

Research Article

Ecological distribution of *Nematopalaemon schmitti* and *Exhippolysmata oplophoroides* (Crustacea: Caridea) near an upwelling area off southeastern Brazil

Daphine Ramiro Herrera¹, Regis Augusto Pescinelli¹ & Rogerio Caetano da Costa¹

¹Laboratório de Biologia de Camarões Marinhos e de Água Doce (LABCAM)

Departamento de Ciências Biológicas, Faculdade de Ciências

Universidade Estadual Paulista (UNESP), Bauru, Brasil

Corresponding author: Daphine Herrera (daphine_herrera@hotmail.com)

ABSTRACT. Regions affected by upwelling show environmental characteristics that may change the distribution of the species. This study evaluated the influence of environmental factors on the spatiotemporal distribution of two caridean shrimps, *Nematopalaemon schmitti* and *Exhippolysmata oplophoroides*, in a region of the Brazilian coast affected by Cabo Frio upwelling. Shrimps were collected monthly from July 2010 through June 2011 off Macaé off the northern coast of Rio de Janeiro State, at six locations: three at 5 m, and the other three at 15 m depth. Shrimp abundance was compared among seasons and sampling sites. *Nematopalaemon schmitti* (n = 1200) was more abundant at 5 m depth while *E. oplophoroides* (n = 2176) occurred predominately at 15 m. There were significant seasonal fluctuations in the distribution of the species in the region, resulting from variation in bottom temperature. The presence of the South Atlantic Central Water (SACW) favors the decrease in the abundance of *N. schmitti* and highest abundance of *E. oplophoroides*. The abundance of *E. oplophoroides* and the percentage of organic matter were significantly and positively correlated. The organic matter content in the sediment and water temperature was among the most important variables affecting seasonal distribution of the species. The distinct environmental characteristic between the bathymetric regions were a determinant factor in their spatial distribution.

Keywords: *Nematopalaemon schmitti*, *Exhippolysmata oplophoroides*, abiotic factors, abundance, spatio-temporal distribution, habitat, SACW, Rio de Janeiro.

INTRODUCTION

The distribution and abundance of benthic organisms may be influenced by many biotic and abiotic factors (Bauer, 1992; Dall *et al.*, 1990). The abiotic factors that shape the coexistence of the caridean shrimps are primarily controlled by habitat types and are influenced by seasonal water temperature changes, salinity fluctuations (Bilgin *et al.*, 2008) and by water masses, through transport and accumulation of nutrients (Coelho-Souza *et al.*, 2012). Sediment also plays an important role in the distribution of carideans because the sediment preferences are related to their burrowing ability (Pinn & Ansell, 1993). Furthermore the organic-matter content can be used as a food source for a high number of preys that feed on this material (Fransozo *et al.*, 2005; Almeida *et al.*, 2012).

Coastal upwelling systems are usually the result of horizontal differences in the surface layer of the ocean,

driven by the wind. Upwelling involves the ascent of cold, nutrient-rich water from subsurface layers to the surface, favoring primary production in the euphotic zone, where mass and energy are transferred through food webs; these physical processes highly impact marine life where they occur (Magliocca *et al.*, 1979; Lehmann & Myrberg, 2008; Merino & Monreal-Gómez, 2009). As a result, upwelling regions are the most productive areas of the ocean (Coelho *et al.*, 2012). The main upwelling area along the Brazilian Coast is off Cabo Frio, state of Rio de Janeiro (23°S), and occurs more frequently and intensely in spring (October to December) and summer (January to March) (Calado *et al.*, 2008; Coelho-Souza *et al.*, 2012). This phenomenon, when combined with the intrusion of South Atlantic Central Water (SACW) with temperatures below 20°C and salinities between 34.6 and 36.0 (Miranda, 1985), makes the Cabo Frio region and adjacent areas highly productive and important for the

distribution and abundance of benthic communities (De Léo & Pires-Vanin, 2006). Studies of Magliocca *et al.* (1979) and Paviglione & Miranda (1985) indicated the occurrence of periodic events of the coastal upwelling off Cabo Frio, with its influence extending up to the proximity of the Cabo de São Tomé (22°S).

The white belly shrimp *Nematopalaemon schmitti* (Holthuis, 1950) is distributed from Venezuela to Brazil (Ferreira *et al.*, 2010). The redleg humpback shrimp or spine shrimp *Exhippolysmata oplophoroides* (Holthuis, 1948) occurs from North Carolina (USA), to Uruguay (Christoffersen, 1998). Even though these two caridean species are currently not commercially exploited, they are part of the trophic structure of soft-bottom environments. Additionally, *N. schmitti* and *E. oplophoroides* are the most abundant species among the caridean shrimps in Macaé region, an area located near of the upwelling in the Cabo Frio region (Silva *et al.*, 2014; Pantaleão *et al.*, 2016). These authors studied the composition and assemblages of shrimps (Penaeoidea and Caridea) in this region; however, the knowledge about the spatial and temporal distribution of the species in this area is scarce.

The Rio de Janeiro State has the highest fishery productivity of the southeastern region of Brazil (IBAMA, 2007), and *N. schmitti* and *E. oplophoroides* form part of the bycatch of penaeid shrimp fisheries, such as *Artemesia longinaris* Spence Bate, 1888, *Pleoticus muelleri* (Spence Bate, 1888), *Xiphopenaeus kroyeri* (Heller, 1862), *Farfantepenaeus paulensis* (Pérez-Farfante, 1967), *Farfantepenaeus brasiliensis* (Latreille, 1817) and *Litopenaeus schmitti* (Burkenroad, 1936) (Costa *et al.*, 2000; Fransozo *et al.*, 2009; Pantaleão *et al.*, 2016). The impact of bottom-trawl shrimp fishing in coastal locations has caused significant losses in the biomass and biodiversity of non-consolidated environments (Pauly *et al.*, 2002; Castilho *et al.*, 2008).

Considering the upwelling system in the Cabo Frio region, which is of great importance for the biological enrichment of the water and the fishery activities in the region, this study analyzed the spatial and temporal distribution of the caridean shrimps *N. schmitti* and *E. oplophoroides* off Macaé, Rio de Janeiro, located within the Cabo Frio upwelling area. This study tested the hypothesis that the abundance of these species varies depending on environmental factors such as bottom temperature and salinity, sediment texture, and organic-matter content.

MATERIALS AND METHODS

Study area

The municipality of Macaé on the northern coast of Rio de Janeiro is located within the limits of the environ-

mental protection area of the Santana Archipelago, near the influence of the Cabo Frio region (Fig. 1). The particular orientation of the Rio de Janeiro coast, with coastline changing abruptly from north-south to east-west direction, moves the coastal water away from the coast and toward the ocean, and favors the intrusion and spread of the SACW. This water mass occurs at the thermocline depth in the open ocean, which intrudes over the inner continental shelf near the bottom, and eventually upwells to the surface near the coast (Moreira da Silva, 1971; Gonzalez-Rodriguez *et al.*, 1992; Campos *et al.*, 2000; Mahiques *et al.*, 2005). The rise of the SACW determines the local upwelling events, and the magnitude of these events is influenced by winds, the configuration of the coast and by the ocean-bottom topography of the Cabo Frio region (Stramma & Peterson, 1990; Rodrigues & Lorenzetti, 2001).

Sampling of specimens and environmental factors

Shrimps were sampled monthly from July 2010 through June 2011 to minimize the possible effect of local trends. Six sampling sites were selected at depths of 5 m (sites 1-3) and 15 m (sites 4-6). A GPS was used to record the position of each sampling site.

The commercial fishing boat used for trawling was equipped with 10 m-long double-rig fishing nets, with a 20 mm mesh size and an 18 mm cod end. Each sampling site was trawled for 30 min at a constant speed of 2.0 knots, covering an area of approximately 18,500 m². During each monthly collection, samples of bottom and surface water were collected with a Van Dorn bottle at each sampling site; temperature was measured with a mercury thermometer (0.1°C scale), and salinity using an optical refractometer (0.1 scale).

Sediment samples were collected seasonally (winter: July-September; spring: October-December; summer: January-March; autumn: April-June) at each site, using a Van Veen grab with a sampling area of 0.06 m² to determine mean grain size of the sediment (ϕ) and organic-matter content (OM) determination. In the laboratory, samples were oven-dried at 70°C for 72 h. For grain size analysis, a 100 g subsample was taken from each site and then treated with 250 mL of a NaOH solution (0.2 mol L⁻¹) for 20 min, to separate the silt and clay particles, and was then rinsed on a 0.063 mm sieve to remove the remaining silt and clay. The subsample was oven-dried again for 24 h at 60°C, and the remaining sediment was rinsed on sieves of different sizes: 2 mm (gravel); 2.0 to 1.01 mm (very coarse sand); 1.0 to 0.51 mm (coarse sand); 0.50 to 0.26 mm (medium sand); 0.25 to 0.126 mm (fine sand), and 0.125 to 0.063 mm (very fine sand); smaller particles were classified as silt-clay. The portions retained on

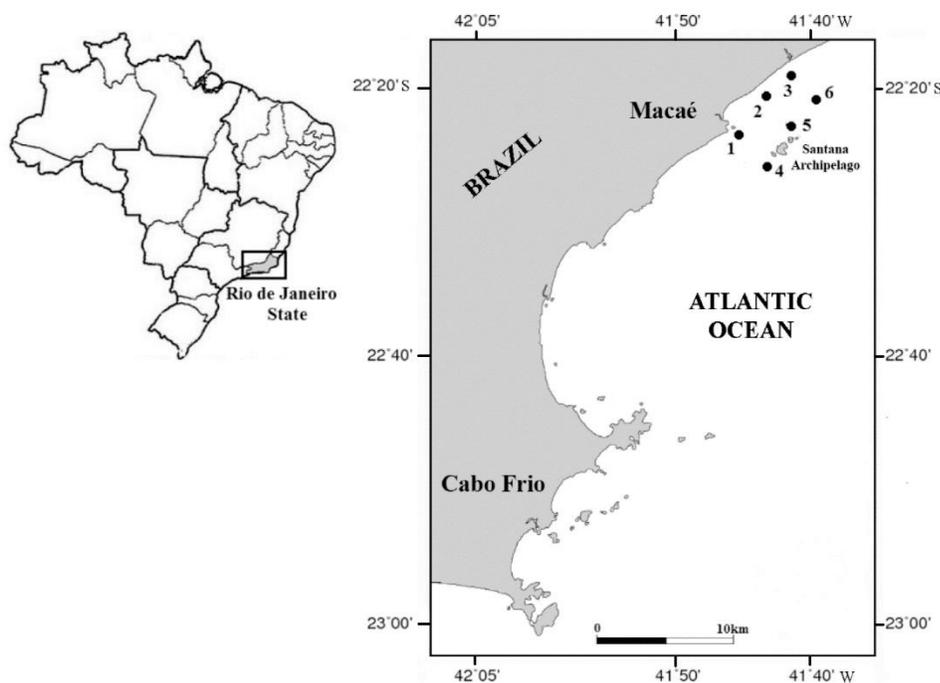


Figure 1. Location of sampling sites off Macaé, Rio de Janeiro State, Brazil. Sites 1, 2, 3 were located at 5 m depth and sites 4, 5, 6 at 15 m depth.

each sieve were weighed on an analytical balance (0.0001 g) to determine the percentage of each grain-size fraction. The particle size classes were expressed in $\phi = -\log_2$ (grain diameter in millimeter), and the following size fractions were obtained: gravel (< -1), very coarse sand ($-1 < \phi < 0$), coarse sand ($0 < \phi < 1$), medium sand ($1 < \phi < 2$), fine sand ($2 < \phi < 3$), very fine sand ($3 < \phi < 4$), and silt and clay (> 4) (Tucker, 1988; Costa *et al.*, 2007). From these grain-size percentages, measurements of central tendency were calculated to determine the most frequent granulometric fractions in the sediment samples. These values were calculated based on data extracted from cumulative frequency-distribution curves of the sediment samples; subsequently the formula $M = \phi_{16} + \phi_{50} + \phi_{84}/3$ was applied (Tucker, 1988).

Sediment samples were classified into three size classes (see Magliocca & Kutner, 1965): Class A: medium sand (MS), coarse sand (CS), very coarse sand (VCS), and gravel ($G > 0.25$ mm) accounting for more than 70% of the sample weight; Class B: fine sand (FS) and very fine sand (VFS) comprising more than 70% of the sample weight (0.25; 0.0625 mm); Class C: more than 70% of the sediment is silt and clay (S+C).

For organic matter (OM) content determination, 10 g from each site was taken from each of the oven dried sediment samples, placed in porcelain crucibles and then heated in an oven at 500°C for 3 h. The percentage of organic matter was estimated as the difference

between the initial and final weight of the crucibles (Mantelatto & Fransozo, 1999).

Data analysis

Tests for homoscedasticity (Levene test) and normality (Shapiro-Wilk test) were performed as pre-requisites for the temporal and spatial abundance data sets. All the data sets for the two species were not normally distributed; shrimp abundances per sampling site and per season were compared using the the Kruskal-Wallis test, with later paired comparisons by the Dunn's test.

The influence of environmental factors on the abundances of the two species was evaluated through a time-series analysis by cross-correlation with the Statistica 7.0 software (StatSoft, Inc). All statistical procedures followed Zar (1999), and the level of significance was set at $P < 0.05$.

The data for abiotic factors were plotted against the presence of *N. schmitti* and *E. oplophoroides* for each sampling location. The analysis of these relationships consisted of distributing the total results for these factors into value classes of abiotic factors (temperature, salinity, sediment texture, and organic-matter content). The number of captured specimens and the frequency of repetitions of the values for each class of the factors were determined by the relative frequency of individuals at each sampling site (Costa *et al.*, 2004, 2005).

RESULTS

The water temperature ranged from 18 to 24.5°C (mean 20.8 ± 1.8) in the bottom and from 19.5 to 26.0°C at the surface (mean 22.8 ± 1.8). Bottom salinity varied between 35 and 39 (mean 36.9 ± 0.8) and between 29 and 39 at the surface (mean 36.4 ± 1.5). Mean monthly surface temperature ranged from 20.5 (July) to 25.7 (March), and bottom temperature fluctuated between 19.4°C (January) and 22.9°C (October) (Fig. 2). The mean surface salinity ranged from 35.2 (December) to 37.4 (November) and bottom salinity ranged from 35.7 (December) to 38 (April) (Fig. 3).

The highest average bottom water temperature was found in site 2 (21.9°C). On the other hand, the lowest values (19.8°C) were recorded in sites 5 and 6 (Table 1). Average temperature values changed with depth, being lowest highest in deeper sites (15 m). The average temperatures at 5 and 15 m depth were 21.6 ± 1.6 °C and 19.9 ± 1.7 °C, respectively. The average bottom salinity was lowest at Site 6 (36.6) and highest at Site 5 (37.3) (Table 1). Average bottom salinity was similar among the sites: at a depth of 5 m, the average salinity was 36.8 ± 0.8 and a depth of 15 m was 37.0 ± 0.8 .

Medium sand and very fine sand predominated at the shallower sites (5 m), and silt and clay at the greater depth (15 m). The highest concentrations of organic matter were found at the points with the highest amounts of silt and clay (15 m) (Fig. 4).

A total of 1200 individuals of *N. schmitti* were collected, and the species was most abundant at Site 3 ($n = 930$). Individuals of *E. oplophoroides* ($n = 2176$) were most abundant at Site 4 ($n = 730$). The abundances of both species differed significantly between the depths (Table 2). *Nematopalaemon schmitti* was more abundant at the shallower sites (5 m), which also contained less organic matter. *Exhippolysmata oplophoroides* was more abundant in deeper water (15 m), where organic-matter concentrations were high (Fig. 5).

The abundances of the two species differed significantly between seasons. *Nematopalaemon schmitti* was more abundant in winter (93.2%). The abundance in winter was statistically different from autumn abundances (1.1%) (Kruskal-Wallis, $P = 0.02$; $H = 8.98$; 3 df). *Exhippolysmata oplophoroides* showed highest abundance in spring (54.2%) and winter (38.9%). The abundance in spring and winter was statistically different from autumn abundances (3.1%) (Kruskal-Wallis, $P = 0.00$; $H = 15.40$; 3 df) (Table 2).

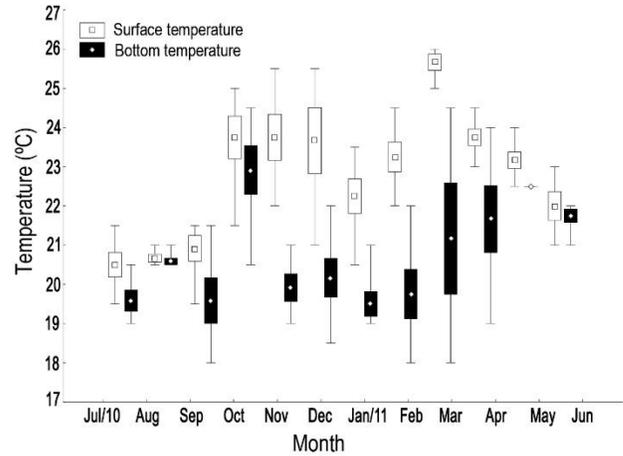


Figure 2. Monthly mean values and standard error (box), and range (whiskers) of surface and bottom water temperatures in the Macaé region, Rio de Janeiro State, Brazil, from July 2010 to June 2011.

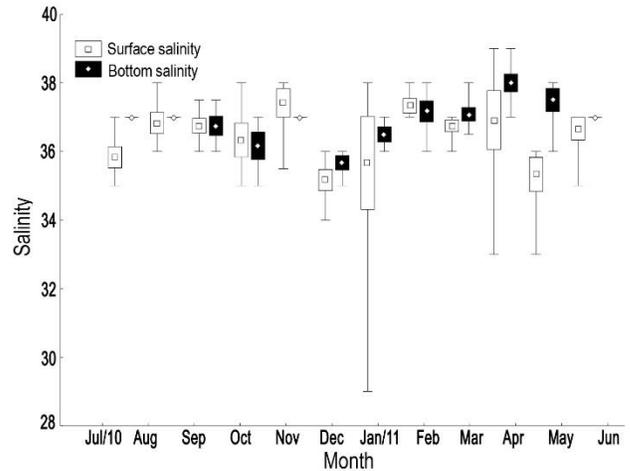


Figure 3. Monthly mean values and standard error (box), and range (whiskers) of surface and bottom water salinity in the Macaé region, Rio de Janeiro State, Brazil, from July 2010 to June 2011.

Nematopalaemon schmitti showed the highest mean number of individuals at sites with water temperatures between 20 and 21°C, salinity of 37 to 38, and lower organic-matter concentrations (0 and 3), with sediment composed of very fine sand ($3 < \phi < 4$) and medium sand ($0 < \phi < 1$) (Fig. 6). The numbers of individuals were negatively correlated with low organic-matter content (as observed graphically). There was no statistically significant correlation between the abundance of this species and environmental factors (cross-correlation, $P > 0.05$). In contrast, *E. oplophoroides* showed the highest mean number of individuals at temperatures between 20 and 21°C and 24 to 25°C, salinity of 35 to 36, and organic-matter concentrations

Table 1. Mean, standard deviation (SD), minimum and maximum bottom temperatures and salinities for each sampling site in the Macaé region, Rio de Janeiro State, Brazil, from July 2010 to June 2011.

Site	Bottom temperature (°C)			Bottom salinity		
	Mean ± SD	Min	Max	Mean ± SD	Min	Max
1	21.2 ± 1.7	19.0	24.5	37.1 ± 0.7	36.0	38.0
2	21.9 ± 1.5	20.0	24.5	36.6 ± 0.9	35.0	38.0
3	21.6 ± 1.5	19.5	24.0	36.8 ± 0.8	35.0	38.0
4	20.2 ± 1.9	18.0	24.5	37.0 ± 0.6	36.0	38.0
5	19.8 ± 1.4	18.0	22.5	37.3 ± 1.0	35.0	39.0
6	19.8 ± 1.7	18.0	22.5	36.6 ± 0.8	35.0	38.0

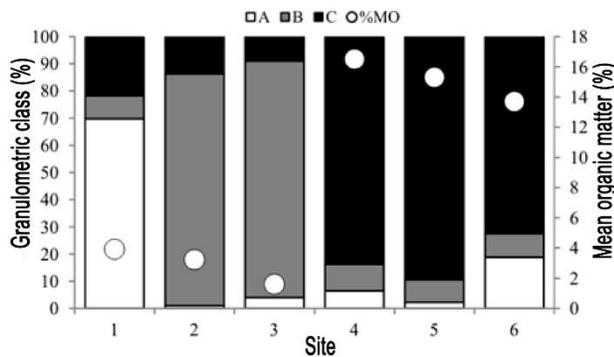


Figure 4. Grain size categories and organic matter content of the sediment at each site sampled, in the Macaé region, Rio de Janeiro State, Brazil. Granulometric class: Class A (gravel, very coarse sand, coarse and medium sand), Class B (fine and very fine sand) and Class C (silt + clay).

between 21 and 24; the species showed a preference for medium sand ($0 < \phi < 1$), and silt and clay ($\phi > 4$) (Fig. 6).

The abundance of *E. oplophoroides* was significantly and positively correlated with the percentage of organic matter (cross-correlation, $P < 0.05$; Fig. 7), and this analysis revealed the highest correlation in the increase in the abundance of individuals two months before the amount of organic matter in the sediment decreased (Fig. 7).

DISCUSSION

The results of this study revealed a well-defined distribution pattern between *N. schmitti* and *E. oplophoroides*, with higher abundances of the species in different seasons, and distinct distributions in space, where environmental characteristics of the sampling site played a key factor to explain the patchy distribution of these two caridean shrimps in Macaé.

Bottom and surface temperatures obtained in this study were, during most of the year, low compared to those usually found in the tropical region, which may be related to the location of the sampling area near the coastal upwelling system of Cabo Frio (Valentin, 1984). Sancinetti *et al.* (2014, 2015) showed that the environmental conditions (temperature and salinity) in the Macaé region differ from those that are usually found in tropical regions. As a result of the influence of the Cabo Frio upwelling, the low mean temperatures and the high nutrient concentrations throughout the year create conditions resembling the cool-temperate southern part of the continent (Sancinetti *et al.*, 2015).

The temperature decreased more sharply when a thermocline was present due to the influence of the SACW (during spring and summer) when upwelling events were more pronounced, mainly by the prevalence of northeasterly winds (Barth *et al.*, 2007; Calado *et al.*, 2008). This phenomenon could be observed during spring-summer of the present study with a decrease in bottom temperature, indicating the presence of the SACW (Fig. 2).

There were seasonal fluctuations in the distribution of the two caridean shrimps studied in the region resulting from variation in bottom temperature. The presence of the SACW promoted a decrease in the abundance of the *N. schmitti* and highest abundance of *E. oplophoroides* in the spring.

Fransozo *et al.* (2009) studying the distribution of *N. schmitti* in Ubatuba Bay, Brazil, concluded that lower temperatures were determinant for the increase in the abundance of this shrimp during the winter. Results of the present study revealed, however, that decreased abundances of *N. schmitti* occurred at temperatures lower than those recorded off the Ubatuba region, suggesting that the optimum temperature for this species is around 20°C.

According to Almeida *et al.* (2012), the decreased abundance of *N. schmitti* in spring and especially in summer may indicate a seasonal migration, occurring together with the transport of the biodebris and plants fragments over the substrata, as a consequence of the intrusion of the SACW. This hypothesis is consistent with our results: the occurrence of this water mass likely induced the animals to migrate to other areas with more favorable temperature conditions because when SACW reaches the bay, it causes a decrease in temperature.

Studies highlighting the use of different areas during the animal's life cycle, suggest that environmental variables, especially temperature, influence the habitat selection of several caridean shrimp species: *Crangon crangon* (Linnaeus, 1758) (Spaargaren, 2000; Siegel *et al.*, 2005), *Palaemon adspersus* Rathke, 1837 (Bilgin *et al.*, 2008), *Palaemon elegans* Rathke, 1837

Table 2. Seasonal abundances of *Nematopalaemon schmitti* and *Exhippolysmata oplophoroides* at each sampling site in the Macaé region, Rio de Janeiro State, Brazil, from July 2010 through June 2011. Different letters indicate significant differences (Kruskal-Wallis, $P < 0.05$).

<i>Nematopalaemon schmitti</i>							
Season	Site						Total
	1	2	3	4	5	6	
Winter	180	21	912	1	0	4	1118 ^A
Spring	37	6	8	3	0	0	54 ^{AB}
Summer	3	0	10	2	0	0	15 ^{AB}
Autumn	13	0	0	0	0	0	13 ^B
Total	233 ^A	27 ^A	930 ^A	6 ^B	0 ^B	4 ^B	1200

<i>Exhippolysmata oplophoroides</i>							
Winter	344	44	99	122	29	208	846 ^a
Spring	59	2	3	562	428	126	1180 ^a
Summer	4	13	22	9	18	17	83 ^{ab}
Autumn	0	1	1	37	27	1	67 ^b
Total	407 ^a	60 ^a	125 ^a	730 ^b	502 ^b	352 ^b	2176

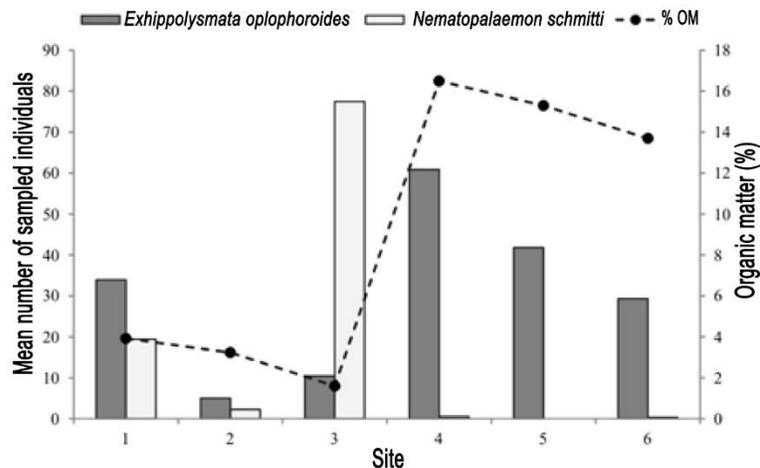


Figure 5. Mean number of sampled individuals of *Nematopalaemon schmitti* and *Exhippolysmata oplophoroides* and percentage of organic matter in the sediment at each sampled site in the Macaé region, Rio de Janeiro State, Brazil, from July 2010 to June 2011.

(Janas & Spicer, 2008), and *N. schmitti* (see Almeida *et al.*, 2011).

The increase in abundance of *E. oplophoroides* occurred in spring, coinciding with a decrease in temperature (Fig. 2); therefore, the species is possibly more tolerant to cold temperatures. In a study on *E. oplophoroides* in Ubatuba, Brazil, Fransozo *et al.* (2005) reported that this species was influenced by temperature variations due to currents. The authors suggested that when SACW reaches the bay, it causes the confinement of this shrimp population in shallower areas (<20 m). However, according to these authors, abundance was not determined only by a specific group of abiotic factors, but also by biotic factors, such as the concentration of organic matter.

The organic matter content in the sediment is a factor that influenced the occurrence of *E. oplophoroides* in Macaé because this species showed a stronger preference for sites with high levels of organic matter content. Sediment characteristics usually influence the abundance patterns of decapod crustaceans (Furlan *et al.*, 2013). Additionally, organic material deposited among sediment particles serves also as a food source for some benthic organisms (Bertini & Fransozo, 1999).

Nematopalaemon schmitti was more abundant at shallower sites, where the sediment was mainly composed of very fine sand with little organic matter, which may be interpreted as sediment preferences probably related to its burrowing ability. Marine shrimps

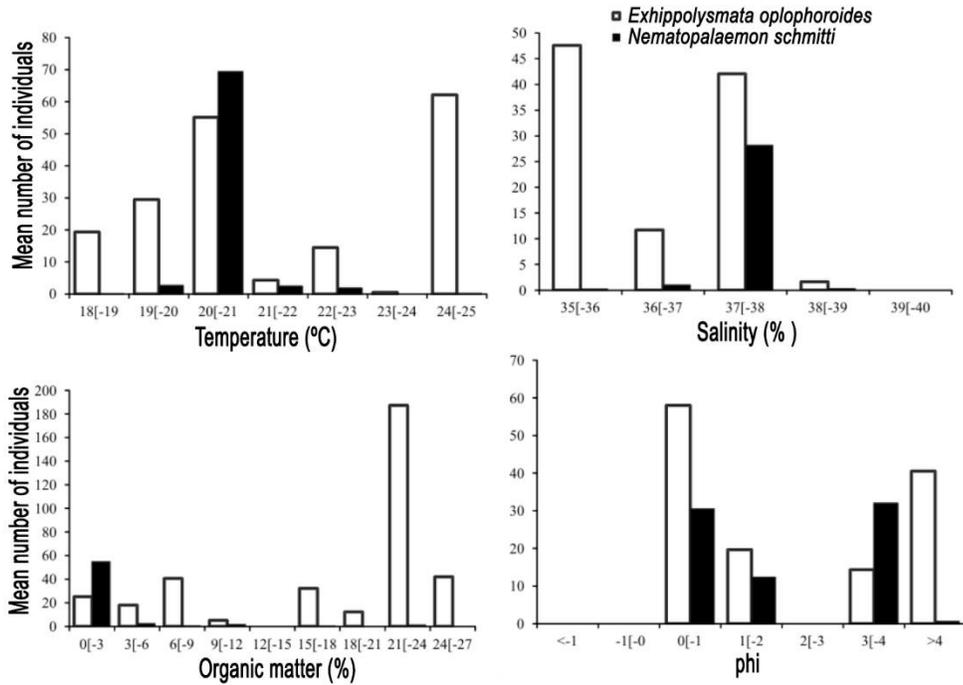


Figure 6. Distribution of the mean number of *Nematopalaemon schmitti* individuals and *Exhippolysmata oplophoroides* specimens in relation to environmental factors (bottom water temperature and salinity, organic matter, and the phi class of the sediment), in the Macaé region, Rio de Janeiro State, Brazil, from July 2010 to June 2011.

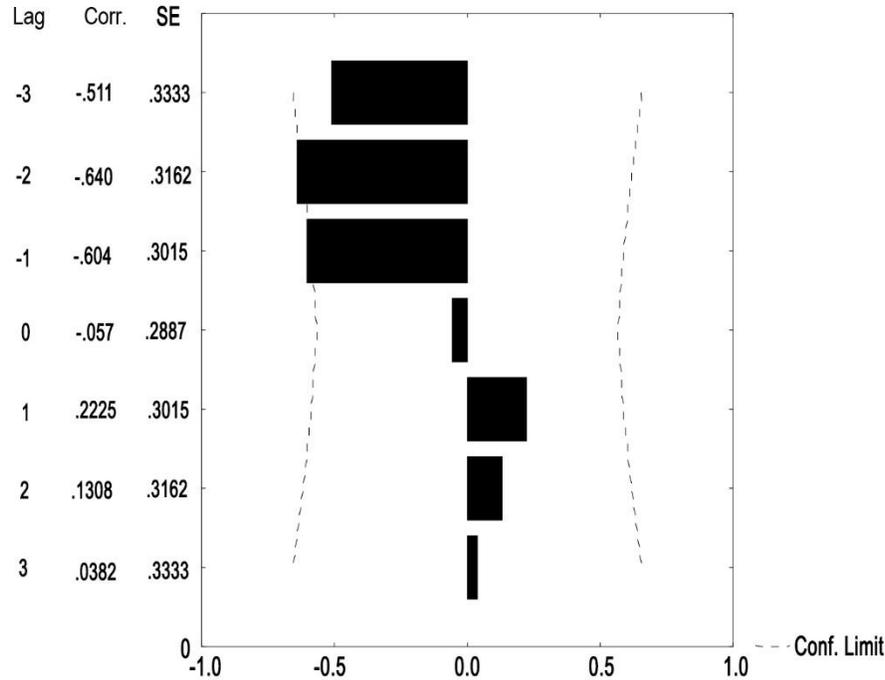


Figure 7. *Exhippolysmata oplophoroides* in the Macaé region, Rio de Janeiro State, Brazil, from July 2010 to June 2011. Cross-correlation analysis between the abundance of individuals and organic matter content, with time lag in months. Bars that reach or pass the curved lines have significant positive (upper) and negative (lower) correlation values. Lag: time, Corr.: correlation value, SE: standard error, Conf. Limit: confidence limit.

burrow to hide from predators, and therefore require a suitable substrate for rapid burying and hiding (Freire *et al.*, 2011). *Exhippolysmata oplophoroides* was caught in higher abundance in water 15 m deep, with higher concentrations of organic matter and muddier substrate, which revealed a close relationship to sediment properties. These properties (such as the organic debris) serve as a protective habitat for many caridean species, and strongly influence the establishment of caridean shrimp populations (Fransozo *et al.*, 2005). Also, these environmental conditions enable the maintenance of caridean populations, particularly females with embryos (Bauer, 1985; Fransozo *et al.*, 2005).

The presence of debris deposits and high organic-matter concentrations can provide a sheltered environment that allows *E. oplophoroides* to establish at a given site, and may also serve as food source for prey of these shrimp. Sumida *et al.* (2005) proposed that changes in the levels of chlorophyll-*a* in the Cabo Frio region could be attributed to upwelling, even during winter. In the Cabo Frio region, high concentrations of chlorophyll-*a* occur with a subsequent organic enrichment of the sediment during upwelling periods. This is probably a result of the higher primary productivity due to these events, because part of the organic matter generated is transferred to the benthos (Sumida *et al.*, 2005).

The species *N. schmitti* and *E. oplophoroides* occurred nearby the coast as indicated in the literature (Fransozo *et al.*, 2005; Almeida *et al.*, 2012; Silva *et al.*, 2014). Silva *et al.* (2014) inferred this distribution due to the local hydrodynamic conditions, proximity to the continent, as well as due to the input from the Macaé River.

Other factors such as competition and predation may also influence the abundance of shrimps (Spaargaren, 2000; Almeida *et al.*, 2012); however, the organic matter content in the sediment and water temperature of the area of the present study offered the most probable explanation for the differences among the abundance patterns of the two caridean shrimps in the Macaé region.

According to the results obtained in the present study, the two caridean species showed different distributions in time and space: the distinct environmental characteristics between the bathymetric regions were a determinant factor in their spatial distributions, and their possible migration was related to environmental factors analyzed.

ACKNOWLEDGMENTS

We thank the LABCAM co-workers for their help during fieldwork and Dr. Alexandre de Azevedo of the

Universidade Federal do Rio de Janeiro/NUPEM for the infrastructure to carry out this work. The authors also thank Dr. Janet W. Reid (JWR Associates) for her great help with English language. The authors are grateful to “Fundação de Amparo à Pesquisa do Estado de São Paulo” (FAPESP) for providing financial support (#2009/54672-4 and #2010/50188-8 to RCC), Research Scholarship (#2010/13008-1 to DRH), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (#159130/2010-7 to RAP and PQ1 #305919/2014-8 to RCC). All experiments conducted in this study comply with current applicable state and federal laws (Authorization of the Instituto Chico Mendes de Biodiversidade/ICMBio - SISBIO number 23012-1).

REFERENCES

- Almeida, A.C., V. Fransozo, G.M. Teixeira, M. Furlan, K.A.N. Hiroki & A. Fransozo. 2011. Population structure and reproductive period of whitebelly prawn *Nematopalaemon schmitti* (Holthuis, 1950) (Decapoda: Caridea: Palaemonidae) on the southeastern coast of Brazil. *Invertebr. Reprod. Dev.*, 55(1): 30-39.
- Almeida, A.C., A. Fransozo, G.M. Teixeira, K.A.N. Hiroki, M. Furlan & G. Bertini. 2012. Ecological distribution of the shrimp *Nematopalaemon schmitti* (Crustacea: Decapoda: Caridea) in three bays on the south-eastern coast of Brazil. *Afr. J. Mar. Sci.*, 34(1): 93-102.
- Barth, J.A., B.A Menge, J. Lubchenco, F. Chan, J.M. Bane, A.R. Kirincich, M.A. Mcmanus, K.J. Nielsen, S.D. Pierce & L. Washburn. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proc. Natl. Acad. Sci. U.S.A.*, 104: 3719-3724.
- Bauer, R.T. 1985. Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea, Decapoda) from seagrass meadows on the north coast of Puerto Rico. *Bull. Mar. Sci.*, 36(1): 150-162.
- Bauer, R.T. 1992. Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. *Invertebr. Reprod. Dev.*, 22(1-3): 193-202.
- Bertini, G. & A. Fransozo. 1999. Spatial and seasonal distribution of *Petrochirus diogenes* (Anomura, Diogenidae) in the Ubatuba Bay, São Paulo, Brazil. *Iheringia, Sér. Zool.*, 86: 145-150.
- Bilgin, S., O. Ozen & A.S. Ates. 2008. Spatial and temporal variation of *Palaemon adspersus*, *Palaemon elegans* and *Crangon crangon* (Decapoda: Caridea) in

- the southern Black Sea. *Estuar. Coast. Shelf Sci.*, 79: 671-678.
- Calado, L., A. Gangopadhyay & I.C.A. da Silveira. 2008. Feature-oriented regional modeling and simulations (FORMS) for the western South Atlantic: Southeastern Brazil region. *Ocean. Model.*, 25: 48-64.
- Campos, E.J.D., D. Velhote & I.C.A. da Silveira. 2000. Shelf break upwelling driven by Brazil current cyclonic meanders. *Geophys. Res. Lett.*, 27: 751-754.
- Castilho, A.L., M.R. Pie, A. Fransozo, A.P. Pinheiro & R.C. Costa. 2008. The relationship between environmental variation and species abundance in shrimp community (Crustacea: Decapoda: Penaeoidea) in southeastern Brazil. *J. Mar. Biol. Assoc. U.K.*, 88: 119-123.
- Christoffersen, M.L. 1998. Malacostraca. Eucarida. Caridea. Crangonoidea and Alpheoidea (Except Glyphocrangonidae and Crangonidae). In: P.S. Young (ed.). *Catalogue of Crustacea of Brazil*. Museu Nacional, Rio de Janeiro, Série Livros, 6: 351-372.
- Coelho-Souza, S.A., M.S. López, J.R.D. Guimarães, R. Coutinho & R.N. Candella. 2012. Biophysical interactions in the Cabo Frio upwelling system, southeastern Brazil. *Braz. J. Oceanogr.*, 60(3): 353-365.
- Costa, R.C., A. Fransozo & A.P. Pinheiro. 2004. Ecologic distribution of the shrimp *Pleoticus muelleri* (Bate, 1888) (Decapoda: Penaeoidea) of southeastern Brazil. *Hydrobiologia*, 529(1): 195-203.
- Costa, R.C., A. Fransozo, A.L. Castilho & F.A.M. Freire. 2005. Annual, seasonal and spatial variation of abundance of the shrimp *Artemesia longinaris* (Decapoda: Penaeoidea) in south-eastern Brazil. *J. Mar. Biol. Assoc. U.K.*, 85: 107-112.
- Costa, R.C., A. Fransozo, F.A.M. Freire & A.L. Castilho. 2007. Abundance and ecological distribution of the "sete-barbas" shrimp *Xiphopenaeus kroyeri* (Heller, 1862) (Decapoda: Penaeoidea) in three bays of the Ubatuba region, south-eastern Brazil. *Gulf Caribb. Res.*, 19: 33-41.
- Costa, R.C., A. Fransozo, F.L.M. Mantelatto & R.H. Castro. 2000. Occurrence of shrimp species (Crustacea: Decapoda: Natantia: Penaeoidea and Carides) in Ubatuba Bay, Ubatuba, SP, Brazil. *Proc. Biol. Soc. Wash.*, 113(3): 776-781.
- Dall, W., B.J Hill, P.C. Rothlisberg & D.J Staples. 1990. The biology of the Penaeidae. In: J.H.S. Blaxter & A.J. Southward (eds.). *Advances in marine biology*. Academic Press, San Diego, pp. 333-355.
- De Léo, F.C. & A.M.S. Pires-Vanin. 2006. A comparison between an upwelling and a non-upwelling ecosystem. *J. Mar. Syst.*, 60: 268-284.
- Ferreira, R.S., R.R.R. Vieira & F. D'Incao. 2010. The marine and estuarine shrimps of the Palaemoninae (Crustacea: Decapoda: Caridea) from Brazil. *Zootaxa*, 2606: 1-24.
- Fransozo, V., R.C. Costa, G. Bertini & V.J. Cobo. 2005. Population biology of spine shrimp *Exhippolysmata oplophoroides* (Holthuis) (Caridea: Alpheoidea: Hippolytidae) in a subtropical region, São Paulo, Brazil. *Rev. Bras. Zool.*, 22(4): 1078-1084.
- Fransozo, V., A.L. Castilho, F.A.M. Freire, M. Furlan, A.C. Almeida, G.M. Teixeira & J.A. Baeza. 2009. Spatial and temporal distribution of the shrimp *Nematopalaemon schmitti* (Decapoda: Caridea: Palaemonidae) at a subtropical enclosed bay in South America. *J. Mar. Biol. Assoc. U.K.*, 89(8): 1581-1587.
- Freire, F.A.M., A.C. Luchiari & V. Fransozo. 2011. Environmental substrate selection and daily habitual activity in *Xiphopenaeus kroyeri* shrimp (Heller, 1862) (Crustacea: Penaeoidea). *Indian J. Geo-Mar. Sci.*, 40(3): 325-330.
- Furlan, M., A.L. Castilho, L.C. Fernandes-Góes, V. Fransozo, G. Bertini & R.C. Costa. 2013. Effect of environmental factors on the abundance of decapod crustaceans from soft bottoms off southeastern Brazil. *An. Acad. Bras. Ciênc.*, 85(4): 1345-1356.
- Gonzalez-Rodriguez, E., J.L. Valentin, D.L. Andre & S.A. Jacob. 1992. Upwelling and downwelling at Cabo Frio (Brazil): comparison of biomass and primary production responses. *J. Plankton Res.*, 14(2): 289-306.
- Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). 2007. *Estatística da Pesca 2005 Brasil-Grandes Regiões e Unidades da Federação*. Brasília, 108 pp.
- Janas, U. & J.I. Spicer. 2008. Does the effect of low temperature on osmoregulation by the prawn *Palaemon elegans* Rathke, 1837 explain winter migration offshore? *Mar. Biol.*, 153: 937-943.
- Lehmann, A. & K. Myrberg. 2008. Upwelling in the Baltic sea. A review. *J. Mar. Syst.*, 74: 3-12.
- Magliocca, A. & A.S. Kutner. 1965. Sedimentos de fundo da Enseada do Flamengo, Ubatuba, SP. *Contr. Inst. Oceanogr.*, 198: 1-15.
- Magliocca, A., L.B. Miranda & S.R. Signorini. 1979. Physical and chemical aspects of transient stages of the upwelling at southwest of Cabo Frio (Lat. 23°S-Long. 42°W). *Bol. Inst. Oceanogr.*, 28(2): 37-46.
- Mahiques, M.M., M.C. Bicego, I.C.A. Silveira, S.H.M. Sousa, R.A. Lourenço & M. M. Fukumoto. 2005. Modern sedimentation in the Cabo Frio upwelling system, southeastern Brazilian shelf. *An. Acad. Bras. Ciênc.*, 77(3): 535-548.
- Mantelatto, F.L.M. & A. Fransozo. 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo State, Brazil. *Rev. Bras. Biol.*, 59(1): 23-31.

- Merino, M. & M.A. Monreal-Gómez. 2009. Ocean currents and their impact on marine life. In: C.M. Duarte & A.L. Helguer (eds.). Marine ecology. Encyclopedia of life support systems (EOLSS). Developed under the Auspices of the UNESCO. Eolss Publishers, Oxford, 1: 52-47.
- Miranda, L.B. 1985. Forma de correlação T-S de massa de água das regiões costeira e oceânica entre o Cabo de São Tomé (RJ) e a Ilha de São Sebastião (SP), Brasil. Bol. Inst. Oceanogr., 33(2): 105-119.
- Moreira da Silva, P.C. 1971. Upwelling and its biological effects in southern Brazil. In: J.D. Costlow (ed.). Fertility of the sea. Gordon and Breach, New York, pp. 469-474.
- Pantaleão, J.A.F., A.C. Batista, A. Fransozo & R.C. Costa. 2016. The influence of the upwelling on the diversity and distribution of marine shrimp (Penaeoidea and Caridea) in two tropical coastal areas of southeastern Brazil. Hydrobiologia, 763: 381-395.
- Pauly, D., V. Christensen, S. Guénette, T.J. Pitcher, U.R. Sumaila, C.J. Walters, R. Watson & D. Zeller. 2002. Towards sustainability in world fisheries. Nature, 418: 689-695.
- Paviglione, A.M. & L.B. Miranda. 1985. Nota sobre a variação sazonal da circulação geostrofica na borda da plataforma continental: cabo de São Tomé (RJ) e a Baía de Guanabara (RJ). Bolm. Inst. Oceanogr., 33(1): 55-68.
- Pinn, E.H. & A.D. Ansell. 1993. The effect of particle size on the burying ability of the brown shrimp *Crangon crangon*. J. Mar. Biol. Assoc. U.K., 73: 365-377.
- Rodrigues, R.R. & J.A. Lorenzetti. 2001. A numerical study of the effects of bottom topography and coastline geometry on the southeast Brazilian coastal upwelling. Cont. Shelf Res., 21: 371-394.
- Sancinetti, G.S., A. Azevedo, A.L. Castilho, A. Fransozo & R.C. Costa. 2014. How marine upwelling influences the distribution of *Artemesia longinaris* (Decapoda: Penaeoidea)? Lat. Am. J. Aquat. Res., 42(2): 322-331.
- Sancinetti, G.S., A. Azevedo, A.L. Castilho, A. Fransozo & R.C. Costa. 2015. Population biology of the commercially exploited shrimp *Artemesia longinaris* (Decapoda: Penaeidae) in an upwelling region in the Western Atlantic: comparisons at different latitudes. Braz. J. Biol., 75(2): 305-313.
- Siegel, V., J. Groger, T. Neudecker, U. Damm & S. Jansen. 2005. Long-term variation in the abundance of the brown shrimp *Crangon crangon* (L.) population of the German Bight and possible causes for its inter-annual variability. Fish. Oceanogr., 14: 1-16.
- Silva, E.R., G.S. Sancinetti, A. Fransozo, A. Azevedo & R.C. Costa. 2014. Biodiversity, distribution and abundance of shrimps Penaeoidea and Caridea communities in region the vicinity of upwelling in southeastern of Brazil. Nauplius, 22(1): 1-11.
- Spaargaren, D.H. 2000. Seasonal and annual variations in the catches of *Crangon crangon* (L., 1758) (Decapoda, Natantia) near the coast of Texel, the Netherlands. Crustaceana, 73(5): 547-563.
- Stramma, L. & R.G. Peterson. 1990. The south-Atlantic current. J. Phys. Oceanogr., 20: 846-859.
- Sumida, P.Y.G., M.Y. Yoshinaga, A.M. Ciotti & S.A. Gaeta. 2005. Benthic response to upwelling events off the SE Brazilian coast. Mar. Ecol. Prog. Ser., 291: 35-42.
- Tucker, M. 1988. Techniques in sedimentology. Blackwell Scientific Publications, Oxford, 394 pp.
- Valentin, J.L. 1984. Analyses des parameters hydrobiologiques dans la remontée de Cabo Frio (Brésil). Mar. Biol., 82: 259-276.
- Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, New Jersey, 663 pp.

Received: 14 December 2015; Accepted: 23 October 2016