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Sublittoral meiofauna and macrofauna of Rocas Atoll (NE Brazil): indirect evidence of a topographically controlled front

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ABSTRACT: Topographically controlled fronts are small-scale phenomena caused by the interaction between currents and complex reef topography, resulting in zones of convergence and eddies where debris and organisms are accumulated. Rocas is the only atoll in the South Atlantic (3° 51' S, 33° 49' W) and it is constructed predominantly by coralline red algae, vermetid gastropods and encrusting foraminiferans. The structure of meiobenthic and macrobenthic communities, particularly nematodes and polychaetes, over the sublittoral carbonate deposits was examined during May 1996. Univariate and multivariate analyses showed a gradual change in the meiobenthic and macrobenthic community structure from the windward to the leeward side of Rocas Atoll, which was significantly correlated with the measured environmental variables. The characteristics of the carbonate deposits, ranging from coarse sands to medium well-sorted sand, and their enrichment process towards the leeward, as shown by the organic content, suggest a strong linkage with the hydrodynamic regime. Even though both components of the benthos are influenced by this hydrodynamic heterogeneity, the meiobenthic and macrobenthic fauna over the sublittoral area of Rocas Atoll are affected in different ways. Changes in the hydrodynamic regime promote a significant increase in diversity and density of the meiofauna, particularly nematodes, but the macrobenthos showed a more complex response, with a decreasing number of taxa and a variable abundance towards the leeward side. The results of this study suggest that the significant changes in the sediment characteristics and benthic community structure along the atoll may be a result of topographically controlled fronts.

KEY WORDS: Meiofauna · Macrofauna · Rocas Atoll · Community structure · Sublittoral · Front · Brazil

INTRODUCTION

Reef habitats are immediately perceived as diverse, abundant and productive. Whilst reef communities do represent one of the most biologically diverse systems (Sale 1980, Alongi 1989b, Sorokin 1993) many of the organisms contributing to the high species diversity of reefs constantly degrade them, converting massive reef structures to sand (Glynn 1997). The surrounding sand deposits, however, normally do not exhibit such high diversity communities as the reef itself (Guzman et al. 1987, Gourbault et al. 1995, Netto et al. 1999), but there is increasing evidence that a variety of reef-associated fauna may be strongly dependent on the peripheral benthos, foraging extensively over the carbonate sediment (Ambrose & Anderson 1990, Frazer et al. 1991, Posey & Ambrose 1994).

The majority of reef systems exist in conditions of permanent and intense hydrodynamic movement of water masses. Interactions between a complex relief, such as an offshore atoll, and oceanic currents generate secondary flows near the reef that result in eddies, upwellings and downwellings (Sorokin 1993). Rather than affecting only the water column processes, increasing plankton biomass and aggregating water-borne eggs and larvae, these small-scale topographically generated fronts influence the sediment composi-

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tion and deposition process (Wolanski & Hamner 1988). As sediment properties have long been recognised as a major factor influencing benthic community structure (e.g. Warwick & Buchanan 1970, Jones 1984, Coull 1988), the topographically controlled fronts may be of particular relevance to the composition and abundance of soft-bottom reef communities.

Several studies detail the benthic community structure on reef-associated carbonate sediments (see review by Alongi 1989b). With respect to atolls, although a number of studies have been carried out in the Pacific (Salvat & Renaud-Mornant 1969, Villiers 1988, Intes & Caillart 1994) and Indian Ocean (Rao & Misra 1983, Narayanan & Sivadas 1986, Naim 1988, Ansari et al. 1991), most of them have only focused on inside habitats, particularly the lagoon.

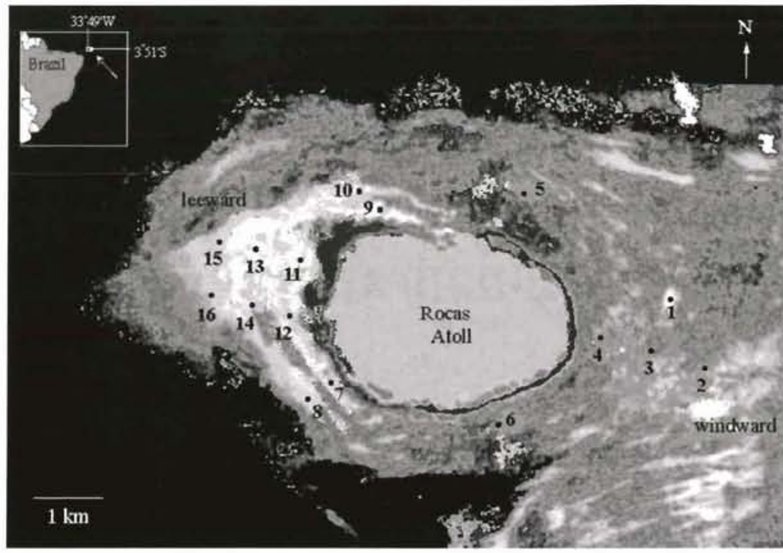

Fig. 1. TM-Landsat image of Rocas Atoll, NE Brazil, showing the sublittoral sampling sites (sand = light patches)

Rocas is the only atoll in the South Atlantic and its reefs are mainly built by encrusting coralline red algae, vermetid gastropods, foraminiferans, molluscs and corals (Gherardi 1996). Studies of the island, located 266 km off the northeast Brazilian coast, are scarce: physical descriptions have been given by Ottman (1962) and Gherardi (1996); references to the occurrences of foraminiferans and mollusc species have been made by Ribas (1966), Tinoco (1967), Matthews (1970) and Rios (1985). Recently, Netto et al. (1999) showed that the patterns in community structure of meiofauna and macrofauna over sublittoral, tidal flat, reef pools and lagoon of Rocas are significantly different and related to the gradation in the physical environment of the atoll.

This paper reports on sublittoral meiobenthic and macrobenthic invertebrate response to a gradation in the physical environment of the offshore Rocas Atoll, NE Brazil, from the more wave-exposed windward area to the leeward. Changes in meiobenthic and macrobenthic community structure, particularly nematodes and polychaetes, are associated with the presence of topographically controlled fronts.

MATERIAL AND METHODS

Study site. Rocas Atoll (3° 51' S, 33° 49' W) is an uninhabited biological reserve located 266 km off the northeast Brazilian coast (Fig. 1). The atoll reef rim (3.5 km long and 2.5 km wide), mainly built by encrusting coralline red algae, has a slightly elliptical shape and it is interrupted by passes in the N and NW. Gherardi (1996) provided a general description of geomorphologic features of the coralline reefs. Sublittoral carbonate sediments range from very coarse to fine sand and from very well to poorly sorted sand (Netto et al. 1999). Sands are patchily distributed (light patches in Fig. 1) and continuously transported towards the leeward side of the atoll, as observed by the satellite image showing the atoll and its shallow platform (Fig. 1). The South Equatorial Current and SE to E winds dominate the Rocas area. Currents can attain velocities up to 70 cm s^{-1} (Silveira et al. 1994) in the region and strong wind-generated waves are normally concentrated upon the eastern portion of the atoll (windward). The regional climate is tropical and dry: minimum air temperature is 26°C and annual average precipitation is 109 mm (Höflich 1984). Local tides have a semi-diurnal regime with maximum amplitudes of 3.8 m (Gherardi 1996).

Sampling. Sixteen stations, from windward to leeward, were sampled at depths between 5.2 and 24.1 m in May 1996 (Fig. 1). The patchy distribution of the sand and the variable thickness of sediment, mainly on the windward side, restricted the number of sampling sites surrounding the atoll. At each station, SCUBA divers collected 3 samples for meiofauna using a 2.5 cm diameter core tube pushed to a depth of 10 cm, and 3 samples with a 10 cm diameter core tube to a depth of 10 cm were taken for macrofauna. On the surface, samples were immediately fixed in 4% buffered formalin. Superficial sediment for granulometric and organic content analyses was collected with a 5 cm core at each station. Meiofauna sample processing followed the procedures described in Somerfield &

Warwick (1996). Macrofauna samples were sieved on a 0.5 mm mesh, sorted, identified to the species or putative species and enumerated. The percentage of silt/clay in the sediment was determined by wet sieving using a 63 µm sieve to separate the fine and sand fractions, which were then dried at 70°C and weighed. Sediment granulometry was determined by sieving dried samples. For the determination of organic content, sediment samples were dried at 70°C and then combusted for 1 h at 550°C.

Data analyses. Univariate and non-parametric multivariate techniques used are described in Clarke & Warwick (1994). For total meiofauna and macrofauna, univariate measures included only number of taxa and abundance because not all organisms were identified to the same taxonomic level. Univariate measures of sublittoral meiobenthic nematode and macrobenthic polychaete assemblages included: number of species (S), total abundance (N), Shannon-Wiener diversity indices calculated using $\log_2$ (H'), Margalef's species richness (d) and evenness (Pielou's J). S and N were converted to approximate normality using a $\log(x+1)$ transformation. Differences in univariate measures between the stations were tested using 1-way ANOVA, and where results were significant ($p < 0.05$), the Tukey multiple comparison tests were applied. Similarity matrices were constructed using Bray-Curtis similarity measure on fourth-root transformed faunal data, therefore reducing contributions to similarity by abundant species. The data were then ordinated by non-metric multidimensional scaling (Clarke 1993). The variability amongst replicate samples over the sublittoral area of the atoll was analysed using the multivariate relative dispersion measure, a procedure used by Warwick & Clarke (1993) to examine an increase of variability between sample replicates with increased levels of perturbation. In order to analyse community pattern for evidence of common biotic structure, the abundance similarity matrices were compared using a Spearman rank correlation (ρ) and significance determined using a permutation procedure (RELATE, Clarke & Warwick 1994).

Environmental data (mean grain size, sorting, fine percentages, organic content and depth) were converted to approximate normality using a $\log(x+1)$ transformation and ordinated using a correlation-based principal component analysis (PCA). Although it is important to obtain information on replicate variability, averaging samples increases the signal-to-noise ratio for displaying patterns of change across sites in relation to an environmental gradient (Somerfield et al. 1995). For this reason, and because only 1 sample for analyses of abiotic data was taken, faunal abundances from 3 replicates at each station were averaged for analyses linking biotic and environmental data. The Bray-Curtis similarity matrices derived from averaged fourth-root transformed biotic data were compared with the environmental distance matrix using the procedure outlined above. The relationships between multivariate community structure and combinations of environmental variables were analysed using the BIO-ENV procedure (Clarke & Ainsworth 1993) to define suites of variables that best explain the faunistic structure.

RESULTS

Meiofauna

The number of total meiobenthic taxa varied significantly over the sublittoral (Fig. 2a), being lower at stations located on the windward side (1, 4, 5 and 6) and higher at Stns 14, 15 and 16, on the leeward side of the atoll (Tukey's HSD test, not shown). Mean population density of total meiofauna varied between 328 and 1476 ind. $10\,\text{cm}^{-2}$. Meiofaunal densities were significantly higher at Stns 14 and 15 (Fig. 2b). Copepods and nematodes were the most abundant taxonomic groups, accounting for 78% of total meiofauna (50 and 27%, respectively). The dominance of the 2 major meio-

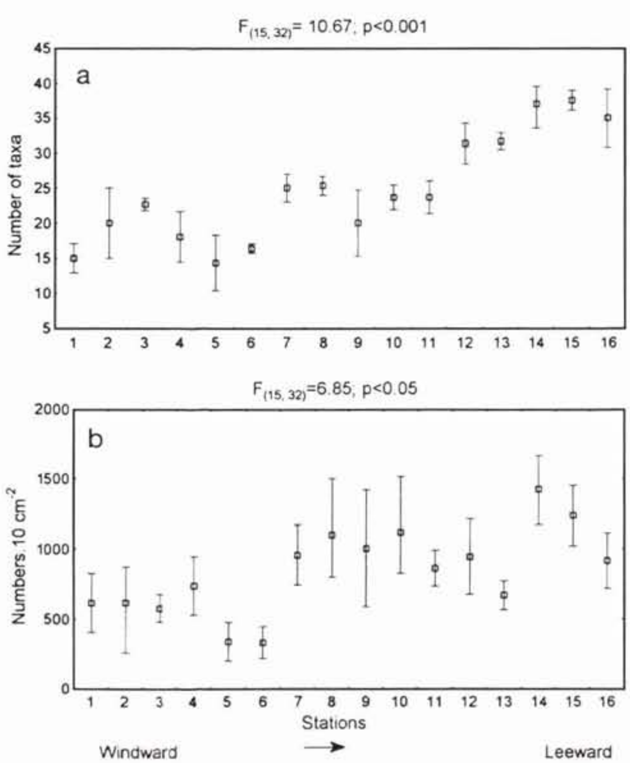

Fig. 2. Means and standard errors for (a) number of taxa and (b) density of total meiofauna

benthic groups was variable along sublittoral stations of the atoll, where the copepods were the dominant group at the windward stations, and the nematodes were more abundant at the leeward stations. The next numerically important meiobenthic groups, such as Ostracoda (9% of total meiofauna abundance), Polychaeta (7%) and Acari (2%), did not show a clear tendency from the windward to the leeward side of the atoll.

A total of 89 putative nematode species was recorded and *Epsilonema* sp. 1 and *Perepsilonema* sp. 1 (Epsilonematidae) were the most abundant forms. All univariate measures of nematode community structure varied significantly between the sublittoral stations (Table 1). Tukey's HSD post hoc comparisons showed that the number of species, abundance, diversity and species richness were significantly higher at stations located on the leeward side of the atoll (Fig. 3). Analyses of nematode feeding types in the sublittoral carbonate sands, according to Wieser's (1953) classification, did not show a clear dominance of one feeding type (Fig. 4). However, whilst the percentage of relative abundance of selective deposit feeders (Fig. 4: 1A) was significantly lower at stations located on the leeward side (Fig. 4), the abundance of epigrowth or diatom feeders (Fig. 4: 2A) displayed an opposite trend, increasing towards the leeward side of the atoll. Non-selective deposit feeder (Fig. 4: 1B) and predator/omnivore (Fig. 4: 2B) groups did not show a clear distribution pattern along the sublittoral stations, always representing less than 25% of total abundance (Fig. 4).

MDS ordination of fourth-root transformed meiofauna and nematode abundance data (Fig. 5a,b) clearly showed that the stations are distributed along a gradient, from the more wave-exposed sites (Stns 1, 2, 3 and 4) to the more leeward sites (Stns 14, 15 and 16).

Table 1. *F* ratios and significance levels ($F_{15,32}$) from 1-way ANOVA tests for differences in some univariate measures derived from meiofauna and macrofauna community structure between sublittoral stations of Rocas Atoll

Univariate measure	Nematodes *F*	Nematodes p	Polychaetes *F*	Polychaetes p
Number of species (*S*)	8.03	0.001	4.97	0.001
Abundance (*N*)	5.1	0.001	3.98	0.006
Diversity (*H'*)	5.1	0.006	4.7	0.006
Richness (*d*)	6.36	0.003	4.8	0.005
Evenness (*J*)	4.55	0.001	4.7	0.008

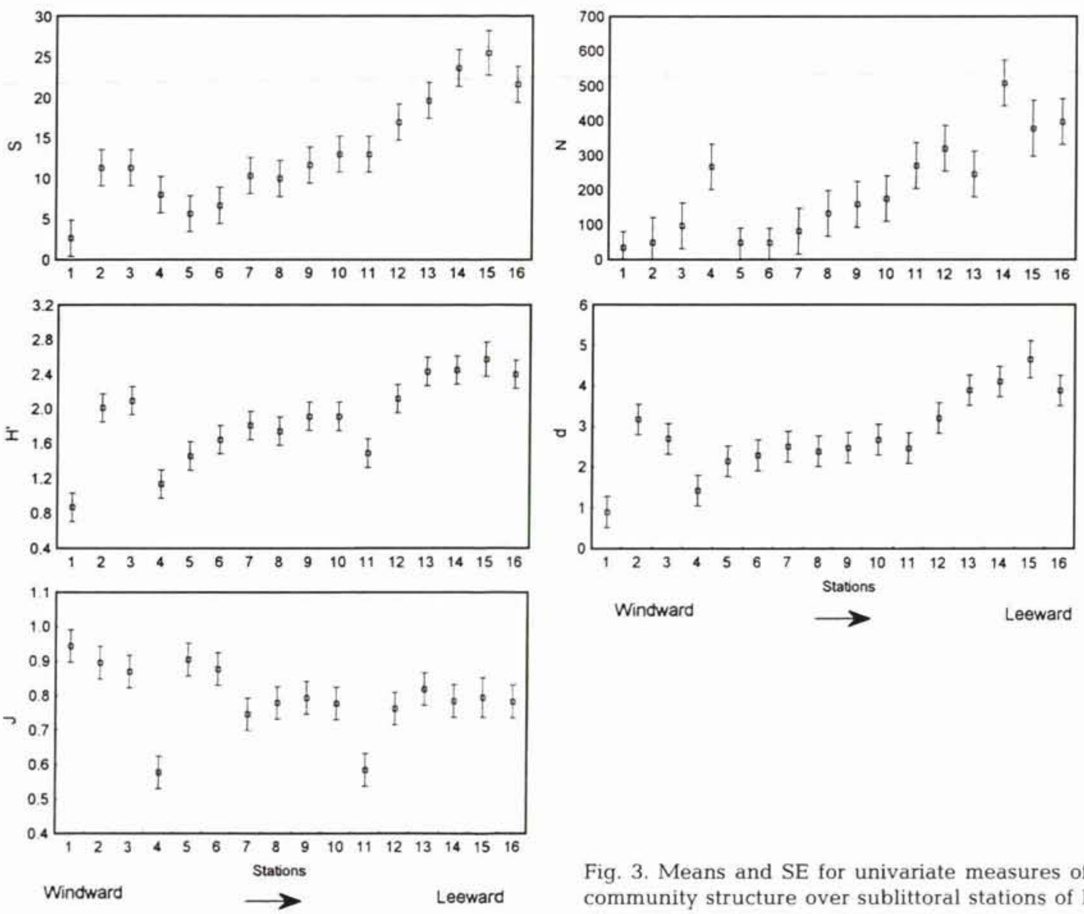

Fig. 3. Means and SE for univariate measures of nematode community structure over sublittoral stations of Rocas Atoll

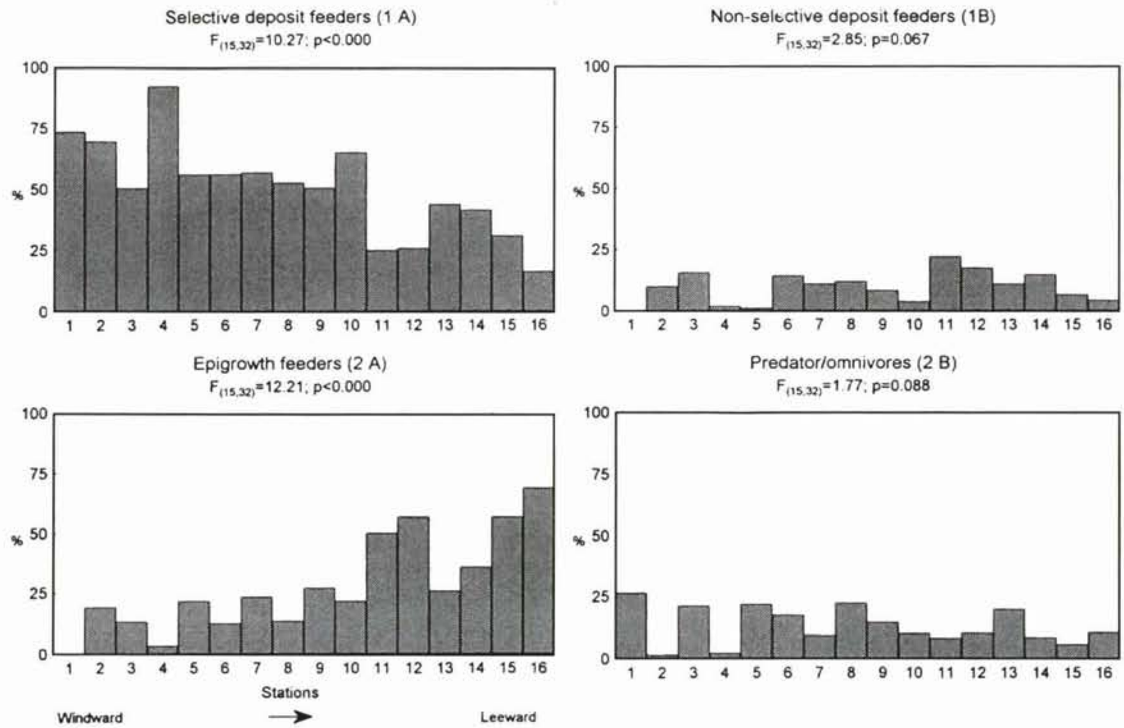

Fig 4. Distribution of nematode feeding types (1A, 1B, 2A and 2B) as mean percentage of abundance, *F* ratios and significance level from 1-way ANOVA tests for differences between sublittoral stations of Rocas Atoll

Both MDS plots also indicate a wide spread of replicate samples on the windward side of the atoll when compared to leeward. Sample relative dispersion values (Fig. 5c), which indicate the variability in meiofauna and nematode multivariate structures within each station, confirmed the decrease in the variability across the atoll.

Macrofauna

The total number of macrobenthic taxa decreased from the windward to the leeward stations (Fig. 6a). Tukey's HSD post hoc comparisons showed that the number of macrofauna taxa was significantly higher at Stns 2 and 3, at the windward, and higher at Stns 13 to 16. Average densities of total macrobenthic invertebrates ranged from 4904 to 25 402 ind. m^{-2}, and did not show a clear trend over the gradient (Fig. 6a). Macrobenthic density was significantly higher at Stn 16. Polychaetes were the dominant taxonomic group at all stations, representing 61 % of the total macrofauna. Oligochaetes and nematodes were numerically the next most important groups accounting, respectively, for 14 and 13 % of the macrofauna. Densities of crustaceans and other groups, such as bivalves and gastropods, were low and decreased towards the leeward side of the island.

A total of 38 species (22 families) of polychaetes were recorded in the sublittoral sands of Rocas. *Eteone heteropoda*, *Saccocirrus papilocerus* and *Macrochaeta clavicornis* were numerically dominant, representing more than 40 % of the total. Univariate measures derived from polychaete data varied significantly across the stations (Table 1). However they did not show a very clear pattern of change from windward to leeward stations (Fig. 7).

Ordination of fourth-root transformed macrofauna and polychaete abundance data (Fig. 8a,b) showed changes in community structure along a gradient, from windward to leeward stations. Replicate variability for macrofauna and polychaete data, as shown by sample relative dispersion (Fig. 8c) did not indicate a clear pattern of change across the sublittoral stations.

The comparison between the benthic communities of sublittoral sediments (Table 2) showed that all similarity matrices were significantly correlated ($p < 0.001$). The highest correlation was between macrofauna and polychaetes, indicating the importance of this group in structuring the macrobenthos.

Environmental variables

Ordination by principal component analysis (Fig. 9) of the environmental data clearly showed that stations were distributed along a marked gradient from wind-

ward to leeward of the atoll. Components 1 and 2 accounted for 77% of the total variance (PC1 = 43% and PC2 = 34%). Carbonate sediments ranged from very coarse, moderately sorted sands at the windward stations (1 to 5) to medium, well-sorted sand in the leeward area (Stns 12 to 15, Fig. 10). Fine percentages

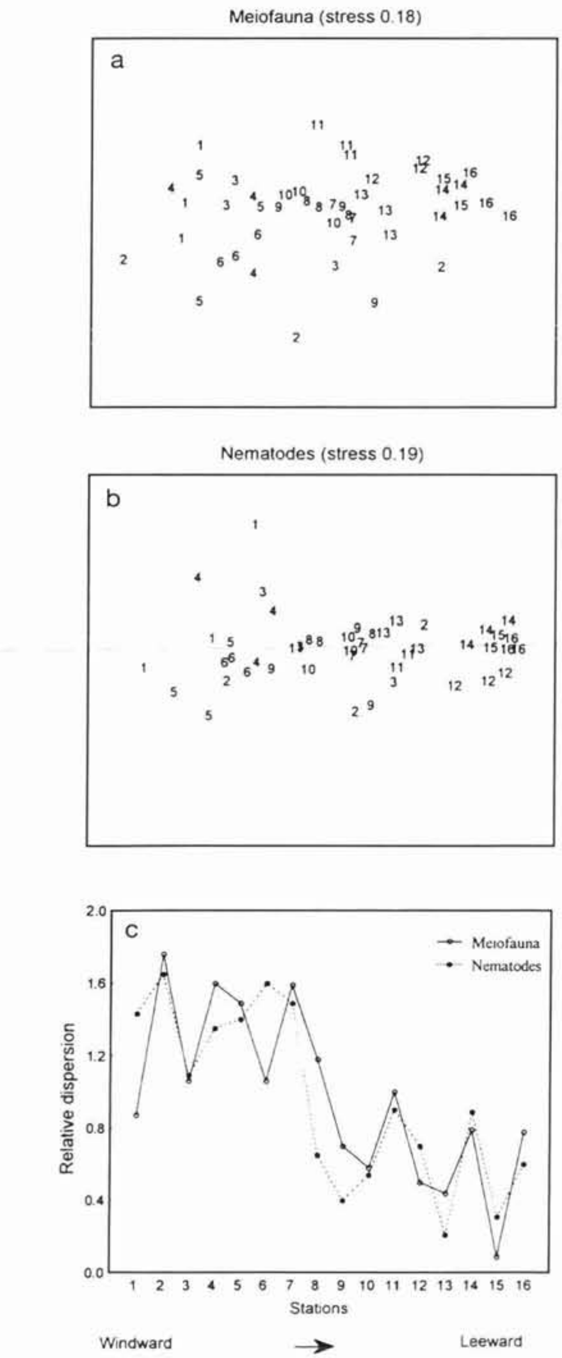

Fig. 5. MDS ordinations from transformed abundances of (a) meiofauna and (b) nematode, and (c) variability among replicate samples at stations over the sublittoral area of the atoll

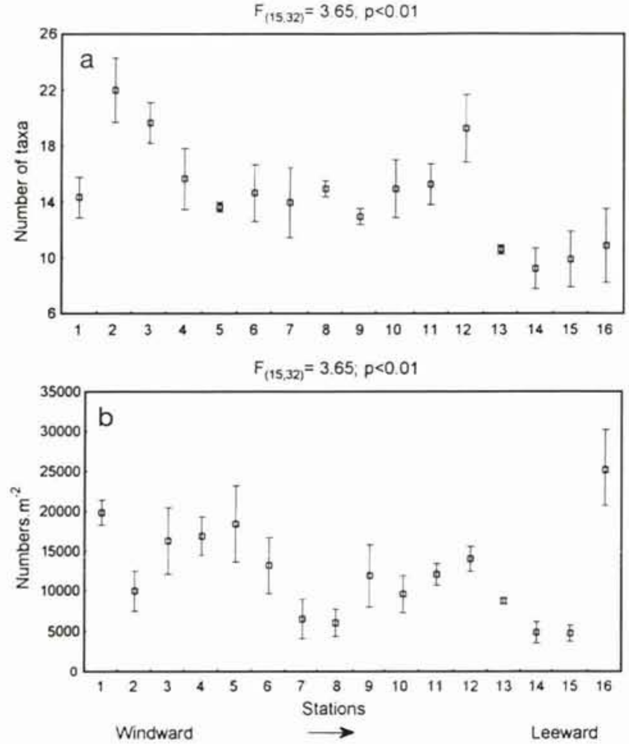

Fig. 6. Means and SE for (a) number of taxa and (b) density of total macrofauna

and total organic content, never higher than 2.81%, also exhibited a tendency to increase their values towards the leeward portion of the atoll (Fig. 10). MDS ordinations, derived from similarity matrices of averaged transformed biotic abundances, all indicated that the distribution of the benthic community also occurred along a gradient (Fig. 9).

Spearman rank correlations between the Euclidean distance matrix from abiotic data and similarity matrices from biotic data presented in Fig. 9 were all significant ($p < 0.001$). The results of BIO-ENV analyses (Table 3) showed a similar result for the meiofauna and nematodes, in which the highest correlation value (0.62) occurred with mean grain size and sorting. Fourth-root transformed macrofauna and polychaete abundance data showed the highest correlations (0.67 and 0.72, respectively) with the same variables as meiofauna and nematodes, with the addition of fine percentages (Table 3).

DISCUSSION

The results of univariate and multivariate analyses showed a gradual change in the meiobenthic and macrobenthic community structure from the windward to the leeward side of Rocas Atoll, which were signifi-

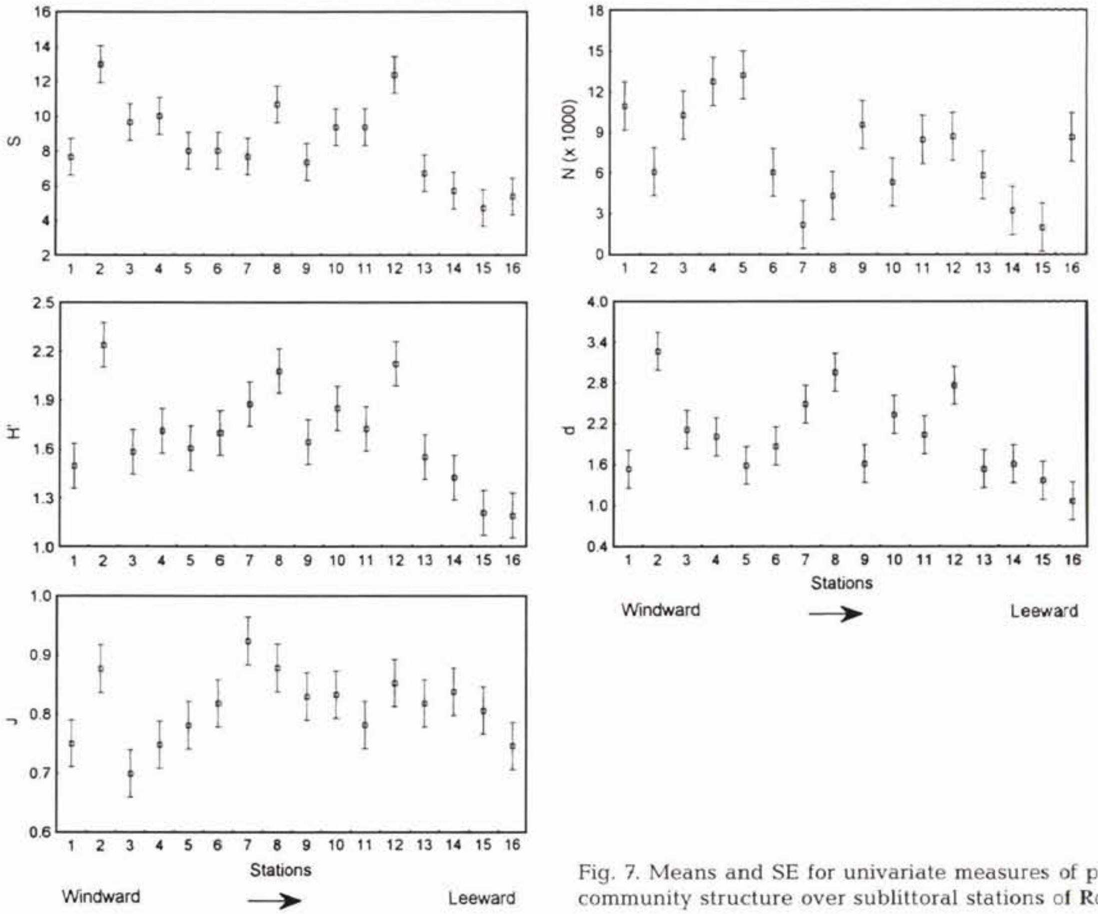

Fig. 7. Means and SE for univariate measures of polychaete community structure over sublittoral stations of Rocas Atoll

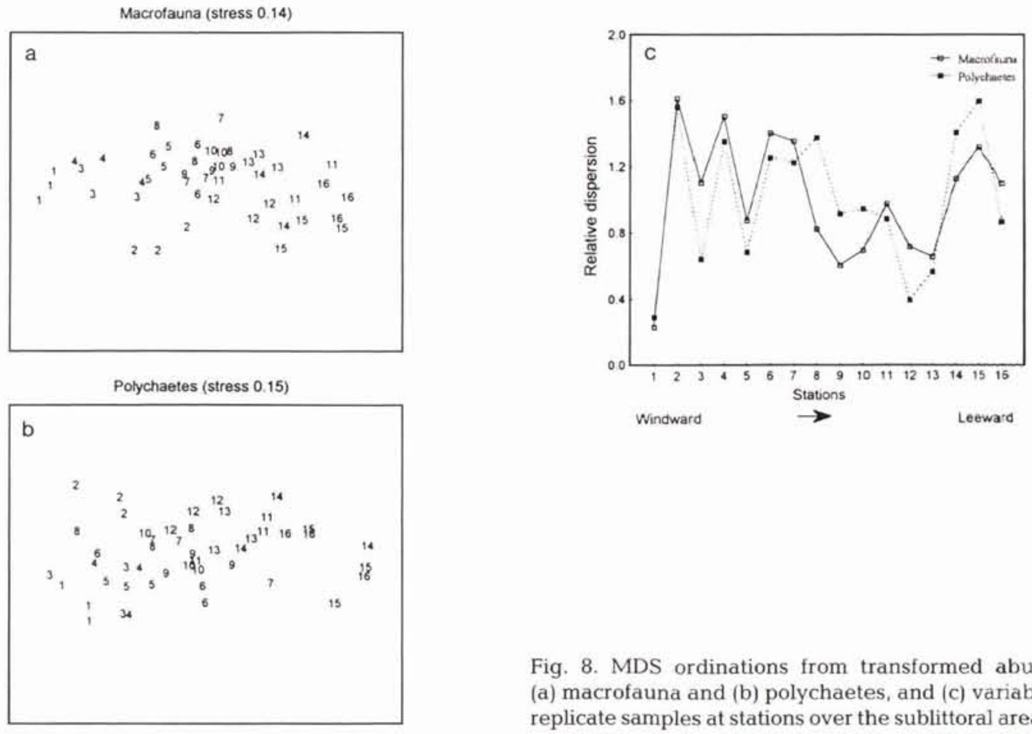

Fig. 8. MDS ordinations from transformed abundances of (a) macrofauna and (b) polychaetes, and (c) variability among replicate samples at stations over the sublittoral area of the atoll

Table 2. Pairwise Spearman rank correlation between similarity matrices derived from fourth-root transformed biotic abundance data. All correlations are significant at $p < 0.001$

	Meiofauna	Nematodes	Macrofauna
Nematodes	0.777		
Macrofauna	0.425	0.452	
Polychaetes	0.429	0.429	0.857

cantly correlated with the measured environmental variables. The characteristics of the carbonate deposits, ranging from coarse, poorly sorted sands to medium, well-sorted sand, and the enrichment process towards the leeward, as shown by the organic content gradient, suggest a strong linkage with the hydrodynamic regime. Even though both components of the benthos are affected by this hydrodynamic heterogeneity, the mechanics of this influence on the meiobenthic and macrobenthic components over the sublittoral area of Rocas Atoll clearly differ.

The changes in the level of stress to which the Rocas fauna is subjected could be detected by the variation in the relative dispersion values of the samples. Both meiobenthic and nematode replicate samples clearly exhibit higher dispersion values in the more wave-exposed sites, decreasing towards the leeward side of the atoll. However, the variability amongst macrobenthic and polychaete data sets did not exhibit a clear trend, although relative dispersion values were generally higher than the meiofauna over the sublittoral station. Warwick & Clarke (1993) suggested that there are 2 potential sources of increased variability among replicate samples: increase in the variability of abundances of the same set of species and changes in species identity. Using multivariate analyses (MDS and index of multivariate dispersion), which exploit both sources of variability, they detected an increase of variability among replicate benthic samples with increase in stress levels. The different responses of the components of the benthos to a similar environmental variability at Rocas Atoll are probably related to the different mechanisms for diversity maintenance between meiofauna and macrofauna. Whilst the meiofauna present a more specialised feeding behaviour and partitioning of food resources, the macrofauna are relatively unselective in their food requirements and may depend on spatial partitioning of the habitat (Whitlatch 1980, Warwick 1984). Thus, the high variability of the macrofauna over the sublittoral area suggests that they are more likely to be affected by the

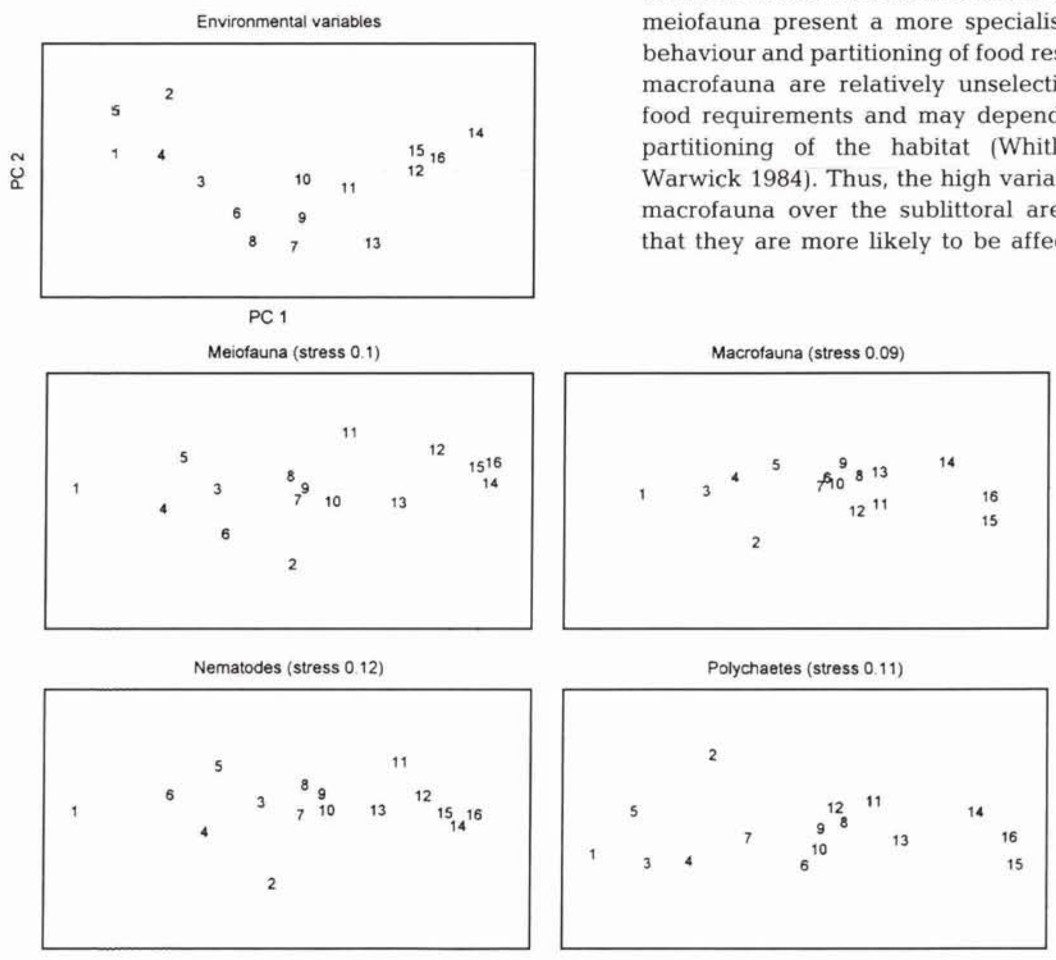

Fig. 9. Ordinations by PCA of environmental variables, and by MDS of averaged abundances from sublittoral stations

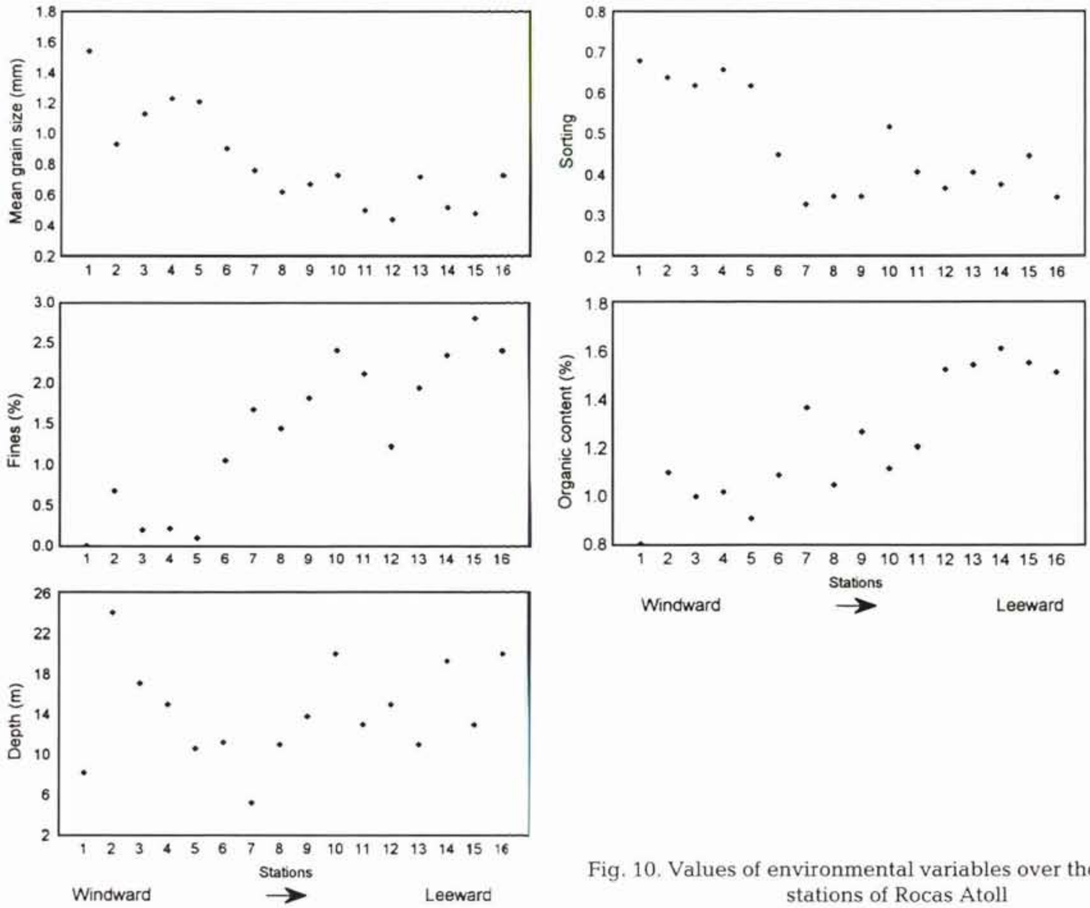

Fig. 10. Values of environmental variables over the sublittoral stations of Rocas Atoll

local physical instability of the sediment than the meiobenthic forms. This differential effect of physical stress on the components of benthos closely corroborates previous observations by McLachlan (1983) and Warwick et al. (1990).

The average macrofauna density in the sublittoral area of Rocas is similar to those recorded from other tropical sand habitats (Alongi 1989b). However, the fauna clearly possesses characteristics that reflect a harsh environmental regime. The macrobenthos is largely dominated (88%) by small surface-dwelling polychaetes, oligochaetes and large nematodes. Abundance of crustaceans, bivalves, gastropods and other groups, such as echinoderms, were very low and relatively important only in some windward sites. The relatively small size of the fauna and their surface-dwelling opportunistic nature probably indicate a low detrital input and may suggest that the macrobenthos could respond rapidly to the local physical instability. These characteristics of the sublittoral macrobenthic forms at Rocas are similar to those described in other shallow subtropical or tropical continental shelves subjected to erratic and low nutrient inputs and physical stress (Yingst & Rhoads 1985, Alongi 1989a).

In contrast to the variable pattern demonstrated by the macrofauna, the meiofauna clearly showed an in-

Table 3. Summary results from BIO-ENV. Combinations of environmental variables yielding the best match of biotic and abiotic similarity matrices, as measured by weighted Spearman rank correlation (ρ_w)

	Meiofauna	Nematode	Macrofauna	Polychaete
Best variable	Mean grain size Sorting	Mean grain size Sorting	Mean grain size Sorting % fines	Mean grain size Sorting % fines
ρ_w	0.62	0.62	0.67	0.72

crease in the number of species and abundance towards the leeward side of the atoll. The progressive change in the meiobenthic community structure is particularly evident for the nematodes. Whilst wind-generated currents and waves may prevent the deposition of organic particles in the windward sediments of the atoll, as well as the establishment of a richer meiobenthic assemblage, there is a clear increase of the sediment organic matter value towards the leeward side. The increase of productivity around oceanic islands, specifically on the leeward side, has been observed by a number of authors (e.g. Alldredge & Hamner 1980, Charpy-Roubaud & Charpy 1994). Wolanski & Hamner (1988) suggested that such enhancement of organism density is mainly caused by topographically controlled fronts, a small-scale interaction between currents, reef topography and island wake resulting in zones of convergence and eddies where debris and organisms accumulate. This aggregation affects the distribution of sediments, waterborne eggs, larvae, and phyto- and zooplankton, consequently influencing the distribution and density of benthic assemblages (Borgne et al. 1985, Hernández-León 1991). Meiobenthic communities are known to be subjected to the same erosion/suspension processes that act on sediments (Palmer & Gust 1985, Gamenick & Giere 1994). Thus, it may be possible that the significantly higher density and diversity of meiofauna and nematodes towards the leeward side of the Rocas Atoll may be a result of 2 main processes caused by the topographically controlled fronts: the passive transport of the fauna, and active aggregation in areas of more abundant and enriched food particles.

Tietjen (1991), studying the ecology of nematodes from the Great Barrier Reef, suggested that assemblages from shallow carbonate sediments are particularly dominated by species belonging to the same families and genera. Species which dominated the sublittoral carbonate sands from the Red Sea (Grelet 1984), Guadaloupe (Boucher & Gourbault 1990) and off North Carolina (Tietjen 1971) were those belonging to the families Desmodoridae, Chromadoridae and Xyalidae, and to a lesser extent Cyatholaimidae, Linhomoeidae, Oncholaimidae and Comesomatidae. However, Netto et al. (1999) showed that the structure of nematode assemblages differs significantly between the habitats of the Rocas Atoll. In the specific case of the shallow sublittoral sediments, they are largely dominated by species belonging to Epsilonematidae, although Draconematidae, Chromadoridae and Desmodoridae are also important. Moreover, as evidenced by the MDS ordination, the area is not homogeneous and there is a gradual change in the structure of the local nematode assemblages; Draconematidae are more abundant on the more wave-exposed windward side whereas Chromadoridae and Desmodoridae are more abundant to the leeward of the atoll. Although there may be some similarities between nematode assemblages from carbonate sands, this similarity is more likely due to the high hydrodynamic conditions which these areas are subjected to rather than the nature of the sediment itself. Similar patterns of dominance in non-carbonate sandy bottoms were recorded by Ward (1975) and Willems et al. (1982).

The absence of a dominant nematode feeding type in the sublittoral area of the atoll, previously described by Netto et al. (1999), conceals the gradual and significant shift in the abundance of selective deposit feeders and epigrowth feeders from the windward to the leeward side of Rocas. Whilst the densities of selective deposit feeders significantly decreased over the sites, the epigrowth or diatom feeders showed an inverse pattern, increasing towards the leeward. The co-dominance by these 2 trophic types probably reflects, on one hand, the availability of the 2 major sources of food and, on the other, the hydrodynamic conditions of the area. The abundance of microbial populations in carbonate sands is known to be heavily dependent upon the density of corals (Sorokin 1993): the largest microbial biomass was found in sands with a rich or medium coral cover, and the smaller in sands of corallinae algae reefs such as Rocas Atoll. High densities of selective deposit feeders or microvores (Moens & Vincx 1997) on the windward side were mostly due to Epsilonematidae and Draconematidae, known to be adapted to extreme substrate instability. This may indicate that picking out bacteria on an individual basis may prove to be energetically favorable where microbial populations are low and/or patchy and where sediment instability is high. Conversely, higher abundances of the epigrowth feeders on the leeward side of the atoll are probably also an effect of the sediment enrichment process of this part of the atoll, where these nematodes scrape off organic coatings that can surround carbonate particles (Tietjen 1991) or directly feed on microalgae (both benthic and recently settled planktonic forms).

The hydrodynamic features that determined the significant accumulation of meiobenthic organisms, particularly nematodes, to the leeward side of Rocas Atoll probably also govern the drifting of plankton. Unfortunately, there are no data on the small-scale physical regime and plankton production at Rocas Atoll. A similar pattern of organism accumulation should indicate that the topographically controlled fronts, as suggested by Wolanski & Hamner (1988), play a key role in the ecology of reef islands.

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