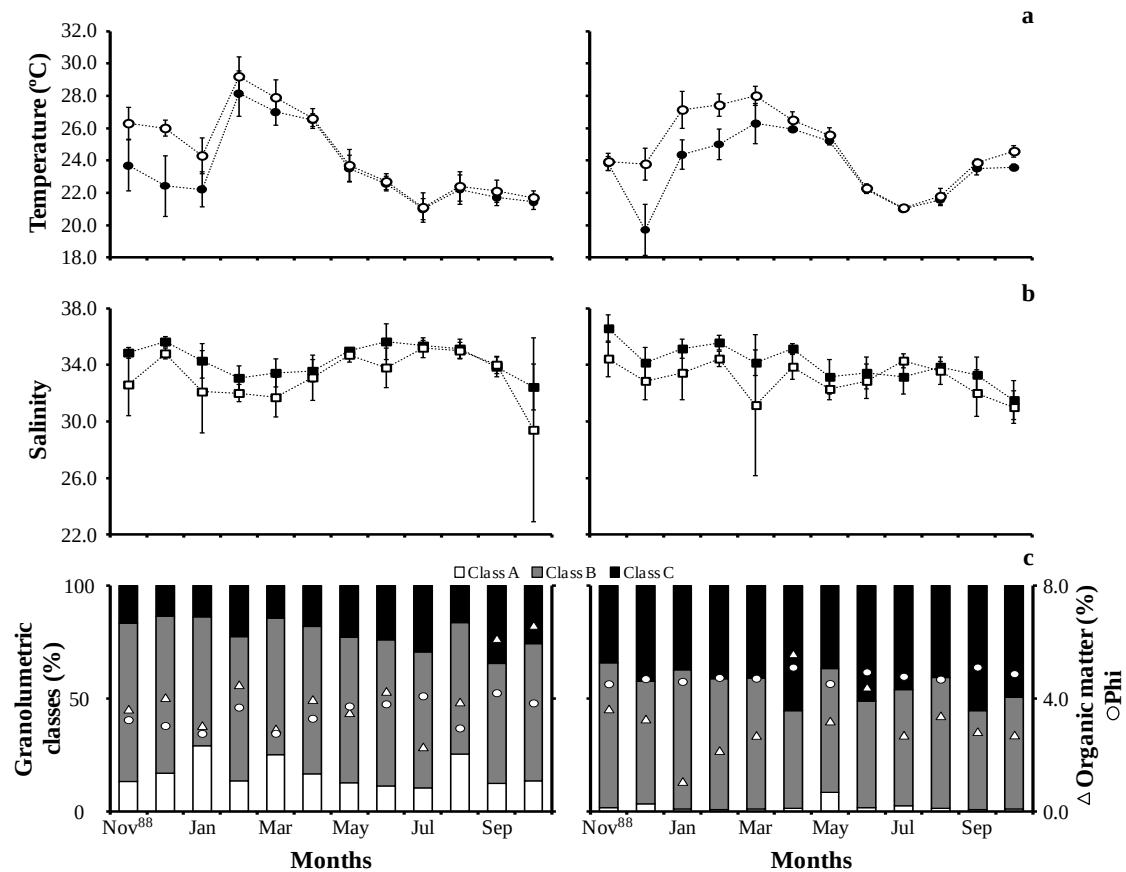


Figure 3: Monthly variations of the environmental variables at Fortaleza Bay during the sampling periods 1 and 2.

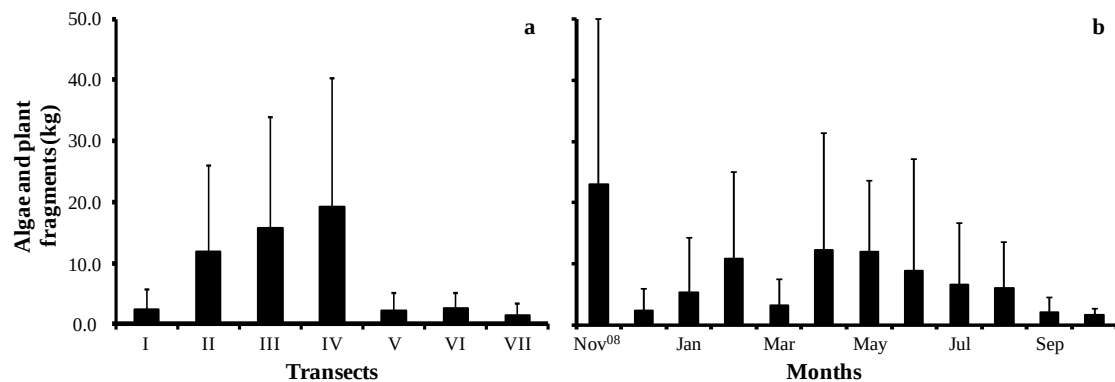


Figure 4: Spatial and monthly variations of the algae and plant fragments biomass at Fortaleza Bay during the sampling period 2.

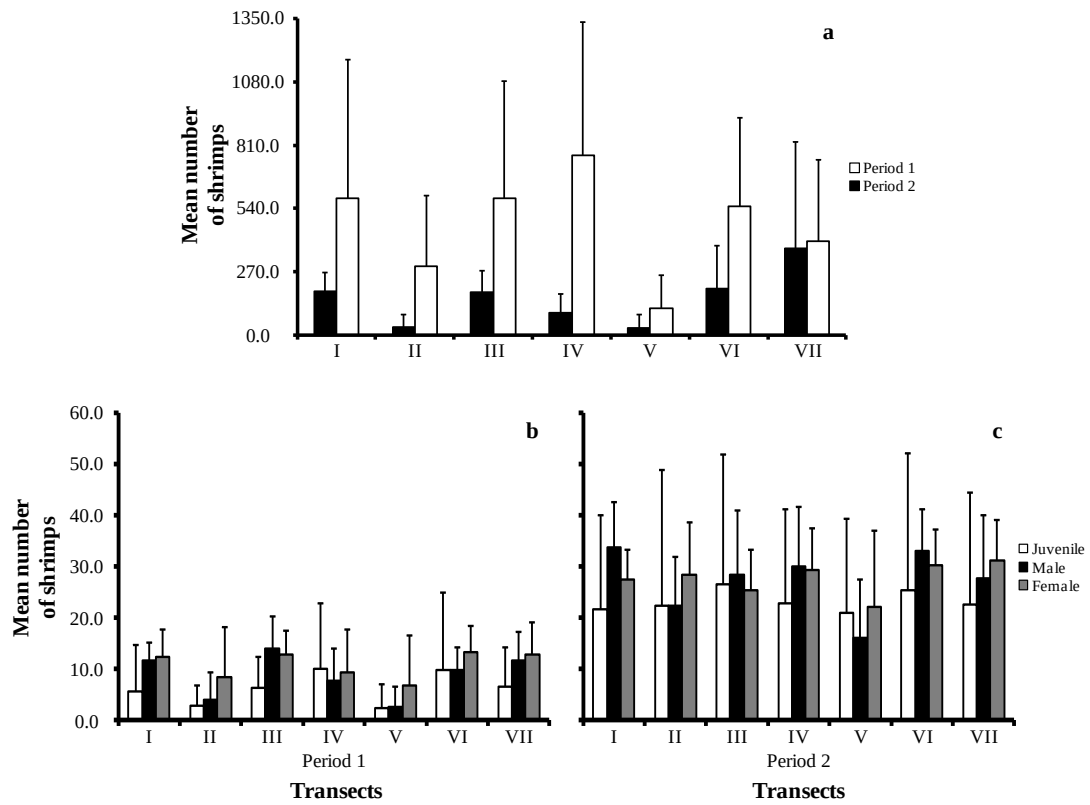


Figure 5: *Xiphopenaeus kroyeri*. Mean number of shrimp by transect during the sampling periods 1 and 2 (error bars denote standard deviation).

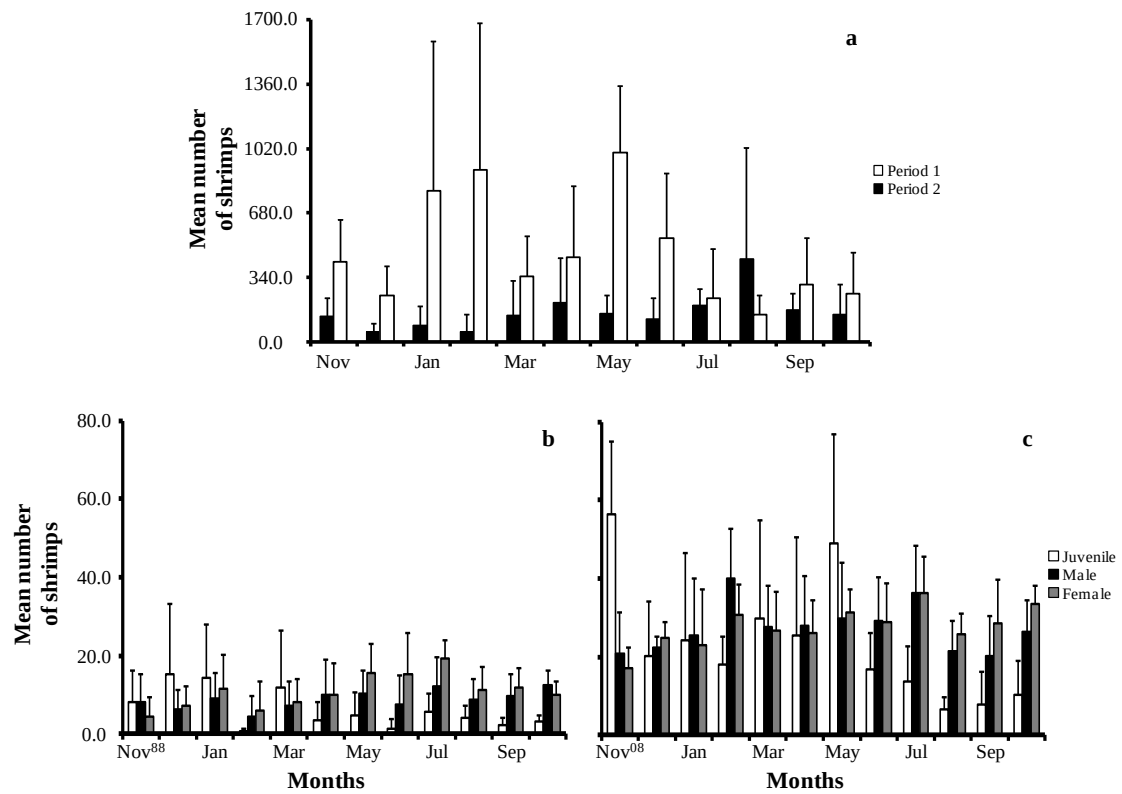


Figure 6: *Xiphopenaeus kroyeri*. Mean number of shrimp by month during the sampling periods 1 and 2 (error bars denote standard deviation).

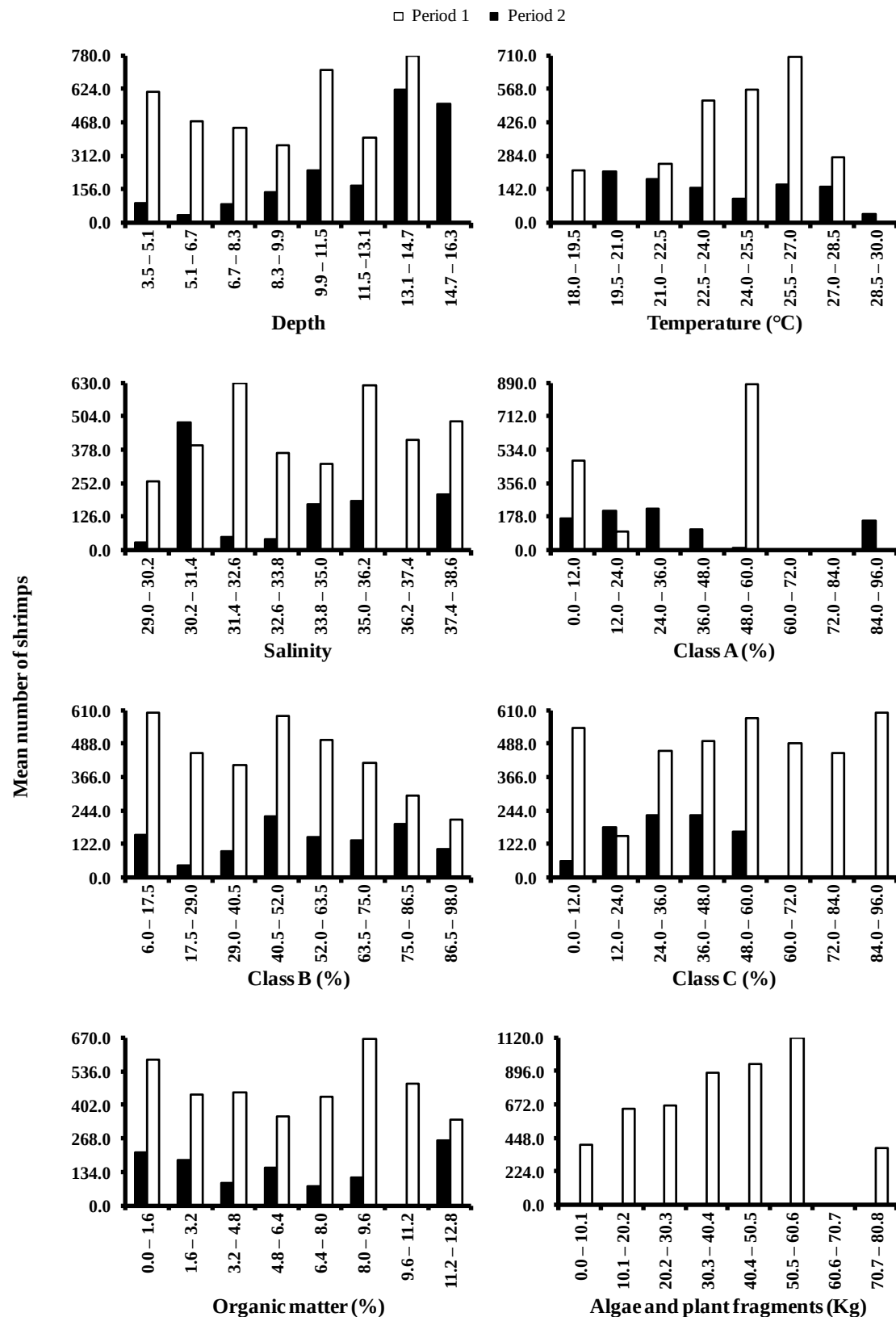


Figure 7: *Xiphopenaeus kroyeri*. Mean number of shrimp per trawling (CPUE) for each class of environmental variable analyzed at Fortaleza Bay.

4. Discussion

Over a range of 20 years, the environmental variables analyzed within Fortaleza Bay showed relevant changes at spatial and temporal scales, resulting in significant associations between them with the abundance of *X. kroyeri*. Such changes in environmental variables might have been caused by natural phenomena, as El Niño / La Niña Southern Oscillation (ENSO / LNSO) events, and hydrodynamic processes, and / or human activities, as urban growth.

A remarkable sedimentation occurred between the first and the second study periods was observed within Fortaleza Bay, especially with respect to the variation of the sediment fraction corresponding to Class C, which resulted in high deposition rates of finer grains during period 2 and considerable reduction of the depth. The interaction of several processes, as wind, water masses circulation, tidal currents, and waves can be responsible for such sedimentation (Mahiques et al., 1998, 2002, 2004, 2005, 2010; Gyllencreutz et al., 2010; Conti et al., 2012). According to Gyllencreutz et al. (2010), the Southeastern Brazilian shelf is very susceptible to wind and wind-driven current systems with opposite directions, comprising the southward-flowing Brazil Current (BC) and the northward-flowing Brazilian Coastal Current (BCC). The confluence of these two main wind-driven current systems around 24°S implies an important influence on sediment transport along the Southeastern Brazilian shelf (Gyllencreutz et al., 2010). During intense events of ENSO and LNSO, fine sediments deposited in the La Plata River, in connection with high discharge and in association with wind pattern in southern Brazil, are resuspended and carried alongshore the Southeastern Brazilian shelf by the BCC, resulting in an elevated contribution of finer grains northward (Gyllencreutz et al., 2010; Mahiques et al., 2010). Importantly, according to the mouth orientation of Fortaleza Bay, it is strongly influenced by hydrodynamic processes

coming from the southern and southwestern (Mahiques et al., 1998). In addition, intense events of El Niño (1990-1993 and 1997-1998) and La Niña (1988-1989 and 2007-2008) were observed during the interval between both study periods (CPTEC, 2012; NOAA, 2012). Therefore, the combination of all these hydrodynamic processes probably resulted in great input of finer sediments to the study region, characterizing the current sedimentation observed.

Another possible cause of the finer sediment accumulation within Fortaleza Bay would be the urbanization. Marine and coastal ecosystems are among the most productive ecosystems, providing a range of important and valuable social and economic benefits to humans (UNEP, 2006; Katsanevakis et al., 2011). However, these ecosystems have been continuously affected and altered by several human activities (UNEP, 2006; Katsanevakis et al., 2011; Parravicini et al., 2012). On the coast of São Paulo State, as well as along the Brazilian coastline, urbanization rates are relatively high, and in association with the fragility of the coastal ecosystem, considerable changes have been identified, as erosion and siltation of Escuro and Comprido rivers and margins of Fortaleza Bay. According to Muehe (2006), 80% of the causes of erosion along the Brazilian coastline are attributed to impacts related to urbanization, which interfere in the sediment flux through construction of rigid structures. The study region is characterized by beautiful sandy beaches surrounded by the exuberant Atlantic Forest, being considered as a tropical paradise very attractive for tourists. As a result, in the recent years there was a noteworthy increase in the number of vacation homes installed around Fortaleza Bay, mainly in permanent protected areas as mangrove and restinga forests (Cunha-Lignon et al., 2009). Furthermore, in an attempt to support and improve such urban growth, a new bridge over the Escuro and Comprido rivers

connecting the cities of Ubatuba and Caraguatatuba was built, which may have further contributed to the accumulation of finer grains within study region.

As observed, Fortaleza Bay has continuously experienced significant changes of natural and anthropogenic origin. Regarding the urban growth, the sedimentation could be considered as a negative effect, but in the present investigation it seemed to play a significant role in the habitat selection by *X. kroyeri*, favoring the high abundance of the species. Previous studies have shown that finer sediments are extremely important in driving spatial distribution patterns of several penaeid shrimps, including *X. kroyeri* (Dall et al., 1990; Costa et al., 2000, 2005a, b, 2007, 2011; Fransozo et al., 2002, 2004; Costa and Fransozo, 2004; Castilho et al., 2008a, b; Simões et al., 2010; Freire et al., 2011; Hiroki et al., 2011), most probably due to their burrowing behavior, which is facilitated in such sediment by reducing energy requirements for excavation (Dall et al., 1990; Freire et al., 2011). During both study periods 1 and 2, the coarse grain amounts observed within some transects, mainly in transect II, resulted in negative associations with the abundance of *X. kroyeri*, since it could interfere in the burrowing behavior of the species. Experimental studies showed that *X. kroyeri*, as well as penaeid shrimps in general, excavate more rapidly in sediment between 62.00 µm and 1.00 mm (Dall et al., 1990; Freire et al., 2011). Indeed, finer sediments might allow these shrimps to excavate deeper and escape from potential predators (Dall et al., 1990; Freire et al., 2011). Interestingly, during period 1, high coarse grain amount was observed in transect I, but the abundance of *X. kroyeri* was similar compared to the other transects characterized mostly by finer sediments. Nevertheless, the transect I was also characterized by considerable silt and clay amount during period 1. The preference of *X. kroyeri* by finer sediments would not be only associated with the burrowing facilities, but also with the turbidity resulting from the excavation processes, in an attempt to distract the predator

and avoid predation due to suspension of silt and clay deposited on the sediment. According to Freire et al. (2011), if a specific substrate used by a species provides differential protection against predators, the predation would exert a strong direct influence on the substrate preference of the species.

All demographic categories, including juveniles, males and females of *X. kroyeri*, showed similar patterns of spatial distribution throughout the study periods 1 and 2, occurring preferentially in transects with sediment composed by fine and very fine sand and silt and clay. In general, finer sediments are associated with elevated organic matter content (Burone et al., 2003), which can constitute an important food source for many marine invertebrates (Lenihan and Micheli, 2001). During period 1, a negative relationship was verified between the abundance of *X. kroyeri* and the organic matter content. Probably, the lower number of specimens sampled in transect II, which showed the highest organic matter content, might result such relationship. Conversely, the other transects, in which the mean phi values were > 3 , with organic matter content varying from 2 to 5, showed an elevated number of individuals, reinforcing the importance of the sediment and its characteristics in explaining the distribution patterns of *X. kroyeri* at Fortaleza Bay. Along the southeastern Brazilian coast, some authors have obtained similar results regarding the distribution patterns of *X. kroyeri* in areas with high percentage of silt and clay phi values (Fransozo et al., 2002, Costa et al., 2007, 2011; Simões et al., 2010). However, correlation positively significant between shrimp abundance and the organic content of the sediment has not been detected. In the present study, beyond the burrowing facilities, the differential sediment preferences of *X. kroyeri* might be also related to food availability in the organic matter content, as related before for the majority of penaeid shrimps (Dall et al., 1990). To the best of the present knowledge, some organic and inorganic debris were described as essential food

items consumed by *X. kroyeri* (Cortés and Criales, 1990; Branco and Moritz-Junior, 2001; Branco, 2005). Therefore, the organic matter content of the sediment at Fortaleza Bay could represent an important food source for *X. kroyeri*, providing conditions extremely favorable for the occurrence and establishment of the species.

In general, the organic matter along the southeastern coast of Brazil is constantly enhanced by upwelling processes and terrigenous input (Mahiques et al., 2004, 2011; Sumida et al., 2005; De Léo and Pires-Vanin, 2006; Carreira et al., 2012). During period 2, considerable biomass of algae and plant floating near the marine floor was recorded at Fortaleza Bay. These floating debris might be exported through the small rivers Escuro and Comprido, and accumulate in transects IV, III and II, given the hydrodynamic circulation within the bay (Mahiques, 1995; Mahiques et al., 1998). Unfortunately, no estimation of debris biomass was recorded during period 1. However, the abundance of *X. kroyeri* correlated positively with the algae and plant biomass during period 2; the highest abundance of the species was registered in transect IV, which showed the highest algae and plant biomass. Such algae and plant biomass also appears to be an important resource in the habitat selection by the caridean shrimp *Nematopalaemon schmitti* (Holthuis, 1950) at Ubatuba Bay, northern coast of São Paulo State (Fransozo et al., 2009; Almeida et al., 2012). Castro et al. (2005) and Almeida et al. (in press) suggested that large amounts of algae and plants floating near the marine floor might provide benefits to juveniles of *X. kroyeri*, protecting them against predators, as this material most probably increases environmental heterogeneity in structurally simple soft bottom habitats (Fransozo et al., 2009). In this study, the juvenile shrimps, as well as male and female shrimps, were caught in all transects during trawl samples, including those with low algae and plants biomass. These algae and plant biomass floating near the bottom might complement the organic matter

content at Fortaleza Bay. Therefore, the availability of this additional food source for all demographic categories of *X. kroyeri* could be much more relevant in controlling the abundance of the species than the protection itself, given that *X. kroyeri* might benefit from a larger quantity of prey that would live on such amounts of floating algae and plants. However, no data about species composition of this debris are available. In this way, future studies will elucidate the standards governing the relationship between the abundance of *X. kroyeri* and algae and plant biomass floating near the marine floor in the study region.

The current analysis demonstrated the importance of bottom temperature in affecting the abundance of the studied shrimp. Significant negative and positive associations were obtained between this environmental variable and the abundance of *X. kroyeri* during study periods 1 and 2, respectively. During period 1, the species was most abundant during the months corresponding to winter (42% of the total specimens caught) in the southern hemisphere (spring: November and December; summer: January–March; autumn: April–June; winter: July–September; spring: October), when bottom temperature reached low mean value (21.6°C). During period 2, the highest abundance of *X. kroyeri* was obtained in summer and fall (36 and 35% of the total specimens caught, respectively), mainly in the months of January 2009, February 2009 and May 2009. Concomitantly, during these seasons the highest mean values of bottom temperature were recorded (25.2 and 24.5°C). Despite the slight variations in bottom temperature observed throughout the study periods 1 and 2, in general it followed a similar pattern, with the exception of the mean value recorded in December 2008 (19.7°C). Interestingly, juvenile specimens were most abundant in spring and summer during both study periods, probably due to the reproductive peaks of *X. kroyeri* usually recorded in late summer + early fall and spring in the same study region (Nakagaki and

Negreiros-Fransozo, 1998; Castro et al., 2005; Almeida et. al, in press; Heckler et al., in press; Castilho et al., submitted).

In previous studies conducted in the Ubatuba region, the largest and smallest catches of *X. kroyeri* were taken mostly during winter and summer, respectively (Costa et al., 2007, 2011; Castilho et al., 2008a; Simões et al., 2010). These authors suggest that seasonal variation in the capture of the species may be related to the interaction of the water masses SACW and TW present over the Southeastern Brazilian shelf (see Material and Methods). According to Costa et al. (2007, 2011) and Castilho et al. (2008a), the intrusion of the SACW into the continental shelf during late spring and summer causes a decrease in bottom temperature and confines the *X. kroyeri* population to shallower areas (< 15 m). The retreat of this cold water mass and the incursion of TW during autumn and winter increase considerably the abundance of the species on the southeastern coast of Brazil. In this investigation, slight thermocline was observed during first months of study, with a possible intrusion of the SACW in December 2008, and surface and bottom temperatures relatively homogeneous from April to October in both study periods. However, based on the mean values of bottom temperature and salinity, the CW (temperature > 20°C and salinity < 36) was constantly present at Fortaleza Bay during both study periods. Therefore, the interaction of SACW and TW did not appear to influence the distribution pattern of *X. kroyeri* at Fortaleza Bay because the species abundance showed distinct patterns between the study periods 1 and 2. Thus, *X. kroyeri* appeared to be most under influence of CW. The high temperature of this water mass (> 20°C) (Castro-Filho et al., 1987), associated with the rich continental suspended material in it (Mahiques et al., 1998, 2004), probably contributed to the great abundance of *X. kroyeri* at Fortaleza Bay, providing suitable conditions for the settlement and life cycle development of the species in the study region.

Climate changes have been suggested before to affect fishing activities, fishers and their communities (Turner et al., 1998; Garcia et al., 2004; Criales et al., 2003; UNEP, 2006; Perry and Sumaila, 2007; Daw et al., 2009; Kalikoski et al., 2010; Overland et al., 2010; Martinho et al., 2012; Pereira and D’Incao, 2012). In South America, the ENSO-related climate anomalies is responsible for changes in salinity, temperature, stratification and water circulation patterns, influencing phytoplankton productivity (Wang and Fiedler, 2006). According to Paes and Moraes (2007), the interaction between the ENSO events and the local oceanographic conditions along the Southeastern Brazilian shelf lie within the primary productivity patterns. These authors suggest that after an intense warm ENSO, the primary productivity and the fishery production should expect an increase, in relation to non ENSO periods. In this sense, the intense El Niño (1990-1993 and 1997-1998) events recorded within the range of 20 years between the study periods 1 and 2, might have contributed to the increase of the primary productivity, and consequently favor the high abundance of *X. kroyeri*. In addition, the species reproduces continuously but with dissimilar intensity throughout the year on the southeastern coast of Brazil, (Nakagaki and Negreiros-Fransozo, 1998; Castro et al., 2005; Almeida et. al, in press; Heckler et al., in press; Castilho et al., submitted). Importantly, the highest reproductive intensity of *X. kroyeri* occurs at a time of the year (spring and summer) when the SACW intrudes into the continental shelf, which is the main source of nutrient transport into the study region (Pires, 1992; Aidar et al., 1993, Odebrecht and Castello, 2001). Thus, high nutrient load entering to the system due to the ENSO events, associated with the nutrient inputs from the SACW intrusions and consequent primary productivity increase, are expected to boost larval condition and/or survival of *X. kroyeri* in the study region. However, modeling analyses are necessary to predict the diversity of processes occurring along the Southeastern

Brazilian shelf, which might be linked to coastal upwelling systems and ENSO events on the primary productivity and increasing fisheries.

Until now, only the importance of some environmental variables in explaining the elevated abundance of *X. kroyeri* at Fortaleza Bay was highlight. However, given that coastal ecosystems represent valuable ecological-economic resources, several measures have been proposed in order to contribute to the correct management of these resources to sustainable levels of exploitation (Palumbi, 2001; Amaral and Jablonski, 2005; Prates, 2007; Gillett, 2008; McCay and Jones, 2011; Rice and Houston, 2011), as well as to the carrying capacity of marine ecosystems for harvestable species (Vasconcellos and Gasalla, 2001), and consequent conservation of the biological diversity (Palumbi, 2001; Amaral and Jablonski, 2005). The most common management measures include controlling fishing effort through permit requirements, restrictions on the size and number of vessels, mesh size regulations, determination of minimum size catch of target species, closed seasons and/or areas, among others (Perez et al., 2001; Amaral and Jablonski, 2005; Gillett, 2008; Devaraj, 2010). Coastal management in Brazil is conducted by a national plan legally enforced, complemented by states and counties plans, and a coastal ecological-economic zoning (EEZ) limited to small portions of the coastal zone (Jablonski and Filet, 2008). The creation of the Anchieta Island State Park integrated into a conservation unit (Proclamation No. 9 629, March 29, 1977, and Federal Law No. 9 985, July 18, 2000), implementation and regulation of the coastal EEZs (Proclamation No 5 300, December 07, 2004), and recent establishment of the special management area at Mar Virado Island and the MPA of the northern coast of São Paulo State (Proclamation No. 53 525, October 08, 2008), reduced drastically the fishing boats operating at Fortaleza Bay in the course of 20 years,

contributing significantly to the stock enhancement of *X. kroyeri* in the study region, in which the abundance almost tripled over a range of 20 years.

Also, the abundance peak recorded in May 2009 is a positive result of the closed season dictated by the Ministry of the Environment (Normative Instruction No. 189, September 23, 2008) for the southeastern and southern regions of Brazil, which comprehends the months from March 01 to May 31. Importantly, during the years of 2006 and 2007, the closed season was defined from October 1 and December 31, motivating the protection of the main peak reproductive of *X. kroyeri*, which occurs during spring along the southeastern and southern Brazilian coastline. According to Pezzuto et al. (2008), the effectiveness of this newly management measure could be jeopardized by excessive levels of fishing mortality that reduce the spawning biomass, limiting levels before the reproductive period of the species. Thus, since the year 2008, the closed season of *X. kroyeri* was again set to the current period, which was priority implemented to protect the coastal recruitment migration of the pink shrimps (*Farfantepenaeus* spp.). However, as *X. kroyeri* occurs and is extensively exploited in depth less than 30 m in the southeastern and southern regions of Brazil (Branco et al., 1999; Costa et al., 2000, 2007, 2011; Fransozo et al., 2000, 2002; Branco, 2005; Castro et al., 2005; Castilho et al., 2008a, submitted; Pezzuto et al., 2008; Simões et al., 2010; Fernandes et al., 2011; Heckler et al., in press), the current closed season also seems to be an efficiently measure to protect the first annual reproductive peak as well as the juvenile recruitment of *X. kroyeri* within this MPA and within non MPAs, contributing to the maintenance and sustainability of this resource. But, the adoption of methods for improving selectivity in the fishing gears used by shrimp boat in the study region, as proposed by Silva et al. (2011, 2012) for canoe-trawl fishery off southern Brazil, might reduce the impacts caused by the trawling activities in the study region, once juveniles

and adults of *X. kroyeri* are caught at the same place and time, probably resulting in imbalances at sustainable levels of this resource upon which the necessary livelihoods of the local traditional human communities depend.

In an abundance monitoring study of the pink shrimps *F. brasiliensis* and *F. paulensis* conducted on the southern coast of Brazil, Freitas Jr et al. (2011) observed that physical disturbances of estuarine environments promote less damage to shrimp stocks than do other potential anthropic influences, such as overfishing pressure on adults and juveniles and excessive discharges of domestic effluents. In the present study, although all hypotheses suggested in order to elucidate such elevated abundance of *X. kroyeri* at Fortaleza Bay over a range of 20 years, as deposition of finer sediments through hydrodynamics processes as well as urban growth, temperature variation and its relationship to water masses interaction, increase of food availability, and finally the primary productivity enhanced in association with natural phenomena El Niño and La Niña, the management measures created, as the absence of industrial fishing through the establishment of the MPA and the closed season, were essential to the settlement and occurrence of *X. kroyeri* at Fortaleza Bay, representing important tools for conservation, preservation and sustainable use of all resources available in the study region.

5. References

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Capítulo III

*Population structure and sex ratio of the
seabob shrimp *Xiphopenaeus kroyeri*
(Heller, 1862) (Decapoda: Penaeidae) on the
southeastern coast of Brazil*

Abstract

The seabob shrimp *Xiphopenaeus kroyeri* constitutes the second most important fishery resource on the southeastern coast of Brazil. In this study, the population structure – based on size frequency distribution – and the sex ratio of the species were recorded monthly during two distinct periods; from November 1988 to October 1989 (period 1), and from November 2008 to October 2009 (period 2), at Fortaleza Bay, northern coast of São Paulo State. In general, the population structure of *X. kroyeri* seemed to be relatively stable throughout both sampling periods, with similar size frequency distribution between males and females, and continuous occurrence of juveniles and adults. Females attained larger body sizes than males in relation to carapace length (CL) ($\sigma = 16.2 \pm 3.0$ mm CL [period 1], 15.3 ± 3.4 mm CL [period 2]; $\phi = 16.9 \pm 4.3$ mm CL [period 1], 15.5 ± 4.6 mm CL [period 2]), showing reverse pattern of sexual dimorphism, most probably related to the reproductive strategies display by *X. kroyeri*. The overall sex ratio of the seabob shrimp at Fortaleza Bay was biased toward females. Interestingly, the sex ratio of juvenile shrimps was female-biased during most of the study periods 1 and 2. By contrast, the sex ratio of adults was male- and female-biased, but in general, it remained in equilibrium. The male mating opportunities, in turn driven by the abundance of reproductively active females, might drive the timing of sexual maturity in males of *X. kroyeri*, resulting in deviations at sex ratio between juveniles and adults. These findings can contribute significantly to the understanding of the population dynamics of *X. kroyeri* in the study region, providing essential information on an effective and sustainable use of this important natural resource on the southeastern Brazilian coast.

Keywords: Sexual dimorphism; size frequency distribution; reproductive strategies

1. Introduction

Studies on population dynamic of the species can lead to a better comprehension of the processes influencing the inter- and intra-species interactions at spatial and temporal scales. Such studies provide a useful evaluation of the vulnerability of the population to fragmentation, which might result from natural or human-induced disturbances (Ricklefs and Miller, 1999). Concerning the fisheries, growth and mortality estimates provide essential information about the population status and its maintenance, since the stock assessment and management rely on these parameters (Kevrekidis and Thessalou-Legaki, 2011).

Fishing activities in marine ecosystem have both temporary and long-term effects on such ecosystem, which might severely impact the structure of many populations, as well as their ability to replenish themselves (Dayton et al., 2002). Along the Brazilian coastline, the long term exploitation of many crustaceans have resulted in a continuous decline in the stocks and reduction in the size of individuals, including the pink shrimps *Farfantepenaeus brasiliensis* (Latreille, 1817) and *F. paulensis* (Pérez Farfante, 1967), the white shrimp *Litopenaeus schimitti* (Burkenroad, 1936), and the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) (Amaral and Jablonski, 2005). Consequently, in the last years there was a steady increase in studies on population dynamics of these species, even as other target penaeid shrimps as *Artemesia longinaris* Bate, 1888 and *Pleoticus muelleri* (Bate, 1888), which have particularly addressed subjects such as age structure, growth, sex ratio, reproductive biology, and juvenile recruitment (e.g., Nakagaki and Negreiros-Fransozo, 1998; Fransozo et al., 2000; Castro et al., 2005; Leite Jr et al., 2006; Castilho et al., 2007a,b, 2008, 2012, submitted; Costa et al., 2008, 2010, 2011; Fernandes et al., 2011; Freitas Jr et al., 2011; Capparelli et al., 2012; Almeida et al., in press; Heckler et al., in press). All these studies have

contributed significantly to a rational management, conservation and preservation of the natural stocks of these shrimp populations.

On the southeastern coast of Brazil, *X. kroyeri* (Heller, 1862) is one of the most valuable species of shrimp targeted by industrial and artisanal fisheries (Vasconcellos et al., 2007, 2011; Ministry of Fisheries and Aquaculture, 2012), constituting the second most important fishery resource (Castro et al., 2005; Costa et al., 2007). In Ubatuba region, northern coast of São Paulo State, the artisanal fishery has high socio-economic importance, where hundreds of fishermen are involved in such activity (Costa et al., 2008). In this region, *X. kroyeri* has been extensively exploited by artisanal fishery in shallow waters down to 20 m (Costa et al., 2007), where the abundance of the species is relatively high (Holthuis, 1980; Costa et al., 2007). According to the authors Castro et al. (2005) and Costa et al. (2007, 2011), juvenile individuals are not dependent on estuaries, completing their life cycle in shallow areas. So, *X. kroyeri* is classified as life cycle type III rather than type II as reported by Dall et al. (1990). In the life cycle type III, the species are restricted to truly marine environments. As a result, both juveniles and adults are largely caught by artisanal fishing boats, causing possible disturbances on population structure of *X. kroyeri* in the Ubatuba region.

The aim of this investigation was contributing to the knowledge of the population dynamics of *X. kroyeri*. The study was conducted at Fortaleza Bay, a Marine Protected Area (MPA) (Proclamation No. 53 525, October 08, 2008) located on the southeastern coast of Brazil. This MPA has recently been established in order to prioritize the conservation, preservation and sustainable use of this and other resources in the region. Variations in population structure, sexual dimorphism, and sex ratio of the species were analyzed monthly during two distinct periods; from November 1988 to October 1989, and from November 2008 to October 2009, in an attempt to provide

essential information about biology of *X. kroyeri*, promoting an effective and sustainable use of this important natural resource on the southeastern Brazilian coast.

2. Material and Methods

2.1. Data collection

The present study comprised two distinct sampling periods: period 1, from November 1988 to October 1989; and period 2, from November 2008 to October 2009. The same methodology was used in both periods.

Shrimp samples were collected monthly during periods 1 and 2 using a fishing boat equipped with double-rig nets (7.5 m wide; 2.0 m mouth; 15 mm and 10 mm mesh diameter at the body and cod end of the net, respectively). A total of 7 permanent transects were established within the Fortaleza Bay (Figure 1). Each transect was trawled for 1 km (each trawl lasted ~ 20 min) covering a total area of 4 km² transect⁻¹.

A total of 13 298 and 39 553 specimens of *X. kroyeri* were captured from 168 trawls conducted throughout the sampling periods 1 (84 trawls) and 2 (84 trawls), respectively. Logistic and time constraints did not permit sexing and measuring each collected individual in such large sample. Thus, subsamples of 100 (period 1) and 250 (period 2) g were randomly separated from each sample for analysis.

Individuals were sexed (presence of petasma in males and thelycum in females; see Bauer, 1986, 1991; Fransozo et al., 2011) and measured using a caliper to nearest 0.1 mm. Carapace length (CL, mm), measured from the orbital angle to the posterior margin of the carapace, was recorded for each shrimp. Next, shrimps were separated into three demographic categories: juveniles, adult males and females. During period 1, shrimps smaller than 13.7 mm carapace length were considered juveniles according to the size at which 50% of the population reached sexual maturity (see Fransozo et al., 2000). Whereas in the period 2, males and females were categorized as juveniles or adults based on macroscopic observations of secondary sexual characters (petasma and

thelycum) and maturity stage of terminal ampoules (in males) and ovaries (in females) (see Almeida et al., in press).

2.2. Data analysis

During periods 1 and 2, monthly length frequency distributions were constructed using 2.0-mm CL size intervals for both males and females, allowing the detection and displacement of modes according to data analyses. A Kolmogorov-Smirnov two sample test (KS; $\alpha = 0.05$) was used to detect any difference between male and female size frequency distribution. Whereas, a Student's t-test ($\alpha = 0.05$) was used to compare differences in the body size of male and female throughout each sampling period. Homoscedasticity and normality of the data set were evaluated and found satisfactory (Zar, 2010).

The sex ratio of *X. kroyeri* was estimated as the quotient between the number of males and the total number of individuals in the samples. Thus, sex ratio values higher or lower than 0.5 indicate a skew toward males or females in the population, respectively. For each sampling month, deviations from a 1:1 sex ratio were tested using a Binomial test ($\alpha = 0.05$) (Wilson and Hardy, 2002). Differences throughout the sampling periods 1 and 2 were also tested using a Chi-square test (χ^2 , $\alpha = 0.05$).

3. Results

A total of 2 180 and 6 569 specimens were sexed and measured throughout the sampling periods 1 and 2. Based on carapace length of the juveniles, adult males and females, the size ranges, means, and standard deviations values are reported in Table I.

The total size frequency distribution of *X. kroyeri* at Fortaleza Bay was similar between the study periods 1 and 2, showing a unimodal size frequency distribution for both sexes (Figure 2). The size classes with interval of 10.0 – 14.0 mm CL showed the most abundance of juveniles, whereas the adults were most abundant in the size classes with interval of 14.0 – 20.0 mm CL. Importantly, during study period 1, the highest abundance of juveniles and adults were recorded in size classes with greater interval compared to the study period 2 (juveniles = 12 – 14 mm CL [period 1]; 10 – 12 mm CL [period 2]; adults = 16 – 18 mm CL [period 1]; 14 – 16 mm CL [period 2]; Figure 2), although both males and females reached the largest size during the latter study period (Table I).

In figures 3 and 4 are represented the monthly size frequency distribution of males and females for the study periods 1 and 2. Overall, the population structure of *X. kroyeri* also followed similar pattern. The presence of juveniles and adults was recorded throughout all study periods. Relatively high occurrence of juveniles was observed in the first sampling months, from November to January during study periods 1 and 2, in March 1989-2009, April 2009 and May 2009, mainly in the size class with interval of 10 – 12 mm CL. In turn, a predominance of adults in the population occurred in February and from June to October during both study periods, usually in the size class with interval of 14 – 16 mm CL.

Differences were statistically obtained in the size frequency distribution of males and females (KS, $p < .001$ [periods 1 and 2]). During study periods 1 and 2, males

measured from 7.5 to 25.8 mm CL, and from 6.0 to 26.6 mm CL, with mean size of 16.2 ± 3.0 and 15.3 ± 3.4 mm CL, respectively. While females showed mean size of 16.9 ± 4.3 and 15.5 ± 4.6 mm CL, ranging from 4.1 to 34.7 mm CL, and from 4.5 to 35.4 mm CL, during study periods 1 and 2, respectively. In general, females reached larger mean body sizes than males (Student's t-test, $p < .001$ [period 1], $p = 0.04$ [period 2]). However, exceptions to this generality were observed in December 1988, November 2008, and March 2009, when the opposite occurred (males > females) and differed statistically (Student's t-test, $p = 0.04$, $p < 0.01$, $p < 0.01$, respectively) (Figure 5).

Taking into account the total number of shrimps collected during the entire sampling periods 1 and 2 (period 1 = 958 males and 1 222 females; period 2 = 3 106 males and 3 463 females), the overall sex ratio was skewed toward females (sex ratio = $0.44 \text{ ♂} : 1.0 \text{ ♀}$, 95% confidence interval = $0.42 \text{ ♂} : 1.0 \text{ ♀} - 0.46 \text{ ♂} : 1.0 \text{ ♀}$, Binomial test, $p < 0.01$ [period 1]; sex ratio = $0.47 \text{ ♂} : 1.0 \text{ ♀}$, 95% confidence interval = $0.46 \text{ ♂} : 1.0 \text{ ♀} - 0.48 \text{ ♂} : 1.0 \text{ ♀}$, Binomial test, $p < 0.01$ [period 2]). Also, the sex ratio estimated for juveniles differed significantly during study periods 1 and 2 (Chi-square test, $\chi^2 = 29.31$, $df = 11$, $p < 0.01$ [period 1]; $\chi^2 = 53.14$, $df = 11$, $p < 0.01$ [period 2]). In turn, the sex ratio estimates for adult individuals only differed significantly in the study period 1 (Chi-square test, $\chi^2 = 27.00$, $df = 11$, $p < 0.01$ [period 1]; $\chi^2 = 15.85$, $df = 11$, $p = 0.15$ [period 2]). Interestingly, all significant differences in the juvenile sex ratio were skewed toward females (Figure 6a). In adults, the sex ratio was skewed toward males in November 1988 and February 2009, and toward females from May 1989 to July 1989, and in September 2009 and October 2009 (Figure 6b).

Table I: *Xiphopenaeus kroyeri*. Size (mm) of the specimens based on carapace length (N = number of individuals; Min = minimum; Max = maximum; SD = standard deviation; P1 = study period from November 1988 to October 1989; P2 = study period from November 2008 to October 2009).

Demographic category	N		Min – Max		Mean ± SD	
	P1	P2	P1	P2	P1	P2
Juvenile males	214	813	7.5 – 13.6	6.0 – 14.0	12.0 ± 1.2	11.2 ± 1.7
Juvenile females	310	1136	4.1 – 13.6	4.5 – 14.4	11.5 ± 1.6	10.5 ± 2.1
Adult males	744	2293	13.7 – 25.8	11.0 – 26.6	17.4 ± 2.2	16.8 ± 2.6
Adult females	912	2327	13.7 – 34.7	12.9 – 35.4	18.8 ± 3.3	17.9 ± 3.4

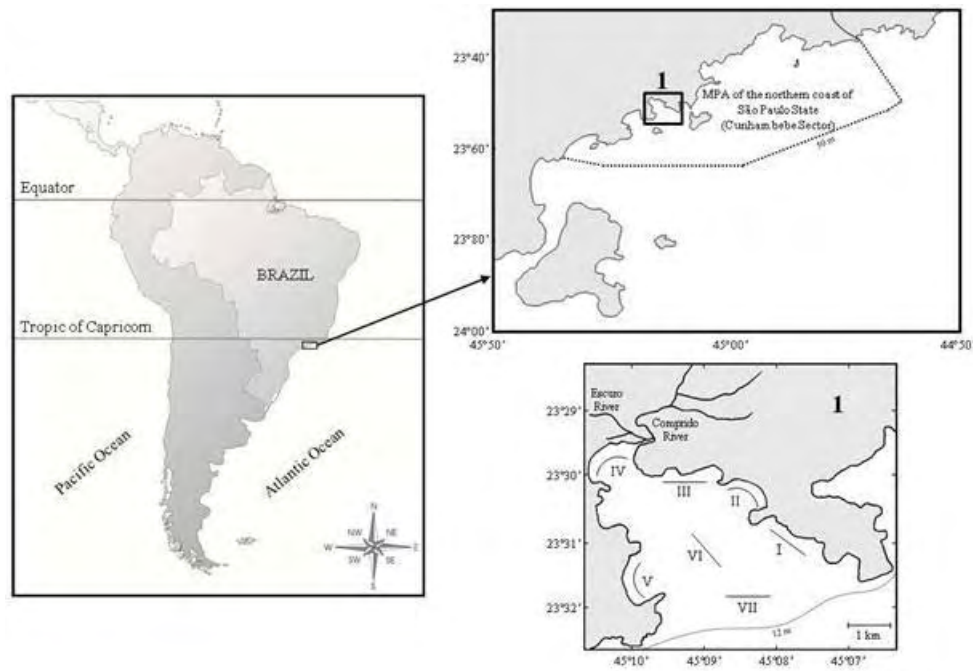


Figure 1: Map of the study region showing the Marine Protected Area (MPA – Cunhambebe Sector) and Fortaleza Bay with the sampling transects.

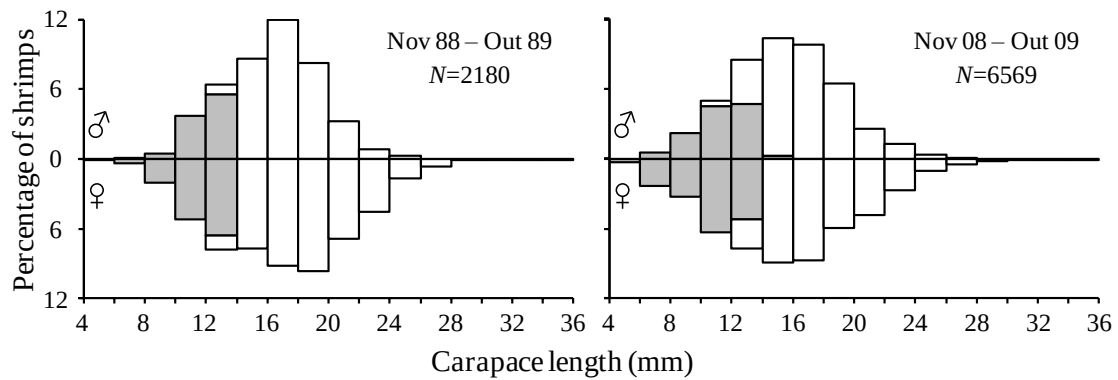


Figure 2: *Xiphopenaeus kroyeri*. Total size frequency distribution of males and females for each study period (gray bar = juvenile; white bar = adult).

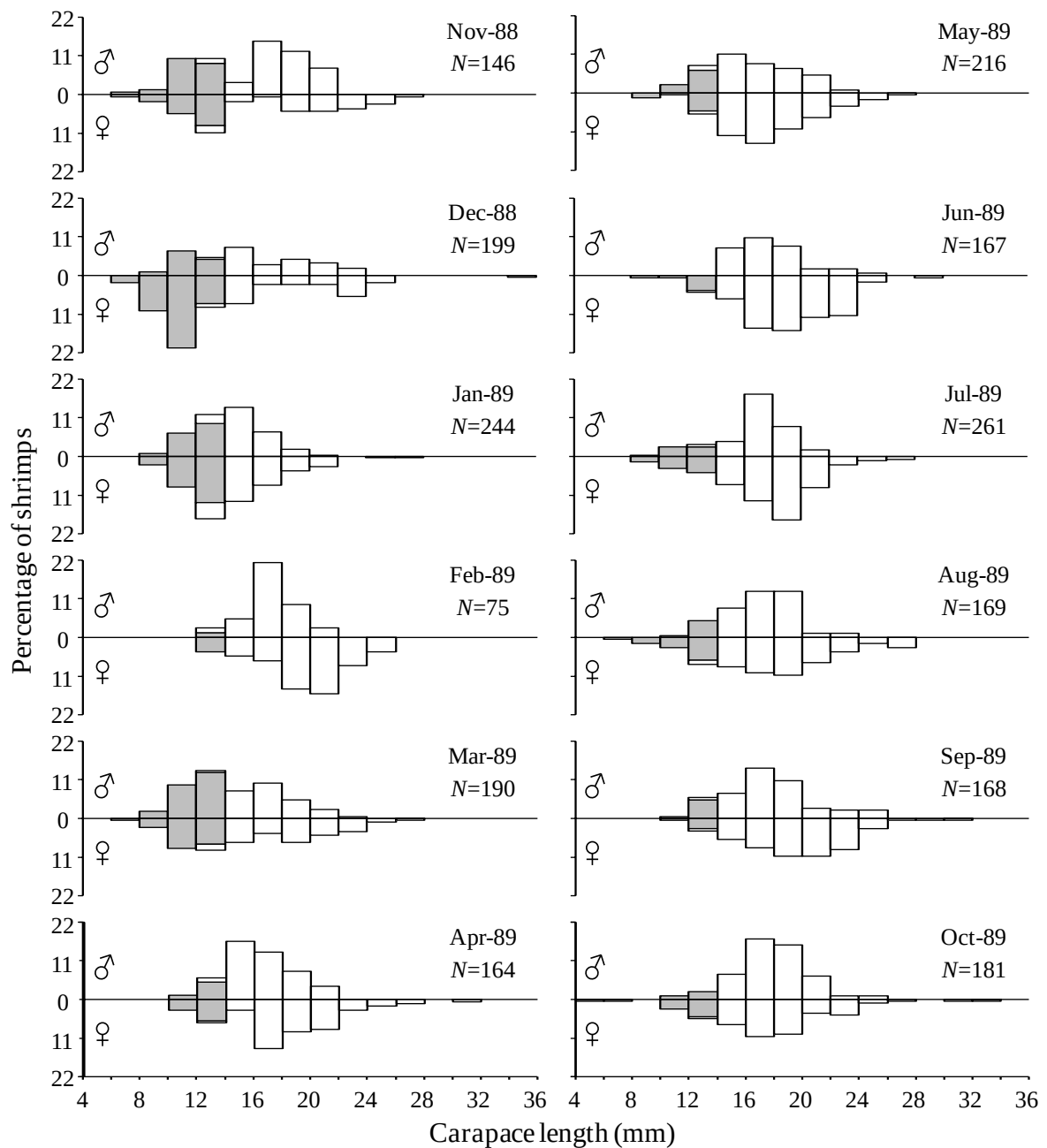


Figure 3: *Xiphopenaeus kroyeri*. Monthly size frequency distribution of males and females for the study period 1 (gray bar = juvenile; white bar = adult).

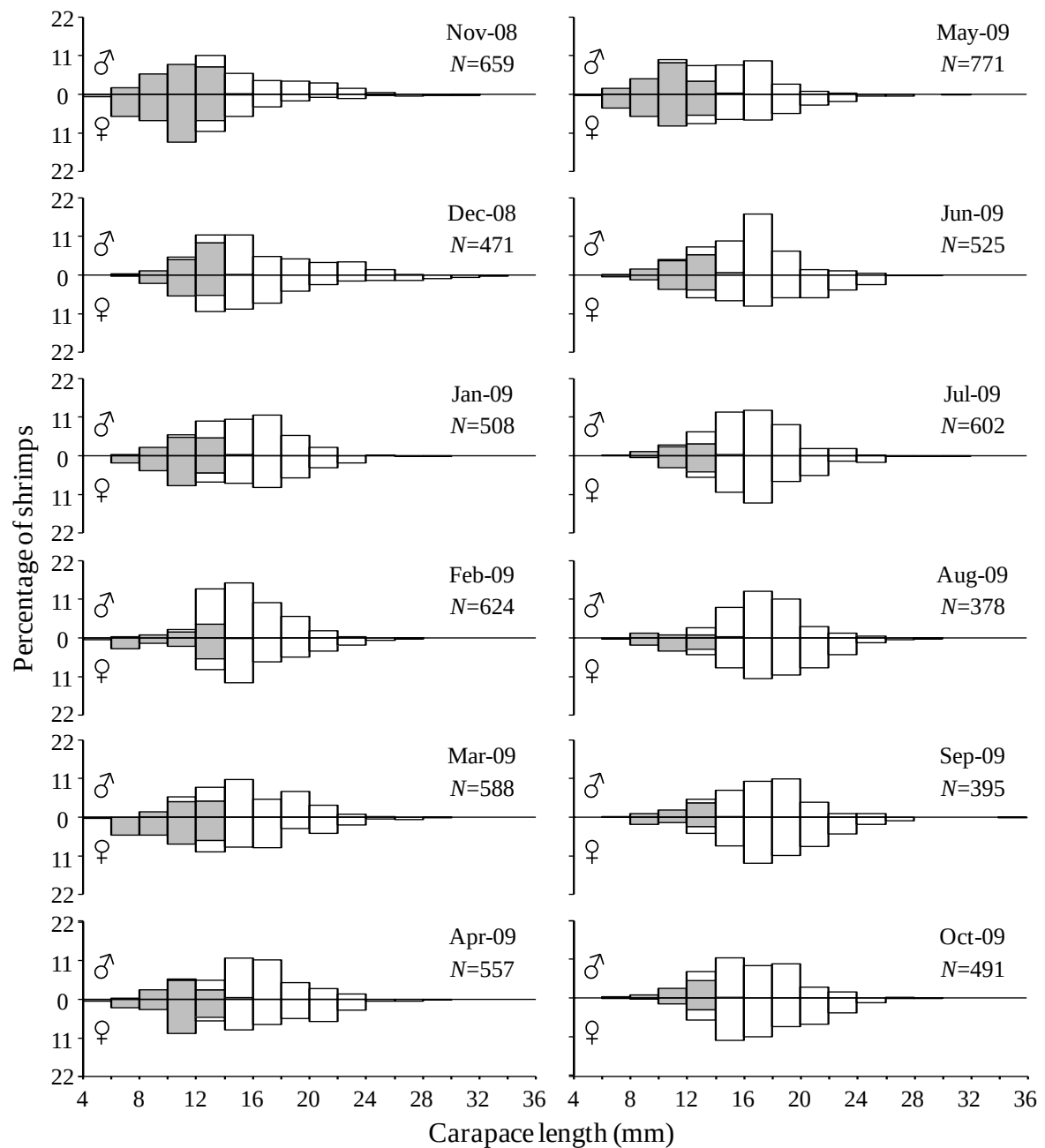


Figure 4: *Xiphopenaeus kroyeri*. Monthly size frequency distribution of males and females for the study period 1 (gray bar = juvenile; white bar = adult).

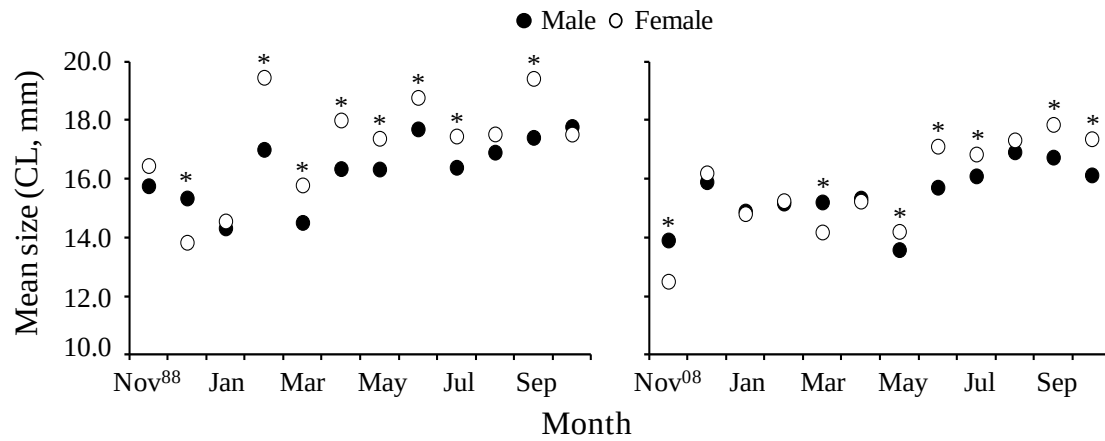


Figure 5: *Xiphopenaeus kroyeri*. Monthly mean size of males and females for each study period (* $\alpha = 0.05$, probability of significance Student's t-test).

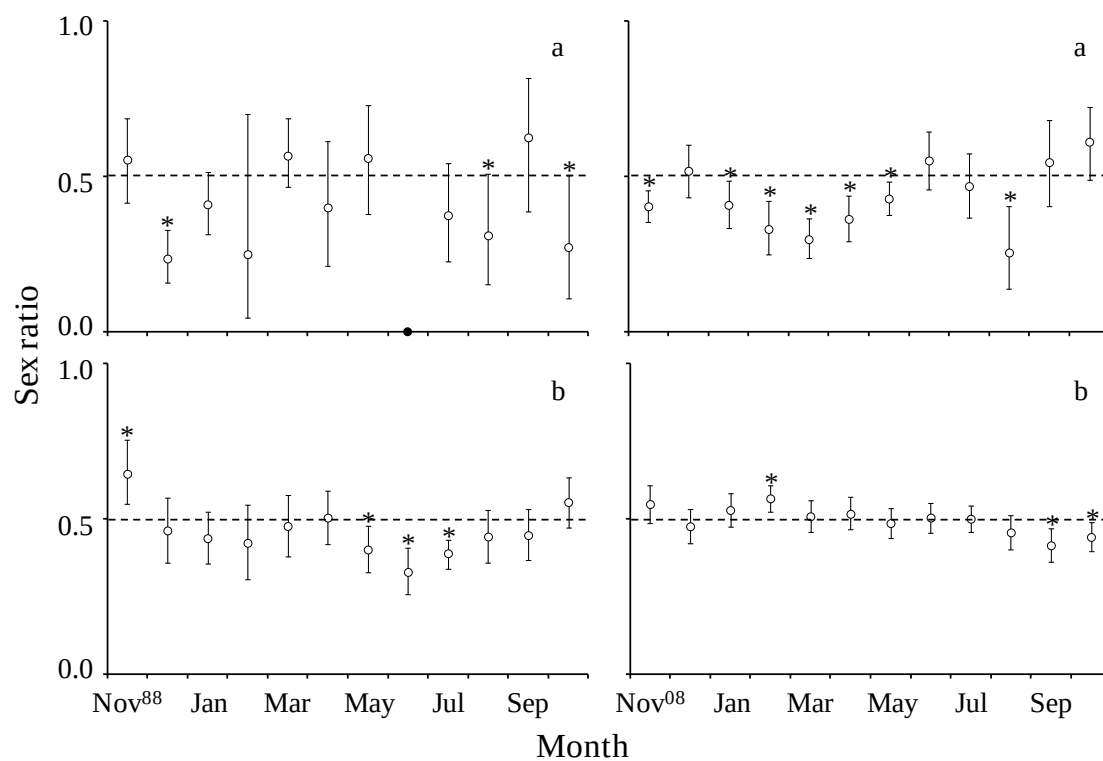


Figure 6: *Xiphopenaeus kroyeri*. Sex ratio estimated as the quotient between the number of males and the total number of individuals (* = statistically significant difference from 1:1 ratio; $\pm$ = 95% confidence interval; • = none male sampled).

4. Discussion

The results obtained in this investigation showed that the population structure of *X. kroyeri* at Fortaleza Bay seemed to be relatively stable throughout the sampling periods 1 and 2. The similar pattern of the size frequency distribution for males and females, and the general unimodality observed, could be explained by the constant birth, mortality and dispersion rates of the individuals in this population. Previous studies on the population dynamic of *X. kroyeri* conducted along the Brazilian coast have also observed a unimodal size frequency distribution for the two sexes (Armação do Itapocoroy – Branco, 2005; Ubatuba Bay – Castro et al., 2005). The above authors concluded that the unimodal size frequency distribution of the seabob shrimp was maintained by the absence of juvenile migration from nursery areas and continuous recruitment of the species. Overall, the stable population dynamic of *X. kroyeri* along the Brazilian coast might be explained if the species displays uniform larval dispersal and settlement rates among populations and similar mortality rates within each population. However, studies on such subjects is warranted because might help understanding the connectivity along small, intermediate and large spatial and temporal scales in different populations of *X. kroyeri*.

The continuous occurrence of juveniles and adults throughout the study periods 1 and 2 at Fortaleza Bay agrees with that reported by previous studies conducted in the southeastern and southern Brazilian coast (i.e., São Paulo State – Nakagaki and Negreiros-Fransozo, 1998; Castro et al., 2005; Castilho et al. submitted; Santa Catarina State – Branco et al., 1999; Branco, 2005). Importantly, the several management measures created and implemented in the study region in the last years, as the creation of the Anchieta Island State Park integrated into a conservation unit (Proclamation No. 9 629, March 29, 1977, and Federal Law No. 9 985, July 18, 2000), implementation and

regulation of the coastal ecological-economic zoning (EEZ) (Proclamation No 5 300, December 07, 2004), recent establishment of the special management area at Mar Virado Island and the MPA of the northern coast of São Paulo State (Proclamation No. 53 525, October 08, 2008), and the closed season dictated for the southeastern and southern regions of Brazil, comprehending the months from March 01 to May 31 (Normative Instruction No. 189, September 23, 2008), probably reduced the fishing boats operating at Fortaleza Bay. As a result, *X. kroyeri* could safely settle and reproduce within Fortaleza Bay, contributing significantly to the stock enhancement of the species in the study region; e.g. the abundance of *X. kroyeri* almost tripled between the first and second study periods; as well as in adjacent not protected areas where this target species has been extensively exploited by commercial fishing fleets.

In the seabob shrimp *X. kroyeri*, females attained larger body sizes than males. This reverse pattern of sexual dimorphism (females > males) agrees with previous observations in the same species along the southeastern and southern Brazilian coast (Nakagaki and Negreiros-Fransozo, 1998; Branco et al., 1999; Branco, 2005; Castro et al., 2005; Fernandes et al., 2011; Heckler et al., in press; Castilho et al., submitted). Reverse sexual dimorphism is also known in several other species of Penaeoidea shrimps (e.g., *Trachysalambria curvirostris* (Stimpson 1860) from the eastern coast of Japan – Yamada et al., 2007; *Penaeus chinensis* (Osbeck, 1765) and *Metapenaeus jolyeri* (Miers, 1880) from the western coast of Korea – Cha et al., 2002, 2004; *Melicertus kerathurus* (Forsk., 1775) from the eastern coast of Greece – Kevrekidis and Thessalou-Legaki, 2006; *Rimapenaeus constrictus* (Stimpson, 1874), *Artemesia longinaris* Bate, 1888, *Pleoticus muelleri* (Bate, 1888), and *Sicyonia dorsalis* Kingsley, 1878, from southeastern coast of Brazil – Costa and Fransozo, 2004; Castilho et al., 2007a, 2008). The above results and those results obtained for *X. kroyeri*, support the

notion that reverse sexual dimorphism is the rule rather than the exception within the Penaeoidea (Boschi, 1989).

The reverse sexual dimorphism in *X. kroyeri* might be explained by a combination of fecundity selection in females and “small male advantage”. Usually, larger body size in females translates into greater fecundity (e.g., Crocos and Kerr, 1983; Crocos, 1987a, b; Dall et al., 1990; Cha et al., 2002, 2004; Choi et al., 2005) and *X. kroyeri* does not appear to be the exception to this general pattern. So, natural selection is expected to favor large body size in females but not necessarily in males of *X. kroyeri*. In turn, small body size might increase mating opportunities in males. Penaeoid shrimps, including *X. kroyeri*, typically live in large aggregations (“schools”), and the monopolization of receptive females via overt aggression by adult males might be expensive (in terms of time and energy) in these schools. Thus, males might attempt to increase mating opportunities by using “pure-search” exploitative rather than interference mating strategies (Bauer, 2004; Baeza and Thiel, 2007). In “pure-search” mating strategies, males are continuously searching for females. Once a receptive female is found, there is no evident courtship, insemination takes place rapidly and males depart immediately after copula in search of other receptive females (Bauer and Abdalla, 2001; Bauer, 2004). This behavior is expected to favor small body size in males because that leads to an increase in agility and encounter rates with receptive females (Shuster and Wade, 2003; Baeza and Thiel, 2007). The description of the relationship between fecundity and body size in females and experiments determining male activity in the presence and absence of receptive females might help revealing the reasons explaining reversed sexual dimorphism in *X. kroyeri* and other members of the Penaeoidea (Bauer, 1996, 2011).

The overall sex ratio of *X. kroyeri* at Fortaleza Bay was biased toward females. Similar population-wise biased sex ratios have been reported before for the same species (e.g., Nakagaki and Negreiros-Fransozo, 1998; Branco et al., 1999; Branco, 2005; Heckler et al., in press) as well as in other Penaeoidea shrimps (Cha et al., 2002; Castilho et al., 2008; Costa et al., 2010; Croos et al., 2011). At first glance, the overall female biased sex ratio in this species might be explained by sex-specific predation (greater in males than in females), in turn driven by the “pure-search” mating tactic played by males (see above). Adult males might be more vulnerable to potential predators (e.g., various fishes from the family Sciaenidae common in region - Souza et al., 2008) while searching for receptive females. Increased mobility and the smaller body size of males compared to that of females might result in increased male mortality and the subsequent female biased sex ratio observed in this study. Importantly, when the sex ratios of juvenile shrimps were examined separately, it was female-biased during most of the study periods 1 and 2. By contrast, the sex ratio of adults was male- and female-biased, but in general, it remained in equilibrium almost during the entire study periods 1 and 2. The above results suggest that mechanisms other than the behavior of adult males are driving the sex ratio of *X. kroyeri* at Fortaleza Bay. Among these mechanisms, the major causes for imbalances in sex ratio among marine invertebrates, include sex-specific growth and/or mortality rates (Wenner, 1972; Cha et al., 2002; Kevrekidis and Thessalou-Legaki, 2006), gender-dependant migration (Wenner, 1972; Costa et al., 2010; Cross et al., 2011), and mating-related behaviors (Willson and Pianka, 1963; Castilho et al., 2008). For *X. kroyeri*, the male mating opportunities, in turn driven by the abundance of reproductively active females, might drive the timing of sexual maturity in males of the seabob shrimp resulting in deviations at sex ratio between juveniles and adults.

In summary, the present investigation showed that Fortaleza Bay provided suitable conditions (biotic and abiotic) for development of life cycle of *X. kroyeri*. The population structure remained stable throughout the study periods 1 and 2 as a function of the continuous occurrence of juveniles, adult males and females, as well as the potential contribution of environmental variables to the settlement of the species within Fortaleza Bay. Over a range of 20 years, the management measures implemented southeastern coast of Brazil, might contributed significantly to the maintenance of *X. kroyeri* population, above all to aid at stock recovery in fishing areas heavily exploited. Nevertheless, future investigations focusing on characteristics such as fecundity, growth, mortality, and larval ecology, will provide additional information necessary for understanding the population dynamic of *X. kroyeri* along its distribution range.

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Capítulo IV

*Reproduction and recruitment of
Xiphopenaeus kroyeri in a Marine
Protected Area in the Western Atlantic:
implications for resource management*

*(Almeida, A.C., Baeza, J.A., Fransozo, V., Castilho, A.L. and
Fransozo, A. [in press], Aquatic Biology)*

Reproduction and recruitment of *Xiphopenaeus kroyeri* in a Marine Protected Area in the Western Atlantic: implications for resource management

RUNNING HEAD: MPA benefits to overfished shrimp populations

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ABSTRACT

The potential of a recently established Marine Protected Area (MPA) in the Western Atlantic, Brazil, as a “seed production” and nursery ground for *Xiphopenaeus kroyeri*, an intensively exploited penaeid shrimp, was investigated in an attempt to reveal any future benefit of this new MPA to adjacent population experiencing heavy exploitation. Overall, we observed that males and females larger than 12 and 20 mm carapace length, respectively, were those individuals contributing the most to reproduction in the studied population. Reproductive activity of *X. kroyeri* was continuous at the MPA; two annual reproductive peaks were recorded from March to April and from November to December, which were followed by recruitment events, occurring from March to April 2009 and November 2009. Sediment, temperature and algae and plant biomass floating near the bottom were relevant environmental variables in driving reproductive activity and recruitment in *X. kroyeri*. The high reproductive potential of the studied population and the occurrence of abundant juveniles throughout the sampling area, supporting the existence of a nursery ground within the region, suggest that this MPA might provide important benefits in the near future. We argue in favor of future long term studies on the larval dispersion, reproductive biology and ecology of *X. kroyeri* in MPAs and non MPAs to construct a base for future management of this species and to aid at stock recovery in fishing areas that are heavily exploited.

KEYWORDS: Marine Protected Area; *Xiphopenaeus kroyeri*; size at first maturity; reproductive potential; nursery ground; environmental parameters; stock recovery

INTRODUCTION

The seabob shrimp *Xiphopenaeus kroyeri* (Heller 1862) is largely distributed in the Western Atlantic, from North Carolina (United States) to Santa Catarina (Brazil) (Holthuis 1980), although there are records of its occurrence in Virginia (United States) and Rio Grande do Sul (Brazil) (D’Incao et al. 2002). This species can reach over 100 mm in total length and is very abundant at depths < 27 m (Holthuis 1980, Branco 2005, Costa et al. 2007). Therefore, *X. kroyeri* is the subject of a globally important fishery (Gillett 2008). The average global catch of this shrimp has increased considerably during the last five decades with captures ranging from 6 000 tons in the 1960s to 42 787 tons in the 2000s (FAO 2011). Approximately 51% (513 785 tones) of the total global catch (1 013 993 tones) is extracted from the Brazilian coast (FAO 2011).

In the northern, northeastern, southeastern and southern regions of the Brazilian coast, which were described by Matsuura (1995) as the major fishing grounds, the seabob shrimp is heavily exploited by trawl fishing boats (Vasconcellos et al. 2007, 2011). Vasconcellos et al. (2007) collected information about the status of stocks of *X. kroyeri* based on the analysis of time-series landings by artisan fisheries during the period 1980-2002. These authors categorized the status of this shrimp as underexploited in the northern region, moderately exploited in the northeastern region, and overexploited in the southeastern and southern regions of Brazil. Furthermore, *Xiphopenaeus kroyeri* is classified as overfished by the Brazilian government because of the high capture rates of specimens from most or all size/age classes throughout the range of distribution of this species (Ministry of the Environment, Normative Instruction 5, 21 May 2004).

Due to overexploitation in the southeastern and southern regions, the stocks of *Xiphopenaeus kroyeri* have presented a continuous decrease in landings since the late

1980s (Valentini et al. 1991, D’Incao et al. 2002, IBAMA/CEPSUL 2006, Vasconcellos et al. 2007). Given the economic significance of this species, research on its ecology, population dynamics, and reproduction has vastly increased over the last years (Nakagaki & Negreiros-Fransozo 1998, Branco et al. 1999, Costa et al. 2000, 2007, 2011, Fransozo et al. 2000, 2002, Branco 2005, Castro et al. 2005, Castilho et al. 2008a, submitted, Simões et al. 2010, Fernandes et al. 2011, Fransozo et al. 2011, Freire et al. 2011, Heckler et al. in press). The highest abundance of *X. kroyeri* occurs at temperatures above 20°C and in areas where the sediment is composed of fine and very fine sand and silt and clay (e.g., Costa et al. 2000, 2007, 2011, Fransozo et al. 2002, Castilho et al. 2008a, Simões et al. 2010, Freire et al. 2011). Previous studies have demonstrated continuous reproduction and recruitment of *X. kroyeri* throughout the year, temporal variations in sex ratio, and differences in the size at the onset of sexual maturity between males and females (e.g., Nakagaki & Negreiros-Fransozo 1998, Branco et al. 1999, Fransozo et al. 2000, Branco 2005, Castro et al. 2005, Fernandes et al. 2011, Heckler et al. in press, Castilho et al. submitted). However, all the studies above have been conducted in populations experiencing high fishing pressure. Additional studies on the population dynamics and reproductive parameters of *X. kroyeri* in protected areas (with low or no fishing) are relevant to guide management of this species throughout its range of distribution.

The aim of this study is describing the reproductive parameters and recruitment of *Xiphopenaeus kroyeri* at Fortaleza Bay, located in a recently established Marine Protected Area (MPA) in the southeastern coast of Brazil, in an attempt to reveal any current or future benefit of this new MPA to adjacent population experiencing heavy exploitation. We have studied monthly variation in size at first sexual maturity, reproductive periodicity and recruitment of *X. kroyeri* from November 2008 to

December 2009 in this MPA. We also analyzed the relationship between various environmental variables and the abundance of different demographic categories of *X. kroyeri* at the study area to examine the role of environmental conditions in driving reproductive activity and recruitment in this species.

MATERIALS AND METHODS

Study site

Fortaleza Bay (23°29'30" S to 45°10'30" W) is situated in Ubatuba, northern coast of São Paulo State, Brazil. Within Fortaleza Bay, 12 sandy beaches are flanked by rocky shores. There is no considerable depth variation within bay; depths range from 1 to 12 m. Two rivers, Escuro and Comprido, originating from the Atlantic coastal forest (Mata Atlântica), flow into the bay and support a diverse intertidal mangrove ecosystem. Fortaleza Bay was established as a MPA (Área de Proteção Ambiental Marinha do Litoral Norte – Setor Cunhambebe) by Proclamation No. 53,525, October 8th, 2008, of the Brazilian Ministry of the Environment in order to prioritize the conservation, preservation and sustainable use of marine resources in the region. In this MPA, fishing is only permitted if it is necessary for the subsistence of traditional human communities. Also, amateur sport and artisanal fishing but not commercial fishing are allowed. These actions attempt to protect, ensure and discipline the rational use of resources in the region, promoting sustainable development.

The Ubatuba region is characterized by innumerable spurs of the Serra do Mar mountain chain that form an extremely indented coastline (Ab'Saber 1955). Exchange of water and sediment between the coastal region and the adjacent shelf is very limited (Mahiques 1995). This region is affected by three water masses: Coastal Water (CW: temperature > 20°C; salinity < 36 PSS), Tropical Water (TW: temperature > 20°C;

salinity > 36 PSS) and South Atlantic Central Water (SACW: temperature < 18°C; salinity < 36 PSS; Nitrogen:Phosphorus – 16:1) (Castro-Filho et al. 1987, Odebrecht & Castello 2001). During summer, the SACW penetrates into the bottom layer of the coastal region and forms a thermocline over the inner shelf located at depths of 10 to 15 m. During winter, the SACW retreats to the shelf break and is replaced by the CW. As a result, no stratification is present over the inner shelf during winter months (Pires 1992, Pires-Vanin & Matsuura 1993). The sediment is composed mainly of fine and very fine sand and silt and clay given the low water movement within the bay and between the bay and the adjacent continental shelf (Mahiques et al. 1998).

Shrimp sampling and description of environmental conditions

Based on previous investigations conducted in the study region (see Castro et al. 2005, Costa et al., 2007, 2011), *Xiphopenaeus kroyeri* is very abundant in depth less than 20 m. Also, the authors suggest that juvenile individuals are not dependent on estuarine regions, completing their life cycle in shallow coastal areas, where both juveniles and adults are largely caught by artisanal fishing boats. Thus, the sampling described below allows capturing all demographic categories (juveniles, adult males and females) of *X. kroyeri*.

Shrimp samples were collected monthly from November 2008 to December 2009 using a fishing boat carrying two rig nets (7.5 m long; 2.0 m horizontal mouth opening; 15 mm and 10 mm mesh diameter at the body and cod end of the net, respectively). A total of 7 permanent transects were established within Fortaleza Bay (Fig. 1) and sampled monthly. One haul per transect and month was made throughout the sampling period. Each transect was trawled for 1 km (each haul lasted ~ 20 min) covering a total area of 4 km² transect⁻¹.

During trawling, bottom water samples were taken with a Nansen bottle in each of the different transects. Water temperature and salinity were measured with a mercury thermometer (accuracy = 0.5°C) and an optical refractometer (precision = 0.5 PSS), respectively.

Sediment samples were obtained during each month and at each transect with a Van Veen grab (0.025 m²) 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 was treated with 250 mL of NaOH solution (0.2 mol l⁻¹) and stirred for 5 min to release silt and clay particles. Next, the subsamples were rinsed on a 0.063-mm sieve. Grain size categories followed 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 $\phi \geq 4$ (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). 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.

Considerable amounts of algae and plant fragments floating near the marine floor that were retained in the trawl nets during sampling were collected, sorted and its biomass (total wet weight, Kg) was recorded with a balance (precision = 0.0001 g)

Reproductive parameters and recruitment of *Xiphopenaeus kroyeri*

We collected a total of 44 029 shrimps during the sampling period. Logistic and time constraints did not permit sexing and measuring each collected individual in such a large sample. Thus, we randomly separated a subsample of 250 g from each sample for analysis. In samples comprising 250 g or less, all individuals were sexed (presence of petasma in males and thelycum in females, see below) and measured using a caliper to nearest 0.1 mm. Carapace length (CL, mm), measured from the orbital angle to the posterior margin of the carapace, was recorded for each shrimp.

Males and females were categorized as juveniles or adults based on macroscopic observations of secondary sexual characters (petasma and thelycum). In males, the endopods of the first pleopods form the petasma. The endopods are completely separated in juveniles but are fused in adults (Bauer 1986, 1991, Fransozo et al. 2011). In females, the thelycum corresponds to any external modification of the posterior thoracic sternites and/or coxae. This structure stores spermatophores transferred by males during insemination. In adult females, the thelycum is a single smooth broad plate and bears an aperture flanked by a transverse ridge that runs from right to left. In

immature (juvenile) females, the ridge has a space between the plates (Bauer 1986, 1991, Fransozo et al. 2011).

Reproductive condition of each shrimp was determined by macroscopic examination of terminal ampullae in males and ovaries in females. Terminal ampullae were classified either as spent (stage I) or developed (stage II) depending upon the absence or presence of spermatophores contained by these structures, respectively (as in Bauer 1991, Bauer & Cash 1991, Nakagaki & Negreiros-Fransozo 1998, Díaz et al. 2002). Maturity of the ovaries was determined based on color and volume of this organ within the cephalothorax of female shrimps. Juvenile females had very thin ovaries lacking any coloration while adult females had thick ovaries varying in color from opaque white to olive green. Ovaries in adult females were also classified as (I) spent, if they were opaque white in color and thicker than the juvenile ovaries; (II) developing, if they were light green; or (III) developed (near spawning), if they were green to olive green (Bauer & Rivera Vega 1992, Nakagaki & Negreiros-Fransozo 1998, Peixoto et al. 2003, Campos et al. 2009).

In the present study, recruitment refers to the smallest individuals (immature stage) vulnerable to fishing gear used. The recruitment was determined monthly by the proportion of juveniles in relation to the total number of adults sampled during study period.

Statistical analysis

Size at first maturity in *Xiphopenaeus kroyeri*

Size at first sexual maturity (overall and per month) in males and females was determined using the proportion of juvenile and adult individuals in size classes of 0.5 mm CL. The procedure used here to estimate sexual maturity was based on fitting the

sigmoid logistic curve to the data above (e.g., Pinheiro & Fransozo 1998). We used the equation $y = 1 / (1 + e^{(-r(CL - CL_{50}))})$; where y is the estimated proportion of adult shrimps, CL is carapace length, CL_{50} is the size at the onset of sexual maturity, and r is the coefficient for the slope of the logistic curve. The logistic curve was fitted by least squares to the aforementioned proportions per size class of all the individuals and samples using maximum-likelihood iterations. After adjusting the regression model, sexual maturity (CL_{50}) was estimated as the size at which 50% of the males and females reached maturity.

Factors correlating with reproduction and recruitment in *Xiphopenaeus kroyeri*

We explored whether or not environmental variables correlate with reproductive activity and recruitment in the studied population. Shrimps were separated into five demographic categories: juveniles (immature males + immature females), males with terminal ampullae in stage I (M-1), males with terminal ampullae in stage II (M-2), females with ovaries in stage I (F-1), and reproductive females (females with ovaries in stage II and stage III grouped together, F-2). The relationship between temperature, salinity, phi, organic matter content of the sediment, and algae and plant fragments floating near the bottom and the abundance of the demographic categories was assessed using Canonical Correspondence Analysis (CCA, $\alpha = 0.05$) in the software R-2.7.1 (R Development Core Team, 2008). This analysis computes a combination of scores for the data set with maximum linear correlations, showing the highest explanation levels of the variance in the data set. For interpreting this ordination technique, the canonical coefficients are used, which permit relating variation in the abundance of the different demographic categories to variation in environmental parameters (Ter Braak 1986, Kindt & Coe 2005). The results of the CCA were plotted in a bi-dimensional graph.

RESULTS

Reproductive parameters and recruitment of *Xiphopenaeus kroyeri*

A total of 7 659 individuals of *Xiphopenaeus kroyeri* were analyzed from a total of 98 hauls (7 hauls per month) taken throughout the sampling period. All specimens were measured and sexed during this study; 2 216 juveniles (941 males and 1 275 females), 2 749 adult males, and 2 694 adult females. Both juvenile and adult specimens were caught in all transects. The size ranges, means, and standard deviations of the carapace length of the specimens analyzed are shown in Table 1.

Macroscopic observations of secondary sexual characters and maturity stage of terminal ampullae (in males) and ovaries (in females) indicated that the smallest body sizes (CL) of adult males and adult females were 11.0 and 12.9 mm, respectively. Taking into account the total number of shrimps collected during the entire sampling period, the overall size at first sexual maturity (CL_{50}) was estimated to be 12.8 mm CL in males and 13.2 mm CL in females (Fig. 2). During most of the studied period, size at first sexual maturity (CL_{50}) was greater in females than in males. Through the year, the CL_{50} varied between 12.1 to 13.6 mm CL in males, and between 13.0 and 13.3 mm CL in females (Fig. 2).

Both in male and female shrimps, the degree of maturity of the terminal ampullae and ovaries, respectively, depended upon body size (Fig. 3). More than 50% of the males with CL < 12.0 mm had terminal ampullae in stage II. The percentage of males with terminal ampullae in stage II abruptly increased from 70% in males with CL ~ 14.0 mm to 90% in males with CL ~ 16.0 mm. Females with ovaries in stage II and III showed higher percentages ($\geq 50\%$) when CL was ~20 mm CL or greater.

The percentage of males with developed terminal ampullae remained relatively constant and above 50% throughout the year (Fig. 3). In turn, two peaks of reproductive activity during the year were identified for females considering the proportion of females with ovaries in different stages of development. One reproductive peak occurred from March to April 2009 and a second peak was observed from November to December 2009. The lowest percentage of females with ovaries in advanced stage of development was registered from May to August 2009.

Juveniles were sampled in all transects at Fortaleza Bay, in which average ($\pm$ standard deviation [SD]) depth varied from 5.6 ± 0.9 to 10.4 ± 1.6 (Table 1). The highest and lowest number of specimens were caught from the transects III and I, respectively (Table 1). The presence of juveniles was also recorded during all months (Fig. 4). The highest percentages of juveniles (compared to the adults) in the population, were observed in November 2008, May 2009, and December 2009 (Fig. 4). These peaks of smaller individuals are probably indicative of recruitment events, occurring after the main reproductive peaks of *Xiphopenaeus kroyeri*, which were registered from March to April 2009 and November 2009. The recruitment peak observed in November 2008 might correspond to the previous reproduction peak, not measured in the present study.

Factors correlating with reproduction and recruitment in *Xiphopenaeus kroyeri*

The average ($\pm$ SD) bottom temperature over the entire study period at Fortaleza Bay was $23.8 \pm 2.1^{\circ}\text{C}$, and varied from 19.7 ± 1.6 to $26.3 \pm 1.3^{\circ}\text{C}$. From January to March 2009 temperature increased in the bay followed by a decrease during the following months up to July 2009 (Fig. 5a). The bottom salinity ranged from 31.5 ± 1.4 to 36.6 ± 1.0 PSS, with an overall average of 34.2 ± 1.6 PSS. The months from May

2009 to July 2009, September 2009 and October 2009, showed the lowest average bottom salinity values (Fig. 5b).

Sediment at Fortaleza Bay was characterized as fine and very fine sand and silt and clay during all the study period; grains with a diameter smaller than 0.25 mm dominated our samples (> 90%). Monthly phi values did not vary throughout the year and, according to the Phi scale, sediment was categorized as silt and clay (average $\pm$ SD: 4.8 ± 0.2 ; range: 4.5-5.3). The highest average percentage of organic matter was observed during April 2009 (5.6%) and the lowest average percentage of organic matter was observed during January 2009 (Fig. 5c).

The total wet weight of algae and plant fragments floating near the marine floor retained in the trawl nets during sampling showed considerable variability during the study (7.1 ± 6.0 Kg) (Fig. 5d). Considering the variation of the organic matter content and algae and plant biomass throughout sampling period, there was a similar pattern between them from August 2009 to December 2009 (Fig. 5c, d).

The CCA used to test for a relationship between environmental variables and abundance of the different demographic categories in *Xiphopenaeus kroyeri* explained 94% of the variance in our dataset (Fig. 6). Temperature (CCA, $p = 0.002$), phi (CCA, $p = 0.033$) and algae and plant fragments floating near the bottom (CCA, $p = 0.009$), all showed a strong correlation with shrimp abundance. On the first axis of the CCA, a positive correlation was observed between the abundance of juveniles and algae and plant fragments floating near the bottom (Table 2, Fig. 6). On the second axis, the abundance of F-2 correlated positively with temperature and phi (a measure of sediment composition) (Table 2, Fig. 6). Overall, the above environmental variables are relevant in explaining abundance of juveniles and adult individuals of *X. kroyeri*.

DISCUSSION

We have described for the first time the reproductive biology and recruitment of *Xiphopenaeus kroyeri* in a MPA (no commercial fishing zone) recently established in the southwestern Atlantic. In the following we discuss three important aspects of *X. kroyeri*; (1) size at first maturity, (2) environmental variables that correlate with reproductive peaks and juvenile recruitment, and (3) the existence of nursery grounds in the studied region. We attempt to reveal the possible role that this recently established MPA might play in the management of this exploited shrimp in the near future.

Size at first maturity in *Xiphopenaeus kroyeri*

Based on the macroscopic observations of sexual traits, size at first sexual maturity (CL₅₀) in *Xiphopenaeus kroyeri* was estimated to be 12.8 mm CL and 13.2 mm CL in males and females, respectively. We have reviewed previous studies reporting size at first sexual maturity in *X. kroyeri* along the Brazilian coast and found considerable variability in this reproductive parameter (e.g., Coelho & Santos 1993, Branco et al. 1999, Branco 2005, Fernandes et al. 2011, Heckler et al. in press, Castilho et al. submitted, Table 3). Our estimates of size at first maturity are similar to those reported by Heckler et al. (in press) and considerably lower than those reported by previous studies in the same region (northern coast of São Paulo State) but before the establishment of the MPA and along the Brazilian coast (Table 3).

Importantly, various of the past studies have not taken into account juveniles when estimating size at first maturity. Some of these studies have (inappropriately) categorized adult males and females with spent terminal ampullae and ovaries, respectively, as juveniles. This misclassification of adult males and females as juveniles most certainly overestimates size at first maturity in *Xiphopenaeus kroyeri*. If we had

considered only adult individuals in our calculations, the estimated size at first sexual maturity (CL_{50}) would correspond to 16.3 mm CL and 17.3 mm CL in males and females, respectively. The above values are similar to those reported by previous studies but incorrect. Overall, uncertainty in size at maturity might have important implications for fisheries stock assessment, including those targeting crustaceans (Anderson et al. 2012). Age-structured models built to evaluate the effect of uncertainty in size at first maturity on stocks of exploited crustaceans have shown that even with low exploitation rates, an overestimation of size at maturity can affect values of the “spawning potential ratio” so that the model incorrectly indicate stock overexploitation. Alternately, an underestimation of size at maturity can cause the failure of models to recognize stock overexploitation when, on reality, overexploitation is indeed taking place (Anderson et al. 2012). We argue in favor of studies constructing age-structured model to evaluate the effect of uncertainty in size at maturity on population assessments of *X. kroyeri*.

Factors correlating with reproduction and recruitment in *Xiphopenaeus kroyeri*

Xiphopenaeus kroyeri reproduced continuously but with dissimilar intensity throughout the year. Two well defined annual reproductive peaks were detected in this study, one during late summer + early fall and a second peak occurring in spring. This reproductive dynamic agrees remarkably well with that reported before for other populations of *X. kroyeri* in the northeastern, southeastern and southern regions of the Brazilian coast (e.g., Coelho & Santos 1993, Nakagaki & Negreiros-Fransozo 1998, Branco 2005, Castro et al. 2005, Fernandes et al. 2011, Heckler et al. in press, Castilho et al. submitted, Table 3). Interestingly, this similarity in reproductive schedules among populations support the notion that continuous reproduction but with dissimilar intensity

(i.e., with breeding peaks in spring and fall) is the rule rather than the exception in Penaeoidea shrimps from tropical and subtropical environments (see Garcia 1988).

Our statistical analyses (CCA) demonstrated a positive correlation between temperature and the abundance of reproductive females during the study period. Importantly, changes in reproductive intensity occurred concomitantly with changes in water temperature during this study; the maximum reproductive activity in females of *Xiphopenaeus kroyeri* (determined by the relative abundance of individuals with developing and developed ovaries that were close to spawning – Bauer & Rivera Vega 1992) occurred at a time of the year when the maximum average values of temperature ($> 25^{\circ}\text{C}$) were recorded at the study site. Thus, temperature appears to drive reproduction in *X. kroyeri* and sudden increases in temperature might be triggering reproduction in this species.

Temperature has been suggested before to affect gonad maturation and/or spawning in other Penaeoidea shrimps (e.g., Sastry 1983, Garcia 1988, Dall et al. 1990, Bauer 1992, Bauer & Rivera Vega 1992, Bauer & Lin 1994, Costa & Fransozo 2004, Castilho et al. 2007a, 2007b, 2008b, 2008c, in press, submitted). In *Xiphopenaeus kroyeri*, high temperature might speed up gametogenesis and sudden increases in temperature (as those observed during the summer, early fall and spring in this study) might also signal to parental females favorable conditions in the water column for egg production and spawning. Importantly, the highest reproductive intensity of *X. kroyeri* observed in this study not only occurred when temperature was high but also at a time of the year (spring and summer) when the SACW intrudes into the continental shelf (Pires 1992). This water mass transports nutrients to the studied region due to its high nitrogen (N) to phosphorus (P) ratio ($\text{N:P} = 16:1$) that favors primary productivity (Aidar et al. 1993, Odebrecht & Castello 2001). Food availability for larvae (e.g.,

primary and/or secondary productivity) is also recognized as another important condition affecting reproduction and spawning in marine invertebrates, including other shrimps (Thorson 1950, Sastry 1983, Bauer 1992, Bauer & Rivera Vega 1992). High nutrient load entering to the system due to the intrusion of the SACW and increased primary productivity (Pires-Vanin & Matsuura 1993) is expected to boost larval condition and / or survival of *X. kroyeri* at Fortaleza Bay.

Sediment characteristics affected the abundance of adult individuals of *Xiphopenaeus kroyeri* at Fortaleza Bay. The positive correlation between sediment type (fine and very fine sand and silt/clay) and abundance of *X. kroyeri* demonstrated by the CCA coincides with that reported by previous studies; shrimps mostly inhabit fine/very fine sand and/or silt/clay along the Brazilian coast (Costa et al. 2000, 2007, 2011, Fransozo et al. 2002, Castilho et al. 2008a, Simões et al. 2010, Freire et al. 2011). Adults of various other Penaeoidea shrimp usually inhabit fine rather than coarse sediments (Dall et al. 1990). Most probably, finer sediments facilitate burrowing in adult shrimps by reducing energy requirements for excavation (Dall et al. 1990, Freire et al. 2011). Indeed, experimental studies have shown that shrimps excavate more rapidly in sediment between 62.00 µm and 1.00 mm (Dall et al. 1990, Freire et al. 2011). Fine sediments might also allow adult shrimps to excavate deeper and escape from potential predators (Dall et al. 1990, Freire et al. 2011).

Interestingly, the abundance of juvenile shrimps was not affected by sediment type; it correlated positively with algae and plant biomass floating near the bottom at Fortaleza Bay. The same relationship between juvenile abundance and such algae and plant biomass was reported before for *Xiphopenaeus kroyeri* at Ubatuba Bay, northern coast of São Paulo State (e.g., Castro et al. 2005). According to previous studies (Dall et al. 1990, Simões et al. 2010), juvenile shrimps are poor excavators, even in fine

sediment. Consequently, they usually settle in shallow water environments rich in detritus, such as seagrass beds, mangrove swamps, or floating sargassum (Garcia 1988). Herein, we propose that large amounts of algae and plants floating near the marine floor, which are associated with local hydrodynamic conditions, proximity to the continent, as well as the input from the small rivers Escuro and Comprido, might represent a nursery ground for *X. kroyeri* in the study region (see also Castro et al. 2005). Such debris could provide protection for juvenile shrimps against potential predators, as this material most probably increases environmental heterogeneity in structurally simple soft bottom habitats (Fransozo et al. 2009a, Almeida et al. 2012). However, additional studies on the ecology of juveniles of *X. kroyeri* both in shallow and deeper nursery grounds is warranted as these might help understanding the early benthic life history of this shrimp and predict adult stock abundance along the Brazilian coast.

Reproductive biology and recruitment of *Xiphopenaeus kroyeri* in a MPA

Overall, our literature review suggests that there are no major differences in the reproductive biology and recruitment schedule of *Xiphopenaeus kroyeri* between Fortaleza Bay and several other localities along the Brazilian coast (see Table 3). However, it is outstanding to detect similarities among different populations of *X. kroyeri* distributed over more than 1 000 km of coast that encompasses approximately 10% of the range of distribution of this species in the south Caribbean and southwestern Atlantic. These similarities are remarkable especially when considering the differences in methodology among studies (e.g., fishing gear, catching effort, and statistical analyses - see references in Table 3). Two aspects emerging from this comparison among populations deserve attention as we believe have important implications for the

future management of the species not only in the Brazilian coast but in the central and southwestern Atlantic.

First, considering previously reported information on the abundance of this shrimp throughout the northern coast of São Paulo State before the establishment of the MPA, Fortaleza Bay appears to sustain larger populations of *Xiphopenaeus kroyeri* than adjacent areas (CPUE = 61.9 shrimp km⁻² in Ubatuba Bay [Nakagaki et al. 1995], 72.5 shrimp km⁻² in Ubatumirim, Ubatuba and Mar Virado bays [Costa et al. 2007], 45.2 shrimp km⁻² in Ubatuba and Caraguatatuba regions [Castilho et al. 2008a]; *versus* 112.3 shrimp km⁻² in Fortaleza Bay [this study]). The above and the occurrence of abundant juveniles in the studied locality suggests that Fortaleza Bay might serve as a “seed production” locality and nursery ground, that might help in the future to replenish nearby (and also far away, see below) fishing grounds of the species during the next decades.

Second, the similarity in reproductive schedules among populations, that in some cases are located thousands of kilometers apart, suggest the existence of an open meta-population with considerable connectivity in the southwestern Atlantic. The relative long larval period reported for this species (~16 days - Fransozo et al. 2009b) supports the idea of considerable connectivity among distantly located populations hundreds and thousands of kilometers apart. The study of meso-scale oceanographic processes (Cowen et al. 2000) and the phylogeography of *Xiphopenaeus kroyeri* along the Brazilian coast (Voloch & Solé-Cava 2005, Gusmão et al. 2006, Francisco et al. 2009) might help revealing the extent of connectivity among populations, that in turn, will help guiding the establishment of sound management strategies in this widely distributed species.

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Table 1: *Xiphopenaeus kroyeri*. Size of specimens based on carapace length. (n = number of hauls; N = number of specimens; SD = standard deviation).

Transect	Hauls (n)	Depth (m)	Juveniles			Males			Females		
			N	Size (mm)		N	Size (mm)		N	Size (mm)	
				Mean (SD)	Range		Mean (SD)	Range		Mean (SD)	Range
I	14	9.1 ± 1.0	286	10.9 ± 2.0	5.4 – 14.0	474	17.1 ± 2.5	11.1 – 25.8	379	17.7 ± 3.1	12.9 – 28.2
II	14	7.2 ± 1.1	313	10.9 ± 1.9	5.3 – 13.8	337	16.6 ± 2.8	11.1 – 25.3	398	18.5 ± 3.5	12.9 – 31.3
III	14	7.0 ± 0.9	349	10.2 ± 2.2	4.5 – 14.2	418	17.2 ± 2.7	11.6 – 26.6	355	18.1 ± 3.4	13.0 – 30.6
IV	14	5.6 ± 0.9	301	10.6 ± 2.1	4.9 – 14.0	414	16.6 ± 2.7	11.0 – 25.8	431	18.1 ± 3.7	12.9 – 35.4
V	14	7.5 ± 1.5	304	11.3 ± 1.7	6.1 – 14.0	233	15.8 ± 2.5	11.0 – 24.6	310	17.2 ± 2.9	12.9 – 30.5
VI	14	8.0 ± 1.1	340	10.8 ± 1.9	5.8 – 14.4	490	16.7 ± 2.3	11.0 – 25.0	400	17.5 ± 2.9	13.0 – 32.9
VII	14	10.4 ± 1.6	323	11.0 ± 1.9	4.8 – 14.0	383	17.2 ± 2.8	11.0 – 25.4	421	18.6 ± 3.5	12.9 – 31.0

Table 2: *Xiphopenaeus kroyeri*. Results of the Canonical Correspondence Analysis ordination for the first two canonical axes, with demographic categories abundance and environmental variables data (T = bottom temperature; S = bottom salinity; OM = organic matter; APF = algae and plant fragments; M-1 = males with terminal ampullae in stage I; M-2 = males with terminal ampullae in stage II; F-1 = females with ovaries in stage I; F-2 = females with ovaries in stage II and stage III).

Environmental variables	Canonical coefficients		R ²	P
	Axis 1	Axis 2		
T	-0.249	-0.968	0.631	0.002*
S	-0.845	-0.535	0.410	0.069
PHI	0.712	-0.703	0.487	0.033*
OM	-0.993	-0.121	0.045	0.798
APF	-0.963	0.270	0.609	0.009*
Demographic categories	Canonical coefficients		R ²	P
	Axis 1	Axis 2		
Juvenile	-0.999	-0.039	0.947	<0.001*
M-1	-0.559	0.829	0.592	0.008*
M-2	0.912	-0.411	0.307	0.166
F-1	0.261	0.965	0.782	0.001*
F-2	0.294	-0.956	0.963	<0.001*

P = probability of significance based on 1000 permutations (Monte Carlo; $\alpha=0.05^*$)

Table 3: *Xiphopenaeus kroyeri*. Reproductive parameters of different shrimp populations along the Brazilian coast. (N.E. = northeastern; S.E. = southeastern; S. = southern; PE = Pernambuco; RJ = Rio de Janeiro; SP = São Paulo; SC = Santa Catarina; CL = carapace length; ^a = total length; ^b = juveniles included at performing of CL₅₀ statistical analysis; ^c = no juveniles included at performing of CL₅₀ statistical analysis; C = continuous; Sp = spring; Su = summer; Fal = fall; Wi = winter).

Reference	Coordinates	Region (State)	Period	Size at sexual maturity (CL mm)		Reproductive periodicity
				♂	♀	
Coelho & Santos (1993)	08°45'S/35°06'W	N.E. (PE)	May 1986 to Dec 1992		19.8	C; Sp-Su
Fernandes et al. (2011)	21°37'S/41°00'W	S.E. (RJ)	Jun 2005 to May 2010	12.0	22.0	C; Sp-Su-Wi
Nakagaki & Negreiros-Fransozo (1998)	23°26'S/45°02'W	S.E. (SP)	Oct 1992 to Sep 1993	68.0 ^a	83.2 ^a	C; Sp-Fal
Castro et al. (2005)	23°26'S/45°02'W	S.E. (SP)	Sep 1995 to Aug 1996	-	-	C; Sp-Fal
Castilho et al. (submitted)	23°48'S/45°23'W	S.E. (SP)	Jan 1998 to June 2003	15.6	17.9	C; Sp-Su
Heckler et al. (in press)	23°26'S/45°02'W	S.E. (SP)	Jul 2005 to Jun 2007	13.3	13.5	C; Sp-Su
Present study	23°29'S/45°10'W	S.E. (SP)	Nov 2008 to Dec 2009	12.8 ^b 16.3 ^c	13.2 ^b 17.3 ^c	C; Sp-Fal
Branco et al. (1999)	26°23'S/48°36'W	S. (SC)	Mar 1996 to Feb 1997	13.9	17.1	-
Branco (2005)	26°47'S/48°38'W	S. (SC)	1996-1997; 1999-2001	14.2	16.0	C; Sp-Fal

FIGURE LEGENDS

Figure 1: Map of the study region showing the Marine Protected Area (MPA) and Fortaleza Bay.

Figure 2: *Xiphopenaeus kroyeri*. Overall and monthly sizes at first sexual maturity for each sex (numbers correspond to the specimens analyzed).

Figure 3: *Xiphopenaeus kroyeri*. Monthly and size variations of the development stage of terminal ampullae and ovaries of males and females, respectively (numbers correspond to the specimens analyzed).

Figure 4: *Xiphopenaeus kroyeri*. Monthly variation of the juvenile specimens obtained (numbers correspond to the specimens analyzed).

Figure 5: Monthly variations of the environmental variables at Fortaleza Bay during the sampling period.

Figure 6: *Xiphopenaeus kroyeri*. Bidimensional graphic resulting from the Canonical Correspondence Analysis between environmental variables and abundance of demographic categories (M-1 = males with terminal ampullae in stage I; M-2 = males with terminal ampullae in stage II; F-1 = females with ovaries in stage I; F-2 = females with ovaries in stage II and III; T = bottom temperature; APF = algae and plant fragments floating near the marine floor).

Fig. 1

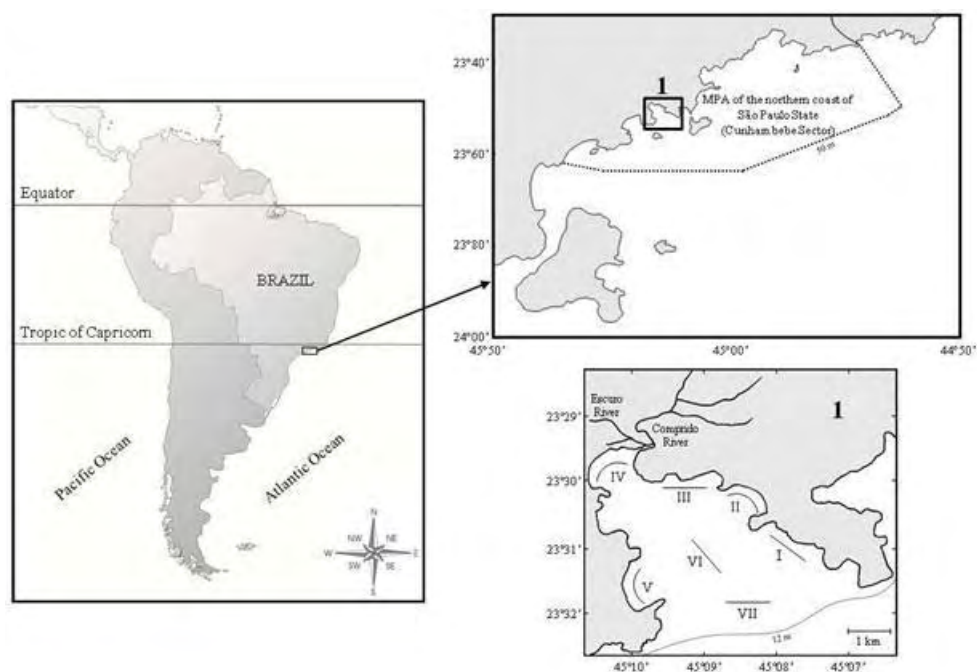


Fig. 2

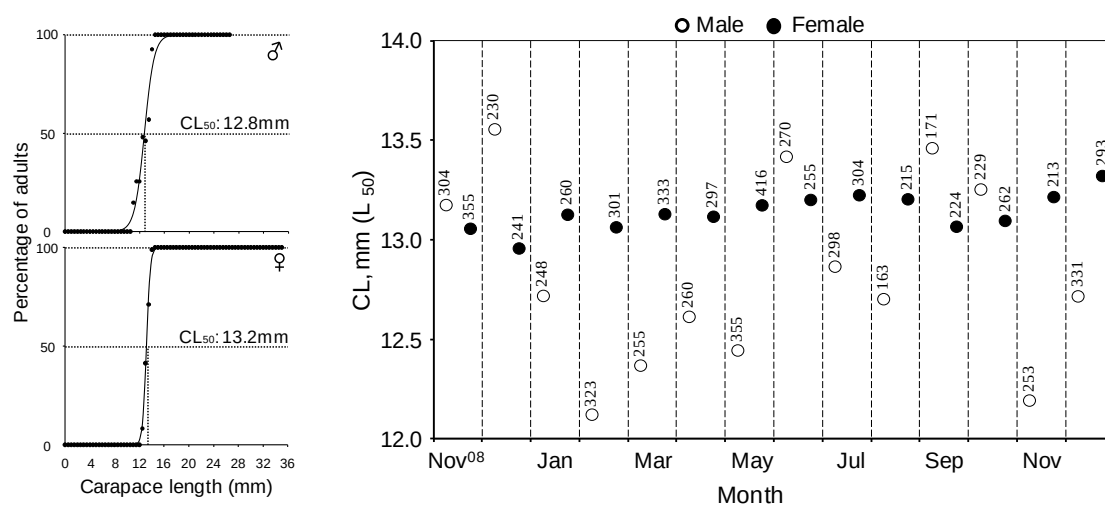


Fig. 3

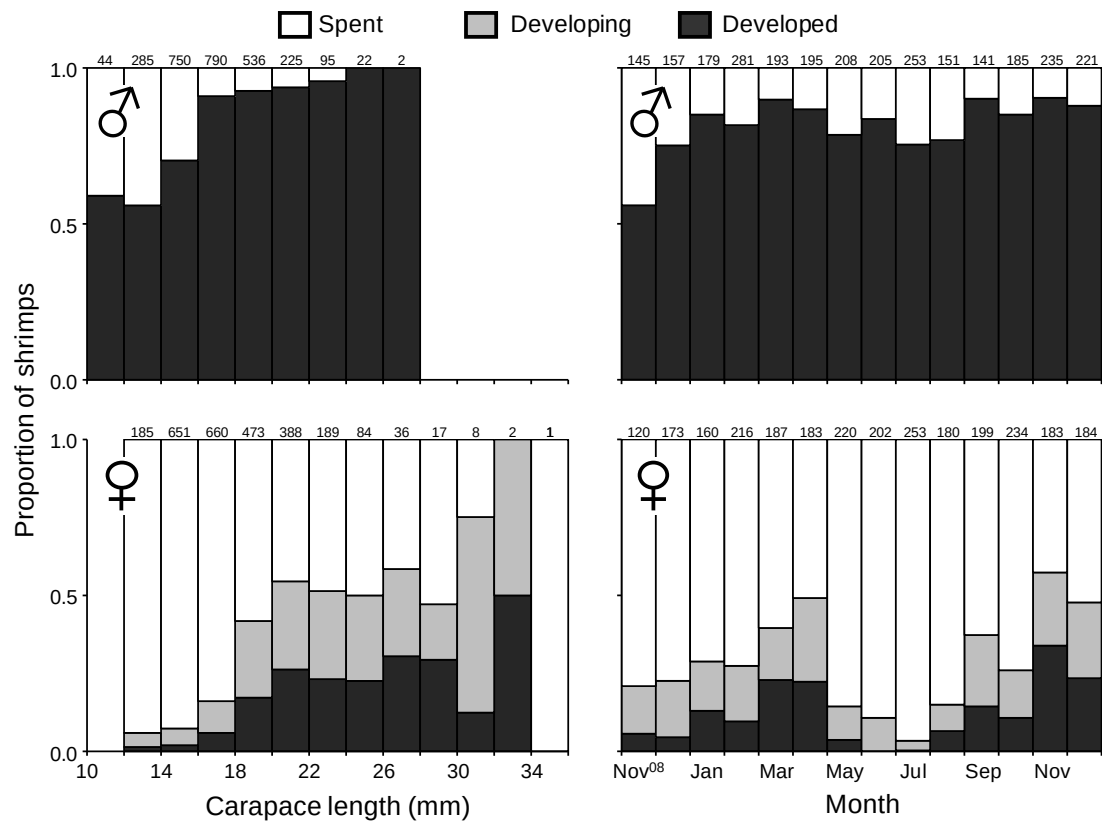


Fig. 4

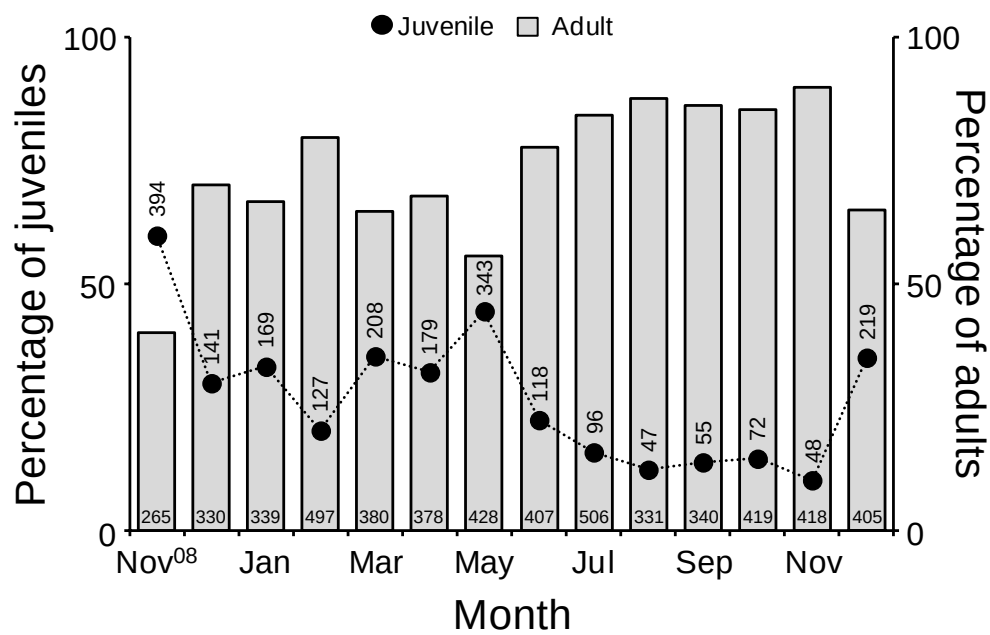


Fig. 5

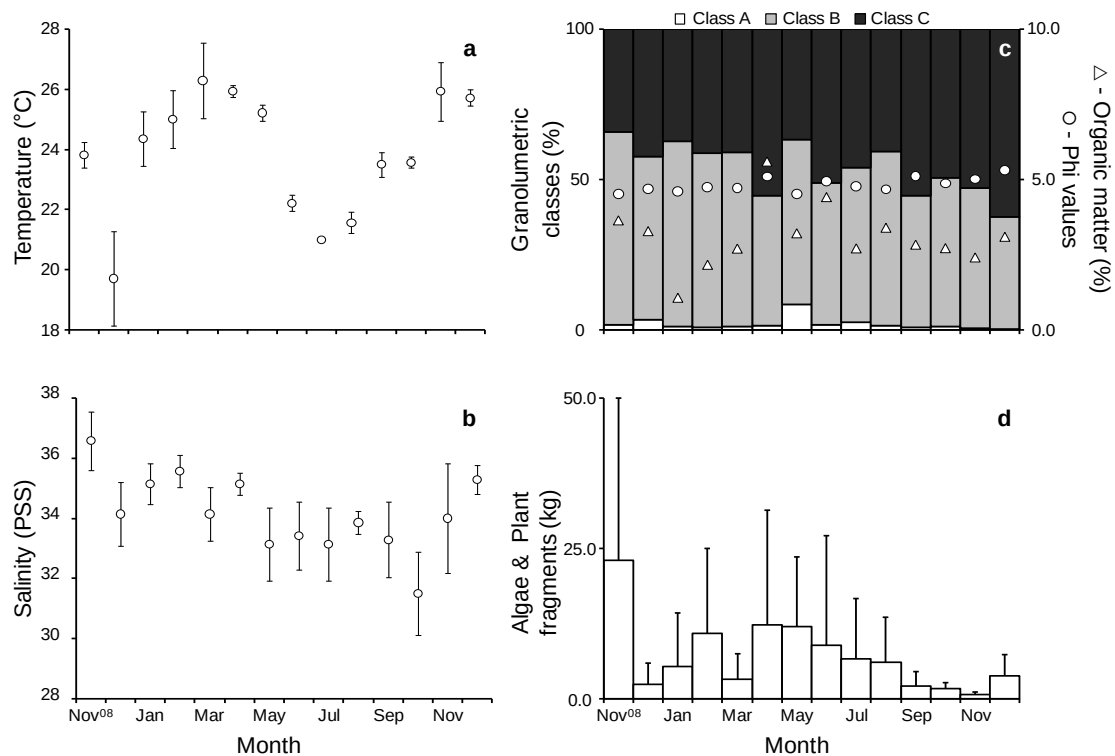
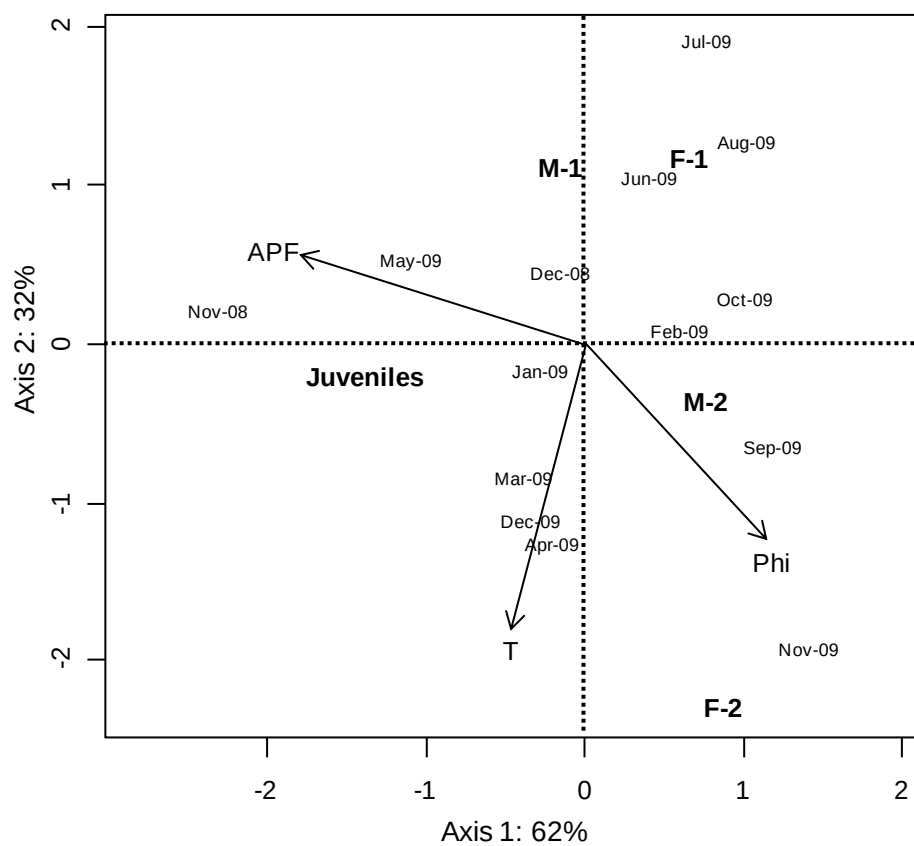


Fig. 6



Considerações finais

1. Considerações finais

O presente estudo gerou importantes resultados sobre a estrutura da comunidade dos camarões pertencentes à infraordem Penaeidea, assim como sobre a dinâmica populacional de *Xiphopenaeus kroyeri* (Heller, 1862) no litoral norte do Estado de São Paulo.

Após um intervalo 20 anos, a riqueza das espécies foi praticamente mantida na Enseada da Fortaleza. Das 61 espécies de camarões peneóideos registradas ao longo do litoral brasileiro, 10 espécies foram obtidas no presente estudo (Figura 1). Considerando a pequena extensão desta enseada em relação ao litoral brasileiro, conclui-se que a Infraordem Penaeidea está bem representada na Enseada da Fortaleza. *Xiphopenaeus kroyeri* correspondeu à espécie mais abundante, tanto espacialmente quanto temporalmente, em ambos os períodos de estudo. É importante ressaltar que apenas *Sicyonia laevigata* Stimpson, 1871 não foi obtida durante as amostragens efetuadas no segundo período de estudo. Porém, esta espécie pôde ser classificada como acidental, visto que apenas um espécime foi obtido durante o primeiro período de estudo.

Os índices ecológicos relativos à dominância (D), diversidade (H'), equidade (J') e similaridade, variaram ao longo dos transectos e meses. Durante o segundo período de estudo, registrou-se os maiores valores de D , e, conseqüentemente, os menores valores de H' e J' , em comparação ao primeiro período de estudo. Tal diferença associou-se, principalmente, à elevada abundância de *X. kroyeri*. Os transectos em que o sedimento foi composto por grãos mais grossos, como os transectos II e V, apresentaram os maiores valores de H' e J' , provavelmente por proporcionar um ambiente mais heterogêneo, facilitando assim a ocorrência de várias espécies. Durante os meses correspondentes ao verão e inverno, também foram registrados os maiores valores de H' e J' . A interação das massas de água presentes na região de Ubatuba,

como Água Costeira (AC: temperatura $> 20^{\circ}\text{C}$; salinidade < 36), Água Tropical (AT: temperatura $> 20^{\circ}\text{C}$; salinidade > 36) e Água Central do Atlântico Sul (ACAS: temperatura $< 18^{\circ}\text{C}$; salinidade < 36), possivelmente influenciaram os padrões de abundância dos camarões peneóideos presentes na região do presente estudo.

Significantes variações no número de indivíduos foram observadas entre o primeiro e o segundo período de estudo; a abundância de *Farfantepenaeus brasiliensis* (Latreille, 1817), *Litopenaeus schmitti* (Burkenroad, 1936), *Rimapenaeus constrictus* (Stimpson, 1874), *X. kroyeri*, *S. dorsalis* Kingsley, 1878 e *S. typica* (Boeck, 1864) aumentou consideravelmente durante o segundo período de estudo. Enquanto que o oposto foi verificado para as espécies *Artemesia longinaris* Bate, 1888, *F. paulensis* (Pérez Farfante, 1967), e *P. muelleri* (Bate, 1888). Porém, os padrões espaciais e temporais da abundância e distribuição dos camarões peneóideos observados na Enseada da Fortaleza corroboraram com investigações anteriores efetuadas na região de Ubatuba, ressaltando a importância das variáveis ambientais na determinação de tais padrões, como exemplo a relação entre *F. brasiliensis*, *F. paulensis*, *R. constrictus*, e *X. kroyeri* e granulometria do sedimento, assim como a relação entre *A. longinaris*, *L. schmitti*, *S. dorsalis*, e *P. muelleri* e a temperatura e salinidade da água.

Em relação à *X. kroyeri*, a abundância desta espécie quase triplicou após um intervalo de 20 anos. Interessantemente, entre o primeiro e o segundo período de estudo, foi observado uma elevada deposição de sedimentos finos na Enseada da Fortaleza, como areia fina e muito fina e silte+argila. Provavelmente, esta sedimentação foi causada pela interação de fenômenos naturais (como as condições hidrodinâmicas locais e os eventos de El Niño/La Niña), e atividades humanas (como o crescimento urbano). Como mencionado anteriormente, sedimentos finos são muito importantes na determinação dos padrões de abundância e distribuição de *X. kroyeri* na região de

Ubatuba. Deste modo, tal sedimentação observada pode ter contribuído significativamente para a elevada abundância da espécie.

Além da deposição de sedimentos finos na Enseada da Fortaleza, demais fatores como o aumento da disponibilidade de alimentos associado à elevada produtividade primária durante os eventos de El Niño e La Niña, e as medidas de gestão e manejo criadas, como a limitação do esforço de pesca, a regulamentação dos equipamentos de pesca e suas restrições de uso, criação de áreas de proteção ambiental e fechamento temporário da pesca, foram essenciais para o estabelecimento e ocorrência de *X. kroyeri* na Enseada da Fortaleza, representando importantes ferramentas para preservação, conservação e uso sustentável deste importante recurso pesqueiro na região do estudo.

Apesar da elevada abundância de *X. kroyeri*, a estrutura da população da espécie pôde ser considerada relativamente estável ao longo dos períodos de estudo, com similar distribuição de frequência de tamanho entre machos e fêmeas, e contínua ocorrência de jovens e adultos. As fêmeas atingiram tamanhos maiores que os machos em relação ao comprimento da carapaça, evidenciando um padrão inverso de dimorfismo sexual (fêmeas > machos), provavelmente relacionado às estratégias reprodutivas desempenhadas por *X. kroyeri*. A razão sexual total da espécie foi direcionada em favor das fêmeas durante ambos os períodos de estudo. Mensalmente, a razão sexual dos jovens variou apenas em favor das fêmeas, enquanto que para os adultos, a razão sexual variou tanto em favor dos machos quanto das fêmeas. Com base nas estratégias reprodutivas desempenhadas por *X. kroyeri*, impulsionado por sua vez pela abundância de fêmeas reprodutivamente ativas, podem exercer influência no tamanho da maturidade sexual de machos, resultando em desvios na proporção sexual entre jovens e adultos. O tamanho da primeira maturação sexual foi estimado em 12,8 mm CC nos machos e 13,2 CC mm nas fêmeas. A reprodução de *X. kroyeri* foi contínua

na Enseada da Fortaleza, porém dois picos foram registrados, os quais foram seguidos por picos de recrutamento juvenil. O alto potencial reprodutivo da população de *X. kroyeri* e a elevada ocorrência de juvenis na Enseada da Fortaleza, demonstram a importância desta região de estudo como áreas de estabelecimento e crescimento da espécie, a qual poderá fornecer importantes benefícios no futuro próximo.

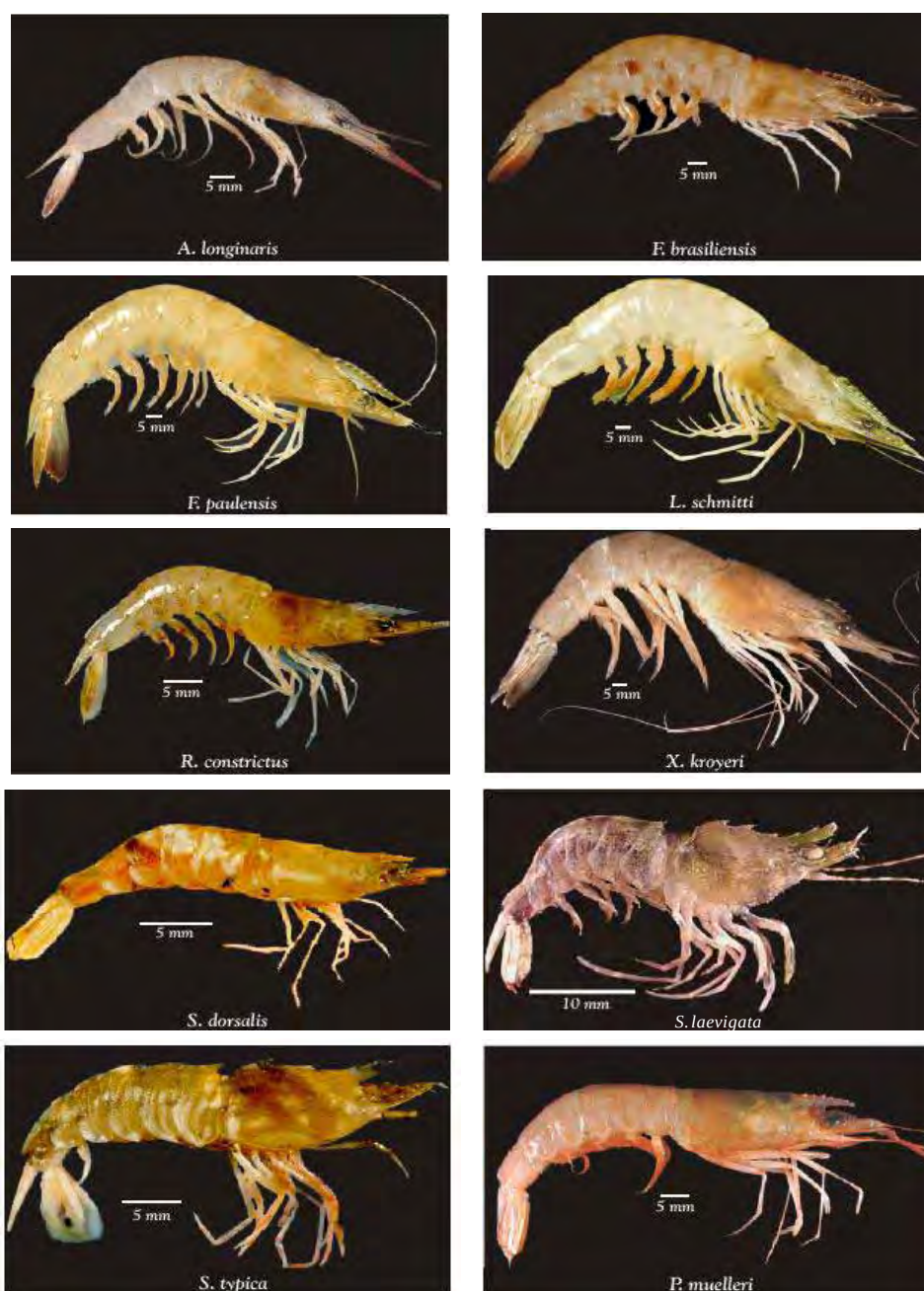


Figura 1: Espécies identificadas no presente estudo (Fotos: Fransozo, A.).