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Trophic structure of a shelf polychaete taxocoenosis in southern Brazil

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Abstract :The distribution patterns of polychaete trophic groups were examined throughout a seasonal cycle of the continental shelf of São Paulo State in southern Brazil. Detritivores (subsurface deposit-feeders, surface deposit-feeders and suspension feeders) were the most important trophic group in the whole area. Subsurface deposit-feeders did not show any temporal variability. Surface deposit-feeders and suspension-feeders underwent pronounced shifts in importance, with higher values in the shallow stations during summer. This variability was probably due to storm-induced disturbances. Other processes such as predation and anthropic action seemed to be spread along the inner shelf. Distribution of trophic groups was related to temperature, $CaCO_3$ content and environmental stability (this being reflected on depth variability). A trophic group importance index is proposed to solve partially problems regarding trophic structure analysis.

Résumé : Le schéma de distribution des groupes trophiques des annélides polychètes au cours d'un cycle saisonnier a été mis en évidence sur la plate-forme continentale au large de l'état de São Paulo, côte sud du Brésil. Les détritivores constituent le groupe trophique le plus important dans l'aire étudiée. Parmi ceux-ci les déposivores de sous-surface ne montrent pas de variations liées à la saison. Par contre, les déposivores de surface et les suspensivores présentent des variations significatives ; les valeurs les plus élevées se mesurent dans les eaux les moins profondes lors des échantillonnages d'été. Cette variabilité semble se retrouver dans l'ensemble de la plate-forme interne. La distribution des groupes trophiques montre une relation avec la température, le taux de calcaire et les caractéristiques de l'environnement. Il est proposé un nouvel index d'importance pour les groupes trophiques afin de rendre plus aisée l'analyse de la structure trophique du macrobenthos.

INTRODUCTION

At the ecosystem level, studies that assess the main energy flows without requiring a more detailed analysis at the specific taxonomic level are desirable. This is specially so for marine tropical ecosystems, where the high biological diversity obscure the recognition of specific food webs responsible for the main part of the energy flow. Analysis of trophic structure of the benthos is one of the most parsimonious ways to evaluate the energy flow in marine ecosystems. The distribution patterns of trophic groups have been proved to be sensitive to several factors including environmental disturbances, food supply, sediment types and hydrodynamic conditions (Sanders, 1958 ; Levinton, 1972 ; Maurer & Leathem, 1981 ; Probert, 1984 ; Gaston, 1987 ; Gaston & Nasci, 1988).

Polychaete worms play a key role in the macrobenthic productivity of continental shelves (Knox, 1977) and their multiple feeding forms allow an evaluation of the macrobenthic trophic structure using only this taxon ; such studies are common in soft-bottom environments (Maurer & Leathem, 1981 ; Gambi *et. al.*, 1982 ; Dauer, 1984 ; Bianchi & Morri, 1985).

The trophic group approach was improved for the polychaetes with the "feeding guild" concept established by Fauchald & Jumars (1979). This concept is more comprehensive than the previous classifications, since it also includes the motility and feeding strategies of the worm in the guild determination. Afterwards, Dauer *et al.* (1981) and Gaston (1987) amended this classification for some families, but maintained the general pattern. The feeding guild approach allows grouping different species with similar roles in the food webs, which work as "ecological units", and may replace species in functional studies.

In this paper, the feeding guild approach is applied to analyze the seasonal and spatial distribution pattern of polychaete worms in the Ubatuba region.

RESEARCH AREA AND STATIONS

The survey cruises were conducted on the continental shelf of São Paulo State, southern Brazil (23°25' to 24°22'S - 44°33' to 45°16'W) at a depth from 15 to 117 m. The whole area covers 3 800 km^2, and is characterized by an inbayed shoreline and by the presence of several islands in the inner shelf. On the southwestern part there is the large Sao Sebastião Island, isolated from the continent by a deep channel (50 m). According to Furtado & Mahiques (1990), the shelf bottom sediment of the survey area is made mainly of fine and very fine sand. Mud content is higher (> 40 %) close to the coast (20 m), near the 50 meters isobath and in the outer shelf below 100 m. The sand fraction prevails in the northern section comprising 80 to 90 % of the sediment. Deposition and resuspension account for the spatial heterogeneity of the sediment on the inner shelf and homogeneity on the outer.

The hydrographic conditions were studied by Emilsson (1961), Matsuura (1986) and Castro Filho *et al.* (1987). Three main water masses have been recognized : the Coastal Water (CW), the Tropical Water (TW) and the South Atlantic Central Water (SACW). The CW is restricted to shallow water (< 20 m) in summer, interacting with the TW in winter when they cover all the inner shelf. The SACW covers the outer shelf all year round, inflowing to the inner shelf during summer. Thus, the inner shelf has a large annual variability, with a strong thermocline at mid-depths (20 m) in summer and almost no stratification during winter.

The grid (Fig. 1) was composed of 9 stations on the inner shelf and 3 stations on the outer shelf, (northern, central and southern). The inner stations at approximately 20, 35 and 45 m depth, were sampled seasonally, whereas the outer stations, at approximately 50, 75 and 100 m depth, were sampled only in summer and winter. A total of 54 stations (36 in the inner and 18 in the outer shelf) were sampled from October 1985 to July 1986.

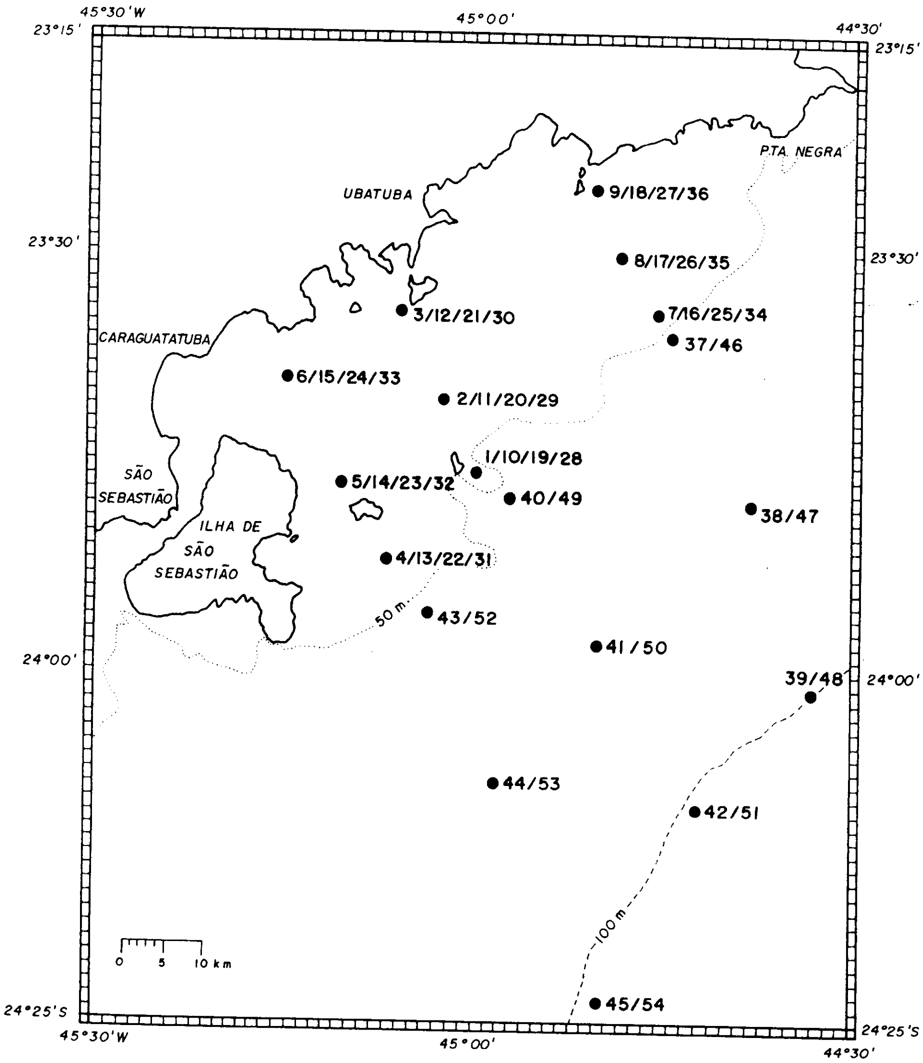

Fig. 1 : Studied area and Sampling stations.

MATERIAL AND METHODS

Samples were taken with a 0,1 m^2 Van-Veen grab. The sediment collected was washed through a 0,5 mm mesh sieve and the material retained was preserved in a 4 % buffered formalin solution before sorting and identification in the laboratory.

Hydrographic data were obtained using Nansen bottles with reversing thermometers. The salinity was measured using an inductive salinometer and the dissolved oxygen content was determined by the Winkler titration method. The sediment was submitted to the standard dry-sieve and pipette method described in Suguio (1973). Four size classes were used in this study : mud, fine sand (from 0,0625 to 0,25 mm), medium sand (0,25 to 0,5 mm) and coarse sand (> 0,5 mm). the $CaCO_3$ content was obtained by HCl 10 % attack and the organic matter content by means of H_2O_2 oxidation.

The species classification into feeding guilds was based on Fauchald & Jumars (1979) and Gaston (1987). Five trophic groups were considered : carnivores, surface deposit-feeders, subsurface deposit-feeders, suspension-feeders and omnivores. The species classified into two trophic groups were included in both.

To evaluate the degree of ecological importance of each trophic group in the sampling stations, a trophic group importance index (Ti) is proposed herein, expressed as :

$$Ti = \sum_{i=1}^{s} \ln ni \quad \text{where,}$$

s = number of species of the trophic group in the sample.

ni = number of individuals of the i^{th} species in the sample.

ln = natural logarithm.

In this case the sampled area was 0,1 m^2 and no extrapolation was made, as the index will overestimate the density or the richness depending on the relation between sampling area and patch sizes.

The dependence of trophic groups on environmental variables was estimated by means of a stepwise multiple regression analysis (Legendre & Legendre, 1983), with a significance level of 0,05.

RESULTS

The importance of each trophic group in the stations is shown in figures 2 to 7 and the variables selected in the regression model are presented in table 1.

Detritivores, represented by surface deposit-feeders and subsurface deposit-feeders, were the dominant group, being followed by suspension-feeders and carnivores.

The surface deposit-feeders were represented by : *Spiophanes missionensis, Cirratulus filiformis, Paraprionospio pinnata, Owenia fusiformis, Amphicteis latibranchiata, Amphicteis gunneri* and *Polydora socialis*. Surface deposit-feeders were very common in the area, in spite of the low values in the spring sampling (10/85). During summer (12/85 and 01/86) they reached their greatest importance at depositional environments such as the 20 m stations and the southern transect on the inner shelf ; on the outer shelf they presented lower values, except for the high values of station 37 (50 m). In autumn samplings (04/86) the values decreased, only the southern transect stations having values higher than 10. The winter samples were similar to autumn ones in the inner shelf, maintaining higher values on the southern transect ; in the outer shelf, the values were similar to that observed in the inner and also to those observed in the outer shelf during summer. The importance of surface deposit-feeders was inversely dependent on depth (t = - 2.07).

TABLE I
Variables selected (0.05 significance level) in the regression model for each trophic group.

	Carnivores	Subsurface dep. feeders		Surface dep. feeders	Suspension feeders	Omnivores
Variables selected	—	Temp.	$CaCO_3$	Depth	$CaCO_3$	—
Coefficient	—	1,84	- 4,57	- 0,78	4,55	—
STD error	—	0,76	2,29	0,38	2,25	—
T - value	—	2,42	- 2,00	- 2,07	0,02	—
Sig. level	—	0,01	0,05	0,04	0,04	—

The carnivorous species were : *Harmothoe lunulata, Pionosyllis pectinata, Sigambra grubii, Parandalia americana, Kinbergonuphis orensanzi, K. difficilis, Lumbrineris cingulata, Goniada maculata, Glycinde multidens* and *Glycera americana*. In spring, carnivores had low importance values, similar to the surface deposit-feeders, but during summer they were uniformly distributed on the inner shelf, while presenting lower values on the outer (except for station 37). In autumn and winter the index values were lower on the inner shelf, although this was the dominant trophic group in the winter. On the outer shelf the winter values were not different from the inner values and were higher than summer ones. Carnivores were not significantly dependent on any environmental variables.

The main subsurface deposit-feeding species were : *Euclymene dalesi, Cirrophorus americanus, Sternaspis capillata, Notomastus lobatus, Axiothella brasiliensis, Asychis brasiliensis, Aricidea (Acesta) simplex, Lumbriclymene noemia, Cirrophorus branchiatus* and *Levinsenia gracilis*. Subsurface deposit-feeders did not present importance values higher than 10. They were evenly distributed throughout the whole area with no seasonal variability such as shown by the other trophic groups. They presented dependence on temperature and inversely on $CaCO_3$ content.

The most important suspension-feeders in the area were *Chone insularis, Hydroides plateni* and *Owenia fusiformis* (also a surface deposit-feeder). The group was not very common in the area, except for some patches in coastal stations. They seldom presented importance values higher than 3. The group was almost absent during spring. In summer they reached their highest values at low depths (20 m) with some occurrences on the outer shelf (75 to 100 m). They were scarce in autumn and nearly absent during winter on the whole shelf. Their winter outer shelf values were similar to the summer ones.

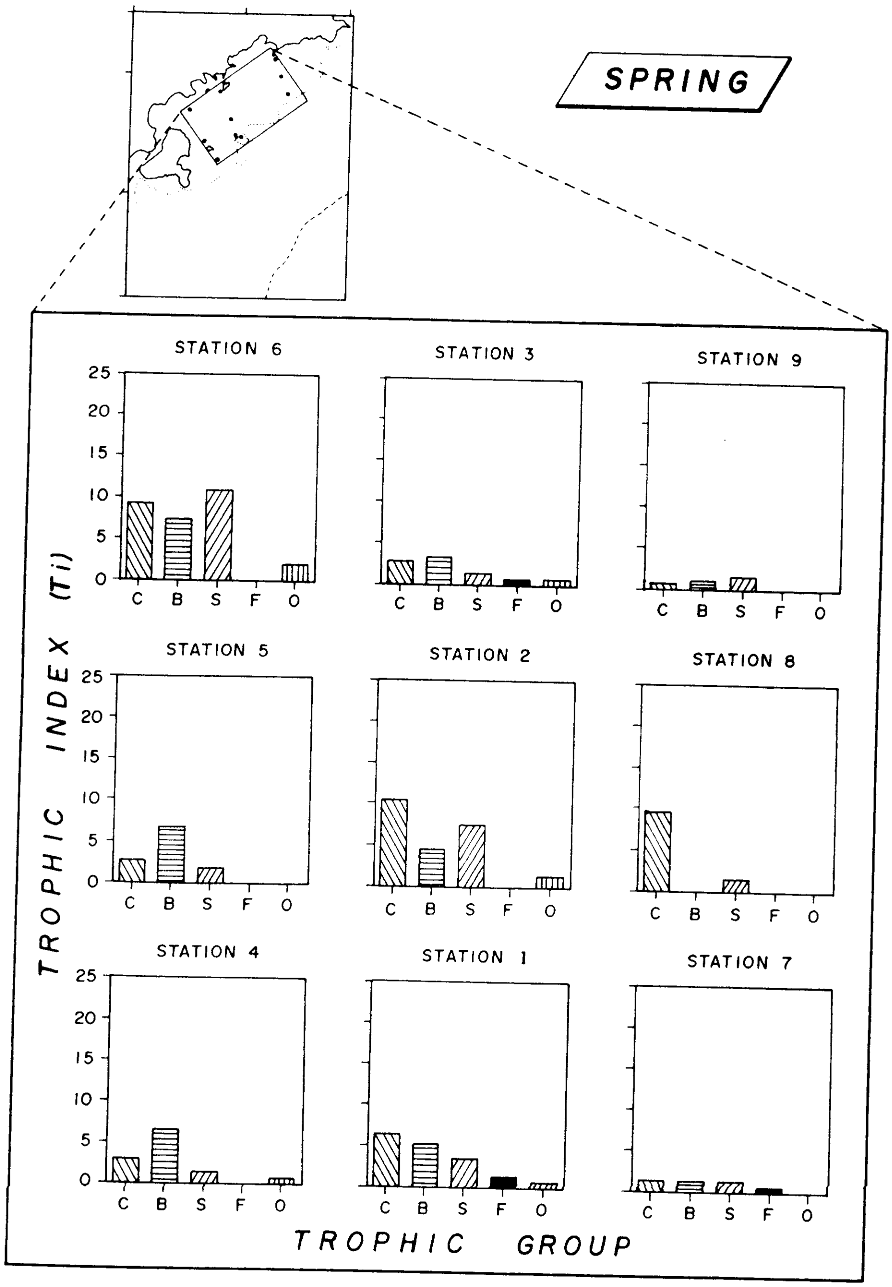

Fig. 2 : Trophic Importance Index of each trophic group for sampling stations during Spring. (C = carnivores ; B = subsurface deposit-feeders ; S = surface deposit-feeders ; F = suspension-feeders ; 0 = omnivores).

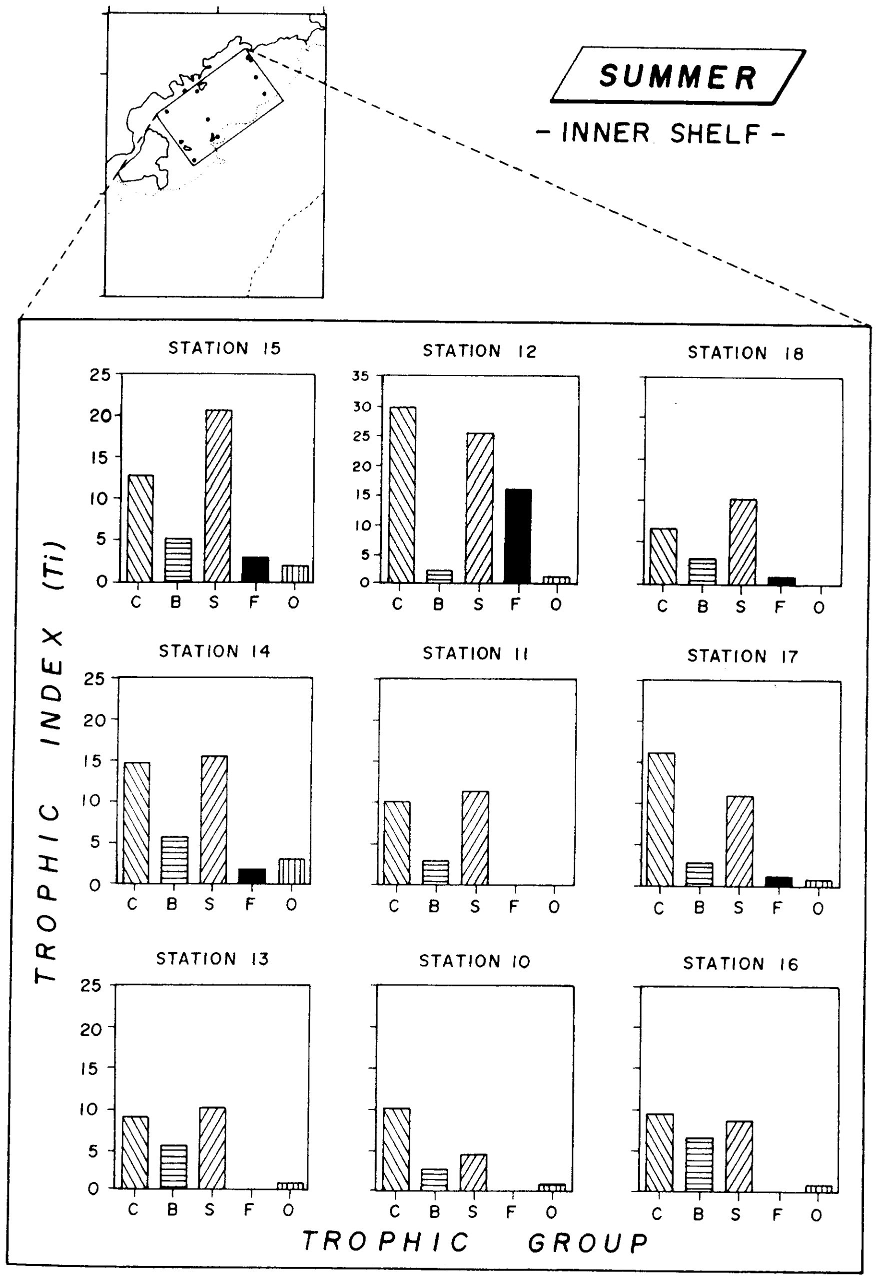

Fig. 3 : Trophic Importance Index of each trophic group for sampling stations of the inner shelf during Summer. (C = carnivores ; B = subsurface deposit-feeders ; S = surface deposit-feeders; F suspension-feeders ; C = omnivores).

Suspension-feeders were more important in sediments with high $CaCO_3$ content. They were also sligthly related to low oxygen contents (not significant at the 0,05 level), owing to the low values in station 12 where they reached their highest index value (15,7).

The omnivores were rare in the area with no obvious pattern, their low importance values being associated to the low number of species and density, even though some species such as *Ceratocephale oculata*, *Neanthes bruaca* and *Nereis broa* were frequent.

As a whole, there was no seasonal pattern on the outer shelf regarding the relative importance of the trophic groups, but there was a difference between summer and winter as regards total density.

On the inner shelf the subsurface deposit-feeders did not show much temporal variability. In the other hand, the surface deposit-feeders and suspension-feeders presented higher values during summer, mainly at the 20 and 30 m stations. The carnivores presented an intermediate pattern of distribution, following the surface deposit-feeders pattern, but without falling too much when these tended to greatly decrease in importance.

DISCUSSION

TROPHIC GROUP IMPORTANCE INDEX

Evaluation of the secondary production for each trophic group allows assesment of their role in the energetic flow of marine food webs. However, this measurement is impracticable in rich and diversified communities such as the tropical and subtropical ones. Wildish (1986) proposed to use the trophic group biomass, but, like the secondary production, it has some restrictions and is hard to assess when working with fragmentary and tiny worms. Because of these problems, some researchers opted to use the species density for evaluation of the trophic group importance (Bachelet, 1981 ; Maurer & Leathem, 1981, Wildish, 1986 ; Gaston, 1987, Gaston & Nasci, 1988 ; Morgado, 1988), while others prefered to use species richness (Gambi *et al.*, 1982 ; Bianchi & Morri, 1985). The density approach is functionally more coherent, mainly when working with polychaete worms, since it indirectly provides the biomass and production when working with communities composed of species with analogous life cycles. However, recruitment events and patchy distribution, not necessarily linked to more intense food supply, lead to an overevaluation of the trophic group concerned. In such cases, the use of the species richness gives more reliable results.

The trophic index proposed in this study is intended to partially solve such problems, reducing the importance of density bu applying log-transformation of abundances and thus preserving the species richness factor, generally underestimated in analyses not subjected to the log-transformation.

DISTRIBUTION OF TROPHIC GROUPS

The dominance of Spionidae among the surface deposit-feeders and their well known capability of colonizing bottoms with high sediment mobility (Maurer & Leathem, 1980)

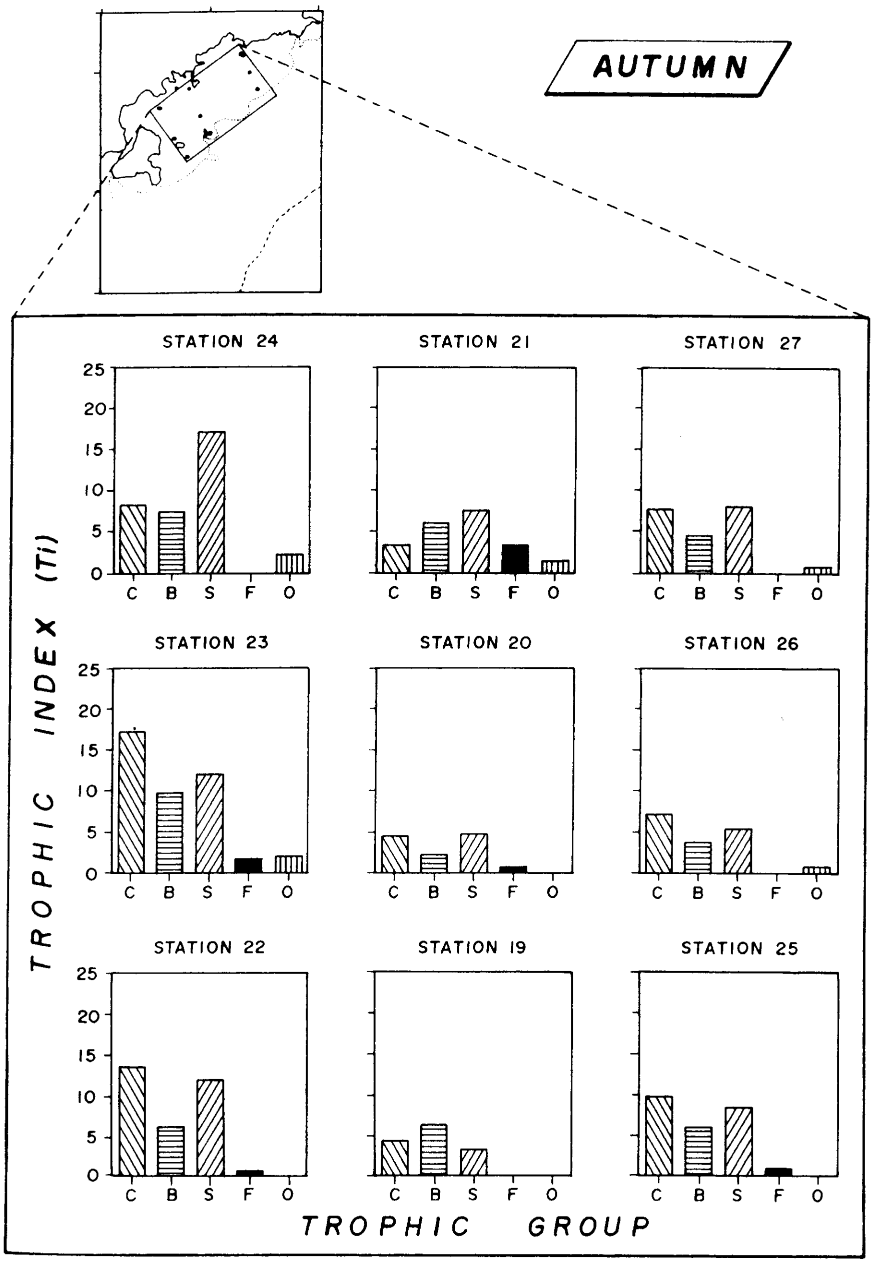

Fig. 4 : Trophic Importance Index of each trophic group for sampling stations during Autumn. (C = carnivores ; B = subsurface deposit-feeders ; S surface deposit-feeders ; F = suspension-feeders ; = omnivores).

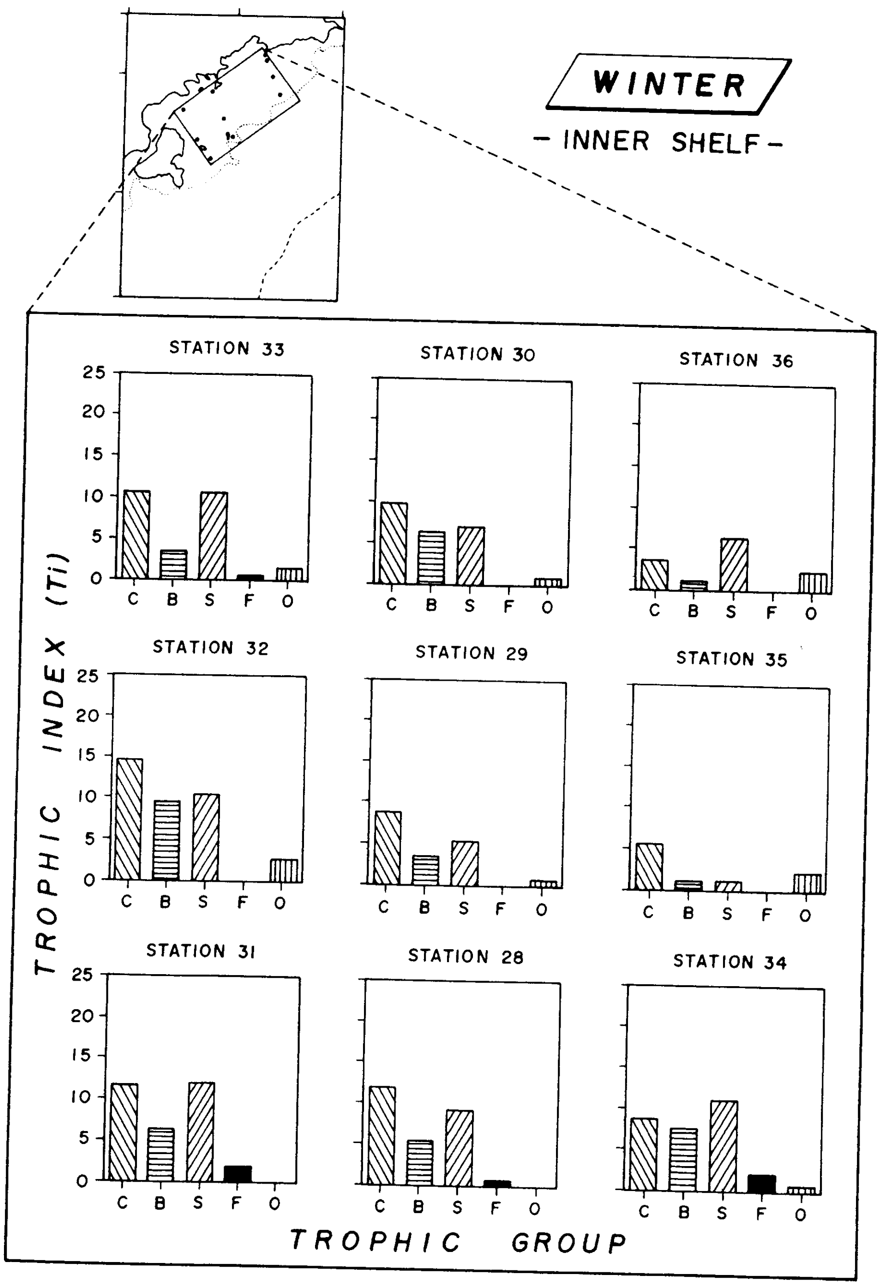

Fig. 5 : Trophic Importance Index of each trophic group for sampling sfations of the inner shelf during Winter. (C = carnivores ; B = subsurface deposit-feeders ; S = surface deposit-feeders ; F suspension-feeders ; O = omnivores).

lead to the higher importance of this trophic group in shallow waters, where the hydrographic conditions induced by surface waves are more intense. The surface detritus accumulation in coarse sediments allows the colonization by surface deposit-feeders (Gaston, 1987). Therefore, there was no dependence of this trophic group on organic matter or mud content, as would be expected for deposit-feeders (Sanders, 1958 ; Gray, 1981). However, this lack of significant dependence is due to the application of a standard sedimentological analysis which provides average values along the whole sediment column, thus resulting in an underestimation of the surface organic matter content.

The inverse dependence of the subsurface deposit-feeders on the $CaCO_3$ content may be a result of the hampering effect of shell fragments in the feeding of species that ingest sediment and digest only organic matter and microorganisms associated to the matrix. The observation of the group distribution along a clay content gradient showed a Gaussian distribution with a peak at 2 to 6 % of clay. This Gaussian distribution is probably related to the non-cohesiveness of such mixed sediments, since the cohesion of sediments with greather clay content inhibits the non-sessile subsurface deposit-feeders, restricting their motility and feeding capability.

The relation of the suspension-feeders to the $CaCO_3$ content in this study is due to the very high densities of *Hydroides plateni* and *Serpula* sp at station 12. This relation seems to be linked to the abundance of shell fragments in the sediment that can be used as a substratum for the tubes of sabellids and serpulids.

Although the carnivores are related to coarser sediments (Maurer & Leathem, 1981 ; Gaston, 1987 ; Morgado, 1988), significant dependence on sand fraction were not recognized, because the sediment that came within the range of this study was mainly composed of sand and sandy-mud. It is likely that the sandy bottoms with low levels of mud are the most suitable for the carnivores since they allow the proliferation of potential preys inside their interstices.

In the distributional analysis of suspension-feeders and deposit-feeders their independent patterns are notewhorthy, probably owing to the lack of interactive inhibitions such as the "trophic amensalism" (Rhoads & Young, 1970) which is a density-dependent factor (Peterson, 1979) and so of little effect on the abundance of macrofauna in low-density assemblages. In such environments the abiotic interactions are more effective than the biotic ones, limiting the distribution patterns of trophic groups and hence influencing the community structure.

The distribution patterns of the trophic groups in the survey area, with a remarkable intra-annual variability characterized by temporal shifts of surface deposit-feeders and suspension-feeders abundances, are frequently referred to as typical of areas subjected to some kind of disturbance. The soft-bottom colonization by surface forms in earlier successional stages is common in estuarine and shelf environments (Rhoads, *et al.*, 1978 ; Probert, 1984 ; Gaston & Nasci, 1988).

In the survey area, the higher importance of surface deposit-feeders and suspension-feeders during summer characterizes this season as a post-disturbance period. The disturbance processes involved are probably linked to the winter period, when the importance of

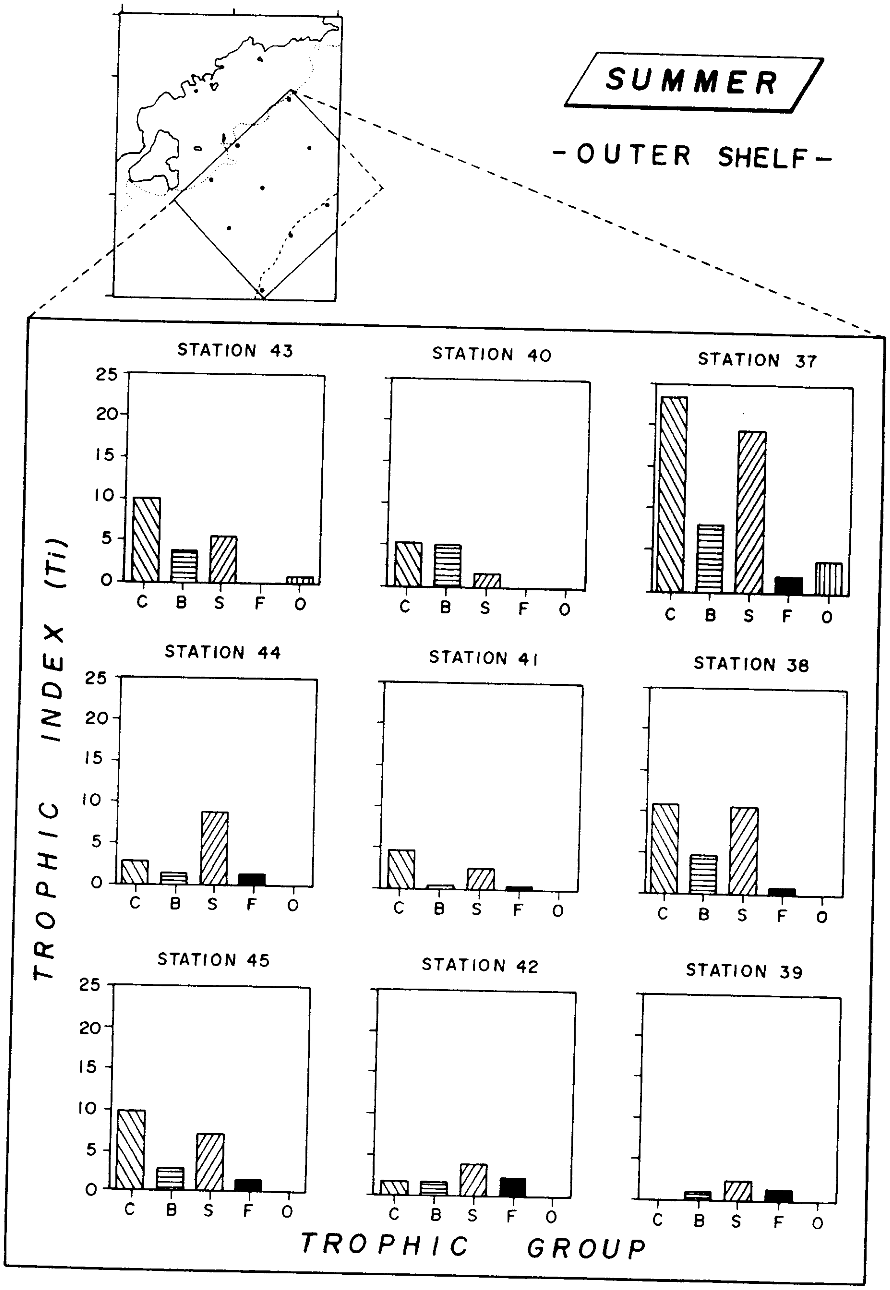

Fig. 6 : Trophic Importance Index of each trophic group for sampling stations of the outer shelf during Summer. (C = carnivores ; B = subsurface deposit-feeders ; S = surface deposit-feeders ; F suspension-feeders ; O = omnivores).

this trophic group fell at the shallow sector (20 and 30 m) in the central and northern transects. Among these winter disturbance processes, the most likely to occur is a revolving movement of bottom sediment induced by surface waves, being according to Tessler (1988) restricted to the inner shelf. These waves are normally generated by strong winds which are characteristic of the pre-frontal zones of cold front systems coming mainly from the south and southwest. These systems may be recognized through the records of the monthly averages of the daily atmospheric pressure variation obtained in the Oceanographic Institute's coastal station in Ubatuba. These records showed a higher frequency of incidence of cold-fronts (higher monthly average) during the winter period and a lower one during summer. The waves and swells generated by the cold front storm have an effect on the bottom that decreases with depth. In this way, there must be a high mortality of surface forms on the inner shelf, mainly at low depths (20 and 35 m depth line). Disturbances caused by winds and storms are widely referred to in the literature on benthic environments (Eagle, 1975, Glémarec, 1978 ; Van Blaricom, 1982 ; Probert, 1984), sometimes giving rise to a complete defaunation of the whole sediment.

Other important disturbance processes in the survey area are predation and anthropic action. Common demersal fishes such as *Paralonchurus brasiliensis*, *Micropogonias furnieri, Ctenosciaena gracilicirrhus*, *Eucinostomus argenteus, Umbrina canosai, Zapteryx brevirostris, Raja agassizi* and *Psammobatis glansdissimilis* (Nonato *et al.*, 1983 ; Rocha, 1990) are active predators of polychaetes (Amaral & Migotto, 1980 ; Soares *et al.*, 1989a, 1989b). Futhermore, Lana (1981) suggested that the predation action of *Paralonchurus brasiliensis* was an important factor in the structuration of polychaete taxocoenosis in sand-muddy bottoms. Some brachyuran crabs such as *Persephona mediterranea*, *Libinia spinosa* and *Portunus spinimanus*, common in the inner shelf, are also predators of polychaetes, making 15 to 90 % of their total diet (Nonato *et al.*, 1990 ; Petti, 1990). Not only the predation upon the polychaetes taxocoenosis by fishes and crabs, but also the mechanic effect, mainly of rays, may disrupt the structure of benthic communities (Fager, 1964, Van Blaricom, 1982). The role of predation in the spatio-temporal variability of the polychaete trophic groups is not clear owing to the variation of the potential predator species distribution, each replacing the other seasonally over the whole area (Rocha, 1990 ; Sartor, 1990). The anthropic action as a disturbance factor is not well determined. However, our observations indicated a sudden fall in density and richness of polychaete worms, specially within the bays over the last 5 years. These alterations in the community structure are probably related to sewage disposal coming from the increasing number of housing projects along the shoreline, noticeable by the striking increase of the fecal coliform index during the period (CETESB, 1984 and 1990). The dredging effect, as a source of disturbance (Conner & Simon, 1979 ; Gaston & Nasci, 1988) resulting from the use of otter-trawls by the intense fishing activities, is likely to be responsible for radical changes in the community structure of the survey area, affecting even the subsurface environnent. This was observed in the "Side Scan Sonar" records of the shallow sector, obtained in the area by the marine Geology Group of the Oceanographic Institute (University of São Paulo).

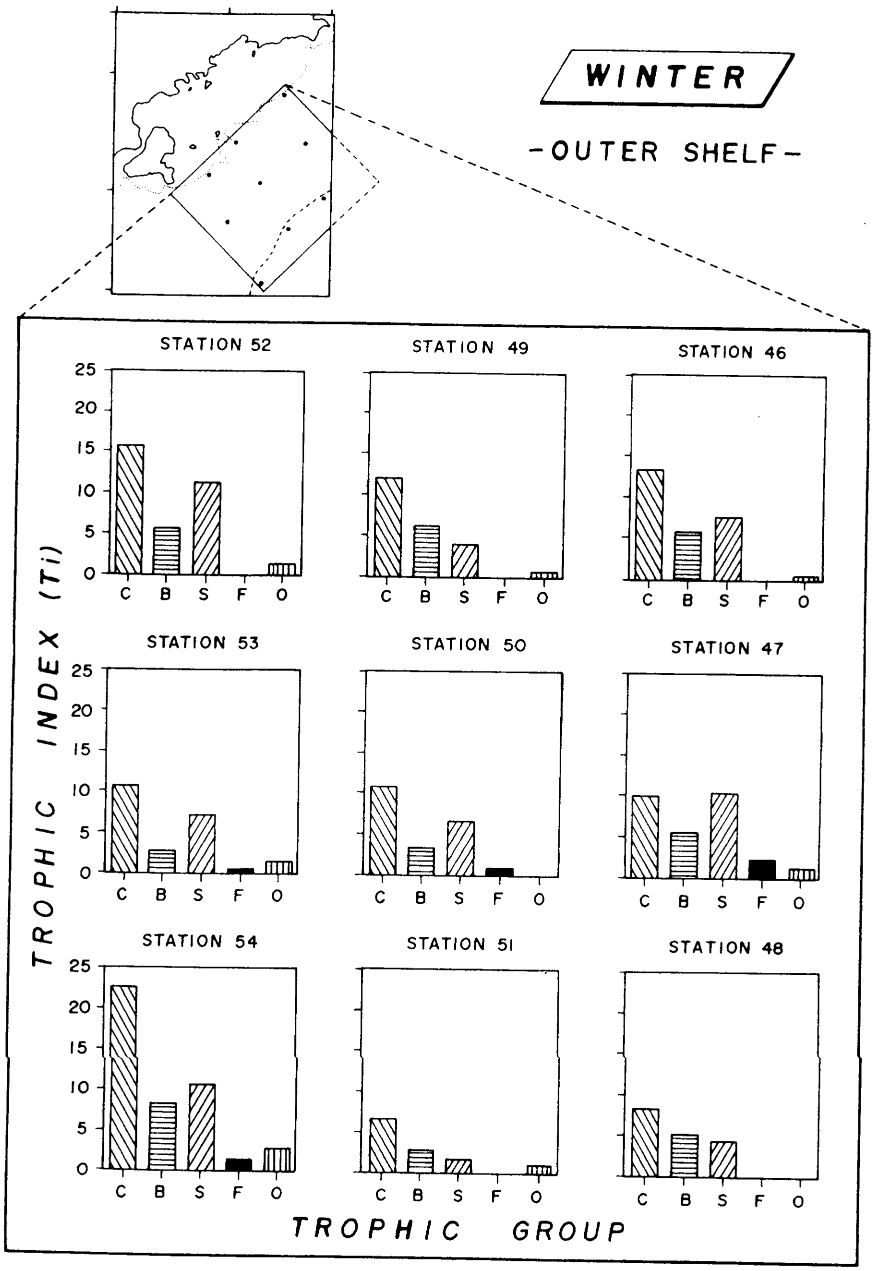

Fig. 7 : Trophic Importance Index of each trophic group for sampling stations of the outer shelf during Winter. (C = carnivores ; B = subsurface deposit-feeders ; S = surface deposit-feeders ; F = suspension-feeders ; O = omnivores).

All the above disturbance processes affect mainly the inner shelf. Those generated by waves and storms are less effective in the southern transect since this is placed in the lee of the large São Sebastião Island, owing to the prevailing southern originating winds. This shaded area gives rise to a more stable community with a low temporal variability of trophic groups. Woodin (1978) characterized the process of protection against disturbance as refuges in function of the position of the organisms in time and space. The summer stratification of the water caused by the entrance of the SACW over the shelf bottom coupled with the low frequency of incidence of cold fronts characterized this period as a temporal refuge for the inner shelf assemblages. The deeper outer shelf and the southern transect of the inner shelf would act as spatial refuges, as also the deeper layers of the sediment column that allow for the maintenance of subsurface forms resulting in the constancy of the subsurface deposit-feeders throughout the year (Figs. 1 to 6).

What happens in the sediment after the winter defaunation process is not known, but it is suggested that it would be a recolonization period, starting with bacterian flourishing and followed by an intense meiofaunal growth (see review by Probert, 1984). This would be facilitated by the SACW entrance during summer since its low speed currents would make uniform the bottom water conditions. Then, the region would be colonized by the more opportunistic species of the sediment-water interface (Rhoads & Germano, 1982 ; Probert, 1984), mainly the spionids that can easily settle in such environments. Barry (1989) stated that such processes of colonization are due to the reproduction induced by physical disturbances, analogous to the fire adaptations of terrestrial plants.

The refuge areas, owing to their predictability and environmental stability, have more structured communities with more specialized and long life-cycles forms, characterizing a more advanced successional stage (Pearson & Rosenberg, 1978 ; Rhoads *et al.*, 1978 ; Rhoads & Germano, 1982) that would seldom be achieved in areas subjected to high frequency of physical disturbances.

It seems that these disturbance processes in the area are responsible for the maintenance of high-diversity and low-density polychaete assemblages (Paiva, in preparation), leaving the less affected zones more subjected to density-dependent interactions. Therefore, the polychaete trophic structure reflected the spatio-temporal disturbance variability, mainly the physical, predictable disturbances.

The key role of the macrobenthic detritivores in the community structuring is noteworthy, in view of the preliminary results of the IOUSP-CIRM Integrated Investigation (IOUSP, 1990) that showed the great importance of the detritus food web in the shelf ecosystem. In this way, the polychaete trophic structure analysis may be a good way to assess the role of some disturbance processes in the structure of detritus-based shelf ecosystems where the polychaetes are the main macrobenthic taxon.

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