



## Impacts of artificial reef spatial configuration on infaunal community structure – Southeastern Brazil



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### ABSTRACT

Degree of isolation among reef modules is a habitat variable that can alter the structure and dynamics of reef-associated groups. This study evaluated the influence of the small-scale spatial distribution of artificial modules on infaunal community structure and associated it with the hydrodynamic and geochemical characteristics of the surrounding sediments and with fish predation pressure. Reefballs™ were placed on a sandy bottom on the northern coast of Rio de Janeiro in modules with a triangular set configuration with side lengths of 0.5, 5 and 15 m. The availability of potential macrobenthic prey for the reef-associated fish community was evaluated using gillnets for each inter-module distance. The input of organic matter and fine sediment into the reef complex during the rainy season favored deposit feeders. Shorter distances showed reduced fine sediment and nutrient deposition and, consequently, a lower density of deposit feeders in the infauna compared with more distant modules, which had a greater number of predators and suspension feeders. The surrounding infauna responded positively to the grain-size composition. This result suggests that transient fishes use the artificial reefs for purposes such as shelter, nursery and breeding habitats. Shifts in infaunal structure reflected the physical disturbance following the deployment of the artificial reefs and the seasonal variations but did not respond to the spatial design, showing the importance of these configuration variables and their influence on the associated infaunal community.

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### 1. Introduction

Artificial reefs (ARs) may influence the environment over a spatial scale of tens to hundreds of meters from the reef itself (Wilding and Sayer, 2002). This influence includes changes in nutrient cycling and transport (Falcão et al., 2007) and in sediment biogeochemistry (Alongi et al., 2008; Cheung et al., 2010) as a response to modifications of water-flow intensity and current direction. Sediment and organic matter removal or deposition on reefs alters the distribution of the sediment grain-size classes in the area and surrounding regions (Fukunaga and Bailey-Brock, 2008; Wilding, 2006). These changes are associated with variations in the composition and abundance of the surrounding infaunal organisms (Langlois et al., 2006; Lorenzi and Borzone, 2009).

The extent and intensity of changes induced by the reef may vary due to the spatial configuration and geometry of the artificial structures (Burt et al., 2009; Thompson et al., 2007). Degree of reef isolation not only physically changes the system but also directly interferes with the occurrence and abundance of benthivorous fishes (Hunter and

Sayer, 2009). Optimal foraging theory suggests that decreased foraging time will increase net energetic gain (MacArthur and Pianka, 1966; Stephens and Krebs, 1986) and reduce the risk of predation (Milinski, 1986 in Jordan et al., 2005). However, closely spaced reef patches can result in overlapping halos, with a concomitant decrease in benthic prey density and, in turn, the density of benthic foragers. This interference then leads to a reduction of infauna near the artificial modules (Barros et al., 2004; Bortone et al., 1998). Lindberg (1996) observed a greater abundance of many reef fish species that forage on the surrounding sediment on configurations in which isolation was 10 times greater (25 vs. 225 m). Therefore, the consumption of prey items by resident fishes likely occurs faster near the reef, resulting in a halo of decreasing benthic prey density (Bortone et al., 1998).

ARs can be easily replicated, accounting for structural variability (e.g., size and complexity), and they can be used in an infinite range of spatial arrangements to further evaluate the significance of reef structural features. However, the use of ARs, either in experimental studies or in coastal resources management, often lacks consideration of reef spacing effects on small scales (i.e., tens to thousands of meters).

Most studies with ARs emphasize the community structure (Santos et al., 2010, 2011), the associated fish-community trophic ecology (Fabi et al., 2006; Herrera et al., 2002) and epifaunal colonization

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(Boaventura et al., 2006; Hunter and Sayer, 2009). Few studies have considered the impact on the surrounding infauna (Barros et al., 2001; Fukunaga and Bailey-Brock, 2008; Machado et al., 2013; Wilding, 2006). Knowledge regarding the influence of reef module distances on infaunal community composition and structure is scarce, but these factors are potentially related to the recruitment and dynamics of associated fishes (Belmaker et al., 2011; Jordan et al., 2005; Schroeder, 1987; Walsh, 1985).

In this context, understanding the influence of reef module distances on infaunal structure is of fundamental importance in AR deployment design because the macrobenthic infaunal organisms have an important ecological role in the marine food chain. The purpose of the present study was to evaluate the influence of the spatial distribution of AR modules on the composition and structure of associated infauna, relating it to the hydrodynamic and geochemical characteristics of the surrounding sediments and to fish predation pressure. The hypotheses were as follows: i) reduced distances between ARs lead to a higher deposition of fine sediment and an accumulation of nutrients due to the decrease in bottom-current intensity and consequently lead to a higher density of infaunal deposit feeders; and ii) reduced distances between reef modules lead to higher infaunal predation and lower density, richness and diversity of the macrobenthic community.

## 2. Materials and methods

The study area (21° 29'S, 41° 00'W) is located on the continental shelf north of Rio de Janeiro State (Brazil) and is adjacent to the mouth of the Paraíba do Sul River (see Santos et al., 2010 for the geographic location and spatial arrangement of the AR complex). The climate of the drainage basin of this river is characterized as warm subtropical, with average annual temperatures ranging from 18 to 24 °C (Marengo and Alves, 2005). The Tropical, Coastal and South Atlantic Central water masses all influence the study area. Primary productivity (chlorophyll a) is low, the Secchi depth does not exceed 4 m, and strong bottom currents are common (Krohling and Zalmon, 2008). The north coast of Rio de Janeiro naturally has little rocky substratum or other hard substrates and is covered by extensive sandy beaches with variable amounts of mud and calcareous nodules (i.e., rhodolites; Zalmon et al., 2002).

The Paraíba do Sul River is an important ecosystem component on the north continental shelf of Rio de Janeiro State, contributing nutrients primarily during the spring and summer, with the export dynamics of dissolved and particulate materials correlated with rainfall (Figueiredo et al., 2011; Silveira et al., 2000; Souza and Knoppers, 2003). Precipitation in the Paraíba do Sul River drainage basin is the primary factor controlling the flow rate and exhibits two distinct periods: dry from May to September and rainy from October to April (Carvalho et al., 2002). The average monthly flow of the Paraíba do Sul River in the region was obtained from the National Water Agency ([www.ana.gov.br](http://www.ana.gov.br)), and the mean pluviosity values were obtained from the National Institute of Meteorology ([www.inmet.gov.br](http://www.inmet.gov.br)).

### 2.1. Experimental design

A total of 18 concrete AR Reefballs™ (~1.0 m<sup>3</sup>; 0.5 t displacement), set 9 m from the surface on a flat bottom, were arranged in sets of three modules or units, each in a triangular configuration with varying distances between the modules (0.5, 5 and 15 m) and a distance >50 m between the groups. The surrounding sediment was collected in September 2009 (D1) and 2010 (D2) (end of the dry period) and in April 2010 (R1) and 2011 (R2) (end of the rainy period). Samples of the first 15 cm of sediment were collected by divers 1 m away from the units for each experimental distance (N = 6 replicates per treatment) using a stainless steel corer (0.018 m<sup>2</sup>).

A 20-g sediment subsample of each replicate was used for analyses of the grain-size distribution, total carbonate (Carb) and total organic

carbon (TOC). Infauna was fixed in 10% formaldehyde, sieved through a 500-µm mesh, sorted and identified to the lowest taxonomic level. The Carb level was determined by acid treatment, with the addition of 20 mL HCl (1.0 M) to 1 g of dry sediment overnight. The grain-size distribution was determined using a particle analyzer by laser diffraction (Shimadzu Model SALD-3101) in several fractions based on the Wentworth scale (Suguio, 1973), and the TOC was determined using a CHN analyzer after removing the Carb with HCl (1.0 M) added directly to silver vials.

Each taxon from the sediment samples was assigned to a functional group according to its trophic group, following Fauchald and Jumars (1979), Kamermans (1994) and Dolbeth et al. (2009) (surface-deposit feeders [SD], subsurface-deposit feeders [SSD], suspension feeders [S], omnivores [O] or carnivores [C]), and according to its mobility (mobile [M], discretely mobile [DM] or sedentary [S]).

Gillnets (25 × 3 m; 30-mm mesh size) were submerged for 24 h over each reef-module group (N = 6 replicates per treatment) during the same infauna-sampling period to identify potential fish predators and their respective reef-associated benthic prey. The captured fishes were identified and counted, and their stomachs were removed. The stomach contents were separated, identified into groups and weighed.

### 2.2. Data analysis

The species density (ind/m<sup>2</sup>), richness, Shannon diversity index and Simpson dominance index were used as descriptors of the reef-surrounding macrobenthic community structure with respect to spatial (between reef distances: 0.5, 5 and 15 m) and temporal (between dry and rainy periods and between years 1 and 2) variations. The descriptors species density (ind/m<sup>2</sup>), richness, diversity and dominance, as well as the sediment-parameter data, were tested using analysis of variance (ANOVA) and a posteriori Tukey's tests to identify spatial and temporal differences between means. The distances and periods were treated as fixed orthogonal factors, and years 1 and 2 were considered random hierarchical factors in the interaction of orthogonal factors. Cochran's test was used before the ANOVA to test for homogeneity of variance. When necessary, a log(x + 1) transformation was used to reduce data heterogeneity (Underwood, 1998).

The pattern of infauna association was compared among the distances (0.5, 5 and 15 m), periods (rainy and dry) and years (1 and 2) through a matrix of the transformed abundance data of the representative species and ordinated (non-metric multidimensional scaling [nMDS]) using the Bray–Curtis similarity index (Clarke and Warwick, 2001). A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001, 2005) was applied for a multivariate comparison of infaunal composition among the distances, periods and years. The Bray–Curtis similarity distance was chosen as a base for the PERMANOVAs. The species density log-transformed data were permuted 9999 times per analysis at a significance level of 0.05. The multivariate analyses were performed using PRIMER v.6 statistical software (Clarke and Warwick, 2001).

The species distributions for the distances (0.5, 5 and 15 m), periods (dry and rainy) and years (1 and 2) and the relationship with the sediment characteristics (total Carb content, organic carbon and grain size), Paraíba do Sul River flow rate and pluviosity mean values were analyzed by canonical correspondence analysis (CCA) using the FITOPAC 2.1 software. The species included in the CCA represented 75% of the total abundance. The significance levels of the canonical axes and variables were determined using a Monte Carlo test ( $p < 0.05$ ) (Ter Braack, 1986).

Fish predation was analyzed through the taxonomic composition of and respective number of food items in the stomachs of the fishes captured in the nets, considering each sampling distance (0.5, 5 and 15 m), period (dry and rainy) and year (1 and 2). The index of relative importance (IRI) was calculated for the main prey categories using the following equation:  $IRI = (\%N + \%M)\%F$ , where N is the number of items, M is the mass (g) and F is the frequency of the prey type in the stomach

**Table 1**

ANOVA results of sediment parameters and nutrients (GRA: gravel; SAND: sand; MUD: mud; CARB: carbonate; TOC: total organic carbon) between sampling distances ( $0.5 \times 5 \times 15$  m), periods (dry  $\times$  rainy) and years ( $1 \times 2$ ).

	df	Factors			
		Distance	Period	Year	Distance*Period*Year
		2	1	1	2
GRA	F	0.357	0.003	1.841	3.899
	p	0.737	0.960	0.352	0.025*
SAND	F	0.712	0.431	6.364	7.994
	p	0.584	0.579	0.136	0.001**
MUD	F	0.985	1.110	2.070	5.567
	p	0.504	0.403	0.326	0.006**
CARB	F	0.075	4.385	0.604	2.140
	p	0.930	0.171	0.623	0.126
TOC	F	0.274	1.883	1.488	9.899
	p	0.785	0.304	0.402	<0.001**

\*  $p < 0.05$ .

\*\*  $p < 0.01$ .

contents (Pinkas et al., 1971). Fish predation was evaluated by Pearson's correlation coefficient between the number of captured fish at the 0.5, 5 and 15 m reef sets and the total number of infaunal individuals at each respective distance, as well as between ichthyofauna food items and the reef-associated infauna at each respective distance. Kolmogorov–Smirnov's test was used before correlation to test for data normality (Zar, 1994).

### 3. Results

#### 3.1. Rainfall and Paraíba do Sul River flow

The mean flow of the Paraíba do Sul River (R1: 1513 m<sup>3</sup>/s; R2: 1647 m<sup>3</sup>/s; D1: 498 m<sup>3</sup>/s; D2: 625 m<sup>3</sup>/s) and the mean precipitation values (R1: 98 mm; R2: 101 mm; D1: 31 mm; D2: 27 mm) were significantly higher in the rainy periods of both years ( $p < 0.05$ ).

#### 3.2. Sediment characterization

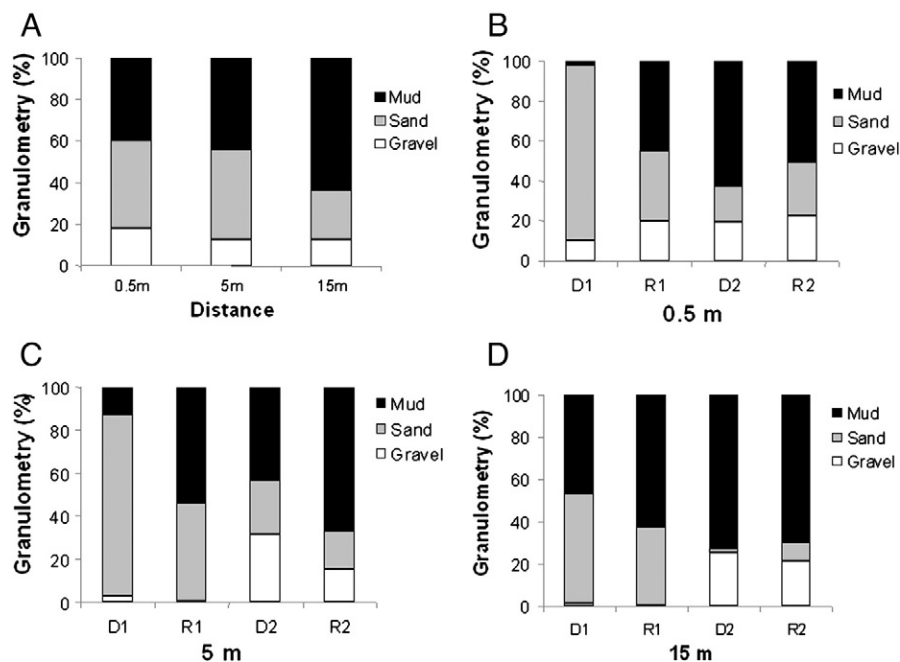
The grain-size compositions were similar 0.5 and 5 m from the reefs, with the highest mean values for sand and gravel (~20% each) and the highest value for mud at 15 m (60%) (Fig. 1A), with no significant spatial differences (Table 1). Temporal variation was significant at the 0.5-m reef distance, with the highest values for sand and gravel in D1 and R1, respectively (Fig. 1B, C, D; Table 1). Significantly higher mud contents were found in year 2 ( $p < 0.05$ ) (Fig. 1B, C, D; Table 1).

The mean Carb percentages did not differ over space or time (Table 1), whereas the TOC was significantly smaller only in periods D1 and D2 at 0.5 m and in R1 at 5 m (Table 1, Fig. 2). A comparative analysis between years revealed significantly higher values for TOC in the rainy period of the second year (Fig. 2).

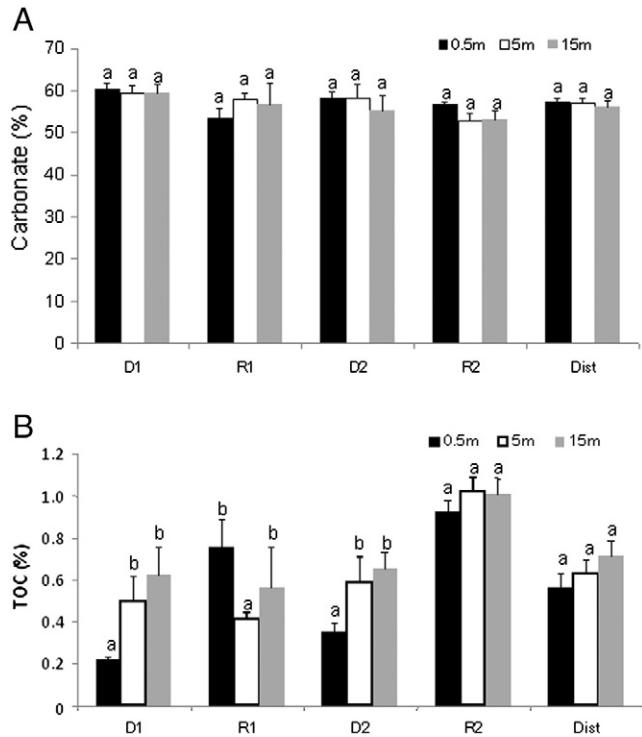
#### 3.3. Infauna

The infauna of the reef area comprised a total of 89 taxa, including 46 Annelida, 27 Mollusca, 13 Arthropoda (Crustacea) and 1 taxon each of Echinodermata, Echyura and Sipuncula. The Annelida predominated at reef distances of 0.5 and 5 m, Crustacea predominated at 0.5 and 15 m, and Mollusca predominated at 15 m (Fig. 3A). Differences in infaunal density were recorded among sampling periods, with the lowest values for Annelida at 15 m during D1 (18.5 ind/m<sup>2</sup>) and R1 (18.5 ind/m<sup>2</sup>) (Fig. 3B, Table 2) and for Crustacea at 5 m during D1 and R1 (0 ind/m<sup>2</sup>) (Fig. 3C, Table 2). The density of Mollusca presented higher values during R1 and D2 than in the other periods (Fig. 3D).

The annelids *Goniadides carolinae*, *Syllis* sp., *Lumbrineris latreilli*, *Exogone* sp. and *Paraonis gracilis gracilis* and the bivalve mollusks *Corbula caribaea* and *Crassinella martinicensis* represented 52% of the total abundance of infauna at the reefs. Two species were common to all 4 periods: *G. carolinae* and *Syllis* sp. A total of 48 exclusive species were found during the rainy periods representing 54% of the total abundance, with an emphasis on the mollusks *Corbula lyoni* and *Calyptolana* sp. During the dry periods, 22 exclusive species were found (25% of the total), particularly *Crassispira cubana* and *Gymmonereis* sp. (Table 3). Among the most abundant species, *G. carolinae* predominated at 0.5



**Fig. 1.** Grain-size composition in the reef complex at the 3 distances (A) and at 0.5 m (B), 5 m (C) and 15 m (D) per sampling period (D1: September 2009; D2 September 2010; R1: April 2010; R2: April 2011) (N = 6 replicates per treatment).



**Fig. 2.** Mean  $\pm$  standard error for carbonate (A) and total organic carbon (B) percentages of the sediment at distances of 0.5, 5 and 15 m per sampling period (D1: September 2009; D2: September 2010; R1: April 2010; R2: April 2011) (N = 6 replicates per treatment). Different letters indicate significant differences ( $p < 0.05$ , Tukey's HSD post hoc test) between distances for the same period.

and 5 m and *C. caribaea* at 15 m (Table 3). The trophic groups of carnivores, suspension feeders and omnivores occurred at higher densities at the shorter distances, whereas the surface-deposit feeders predominated at the 15-m intermodules (Table 3).

The structure indicators species richness and density differed significantly with AR spacing, exhibiting higher values at 0.5 m during the

period R1, with the dominance index increasing during D1 (Fig. 4, Table 4). The lowest richness, density and diversity values were recorded in the dry period of the first year (Fig. 4).

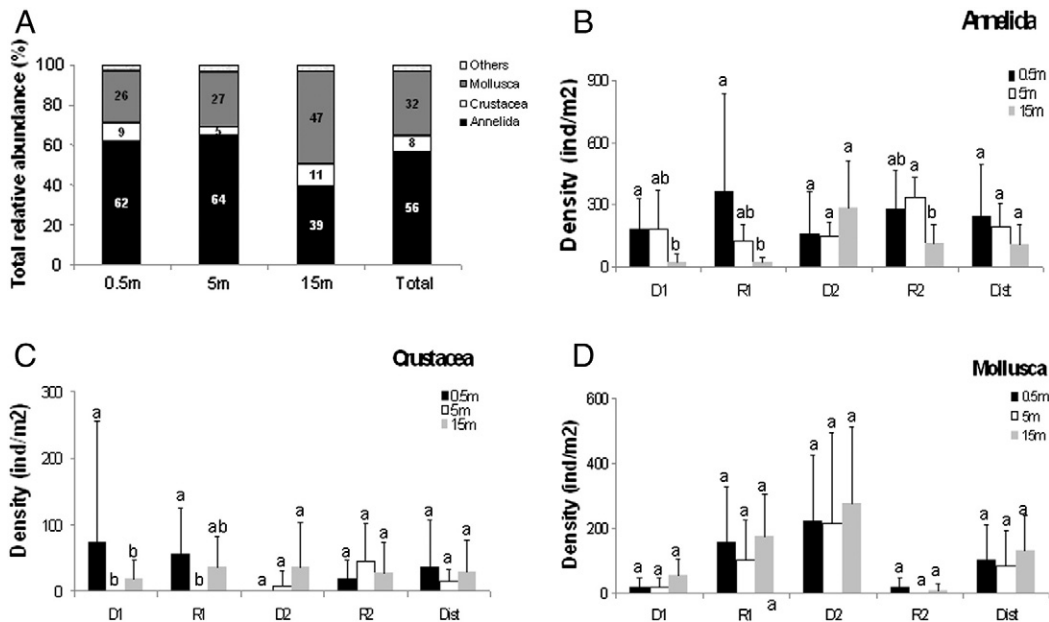
The nMDS diagram showed no clear spatial separation of the distances in either of the sampled years (Fig. 5A, B) but showed a temporal variation (dry vs. rainy) of the infauna in year 2 (Fig. 5B).

The PERMANOVA analysis detected no significant differences in infaunal composition or abundance between the reef distances and sampling periods. However, a significant difference was detected between years (Table 5). The a posteriori test indicated that such differences occurred between the same periods of different years ( $D1 \times D2: p = 0.049$ ,  $R1 \times R2: p = 0.021$ ).

The CCA confirmed the strong influence of the Paraíba do Sul River during both rainy periods, with a higher flow rate in R1 (Fig. 6). The 2 canonical axes extracted by the CCA accounted for ~37% of the species variance, and ~74% of the total variance was explained by the abiotic variables. The 2 axes were significant ( $p = 0.002$ ) and did not show any correlation with the spatial configuration. Canonical Axis 1 identified the parameters of the Paraíba do Sul River flow rate and TOC as the most explanatory variables, with rainy period 1 positively associated with the flow rate and rainy period 2 associated with the TOC (Fig. 6). Canonical Axis 2 emphasized grain-size as the most explanatory variable, with dry period 1 positively associated with sand and dry period 2 associated with mud. *C. lyoni*, *C. marplatensis* and *L. magalhaensis* were highlighted as associated taxa in R1, and *L. latreilli* and *P. gracilis* were the most-associated taxa in R2 (Fig. 6).

3.4. Predation

A total of 13 fish species that were captured at the artificial modules contained infaunal specimens in their stomachs, with crustaceans and mollusks having the highest IRI values in the fishes' diets (Table 6). The correlation of the reef-associated infauna at the different distances with the fishes' stomach contents was not significant ( $r < 0.2$ ;  $p > 0.05$ ). Similarly, no significant relationship was found between infaunal abundance and the abundance of fishes captured near the modules at the reef distances of 0.5, 5 and 15 m ( $p > 0.05$ ).



**Fig. 3.** Total relative abundance (%) of the large taxonomic groups (A) and mean density (ind/m<sup>2</sup>)  $\pm$  standard error for Annelida (B), Crustacea (C) and Mollusca (D) at distances of 0.5, 5 and 15 m per sampling period (D1: September 2009; D2: September 2010; R1: April 2010; R2: April 2011) (N = 6 replicates per treatment). Different letters indicate significant differences ( $p < 0.05$ , Tukey's HSD post hoc test) between distances for the same period.

**Table 2**

ANOVA results for Annelida, Mollusca and Crustacea density between sampling distances (0.5 × 5 × 15 m), periods (dry × rainy) and years (1 × 2).

	df	Factors			
		Distance	Period	Year	Distance * period * year
		2	1	1	2
ANNELIDA	F	0.761	0.134	0.571	7.297
	p	0.569	0.749	0.637	0.001*
MOLLUSCA	F	1.942	0.213	41.452	0.363
	p	0.339	0.689	0.124	0.696
CRUSTACEA	F	0.258	35.166	0.015*	3.722
	p	0.795	0.027	0.985	0.029*

\*  $p < 0.05$ .

#### 4. Discussion

The presence of rigid submerged structures in the marine environment changed the water-circulation pattern and hence also sediment deposition (Davis et al., 1982; Machado et al., 2013). The significant spatial differences in grain size around the reef structures during year 1 most likely reflected the introduction of ARs to the marine sediment and the resulting changes in the grain-size characteristics of the substrate. Depending on the spatial arrangement of the substrate (in this case, the distance between reef modules), this effect can be more or less intense.

Studying the area of influence of this AR complex on infaunal variation, Zalmon et al. (2011) found a low-magnitude relationship between sediment grain size and organic material with increasing distance to the reef complex. This result suggests that the reef effect quickly dissipates due to the strong bottom currents, which are on average greater than 4–5 m/s. Thus, we have verified that temporal effects surpass spatial effects in response to the Paraíba do Sul River influence. This result indicates that changes in the composition and structure of the macrobenthic community are associated with the seasonality of the river flow, which is more intense during the rainy period. The influence of river discharge on soft-bottom community structure and complexity was observed by Pagliosa (2006) and Macdonald et al. (2012), who also suggested that temporal shifts in the community were associated with variations in the sediment and nutrient inputs from rivers, especially during the rainy period.

The relationship of infauna with soft-bottom grain-size composition is typical (Snelgrove and Butman, 1994) and is usually associated with trophic guilds (Putro, 2009; Taurusman, 2010). In the ARs, as expected, deposit feeders prevailed in muddy sediments with higher organic content, whereas carnivores and filter feeders were more abundant in coarser sediments with lower levels of organic matter. Thus, the inputs of organic matter and fine sediment into the reef complex, especially during the rainy period when a greater water flow of the Paraíba do Sul River was observed, favored the deposit feeders by increasing food availability, as observed by Santos and Pires-Vanin (2004) and Macdonald et al. (2012). An association with reef distance was not observed, as a reduced degree of isolation led to a decline in the deposition of fine sediment and nutrients and to a lower density of infaunal deposit feeders compared with those at more distant modules with a greater number of predators. Thus, the hypothesis that hydrodynamics are related to the AR intermodule distance is rejected, most likely due to the strong bottom currents throughout the entire studied area.

In the AR-associated infauna, Polychaeta predominated at reef distances of 0.5 and 5 m and Mollusca at 15 m. The high abundance of these groups is commonly recorded in soft-bottom substrata in natural and AR areas (Fabi et al., 2002; Fukunaga and Bailey-Brock, 2008; Lorenzi and Borzone, 2009; Machado et al., 2013; Zalmon et al., 2011). Ambrose and Anderson (1990) noted that one of the major effects of ARs on the macrobenthic community is the strong association of polychaete predators in the sandy sediments closer to the modules. The

predominance of *Goniadides caroliniae* and the high frequency of carnivores associated with the sediment surrounding the ARs, especially at the shorter distances, are related to the higher sand content, which corroborates the preference of this trophic group for environments with a coarser grain-size composition (Boaventura et al., 1999; Brasil and Silva, 2000).

In general, ARs have a negative effect on macrobenthic community structure, with abundance decreasing as a consequence of changes in the bottom current and the surrounding grain-size distribution soon after the establishment of the ARs (Ambrose and Anderson, 1990; Fabi et al., 2002; Fukunaga and Bailey-Brock, 2008; Wilding, 2006). In the reefs studied here (especially in year 1), the low-density values highlight the influence of the AR installation on the seafloor and the consequent physical disturbances on the associated infauna. However, during the subsequent periods, the density increase was not significant, suggesting the effects of other factors or stressors on the community, such as the high local hydrodynamics. According to Zalmon et al. (2011) and Machado et al. (2013), these may be responsible for maintaining the community at low abundance and high diversity levels.

Although Lindquist et al. (1994) and Fabi et al. (2006) suggested that ARs influence their surrounding environment primarily by affecting the predation by ichthyofauna on associated benthic invertebrates, Ambrose and Anderson (1990) suggested that physical variables are the main determinants of the abundance patterns of the infauna surrounding ARs.

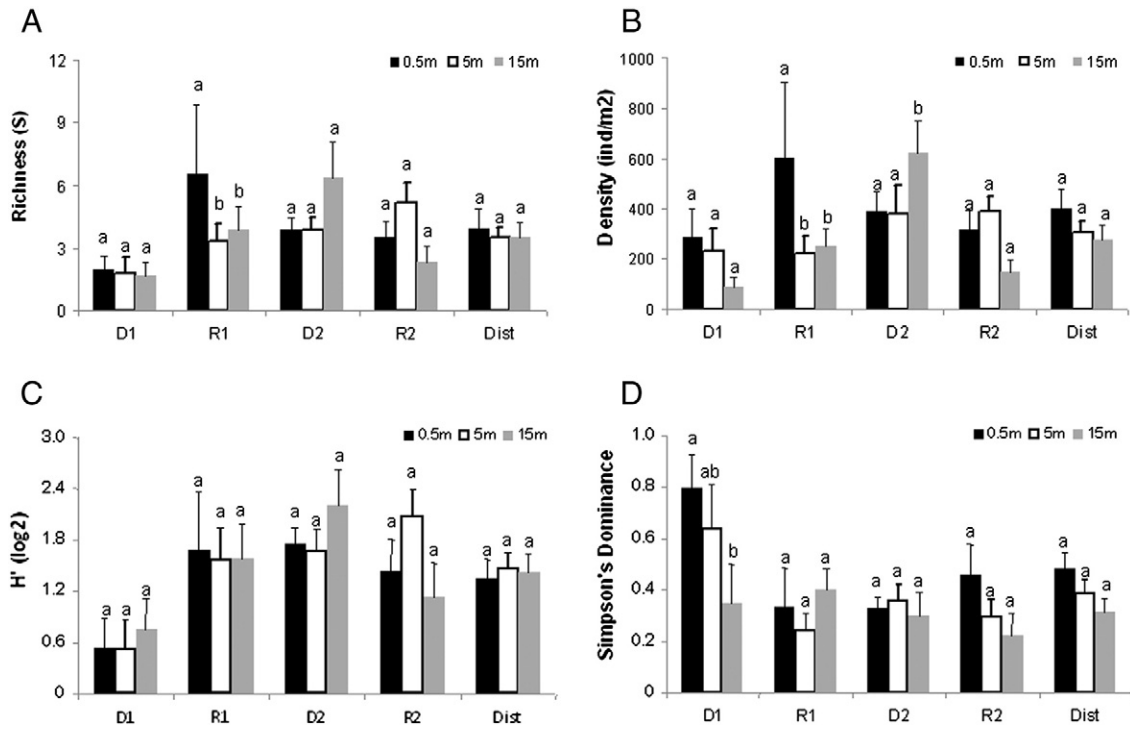
According to Langlois et al. (2006), in an environment with large hydrodynamic disturbances, larger-bodied fauna (>4 mm) may be more likely to exhibit patterns in response to biological processes such as predation. These observations support the model of Menge and Sutherland (1987) for infaunal community structure control, in which evidence of biotic processes is detectable below certain thresholds of physical disturbance.

Jordan et al. (2005) evaluated the effect of distance between reef modules on the structure of the associated fish community and found higher richness and abundance values with an increasing degree of isolation in response to predation haloes caused by the reduction of benthic prey density at the shorter reef distances. However, the higher densities and species richness of infauna and fishes at our studied reefs with the shortest distance between the modules suggest that the haloes of large-bodied infauna (>5 mm: 500- $\mu$ m mesh) around reefs are not consistent, particularly on open coast sediment. These results indicate that predation by transient fishes is not the structuring factor of the macrobenthic community. Herrera et al. (2002) emphasized that predation pressure is less evident at sites where the predators are not resident species, which is a characteristic of many species found in the studied reef area (Santos et al., 2010, 2011).

Barros (2005) also observed that the changes in macrobenthic communities surrounding rocky reefs could be explained not by fish predation but by the dissimilarities in the sandy bottom close to and far from the reefs. Our results showed that the 15-m reefs had finer sediment (>60% mud) than those separated by 0.5 and 5 m, with sand, gravel and mud. An increase in coarser sediment fractions close to the 0.5 and 5 m modules led to an increase in the spatial heterogeneity of the sediments compared with those at the 15-m distance, which were more homogeneous, being composed essentially of mud. As the complexity of the physical structure of the habitat increased, the species richness and abundance of the associated organisms also increased. Furthermore, spatial heterogeneity can alter the effects of predation by lessening its impact on the benthos through the provision of a spatial refuge and by decreasing the foraging efficiency of predators (Gilinsky, 1984; Sih et al., 1985).

In summary, the infauna surrounding the reef complex exhibited a stronger response to variations in the sediment grain-size composition associated with the intense hydrodynamics in the region than to predation. This finding suggests that transient fishes use the reef for other purposes, most likely as shelter (Brotto and Zalmon, 2007; Brotto





**Fig. 4.** Mean ± standard error for species richness (A), species density (B), Shannon diversity index (C) and Simpson dominance index (D) at distances of 0.5, 5 and 15 m per sampling period (D1: September 2009; D2: September 2010; R1: April 2010; R2: April 2011) (N = 6 replicates per treatment). Different letters indicate significant differences (p < 0.05, Tukey's HSD post hoc test) between distances for the same period.

**Table 4**

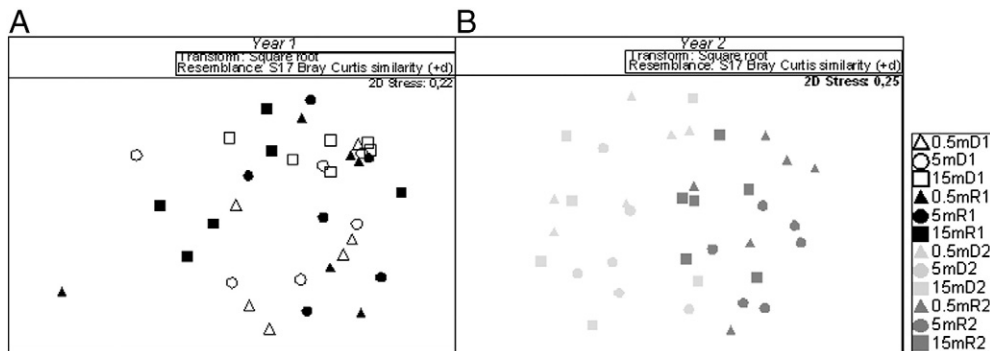
ANOVA results for species richness (S), density (Dens), diversity (H') and dominance between sampling distances (0.5 × 5 × 15 m), periods (dry × rainy) and years (1 × 2).

Factors	S		Dens (ind/m <sup>2</sup> )		H' (log <sub>2</sub> )		Simpson's dominance	
	F	p	F	p	F	p	F	p
Distance	0.0574	0.946	0.2830	0.779	0.0376	0.964	0.5787	0.633
Period	0.2301	0.679	0.0702	0.816	0.5221	0.545	2.0788	0.286
Year	1.6683	0.326	2.3045	0.268	1.6388	0.329	2.0000	0.293
Distance × period × year	3.1304	0.050*	4.5041	0.015*	2.2148	0.118	4.0551	0.022*

\* p < 0.05.

et al., 2006a,b; Krohling et al., 2006), nursery and/or breeding habitats (Gomes et al., 2001; Santos et al., 2011). The changes detected in the composition, richness and abundance of the macrobenthic community reflected the physical disturbance following the AR implantation as well as temporal environmental variations (especially of the Paraíba do Sul

River) but were not as strongly related to the spatial configuration of the ARs. Most likely, the results stem from a combination of several factors acting together, with sediment composition as the major structuring force for infauna associated with variable small-scale spatial arrangements of ARs subject to periodic environmental disturbances.



**Fig. 5.** The nMDS ordination diagram (similarity coefficient of Bray–Curtis) of infaunal assemblages at distances of 0.5, 5 and 15 m for each period (D1: September 2009; D2: September 2010; R1: April 2010; R2: April 2011) per sampling year (A: year 1; B: year 2). Transformed data: log (x + 1).

**Table 5**  
PERMANOVA results of the infauna between distances, periods, years and respective interactions (d.f.: degrees of freedom; p (MC): significance of Monte Carlo permutation).

	DF	F	p	p (MC)
Distance	2	1.315	0.221	0.1770
Period	1	0.560	0.889	0.8660
Year (per)	2	6.007	0.001**	0.0001**
Distance × period	2	0.645	0.883	0.9470
Distance × year (per)	4	1.302	0.245	0.2120
Residual	48			
Total	71			

\*\* p < 0.01.

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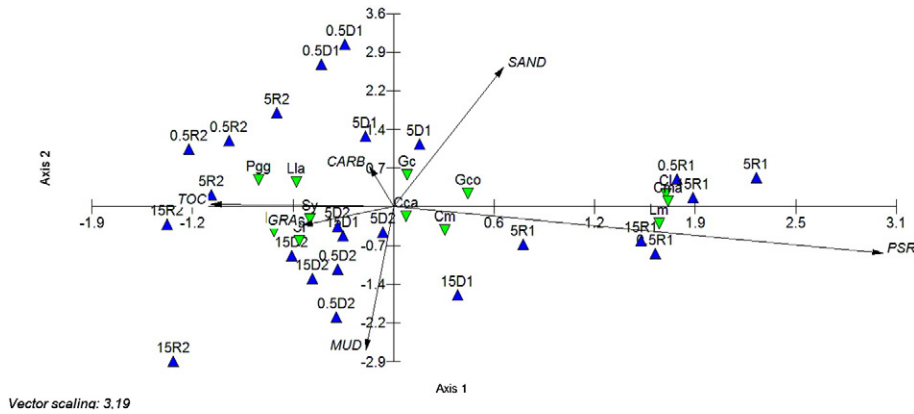
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**Fig. 6.** Canonical correspondence analysis (CCA) including species representing > 75% of the total abundance in each sampling distance (0.5, 5 and 15 m), period (D: dry; R: rainy) and year (1 and 2), and the environmental parameters gravel, sand, mud, carbonate (Carb), total organic carbon (TOC) and flow rate of the Paraíba do Sul River (PSR).

**Table 6**  
The index of relative importance (IRI) for the main prey categories of fish at distances of 0.5, 5 and 15 m per sampling period (D1: September 2009; D2: September 2010; R1: April 2010; R2: April 2011) (N = 6 replicates per treatment). OST: Osteichthyes; CRUS: Crustacea; MOL: Mollusca; ANNEL: Annelida.

Year 1									
		Dry 1				Rainy 1			
0.5 m	<i>Bagre marinus</i>	<i>Cynoscion virescens</i>	<i>Cynoscion microlepidus</i>	<i>Stellifer rastrifer</i>	0.5 m	<i>Aspistor luniscutis</i>			
OST		20,000.0	7467.7	14,984.1	OST	4324.3			
CRUS	20,000.0		2532.3		CRUS	1809.4			
5 m	<i>Bagre marinus</i>	<i>Cynoscion virescens</i>	<i>Cynoscion microlepidus</i>	<i>Larimus breviceps</i>	<i>Genidens genidens</i>	5 m	<i>Aspistor luniscutis</i>		
OST	14,655.0	17,680.5	5066.7		OST	1317.5			
CRUS	5345.0	155.0		20,000.0	20,000.0	CRUS	6864.9		
MOL		308.9	14,933.3			MOL	386.3		
15 m	<i>Bagre marinus</i>	<i>Cynoscion virescens</i>	<i>Cynoscion microlepidus</i>	<i>Larimus breviceps</i>	<i>Genidens genidens</i>	<i>Paralichthys brasiliensis</i>	15 m	<i>Aspistor luniscutis</i>	<i>Rhizopriodon porosus</i>
OST	20,000.0	20,000.0	20,000.0				OST		13,629.0
CRUS				20,000.0	20,000.0	18,233.2	CRUS	2912.5	
MOL						441.7			
Year 2									
		Dry 2				Rainy 2			
0.5 m	<i>Cynoscion jamaiscenses</i>	0.5 m	<i>Aspistor luniscutis</i>	<i>Chloroscombrus chrysurus</i>	<i>Orthopristis ruber</i>	15 m	<i>Larimus breviceps</i>	<i>Odontognathus mucronatus</i>	
OST	19,970.7	OST	197.8			OST	8333.3		
MOL	12,500.0	CRUS	1473.9	20,000.0	3797.8	CRUS	11,666.7	20,000.0	
		MOL	670.9						
		ANNEL			1994.5				
		5 m	<i>Rhizopriodon porosus</i>						
		OST	5137.7						



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