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Trophic structure of polychaetes in the São Sebastião Channel (southeastern Brazil)

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Abstract Between November 1993 and August 1994, the spatial and seasonal trophic structures of polychaete annelids were studied in the São Sebastião Channel, southeastern Brazil, located between the mainland of São Paulo State and São Sebastião Island. Four sampling surveys were carried out with a van Veen grab of 0.1 m^2 at 15 stations. A total of 12 003 individuals (126 species) was recorded and separated into 14 feeding guilds. Data were analysed with univariate and multivariate techniques (cluster and canonical correspondence analysis). Results showed a strong correlation between trophic groups and sediment variables such as grain size and organic carbon content. The Channel was dominated by surface deposit-feeders, followed by carnivores. Suspension-feeders were confined to medium and coarse sandy sites, environments with high energy. Bottoms where silt, clay and organic carbon predominated showed low polychaete densities. In these places the pollution induced by the sewage discharge from Araçá underwater emissions and by the oil terminal Dutos e Terminais Centro Sul was evident. There were no significant seasonal variations in the trophic structure over the study period, except in fall when densities were low. The polychaetes' relationships within the benthic system are discussed.

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Introduction

The analysis of benthic community structure is an important tool to describe changes in space (with applications on point source pollution monitoring) and in time (including the descriptions of changes in system health) (Heip 1992). In temperate and high-latitude regions the benthic systems have been thoroughly studied (Hughes et al. 1972; Maurer and Leathem 1980). However, in tropical areas, comprising nearly one-third of the continental shelf, they are not well understood, despite their quantitative significance. According to Wiebe (1987), tropical marine systems have been inadequately studied and in most cases have been sampled at only a few sites by short-term expeditions.

The analysis of the trophic structure of benthic communities is a widely used method to determine energy flow in marine sediments. Many authors have demonstrated that the distribution patterns of trophic groups are sensitive to multiple factors, including environmental disturbance, food supply, sediment types, hydrodynamic conditions and anthropogenic effects (Probert 1984; Gaston 1987; Gaston and Nasci 1988).

Polychaetes are frequently the main component of the benthic macrofauna, both in number of individuals and number of species (Boesch 1972). In addition, they play a key role in the macrobenthic secondary production on continental shelves (Paiva 1993).

Classifying benthic animals into feeding categories dates back to the work of Hunt (1925), and this approach has been used extensively in soft-bottom environments (Maurer and Leathem 1981; Dauer 1984; Bianchi and Morri 1985). Along the southern Brazilian coast, only Lana (1981) and Paiva (1993) have attempted to characterize the polychaete fauna of the Ubatuba region according to trophic groups. Fauchald and Jumars (1979) applied the concept of "feeding guilds" as a more comprehensive classification of trophic groups, since it includes both the motility and feeding strategies of the animals. This functional approach permits grouping of species as "ecological units" according to the similarity of their role in the food web and may replace the use of species populations in ecological studies. Fauchald and Jumars' classification has been revised for several polychaete families (Dauer et al. 1981; Gaston 1987) and, more recently, for several species on the Brazilian coast (Pardo 1995).

The aim of the present paper is to understand the spatial and seasonal patterns of the polychaete associations in the São Sebastião Channel, using the feeding guild approach combined with multivariate analysis. This area is peculiar for the northern São Paulo coast since it is affected by multiple human impacts. This study is part of a broader interdisciplinary research program carried out to understand the structure and function of the São Sebastião tropical inner shelf ecosystem.

Materials and methods

Sampling area

The São Sebastião Channel is located on the northern coast of São Paulo State (23°41′–23°53.5′S; 45°19′–45°30′W), Brazil (Fig. 1). It is situated parallel to the coast, separating the continent from São Sebastião Island and forming a barrier to the open sea. The Channel itself is about 25 km long with two relatively large openings (6 to 7 km wide) and a narrow central part of nearly 2 km in width. Its topography presents fan-like features in the south, and a well-sorted sand barrier in the north (Furtado 1995). Also, its northern region has a counter-clockwise vortex, which transports fine grains to the south, causing deposition of fine sediment at the continental margin, an area with low hydrodynamic energy conditions. In the central, deepest parts of the Channel no deposition of sediments occurs, probably due to the increase in current speed caused by the narrowing of the Channel (Furtado 1995).

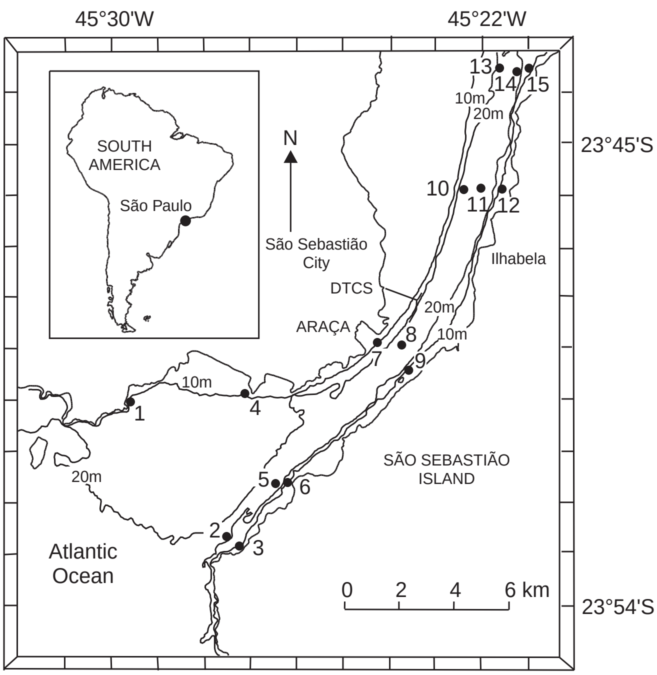

Fig. 1 Map of the study area with the 15 sampling stations. The 10- and 20-m isobaths are indicated

Although marine currents in the Channel are variable in space and time, they mainly move towards the NE (Castro Filho 1990), except in summer (Fontes 1995), when there is a two-layer water flow, the superficial one directed to the SW and the deep one towards the NE. The bottom current is not influenced by the wind but may be associated with the penetration of South Atlantic central water (SACW), which is characterized by low temperature (<18 °C) and high salinity (>36 psu). For the rest of the year the prevailing water mass has coastal water (CW) characteristics, with temperatures higher than 20 °C and salinities lower than 34.5 psu (Castro Filho et al. 1987).

The São Sebastião Channel is also affected by multiple human activities. It harbors one of the largest oil terminals in Brazil (Dutos e Terminais Centro Sul, DTCS), a commercial port and is also an important center of tourism. Given the frequent oil spills, dredging activities and sewage discharge from both the Araçá pipe and the neighboring cities, São Sebastião Channel is subjected to great environmental stress.

Data collection

Between November 1993 and August 1994 four surveys were carried out at 15 oceanographic stations distributed systematically in three radials parallel to the axis of the Channel (Fig. 1). The surveys were conducted with the R.V. "Veliger II" from the Oceanographic Institute of the University of São Paulo. Sampling was carried out with a 0.1 m^2 van Veen grab at 15 stations on four seasonal cruises. Depth varied between 10 and 45 m (see Table 1).

The sediment was washed in situ through 2.0, 1.0 and 0.5 mm mesh sieves, and the material retained was preserved in 70% ethanol. In the laboratory, the sediment was washed again applying the elutriation technique (Santos et al. 1996) before sorting and identification under a stereoscopic microscope.

Hydrographic data were obtained at 1 m intervals in the water column using Nansen bottles with digital thermometers. Salinity was measured by means of an inductive salinometer. Dissolved oxygen concentration was determined by the Winkler titration method (Strickland and Parsons 1968), and the saturation levels were calculated.

Nearly 100 g of the grab sediment was submitted to the standard dry-sieve and pipette method described in Suguio (1973). Parameters described by Folk and Ward (1957) were obtained for sedimentological data. Five size classes were distinguished in this study: clay, silt, fine sand, medium sand and coarse sand. The organic carbon content was calculated as described by Gaudette et al. (1974), and the nitrogen was estimated according to Kabat and Mayer (1948). The biodetritic carbonate content was obtained by HCl 10% attack.

The classification of species into trophic groups and feeding guilds was based on Fauchald and Jumars (1979), Gambi and Giangrande (1985), Gaston (1987), Paiva (1993) and Pardo (1995). However, the classification of the macrofauna, especially of polychaetes, still remains questionable (Fauchald and Jumars 1979; Gaston 1987). Although one of the best ways to classify an organism and/or verify its trophic classification is by examining its gut content, with the usually minute tropical polychaetes this is almost impossible. As investigations on polychaete trophic structure in Brazil are scarce and the few studies published employed Fauchald and Jumar's classification, we decided to also adopt this system in the interest of making results comparable.

Species classified into two trophic groups were included in both. We considered five trophic groups: carnivores (C), surface deposit-feeders (S), subsurface deposit-feeders (B), suspension-feeders (F) and omnivores (H); three categories of motility: motile (M), discretely motile (D) and sessile (S); and three types of morphological structures used in feeding: jawed (J), tentaculate (T) and other structures (X, usually eversible sac-like pharynges).

Table 1 Environmental variables studied at the 15 stations in the four surveys carried out in São Sebastião Channel (*Oxyg* percentage of saturation; *CS* coarse sand; *MS* medium sand; *FS* fine sand; *S* silt; *C* clay; *Org. C* organic carbon; *Org. N* organic nitrogen; *Diam.* mean diameter; *SF* fine silt; *SC* coarse silt; *SM* medium silt; *VFS* very fine sand)

Stations	Lat. (S)	Long. (W)	Depth (m)	Sal. (psu)	Temp. (°C)	Oxyg (% sat.)	CS (%)	MS (%)	FS (%)	S (%)	C (%)	Org. C (%)	Org. N (%)	Diam.	Type
Spring															
1	23°50.4′	45°29.7′	15	33.59	20.71	74.9	2.62	11.7	85.48	0.23	0	0.072	0.001	2.98	FS
2	23°52.7′	45°27.5′	26	34.18	20.42	72.2	0	0.25	12.42	59.07	28.25	0.919	0.12	6.35	SF
3	23°53′	45°27.1′	10	32.53	21.64	92.4	56.13	21.24	14.63	0.52	0	0.716	0.05	0.72	CS
4	23°50′	45°27′	10	31.45	23.61	97.6	0.06	0	95.35	2.51	2.08	0.175	0.02	3.47	VFS
5	23°51.8′	45°23.4′	23	34.79	19.69	59.2	1.11	2.12	79.37	10.45	6.96	0.610	0.05	3.44	VFS
6	23°51.8′	45°26′	10	31.40	23.51	101.2	7.19	7.07	37.1	32.43	16.21	1.516	0.08	4.68	SC
7	23°49′	45°24′	10	31.60	23.10	93.4	0	0.37	32.23	49.85	17.45	1.690	0.10	5.64	SM
8	23°49.1′	45°23.7′	45	35.57	16.81	70.2	15.83	8.13	18.23	38.53	14.62	1.203	0.09	4.25	SC
9	23°49.6′	45°23.4′	10	32.01	22.70	98.1	23.54	41.81	33.07	0.16	0	0.205	0.02	1.53	MS
10	23°46.1′	45°22.3′	10	32.14	22.39	99.2	0	0.18	29.19	53.62	17	1.422	0.14	5.61	SM
11	23°46.1′	45°21.9′	28	33.86	20.21	74.7	54.43	25.39	6.33	0.19	0	0.071	0.02	0.35	CS
12	23°46.1′	45°21.4′	9	31.42	22.36	100.7	5.01	10.78	50.91	23.65	9.46	0.887	0.05	3.85	VFS
13	23°44.3′	45°20.9′	11	33.00	21.29	85.6	2.48	4.15	34.11	41.76	17.51	1.498	0.09	5.2	SM
14	23°43.8′	45°21.2′	26	34.19	19.69	75.7	52.74	26.36	12.72	4.94	3.25	0.297	0.03	1.06	MS
15	23°43.4′	45°20.7′	8	32.55	22.00	88.5	26.8	9.36	49.65	8	2.67	0.183	0.03	2.17	FS
Summer															
1	23°50.4′	45°29.7′	15	34.97	29.85	101.1	0.15	1.05	90.14	8.65	0	0.192	0.02	3.47	VFS
2	23°52.7′	45°27.5′	26	34.87	27.50	98.7	0.41	0.42	37.42	41.17	20.59	1.660	0.11	5.55	SM
3	23°53′	45°27.1′	10	34.95	26.83	–	22.09	48.41	24.45	3.94	0	0.207	0.03	1.56	MS
4	23°50′	45°27′	10	35.01	27.35	–	0.18	0.19	93.84	4.6	1.06	0.336	0.03	3.45	VFS
5	23°51.8′	45°23.4′	23	35.34	24.58	–	0.19	0.49	89.48	8.56	1.07	0.637	0.03	3.25	VFS
6	23°51.8′	45°26′	10	34.88	27.33	99.4	4.18	9.8	65.08	16.25	4.64	0.842	0.05	3.49	VFS
7	23°49′	45°24′	10	34.76	27.90	103.1	0.22	0.36	37.57	44.87	16.98	1.260	0.13	5.51	SM
8	23°49.1′	45°23.7′	45	35.31	22.86	80.7	10.05	6.54	14.65	49.22	18.62	1.381	0.25	5	SM
9	23°49.6′	45°23.4′	10	34.76	27.97	104.6	24.86	38.9	35.07	0	0	0.080	0.02	1.55	MS
10	23°46.1′	45°22.3′	10	35.07	28.27	108.9	0	0.09	29.5	55.48	14.94	1.512	0.19	5.42	SM
11	23°46.1′	45°21.9′	28	35.15	23.21	87.3	34.63	38.56	19.45	4.25	1.06	0.176	0.03	1.35	MS
12	23°46.1′	45°21.4′	9	34.84	26.89	106.7	38.43	12.38	15.97	11.02	18.73	0.479	0.04	3.18	VFS
13	23°44.3′	45°20.9′	11	34.98	26.95	101.4	31.43	8.87	48.48	6.19	1.25	0.175	0.02	1.97	MS
14	23°43.8′	45°21.2′	26	35.15	25.74	87.7	44.13	21.6	16.41	5.85	1.08	0.239	0.03	0.91	CS
15	23°43.4′	45°20.7′	8	35.35	26.29	94.5	0.33	0.63	38.03	46.28	14.72	1.530	0.12	5.31	SM
Fall															
1	23°50.4′	45°29.7′	15	34.79	24.49	69.3	0.04	0.14	94.01	5.8	0	0.127	0.02	3.47	VFS
2	23°52.7′	45°27.5′	26	35.78	24.11	77.9	0	0	25.75	50.02	23.92	1.911	0.10	5.92	SM
3	23°53′	45°27.1′	10	33.91	26.01	93.1	28.26	33.07	35.67	1.34	0	0.190	0.03	1.55	MS
4	23°50′	45°27′	10	33.73	25.06	107.3	0.08	0.15	98.16	1.6	0	0.190	0.03	3.41	VFS
5	23°51.8′	45°23.4′	23	35.29	24.16	72.9	0.14	0.48	71.16	19.2	9.04	0.698	0.08	4.2	SC
6	23°51.8′	45°26′	10	34.02	25.82	86.2	3.15	7.27	67.93	17.31	4.33	0.678	0.06	3.72	VFS
7	23°49′	45°24′	10	33.95	25.21	95.4	0.17	0.26	20.92	61.16	17.47	1.806	0.10	5.91	SM
8	23°49.1′	45°23.7′	45	35.5	23.16	83	27.36	13.14	18.58	25.71	11.57	1.052	0.07	3.24	VFS
9	23°49.6′	45°23.4′	10	34.16	25.26	90.3	23.88	42.77	31.43	0.005	0	0.126	0.03	1.51	MS
10	23°46.1′	45°22.3′	10	34.25	24.95	92.6	0.09	0.33	20.63	62.7	16.26	1.492	0.09	5.76	SM
11	23°46.1′	45°21.9′	28	34.92	24.30	82.5	53.23	24.11	8.46	2.34	0	0.157	0.02	0.5	CS
12	23°46.1′	45°21.4′	9	34.56	24.25	90	2.93	6.1	49.34	31.71	9.76	1.247	0.07	4.22	SC
13	23°44.3′	45°20.9′	11	34.35	25.02	87.9	14.36	8.07	54.43	17.1	3.95	0.315	0.03	3.1	VFS
14	23°43.8′	45°21.2′	26	34.76	24.31	99.8	47.95	16.81	12.65	8.26	1.18	0.299	0.03	0.83	CS
15	23°43.4′	45°20.7′	8	34.71	24.70	86.2	32.58	40.1	22.82	2.91	0	0.111	0.03	1.41	MS
Winter															
1	23°50.4′	45°29.7′	15	33.16	20.40	80	2.85	9.82	85.42	1.93	0	0.047	0.02	3.08	VFS
2	23°52.7′	45°27.5′	26	33.76	20.20	92	0.16	0.36	31.84	40.98	26.64	1.647	0.13	5.87	SM
3	23°53′	45°27.1′	10	33.24	20.40	95.1	0.96	7.39	80.14	11.51	0	0.431	0.05	3.04	VFS
4	23°50′	45°27′	10	33.19	20.40	83.8	0.21	0.28	91.72	4.4	3.3	0.365	0.05	3.48	VFS
5	23°51.8′	45°23.4′	23	33.16	20.40	93.8	0.35	1.22	86.23	8.86	3.32	0.509	0.06	3.13	VFS
6	23°51.8′	45°26′	10	33.25	20.60	92.7	2.43	5.36	69.51	20.63	2.06	0.699	0.06	3.84	VFS
7	23°49′	45°24′	10	33.60	20.70	95.9	0.08	0.21	17.8	58.8	23.1	1.700	0.12	6.15	SF
8	23°49.1′	45°23.7′	45	33.84	20.70	99.7	13.87	9.63	19.48	39.75	15.46	0.820	0.07	4.52	SC
9	23°49.6′	45°23.4′	10	33.39	20.70	98.3	21.71	40.78	36.42	0.27	0	0.171	0.02	1.61	MS
10	23°46.1′	45°22.3′	10	33.29	20.50	99.4	0.04	0.12	31	56.32	12.52	1.480	0.10	5.4	SM
11	23°46.1′	45°21.9′	28	34.22	20.70	90.8	43.65	29.94	10.5	2.51	0	0.110	0.02	0.62	CS
12	23°46.1′	45°21.4′	9	33.78	20.50	91.9	19.03	17.82	44.5	14.11	4.03	0.525	0.05	2.54	FS
13	23°44.3′	45°20.9′	11	33.74	20.60	100.2	12.16	8.16	68.82	7.46	1.24	0.510	0.04	2.72	FS
14	23°43.8′	45°21.2′	26	34.10	20.60	96.1	34.95	26.51	14.28	9.09	3.41	0.302	0.04	1.22	MS
15	23°43.4′	45°20.7′	8	34.05	20.60	100.5	31.15	32.75	19.94	9.28	5.3	0.413	0.04	1.86	MS

Data analysis

To evaluate the degree of ecological importance of each trophic group at the sampling stations the biomass was measured (g wet weight per 0.1 m^2, with 0.001 g accuracy). Both the percentage of each trophic group and the trophic importance index (Ti) proposed by Paiva (1993) were calculated. The latter has modified to avoid the loss of data from those stations with only one individual per trophic group. The use of Ti reduces the importance of density by applying the log-transformation of abundance, thus preserving the species richness factor (Paiva 1993) generally underestimated in analyses not subjected to log-transformation. Ti is expressed as:

$$\mathrm{Ti} = \sum_{i=1} \ln n_i + 0.1 \ ,$$

where s is the number of species of the trophic group in the sample; n_i is the number of individuals of the ith species in the sample and 0.1 is a constant when $n_i = 1$, then $\mathrm{Ti} > 0$.

The correlation between the trophic groups (biomass and Ti) and the environmental variables was estimated through Pearson's index (Snedecor and Cochran 1980), considering a significance level of 0.05.

With the percentages of the three most dominant trophic groups (C, F and S) a ternary diagram was constructed to illustrate the trophic composition of individual sites in the Channel. Each point on the diagram represents a collection site (station), and the ratio of the three feeding groups was used to plot each point on the ternary diagram.

Data on the abundance of feeding guilds of polychaetes were analysed employing multivariate statistical methods of classification and ordination. Following the log-transformation ($y = \log x+1$) of feeding guild abundance data, a dissimilarity matrix was constructed among stations (15 × 4) and among feeding guilds (14) using the Bray–Curtis quantitative coefficient. The matrix was submitted to a cluster analysis (Q-mode and R-mode) with the UPGMA (unweighted pair-group method using arithmetic means) method of linkage. The FITOPAC program (developed by G. Shepard, Universidade Estadual de Campinas, Brazil) was used to generate Q- and R-mode dendrograms. The ordination method chosen was canonical correspondence analysis (CCA) using the CANOCO program (ter Braak 1986, 1988). By this technique the species or biological data are arranged on an environmental basis, offering in a single diagram the direct interpretation of possible relationships between species, stations and environmental variables (Nielsen and Hopkins 1992). The environmental variables were selected through the forward option in the CANOCO program. The relationship between feeding guilds and environmental variables was tested by the Monte-Carlo permutation test (ter Braak 1990).

Results

Environmental data

Temperature and salinity data analysis showed that the São Sebastião Channel was dominated by coastal water (CW) over the study period, except in spring when South Atlantic central water (SACW) was present in the deepest part (45 m) (Table 1). The concentration of dissolved oxygen and the saturation levels in the bottom water varied, with the lowest values in spring and the highest values in winter. A heterogeneous sediment texture was present on the bottom. However, deposition of fine and very fine sands occurred at the southern mouth of the Channel and coarse sediments in the north. The continental margin was dominated by fine fractions. In the central zone the pelitic fractions (silt and clay) prevailed, and the highest values of organic carbon were found there.

Trophic structure

Univariate methods

A total of 12 003 individuals of 126 species belonging to 34 families were separated into 5 trophic groups and 14 feeding guilds. The trend shown by the distribution of Ti-values for each trophic group in the whole area were similar throughout the study period, except in fall when densities were low (Table 2). However, there were important differences among stations, probably related to the high sediment heterogeneity of the Channel (Table 1). The overall trend of Ti was different from that of biomass (Tables 2, 3). Very large body size and low abundance of suspension-feeder and subsurface deposit-feeder species may have influenced these findings.

Detritivores, represented by surface and subsurface deposit-feeders, were generally the dominant group, followed by carnivores. Suspension-feeders and omnivores contributed little to the total abundance of polychaetes in the Channel.

Surface deposit-feeders were very frequent and abundant in the whole area all the time, with the sole exception of fall, when all the groups showed a dramatic decrease in number and biomass. The main deposit-feeders were *Neanthes bruaca*, *Aricidea* (*Acmira*) *taylori*, *Cirrophorus americanus*, *Spiophanes missionensis*, *Owenia fusiformis* and Magelonidae species. Amongst these, *N. bruaca* and *O. fusiformis* were considered ditrophic. The Ti-values of the surface deposit-feeders were positively correlated with the coarser fractions of sediment, and negatively with the mean diameter, percentages of organic carbon, silt and clay, and bottom temperature. The same trend was observed for biomass values (Table 4).

Carnivores were always very abundant in the Channel area. They presented a very high abundance at the stations where sand fractions predominated (north coast of island). This trophic group was represented by *Ninoe brasiliensis*, *Lumbrineris tetraura*, *Exogone arenosa*, *Odontosyllis heterofalchaeta*, *Typosyllis hyalina*, *Typosyllis* sp., *Goniadides carolinae* and *Diopatra tridentata*. Considering both biomass and Ti, carnivores were positively correlated with medium and coarse sand fractions, and negatively with the percentage of silt, clay and organic carbon (Table 4).

The main subsurface deposit-feeding species were *Clymenella dalesi*, *Axiothella brasiliensis*, *Eunice rubra*, *Nematonereis schmardae* and *Scoloplos* (*Scoloplos*) *treadwelli*. Their overall abundance was low but always slightly higher in the northern region of the Channel. The Ti-values for this group were positively correlated with medium and coarse sand fractions, and negatively with percentage of organic carbon and mean sediment

Table 2 Ti (trophic importance index)-values for each trophic group at 15 stations for the four surveys carried out in São Sebastião Channel (*C* carnivores; *S* surface deposit-feeders; *B* subsurface deposit-feeders; *H* omnivore; *F* suspension-feeders)

Stations	C	S	B	H	F
Spring					
1	8.2	17.4	0	0.1	2.6
2	0.3	4.3	1.6	0	0
3	12.8	22.8	0	0	4.3
4	9.1	13.2	2	2.7	1.2
5	3	3.6	3.1	1.2	1.3
6	3.9	9.3	6.5	4.6	0
7	1.9	3.6	1.2	0.8	0
8	6	9.5	4.7	4.4	7.3
9	19.3	11.4	7.5	6.4	11.3
10	1.6	3.7	0.1	1.6	0.8
11	6.5	4.4	2.9	3.6	0
12	5.8	16.4	3.1	4.2	0.8
13	5.6	12.9	3	3.8	1.3
14	31.7	31.6	11.4	6.6	7.9
15	29.2	18.5	8.9	1.9	1.5
Summer					
1	9.7	18.3	0.9	0	0
2	12.4	7.7	2	3.1	1.2
3	20.2	12.3	2.3	6.9	5.2
4	12.1	16.8	2.3	1.6	0.9
5	4.8	14.1	6.9	2.3	0.1
6	10.8	15.9	8.3	1.5	3.9
7	3.5	2.9	4.6	0.8	1.5
8	6.4	18.1	3.1	3.1	2.9
9	13.7	4.2	5.6	5.7	4.1
10	4.4	7.2	4.2	1.3	0.8
11	34.3	27.6	11.1	6.9	6
12	21.1	17.7	3.1	6.8	0
13	18.4	4.1	9.2	3.5	7.2
14	26	10.3	8.7	4	2.9
15	3.2	3.2	4.8	1.3	0
Fall					
1	6.6	8.6	1.7	0.1	1.9
2	0.3	5.1	2.8	1.6	0.1
3	6.4	2.2	2.6	3.4	1.9
4	13.6	16.3	2.4	2.2	3.6
5	1.5	9.7	2.1	2.7	0
6	4.3	3.2	2.3	0.8	0.1
7	1.9	2.4	1	0.1	0
8	2.1	9.1	0.2	2.3	1.5
9	7.7	5.4	5	3.2	4.9
10	5.6	6.1	0.2	1.5	0
11	3.1	1.5	3.7	1.5	0
12	4.2	7.3	4.2	2.3	0.1
13	18.8	16.4	6.5	0	5
14	23.9	18.5	12.9	0	4.6
15	13.5	22.4	10.7	1.5	1.5
Winter					
1	9.2	10.4	0.1	0	1.5
2	3.6	6.5	0.8	1.3	3.5
3	22.8	18	2.5	3.4	7.5
4	12.5	17.3	0	2.2	0.8
5	4.3	19	11	1.9	2.9
6	24.5	25	9.6	3.9	5
7	3.4	4.1	1.3	2.3	0
8	30.4	32	12.7	3.2	10.1
9	23.9	21.7	7	14	7.7
10	4.9	5.6	3	0.8	0
11	13.5	15.8	8.8	6.7	4.9
12	4.5	10.7	6.5	1.8	0.2
13	28.3	31.4	11.4	4.4	6.6
14	31.5	23.4	10.6	7.8	7.3
15	21.5	21	16.3	7.6	3.5

Table 3 Biomass values (g 0.1 m^{-2}) for each trophic group at 15 stations for the four surveys carried out in São Sebastião Channel (*C* carnivores; *S* surface deposit-feeders; *B* subsurface deposit-feeders; *H* omnivores; *F* suspension-feeders)

Stations	C	S	B	H	F
Spring					
1	3.801	0.234	0.007	0.004	0.000
2	0.003	0.016	0.149	0.000	0.061
3	0.091	0.120	0.108	0.000	0.051
4	0.971	0.061	0.006	0.007	0.009
5	0.323	0.018	0.017	0.008	0.216
6	0.511	0.112	0.326	0.005	0.069
7	0.006	0.010	0.645	0.002	0.000
8	0.063	0.079	0.039	0.041	32.102
9	0.411	0.612	0.066	0.000	0.191
10	0.012	0.018	0.024	0.016	0.001
11	0.018	0.013	0.106	0.000	0.003
12	0.006	0.005	0.232	0.076	0.034
13	0.460	0.215	0.028	0.015	0.113
14	7.581	6.475	0.357	0.013	5.890
15	0.796	0.263	0.471	0.056	0.011
Summer					
1	0.292	0.057	0.001	0.000	0.000
2	0.105	0.443	0.662	0.028	0.104
3	0.443	1.253	0.062	0.022	0.311
4	0.050	0.179	0.024	0.006	0.785
5	0.025	0.132	0.184	0.028	0.091
6	0.182	0.751	0.511	0.004	0.196
7	0.006	0.121	1.462	0.003	0.015
8	0.167	0.307	0.052	0.010	0.099
9	0.030	0.126	0.026	0.000	0.121
10	0.004	0.140	2.124	0.005	0.039
11	1.348	0.105	0.485	0.046	9.377
12	0.232	0.462	0.017	0.027	0.000
13	1.382	4.695	0.330	0.000	5.000
14	0.657	0.124	0.130	0.000	0.106
15	0.010	0.021	0.131	0.009	0.000
Fall					
1	0.037	0.046	0.021	0.000	0.015
2	0.003	0.052	2.411	0.031	0.014
3	0.014	0.001	0.502	0.000	0.002
4	0.041	0.035	0.032	0.001	0.455
5	0.002	0.261	0.022	0.029	0.000
6	0.015	0.120	0.005	0.000	0.007
7	0.028	0.018	0.146	0.021	0.000
8	0.004	0.234	0.002	0.029	16.760
9	0.005	0.050	0.017	0.000	0.044
10	0.217	0.155	0.009	0.009	0.000
11	0.021	0.004	0.009	0.004	0.000
12	0.004	0.017	0.604	0.013	0.007
13	0.826	0.128	0.136	0.000	0.032
14	1.720	3.938	0.419	0.000	3.641
15	0.037	0.076	0.266	0.007	0.010
Winter					
1	0.613	0.488	0.002	0.000	0.040
2	0.009	0.112	0.360	0.055	0.044
3	0.282	0.317	0.194	0.000	0.0164
4	0.108	0.191	0.000	0.007	0.071
5	0.052	0.495	0.622	0.015	0.206
6	0.240	0.592	0.100	0.002	0.247
7	0.009	0.077	1.414	0.000	0.000
8	0.828	3.281	0.570	0.004	91.861
9	0.073	1.400	0.016	1.032	0.412
10	0.229	0.125	0.749	0.008	0.194
11	0.029	0.061	0.318	0.002	0.034
12	0.007	0.106	0.966	0.003	0.003
13	1.073	0.127	0.480	0.003	0.076
14	1.133	1.228	0.584	0.017	1.365
15	0.247	0.093	0.505	0.004	0.048

Table 4 Correlation levels between environmental variables and trophic importance index or biomass. Only values that were found significant at a 5% level are shown. For every trophic group data obtained in four surveys at 15 stations were pooled (*C* carnivores; *S* surface deposit-feeders; *B* subsurface deposit-feeders; *H* omnivores; *F* suspension-feeders)

Variables	Trophic importance index					Biomass				
	C	S	B	H	F	C	S	B	H	F
Depth	–	–	–	–	–	–	–	–	–	0.4627
Temperature	–	−0.2928	–	–	−0.2793	–	–	–	–	–
Salinity	–	–	–	–	–	–	–	–	–	–
Oxygen	0.3273	0.268	0.2705	0.3192	0.2862	–	–	–	–	–
$CaCO_3$	–	–	–	–	–	–	–	–	–	–
Gravel	0.4102	–	0.3842	0.2847	0.3226	–	–	–	–	–
Sand	0.4652	0.4167	0.3097	0.289	0.358	–	–	−0.4155	–	–
Coarse sand	0.5019	0.2686	0.4456	0.3556	0.3564	0.2903	0.3687	–	–	–
Medium sand	0.521	0.3112	0.4704	0.6027	0.5286	–	–	–	–	–
Fine sand	–	–	0.3541	0.3687	0.3384	–	–	–	–	–
Silt	−0.4291	−0.3266	–	−0.3302	−0.3656	–	–	0.4166	–	–
Clay	−0.3951	−0.295	–	–	−0.3583	–	–	0.3917	–	–
Mean diameter	−0.5611	−0.3787	−0.4625	−0.4205	−0.447	−0.2779	−0.277	0.3214	–	–
Selection coefficient	–	–	–	–	–	–	–	–	–	0.3508
Organic carbon	−0.4991	−0.3404	−0.2923	−0.2844	−0.3649	−0.2593	–	–	–	–

diameter (Table 4). Biomass presented an opposite trend compared to Ti. It was positively correlated with percentage of silt and clay and mean diameter of the sediment, and negatively correlated with the percentage of sand.

Suspension-feeding was not very common in the area. The most abundant species were *Owenia fusiformis* (at the same time a surface deposit-feeder) and *Chone insularis*. In the central portion of the Channel, *Spirographis brasiliensis* was very frequent. Due to its large body size (approximately 15 cm), the biomass of suspension-feeders showed a positive linear correlation with depth. On the other hand, their Ti correlated positively with medium and coarse sand, and negatively with bottom temperature, mean sediment diameter, silt and clay fractions and percentage of organic carbon (Table 4).

Omnivores were rare in the Channel area and always considered as ditrophic species. Their low Ti-values were associated with the low density and limited number of species, even though some species such as *Exogone arenosa*, *Neanthes bruaca*, *N. succinea* and *Nereis broa* were frequent.

No seasonal pattern in relative abundance and biomass of the trophic groups was found; in total density there was an important difference between fall and the rest of the year. Additionally, in those regions where sand fractions predominated the total density was always higher.

Fig. 2 shows the overall trophic tendency in the Channel. The surface deposit-feeders and carnivores grouped the majority of the sampling stations, independent of the season, with some contribution of suspension-feeders. The latter were always present at those sites where coarse sand was more abundant. Northern stations showed a high abundance of carnivores, and the south-continental and central portions of the Channel were dominated by surface deposit-feeders (Table 2; Fig. 2).

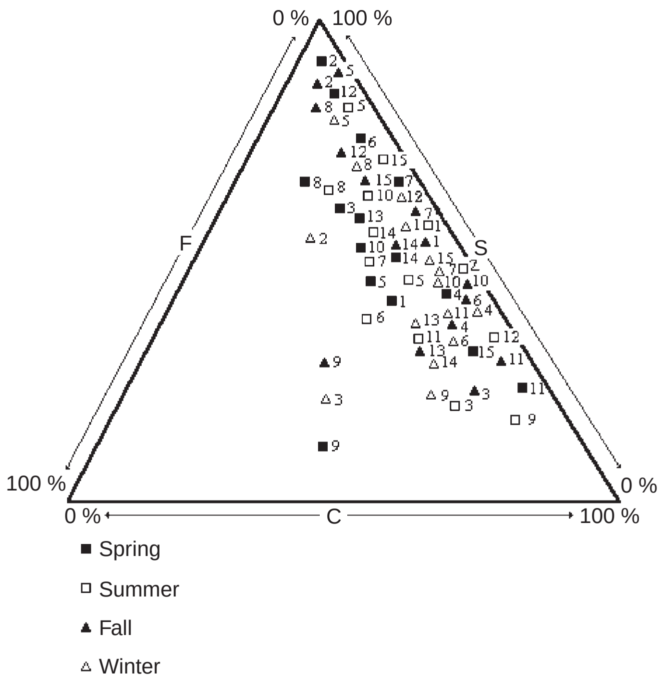

Fig. 2 Ternary diagram of sampling stations (data see Table 1). Stations are distributed by percentages of the three most abundant polychaete trophic groups (*C* carnivores; *S* surface deposit-feeders; *F* suspension-feeders)

Multivariate analysis

Classification analysis

The dendrogram of dissimilarities among sampling stations shows three main groups directly related to the bottom sediment type (Fig. 3A). The first contains sites where silt and clay fractions prevailed and the organic content of the sediment was high (sites of the central and continental regions of the Channel). Sites with a high

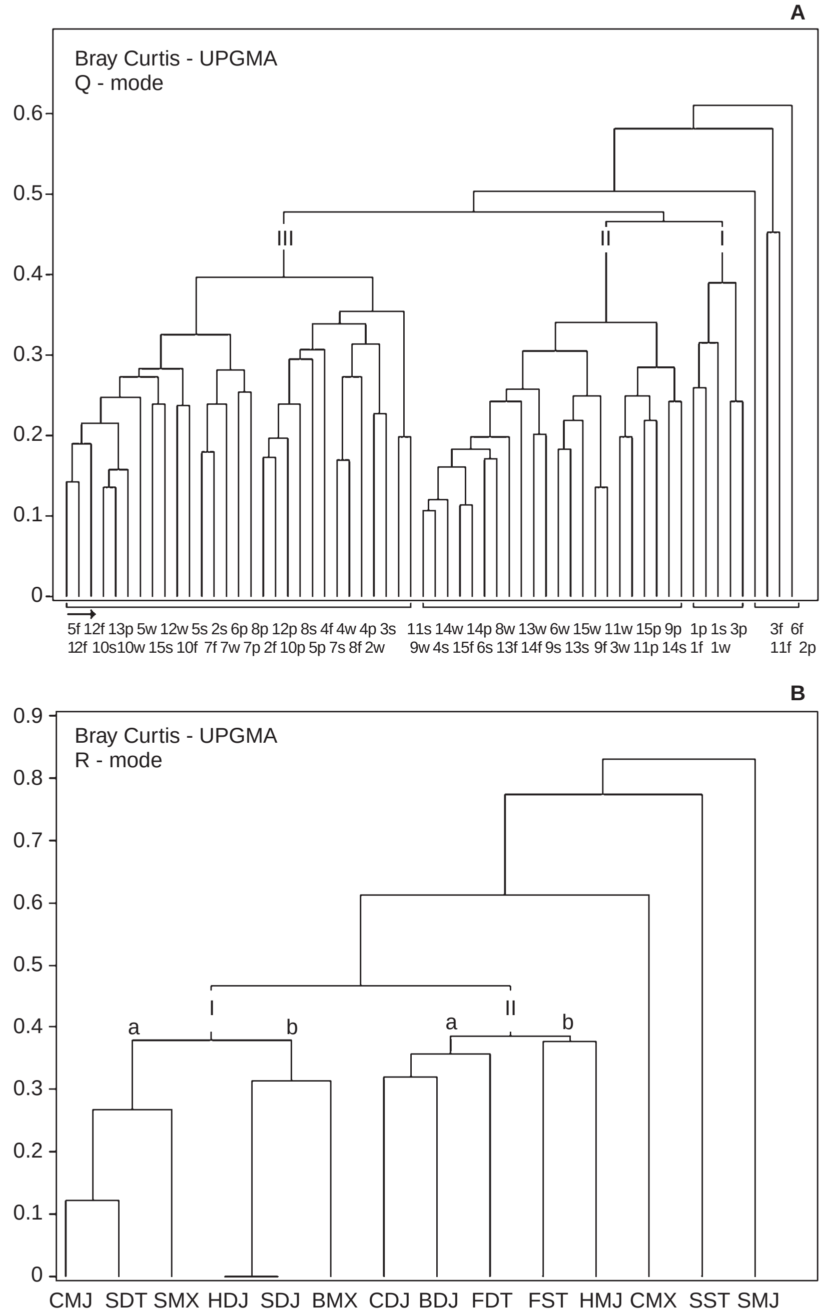

Fig. 3 Dendrograms showing the results of cluster analysis. **A** Grouping the sample stations (I, II, III) (Q-mode). **B** Grouping the feeding guilds (I and II) (R-mode) (*CMJ* carnivore, motile, jawed; *SDT* surface deposit-feeder, discretely motile, tentaculate; *SMX* surface deposit-feeder, motile, with eversible pharynge; *HDJ* omnivore, discretely motile, jawed; *SDJ* surface deposit-feeder, discretely motile, jawed; *BMX* subsurface deposit-feeder, motile with eversible pharynge; *CDJ* carnivore, discretely motile, jawed; *BDJ* subsurface deposit-feeder, discretely motile, jawed; *FDT* suspension-feeder, discretely motile, tentaculate; *FST* suspension-feeder, sessile, tentaculate; *HMJ* omnivore, motile, jawed; *CMX* carnivore, motile with eversible pharynge; *SST* surface deposit-feeder, sessile, tentaculate; *SMJ* surface deposit-feeder, motile, jawed; *p* spring survey; *s* summer survey; *f* fall survey; *w* winter; the numbers represent the sampling stations)

percentage of very fine sands (southern margin of the continent) formed the second group, and the third group is composed exclusively of samples from places where coarse and medium sand dominated, i.e. the northern Channel and island margin of the study area.

The dendrogram of dissimilarities among feeding guilds (Fig. 3B) shows two main groups (Group I and II at 0.5 level of dissimilarity), each of these can be further divided into two subgroups. In this way, Group Ia is formed by CMJ, SDT and SMX, and Group Ib by HDJ, SDJ and BMX (for group nomenclature see Fig. 3). CDJ, BDJ and FDT form Group IIa, and IIb is formed only by FST and HMJ. The feeding guilds CMX, SST and SMJ are external to the groups mentioned above.

Ordination analysis

Fig. 4 illustrates the resulting ordination diagram. Basically, the same groups of classification were formed. Again, the CMX, SST and SMJ feeding guilds were external to the two main groups formed in the CCA diagram. The correlation of feeding guilds to environmental data was approximately 0.81 for the first axis and 0.70 for the second one. The Monte-Carlo test showed a significant relation ($p \leq 0.001$) between feeding guilds and sediment type variables. Therefore, only the first two canonical axes were interpreted, representing 61% of the variation between feeding guilds and environmental data. In this model only the environmental

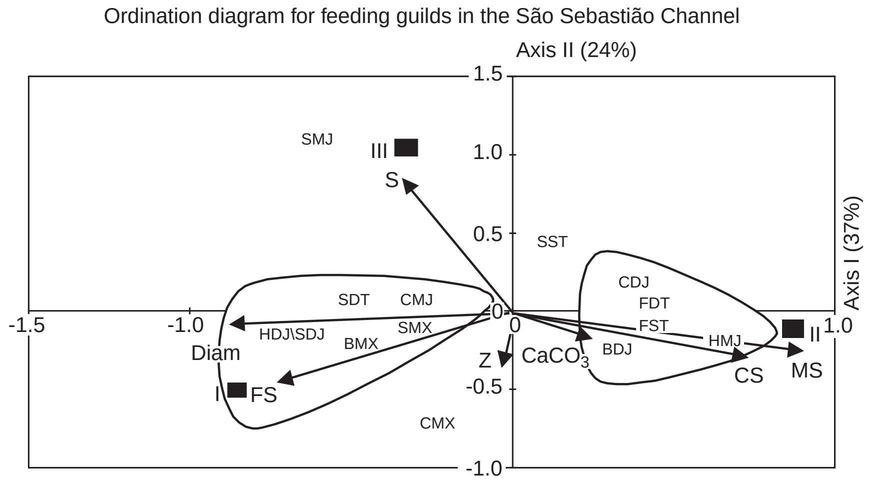

Fig. 4 Ordination diagram obtained from the canonical correspondence analysis (CCA), showing the main groups formed: (I) fine sediments, continental margin and southeastern Channel; (II) medium and coarse sand, island margin and northeastern Channel; (III) central-continental margin, including Stations 7 and 10. Arrows indicate the importance of each variable included in the analysis (*S* silt; *FS* fine sand; *MS* medium sand; *CS* coarse sand; *Diam* mean diameter; *D* depth; *CaCo₃* carbonates; abbreviations used for the feeding guilds are as in Fig. 3)

variables that showed a significant relation ($p \leq 0.001$) in the forward selection procedure were included, i.e. percentage of coarse sand (CS), percentage of medium sand (MS), percentage of fine sand (FS), mean sediment diameter (Diam.), calcium carbonate ($CaCO_3$), percentage of silt (S) and depth (Z).

Discussion and conclusions

The trophic groups and their evaluation

Ecologists are always trying to classify benthic organisms, especially infaunal species into discrete categories with the aim of thoroughly understanding their spatial and temporal patterns. Hunt (1925) was one of the pioneers in classifying benthic organisms into surface deposit-feeders, carnivores and suspension-feeders.

There are many ways of classifying carnivores according to behavioral aspects. There are active and passive predators, scavengers, etc. According to Matthews et al. (1984) carnivores are organisms that "obtain their food by killing the prey". This excludes parasitism, commensalism and the partial consumption of prey. However, in the case of *Diopatra* species, a very common animal in the study area, it is hard to distinguish whether prey was consumed that was already dead or that was alive with low motility (Paiva 1993). So, the organisms classified here as carnivores were those that ingested the body or part of the body of a "food item", and the "death" event was not taken into account for classification.

The omnivore group was included in this work due to the difficulty of inserting some nereids in any other trophic group. Fauchald and Jumars (1979) classified several nereid species (e.g. *Neanthes succinea*, *Eunereis longissima*, *Dendronereis* sp.) as both carnivores and herbivores. Later, Gaston (1987) characterized them as surface deposit-feeders, and Bianchi and Morri (1985) once again as herbivores. According to Mann et al. (1984), herbivory is related to organisms that feed on living autotrophic cells. As there are some doubts in the literature and since the feeding plasticity is high, we preferred to classify the nereids of the São Sebastião Channel as omnivores.

There are many species of polychaetes cited as ditrophic in the literature, that is, organisms that can feed in two different ways. The most typical examples are for spionid and owenid species that act both as surface deposit-feeders and suspension-feeders (Dauer et al. 1981; Maurer and Leathem 1981). Although the latter authors proposed a new group called "interface consumer", which includes the ditrophic forms; in the present study the spionid species were classified as surface deposit-feeders and the owenids as suspension and surface deposit-feeders, according to Paiva (1993). Using this classification we can compare our results with the scarce data published from the Brazilian coastal zone.

From a functional point of view, estimates of the secondary production for each trophic group allow assessment of its role in the energy flow of marine food webs. This measurement, nevertheless, cannot be done in communities as rich and diversified as those which exist in the São Sebastião Channel. Most of the work done on trophic structure of polychaete annelids considered the percentage or number of individuals in each trophic group (Maurer and Leathem 1981; Gambi and Giangrande 1985; Gaston and Nasci 1988; Tena et al. 1993) as a measure of its importance. Other investigations employed the number of species per trophic group, calling this measure "qualitative dominance" (Gambi et al. 1982; Bianchi and Morri 1985). Later, Paiva (1993) suggested the use of what he called the "trophic group importance index" (Ti). In this work we applied Paiva's Ti as it proved to be robust and very informative.

The biomass of each trophic group was also estimated as an alternative indicator of the importance of each trophic group. We then compared the biomass and Ti results to verify whether the two methodologies are comparable or not. We found that the biomass approach is a good approximation of the quantity of organic material available for subsequent links in the food web.

Trophic structure

The São Sebastião Channel is trophically dominated by strict detritivores (S + B), with a low contribution of subsurface deposit-feeders (B) (Fig. 2; Table 2). This group predominates both in number of species and number of individuals. These results are in agreement with data commonly reported for soft bottom coastal ecosystems (Levinton 1977; Gaston and Nasci 1988; Paiva 1993; Muniz et al. 1996). In the São Sebastião Channel detritivores were shown to be more tolerant to environmental changes and, thus, able to explore more habitats.

The low frequency of surface deposit-feeders where mud fractions predominated in the Channel was confirmed by the negative linear correlation between this group and the percentage of silt, clay and organic carbon in the sediments. Even though no previous results for the study area were available for comparison, we had expected to find more surface deposit-feeders in sediments where mud predominates (Sanders 1958; Gray 1981). However, some of these locations were situated near sources of pollution, such as the DTCS and the sewage pipe, which could explain the relatively few trophic groups found.

Subsurface deposit-feeders behaved somewhat peculiarly in relation to the environmental variables studied. Considering their feeding mechanisms, their distribution should be affected by (i) the presence of high quantity food sources in the subsurface sediment layer and (ii) an adequate exchange of solutes between the sediment and the overlying water layer. One would also expect positive correlations among the subsurface deposit-feeders, muddy sediments and organic carbon content. Frequently subsurface deposit-feeders are associated with an environment of low hydrodynamics and consequently with high concentrations of organic matter (Bianchi and Morri 1985; Gambi and Giangrande 1985; Tena et al. 1993). Nevertheless our results show Ti-values with an opposite trend: positive correlation with the coarser fractions of sediment and negative correlation with the percentage of organic carbon, reflecting the human impact near the silt-clay region of the Channel (Weber and Bícego 1991; Ehrhardt et al. 1995; Zanardi et al. 1999).

The abundance of carnivores in the São Sebastião Channel area, where sand was the dominant sediment type, was evidenced by the positive correlation between Ti-values and the percentage of different fractions of sand and gravel. The preference of this trophic group for coarse sediments with low levels of mud is well known (Maurer and Leathem 1981; Gaston and Nasci 1988; Tena et al. 1993). Sandy bottoms are most suitable for carnivores since the proliferation of potential prey organisms occurs in their interstitial spaces. The majority of the carnivores collected were small individuals of interstitially feeding species, whose feeding and movement are grain-size dependent. In this kind of sediment the larger pore space between sand grains allows prey to move easily. According to Fenchel (1970) the increased movement of the carnivores enhances oxygen penetration in the sediment. On the other hand, fine-grained bottoms support only carnivorous polychaetes that feed in the sediment–water interface. The small interstitial spaces of such sediments were possibly unfavorable for prey. The negative correlation obtained between carnivores and mud fractions and the content of organic carbon of the sediment support this idea. In terms of biomass the above trend was not as evident. It presented only a positive correlation with coarse sand, and a negative one with mean sediment diameter, probably linked to the small size of the most dominant sillid species, *Exogone arenosa*.

Due to the carnivores' superior position in the food web, their percent of dominance and Ti-values can be considered a good measure of the high degree of community structuralization. Accordingly, we observed that the polychaete associations in the northern part of the area and at the island margin may be submitted to comparatively less environmental stress since they present high values of density, species richness and diversity.

The relationship between suspension-feeders and sand fractions tends to indicate the greater hydrodynamic forces at work on sandy bottoms. Generally, suspension-feeders were poorly represented in the Channel area and showed the same trends as the carnivores. The optimal habitat for these organisms should be fine, well-sorted sandy bottoms, since the energy here is sufficient to resuspend small quantities of material without causing obstruction of the organism's filtration structures (Sanders 1958; Hily 1984). In the Channel, suspension-feeding forms were related to all fractions of sand most abundant in sandy locations (Station 9 and the northern region of the São Sebastião Channel). Regarding biomass, suspension-feeders showed a positive correlation with depth, due to the large size of *Spirographis brasiliensis* (approximately 15 cm) found only at Station 8, located in the deepest area of the Channel (45 m) and subjected to the highest current velocities (Fontes 1995).

Few omnivores were important in the study area. They followed the same trend as deposit-feeders and carnivores because these species were considered ditrophic. The multivariate analysis applied to the feeding guild data separated the groups according to their sediment preferences and the bottom stability. The position of each feeding guild in multivariate space gives an idea of the physical characteristics of their ecological niche. The distribution patterns probably reflect fitness among species, both from an ecological and an evolutionary point of view (Dueser and Shugart 1978, 1979).

Fauchald and Jumars' method of classification (1979) allowed us to understand why several trophic groups can coexist in the same habitat and perfer the same environmental characteristics. According to the multivariate results, the São Sebastião Channel seems to have two main groups of polychaetes with different environmental preferences. The first one is abundantly represented in the places where coarser sediments predominate (medium and coarse sand), and the second group is found where fine mixed sediments and low hydrodynamic conditions prevail. In the first group a clear division in the habitat structure of the species is observed (Fig. 5A). We have HMJ well represented by the small motile sillid, *Exogone arenosa*, feeding on small prey between the sand interstices and on the remains of organisms. We also have CDJ, mainly represented by species of Glyceridae, as members of the surface-feeding infauna, and the suspension-feeders, FDT, highly dominated by *Owenia fusiformis*. This species is a discretely motile tubicole with a ciliar crown that permits its feeding both as a suspension-feeder and as a surface deposit-feeder. Another suspension-feeder is *Chone insularis* that acts exclusively as a sessile filtrator. According to Warwick (1982), the suspension-feeding component of benthic communities is usually dominated by a single species. The last group consists of the subsurface deposit-feeders (BDJ), discretely motile eunicids that move between the sand grains and inhabit the deep layers of the sediment column, sucking the organic debris present there.

A similar division is found in the other main group obtained by classification (Fig. 5B), where motile and discretely motile polychaetes prevail and suspension-feeders were absent. Low hydrodynamic conditions in this region of the Channel may be responsible for these results. In this group the CMJ is represented by several species of Pilargidae, Polynoidae, and Syllidae, preferentially feeding on the surface sediment layer (Fauchald and Jumars 1979). In addition, we have the surface deposit-feeders like SMX, SDT and SDJ represented by spionid, magelonid, paraonid and nereid species. The species of this group exploit the same food resource, but do not compete with each other because they have different motile capabilities and different feeding structures. For example, the SMX obtain their food with their pharynx, the SDT by ciliate tentacles or by papillae, and the SDJ with the help of their jaws. Moreover, this group contains species of motile subsurface deposit-feeders (BMX) feeding in the sediment column by means of their pharynx. Typical representatives of the last

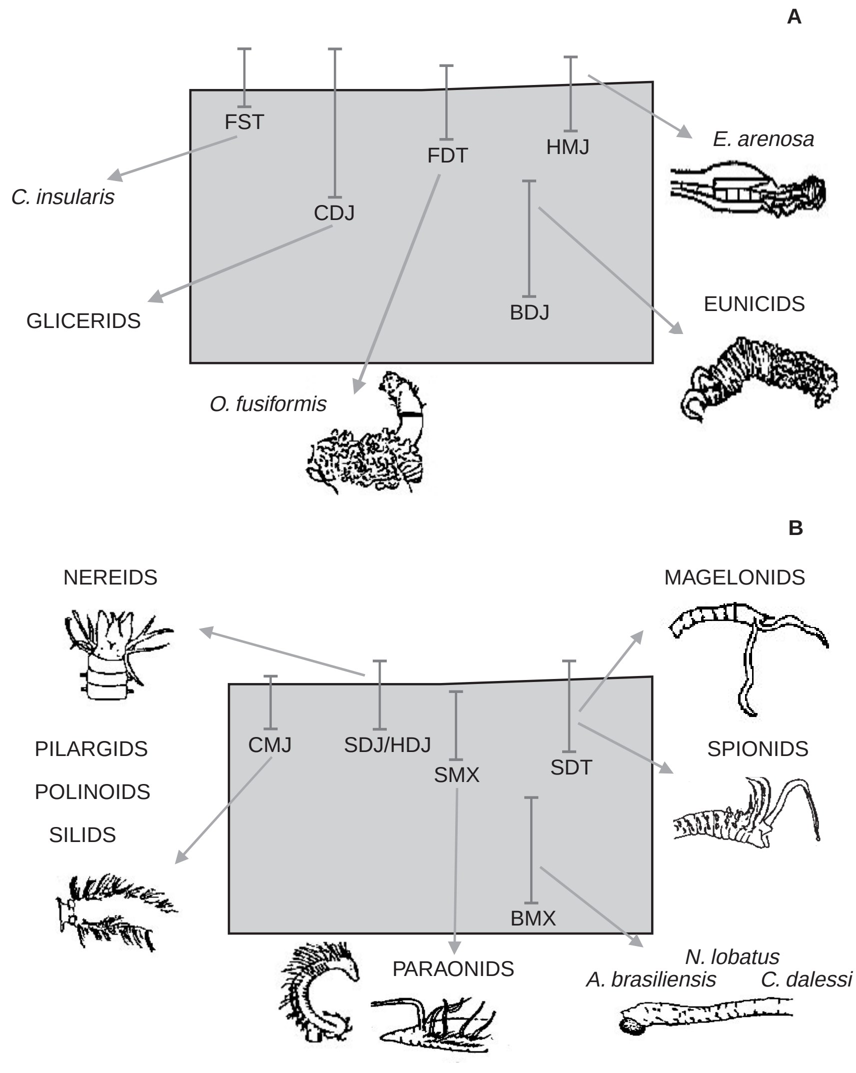

Fig. 5 Theoretical models of the possible vertical distribution of the most representative polychaetes of **A** Group II and **B** Group I, obtained by cluster analysis. Abbreviations used for the feeding guilds are as in Fig. 3

feeding guild are the capitellid *Notomastus lobatus* and the maldanids *Axiothella brasiliensis* and *Clymenella dalesi*, all of which predominate in the most sheltered region of the Channel.

In this work we could not find any clear preference of the species for the muddiest environments of the Channel, presumably due to the strong anthropogenic impact on the macrobenthic fauna in these areas.

On a temporal scale, the only remarkable change was the low abundance of polychaetes in autumn. Frequently the macrobenthos is very restricted in abundance and species richness in that season (Pires-Vanin et al. 1997). This decrease might be explained by the very high density of the peneid shrimp *Xiphopenaeus kroyeri* throughout the Channel in fall, which probably feeds on the benthic macrofauna, especially the infauna (Pires 1992).

Regarding the dominance of detritivores in the surveyed area, the benthic system of the São Sebastião Channel seems to be based on a detritus food web, where the organic input has both continental and oceanic origin, as indicated by the C/N relationship. Such a model follows that proposed for the Ubatuba system, a region nearby and to the north of the São Sebastião Channel (Pires-Vanin et al. 1993). Thus, polychaete associations play an important role in the local benthic system, forming a link between its lowest and uppermost levels. This is even more obvious if we consider that they represent 51% of the total benthic fauna in the Channel (Pires-Vanin et al. 1997). The identification of polychaete trophic guilds has been demonstrated to be a good tool to describe the benthic ecosystem structure.

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