

## SPATIO-TEMPORAL AND FUNCTIONAL STRUCTURE OF THE AMPHIPOD COMMUNITIES OFF SANTOS, SOUTHWESTERN ATLANTIC

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### ABSTRACT

The amphipod fauna was employed to investigate a bottom environmental gradient in the continental shelf adjacent to Santos Bay. The constant flow of less saline water from the estuarine complex of the Santos and São Vicente rivers besides the seasonal intrusion of the cold saline South Atlantic Central Water (SACW) bring a highly dynamic water regime to the area. Density, distribution, diversity and functional structure of the communities were studied on a depth gradient from 10 to 100 m on two cruises in contrasting seasons, winter 2005 and summer 2006. Twenty-one sediment samples were taken with a 0.09m<sup>2</sup> box corer. Temperature and salinity were measured at each station and an additional surface sediment sample was obtained with the box corer for granulometric and chemical analyses. Sixty species were collected on each survey and higher density values were found in summer. A priori one-way Analysis of Similarities (ANOSIM) indicated the existence of three different groups of amphipods related to the depth gradient: the Coastal group, the Mixed Zone group and the Deep Zone group. The Coastal Zone in both cruises was inhabited by a community presenting low diversity and density, besides high dominance of the infaunal tube-dweller *Ampelisca paria*; the area around 30 m presented the highest values of all the ecological indicators and the species showed several life styles; the outer area, situated between 50 and 100 m depth in the SACW domain, presented a community characterized by lower diversity and high biomass and density values. A season-depth ANOSIM showed the influence of depth and season for the Coastal and Mixed Zone groups whereas no seasonal difference was obtained for the Deep Zone group. The synergistic effect of the SACW and depth in the first place, followed by physical changes in substrate, seem to be the main factors controlling the fauna's distribution. In addition, the estuarine waters from Santos Bay apparently had no effect on the establishment of the environmental gradient observed on the adjacent shelf. Diversity, distribution, functional groups and trophic conditions of superficial sediments are discussed in the light of the main oceanographic processes present on the southern Brazilian shelf.

### RESUMO

A fauna de anfípodes foi empregada para investigar o gradiente ambiental na plataforma continental adjacente a Baía de Santos. A entrada constante de uma água menos salina proveniente do complexo estuarino de Santos e São Vicente e a intrusão sazonal da água fria e salina da Água Central do Atlântico Sul (ACAS) faz com que a área seja um ambiente hidrodinamicamente instável. Densidade, distribuição, diversidade e estrutura funcional das comunidades de anfípodes foram estudadas em um gradiente de profundidade entre 10 e 100 m, em dois cruzeiros realizados em épocas contrastantes, inverno (2005) e verão (2006). Vinte e uma amostras de sedimento foram coletadas com um box corer de 0,09 m<sup>2</sup>. Temperatura e salinidade foram coletadas em cada estação com CTD e uma amostra adicional de sedimento superficial foi obtida com box corer para análises granulométricas e químicas. Sessenta espécies estiveram presentes em ambos os cruzeiros e altos valores de densidade foram encontrados especialmente no verão. A Análise de Similaridade (ANOSIM) realizada a priori indicou a existência de três grupos diferentes de anfípodes relacionados ao gradiente de profundidade: um grupo Costeiro, um grupo da Zona de Mistura e um grupo da Zona Profunda. A zona Costeira, em ambos os cruzeiros foi habitada por uma comunidade que apresenta baixa diversidade e densidade, além de alta dominância do tubícola infaunal *Ampelisca paria*; a área em torno de 30 m apresentou os maiores valores de todos os indicadores ecológicos e as espécies de anfípodes mostraram grande diversidade funcional; a área externa, entre 50 e 100 m de profundidade e no domínio da ACAS, apresentou uma comunidade caracterizada por baixa diversidade e altos valores de biomassa. A ANOSIM sazonal-profundidade mostrou diferença sazonal significativa para os grupos Costeiros e da Zona de Mistura, enquanto que para o grupo da Zona Profunda não foi encontrada diferença temporal significativa. O efeito sinérgico da ACAS e da profundidade em primeiro lugar, seguido pelas mudanças físicas do substrato, parecem ser os principais fatores controladores da distribuição da fauna. As águas estuarinas provenientes da Baía de Santos aparentemente não tiveram efeito no estabelecimento do gradiente ambiental observado na plataforma adjacente. Diversidade, distribuição dos grupos funcionais, condições tróficas dos sedimentos superficiais, além de outros aspectos ecológicos das comunidades são discutidos à luz dos processos oceanográficos dominantes na plataforma sudeste brasileira.

Descriptors: Amphipod communities, Life style distribution, Southern Brazilian shelf, Baixada Santista.

Descritores: Comunidades de anfípodes, Distribuição do modo de vida, Plataforma do sul do Brasil, Baixada Santista.

## INTRODUCTION

Benthic systems of the continental shelf play an important role in the economy of many coastal populations through the provision of food and non-living resources (HALL, 2002; NICHOLLS et al., 2007). Although, in general, data on the distribution and abundance of species are rather limited and few areas have been studied comprehensively, greater efforts have been made over the last twenty years due, in part, to seabed survey work related to oil and gas exploration (OSLGARD; GRAY, 1995; SANTOS et al., 2009). In coastal areas, marine soft bottom fauna is frequently composed of a large number of species with different patterns of distribution and temporal dynamics (RHOADS; YOUNG, 1970; VAN HOEY et al., 2008). In their turn, the benthic infaunal communities are organized structurally and functionally in relation to gradients of resource availability, modified by complex interactions with many environmental factors (PEARSON; ROSENBERG, 1987; WIEKING; KRÖNCKE, 2005).

The estuarine complex of Santos, São Paulo state, on the southeastern Brazilian coast, opens into the Santos Bay through the São Vicente and the Santos Channels, carrying organic components and heavy metals from the upper estuary (MARTINS et al., 2011), besides nutrients (MOSER et al., 2005). The waters from the bay flow onto the adjacent shelf and might transport and deposit these materials on the nearby coast. The area is also influenced by the oceanographic regime of the southwestern Atlantic (CASTRO et al., 2008) with the spring/summer intrusion of the South Atlantic Coastal Water from the slope onto the coastal continental shelf.

There have been reports of the ecological influence of water mass dynamics on the benthic fauna of the southeastern Brazilian shelf (PIRES-VANIN, 1992; SANTOS; PIRES-VANIN, 2004; SOARES-GOMES; PIRES-VANIN, 2005), but the available data do not take the role of the estuarine system on the shelf into consideration. The main objective of the present study was, therefore, to examine the changes in diversity, density and life style of the amphipod community of the shelf adjacent to Santos Bay in the attempt to understand the environmental gradient addressed by the coastward SACW intrusion combined with the influence of the oceanward estuarine waters on superficial sediment communities.

Amphipods are abundant, sensitive organisms on the shelf (VALÉRIO-BERARDO et al., 2000c) and may be used as a proxy in the determination of the system's dynamics and health (SCHAFFNER; BOESCH, 1982). Amphipods play an important role in the benthic systems of tropical and subtropical continental shelves, acting as principal, secondary and tertiary

producers (MARQUES; BELLAN-SANTINI, 1993) and also as reducers in the cycling of nutrients (VALÉRIO-BERARDO et al., 2000a).

In view of the above we expected to find an impoverished population in the stressful inner shelf zone and a seasonal structural difference in the communities allied to a shift in the dominance of the functional groups.

## MATERIAL AND METHODS

### Study Area

The area of study is located in an economically important area of Brazil, the Baixada Santista, a metropolitan coastal region which embraces many cities. The Baixada Santista contains one of the most important petrochemical and metallurgical poles in Brazil, the Cubatão industrial complex. Further, the main city, Santos, possesses the largest commercial harbor in South America (MARTINS et al., 2008). The area sampled is located between the cities of São Sebastião and Peruíbe (23°50'S to 25°23'S and 45°12'W to 46°54'W) in São Paulo State, southeastern Brazil, and includes the mouth of Santos Bay into which flows the input from the Santos estuary.

The superficial sediments of the inner and middle shelf are characterized by the prevalence of fine to very fine sand and the absence of any great modification of the submarine relief (FURTADO et al., 2008). Such characteristics indicate such effective wave action over the inner and middle shelf as to hinder the deposition of muddy sediments and organic matter (MAHIQUES et al., 1999; 2004). The muddy belt situated on the outer shelf at around 90-100 m depth is related to relict sediments (TESSLER; GOYA, 2007; FURTADO et al., 2008). Thus there is a relatively simple granulometric pattern in the study area that contrasts sandy and scant organic matter bottoms with muddy substrates relatively rich in organic content.

The inner and middle shelf dynamics are determined by the displacement of three water masses with strong seasonal variation (CASTRO-FILHO et al., 1987). The Tropical Water (TW), warm ( $T > 20^{\circ}\text{C}$ ) and saline ( $S > 36.4$ ), covers the whole shelf and forms the main stream of the Brazilian Current (BC); the South Atlantic Central Water (SACW), relatively cold ( $< 20^{\circ}\text{C}$ ) and less saline ( $< 36.4$ ), is present seasonally on the shelf; the Coastal Water (CW), result of the mixture between continental runoff and the Shelf-Water (SW), flows shallower along the coast (CASTRO-FILHO; MIRANDA, 1998). Between November and March, the SACW moves coastward close to the bottom, leading to the oceanward displacement of the less dense CW and keeping the TW relatively distant from the coastline. This period corresponds to the rainy season in SE Brazil and, thus,

to the increase of terrigenous input to coastal waters. From March to November, the retreat of the SACW to the slope increases the influence of the TW in the outer shelf processes, whereas CW occupies the inner shelf area. Consequently, a homogeneous water column is to be observed in the inner and middle sectors of the shelf at this time (CASTRO et al., 2008; PIOLA et al., 2008).

#### Sampling

Two oceanographic cruises were carried out in winter 2005 and summer 2006 on board the R/V "Prof. W. Besnard" of the University of São Paulo. On each cruise a grid of 21 stations, located between 10 and 100 m depth, denser in the vicinity of the bay's opening, was established for data collection (Fig. 1). The temperature and salinity of the water column were obtained by means of a device profiler (CTD, SeaBird – MCTD-MBP-S model).

Two replicates of 0.09 m<sup>2</sup> were taken at each station on each cruise using a box corer. Subsamples for sediment analysis and for sedimentary chlorophyll *a* and pheopigment content were extracted from each box corer with a 3 cm diameter cylinder, 5 cm long. Sediment samples were frozen until ready for analysis. Sediment particle size analysis was conducted for each station according to the sieve and pipette techniques described in Suguio (1973) and classified after Folk and Ward's triangular diagram (FOLK; WARD, 1957). The quantity of carbonates and total sedimentary organic matter were measured, respectively, by acid dissolution and oxidation on H<sub>2</sub>O<sub>2</sub> (GROSS, 1971). The concentrations of chlorophyll *a* (Cloro-*a*) and pheopigments (Pheo) were determined following the methodology set out in Lorenzen (1967) modified for sediments.

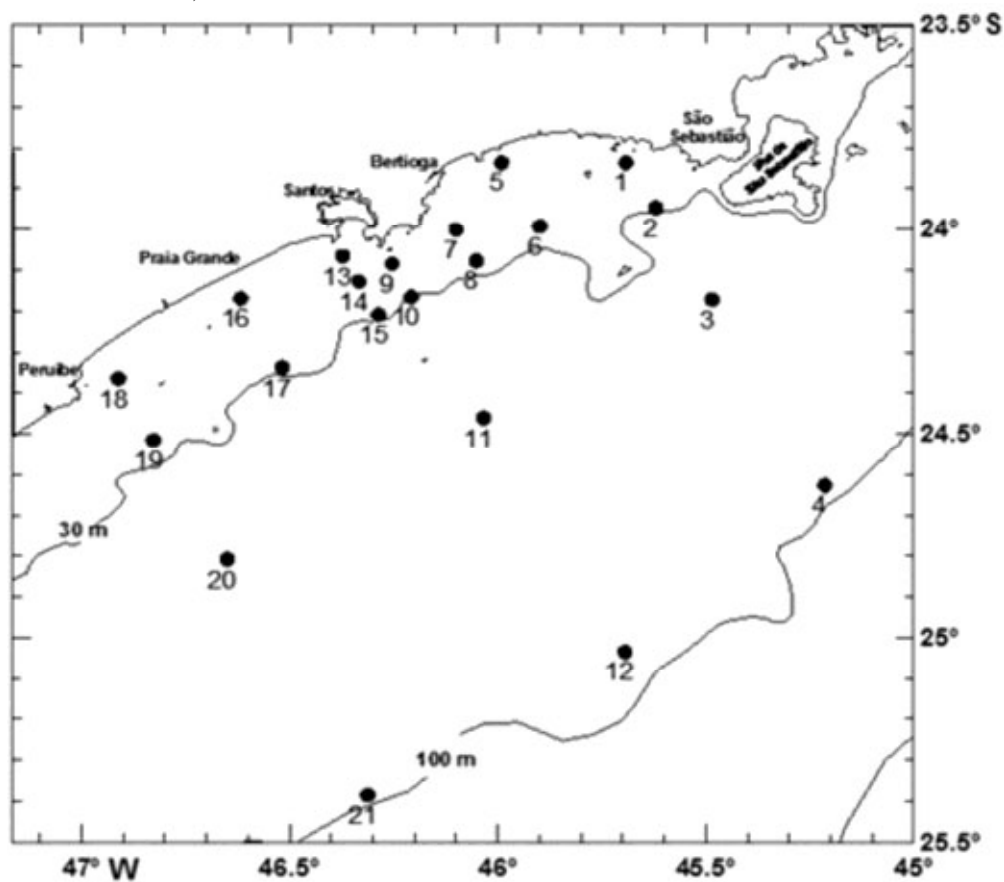


Fig. 1. Area of study showing the 21 sampling sites in the continental shelf between São Sebastião and Penúbe. Isobaths presented in solid lines.

Sediments were washed through a 0.5 mm sieve and the material retained preserved in 70% ethanol. In the laboratory, samples were sorted out and the amphipods counted and weighed (wet weight) with the aid of a semi-analytical digital balance accurate to 0.1 mg. Prior to weighing the excess fixate was removed by the drying of individuals on filter paper for one minute (WETZEL et al., 2005). Then the amphipods were recounted and identified to species level, or to the lowest taxonomic level possible.

The amphipod species were classified according to their life style in five functional groups: infaunal tube-dweller (ITd), epifaunal tube-dweller (ETd), nestler (N), free-surface dweller (FSd) and burrower (B), based on Biernbaum (1979); Dauby et al. (2001) and De Broyer et al. (2003).

Each biological sampling unit was considered individually. Each station was labeled with a number (1 to 21) prefixed to the initial letter of the season sampled (W or S) and followed by the number of the replicate (1 or 2). Density was estimated as number of individuals ( $N$ ) per unit area ( $0.09\text{m}^2$ ), and species richness was determined as the total number of species ( $S$ ). Diversity ( $H'$ ,  $\log_e$ ) (SHANNON; WEAVER, 1963) and evenness ( $J'$ ) (PIELOU, 1975) were estimated. To test significant differences between richness, diversity, evenness and biomass on the two cruises, the non-parametric Mann-Whitney U-test was applied.

The environmental matrix (21 stations x 15 variables x 2 replicates x 2 periods) was constructed with the standardized selected abiotic factors (bottom temperature, bottom salinity, depth, biodegradable carbonate, organic matter, chlorophyll-a, pheopigments, gravel, very coarse sand, coarse sand, medium sand, fine sand, very fine sand, silt and clay). Principal component analysis (PCA) was performed to order the sampling stations as a function of the environmental variables.

The one-way crossed analysis of similarity (ANOSIM) (CLARKE; WARWICK, 2001) was performed to test the null hypothesis regarding the influence of depth. Then the nMDS analysis was applied to order the sampling stations of both cruises, according to species abundance. A second one-way ANOSIM analysis was applied to test the combined influence of season and depth. To perform this test, six groups of stations were established based on depth (< 20m; 20 – 40m; > 50 m) for each season (winter 2005; summer 2006).

To investigate the relationship between the environmental variables and the species abundance data the Canonical Correlation Analysis (CCA) was applied to the data (CLARKE; AINSWORTH, 1993) and to establish which species contributed most to the differences observed among groups, the similarity

percentages analysis (SIMPER) was performed (CLARKE, 1993).

## RESULTS

### Environmental Variables

The oceanographic characterization of the study area in each sampling period is showed by the T-S diagram in Figure 2. The analysis indicated the presence of the three water masses, Coastal Water (CW), Tropical Water (TW) and South Atlantic Central Water (SACW), on both cruises and the existence of some seasonal variation in the degree of interaction among them. In summer, both CW and SACW were detected close to the bottom (Table 1) but TW was restricted to the pelagic system. In this season the three water masses presented a continuous signature that indicated the area of mixing between TW and CW as lying in the surface layer and that between SACW and CW in the bottom layer. The data indicated also that in this sampling period, SACW advanced on the shelf up to nearly 50 m depth (as shown by T and S values at stations 3, 11 and 20), and the thermal front, or mixing zone between CW and SACW, fluctuated from 50 to about 28 m depth, as seen at stations 2, 8, 10 and 15 (Table 1). During the winter cruise, CW and SACW were present on the shelf but with little interaction between them. At this time the water column was homogeneous on the inner and middle shelf to about 50 m depth due to the retreat of SACW to the outer shelf (Table 1).

In the winter sampling, bottom temperature ranged between 16.7°C and 21.6°C, the lowest being recorded at station 21 and the highest at station 1. In summer, as expected, the range was greater, from 15°C to 26.8°C (Table 1). The bottom salinity varied between 34 and 35.9 in the winter and between 33.0 and 35.8 in summer. In general, the lowest values were related to coastal stations, such as 5 and 7 near the mouth of the Bertioga estuary and station 18 near the Itanhaém estuary.

Sand was the predominant sediment fraction on the inner and middle shelf, whereas muddy bottoms were found at the outer shelf stations. Among the sandy stations, very fine sand was the predominant fraction with values ranging between 45.9 and 92% (Fig. 3). At station 18, near the Itanhaém estuary, a seasonal variation in granulometry occurred, with an increase of silt and clay and a decrease of the very fine sand fraction in summer, probably due to the increase in the influence of the Itanhaém river (Fig.3). The muddy outer stations were characterised by bottoms with more than 70% of silt and clay and heterogeneous sediments were found at various depths, though only in a few places (sts. 2, 4 and 11) (Table 1, Fig. 3).

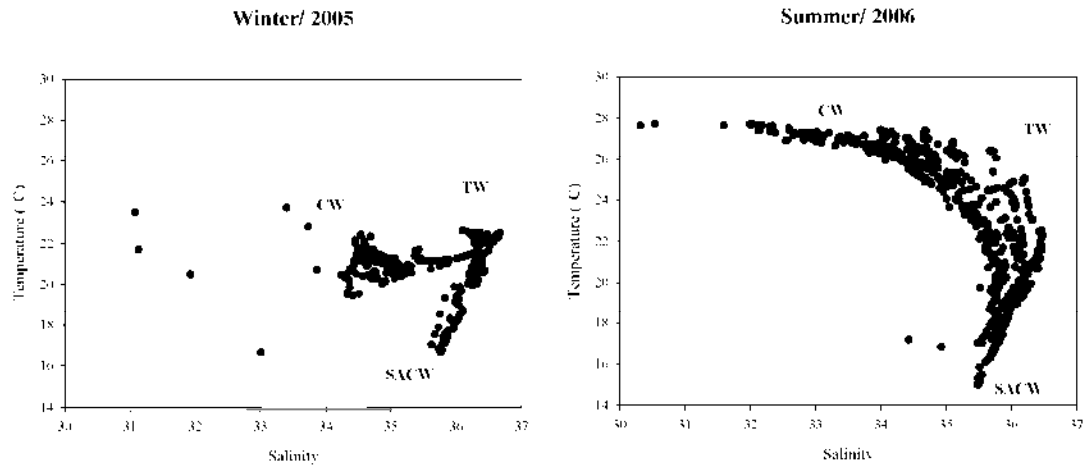


Fig. 2. Temperature - Salinity diagram (T-S) of the principal water masses sampled during winter 2005 and summer 2006 in the continental shelf between São Sebastião and Peruíbe, SP. CW = Coastal Water; TW = Tropical Water and SACW = South Atlantic Central Water.

Table 1. Environmental variables from the 21 stations of the two surveys carried out in the continental shelf between São Sebastião and Peruíbe. St = stations; Temp = bottom temperature; Sal = bottom salinity; GR = gravel; VCS = very coarse sand; CS = coarse sand; MS = medium sand; FS = fine sand; VFS = very fine sand; MD = mean diameter; S<sub>o</sub> = sort coefficient; TOM = total organic matter; VWS = very well sorted; WES = well sorted; MOS = moderately sorted; VPS = very poorly sorted; POS = poorly sorted.

	St.	Depth (m)	Temp. (°C)	Sal.	GR (%)	VCS (%)	CS (%)	MS (%)	FS (%)	VFS (%)	Silt (%)	Clay (%)	MD (φ)	S <sub>o</sub> (?)	TOM (%)	CaCO <sub>3</sub> (%)
Winter 2005	1	20.10	21.60	34.60	0.0	0.0	0.1	0.1	3.1	84.5	4.5	7.8	3.77	MOS	5.48	6.70
	2	34.00	21.40	34.00	6.40	2.5	1.4	1.7	16.4	55.8	5.1	10.7	4.08	POS	3.13	7.63
	3	58.30	20.60	35.20	0.2	0.3	0.4	0.6	9.6	73.7	3.4	11.8	3.63	POS	3.46	9.65
	4	85.10	17.40	35.90	3.8	3.1	1.6	2.6	43.8	30.1	4.4	10.5	3.11	POS	2.99	19.39
	5	15.10	21.20	34.60	0.0	0.0	0.0	0.1	4.7	90.1	2.3	2.8	3.56	WES	1.47	4.90
	6	27.40	20.90	35.70	0.8	0.1	0.2	0.2	10.8	78.5	2.8	6.7	3.38	POS	1.37	2.33
	7	19.20	21.20	34.70	0.0	0.0	0.1	0.2	8.4	80.1	6.8	4.5	3.57	POS	4.16	2.88
	8	27.10	21.20	35.10	0.4	1.4	1.2	1.1	27.6	62.3	2.2	3.8	3.13	MOS	1.19	7.92
	9	24.10	21.10	34.90	0.0	0.0	0.1	0.3	6.0	72.3	12.1	9.2	4.29	WES	3.03	4.17
	10	31.20	20.90	35.20	1.2	1.4	1.4	1.2	41.3	51.5	0.6	1.1	3.01	VWS	1.03	8.39
	11	53.60	21.10	35.90	5.1	2.5	1.7	1.6	14.7	59.1	4.0	11.3	3.39	POS	2.11	23.09
	12	93.50	17.10	35.80	0.1	0.1	0.1	0.2	0.6	2.4	35.1	61.4	7.7	POS	8.73	26.02
	13	16.20	21.10	34.90	0.0	0.0	0.0	0.1	0.5	87.3	7.5	4.6	3.7	MOS	2.61	3.13
	14	26.30	21.00	35.10	0.0	0.1	0.2	0.7	44.9	46.5	3.3	4.3	3.11	MOS	1.00	3.30
	15	31.60	20.70	35.20	0.0	0.6	0.7	1.0	50.2	47.3	0.0	0.0	2.98	VWS	0.91	5.12
	16	13.50	21.00	34.90	0.1	0.0	0.1	0.4	3.5	89.3	1.7	5.0	3.55	WES	1.12	4.17
	17	30.70	20.50	35.00	0.2	0.2	0.4	1.2	22.5	73.8	0.0	1.7	3.18	VWS	1.10	4.46
	18	15.30	21.00	34.60	0.0	0.0	0.1	0.2	3.0	90.0	3.9	2.8	3.62	WES	1.35	2.25
	19	27.40	20.90	34.60	0.1	0.3	0.3	1.6	28.3	69.4	0.0	0.0	3.12	WES	1.76	3.50
	20	49.70	21.00	35.80	1.4	0.8	0.8	0.9	6.5	77.7	3.9	7.9	3.58	POS	1.75	10.72
	21	97.10	16.70	35.80	10.60	5.2	5.9	5.0	3.1	1.4	20.1	48.9	5.52	VPS	6.71	15.69
Summer 2006	1	19.10	25.80	34.50	0.0	0.0	0.1	0.2	4.4	90.8	1.7	2.8	3.4	VWS	1.24	4.26
	2	33.50	19.70	35.70	2.0	1.6	1.2	1.3	13.0	64.4	4.4	12.1	4.1	POS	9.81	6.32
	3	57.20	16.80	34.90	0.1	0.3	0.4	0.5	9.3	73.8	5.6	10.1	3.5	POS	2.70	8.83
	4	84.60	15.00	35.50	4.1	3.3	2.0	2.8	43.4	31.5	5.0	7.9	3.0	POS	3.51	21.20
	5	14.50	26.10	34.20	0.0	0.0	0.0	0.1	3.9	92.0	2.3	1.7	3.5	VWS	2.14	4.79
	6	27.40	21.00	35.70	0.0	0.1	0.1	0.2	10.1	68.2	4.3	16.8	4.7	POS	9.06	3.37
	7	20.10	24.90	34.70	0.0	0.0	0.1	0.1	10.4	82.6	3.4	3.4	3.5	WES	7.01	2.15
	8	28.20	19.60	35.70	0.1	1.0	1.1	1.2	31.2	65.4	0.0	0.0	3.1	WES	1.30	6.60
	9	24.60	21.50	35.80	0.0	0.0	0.1	0.2	7.9	69.7	8.3	13.8	4.6	POS	6.63	3.38
	10	31.20	19.10	35.70	4.1	2.1	1.6	1.4	39.8	48.2	0.6	2.3	3.0	VWS	1.68	14.25
	11	56.20	17.20	34.40	3.7	3.1	2.1	1.8	14.6	62.1	7.4	5.1	3.4	POS	2.46	23.27
	12	93.30	16.50	35.70	0.0	0.0	0.0	0.0	0.0	3.5	68.7	27.8	7.1	POS	11.32	27.81
	13	15.40	25.90	34.00	0.0	0.0	0.0	0.1	0.3	90.9	3.3	5.5	3.7	MOS	12.20	2.55
	14	24.60	22.20	35.80	0.2	0.2	0.3	0.7	49.3	45.9	1.1	2.2	3.1	WES	0.88	3.77
	15	31.20	18.60	35.70	0.2	0.7	0.7	1.1	49.8	47.3	0.0	0.0	3.0	VWS	1.43	4.35
	16	14.10	26.30	33.80	0.0	0.1	0.1	0.3	3.7	91.2	1.7	2.8	3.5	VWS	1.10	5.13
	17	30.10	20.00	35.80	0.1	0.1	0.2	0.5	15.3	78.7	0.6	4.4	3.3	MOS	1.55	4.37
	18	14.50	26.80	33.00	0.0	0.0	0.1	0.2	2.8	57.1	17.6	5.3	5.3	VPS	9.89	4.42
	19	28.60	20.60	35.80	0.1	0.2	0.3	1.5	28.2	68.2	0.0	1.7	3.1	VWS	1.15	4.21
	20	49.50	17.20	35.70	0.2	0.4	0.7	0.8	6.5	81.8	3.4	6.2	3.6	MOS	2.69	9.60
	21	96.20	17.00	35.50	0.7	0.3	0.5	0.6	1.6	1.4	36.5	58.4	7.6	POS	12.54	26.02

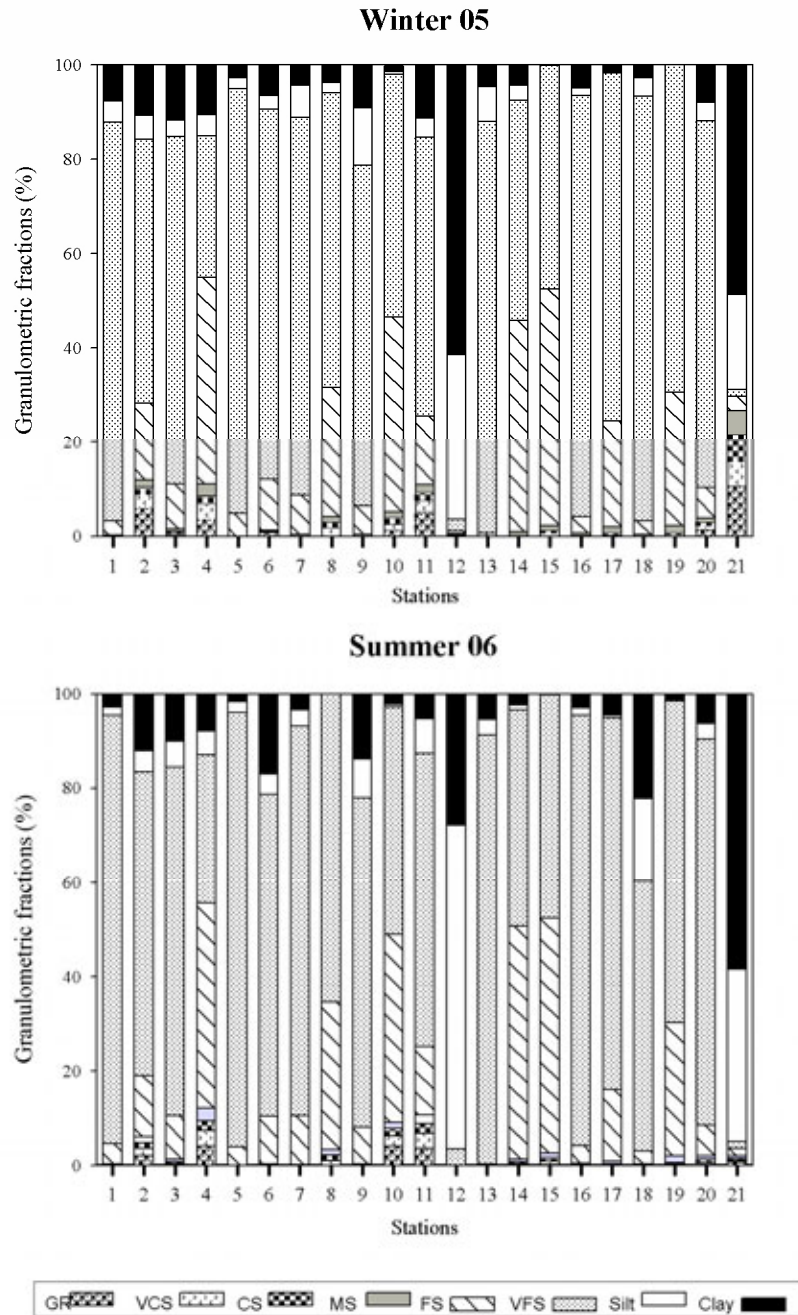


Fig. 3. Distribution of grain sizes among the stations of the two surveys carried on the continental shelf between São Sebastião and Peruibe. St = stations; Sal = salinity; Temp = temperature; GR = gravel; VCS = very coarse sand; CS = coarse sand; MS = medium sand; FS = fine sand; VFS = very fine sand.

Total organic matter ranged from 0.8 to 12.5% and presented a strong correlation with finer sediments, as seen at the deep stations 12 and 21 and at 13 and 18, nearer the estuaries, in summer. Values

of biotritric carbonate were situated within a broad range, between 2 and 28%, and those above 15% were associated with the muddy stations and the highly heterogeneous station 11 (Table 1).

Results of the PCA with environmental variables for both cruises are shown in Figure 4. The first two axes explain 82.8 % of the total variance. Axis I (62.8%) distinguishes the percentages of silt, clay, total organic matter, pheopigments and carbonates on the positive side from the very fine sand and temperature on the negative side. This axis represents the environmental gradient of temperature and depth, since it distinguishes the cold and deeper stations 12 and 21 from the warm, shallower stations 13 and 18 in the winter and stations 5 and 16 in summer.

Axis II (20%) separates temperature, very fine sand and organic matter content on the positive side from fine sand on the negative side. This axis discriminates the organically enriched sandy stations of the Santos Bay mouth and Bertioga estuary area (represented by sts 7 and 13) from the organically depleted sandy stations (10, 14 and 15) a little farther from the bay's mouth.

#### Composition and Distribution of the Amphipod Fauna

A total of 3,394 amphipods belonging to 60 species were identified on the two cruises. The total density was 1,586 individuals/0.09 m<sup>2</sup> on the winter

cruise, and rose to 1,808 individuals/0.09m<sup>2</sup> in the summer sampling. Ampeliscidae and Phoxocephalidae were the most important families since they presented a high number of species (15) and comprised about 55% of the fauna.

A high density of the gammarids *Ampelisca paria* and *Metharpinia* sp. characterized both cruises, but the first species was numerically dominant in winter (about 30% of the total fauna). *Urothoe* sp. was abundant only in the winter whereas *Gitanopsis* sp. and *Pseudomegamphopus* sp. characterized the summer. A remarkable abundance of a few species occurred in the winter, when 70% of the individuals belonged to 15 species in 2 families. Altogether, *Ampelisca paria* (188 individuals), *Metharpinia* sp. (96), *Urothoe* sp. (46) and *Heterophoxus videns* (41) accounted for more than half of the individuals collected in this season. Conversely, a greater diversity occurred in summer, when 19 species of 5 families comprised almost 70% of the fauna. *Ampelisca paria* (83 individuals), *Pseudomegamphopus* sp. (75), *Gitanopsis* sp. (71), *Metharpinia* sp. (70), *Microphoxus moraesi* (60) and *Resupinus coloni* (49) accounted for about 49% of the total amphipod abundance.

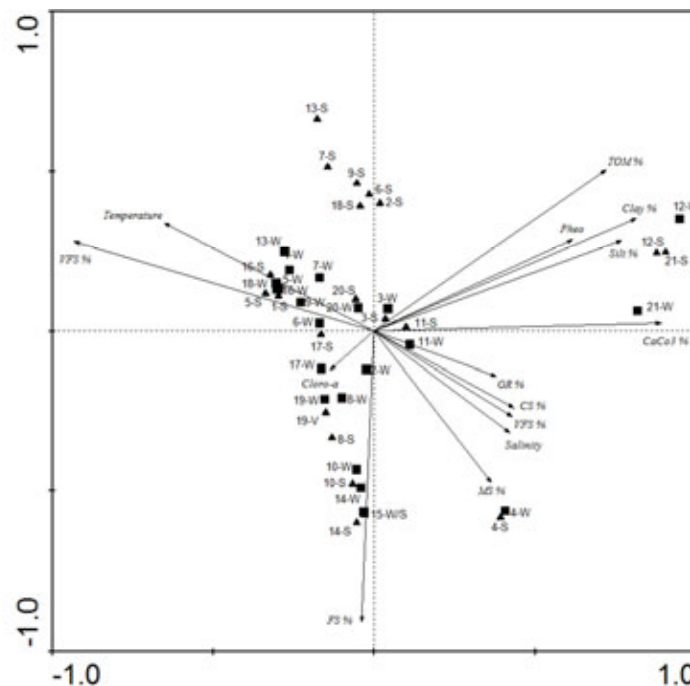


Fig. 4. Principal component analysis (PCA) of environmental variables in the two campaigns. Black squares: winter stations (W); Black triangle: summer stations (S). GR = gravel; CS = coarse; MS = medium sand; FS = fine sand; VFS = very fine sand; Pheo = Pheopigments; Chloro-a = Chlorophyll-a; TOM = total organic matter.

The highest density values were found at station 20 on the winter cruise with a mean number of 132 individuals/0.09m<sup>2</sup>. In the summer the density rose at station 14, with a mean number of 166 individuals/0.09m<sup>2</sup>, followed by station 20 (128 individuals/0.09m<sup>2</sup>) (Fig. 5).

Biomass values were similar for both cruises (Mann-Whitney U-test,  $p = 0.09$  at  $\alpha = 0.05$ ). High mean values, between 41 and 71 g/0.09m<sup>2</sup>, were found at stations 2 and 3, 11W and 20S. The greatest value was observed at station 11W<sub>1</sub> (116 g/0.09m<sup>2</sup>) (Fig. 5)

Table 2 presents the values for richness, diversity and evenness obtained by each sampling unit on each cruise. The number of species ranged between 2 and 17 in the winter sampling and from 1 to 21 in summer. In general, low values were found both at the shallower ( $\leq 20$ m) and deeper stations ( $\geq 80$ m) (Table 2).

Diversity and evenness were quite variable spatially and presented similar patterns to that shown for richness (Table 2). This latter ranged from 0.10 (st. 18 W<sub>1</sub>) to 2.45 (st. 3 W<sub>1</sub>) in the winter and from 0.47 (st. 9 S<sub>1</sub>) to 2.58 (st. 10 S<sub>2</sub>) in the summer,

and a significant temporal difference was found between the cruises (Mann-Whitney U-test,  $p = 0.04$  at  $\alpha = 0.05$ ). Evenness presented high variability, it was quite low (0.14) at st. 18 W<sub>1</sub> and high (1.00) at st. 13 S<sub>2</sub> (Table 2). No statistically significant difference was observed between the data from the two cruises (Mann-Whitney U-test,  $p \geq 0.13$  at  $\alpha = 0.05$ ).

The amphipods collected were placed in five different classes according to their life styles. This classification included mode of occupation of the substrate, species mobility and trophic group (Table 3). Spatially, infaunal tube dwellers (It<sub>d</sub>) dominated at the innermost stations in both sampling periods, and *Ampelisca paria* was the main species of this group (Fig. 6). The stations located as deep as 30 m presented four or five classes, especially in summer, when species of all functional guilds with similar abundance could be observed. Stations deeper than 50m exhibited a dominance of burrowers; however, the same did not occur at stations 4 and 21, where epifaunal tube dwellers dominated in summer (Fig. 6).

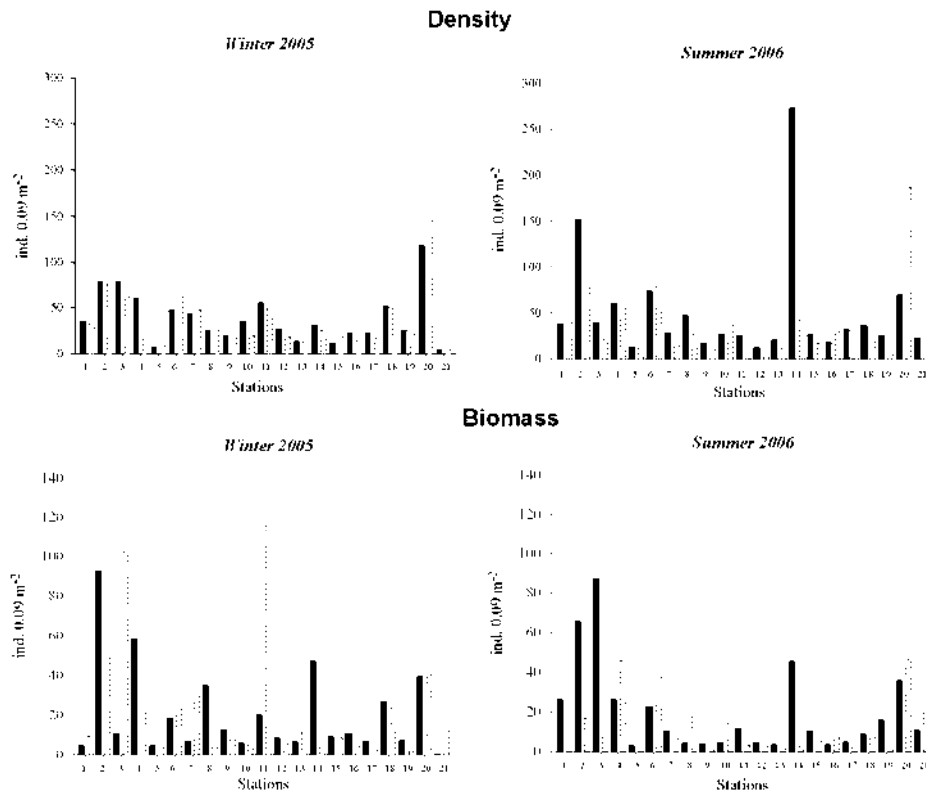


Fig. 5. Density (ind. 0.09m<sup>-2</sup>) and biomass (mg 0.09m<sup>-2</sup>) of amphipods in all 84 stations sampled at the continental shelf between São Sebastião and Peruibe, SP in winter 2005 and summer 2006. Replicate 1 = black and Replicate 2 = diagonal lines.



Table 2. Values of all the stations of richness (S), diversity (H') and evenness (J') obtained for each replicate station in the two cruises (winter 2005 and summer 2006). The letters A and B represent the replicates.

Stations	Winter 05			Summer 06		
	S	H'	J'	S	H'	J'
1A	4	0.68	0.49	9	1.47	0.67
1B	3	0.44	0.40	9	1.61	0.73
2A	12	1.62	0.65	21	2.24	0.74
2B	9	1.70	0.77	14	1.72	0.65
3A	16	2.45	0.88	14	1.74	0.66
3B	17	2.41	0.85	7	1.62	0.83
4A	12	1.87	0.75	14	2.38	0.90
4B	6	1.51	0.84	12	1.94	0.78
5A	2	0.66	0.95	7	1.82	0.94
5B	2	0.35	0.50	5	1.47	0.91
6A	12	1.98	0.80	10	1.74	0.76
6B	15	1.96	0.72	15	2.21	0.82
7A	2	0.19	0.27	8	1.50	0.72
7B	4	0.49	0.35	3	0.73	0.66
8A	9	2.00	0.91	13	2.25	0.88
8B	11	2.09	0.87	12	2.20	0.88
9A	3	0.69	0.63	2	0.47	0.67
9B	1	****	****	4	1.09	0.79
10A	10	1.72	0.75	11	2.18	0.91
10B	9	2.02	0.92	16	2.58	0.93
11A	17	2.39	0.84	9	1.74	0.79
11B	13	2.07	0.81	1	****	****
12A	6	1.52	0.85	4	1.27	0.91
12B	4	0.90	0.65	1	0.00	****
13A	2	0.41	0.59	5	1.13	0.70
13B	2	0.26	0.37	2	0.69	1.00
14A	8	1.73	0.83	15	1.84	0.68
14B	7	1.30	0.67	14	2.25	0.85
15A	6	1.58	0.88	10	2.19	0.95
15B	9	1.91	0.87	8	1.98	0.95
16A	5	1.29	0.80	5	1.34	0.83
16B	4	0.99	0.72	7	1.47	0.75
17A	6	1.17	0.65	7	1.58	0.81
17B	7	1.82	0.94	11	1.99	0.83
18A	2	0.10	0.14	4	0.80	0.58
18B	3	0.39	0.36	3	0.73	0.66
19A	10	1.96	0.85	9	2.12	0.97
19B	10	2.07	0.90	3	1.08	0.98
20A	11	1.67	0.70	14	1.85	0.70
20B	8	1.07	0.51	18	1.88	0.65
21A	2	0.50	0.72	6	1.54	0.86
21B	4	1.32	0.95	5	1.28	0.79

Table 3. Classification of the amphipod species obtained in the two cruises (winter 2005 and summer 2006) according with their life styles. ITd = Infaunal Tube-dweller; ETd = Epifaunal Tube-dweller; B = Burrower; FSd = Free-Surface dweller; N = Nestler.

Abbrev.	Species	Life Style	Abbrev.	Species	Life Style
<i>A bre</i>	<i>Ampelisca brevisimulata</i>	ITd	<i>Me sp</i>	<i>Metharpinia</i> sp.	B
<i>A cris</i>	<i>Ampelisca cristata</i>	ITd	<i>Me ia</i>	<i>Metharpinia</i> cf. <i>iado</i>	B
<i>A mor</i>	<i>Ampelisca moreirai</i>	ITd	<i>Mi mo</i>	<i>Microphoxus moraesi</i>	B
<i>A par</i>	<i>Ampelisca paria</i>	ITd	<i>Pse den</i>	<i>Pseudoharpinia dentata</i>	B
<i>A pug</i>	<i>Ampelisca pugetica</i>	ITd	<i>Eud gra</i>	<i>Eudevenopus gracilipes</i>	B
<i>A rod</i>	<i>Ampelisca rodriguesi</i>	ITd	<i>Ti vis</i>	<i>Tiburonella viscana</i>	B
<i>A rom</i>	<i>Ampelisca romigi</i>	ITd	<i>Syr cre</i>	<i>Syrrhoce crenulata</i>	B
<i>A sub</i>	<i>Ampelisca subtropicalis</i>	ITd	<i>T bio</i>	<i>Tiron biocellata</i>	B
<i>Git sp</i>	<i>Gitanopsis</i> sp.	ETd/N	<i>T tro</i>	<i>Tiron tropakis</i>	B
<i>Ka sp</i>	<i>Kamehatylus</i> sp.	ETd/N	<i>P ni</i>	<i>Parametopella ninis</i>	ETd/N
<i>E sp</i>	<i>Eusirus</i> sp.	ETd/FSd	<i>Hu sp</i>	<i>Huerpa</i> sp.	B
<i>L dub</i>	<i>Liljeborgia dubia</i>	ETd/N	<i>Ca sp</i>	<i>Carangolia</i> sp.	B
<i>L qui</i>	<i>Liljeborgia quinqueidentata</i>	ETd/N	<i>U sp</i>	<i>Urothoe</i> sp.	B
<i>Ls tit</i>	<i>Listriella titinga</i>	ETd/N	<i>Le sp</i>	<i>Lembos</i> sp.	ETd
<i>Prasp</i>	<i>Prachynella</i> sp.	ETd/FSd	<i>Am ra</i>	<i>Ampithoe ramondi</i>	ETd
<i>Try sp 1</i>	<i>Tryphosella</i> sp. 1	ETd/FSd	<i>Mo ach</i>	<i>Monocorophium acherusicum</i>	ETd
<i>Try sp 2</i>	<i>Tryphosella</i> sp. 2	ETd/FSd	<i>Lep sp</i>	<i>Corophiidae</i> cf. <i>Leptocheirus</i>	ETd
<i>Cd sp</i>	<i>Ceradocus</i> sp.	ETd/FSd	<i>Che meg</i>	<i>Cheirophotis megacheles</i>	ETd
<i>D ani</i>	<i>Dulichtiella anisochir</i>	ETd/FSd	<i>Che neo</i>	<i>Cheirophotis neotropicalis</i>	ETd
<i>G my</i>	<i>Giberosus myersi</i>	B	<i>Par pu</i>	<i>Paracaprella pusilla</i>	ETd/FSd
<i>M sp</i>	<i>Maera</i> sp.	ETd/FSd	<i>Par te</i>	<i>Paracaprella tenuis</i>	ETd/FSd
<i>R col</i>	<i>Resupinus coloni</i>	B	<i>Po br</i>	<i>Podocerus brasiliensis</i>	ETd/FSd
<i>Mo ny</i>	<i>Monoculodes nyei</i>	B	<i>Pseu sp</i>	<i>Pseudomegamphopus</i> sp.	ETd
<i>Par ac</i>	<i>Paramonoculopsis acuta</i>	B	<i>Pseu ba</i>	<i>Pseudomegamphopus barnardi</i>	ETd
<i>Oed cin</i>	<i>Oediceroides cinderella</i>	B	<i>C sp</i>	<i>Cerapus jonsoni</i>	ETd
<i>Syn am</i>	<i>Synchelidium americanum</i>	B	<i>Ar sp</i>	<i>Kamakidae</i> cf. <i>Aorcho</i>	ETd
<i>We rec</i>	<i>Westwoodilla rectirostris</i>	B	<i>Amp po</i>	<i>Ampelisciphotis podophthalma</i>	ETd
<i>H sp</i>	<i>Pardaliscidae</i> cf. <i>Halicoides</i>	B	<i>Ph bre</i>	<i>Photis brevipes</i>	ETd
<i>Ht vid</i>	<i>Heterophoxus videns</i>	B	<i>Ph lon</i>	<i>Photis longicaudata</i>	ETd

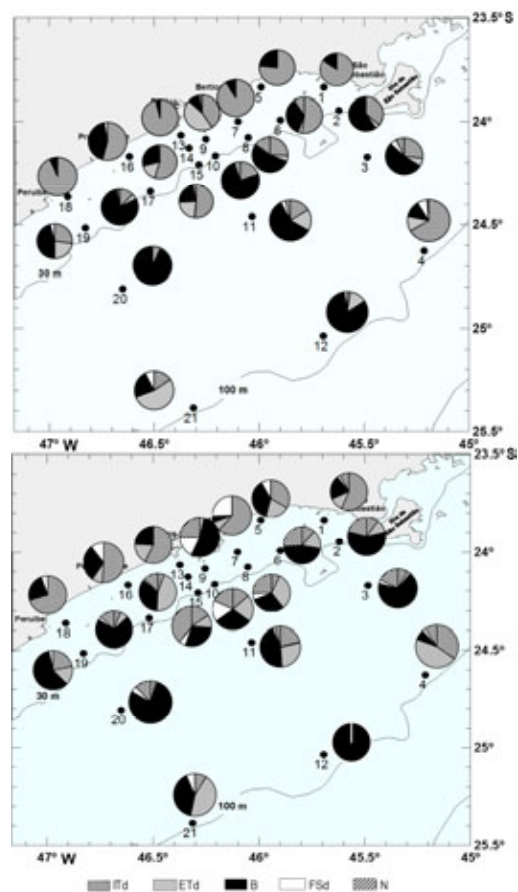


Fig. 6. Distribution of the relative abundance of different life styles of amphipods at the 21 sampled stations. ITd = Infraunal Tube-dweller; ETd = Epifaunal Tube-dweller; B = Burrower; FSd = Free-Surface dweller and N = Nestler.

#### Amphipod Communities

The ANOSIM one-way test of similarity showed that the amphipod fauna differed significantly between the three groups of sites (shallower than 20 m; between 20 and 40 m; deeper than 50 m) ( $R_{Global} = 0.64$ ; significance level = 0.1). The pairwise comparison between groups showed that the greatest difference was found between the shallowest site and the stations deeper than 50 m. There was also a great difference between the stations located between 20 and 40m and those deeper than 50 m, whereas relatively little segregation of the groups can be seen on the inner shelf (Table 4).

Three groups of stations were identified by means of the n-MDS ordination analysis applied to the data. A clear depth gradient could be detected, but with some seasonal influence at the stations shallower than 50 m. The 0.18 stress showed considerable

accuracy in interpreting the spatial distribution on only two planes (Fig. 7).

Table 4. Results obtained from depth and season-depth one-way analyses of ANOSIM sl = significance level; Perm = number of permutations. A = < 20 m winter; B = 20 – 40 m winter; C = > 50 m winter; D = < 20 m summer; E = 20 – 40 m summer and F = > 50 m summer.

ANOSIM			
One-way			
<i>Depth:</i> Global $R = 0.64$ , $p = 0.1\%$			
	<b>R</b>	<b>sl (%)</b>	<b>Perm.</b>
< 20m, 20-40 m	0.534	0.1	999
< 20 m, > 50 m	0.81	0.1	999
20 - 40 m, > 50 m	0.66	0.1	999
<i>Season-Depth groups:</i> Global $R = 0.625$ , $p = 0.1\%$			
	<b>R</b>	<b>sl (%)</b>	<b>Perm.</b>
A, B	0.548	0.1	999
A, C	0.932	0.1	999
A, D	0.594	0.1	999
A, E	0.94	0.1	999
A, F	0.919	0.1	999
B, C	0.685	0.1	999
B, D	0.515	0.1	999
B, E	0.445	0.1	999
B, F	0.687	0.1	999
C, D	0.755	0.1	999
C, E	0.647	0.1	999
C, F	-0.043	73.9	999
D, E	0.521	0.1	999
D, F	0.744	0.1	999
E, F	0.587	0.1	999

The one-way ANOSIM with the sampling season (winter 2005 and summer 2006) and depth range indicated a significant coupled influence of season and depth on the amphipod communities (Season-Depth Global  $R = 0.625$ , significant level = 0.1%). According to season-depth ANOSIM, there is no difference between the deeper winter and summer groups (C and F:  $R = -0.043$ ), consequently the deeper groups can be considered as one (Table 4).

The pairwise comparison between season-depth groups showed that the greatest differences occurred between the shallower (< 20 m winter and summer) and the deeper groups (> 50m) (A and C:  $R = 0.932$ , A and F:  $R = 0.919$ , C and D:  $R = 0.755$  and D and F:  $R = 0.744$ ,  $p = 0.1\%$ ), and that the difference was greater in the winter than in summer. A marked difference could be observed also between the winter Coastal (shallow) group and the summer Mixed group (A and E:  $R = 0.94$ ) (Table 4).

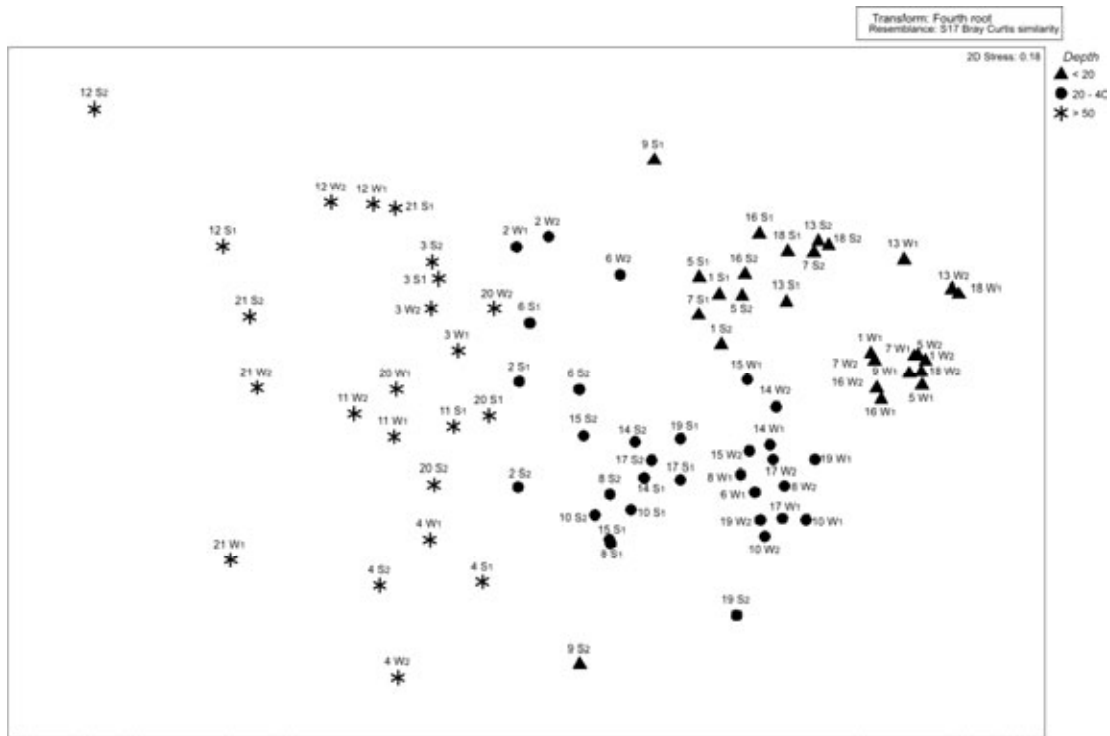


Fig. 7. Component analysis (nMDS) of the 84 stations based on the amphipod species abundance in the two periods studied (W = winter and S = summer). It is indicated the three depth groups. Black triangle = Coastal stations (< 20 m); Black circle = Mixed Zone stations (20 – 40 m) and Black star = Deep Zone stations (> 50 m). The numbers of the replicates are subscripts (e.g. W<sub>1</sub> = Replicate 1 for winter).

With respect to faunal composition, the first four high percentages of dissimilarity were observed between the Deep group and the other groups (A, C = 90.41%; D, C = 86.65%; B, C = 85.98% and E, C = 84.45%) (Table 5). Species that contributed most to the seasonal dissimilarity were *Ampelisca paria* (more abundant in the winter) and *Metharpinia* sp., *Gitanopsis* sp. and *Liljeborgia quinquedentata* (significantly abundant in summer). When considering species dissimilarity between the season-depth groups, *Pseudoharpinia dentata*, *Urothoe* sp. and *Heterophoxus videns* were abundant in the Deep group, but totally or almost absent from the other groups. *Ampelisca paria* was present at the stations shallower than 40 m, with higher numbers in the winter. In summer, *Metharpinia* sp. and *Eudevenopus gracilipes* were denser in the Coastal group, whereas *Gitanopsis* sp. and *Liljeborgia quinquedentata* were more abundant in the Mixed Zone group (Table 5).

The average values of the main biological variables (density, biomass, species richness, diversity, evenness) and of the environmental variables (depth, temperature, total organic matter, percentage of sand, mud, chlorophyll a and pheopigments) were calculated (Table 5).

for each group identified (Table 6). Sand was considered as the sum of fine sand and very fine sand fractions, whereas mud was composed of the sum of silt and clay.

The Coastal groups were represented by the stations 1, 5, 7, 9, 13, 16 and 18. In the winter this group was almost entirely dominated by *Ampelisca paria* (infaunal tube-dweller) and *Microphoxus moraesi* (burrower) which together accounted for more than 90% of the total abundance. As a consequence, species richness, diversity and evenness showed the lowest values in this group (Tables 5 and 6). In summer, *Ampelisca paria* was still present but conceded its dominance to *Metharpinia* sp. (burrower), followed by *Eudevenopus gracilipes* (burrower) and *Resupinus coloni* (free-surface dweller). Differently from the winter, *Microphoxus moraesi* was found in low abundance in summer. The Coastal group at this time presented the lowest biomass value though densities were near to the winter ones. In the summer sampling an increase in mud content was observed, mainly at those stations near the Santos Bay mouth and the Itanhaém River (stations 13, 16 and 18) (Tables 5 and 6).

Table 5. Species abundance and average dissimilarity among groups obtained in winter 2005 and summer 2006. Species which contributed most to the differences among groups are indicated in bold.

Species	< 20 m W		< 20 m S		20 - 40 m W		20 - 40 m S		> 50 m W/S	
	Av. Abund.	% Contrib.	Av. Abund.	% Contrib.	Av. Abund.	% Contrib.	Av. Abund.	% Contrib.	Av. Abund.	% Contrib.
<i>Ampelisca paria</i>	<b>1.96</b>	<b>61.99</b>	<b>0.83</b>	<b>9.54</b>	<b>1.31</b>	<b>27.99</b>	<b>0.68</b>	<b>8.98</b>	-	-
<i>Metharpinia</i> sp.	-	-	<b>1.21</b>	<b>23.24</b>	0.54	1.87	<b>1.07</b>	<b>25.21</b>	0.40	3.52
<i>Microphoxus moraesii</i>	<b>1.17</b>	<b>32.54</b>	0.07	0.00	<b>1.02</b>	<b>19.31</b>	0.14	0.27	0.10	0.07
<i>Urothoe</i> sp.	-	-	-	-	0.26	0.28	0.47	1.47	<b>0.67</b>	<b>11.79</b>
<i>Pseudoharpinia dentata</i>	-	-	0.07	0.00	0.30	1.00	-	-	<b>0.67</b>	<b>19.69</b>
<i>Heterophoxus videns</i>	-	-	0.28	0.25	0.33	0.81	0.48	2.19	<b>0.67</b>	<b>10.76</b>
<i>Gitanopsis</i> sp.	0.07	0.00	<b>0.94</b>	<b>6.88</b>	0.06	0.00	<b>0.88</b>	<b>9.83</b>	0.14	0.64
<i>Photis brevipes</i>	0.14	0.19	<b>0.83</b>	<b>6.00</b>	0.21	0.60	<b>0.63</b>	<b>5.04</b>	0.11	0.14
<i>Ampelisca pugetica</i>	0.07	0.00	0.08	0.00	0.28	0.99	0.34	1.70	0.24	2.28
<i>Monoculodes nyei</i>	0.34	1.38	<b>0.78</b>	<b>7.91</b>	<b>0.50</b>	<b>5.45</b>	0.19	0.16	-	-
<i>Eudevenopus gracilipes</i>	0.24	0.56	<b>0.96</b>	<b>13.91</b>	<b>0.65</b>	<b>8.36</b>	0.21	0.50	-	-
<i>Resupinus coloni</i>	0.18	0.41	<b>1.02</b>	<b>11.17</b>	<b>0.60</b>	<b>9.14</b>	<b>0.60</b>	<b>5.99</b>	0.18	1.39
<i>Liljeborgia quinquecostata</i>	0.14	0.23	<b>0.72</b>	<b>5.87</b>	0.29	1.41	<b>0.79</b>	<b>13.41</b>	0.18	0.65
<i>Carangolia</i> sp.	-	-	-	-	0.06	0.00	-	-	<b>0.43</b>	<b>7.43</b>
<i>Pseudomegamphopus</i> sp.	0.27	0.75	0.61	1.90	0.36	3.24	0.23	0.60	0.37	4.79
<i>Ampelisca cristata</i>	0.07	0.00	0.36	1.23	0.26	1.55	0.52	4.02	0.14	0.57
<i>Ampelisca moreirai</i>	-	-	0.18	0.13	0.34	1.41	0.34	1.81	0.35	2.48
<i>Ampelisca brevisimulata</i>	-	-	0.49	1.83	0.64	4.47	0.39	1.71	0.24	1.93
<i>Lembos</i> sp.	-	-	0.48	4.23	0.14	0.28	0.20	0.70	0.36	5.66
<i>Paramonoculopsis acuta</i>	-	-	0.19	0.40	0.14	0.15	0.43	0.36	0.26	2.50
<i>Ampelisca rodriguesi</i>	-	-	-	-	-	-	-	-	0.33	1.69
<i>Tiron biocellata</i>	0.14	0.00	-	-	0.41	3.34	0.26	0.98	0.14	0.44
<i>Oediceroides cinderella</i>	0.14	0.54	-	-	-	-	-	-	-	-
<i>Synchelidium americanum</i>	-	-	-	-	0.31	0.97	0.25	0.98	0.11	0.13
<i>Cheirophotis neotropicalis</i>	-	-	0.19	0.11	0.31	1.84	-	-	-	-
<i>Liljeborgia dubia</i>	0.14	0.42	0.07	0.00	0.27	1.19	-	-	0.08	0.00
<i>Gyberosus myersi</i>	0.25	0.98	0.10	0.00	0.20	0.54	-	-	-	-
<i>Ampelisca</i> sp.1	-	-	-	-	0.17	0.17	-	-	0.07	0.00

Table 6. Mean value of the biological and environmental variables in each of the five groups obtained for the two cruises (winter 2005 and summer 2006). W = winter; S = Summer; S = number of species; H' = Shannon's diversity; J' = Pielou's evenness; D = density; FS = fine sand; VFS = very fine sand; Chloro-a = Chlorophyll -a; Pheo = Pheopigments; TOM = total organic matter and Temp = temperature.

	< 20 m W	< 20 m S	20 - 40 m W	20 - 40 m S	> 50 m W/S
<b>S</b>	3	5	9	12	10
<b>H'</b>	0.53	1.16	1.79	2.01	1.60
<b>J'</b>	0.50	0.75	0.81	0.93	0.75
<b>D</b>	28.4 ± 16.9	21.8 ± 10.3	36.7 ± 20.9	61.5 ± 66.4	50.6 ± 46.3
<b>Biomassa</b>	0.012 ± 0.01	0.006 ± 0.01	0.021 ± 0.02	0.018 ± 0.02	0.032 ± 0.03
<b>FS + VFS (%)</b>	91.7	88.3	92.4	93.2	55.2
<b>Silt + Clay (%)</b>	8.0	11.4	3.9	4.5	38.8
<b>Chloro-a</b>	1.3	1.51	3.89	5.56	1.49
<b>Pheo</b>	5.09	4.86	2.41	4.18	12.71
<b>TOM (%)</b>	1.61	4.21	1.31	2.60	5.40
<b>Depth</b>	17.6	17.5	29.5	29.4	72.8
<b>Temp (°C)</b>	21.2	25.3	20.9	20.1	17.8

The Mixed Zone stations 2, 6, 8, 10, 14, 15, 17 and 19 were characterized by having species that occurred both in the Coastal and Deep Zones. This group had a similar species composition and dominance in both the seasons sampled. In the winter it presented the second largest biomass value for the area, whereas in summer all the biological variables were higher (Tables 5 and 6).

The Deep Zone group was represented by stations 3, 4, 11, 12, 20 and 21 and was characterized by having the highest biomass, mud and total organic matter values and a low temperature (17.8°C). The four dominant species were all burrowers: *Pseudoharpinia dentata*, *Urothoe* sp., *Heterophoxus videns* and *Carangolia* sp. This group was the only one in which *Ampelisca paria*, *Monoculodes nyei* and *Eudevenopus gracilipes* did not occur.

Relationships between amphipod species, stations and environmental variables are shown in the CCA diagram of Figure 8. The first two axes explained 50.9% of the total variance of the data. Axis I (30.3%) separated the deeper stations with poorly selected muddy bottoms, high biodebitric carbonate values and burrower species from the other groups of stations with high values of bottom water temperature. Station 4 (in both winter and summer) was more related to the presence of the infaunal tube-dweller *Ampelisca rodriguesi* and higher coarse sand values,

whereas the other deeper stations were characterized by burrower species. The coastal stations in the winter received a major contribution of very fine sand and were dominated by *Ampelisca paria* (infaunal tube-dweller) and *Oediceroides cinderella* (burrower).

Axis II accounted for 20.6% of the total variance and distinguished the Mixed Zone groups from the others. Fine sand and more than ten species are related to this axis, confirming the high diversity values described for the groups in this area.

## DISCUSSION

The study area is characterized by high precipitation in summer and low rainfall in winter, though without any marked dry season (CAMARGO et al., 1996). The amount of rainfall is particularly important to the system, since it decreases salinity and provides transport of internal waters rich in nutrients to Santos Bay (SB), enhancing eutrophication of the waters (MOSER et al., 2005). However, despite this importance, few studies have focused on the fluxes of estuarine properties from the Santos and São Vicente estuaries into the SB (HORTELLANI et al., 2005; MOSER et al., 2005).

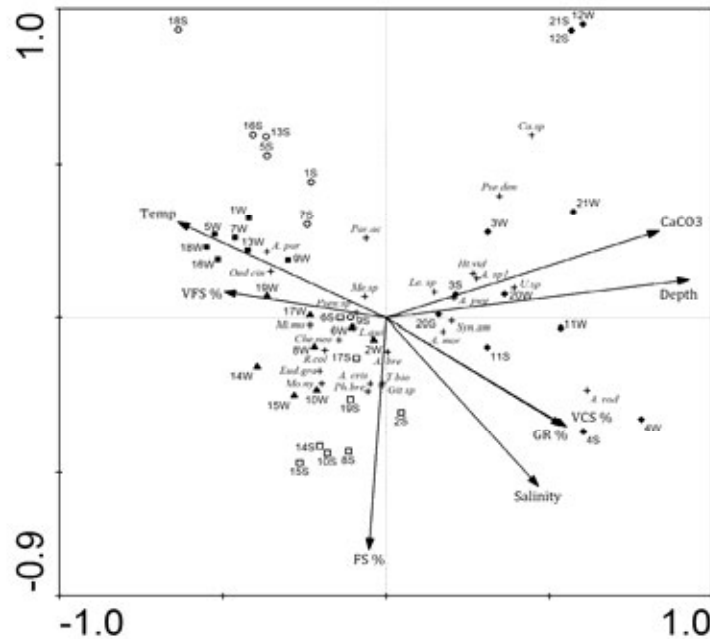


Fig. 8. Canonical correspondence analysis (CCA). With the species that most contributed to the groups identified with SIMPER analysis. Black square = Coastal winter; Empty circle = Coastal summer; Black triangle = Mixed Zone winter; Empty square = Mixed Zone summer; Black diamonds = Deep Zone winter and summer; Cross = Simper species. W = winter; S = summer; Temp = Temperature; GR = gravel; VCS = very coarse sand; FS = fine sand; VFS = very fine sand.

The internal hydrodynamics of the SB flow clockwise and together with the sedimentary processes are considered the main cause of distribution of nutrients, contaminants and suspended solids inside the bay (FUKUMOTO et al., 2004). Despite the major part of the particulate matter's being trapped in the SB, an estuarine plume was detected at the water surface transporting sediments to the north (onto the northern part) of the adjacent shelf (MARTINS et al., 2008). Our results did not detect any effect of this plume on the bottom sediment of the adjacent shelf, either in terms of an increase in the organic matter content or as structural differences in the amphipod communities. The data of this present study indicate that the SB acts as a "dilution box" for the material transported from the estuarine channels of Santos and São Vicente, especially in summer when rainfall is heavy. Also, during the study periods the sign of the estuarine plume was weak and localized near the entrance of SB, as the low values of salinity and high values of organic matter found at the surface of those stations showed.

A distinct situation occurs in the south of the study area, where the estuary faces the open sea and an effective transport of less saline waters to the adjacent shelf occurs. In that region, in summer, low values of salinity were currently found (CAMARGO et al., 1996; SOUZA-PEREIRA; CAMARGO, 2004) and indicate the decrease of marine influence due to the concurrent increase in both rainfall values and river drainage. A notable summer estuarine input of fine sediments and organic matter was detected at station 18, where the organic matter content was about 7.3 higher in the summer than in the winter sampling.

It seems that the Itanhaém estuary plays a different role on the shelf than do the Santos-São Vicente estuaries, mainly by virtue of the absence of the above-mentioned "dilution box". Thus, especially in summer, the transport of material from the estuary to the shelf is greater and changes the bottom sediment composition of the inner shelf, which becomes finer and organically enriched. As a consequence, the dominant amphipod species in the inner southern area are different from those of the northern part.

The southwestern Atlantic continental shelf is characterized by the presence and interaction of three water masses (Coastal Water, Tropical Water and South Atlantic Central Water) as observed in earlier studies (CASTRO-FILHO et al., 1987; MAHIQUES et al., 1999; 2004). The summer coastward intrusion of the cold, dense SACW near the bottom from the slope may contribute to changes in the species composition and structure of the megafauna (PIRES-VANIN, 1992; DE LÉO; PIRES-VANIN, 2006) and macrofauna communities (PIRES-VANIN, 1993) by displacing warm water species into shallower areas and favoring the presence of

carnivores. The data on amphipod communities here presented suggest that the five groups of species could be maintained mainly by the influence of depth and water masses. In fact, the greater dissimilarity between the amphipod fauna on the middle and inner shelf demonstrates the influence of the water mass dynamics on the benthic fauna, as shown for other macrofauna components such as polychaete and mollusk species, as also for megafauna (SOARES-GOMES; PIRES-VANIN, 2003; PIRES-VANIN, 2008).

Studies on macrobenthos composition and community structure from tropical and sub-tropical continental shelves of southern oceans are relatively few (ALONGI, 1990; GRAY, 2002; BIGOT et al., 2006; CAPITOLI; BEMVENUTI, 2006). However, all of them suggest that the amount of hydrodynamic energy and available organic matter are the main driving forces in structuring the soft-bottom communities, with depth and sediment grain size as secondary correlates. Depth and grain size are intrinsically related factors that act on the variability of the macrofauna diversity, integrating effects of the hydrodynamic environment over time (ELLINGSEN, 2002; JAYARAJ et al., 2008; MOHAMMED; COPPARD, 2008). The results obtained in the present study support these findings, since it was possible to observe 3 spatially distinct groups of amphipods that corresponded to different hydrodynamic areas.

Many factors are currently evoked to explain the spatial and temporal distribution of amphipod communities on continental shelves. They are physical and/or biological in nature and their effects are frequently difficult to evaluate, especially when they occur on coastal shelves subject to human influence (POSEY, 1987; SCHAFFNER; BOESCH, 1982). The study of the amphipod fauna off the west coast of Portugal (CUNHA et al., 1999) showed that the pattern of density and species diversity could be related not only to sediment composition, water temperature, depth, local hydrodynamics and food availability, but also to the biology of the species. According to those authors, the seasonal pattern of the assemblages was mainly associated with fluctuations in the density of the dominant species. Amphipods breed almost continuously in tropical and subtropical areas, but some species exhibit conspicuous breeding peaks, a fact that may influence the inter- and intra specific interactions and the community structure (DAUVIN et al., 1994; MOREIRA et al., 2008).

Ocean dynamics, together with the sediment pattern, have been observed to be the main factors which explain the amphipod community structure on the subtropical Brazilian shelf (SANTOS; PIRES-VANIN, 2000; VALÉRIO-BERARDO et al., 2000a, c). The latter authors found that the diversity of

tube-dwellers on the Ubatuba shelf off the northern coast of São Paulo state, decreased with the increase of sedimentary silt and clay and showed the importance of the muddy belt of the outer shelf area in changing the community composition of the shelf.

The species of the cosmopolitan tube-dweller genus *Ampelisca* occurred throughout the study area, but only *Ampelisca paria* presented a marked and characteristic dominance in the Coastal Zone. Although species of *Ampelisca* are distributed worldwide and commonly dominate many soft-bottom communities, the data available on their biology are still fragmentary (KAÏM-MALKA, 2000). There is little information about *Ampelisca paria* but the species is reported to live in mud, fine and silty sand, within a depth range of 4-23 m (SEREJO et al., 2000). Studies carried out on a few other species have shown that they live in the sediment, mainly in the sandy bottoms of shallow waters, and can attain very great abundance (DAUVIN; BELLAN-SANTINI, 1988; SHEADER, 1998).

As occurs with other amphipods, it is difficult to analyze the species of *Ampelisca* according to the r- and K- selection theory. Some *Ampelisca* approach the criteria for being considered K-strategist (period of reproduction and recruitment limited in time, slight dispersion and limited capacity to build up their populations) (DAUVIN, 1989); other species have been described as opportunistic (r-strategist) due to their rapid development and early maturation (SANTOS; SIMON, 1980; FRANZ; TANACREDI, 1992; CAIN et al., 2009). *Ampelisca paria* seems to behave opportunistically, because it has been reported as always being highly abundant in hydrodynamically unstable areas of the Brazilian shelf (SANTOS; PIRES-VANIN, 2000; 2004). On the Santos shelf, the species was dominant in the Coastal Zone, especially in the winter, when the area is characterized by the constant disturbance of superficial bottom sediments on different time scales. On the Southern Brazilian shelf resuspension of sediments is more frequent in winter and has been associated with the constant passage of cold fronts (PAIVA, 1993; MAHIQUES et al., 1998). Bottom resuspension affects micro-environmental structure as well as the organic content levels of sediments and directly influences macrofaunal communities by removing young and adults. Consequently, a decrease in density and diversity has been observed in the shallow shelf area, i.e., the Coastal Zone (VALÉRIO-BERARDO et al., 2000a,b; CAPÍTOLI; BEMVENUTI, 2004; VAN HOEY et al., 2004).

Although information on recolonization and the successional process in soft-bottom communities is vast, it is not possible to fit a general predictable model to most of the habitats (LU; WU, 2000; MCALLEN et al., 2009; PACHECO et al., 2010).

Nevertheless, the strategy of tube construction seems to be highly favorable for *Ampelisca paria*, which protects itself against winter disturbances. *Ampelisca* lies on fine sand substratum and constructs a larger tube extending deeper into the sediment (SANTOS; SIMON, 1980) burrowing rapidly with the dorsal surface uppermost (MILLS, 1967). On the other hand, neither other infaunal or tube-dwelling species can do so and they may thus be easily removed from the area. After any disturbance *A. paria* is able to recolonize the unstable areas quickly and successfully and, consequently, become the dominant species. In early spring and during the summer the bottom surface remains more stable due to the absence of cold fronts and this stability lasts longer, since the intruding SACW is a slow moving current, with velocities of less than 0.20 m/s (CASTRO et al., 1998). This new water flux over the bottom seems to be unable to remove and resuspend the sand grains of the sediments (PAIVA, 1993).

Hence, under the SACW's influence, species with diverse life styles can inhabit the area and may compete with *Ampelisca paria* and reduce its abundance. The increase in diversity and the consequent decrease in the relative importance of *A. paria* verified in summer corroborate this hypothesis.

A general relationship between primary production, water depth and abundance of benthos has been recognized for the southern Brazilian shelf (SANTOS; PIRES-VANIN, 2004; DE LÉO; PIRES-VANIN, 2006). The pulsed seasonal input of new production promoted by the SACW may be responsible for the enhancement of biomass and density found in the Mixed Zone, especially in summer, when compared to the coastal areas. With regard the Deep Zone, with the constant input of SACW nutrients, temporal stability is greater and the species present high density and biomass. The same result has been obtained for mollusks (SOARES-GOMES; PIRES-VANIN, 2005) and for polychaetes (PAIVA, 1993) in northern areas of the southwestern Atlantic shelf. The higher biomass of amphipods found in the Deep Zone may be due to the temperature-dependent life histories of the species, because their growth and molting rates appear to be decoupled, resulting in small adults at warm temperatures (e.g. in the Coastal Zone) and large adults at lower temperatures (e.g. in the Deep Zone) (AYDIN et al., 2007). Highsmith and Coyle (1991) reported that the pattern of early maturation, small adult size, and short lifespan at warmer temperatures and the pattern of late maturation, large adult size, and long lifespan at cold temperatures may be a widespread phenomenon among marine invertebrates.

While the shallower coastal area is subject to different kinds of disturbance, the muddy outer shelf region is a relatively less disturbed and predictable

environment. In consequence, this stability helps to maintain a community of low diversity but high evenness, i.e., that of the Deep Zone. The major part of the fauna is of burrower species but other trophic groups are present in low numbers, which agrees with the pelitic characteristic of these sediments. *Pseudoharpinia dentata*, the characteristic species of the group, is reported to live in muddy bottoms under low temperatures (WAKABARA et al., 1991; VALÉRIO-BERARDO et al., 2000a; ALONSO DE PINA, 2008).

The interaction between the South Atlantic Central Water (SACW) and the Coastal Water (CW) is also important in changing the species composition of the amphipod communities in the area. The coastal and the mixed zone groups were highly similar in the winter but quite different in the summer. Besides the seasonal variation in species composition, the Mixed Zone presented species with contrasting mobility and feeding habits, as burrowers, infaunal and epifaunal tube-dwellers, free-surface dwellers and nestlers, indicating the existence of a complex food web and inter-specific relationships (PIRES-VANIN et al., 2011).

According to Levin et al. (2001), a hydrologically unstable area such as the present mixed area, could be called a Critical Transition Zone (CTZ), since it provides essential ecological functions, including decomposition, nutrient cycling and nutrient production, as well as regulation of fluxes of nutrients, water and particles. A wide variety of animals move into, out of, or across marine transitional zones (KNEIB, 2000) and they have different life history patterns and use these habitats in different ways. Besides this, diversity is indeed important to ecosystem functioning in marine CTZs because high diversity maintains positive interactions among species, promoting stability and resistance to invasion or other forms of disturbance (LEVIN et al., 2001).

Previous studies carried out on the Ubatuba shelf, north of the study area, have also reported the presence of mixed communities at around 40 - 50 m depth, and suggested that the broad variation in bottom temperature together with the increase in depth were the main factors influencing density and diversity of peracarid communities (PIRES-VANIN, 1993), polychaetes (PAIVA, 1993), mollusks (SOARES-GOMES; PIRES-VANIN, 2003) and megafauna invertebrates (PIRES-VANIN, 1992; PIRES-VANIN, 2008). Transitional or mixed communities are well known in estuarine systems around the world (PILAR et al., 2002; CRUZ et al., 2003; LOURIDO, et al., 2008) and reflect the chemical and physical changes in the water's characteristics. For the continental shelf, the effects of the interaction of water masses upon benthic invertebrate communities are less well known (SALAT et al., 2002; MUELBERT et al., 2008), but

studies have shown that these environments are populated by species from the adjacent well defined systems. The mixed communities observed for several groups of invertebrates at the interface between CW and SACW correspond to the general pattern of benthic community distribution in the transitional environments of the southeastern Brazilian shelf.

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