BIVALVE MOLLUSK ASSEMBLAGES ON SÃO PAULO’S NORTHERN CONTINENTAL SHELF, SOUTHEAST BRAZIL

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ABSTRACT

Soft bottom bivalve mollusc assemblages were sampled along a depth gradient (10 to 100 m) on the northern São Paulo shelf during the austral summer and winter. A one-way analysis of similarity permutation test revealed there was no seasonal difference in the structure of the bivalve assemblages in the area. A clustering analysis indicated 3 groups of stations corresponding to the bathymetric gradient. Both K-dominance curves and Shannon and Pielou indexes showed higher biological diversity and higher evenness for the shallower area. Most of the bivalves found were classified as suspension-feeders, co-occurring with deposit-feeder species, suggesting an absence of negative interactions between these trophic groups. Differences in the frequency of disturbance along the depth gradient caused by wave storms – more common in winter – and also by predation and anthropogenic activities, such as dredging of fishing boats and input of gross sewage, likely explain the higher diversity found on the inner shelf of Ubatuba.

Keywords: soft bottom, sublittoral, biodiversity, spatial distribution, macrobenthos.

RESUMO

Associações de moluscos bivalves na plataforma continental norte de São Paulo, sudeste do Brasil

Moluscos bivalves de fundos não-consolidados foram amostrados no verão e no inverno entre as profundidades de 10 a 100 m na plataforma norte de São Paulo. Baseado na análise de variância por similaridade não foi verificada diferença sazonal significativa nas associações de bivalves. A análise de agrupamento evidenciou três grupos de estações que correspondem ao gradiente batimétrico. Tanto as curvas de dominância-K, quanto os índices biológicos usados (Shannon e Pielou) mostraram uma maior diversidade biológica e uma maior uniformidade na distribuição dos indivíduos nas áreas rasas. A maioria dos bivalves coletados pode ser classificada como de hábito alimentar suspensívoro. Estes, porém, co-ocorreram com espécies depositívoras, o que sugere uma ausência de correlação negativa entre esses dois grupos tróficos. Diferenças na freqüência de ocorrência de distúrbios ao longo do gradiente batimétrico, causados por ondas de tempestade, mais comuns no inverno, e também causados por predação e atividades antrópicas, tais como dragagens realizadas por barcos de pesca e despejo de esgoto in natura, podem explicar os padrões de diversidade observados.

Palavras-chave: biodiversidade, sedimentos marinhos, distribuição espacial, plataforma continental.

INTRODUCTION

Invertebrate species are an important link in the food chain, from primary producers such as phytoplankton and microphytobenthos to predators such as fish and birds (Kamermans, 1992).

Mollusks are relevant components of the tropical soft sediments, in terms both of abundance and of species richness (Jones *et al.*, 1990), and are the second diversity group of marine invertebrates (Merlano & Hegedus, 1994). On tropical and subtropical shelves, mollusks, which are important living resources, may represent 38% of the invertebrate fauna (Longhurst & Pauly, 1987), and in some regions their biomass is equivalent to the total benthic biomass (Antipova, 1976).

Bivalve mollusks play an important role in some marine ecosystems, acting as keystone species by controlling the flux of material and energy (Dame, 1996; Gosling, 2003). They also respond to pollutants and are used as indicator and monitoring species in pollution studies (Akberali & Treuman, 1985). In some situations, bivalves have been shown to control eutrophication in shallow water habitats (Loo & Rosenberg, 1989). Furthermore, because these invertebrates display mostly sedentary behavior, they show a good correlation with abiotic components of the environment, such as sedimented organic matter and granulometry (Franz, 1976; Cornet, 1985). Not least, bivalves are fundamental components of the macrobenthos, thus helping increase our knowledge about the large-scale marine biodiversity pattern (Crame, 2000).

Many studies of the benthic fauna of the Ubatuba shelf on Brazil's southeastern coast have aimed to shed light on the functioning of this ecosystem (Paiva, 1993a, 1993b; Pires-Vanin, 1993; Pires-Vanin *et al.*, 1995; Santos & Pires-Vanin, 1999). However, none of these studies has been dedicated to a detailed investigation of the species' composition or the structure of assemblages. This area is strongly influenced by the dynamics of three water masses (Castro-Filho *et al.*, 1987) that control the main biological processes of energy input to the benthos. Therefore, bivalves serve a useful function as indicators of the benthic patterns of the faunal distribution on that shelf, for these organisms are frequently collected by commonplace benthic equipment such as dredges and grabs. This work describes the composition, relative abundance, diversity and spatial distribution of bivalve mollusk assemblages and their relation to abiotic variables of Brazil's southeast continental shelf.

MATERIAL AND METHODS

Study area

Ubatuba continental shelf is part of the southeastern Brazilian Bight and the sampling stations were located between São Sebastião Island and Ubatumirim Bay (23° 25' to 24° 22' S and 44° 33' to 45° 16' W). The area was divided into the inner shelf (from the coastline to a 50 m depth), and the outer shelf (from 50 m to 100 m depth), based on physical and biological features, according to Castro-Filho *et al.* (1987) and Pires (1992).

Three water masses, the Coastal water (CW) – high temperature (> 20 °C) and low salinity (< 36); Tropical Water (TW) – with both high temperature (> 20 °C) and salinity (> 36); and South Atlantic Central Water (SACW) – low temperature (< 18 °C) and salinity (< 36), can affect the shelf (Castro-Filho *et al.*, 1987). During spring and summer, the SACW intrudes into the shelf near the bottom layer and a strong thermocline develops in midwater in the coastal region, while the CW is compressed and lies in the superficial layer. This two-layer water structure is disrupted in winter, when the SACW retreats to the shelf break and occupies the entire column of the inner shelf. Frontal eddies occur aperiodically on the outer shelf throughout the year (Pires, 1992).

The presence of the SACW promotes an input of nutrients (N and P) in the euphotic zone, enhancing the primary production by 7 to 10-fold during summer (Aidar *et al.*, 1993). According to Pires (1992), this enhancement increases the availability of pelagic food to the benthos, promoting a seasonal variation in faunal biomass.

Sediments in the area are heterogeneous, although a general pattern of mean particle size distribution can be drawn. Very fine sand covers most of the inner shelf. Coarser-grained sand is deposited both near the shelf break and northwards, while silt dominates in two areas, from the coast to a depth of almost 70 m south of the region, and close to the 100 m isobath in the center of the area In the north, sand is well-sorted from the coast to a depth of 75 m (Pires, 1992).

Sampling design and analytical techniques

Sampling was carried out at 18 stations in three transects perpendicular to the coast, between 10 and 100 m depths, once during the summer of 1986 and in the winter of 1987, aboard the research vessels "Prof. W. Besnard" and "Veliger II", both the property of the University of São Paulo (Fig. 1).

Sediments were collected with a 0.1 m^2 van Veen grab, a rectangular dredge and a beam-trawl net so as to allow for a comprehensive taxonomic survey. Dredge and beam-trawl samples were standardized to 20 L of sediment. The macrozoobenthos was sieved out through 0.5 mm mesh size and sorted under a stereomicroscope.

Data from the three samplers were used to calculate the frequency of occurrence (F), and species were classified as constant ($F > 50\%$), common ($10\% \leq F \leq 50\%$), and rare ($F < 10\%$) (Guille, 1970).

Dredge and grab data were arranged separately in two matrices. The one-way analysis

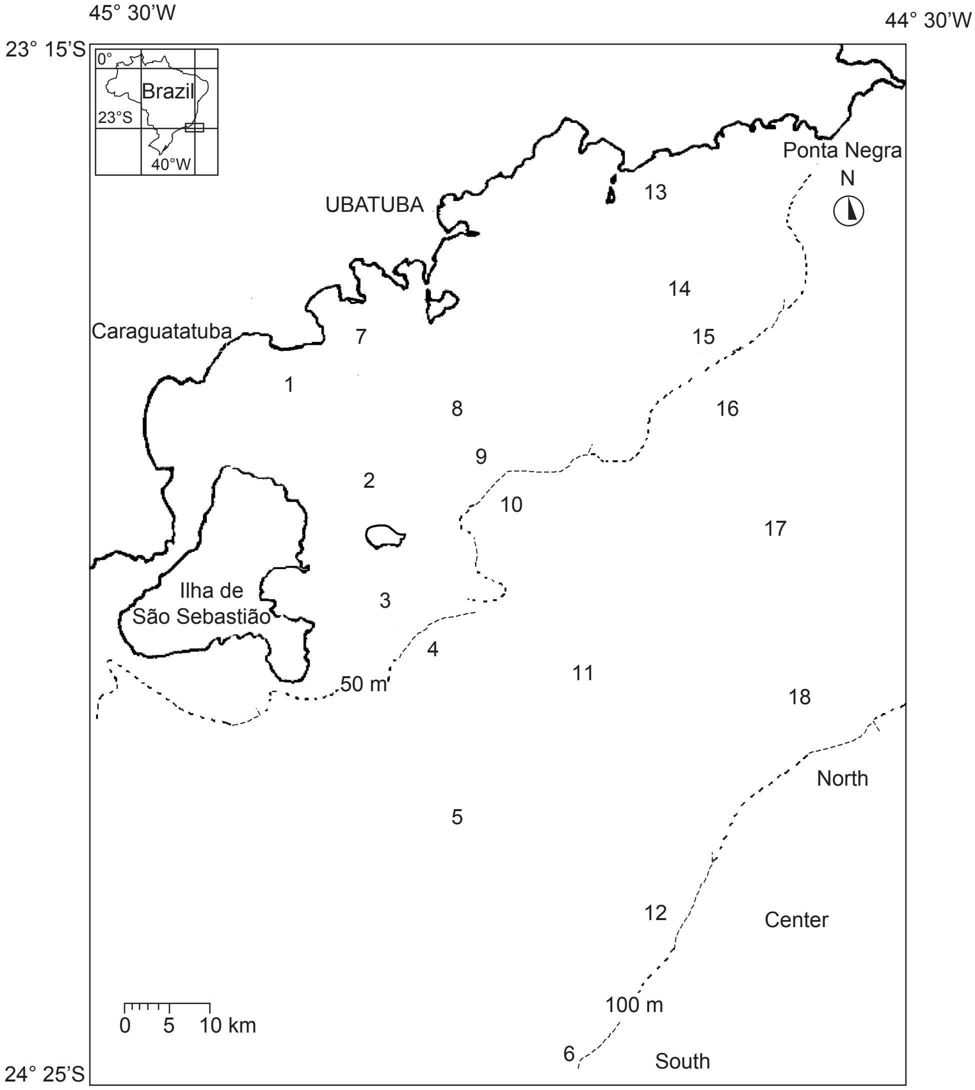

Fig. 1 – Map of the study area with location of sampling stations.

of similarity permutation test (ANOSIM) proposed by Clarke & Green (1988), employing the Bray-Curtis similarity index, was used to test the null hypothesis of seasonal difference in the structure of the bivalve assemblages.

When no variation between winter and summer seasons was detected, the mean values of dredge data were used to analyze the spatial pattern. This pattern was assessed by cluster exploratory analysis, using the Bray-Curtis similarity index for fourth root transform data. The Unweighted Pair Group Method Average (UPGMA) hierarquical clustering and the Non-Metric Multidimensional Scaling (NMDS) ordination analysis were employed. The species' contribution to the set of stations considered homogeneous by exploratory data analysis was determined by the SIMPER procedure, Primer software routine (Clarke & Warwick, 1994).

Stations having the same isobath were pooled to draw K-dominance curves (Lambshead *et al.,* 1983). Furthermore, Shannon diversity and Pielou's evenness were calculated for each group of stations and tested by Kruskal-Wallis non-parametric variance analysis (Clarke & Warwick, 1994).

Granulometric fractions of the sediments were determined by the standard dry-sieve and sedimentation method (Suguio, 1973), and mean grain size and sorting coefficient were calculated according to Folk & Ward (1957). Organic matter content was determined by the H_2O_2 oxidation method (Gross, 1971) and biodetritic carbonate ($CaCO_3$) was obtained by HCl 10% attack. The Euclidean Distance was calculated for the set of abiotic variables and applied to test the hypothesis of no difference between the inner (from 10 to 40 m depth), intermediary (50 m), and outer sectors (from 70 to 100 m) of the shelf, employing the ANOSIM procedure.

RESULTS

A total of 65 species belonging to 31 families were collected, of which 25 species were restricted to the inner shelf and 6 to the outer shelf. The following species showed a continuous distribution along the bathymetric gradient in the area: *Abra lioca, Corbula patagonica, Crassinella marplatensis, Entodesma alvarezi, Macoma tenta, Nucula puelcha, Periploma ovata, Americuna besnardi, Chlamys tehuelchus* and *Trachycardium muricatum.* According to the classification proposed by Guille (1970), only 3 species were constant throughout the bathymetric gradient (*Abra lioica, Carditamera micela* and *Nucula puelcha*), while 11 and 7 species were constant on the inner and outer shelves, respectively. The majority of species showed a common frequency of occurrence in the whole area, and only 10 species were classified as rare (Table 1).

The ANOSIM test employed for both grab and dredge data indicated that there was no summer/winter difference in the structure of bivalve assemblages (Table 2).

A clustering analysis indicated 3 groups of stations, corresponding approximately to the shelf sectors. Stations 10, 11 and 12, located at the 50 m isobath, appeared as an independent group, and stations 6 and 9 as outliers (Fig. 2). According to the SIMPER procedure, *Corbula caribaea, Adrana patagonica* and *Periploma compressa*, on the inner shelf, and *Carditamera micella, Cyclinella tenuis* and *Musculus lateralis*, on the outer shelf, were the 6 species that most contributed to the groups' formation (Table 3). The group assembling from 50 m depth was the most homogeneous (intragroup similarity of 58%), while the highest intergroup dissimilarity (85%) was found between the inner and outer shelves (Table 4).

Both the K-dominance curves and biological indexes applied (Shannon & Pielou) revealed a higher biological diversity and greater evenness for the inner shelf sector (Figs. 3 and 4).

The set of abiotic variables showed a marked difference between the inner and outer shelves. The intermediary sector was more related to the inner shelf environment. The shelf of the inner sector presented higher values of organic matter and silt content, lower mean grain size, and hence, lower sand and clay content (Fig. 5). The 3 sectors showed statistical differences in relation to abiotic variables (Table 5).

DISCUSSION

Phenomena of improving productivity could lead to structural changes in the benthic community as a result of the dynamics of organic matter input. Levinton (1972) speculated that temporal variations in the abundance of suspension-feeding bivalves are caused by seasonal variability

TABLE 1
Frequency of occurrence (%) and feeding mode of the 65 species sampled by grab and dredge on the bathymetric zones. DF = deposit-feeders; SF = suspension-feeders; CA = carnivorous; nd = not determined.

		Isobaths (metres)					
Species	**Feeding Mode**	**10**	**20**	**40**	**50**	**70**	**100**
Solemya patagonica	DF	0	8.3	16.7	0	16.7	0
Núcula puelcha	DF	66.7	33.3	33.3	100	66.7	50.0
Núcula semiornata	DF	8.3	0	16.7	0	0	0
Adrana electa	DF	25.0	0	0	0	0	0
Adrana patagonica	DF	58.3	75.0	58.3	100	0	0
Nuculana acuta	DF	0	0	0	0	50.0	50.0
Nuculana larranagai	DF	0	0	0	0	50.0	83.3
Nuculana platessa	DF	0	0	0	0	0	33.3
Anadara brasiliana	SF	58.3	33.3	16.7	16.7	0	0
Anadara notabilis	SF	25.0	0	0	0	0	0
Anadara ovalis	SF	50.0	0	8.3	0	0	0
Limopsis antillensis	SF	0	0	0	16.7	16.7	83.3
Cosa brasiliensis	ND	0	0	25.0	16.7	50.0	33.3
Crenella divaricata	SF	0	25.0	8.3	0	50.0	0
Musculus lateralis	SF	0	8.3	0	50.0	50.0	16.7
Pteria hirundo	SF	0	0	0	16.7	33.3	16.7
Atrina seminuda	SF	8.3	0	0	0	0	0
Limaria thryptica	SF	8.3	0	8.3	0	0	0
Limatula hendersoni	SF	0	0	25.0	0	0	50.0
Ostrea puelchana	SF	0	0	0	33.3	0	0
Plicatula gibbosa	ND	0	0	8.3	0	16.7	0
Chlamys tehuelchus	SF	33.3	33.3	0	16.7	16.7	50.0
Ctena orbiculata	SF	50.0	41.7	25.0	16.7	33.3	0
Linga amiantus	SF	8.3	0	0	0	0	0
Thyasira croulinensis	SF	0	8.3	0	0	0	0
Felaniella candeana	SF	8.3	0	0	0	0	0
Timothynus rehderi	ND	0	0	0	0	0	16.7
Carditamera floridana	SF	0	0	8.3	0	16.7	0
Carditamera micella	SF	0	16.7	33.3	83.3	83.3	100
Pleuromeris sanmartini	SF	0	0	25.0	0	16.7	16.7
Americuna besnardi	SF	8.3	16.7	0	33.3	0	16.7
Crassatella riograndensis	SF	0	0	0	16.7	16.7	50.0
Crassinela marplatensis	SF	16.7	33.3	33.3	16.7	33.3	33.3
Crassinela martinicensis	SF	41.7	16.7	16.7	16.7	33.3	0
Trachycardium muricatum	SF	25.0	16.7	16.7	50.0	0	33.3
Mactra janeiroensis	SF	25.0	16.7	50.0	0	0	0
Mactrelona alata	SF	16.7	8.3	0	0	0	0
Raeta plicatela	SF	33.3	0	0	0	0	0
Macoma tenta	DF	41.7	25.0	33.3	33.3	50.0	16.7
Tellina martinicensis	SF	16.7	0	0	0	0	0
Tellina versicolor	SF	8.3	16.7	8.3	0	16.7	0
Abra lioca	DF	75.0	41.6	41.7	33.3	50.0	83.3

TABLE 1
Continued...

		Isobaths (M)					
Species	**Feeding Mode**	**10**	**20**	**40**	**50**	**70**	**100**
Ervilia concentrica	SF	8.3	0	0	0	0	0
Semele casali	SF	0	8.3	0	0	0	0
Semele proficua	SF	8.3	8.3	0	0	0	0
Amiantis purpuratus	SF	8.3	0	0	0	0	0
Chione cancelata	SF	8.3	0	25.0	0	0	0
Cyclinella tenuis	SF	0	0	0	33.3	50.0	83.3
Pitar rostratus	SF	58.3	41.7	58.3	66.7	0	50.0
Corbula caribaea	SF	91.7	41.7	83.3	83.3	0	0
Corbula cubaniana	SF	0	25.0	16.7	83.3	0	16.7
Corbula cymella	SF	0	16.7	8.3	0	0	0
Corbula dietziana	SF	8.3	16.7	8.3	16.7	16.7	0
Corbula lyoni	SF	0	0	8.3	16.7	16.7	0
Corbula patagonica	SF	25.0	50.0	33.3	50.0	100	66.7
Periploma compressa	SF	41.7	33.3	33.3	16.7	0	0
Periploma ovata	SF	58.3	75.0	83.3	33.3	33.3	33.3
Entodesma alvarezi	SF	25.0	25.0	16.7	33.3	50.0	16.7
Pandora braziliensis	SF	0	0	0	16.7	0	0
Pandora bushiana	SF	0	8.3	8.3	83.3	16.7	50.0
Poromya cymata	SF	0	0	25.0	50.0	0	16.7
Poromya granulata	SF	0	0	0	0	0	16.7
Cardiomya perrostrata	CA	0	8.3	8.3	66.7	0	16.7
Cuspidaria platensis	CA	0	0	0	16.7	0	16.7
Verticordia ornata	ND	0	8.3	0	0	16.7	33.3

TABLE 2
Result of one-way analysis of similarity (ANOSIM) for grab and dredge data.

	Grab	**Dredge**
Global R	- 0.05	0.063
Significant level of sample statistic (%)	75.3	10.6
Number of permutations	999	999
Number of permuted statistics greater than or equal to Global R	752	105

in the phytoplanktonic food source, and that these animals have evolved mechanisms to rapidly increase their numbers in response to periods of food abundance.

On the Ubatuba shelf, the enhancement of primary production induces changes in the density and species composition of the benthic mega-and macrofauna (Pires, 1992; Paiva, 1993a, 1993b; Santos & Pires-Vanin, 1999). However, during the period studied here, the structure of the bivalve assemblages did not change temporally in the region, and increments in phytoplankton biomass were probably insufficient to shift the patterns of species dominance or bivalve density. Extra organic matter in summer was also consumed by pelagic species in the water column itself, with

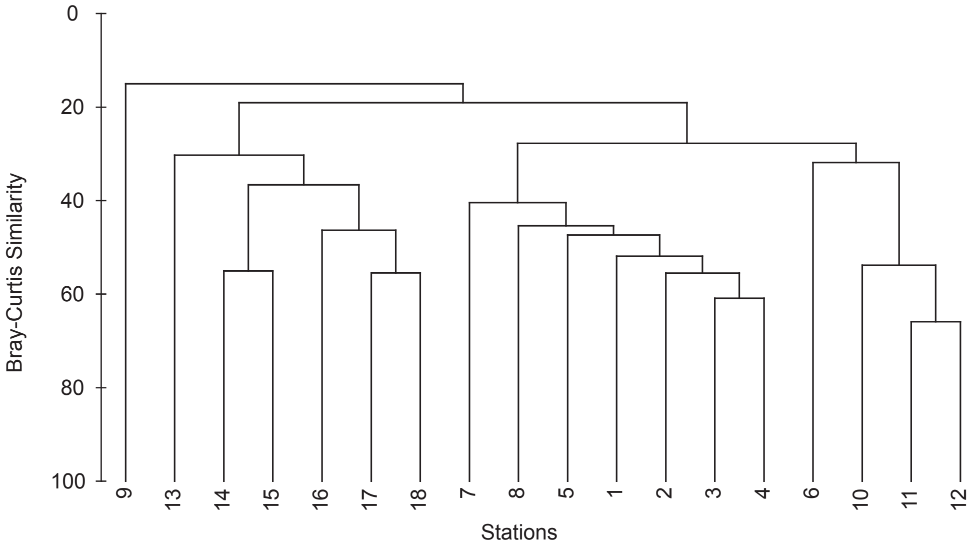

Fig. 2 — Mode-Q dendrogram based on dredge fourth root transformed data.

TABLE 3
Species contribution (%) for groups determined by SIMPER procedure.

Species	Inner Shelf	Intermediary	Outer Shelf
Abra lioca	9.63	-	-
Adrana patagonica	10.90	15.26	-
Anadara brasiliana	3.64	-	-
Cardiomya perrostrata	-	2.65	-
Carditamera micella	-	9.18	17.10
Chlamys tehuelchus	-	-	3.33
Corbula caribaea	13.73	9.66	-
Corbula cubaniana	-	18.56	-
Corbula patagonica	2.74	15.88	-
Cosa brasiliensis	-	-	6.42
Crassatella riograndensis	-	-	3.04
Crassinela marplatensis	2.32	-	-
Crassinela martinicensis	2.38	-	-
Ctena orbiculata	7.08	-	-
Cyclinella tenuis	-	-	12.22
Entodesma alvarezi	-	-	3.20
Limopsis antillensis	-	-	5.68
Mactra janeiroensis	2.82	-	-
Musculus lateralis	-	-	6.76
Nucula puelcha	3.64	-	5.13
Pandora bushiana	-	13.79	2.64
Periploma compressa	10.31	-	-
Periploma ovata	8.54	-	-
Pitar rostratus	9.98	-	-
Poromya cymata	-	2.94	-
Trachycardium muricatum	-	2.94	-

TABLE 4
Average intragroup similarity and intergroup dissimilarity (%) determined by SIMPER procedure.

		Inner Shelf	**Intermediary**	**Outer Shelf**
Intragroup Similarity		37.34	57.85	38.29
	Inner Shelf	0	73.57	84.69
Intergroup Similarity	**Intermediary**	73.57	0	72.98
	Outer Shelf	84.69	72.98	0

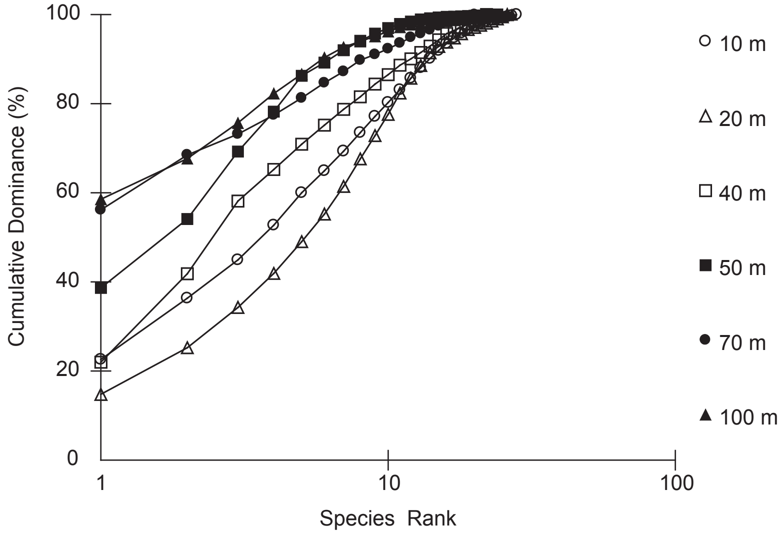

Fig. 3 — K-Dominance curves for the different isobaths of the studied area.

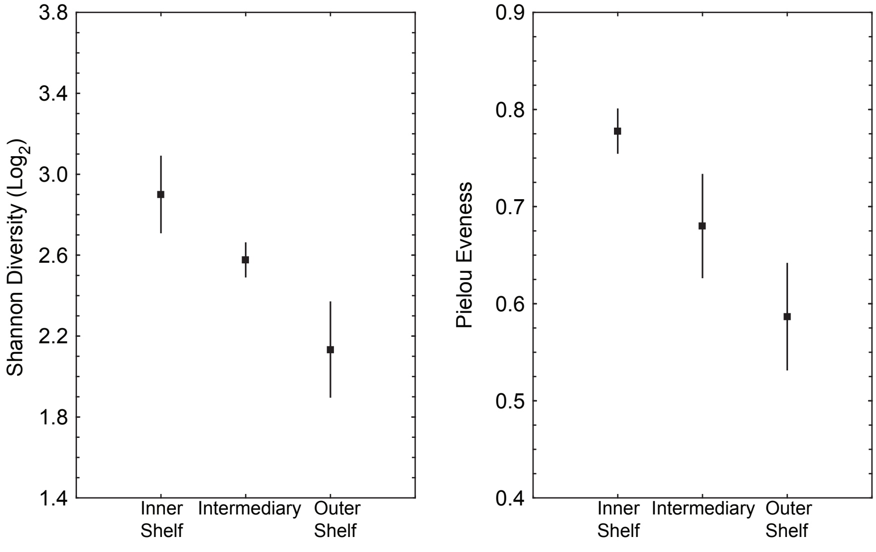

Fig. 4 — Mean Shannon's diversity and Pielou's eveness in the different sectors of the continental shelf of Ubatuba.

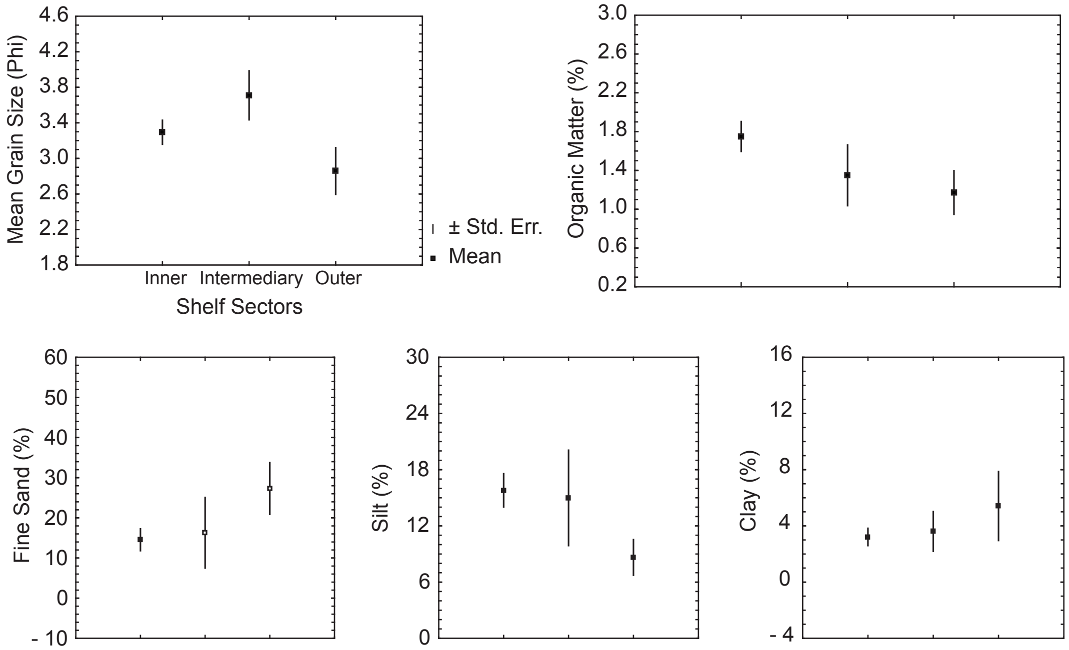

Fig. 5 — Means of the abiotic variables in the different sectors of the continental shelf of Ubatuba.

TABLE 5
Result of one-way analysis of similarity (ANOSIM) for abiotic variables.

Global Test		
Global R	0.005	
Significant level of sample statistic (%)	44.2	
Number of permutations	999	
Number of permuted statistics greater than or equal to Global R	441	
Pairwise Test (Shelf Sectors)	**R Statistic**	**Significance Level(%)**
Inner and Intermediary	0.037	38.3
Inner and Outer	- 0.016	54.9
Intermediary and Outer	0.048	31.2

low sedimentation to the seafloor. The population dynamics of the bivalve species occurring in the area cannot be related with food availability. A similar lack of correlation between bivalve dynamics and increases in pelagic food was found by Soares-Gomes & Fernandes (2005) in the Cabo Frio region, northern Ubatuba shelf.

Temporal food availability is not the only factor that promotes changes in the biotic structure. Assemblages of more mobile species can show a faster shift in their composition in response to changes in environmental temperature. On the Ubatuba shelf, this behavior was described for the crab *Portunus spinicarpus* and the snail *Zidona dufresnei* by Pires-Vanin *et al*. (1995). In the Cabo Frio region (north of Ubatuba), Netto & Gaelzer (1991) reported the same behavior for benthic and demersal fish such as the red porgy, *Pagrus pagrus*, the cusk-eel, *Genypterus brasiliensis*, the silver hake, *Merluccius hubbsi*, and the anglerfish, *Lophius gastrophysus*. Benthic sedentary and sessile species such as bivalve mollusks, however, may not exhibit this behavior, and may be not structured temporally if they are unaffected by any other environmental variable or by intrinsic factors.

In relation to the spatial distribution, the bivalve assemblage is clearly structured along the depth gradient. Both the exploratory data analysis (cluster and NMDS ordination) and the hypothesis testing (ANOSIM) results showed a consistent change in the assemblage structure on the inner and outer shelves. The 50 m isobath seems to be a transition zone between the two areas. This spatial pattern was also found for bivalve mollusks and other macrobenthic components of Cabo Frio's inner shelf (Soares Gomes & Fernandes, 2005; Ventura & Fernandes, 1995; Netto & Gaelzer, 1991). Such a spatial pattern in a narrow depth gradient shows a good relation with sediment types, and has been related to feeding types.

According to Levinton (1972), sediments with high coarse particle content are typical of high-energy habitats. Due to the action of currents and waves, those habitats offer a greater availability of suspension-feeding particles than habitats of fine sediments. Moreover, coarse sediments are less often subject to resuspension by the activities of burrowing fauna. Fine sediment habitats may be unsuitable for filter-feeding species, since resuspended sediment may cause clogging of filtering structures. On the other hand, because these habitats are rich in organic content, they favor the occurrence of deposit-feeding species (Rhoads & Young, 1970). This dichotomy in the distribution of feeding types according to the type of sediment is known as animal-sediment relationship and was described by Sanders as early as 1958. Franz (1976) found that the deposit-feeder *Nucula proxima* is most abundant in the finest sediments and declines in importance as sediments become coarser and the silt-clay component decreases. The suspension-feeder *Tellina agilis*, on the other hand, becomes dominant as the sediment texture shifts from silty sand to medium-grained sand.

The majority of bivalve species found in the present study were classified as suspension-feeders (44 species), while only 11 species were classified as deposit-feeders. Furthermore, these trophic groups co-occur in all samples and even showed a significant positive correlation (Spearman correlation = 0.56), suggesting an absence of negative interactions between these trophic groups. But, for polychaetes from the same area, trophic separation between isobaths was revealed (Paiva, 1993a). The deposit-feeders polychaetes were more abundant in the inner shelf due to the hydrodynamic pattern in the Ubatuba's shelf. Some bivalves species, however, shift their feeding behavior depending upon the water flux and transport of particles in the bottom layer (Levinton, 1991). Among the bivalves, tellinideans, traditionally classified as deposit-feeders, could show a suspension-feeding behavior in response to availability of suspended organic matter relative to that of sedimentary organic matter (Reid & Reid, 1969). The co-occurrence of suspension and deposit-feeders bivalve mollusks is generally common in marine soft-bottoms (Snelgrove & Butman, 1994).

The diversity pattern showed that the inner shelf sector have higher biological diversity. Shallower areas of Ubatuba (< 10 m) studied by Santos & Pires-Vanin (1998) are as rich as the inner shelf in these work. However, the shallow area of Ubatuba's bay has a different assemblage of bivalve; only 15 species (c.a. 20%) found by Santos (1998) occurred in the inner shelf. Type of sediments, and organic content of sediments are possible causes of this spatial pattern.

Some degree of disturbance enhances diversity of soft-bottom because it prevail competitive exclusion between species. Higher diversity is expected to be found at sites where intermediary frequency of disturbance occur (Hall, 1994). Differences in the frequency of disturbance along the depth gradient, caused by changes in the hydrodynamic regime could explain the higher diversity found in the inner shelf of Ubatuba. The inner shelf of Ubatuba is more frequently disturbed than the outer shelf (Pires, 1992; Pires-Vanin, 1993). Those disturbances are caused by wave storms, more common during winter season, and also by predation and anthropogenic activities, such as dredging of fishing boats and input of gross sewage (Paiva, 1993a).

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