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The relationship between benthic fauna, carbonate sediments and reef morphology in reef-flat tidal pools of Rocas Atoll (north-east Brazil)

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The composition of meiobenthic and macrobenthic communities between different intertidal reef-flat pools on Rocas Atoll (South Atlantic) was compared, and related to properties of the carbonate sediments and patterns of reef growth. Both univariate and multivariate statistical analyses showed that the reef height and size influenced the properties of the reef-derived sediments and were correlated with the composition and abundance of the benthic fauna in the intertidal pools. The temperature and the salinity between Rocas tidal flat reef pools did not vary significantly, despite the differences in size, exposure degree and elevation, suggesting that percolation through the porous lime body of the reef and/or the connection between the tidal pools and seawater by blowholes have a significant effect on the tidal pools. The major asymmetry in the reef topography of Rocas Atoll was observed between the leeward and windward reefs, which paralleled the largest changes in sediment properties and faunal structure inside intertidal reef pools. Sediments from the tidal pools located in the windward side of the atoll were significantly finer, the organic content higher and the benthic fauna more abundant and diverse. The results of this study suggest that significant changes in the sediment properties and benthic community structure between the intertidal reef-flat pools of Rocas Atoll may be primarily conditioned by different patterns in reef growth.

INTRODUCTION

Intertidal reef-flat pools represent a conspicuous and typical feature of reef formations within the tropical belt (Guilcher, 1988). However, contrary to the intertidal rocky pool environment, which has been the focus of investigations since the beginning of this century (Raffaelli & Hawkins, 1999), tropical reef-flat pools tend to be systematically excluded from studies and descriptions of reefs. As a result, no attempts have been made to describe the dynamics of these specialized habitats.

The optimum activity of reef organisms, whether constructive or destructive, is dependent on a series of processes from macroscale (e.g. sea level change) to microscale (e.g. bioerosion; Hubbard, 1997). Thus, the resulting reef morphology, as well as the composition of the reef-derived sediments, will be due to both mechanical and biological factors. Typically, reef growth is greatest on the wave-influenced margins, where a wave-resistant skin of massive encrusting algae encloses and protects a less rigid structure of skeletons and sediments (Preobrazhensky, 1993). For intertidal rock pools, it has long been recognized that the degree of exposure, the isolation from the shore, the height and size of the pools have a major influence on the structure of the benthic organisms (Huggett & Griffiths, 1986; Kooistra et al., 1989). The walls of intertidal reef-flat pools, despite their rigid appearance, are remarkably permeable. Nevertheless, variations in the degree of exposure, height and size also exist for reef pools and it is likely that they may have a similar effect on the fauna.

Despite the considerable research effort into the ecology of benthic communities associated with carbonate reef sediments as a whole (see review by Alongi, 1989), studies conducted in atolls are still scarce, geographically restricted to the Pacific and Indian oceans and primarily focused on the lagoon habitat (Salvat & Renaud-Mornant, 1969; Rao & Misra, 1983; Narayanan & Sivadas, 1986; Naim, 1988; Ansari et al., 1991; Intes & Caillart, 1994; Villiers & Bodiou, 1996). The only existing study conducted on intertidal reef-flat pools was by Fricke & Fricke (1979), who analysed the tidal-linked behaviour of a caridean shrimp at Aldabra Atoll (Indian Ocean).

Rocas is the only atoll in the South Atlantic and its reef is mainly built by encrusting coralline red algae (Gherardi, 1996; Kikuchi & Leão, 1997; Gherardi & Bosence, 2001). The reef perimeter, which can be as wide as 600 m, presents a number of intertidal pools, from narrow fissures to large pools with sandy bottoms. The intertidal pool environments have been considered a non-selective sedimentary trap, retaining a heterogeneous sediment related to wave action (Villora-Moreno, 1997). However, it has also been shown elsewhere (Netto et al., 1999a,b) that a strong gradient in the hydrodynamic regime from windward to the leeward side of the atoll affects the composition and abundance of benthic communities, particularly on the subtidal and intertidal habitats.

The aim of this study is to analyse comparatively the structure of meiobenthic (particularly nematodes) and macrobenthic communities in different intertidal reef-flat tidal pools of Rocas Atoll, Brazil and thus provide one of the few existing studies on this marine habitat. The patterns of reef growth (size and height) exhibited along the atoll are also examined and related to the carbonate sediments and benthic fauna of the reef-flat pools.

MATERIALS AND METHODS

Study site

Rocas Atoll is located 266 km off the north-east Brazilian coast (03°51′S 33°49′W; see Figure 1 in Netto et al. (1999a)) and it is built up on the western side of a flat-topped seamount within the Fernando de Noronha Ridge (Ponte & Asmus, 1976). The regional climate is tropical and dry: minimum air temperature is 26°C and annual average precipitation is only 109 mm (Höflich, 1984). South-easterly and easterly winds predominate with velocities up to 15 m s^{-1}. Local tides have a semi-diurnal regime with maximum amplitudes of 3.8 m (hurricane warning system; Gherardi, 1996). The atoll reef rim, mainly built by encrusting coralline red algae, has a slightly elliptical shape (3.5 km long and 2.5 km wide) and it is interrupted by north and north-west passes. There is a large number of intertidal pools on the reef perimeter. However, those with sand bottoms are less numerous (four reef-pools). The pools are located at both leeward and windward side, and on the southern margin of the atoll. Although the size and morphology of the reef-pools vary, depth is roughly similar (around 2.5 m). The central part of the atoll has a flat surface covered by discontinuous sheets of sediment, exposing underlying hard rock in places. There are two sand cays on the west part of the atoll (Farol and Cemitério Islands) with a maximum height of 3.7 m (mean tidal level, MTL). The lagoon, restricted to the north-east area of the atoll, has an average depth of 3.5 m and is connected to oceanic waters by the north reef pass. A full description of the atoll physiography is provided by Ottman (1962), Gherardi (1996) and Kikuchi & Leão (1997).

Sampling and sample processing

Samples were collected by SCUBA diving, during May 1996 at low spring tide. Three stations were established within each of the four available intertidal reef-flat pools, from the windward to the leeward margins of the atoll: pool 1, located at the leeward side; pools 2 and 3, both located at an intermediate area on the south margin of the reef perimeter; pool 4, the only one located on the windward side of the atoll. At each station, three samples for meiofauna were taken using a 2.5 cm diameter core tube pushed to a depth of 10 cm, and three samples with a 10 cm diameter core tube to a depth of 10 cm were taken for macrofauna. 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 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 sand fractions, which were then dried at 70°C and weighed. Sediment granulometry was determined by sieving dried samples (to one phi interval). For the determination of organic content, sediment samples were dried at 70°C and then combusted for 1 h at 550°C (Dean, 1974).

The reef pool size (longest axis) and the degree of exposure (measured as the lowest distance between the reef pools and the reef front) were recorded. Data from Gherardi (1996), who recorded the reef rim height based on topographic profiles, were also used to give an indication of the exposure of the reef pools. The salinity of water (temperature-compensating refractometer), temperature (hand-held mercury thermometer) and depth (digital depth gauge) were also recorded on site.

Data analyses

Univariate and multivariate statistical techniques used are described in Clarke & Warwick (1994). Environmental data (sediment mean grain size, sorting, % fines and % organic content, water temperature and salinity, reef pool size, distance of pools from reef crest and reef height) were converted to approximate normality using a log (x) transformation and ordinated using a correlation-based principal component analysis (PCA). The significance of the differences in textural composition of the sediment, temperature, salinity and depth between the four reef pools was tested using one-way analysis of variance (ANOVA). The Tukey honestly significant difference (HSD) multiple comparison test was used when significant differences were detected ($P<0.05$).

Differences in univariate measures of the meiofauna, nematodes and macrofauna (number of species or taxa and abundance) between the reef pools were tested using one-way ANOVA, and where results were significant ($P<0.05$), the Tukey test was applied. A fourth-root transformation was applied to the meiofauna, nematode and macrofauna abundance data, and lower triangular similarity matrices were constructed using the Bray–Curtis similarity measure. The data were then ordinated by non-metric multidimensional scaling. Formal significance tests for differences in meiofauna, nematode and macrofauna community structure between the reef pools were performed using the one-way analysis of similarities (ANOSIM) test. Evidence for a consistent biotic assemblage structure within the tidal pools of Rocas Atoll was analysed using the Spearman rank correlation (ρ) between the similarity matrices and environmental distance matrix and the significance determined using a permutation procedure (RELATE). The species (or taxa) contributing to dissimilarities between tidal pools were assessed using similarities percentages procedure (SIMPER).

The relationships between reef morphology, carbonate sediments and the univariate measures from the benthic fauna were investigated using a standard product-moment correlation analysis. The association between abiotic and

Table 1. *Mean values of the environmental variables and significance levels from one-way ANOVA tests for differences between the reef-flat tidal pools of Rocas Atoll. Analyses performed on log (x) transformed data. Significant differences evaluated with Tukey's HSD multiple comparison tests.*

	Tidal pools					
Variables	1	2	3	4	*P*	Comparison
Mean grain size (mm)	0.94	0.31	0.39	0.50	0.0001	1>2, 3>4
Sorting	0.68	1.25	1.01	0.86	0.019	4, 3>1, 2
Fines (%)	3.18	6.30	3.21	5.61	0.0006	2, 4>1, 3
Organic content (%)	1.67	2.83	2.97	3.30	0.021	4>2, 3>1
Temperature (°C)	31	29	29	29	0.38	–
Salinity (psu)	37	37	37	37	–	–
Depth (m)	2.15	2.27	2.60	2.70	0.23	–

biotic multivariate structure was then analysed using the RELATE procedure. Finally, the relationships between multivariate patterns of community structure and combinations of environmental variables were analysed using the BIO-ENV procedure to define suites of variables which best explain the faunistic structure.

RESULTS

Reef morphology and carbonate sediments

The major asymmetry in the reef topography at Rocas Atoll was observed between the leeward and windward reefs, where tidal pools 1 and 4 respectively are located. The reef crest was higher and the reef-flat wider at the windward (pool 4) when compared to the leeward side (pool 1) of Rocas Atoll. The shortest distance between the tidal pools and the reef front, which is dependent on the size of the reef-flat, was for pool 1 (22 m), at the leeward side, and the largest for pool 4 (353 m). The reef crest height and the size of the reef-flat, on which the remaining tidal pools 2 an 3 are located, showed intermediate values between these two extreme conditions of the leeward and windward sides of the atoll.

The carbonate sediments in the reef-flat tidal pools ranged from coarse and moderately well sorted sand in pool 1 to medium and poorly sorted sand in pool 4 (Table 1). Percentage fines in reef pools 2 and 4 (around 6%) were significantly higher than at the remaining sites (Table 1). Total sediment organic content was significantly higher in reef pool 4 (mean of 3.30%) and lower in reef pool 1 (1.67%, Table 1). Water temperature, depth and salinity did not vary significantly between the reef-flat tidal pools (Table 1).

Ordination by principal component analysis of all the environmental data showed a clear distinction between each of the reef-flat pools (Figure 1). The first two principal components accounted for 77% of the data variance (PC1- 58%; PC2- 19%). High positive values along PC1 were associated with reef height and distance from reef pool to reef crest, whilst negative values related to temperature and mean grain size. For PC2, high positive scores were due to % fines and sorting, and negative values with sediment organic matter.

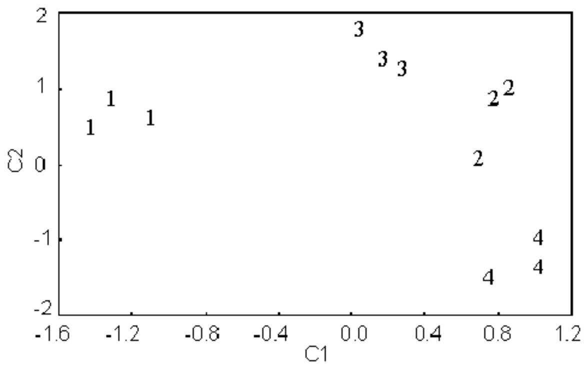

Figure 1. Ordination of the environmental variables by a correlation-based principal component analysis. Numbers refer to replicates from pools 1–4.

Meiofauna and macrofauna diversity

The meiofauna community within the reef-flat pools of Rocas Atoll was composed of 95 taxa. The number of meiobenthic taxa was lower in the leeward reef pool 1 (Tukey's HSD test, Figure 2A), but did not vary significantly between the other sites. Mean population density of total meiofauna varied between 278 and 4165 ind $10\,cm^{-2}$, being significantly higher in the windward reef-flat pool 4 and lower on pool 1 (Figure 2B). Nematodes (45%) and copepods (44%) numerically dominated the meiofauna over the sites, except for the leeward reef pool 1, where the polychaetes were more abundant (55% of total meiofauna).

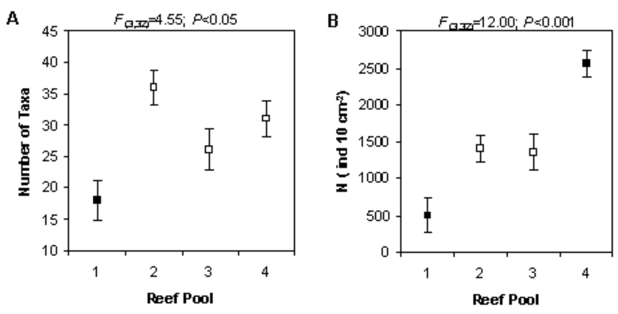

Figure 2. *F*-ratios and significance level from one-way ANOVA tests, means and standard errors for: (A) number of taxa; and (B) density of total meiofauna within the four reef pools of Rocas Atoll. ■, significant difference at $P<0.05$.

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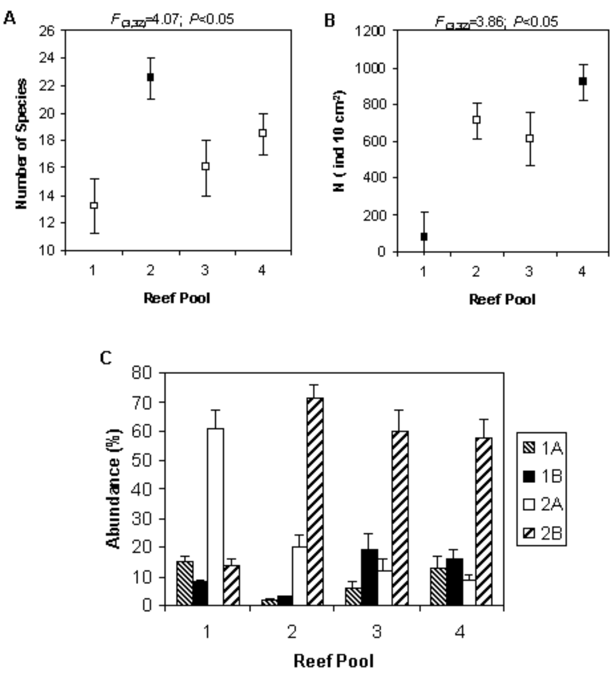

Figure 3. Means and standard errors for: (A) nematode number of species; (B) abundance; and (C) feeding types as mean percentage of abundance within the four reef pools of Rocas Atoll. ■, significant difference at $P<0.05$.

Among the 29 putative species of meiobenthic polychaete recorded, 87% belonged to the families Nerillidae (47%) and Syllidae (40%), with *Nerillidium* sp. 1 and *Syllis* (*Ehlersia*) *cornuta* the most abundant taxa. For the nematodes, a total of 61 putative nematode species was recorded from the reef-flat pools, and their number was significantly higher in pool 2 (Figure 3A). *Chromaspirinia* sp. 1 (Desmodoridae), *Metoncholaimus* sp. 1 (Oncholaimidae), *Gomphionema* sp. 1 (Ethmolaimidae) and *Paralinhomoeus* sp. 2 (Linhomoeidae) were the most abundant. The population density of nematodes, ranging from 53 to 2592 ind 10 cm^{-2}, was significantly higher in reef pool 4 and lower in pool 1 (Figure 3B). Analysis of nematode feeding types according to Wieser's (1953) classification showed a significant dominance ($P<0.001$) of predator/omnivore feeding type (2B), except for leeward pool 1 where epigrowth feeders dominated (type 2A, Figure 3C).

The macrofauna community at these sites was composed of 79 taxa, the number of macrobenthic taxa varying significantly between the sites, being lower in the reef pool 1 (Tukey's HSD test, Figure 4A). Macrofauna density, ranging from 5000 to 167,000 m^{-2}, also followed the same trend of meiofauna and nematodes: significantly higher in the windward reef pool 4 and lower in pool 1 (Figure 4B). Tubificidae oligochaetes largely dominated, accounting for 55% of total macrofauna. The next most abundant groups were nematodes (23% of the total macrofauna) and polychaetes (16%). Among the 26 putative macrobenthic nematode species recorded, *Metoncholaimus* sp. 1, *Paralinhomoeus* sp. 2, and *Anticoma* sp. 1 (Anticomidae) were the most abundant forms. For the polychaetes, 36 putative species were recorded and the numerically important ones were *S. cornuta*, *Caulleriella* cf. *alata* (Cirratulidae) and *Hermodice carunculata* (Amphinomidae).

The multidimensional scaling (MDS) ordinations derived from meiofauna, nematodes and macrofauna data are presented in Figure 5. All MDS plots demonstrated a similar pattern in which pool 1, located at the leeward reefs, represented the most distinctive site out of the reef-flat tidal pools of Rocas. The remaining reef-flat pools (2, 3 and 4) formed a more compact group of stations, although each of the pools were clearly apart from each other. The results of ANOSIM tests for differences in benthic community structure between the reef-flat tidal pools revealed that the differences between pools were all highly significant (Global R values: meiofauna 0.64, nematodes 0.52, macrofauna 0.75, all $P<0.001$). An examination of the pairwise comparisons demonstrated that each pair of pools differed in community structure (minimum $R=0.27$, $P=0.028$ for nematodes in pools 3 and 4). The relative differences were higher between leeward reef pool 1 and windward pool 4, with particularly high R values for the macrofauna (all $R>0.66$, all $P<0.001$).

The analysis of the community patterns for evidence of a common biotic structure between the reef pools (RELATE procedure) showed that all similarity matrices derived from meiofauna, nematodes and macrofauna were significantly correlated ($P<0.001$). The highest correlation was detected between the meiofauna and nematode abundance (0.83), whilst the lowest was between macrofauna and nematodes (0.66). Correlation between meiofauna and macrofauna matrices was 0.69.

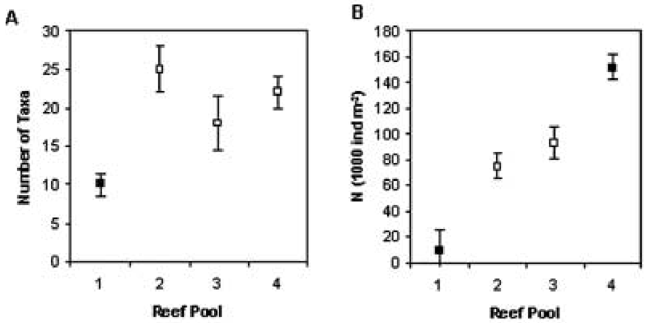

Figure 4. F-ratios and significance level from one-way ANOVA tests, means and standard errors for: (A) number of taxa; and (B) density of total macrofauna within the four reef pools of Rocas Atoll. ■, significant difference at $P<0.05$.

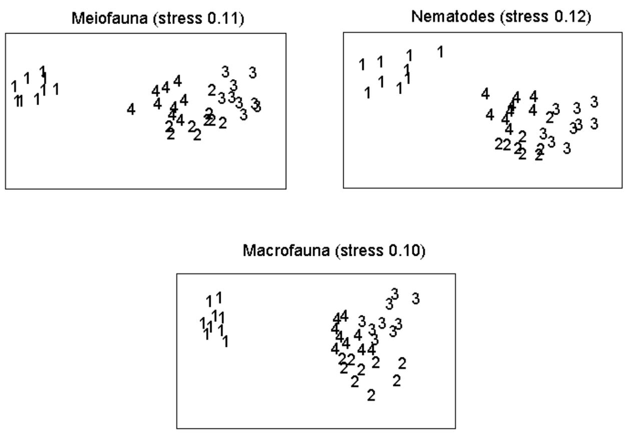

Figure 5. The MDS ordinations of transformed abundance data for meiofauna, nematodes and macrofauna within the reef pools of Rocas Atoll.

Table 2. *Summary results from BIO-ENV analysis derived from abiotic and faunal data of the reef-flat tidal pools of Rocas Atoll. Analysis performed by combining the environmental variables,* k *at a time, yielding the best match of biotic and abiotic similarity matrices, as measured by weighted Spearman rank correlation. Bold values indicates the highest correlations.*

k	Best variable combinations		
Meiofauna			
1	reef height 0.79	organic content 0.75	distance pools-reef front 0.71
2	reef height organic content **0.83**	distance pools-reef front organic content 0.80	
3	reef height distance pools-reef front organic content 0.81		
Nematode			
1	reef height **0.80**	distance pools-reef front 0.74	mean grain size 0.63
2	reef height mean grain size 0.75	reef height pool size 0.73	
3	reef height distance pools-reef front mean grain size 0.76		
Macrofauna			
1	reef height 0.70	pool size 0.68	temperature 0.65
2	reef height temperature 0.72	pool size temperature 0.71	
3	reef height pool size temperature **0.77**		

The SIMPER analysis of meiofauna, nematodes and macrofauna abundance data was used to determine the contribution from individual taxa or species to the Bray–Curtis dissimilarities between reef-flat tidal pools and to similarities within a pool. Samples from reef pool 1, at the leeward side of the atoll, was mainly distinguished by the low number of species and abundance of both meiofauna and macrofauna. Species important in discriminating reef pool 1 were the polychaetes *Nerillidium* sp. 1 (16%) and *Pionosyllis gesae* (14%), and to a lesser extent the nematode *Desmodora* sp. 1 (9%). Variation in abundance of a range of species common to the remaining sites accounted for most of the pairwise dissimilarities between reef-flat pools 2, 3 and 4. The community at the tidal pool 2 were characterized by the nematodes *Metoncholaimus* sp. 1, both meiobenthic and macrobenthic forms (14.9% and 16% respectively), and to a lesser extent *Chromaspirinia* sp. 1 (8%). The predator/omnivorous nematode *Gomphionema* sp. 1 (18%) and the cirratulid polychaete *Caulleriella* cf. *alata* (15%) were the species that contributed most to the similarities within samples from reef-flat pool 3. Pool 4, at the windward reef of the atoll, was mainly characterized by high densities of both meiofauna and macrofauna, especially oligochaetes and the nematode *Chromaspirinia* sp. 1 (15.6%).

Correlations between reef morphology, carbonate sediments and benthic fauna

The relationships between the multivariate community structure and all the environmental variables (reef morphology and sediments properties) were analysed firstly by comparing the biotic similarity matrices, constructed from averaged transformed data, with the distance matrix derived from abiotic data. The results of the RELATE analysis showed that all biotic matrices were significantly correlated with the abiotic matrix (meiofauna ρ=0.747, Nematoda=0.799, macrofauna=0.726, all $P<0.006$).

The interrelationships between the multivariate community structure and combinations of environmental variables were also examined using the BIO-ENV procedure, the results of which are summarized in the Table 2. The highest correlation shown for the fourth-root transformed meiofauna abundance was 0.83 with two variables, reef height and organic content. Fourth-root transformed nematode abundance data showed a highest correlation (0.80) with a single variable, reef height (Table 2). Adding further variables into the analysis degraded the correlation. For the macrofauna data, the highest correlation was 0.77 also with reef height, but with the addition of pool size and temperature.

DISCUSSION

The results of this study showed that the structure of meiobenthic and macrobenthic communities differs between the intertidal reef-flat pools of Rocas Atoll. Both univariate and multivariate statistical analyses indicated that variable patterns in reef morphology and distance of reef pools relative to the incident waves affect the textural properties of the tidal pools' carbonate sediments and correlate with the composition and abundance of the benthic fauna. Although the structure of the meiofauna and macrofauna communities display a similar trend in the distribution along the intertidal reef pools, the taxonomic composition suggests a differential response of the two components of the benthos.

The reef-flat zone of Rocas Atoll consists mainly of a poorly cemented pavement of coralline algae with a rugged surface, together with a range of detrital material derived from the other parts of the reef. Due to this morphology, and the action of bioerosion, cavities are generated within the framework (Tucker & Wright, 1990) resulting in extremely porous internal parts of the reef (Guilcher, 1988; Sorokin, 1993). Consequently, there is potentially a significant exchange process between the tidal pools and the nearby oceanic water. Whilst physico-chemical variability in rocky shore intertidal pools of different sizes can be extremely high, and differ considerably from the adjacent seawater (Morris & Taylor, 1983), due to the porosity of the reef, the environmental instability of intertidal reef pools is likely to be much less. Indeed, at Rocas Atoll neither temperature nor salinity varied significantly between the reef pools and the adjacent sea (Netto et al., 1999a). This result suggests that percolation through the porous lime body of the reef and/or the connection between the tidal pools and the seawater by blowholes have a significant effect on the tidal pools. The Rocas pools did, however, differ significantly in the particle size of their carbonate sediments which reflects the gradient in exposure across the reef that is correlated with reef growth and subsequent morphology (Gherardi, 1996) and thus influences the nature and textural attributes of reef-derived carbonate sediments. As the reef-flat normally contains little loose sediment (Netto et al., 2000), the tidal pools act as traps for the carbonate particles. The high exposure to wave action characteristic of the reef tract, even on the leeward side, is reflected by the general coarseness of the sediment found in the Rocas tidal pools. However, the higher and wider the reef (i.e. higher exposure), the finer the sediment in the tidal pools. This relationship, evidenced by the significant correlations between the reef morphology and mean grain size (negatively correlated) and percentage fines (positive correlation), probably reflects the comparative amount of transport and abrasion that the biological-derived grains have undergone over the leeward and windward margins of Rocas Atoll reefs.

Although there is a complete lack of data on the structure of benthic communities in reef-flat tidal pools, the composition of the meiofauna, especially the nematodes, showed similarities with assemblages from the shallow tropical carbonate benthos (Salvat & Renaud-Mornant, 1969; Rao & Misra, 1983; Tietjen, 1991; Gourbalt et al., 1995). These similarities were particularly evident for nematodes at family level, mainly composed by Desmodoridae (40%), Oncholaimidae (19%), Ethmolaimidae (11%) and Linhomoidae (10%). At lower taxonomic levels, however, the affinities between the communities were less apparent. Whilst the nematodes in the windward reef pools were dominated by omnivorous/predatory species (*Chromaspirinia* sp. 1, *Gomphionema* sp. 1, *Metoncholaimus* sp. 1), reef pool 1 (leeward) was dominated by epigrowth feeding species such as *Desmodora* sp. 1 and *Spirinia* sp. 1. The higher abundance of omnivores/predators clearly contrasts with some findings in the reef system from the Pacific or Indian oceans which are largely dominated by non-selective deposit feeders (Gourbalt & Renaud-Mornant, 1990; Tietjen, 1991). Although the precise nature of Wieser's (1953) group 2B omnivore/predator is poorly understood, it has been suggested that species belonging to this group may scavenge off dead animal remains, forage in detrital material, are opportunistic feeders or even facultative predators (Moens & Vincx, 1997). Nevertheless, the discrepancies in nematode population structure and trophic composition in reef sediments are more likely to be related to the variability within different reef zones. Most of the meiofauna data from atolls or other reef systems were derived from studies focused on the lagoon or on the shallow platform, which probably do not represent the meiobenthic community structure of the whole system. Netto et al. (1999a) have already shown that meiobenthic community structure and nematode feeding types differ significantly between contrasting zones of Rocas Atoll. This is further supported by the report of Alongi (1986) that population structure and trophic composition of nematodes differ between zones of Davis Reef, Australia, and that the sediments from the reef crest were also dominated by predatory and omnivorous species. In the specific case of differences observed in nematode composition within Rocas Atoll reef pools, these changes in the community structure are probably related to the differential pattern in growth-related morphology of the reefs, or some variable correlated with it, such as the quality and amount of the food particles carried from the reef to each tidal pool.

In contrast to the similarities exhibited within the nematode community, the macrofauna of Rocas Atoll reef pools did not show the typical taxonomic composition recorded in other tropical carbonate bottoms (Riddle, 1988; Naim, 1988; Alongi, 1989; Ansari et al., 1991; Nacorda & Yap, 1997). Netto et al. (1999a,b, 2000) suggested that the benthic macrofauna at Rocas Atoll evidenced a stressed assemblage, but the intertidal reef pools, although located in the very limit of the reef, are subjected to a less harsh environment than other parts of the atoll. Furthermore, the number of macrobenthic species in the pools is normally higher than other zones of an atoll. However, the differential effect of physical stress on the meiofauna and macrofauna was evidenced by the dominance of oligochaetes, large nematodes and small surface-dwelling polychaetes. Other groups such as molluscs, crustaceans, and echinoderms accounted for less than 5% of the macrofauna. This result probably suggests that the relatively small sized macrofauna with a surface-dwelling opportunistic nature, may respond rapidly to intermittent (albeit low) nutrient inputs and physical stress. Similar differential responses of both components of the benthos, in which the macrofauna was more affected than the meiofauna by physical stress, have been found in other intertidal areas (Austen et al., 1989) and subtidally (Josephson & Wildbom, 1988; Warwick et al., 1990; Netto et al., 1999b).

The average density of the benthic fauna in the intertidal reef-flat pools of Rocas Atoll, particularly the macrofauna, was generally higher than those summarized by Alongi (1989) or recorded in more recent studies from other reef habitats (Arlt, 1995; Nacorda & Yap, 1997). Similarly, the meiofauna and macrofauna abundances in the reef-flat pools are significantly higher than other reef zones of Rocas Atoll (Netto et al., 1999a). Kinsey (1985) suggested that reef-flats are the most productive zone of the reef, although major imbalances may occur within particular zones over short periods of time. In turn, Yap et al. (1994) argued that some components of the reef-flat are likely to export organic matter to the more heterotrophic portions of the reef, such as some areas covered by sediments. The detritus fuelling tidal pool meiobenthos and macrobenthos may be derived from a variety of sources including that from the reef-flat and other hard substrates, *in situ* benthic production as well as those derived from the water column biota. Both the meiofauna and the macrofauna of Rocas reef-flat pools showed a significant increase in densities from leeward (pool 1) to windward margins of the atoll (pool 4). The increase in organism density is paralleled by an increase in the sediment organic content towards pool 4, which was positively correlated with both reef height and size. Therefore, it is likely that the variability in meiofauna and macrofauna abundance between leeward and windward reef-flat pools of Rocas Atoll is a result of two main factors caused by the differential morphology of coralline algal reef. Firstly, the amount of organic matter derived from a wider and active-growing reef is probably higher than those from the featureless leeward side, material from the active-growing reef combining with comparatively large amounts of organic matter derived from the reef flat flora and fauna. Secondly, the maximum windward reef growth, which is reflected by a higher reef ridge height and reef-flat size, may prevent a more direct wave action on the shallow bottom of the tidal pool which would increase sediment instability and resuspension. The macrofauna abundance, as evidenced by the BIO-ENV analysis, was also related to temperature and reef pool size. However, temperature did not differ significantly between pools, but mean values were high in the small reef pool (pool 1- at the leeward). Morris & Taylor (1983), suggested that any increase of water temperature will also decrease gas solubility, in particular the oxygen. Moreover, diffusion across the air–water interface is also affected by temperature (Huggett & Griffiths, 1986). Thus it is possible that the small leeward reef pool, which has a small area for gas diffusion across air–water interface, is more affected by the temperature variability and the fauna subjected to higher physiological stress.

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