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ORIGINAL ARTICLE

Ecological distribution and population features of *Hexapanopeus paulensis* Rathbun, 1930 (Crustacea: Decapoda: Xanthoidea) caught by bottom trawling in the southeastern coast of Brazil: implications for its population structure

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ABSTRACT

We analyzed the spatio-temporal variations of the abundance, distribution and the population structure of *Hexapanopeus paulensis* Rathbun, 1930 from the southeastern Brazilian coast. Monthly samples were taken from January 1998 to December 1999 at Ubatumirim, Ubatuba and Mar Virado bays. A total of 1084 individuals were obtained, 76 specimens at Mar Virado, 322 at Ubatuba and 686 at Ubatumirim. It was possible to verify an association between the abundance of *H. paulensis* and bottom temperature (positive correlation), grain size of sediment and organic matter content (both negatively). This explains the higher number of individuals in the stations nearest to the continent (with higher temperature values and heterogeneous substrate). Juveniles were recorded throughout the study period, constituting 39.5% of the sampled population, which highlights the importance of the region (especially Ubatumirim Bay, due the highest abundance) for the establishment of the species. Only females occupied the largest size classes, which could mean differential mortality between the sexes or growth rate. Nevertheless, further studies should be accomplished to a better comprehension of such difference.

KEY WORDS

Panopeidae, environmental variables, recruitment, sex ratio.

INTRODUCTION

Crabs of the superfamily Xanthoidea are well represented along the Brazilian coast, totaling approximately 32 described species (Melo, 1996), of which eight have been recorded on the northern coast of São Paulo state (Mantelatto and Fransozo, 2000; Bertini *et al.*, 2010a). Given the high abundance of some species of this superfamily showing predatory habits, these crabs play an important ecological role in marine ecosystems due to its interactions among different trophic levels.

On the southeastern coast of Brazil, many xanthoid species are often caught by shrimp trawling (Bertini *et al.*, 2010a), which is considered a predatory and destabilizing activity of benthic communities (Ruffino and Castello, 1992; Branco and Fracasso, 2004). The captured species (bycatch) are discarded indiscriminately, including *Hexapanopeus paulensis* Rathbun, 1930, a crab poorly studied with only two previous studies: Fransozo *et al.* (1991) and Silva *et al.* (2014) on the larval development and morphometric analysis, respectively.

The abundance and distribution patterns of the decapod crustaceans are strongly influenced by several environmental variables, determining the occurrence of a species in a given habitat (Mantelatto *et al.*, 1995; Mantelatto and Fransozo, 1999a). The different interactions between biotic and abiotic variables, and the wide oceanic extension, make the comprehension of such patterns very complex (Shirley *et al.*, 1990). In this sense, studies in small areas such as bays can significantly contribute to the understanding of these interactions (Mantelatto *et al.*, 1995; Braga *et al.*, 2007).

Most studies involving analysis of abundance and distribution variations and population structure of decapod crustaceans in unconsolidated regions are directed toward commercial species, such as *Farfantepenaeus paulensis* (Pérez-Farfante, 1967), *Farfantepenaeus brasiliensis* (Latreille, 1817), *Litopenaeus schmitti* (Burkenroad, 1936) and *Xiphopenaeus kroyeri* (Heller, 1862) (Severino-Rodrigues *et al.*, 2002; Bertini *et al.*, 2010a). Fransozo *et al.* (2013) performed the only populational study on a xanthoid crab analyzing the ecological distribution and population structure of *Acantholobulus schmitti* (Rathbun, 1930). Alves *et al.* (2012) published a checklist of Brachyuran species which provides some information about xanthoid crabs (including *H. paulensis*), such as the total abundance and average size of the individuals.

Therefore, the objective of this study was to analyze the spatio-temporal variations of the abundance and distribution of *H. paulensis* in three bays in Ubatuba region on the southeastern coast of Brazil, as well as the influence of some environmental variables on such abundance and distribution. Also, the recruitment period, sex ratio and length frequency distribution of *H. paulensis* were investigated in order to evaluate how this population responds to such variations in a region under fishing pressure.

MATERIAL AND METHODS

Study site

According to Ab'Saber (1955) and Mahiques (1995), the north coast of the São Paulo state, Brazil, is characterized by its proximity to the Serra do Mar, resulting in an extremely indented coastline with many inlets and bays, favoring the establishment of different marine communities. Recent studies have demonstrated the importance of the region as a local of high biodiversity, with optimal conditions for the colonization of many decapod species (Bertini *et al.*, 2004; 2010a; Fransozo *et al.*, 2011).

Despite these environmental particularities, the region is strongly influenced by three water masses, with distinct effects during the summer and winter: South Atlantic Central Water (SACW), with low temperature and salinity ($T < 20°C$; $S < 36$), Tropical Water (TW), with high temperature and salinity ($T > 20°C$; $S > 36$) and Coastal Water (CW), with high temperature and low salinity ($T > 20°C$; $S < 36$) (Castro-Filho *et al.*, 1987).

In this region, Ubatumirim, Ubatuba and Mar Virado bays present different physiographic features, both regarding their configuration and the orientation of the bay mouth. The seaward end of Mar Virado Bay faces the southeast, and Mar Virado Island is situated at the eastern border of the bay mouth. Ubatuba Bay faces the east and presents a seaward constriction formed by rocky projections, thus delimiting a shallower inner area and an outer area (Mahiques, 1995). Finally, the Ubatumirim Bay faces the southwest with several small islands close to its mouth. Prumirim and Porcos Islands are situated at the bay entrance, and Couves Island, the largest one, is located further north.

Biotic and abiotic sampling

Crabs were collected monthly, from January 1998 to December 1999 in Ubatumirim, Ubatuba, and Mar Virado (north limit: 23°32'S 44°90'W; south limit: 23°56'S 45°18'W). Six sampling sites were established in each bay, three in areas protected from wave action (with depths of 5, 7.5, and 10 m) and three in exposed areas (10, 15, and 20 m) (Fig. 1).

Sampling was carried out using a shrimp fishing boat equipped with double-rig nets consisting of a main net body with 20 mm mesh and a terminal cod with 15 mm mesh. Trawling was carried out for 30 min each, sampling a total area of approximately 18,000 m^2. An ecobathymeter coupled with a global positioning system was used to record the depth (m) at the sampling sites.

Captured crabs were identified according to Melo (1996), with sex determined by observing the abdominal morphology. The maximum carapace width (CW) was measured using a caliper (0.01 mm). The

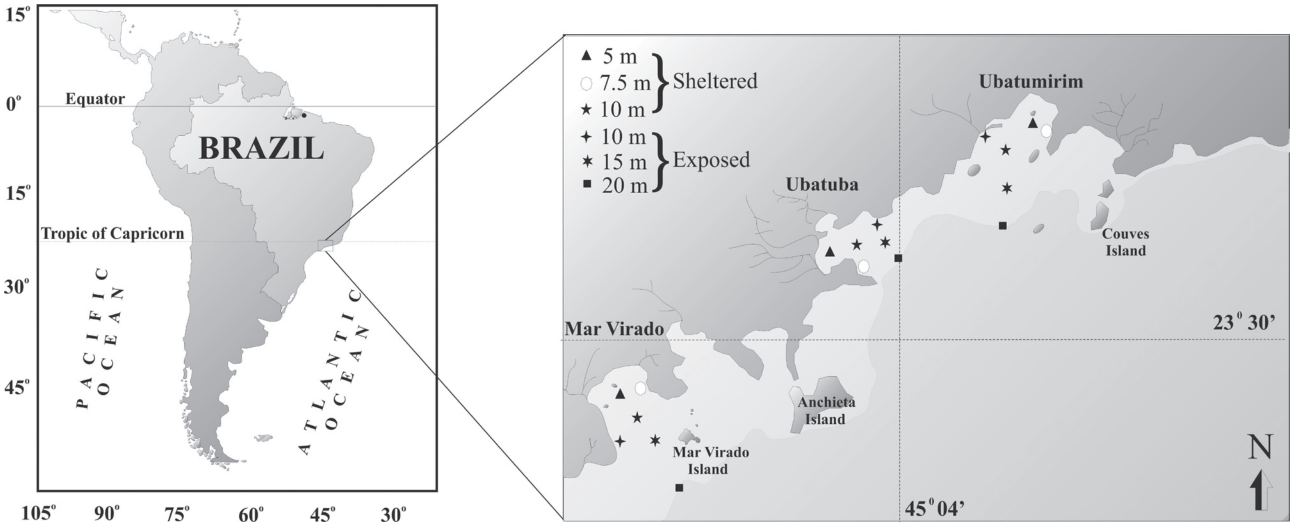

Figure 1. Map of the Ubatuba region, northern coast of the São Paulo state, Brazil, showing bays, areas (exposed and sheltered) and sampling points.

specimens were categorized into five demographic categories: juvenile males (JM), juvenile females (JF), adult males (AM), adult females (AF) and ovigerous females (OF). The differentiation between juvenile and adult individuals were considered following Silva *et al.* (2014), which documented that males and females showing CW larger than 6.7 and 6.3 mm, respectively, could be considered adults based on morphometric analysis.

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

Sediment samples were obtained during each season at each station with a Van Veen grab (0.06 m^2) in order 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. For the detailed procedure, see Hiroki *et al.* (2011) and Almeida *et al.* (2012).

The organic matter content of sediment was estimated as the difference between initial and final ash-free dry weights of three subsamples (10 g each) incinerated in porcelain crucibles at 500°C for 3 h.

Data analysis

Initially, the assumptions of homoscedasticity (Levene test) and normality (Shapiro-Wilk test) of the data set were tested. So, non-parametric tests were used because the data do not meet these assumptions.

The bottom and surface temperature (BT and ST), salinity (S) and organic matter content (OM%) values were compared between the bays, stations and seasons (summer from January to March; fall from April to June; winter from July to September; and spring from October to December) using the Kruskal-Wallis test, followed by Dunn's *a posteriori* test (Zar, 2010).

To verify the correlation between the abundance of these demographic groups and environmental variables, we carried out a redundancy analysis (RDA). The data matrix of environmental variables was standardized to mean 0 and variance 1. The Variance Inflation Factor (VIF) was used to check for collinearity and environmental variables with VIF above 3 were considered collinear and excluded from further analyzes. The matrix of environmental variables and matrix of abundance of individuals (males and females) were correlated using a redundancy analysis (RDA) (Oksanen *et al.*, 2013). Only scores of environmental variables above 0.4 and less than -0.4 were considered biologically meaningful for RDA axis (Rakocinski *et al.*, 1996).

The abundance of the species was also analyzed on spatial (bays, areas and stations) and temporal (seasons) scales, performing the Mann-Whitney and Kruskal-Wallis tests followed by Dunn's *a posteriori* test (Zar, 2010).

The sex ratio, total and size classes were estimated as the quotient between the number of males and the total number of individuals in the samples. For each analysis, deviations from a 1:1 were tested using a Binomial test (Wilson and Hardy, 2002).

Automatic Peak Detection and Fitting – "Method I" was used for the identification of peaks, included in the total individual frequency distribution by size classes. This method was calculated in the PeakFit software package, version 4.12 (Sea Solve Software Inc. 1999 – 2003). A Kolmogorov-Smirnov two-sample test was used to detect any difference between male and female length frequency distribution.

Mann-Whitney test was used to compare differences in the body sizes of males and females, while the Kruskal-Wallis test was performed for the same purpose, but among the bays. The significance level used for all tests was $\alpha = 0.05$ (Zar, 2010).

RESULTS

Environmental variables

The bottom temperature ranged from 16.0 to 29.7°C, 16.5 to 30.0°C and 16.5 to 29.7°C in Ubatumirim, Ubatuba and Mar Virado bays, respectively. Considering the surface temperature, it ranged from 20.0 to 31.4°C in Ubatumirim, from 20.0 to 30.2°C in Ubatuba and from 19.0 to 30.8°C in Mar Virado. However, there was no significant difference between both bottom and surface temperatures among the bays (Kruskal-Wallis: $p > 0.05$; $H = 1.52$ for bottom temperature; $H = 1.80$ for surface temperatures). The highest and the lowest mean values of bottom temperature were observed during the summer (25.7 ± 3.0°C) and spring (20.6 ± 23°C), respectively, resulting in significant differences (Kruskal-Wallis: $p < 0.05$; H = 188.32). The higher mean value of surface temperature was also observed during the summer (29.0 ± 2.0) while the lower mean value was recorded during the winter (22.6 ± 0.9), which differed statistically (Kruskal-Wallis: $p < 0.05$; H = 271.36). In general, a remarkable thermocline was observed between the spring and summer (Fig. 2).

The bottom salinity mean values observed in Mar Virado (34.3 ± 1.5) were lower and statistically distinct (Kruskal-Wallis: $p < 0.05$; H = 5.16) from those recorded in Ubatumirim (34.8 ± 1.3) and Ubatuba (34.8 ± 1.3). Among the seasons, the lower mean value of this environmental variable was also observed during the winter (Kruskal-Wallis: $p < 0.05$; H = 59.13) (Fig. 3).

In analyzing the sediment samples, there was an increase of phi values from the north (Ubatumirim) to the south (Mar Virado), with mean values of 3.8 ± 1.0, 4.4 ± 0.9 and 5.5 ± 0.6 in Ubatumirim, Ubatuba and Mar Virado bays, respectively. Considering each bay, the highest mean value was significantly recorded

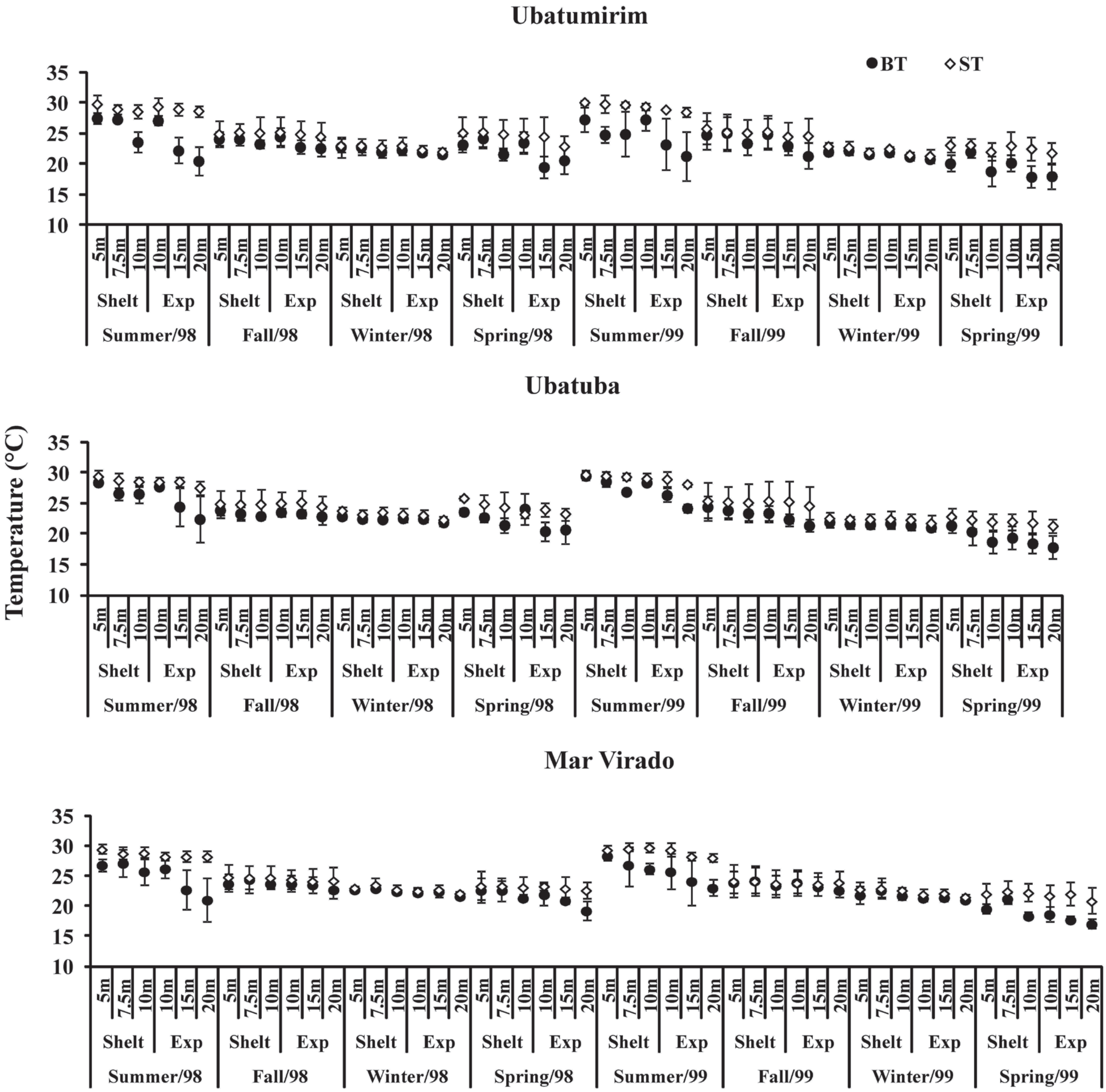

Figure 2. Bottom (BT) and surface (ST) temperature variation per seasons, areas and sampling points in 1998 and 1999.

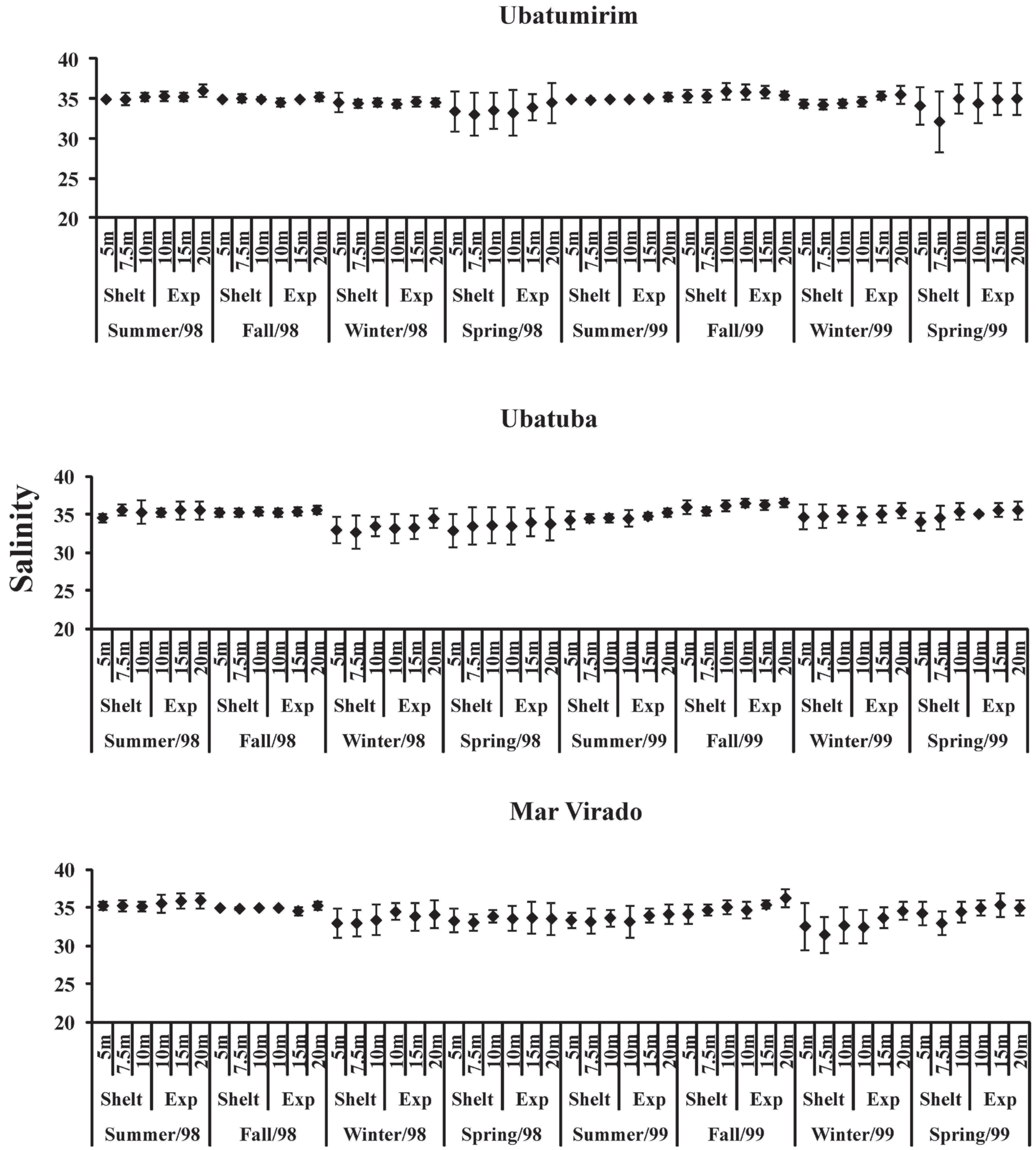

Figure 3. Salinity values variation per seasons, areas and sampling points in 1998 and 1999.

in Mar Virado (Kruskal-Wallis: $p < 0.05$; H = 179.10). Spatially, the lowest mean value of phi was observed at 20 m in all bays. Additionally, the percentage of organic matter content was higher in Ubatuba (5.8 ± 4.0), followed by Mar Virado (4.5 ± 2.8) and Ubatumirim (3.6 ± 2.3), which differed statistically from the other bays (Kruskal-Wallis: $p < 0.05$; M = 21.7) (Fig. 4).

Spatio-temporal variations of the abundance

From the 1084 specimens sampled, 686 were caught in Ubatumirim, 322 in Ubatuba and 76 in Mar Virado. The results of the Kruskal-Wallis test, followed by Dunn's test, revealed that only the abundance of *H. paulensis* caught in Ubatumirim was significantly higher than in Mar Virado (Kruskal-Wallis: $p < 0.05$; H = 14.4).

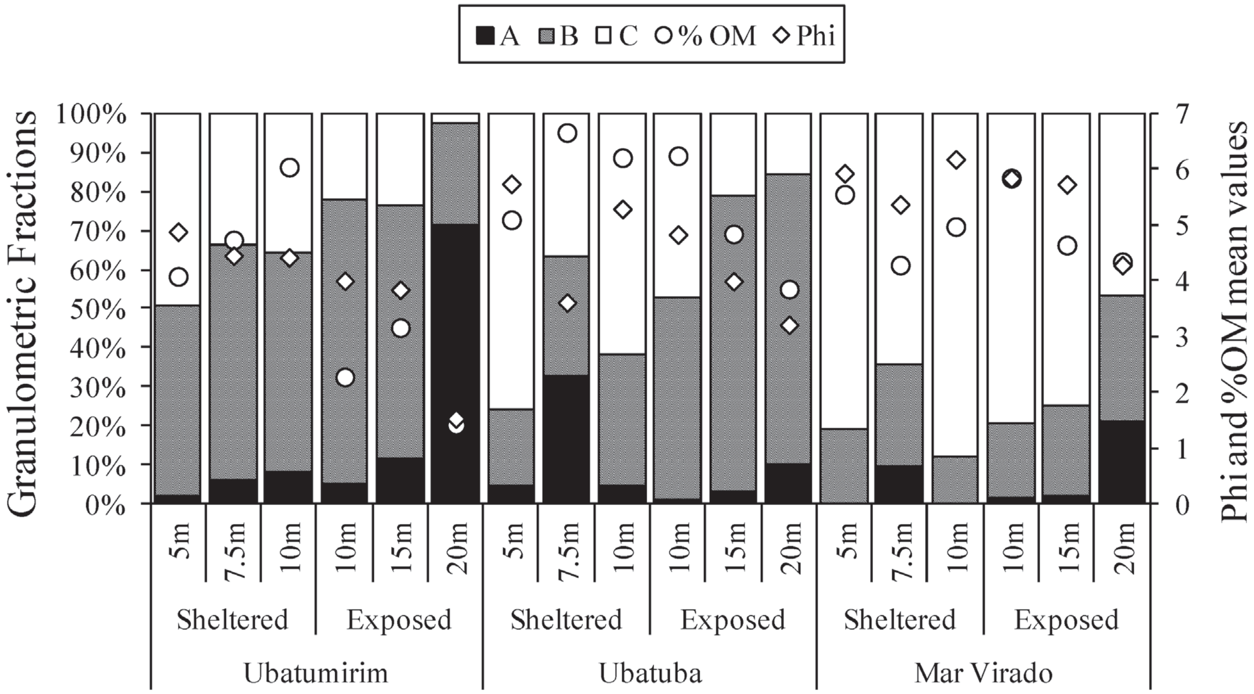

Figure 4. Sedimentological analysis showing grain size fractions (columns) and mean values of phi and %OM (percentage of organic matter) obtained from January 1998 to December 1999. A = median sand + coarse sand + gravel, B = fine sand + very fine sand and C = silt + clay.

In Ubatumirim Bay, the abundance of the species at 10 m of the exposed area was significantly higher compared to other depths (Kruskal-Wallis: $p < 0.05$; $H = 26.9$), with exception to the depth of 7.5 m (Fig. 5). In Ubatuba Bay, the highest abundance was statistically recorded at a depth of 7.5 m in the protected area (Kruskal-Wallis: $p < 0.05$; $H = 36.2$) (Fig. 5). In Mar Virado Bay, there was no significant difference in the abundance among the stations sampled (Kruskal-Wallis: $p > 0.05$; $H = 2.8$).

In general, the lowest number of individuals of *H. paulensis* was obtained during spring months in all bays (Fig. 6). In Ubatumirim Bay, the abundance of the individuals differed significantly during the summer compared to the spring and fall (Kruskal-Wallis: $p < 0.05$; $H = 14.8$), while in Ubatuba and Mar Virado bays, there was no difference between the abundance of *H. paulensis* in the seasons (Ubatuba: Kruskal-Wallis: $p > 0.05$; $H = 5.9$; Mar Virado: Kruskal-Wallis: $p > 0.05$; $H = 5.9$).

The variation of the individual numbers by environmental variable classes is shown in Fig. 7. An elevated abundance of the species was noted at bottom temperature classes ranging from 25.9 to 28.7°C in Ubatumirim, from 24.5 to 28.7°C in Ubatuba and from 20.3 to 24.5°C in Mar Virado (Fig. 7A). Considering bottom salinity, most individuals were recorded at classes with values from 33.5 to 35.3 in Ubatumirim and Ubatuba, while in Mar Virado there is no preference for a specific environmental class of bottom salinity, the individuals were distributed at the classes with values from 29.9 to 37.1 (Fig. 7B).

Most individuals were obtained in classes of organic matter content ranging from 0.2 to 3.2% and 4.7 to 6.2% in Ubatumirim. Interestingly, no specimen was recorded in classes with values above 9.2%. In Ubatuba, the classes with the highest occurrence of individuals ranged from 1.7 to 3.2%. In Mar Virado, the frequency distribution of the individuals was similar among the environmental classes, up to 12.2% of organic matter content (Fig. 7C).

In relation to the phi classes, the frequency distribution of the individuals did not vary among Ubatumirim, Ubatuba and Mar Virado. Most individuals were concentrated at classes with values of 3.8 to 4.2 in Ubatumirim, 3.4 to 3.8 in Ubatuba and 4.2 to 4.6 and 5.0 to 6.3 in Mar Virado, which represented the finer sediment (phi values from 3 to 4 = very fine sand and phi values up to 4 = silt and clay) (Fig. 7D).

The first RDA axes represented 98% of the variation in the abundance of individuals (males and females) (Tab. 1). Bottom temperature presented positive

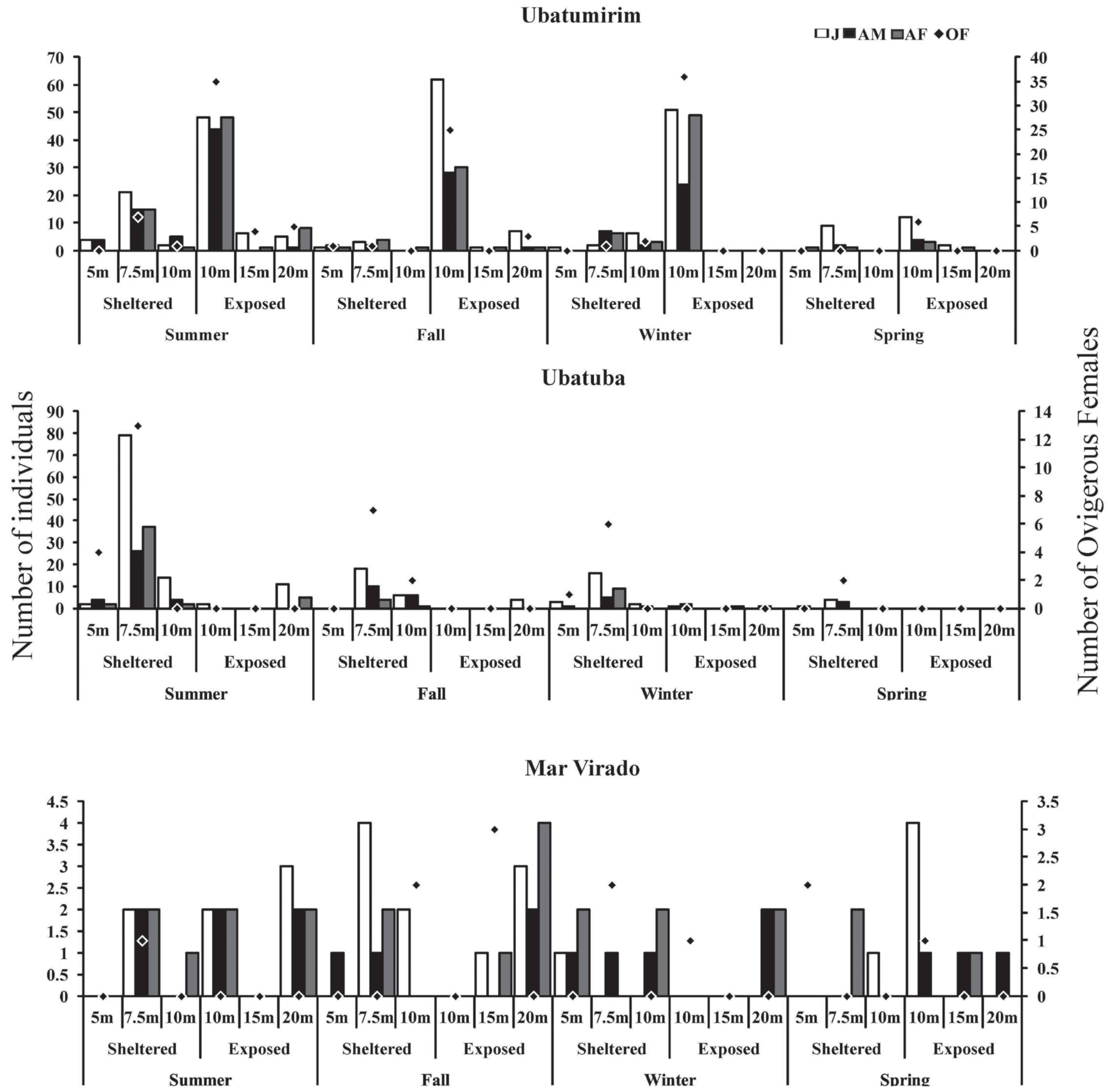

Figure 5. *Hexapanopeus paulensis*. Spatiotemporal distribution of individuals by bays, seasons, areas and sampling points, from January 1998 to December 1999. J = juveniles, AM = adult males, AF = adult females and OF = ovigerous females.

correlation to the abundance of individuals while percentage of organic matter and phi values showed negative correlation.

Population structure

From the total individuals collected, 428 were juveniles (39.5% - 217 males and 211 females), 223 adult males (20.6%) and 433 adult females (39.9%), of which 174 were ovigerous (16.1%). Juveniles were recorded during all seasons, but in smaller values during the spring months. In Ubatumirim and Ubatuba bays, the highest abundance of juveniles occurred during the summer, while in Mar Virado, it was observed during the fall (Fig. 6).

Table 1. *Hexapanopeus paulensis*. Summary of results of Redundancy Analysis (RDA) for abundance of individuals (males and females) and environmental factors.

	RDA 1	RDA 2
Eigenvalue	17.28	0.29
% of Variance	98	1
Environmental Factors		
Bottom Temperature	**0.68**	-0.32
Salinity	0.25	-0.56
% of Organic Matter	**-0.49**	-0.08
Phi	**-0.44**	-0.24
Abundance of Individuals		
Females	3.35	0.31
Males	2.43	-0.43

Bold values denote those variables that were considered to the biologically meaning for that RDA axis (i. e. > 0.4 and <-0.4) Rakocinski *et al.* (1996).

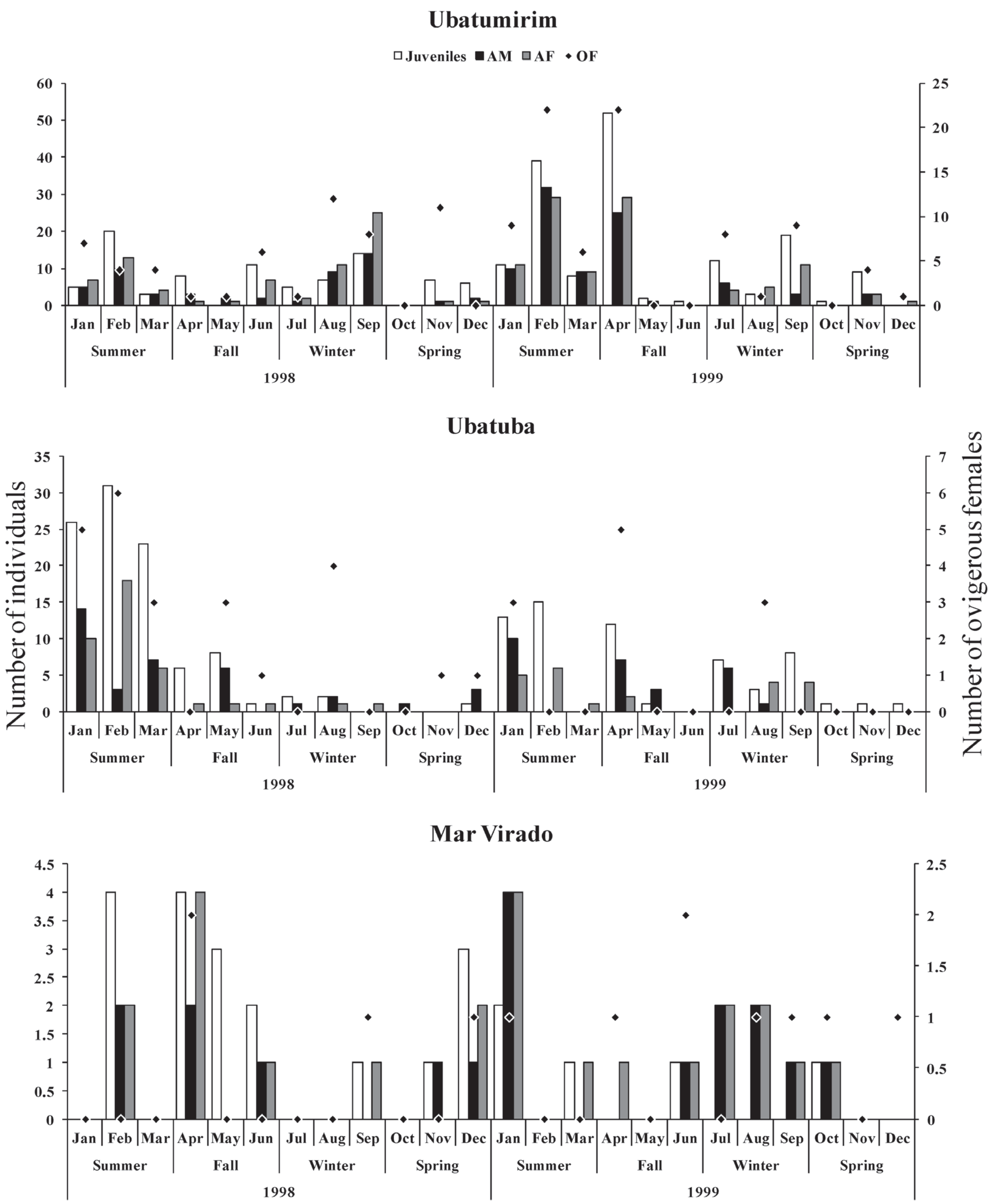

Figure 6. *Hexapanopeus paulensis*. Temporal distribution of individuals in Ubatumirim, Ubatuba and Mar Virado bays, from January 1998 to December 1999. AM = adult males, AF = adult females and OF = ovigerous females.

The ratio between males and females differed from the 1:1, considering the total individual numbers caught during the study period (Binomial test, $p < 0.05$). In analyzing it by bay, it was possible to notice differences from the proportion expected only in Ubatumirim (Binomial test, $p < 0.05$). Additionally, the sex ratio throughout the size classes was equal 1:1 only in the two first classes (2.5[--3.8 and 3.8[--5.1) in all bays (Tab. 2).

The male size ranged from 3.0 to 12.9 mm, 2.9 to 17.0 mm and 3.2 to 11.4 mm in Ubatumirim, Ubatuba and Mar Virado, respectively, while the female size

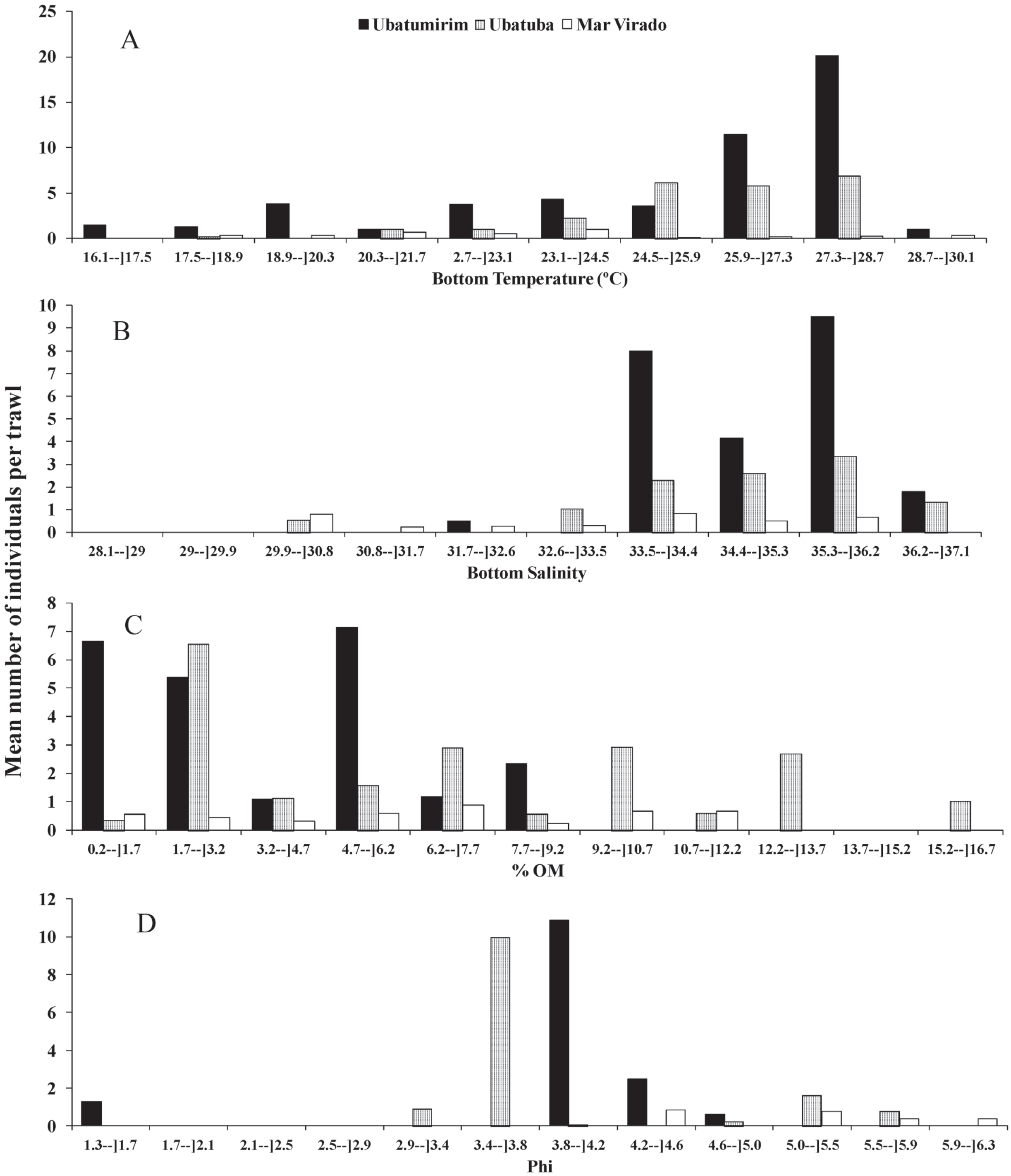

Figure 7. *Hexapanopeus paulensis*. Abundance of individuals, distributed according to environmental factors classes (A: bottom temperature; B: bottom salinity; C: percentage of organic matter; D: phi) at Ubatumirim, Ubatuba and Mar Virado, from January 1998 to December 1999.

ranged from 3.4 to 13.0 mm in Ubatumirim, 2.9 to 13.5 mm in Ubatuba and 4.9 to 12.8 mm in Mar Virado. However, there is no significant difference in the sizes between sexes (Mann-Whitney: $p > 0.05$, UUBM = 54803.5, UUBA = 11491.0 and UMV = 605.0), only among the three bays (Kruskal-Wallis: $p < 0.05$, H = 14.27) where individuals at Mar Virado bay were bigger than the others (7.16 ± 2.06 mm at UBM, 6.83 ± 2.62 mm at UBA and 7.59 ± 2.19 at MV).

The frequency distribution of the individuals by size classes differed significantly between males and females in Ubatumirim (Kolmogorov-Smirnov test:

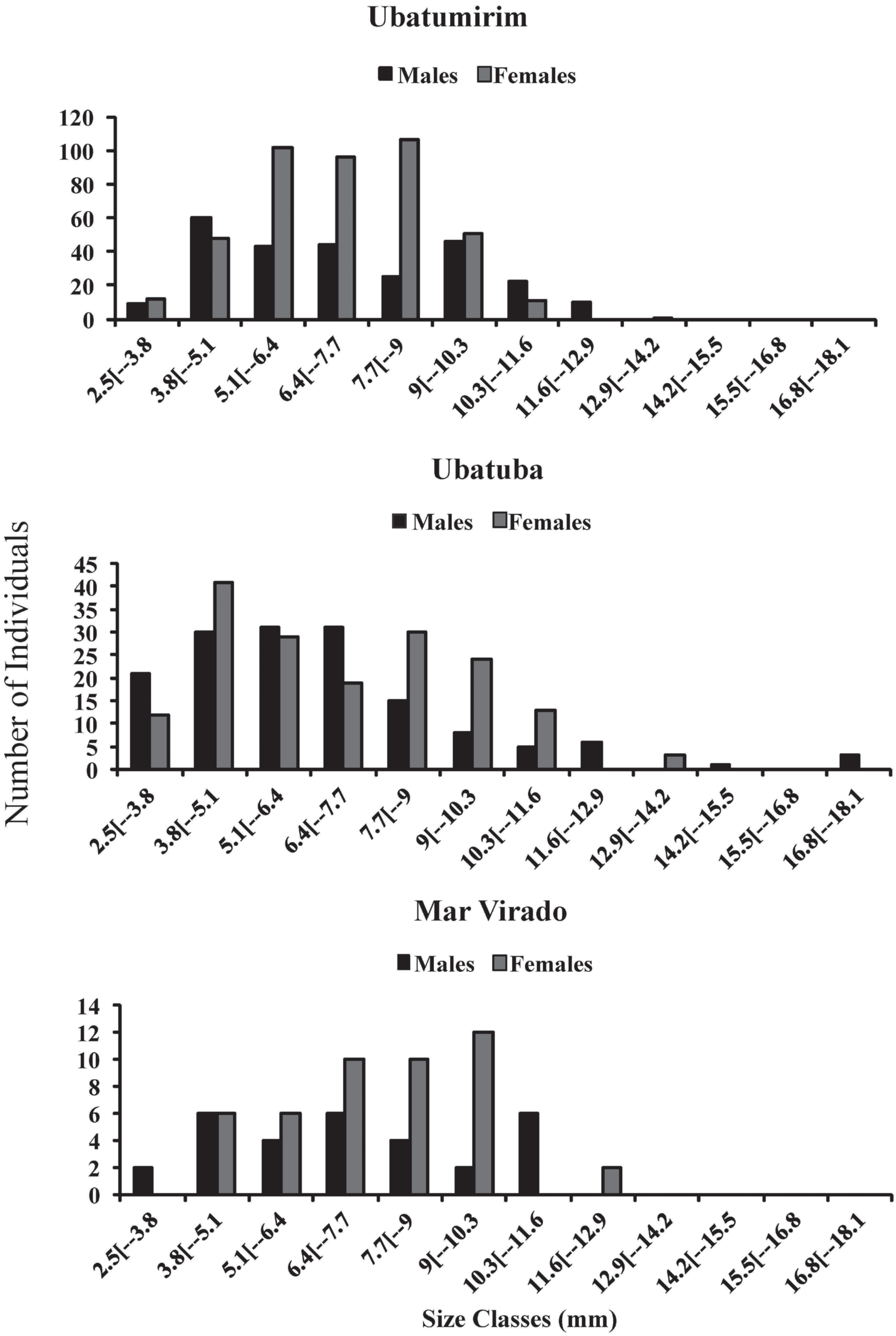

Figure 8. *Hexapanopeus paulensis*. Frequency distribution of individuals in size classes at the sampled bays.

Table 2. *Hexapanopeus paulensis.* Frequency distribution of demographic groups in size-classes with binomial test results for sex ratio.

Bay	Size Classes	Males			Females			Proportion	p
		JM	AM	TM	JF	AF	TF	M:F	
UBM	2.5[--3.8	9	0	9	12	0	12	1:1.3	0.52
	3.8[--5.1	60	0	60	47	1	48	1:0.8	0.23
	5.1[--6.4	43	0	43	66	36	102	1:2.4	0.00*
	6.4[--7.7	6	38	44	0	96	96	1:2.2	0.00*
	7.7[--9	0	25	25	0	106	106	1:4.2	0.00*
	9[--10.3	0	46	46	0	51	51	1:1.1	0.61
	10.3[--11.6	0	22	22	0	11	11	1:0.5	0.06
	11.6[--12.9	0	10	10	0	0	0	1:0	0.00*
	12.9[--14.2	0	0	0	0	1	1	0:1	0.5
	14.2[--15.5	0	0	0	0	0	0	-	-
	15.5[--16.8	0	0	0	0	0	0	-	-
	16.8[--18.1	0	0	0	0	0	0	-	-
	Total	118	141	259	125	302	427	1:1.6	0.00*
UBA	2.5[--3.8	21	0	21	12	0	12	1:0.6	0.12
	3.8[--5.1	30	0	30	38	3	41	1:1.4	0.17
	5.1[--6.4	31	0	31	25	4	29	1:0.9	0.84
	6.4[--7.7	5	26	31	0	19	19	1:0.6	0.09
	7.7[--9	0	15	15	0	30	30	1:2	0.02*
	9[--10.3	0	8	8	0	24	24	1:3	0.00*
	10.3[--11.6	0	5	5	0	13	13	1:2.6	0.06
	11.6[--12.9	0	6	6	0	0	0	1:0	0.01*
	12.9[--14.2	0	0	0	0	3	3	0:1	0.12
	14.2[--15.5	0	1	1	0	0	0	1:0	0.5
	15.5[--16.8	0	0	0	0	0	0	-	-
	16.8[--18.1	0	3	3	0	0	0	1:0	0.12
	Total	87	64	151	75	96	171	1:1.1	0.27
MV	2.5[--3.8	2	0	2	0	0	0	1:0	0.25
	3.8[--5.1	6	0	6	5	1	6	1:1	0.88
	5.1[--6.4	4	0	4	6	0	6	1:1.5	0.54
	6.4[--7.7	0	6	6	0	10	10	1:1.7	0.39
	7.7[--9	0	4	4	0	10	10	1:2.5	0.11
	9[--10.3	0	2	2	0	12	12	1:6	0.02*
	10.3[--11.6	0	6	6	0	0	0	1:0	0.01*
	11.6[--12.9	0	0	0	0	2	2	0:1	0.25
	12.9[--14.2	0	0	0	0	0	0	-	-
	14.2[--15.5	0	0	0	0	0	0	-	-
	15.5[--16.8	0	0	0	0	0	0	-	-
	16.8[--18.1	0	0	0	0	0	0	-	-
	Total	12	18	30	11	35	46	1:1.5	0.07
General Total		**217**	**223**	**440**	**211**	**433**	**644**	**1:1.5**	**0.00***

UBM = Ubatumirim, UBA = Ubatuba, MV = Mar Virado, JM = juvenile males, AM = adult males, TM = total males, JF = juvenile females, AF = adult females, TF = total females, M = males, F = females. * $p < 0.05$.

dmax = 0.1536; $p < 0.05$) and in Ubatuba (Kolmogorov-Smirnov test: dmax = 0.1577; $p < 0.05$), but did not differ in Mar Virado (Kolmogorov-Smirnov test: dmax = 0.1565; $p > 0.05$). There is a polimodality for the males in all bays, while for females a bimodality was observed in Ubatumirim, and a polimodality in Ubatuba and Mar Virado bays (Fig. 8).

DISCUSSION

Spatio-temporal variations of the abundance

Considering the sediment texture of the Ubatumirim, Ubatuba and Mar Virado bays, the three bays exhibited distinct characteristics. Many researchers observed that the sediment in Ubatumirim is more heterogeneous, contrasting that observed in

Mar Virado, which can be characterized by a large amount of silt and clay (Bertini *et al.*, 2004; Braga *et al.*, 2005). Also, the sedimentary homogeneity in Mar Virado probably provides fewer shelters for the present species. In Ubatuba, the sediment texture was intermediary compared to Ubatumirim and Mar Virado.

Most individuals of *H. paulensis* were found to be associated with biodetritus and tree branches, which were observed in large amounts in Ubatumirim Bay (A. Fransozo, pers. obs.). The low hydrodynamics associated to the great influence of the Ubatumirim River allows this type of material to accumulate in this bay. Such material provides greater shelter availability for small species and with cryptic habits, such as *H. paulensis*. Furthermore, this condition provides heterogeneous substrate for this region, with greater grain sizes.

Fransozo *et al.* (2013) found similar results for a sympatric species, which some time ago was a congener of *H. paulensis;* the panopeid crab *A. schmitti*. The authors pointed out that the heterogeneity of the sediment and the large amount of biodetritus and plant fragments observed in Ubatumirim Bay could be an important variable influencing the abundance and distribution of the species.

Another similarity between *H. paulensis* and *A. schmitti* was related to the distribution of individuals along the stations sampled in Ubatumirim and Ubatuba bays. Both species occurred in greater values in the stations nearer to the continent. According to Melo (1996), beyond unconsolidated bottoms, *H. paulensis* might occur on substrates composed of shells, sponges, ascidians and/or bryozoans. The occurrence of individuals in the stations nearer to the continent and exposed to wave action (7.5 and 10 m) was remarkable in this study. This is probably due to their proximity to the rocky shores, where *H. paulensis* is frequently found (Alves *et al.*, 2012) as this kind of habitat receives deposits of allochthonous material from the continent and small rivers.

The strong positive correlation between bottom temperature and abundance of individuals is evident during the summer. At this time the higher temperatures were recorded in the same sites where the animals were more abundant.

The high number of individuals caught during the summer coincides with the period of greatest SACW incidence, enhancing the waters with nutrients that favor primary productivity (Castro-Filho *et al.*, 1987). According to the same author, this water mass intrudes into the continental shelf in late spring. This may facilitate the availability of food for the larvae of this and other species. For Vega-Pérez (1993), the temporal variation of the planktonic productivity can be an essential factor in the reproductive activity of crustaceans, which is closely related to the availability of food (phytoplankton) for the larvae. Thus, this water mass may be an indirect factor that affects the individuals abundance.

Associated with the enrichment of the water by the SACW, the input of organic matter from the continent is higher during the summer due to elevated precipitation. Thus, shelter availability and the dynamics of water masses of the north coast of São Paulo state might be a key factor modulating the spatial and temporal variations of the abundance of *H. paulensis*.

Population structure

At birth, the ratio of male to female tends to be 1:1 (Fisher, 1958). However, several factors during the life cycle of the species such as longevity, mortality and differential growth between the sexes may affect such sex ratio (Wenner, 1972; Hartnoll, 1982). In the present study, a deviation from 1:1 in favor of the females was recorded for *H. paulensis*. Alves *et al.* (2012) also observed the occurrence of an elevated number of females compared to males of the same species, but in a consolidated substrate. Such deviations might indicate a common pattern for *H. paulensis* in the study region.

According to Hartnoll (2006), males of some decapod species may exhibit high mortality as a result of reproductive activities, such as courtship and searching for receptive females. These behavioral displays can increase the exposure of the males to predators. Such a hypothesis is supported by the deviations in the sex ratio of *H. paulensis* after individuals attaining sexual maturity (from the size class with amplitude of 5.1 to 6.4 mm CW). Similar results were recorded for another xanthoid crab, *Panopeus americanus* Saussure, 1857 by Vergamini and Mantelatto (2008). Therefore, the occurrence of females in the last size classes may be associated to the high mortality rate of males of *H. paulensis* due to reproductive behavior, since the males need to leave their shelters to seek receptive females, becoming potential prey considering the small size of the species.

The bi and polimodal patterns of the length frequency distribution generally suggest recruitment pulses, distinct or catastrophic mortality, and/or differential behavior (Díaz and Conde, 1989). In fact, no environmental catastrophe or spatial segregation among the demographic categories were recorded during the sampling period. Thus, the bi and polimodal patterns observed for *H. paulensis* can be related to the several reproductive and recruitment pulses of the species, once the presence of juveniles and ovigerous females were recorded throughout the study period.

In general, the recruitment of *H. paulensis* on the north coast of São Paulo state might be considered continuous because of the occurrence of juveniles throughout the year, with peak abundance in the summer. For Vega-Pérez (1993), the temporal variation of planktonic productivity may represent an essential rule in the reproductive activity of crustaceans, which is closely related to food availability (phytoplankton) for the larvae. The recruitment peaks recorded in the summer coincide with intrusion of the SACW in the study area (Castro-Filho *et al.*, 1987), showing that the nutrient enrichment caused by this water mass during the late spring and summer (Aidar *et al.*, 1993) can benefit the increase of the abundance of *H. paulensis*.

Several authors have reported the importance of the SACW on the breeding period and recruitment of many species of brachyurans. Among those studies, we can point out those on: *Callinectes ornatus* Ordway, 1863; *Mithraculus forceps* (A. Milne-Edwards, 1875), *Libinia spinosa* H. Milne Edwards 1834, *Persephona mediterranea* (Herbst, 1794), *Persephona punctata* (Linnaeus, 1758), *Persephona lichtensteinii* Leach, 1817 and *A. schmitti*, which were studied, respectively, by Mantelatto and Fransozo (1999b), Mantelatto *et al.* (2003), Braga *et al.* (2007), Bertini *et al.* (2010b), Almeida *et al.* (2013), Almeida *et al.* (2013), and Fransozo *et al.* (2013). Therefore, in addition to influencing the temporal abundance variations of *H. paulensis*, the SACW plays a fundamental role in juvenile recruitment.

Future studies on the mating behavior of *H. paulensis* might elucidate a question discussed in this study: are deviations from 1:1 in the sex ratio due to a differential mortality for males because of their reproductive displays? In general, studies about spatio-temporal variations on abundance and population dynamics of xanthoid crabs are scarce or non-existent for some species, however, they are very important as tools for development of management projects and environmental conservation.

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