



Influence of *Palythoa caribaeorum* (Anthozoa, Cnidaria) zonation on site-attached reef fishes

JOSÉ P. MENDONÇA-NETO¹, CARLOS E.L. FERREIRA¹, LAÍS C.T. CHAVES² and RENATO C. PEREIRA¹

¹Departamento de Biologia Marinha, Universidade Federal Fluminense, Outeiro São João Batista s/n Morro do Valonguinho, Centro, 24001-970 Niterói, RJ, Brasil

²Departamento de Oceanografia, Universidade Federal de Pernambuco, UFPE, Av. Arquitetura s/n Cidade Universitária, 50670-901 Recife, PE, Brasil

Manuscript received on January 14, 2008; accepted for publication on April 30, 2008;
presented by LUCIA MENDONÇA PREVIANO

ABSTRACT

This work aimed to test the influence of *Palythoa caribaeorum*, a widely distributed zoanthid in the Atlantic, on site-attached reef fish in a subtropical rocky shore. Density, richness and vertical distribution of reef fish inside (ID) and outside (OD) previously chosen *P. caribaeorum* dominance patches were compared through stationary visual censuses along three different periods. Fishes were grouped in different trophic guilds to evidence differences in resources uses in both treatments. A complexity index was estimated by the chain link method and percentage covering of benthic organisms was obtained analyzing random points from replicated photo-quadrats. We observed thirty-eight species of fishes, belonging to twenty-five families. Reef fish communities between studied patches were similar, both in terms of species composition and vertical distribution. Considering only the most site-attached fishes, which were the most frequent and abundant species, data showed that ID sustains higher diversity and abundance than OD. Results showed that benthic composition differ significantly among patches whereas complexity remained without differences. Otherwise, results indicated that these areas might play an important role in space limitation, structuring neighboring benthic community and consequently reef fish assemblages.

Key words: benthic covering, habitat complexity, reef fish community, rocky shore, zoanthid.

INTRODUCTION

Studies on coral reefs dealing with fish and available complexity provided by live coral cover had pointed out the most usual examples of positive relationships (Carpenter et al. 1981, Sano et al. 1984, Lewis 1997), which are an increase in richness (Risk 1972, Luckhurst and Luckhurst 1978, Bell and Galzin 1984, Harmelin 1990, McClanahan 1994, Caley and John 1996, Beukers and Jones 1997) and in some cases abundance (Roberts and Ormond 1987, Sano et al. 1984, Gratwicke and Speight 2005). However, fewer reports made assumptions regarding fish relationships with benthic cover (Bouchon-

Navarro and Bouchon 1989, Syms and Jones 2000, Munday 2002) or with the rocky reefs complexity indicators (Aburto-Oropeza and Balart 2001, Ferreira et al. 2001).

The influence of habitat complexity on reef fish has been extensively studied (Sale and Dybdahl 1975, Luckhurst and Luckhurst 1978, Gratwicke and Speight, 2005) and has been considered an important determinant of local abundance and diversity by influencing the outcomes of predation, competition and trophic dynamics (Roberts and Ormond 1987, Bell et al. 1991, Hixon and Menge 1991, Almany 2004). This influence may reduce predation and competition providing more refuges, contributing to decrease encounter rates between predators and preys, and increasing resource availability (Murdoch and Oaten 1975, Almany 2004).

Correspondence to: José Policarpo de Mendonça Neto
E-mail: zepolicarpo@gmail.com

Benthic biota has a fundamental role on reef ecology as important trophodynamic components. For example, the high algal turnover and primary production on tropical regions sustaining large sizes and high biomass of herbivorous fishes (Choat 1991) or even the positive relationships of chaetodontids and live coral cover (Bell and Galzin 1984, Bouchon-Navarro and Bouchon 1989). Benthic composition may yet be considered as important complexity contributor (Hixon and Brostoff 1983, Jones 1986, Jones et al. 1991), adding niches to a diverse fauna of mobile and sessile invertebrates. Both in low as in high latitude reefs, benthic associated mesofauna of invertebrates consists in an abundant food resource for reef fishes (Lobel 1980, Hixon and Brostoff 1982, Klumpp et al. 1988, Zeller 1988, Moyer et al. 2003). Benthic organisms may also interfere on reef relief by increasing structural complexity provided by boring and arborescent organisms; whose on a scale of centimeters can provide mesoscale habitat modification for small benthic fishes (Stephen et al. 2006).

Branching corals are among the most reported ecological engineers on tropical coral reefs, enhancing the available substrate and providing a multitude of niches and refuges (Shima 2001, Shima and Osenberg 2003, Gratwicke and Speight 2005). In rocky shores, the size of boulders and geology providing holes of different sizes and shapes, are together with benthic organisms, the most important complexity generators (Ferreira et al. 2001, Floeter et al. 2007). Conversely, zoanthids do not generate complexity, and by covering huge portions of the reef substratum, can actually flatten the available complexity (Haywick and Mueller 1997, Mueller and Haywick 1995).

Palythoa caribaeorum have large distribution in the Atlantic (Mueller and Haywick 1995) and was reported to dominate large bottom extensions with low exposure and high luminosity (Sebens 1982, Acosta 2001, Leão 1996). It is recognized as an aggressive competitor against neighbors for vital resources (Suchanek and Green 1981, Sorokin 1995) and space (Lang 1973, Bak et al. 1982) and to be tolerant to high environmental variability (Cooke 1976, Sebens 1982, Sorokin 1991, Kemp et al. 2006). Nevertheless, there are still a lot of ecological processes encompassing its dominance which is less investigated, like the effects it could fulfill on the structure of reef communities (Sheppard 1982, Carlon and

Olson 1993, Acosta et al. 2005, Boscolo and Silveira 2005, Pérez et al. 2005). The *P. caribaeorum* tissue contains a powerful high molecular weight toxin known as palytoxin (PTX) (Gleibs et al. 1995). It is described as the most potent non-protein marine toxin known (Gleibs et al. 1995, Mueller and Haywick 1995) and is primarily found (or produced) in zoanthids (Moore and Scheuer 1971, Gleibs et al. 1995) and in dinoflagellates (Usami et al. 1995). Despite of this several marine organisms are reported to forage on *Palythoa* (Bonaldo et al. 2005, Bozec et al. 2005, Stampar et al. 2007). The PTX apparently does not affect some species, probably because different levels of resistance or tolerance to toxic secondary metabolites (Gleibs and Mebs 1999). Actually, the transport and accumulation of toxins in food chains are a common phenomenon in marine biota with toxic products eventually consumed by human through clams, crustaceans and fish consumption (Mebs 1998, Gleibs and Mebs 1999).

In Brazilian reefs *P. caribaeorum* colonies are well developed and widespread (Castro et al. 1995, Leão 1996, Villaça and Pitombo 1997, Ferreira et al. 2001, Oigman-Pszczol et al. 2004, Pérez et al. 2005, Floeter et al. 2007). In the Southeastern Brazilian coast, rocky reefs dominate, while in the Northeastern coast, coral and sandstone reefs are the dominant component (Maida and Ferreira 1997, Floeter et al. 2001). The distribution and composition of benthic communities along the Brazilian coast are strongly correlated with general environmental and geographical variables (Lana et al. 1996, Floeter et al. 2001, Ferreira et al. 2004). With more than 8,000 km of coast extension, a diverse scenario provides different ecological processes which generate diverse communities and trophodynamics processes (Kempf 1970, Eston et al. 1986, Rosa and Moura 1997, Ferreira et al. 1998a, b, Reis and Yoneshigue-Valentin 1998). Despite this, few studies investigated the vertical distribution and the influence of benthic communities and complexity on reef fishes (Ornellas and Coutinho 1998, Ferreira et al. 2001, Floeter et al. 2007).

This study examines the influence of *P. caribaeorum* dominance patches on distribution of conspicuous site-attached reef fishes in a subtropical rocky shore of Southeastern Brazilian coast. We investigated reef fish densities and richness outside and inside of *P. caribaeorum* dominance patches. We sustain the hy-

pothesis that these dominant patches of *P. caribaeorum* may reduce the amount of shelter available to fishes by overgrowing reef crevices and also reducing benthic diversity, consequently limiting food resources.

MATERIALS AND METHODS

STUDIED AREA

This study was carried out in sheltered rocky shores of Maramutá Inlet at Cabo Frio Island on Arraial do Cabo, RJ (23°44'S-42°W). This site is a high latitude tropical region located on the Brazilian Southeastern coast (Fig. 1). The marine environment of this region sustains a very rich reef fauna and flora (Castro et al. 1995, Guimaraens and Coutinho 1996, Ferreira et al. 2001) that flourish either in embayment as well as in exposed conditions upon a granitic rocky shore formation. This area is under influence of the convergence of tropical and subtropical water masses, where rocky shores and rocky reefs are the main systems (Floeter et al. 2001).

Maramutá Inlet presents areas with patches on different levels of *Palythoa caribaeorum* cover. These differences were probably mainly associated to distinct wave surge conditions. Two rocky shore profiles were determined in this study, considering benthic composition analysis: outside and inside *P. caribaeorum* dominance. Patches in areas outside dominance (OD) were configured by the presence of a great variety of benthic organisms but including only ~10% of *P. caribaeorum* mean benthic cover; whereas patches inside dominance (ID) areas were composed by large colonies of *P. caribaeorum*, which represented ~70% of mean benthic cover.

REEF FISH COMMUNITY STRUCTURE

Density, richness, vertical and temporal distribution of reef fish outside (OD) and inside (ID) previously chosen patches of *P. caribaeorum* dominance were compared through replicated visual stationary censuses. Randomly plots of 1.5 × 1.5 m (2.25 m²) delimited with a measure tape were used to estimate fish density. These censuses were conducted through different depth zones: shallow (~ 0-3 m); intermediate (~ 3-9 m) and interface (~ 9-12 m). Every fish sighted inside plots were counted, with carefully searching for cryptobenthic fishes. Each area were visited on three samples events along

7 months period (January to July 2006) and censuses were conducted at OD and ID patches on the same period, always between 8:00 and 12:00 a.m. A total of 180 censuses were conducted; 30 censuses on each depth zone; representing 90 censuses on OD patches and 90 censuses on ID patches. Time spent on each fish counts was approximately 3 minutes, and all censuses were performed by the same observer along the study development (J.P.M.N.) in order to minimize bias. Fishes were counted with data being recorded on a prepared acrylic sheet. In order to analyze differences on resources use, reef fishes were grouped by trophic guilds (Ferreira et al. 2004).

BENTHIC AND HABITAT COMPLEXITY

Benthic relative abundance and complexity data were collected on two sample events in July 2006. Percentage cover of *P. caribaeorum* and other benthic organisms were obtained from *in situ* replicated photo-quadrats (n = 30). These data were obtained through replicated transects with 50 × 50 cm quadrat on each bathymetric zones on OD and ID patches. Some organisms were identified to species level: *Palythoa caribaeorum*; *Phyllogorgia dilatata*; *Millepora alcicornis* and *Siderastrea stellata*; whereas other was pooled into major groups: urchins; macroalgae; articulate coralline algae; encrusting calcareous algae; sponges (green, orange and yellow) and other sessile organisms.

Habitat complexity was estimated by the 'chain link method', where a chain of 1.5 m was positioned to follow the contours and crevices as closely as possible. The mean ratio of contour length/stretched length was used as a comparative index, where 1.0 indicates a flat surface and higher values indicates substrata with more complexity (Cheney and Côté 2003).

DATA ANALYSIS

Spatial (depth) and temporal differences in fish density and richness were compared by one-way ANOVA among patches outside (OD) and inside (ID) *P. caribaeorum* dominance. When homogeneity of variances was not reached (Levene's test), data were log transformed (Underwood 1997). Additional Tukey multiple comparisons of means test were performed as a *post hoc* test (Zar 1996). In order to indicate which variables (% cover of benthic organisms and habitat complexity)

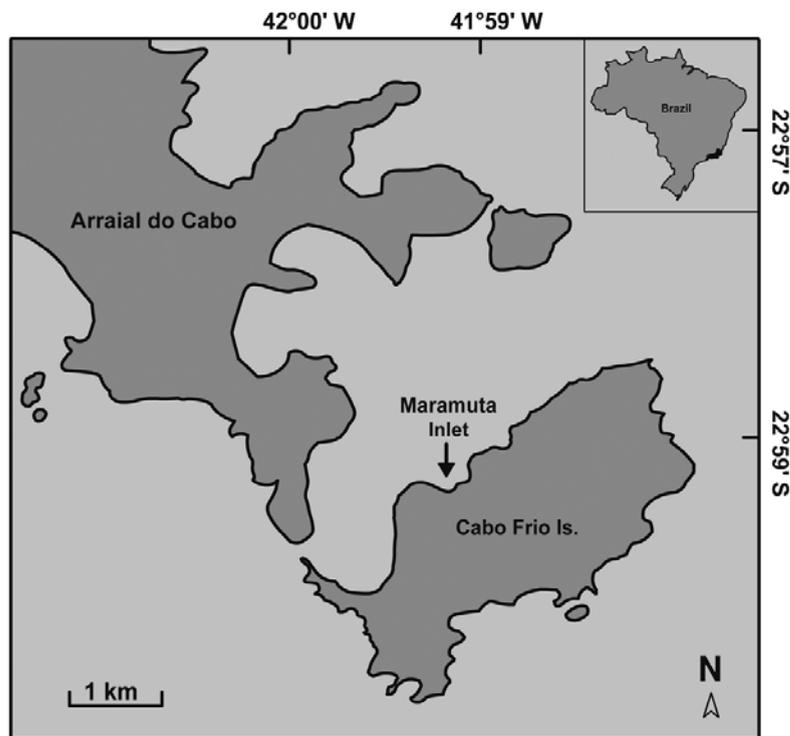


Fig. 1 – Map showing Maramutá Inlet on Cabo Frio Island at Arraial do Cabo.

were better correlated with fish community variables, a Multi Dimensional Scaling ordination (MDS) was used with a posterior ANOSIM (analysis of similarity) significance test. Cluster analyses were also used to group trophic guilds by similarities. Both procedures were performed with *PRIMER 5* software. Although this ordination method makes few assumptions about the data, distances between the points within the MDS configuration have the same rank order as the corresponding dissimilarity between samples (Clarke 1993).

Percent covers of benthic organisms were provided by random points generated by CPCe Program on each photo-quadrat (Kohler and Gill 2006). These data were treated by the same statistical procedure utilized to reef fish being analyzed by one-way ANOVA comparing patches outside (OD) and inside (ID) *P. caribaeorum* dominance.

Fish and benthic organisms' vertical distribution plus relationships among them were analyzed through a Canonical Correspondence Analysis (CCA) utilizing *Canoco 4.0* for windows software (Ter Braak and Verdonschot 1995).

RESULTS

REEF FISH COMMUNITY

Visual census listed 38 species belonging to 25 families. The ten most abundant fishes, considering both OD and ID areas, in decreasing order were: *Stegastes fuscus*, *Stephanolepis hispidus*, *Halichoeres poeyi*, *Labrisomus nuchipinnis*, *Serranus baldwini*, *Stegastes pictus*, *Coryphopterus glaucofraenum*, *Parablennius pilicornis*, *Abudefduf saxatilis* and *Acanthurus chirurgus*. These species together corresponded to approximately 65% of all fishes recorded during the study development (Table I). Significant temporal differences in fish abundance were observed during the sampling effort to shallow and intermediate zones, both in OD and ID patches. No differences were noted to interface zone among samples and patches (Fig. 2).

On OD patches 370 fishes belonging to 26 species were recorded (Table I). Sample 1 showed the highest density and richness per census and was significant different than samples 2 and 3 (Fig. 2). Interface zone is distinguished from other depths showing similarities in

TABLE I

Total composition of reef fish on Maramutá shores detected by visual census and trophic guilds: Total number of specimens counted (n); density per 2.25m² (mean ± SE) and percent of total observed on each patch.

Families	Species	Trophic guild	OD			ID		
			n	Density	%	n	Density	%
ACANTHURIDAE	<i>Acanthurus bahianus</i>	Roving Herbivore	18	0.2 ± 0.56	4.86	–	–	–
	<i>Acanthurus chirurgus</i>	Roving Herbivore	13	0.14 ± 0.53	3.51	10	0.11 ± 0.38	2.43
APOGONIDAE	<i>Apogon americanus</i>	Mobile invertebrate Feeder	4	0.04 ± 0.25	1.08	–	–	–
BALISTIDAE	<i>Balistes vetula</i>	Omnivore	–	–	–	11	0.12 ± 0.39	2.68
BLENIIDAE	<i>Parablennius marmoratus</i>	Mobile invertebrate Feeder	–	–	–	4	0.04 ± 0.25	0.97
	<i>Parablennius pilicornis</i>	Mobile invertebrate Feeder	17	0.18 ± 0.49	4.59	9	0.10 ± 0.33	2.19
CHAENOPSIDAE	<i>Emblemariopsis signifera</i>	Mobile invertebrate Feeder	8	0.08 ± 0.32	2.16	14	0.15 ± 0.47	3.41
CHAETODONTIDAE	<i>Chaetodon sedentarius</i>	Sessile Invertebrate Feeder	–	–	–	11	0.12 ± 0.41	2.68
	<i>Chaetodon striatus</i>	Sessile Invertebrate Feeder	–	–	–	13	0.14 ± 0.46	3.16
DACTYLOPTERIDAE	<i>Dactylopterus volitans</i>	Mobile invertebrate Feeder	7	0.07 ± 0.26	1.89	–	–	–
GOBIIDAE	<i>Coryphopterus glaucofraenum</i>	Mobile invertebrate Feeder	17	0.18 ± 0.53	4.59	10	0.11 ± 0.38	2.43
	<i>Elacatinus figaro</i>	Mobile invertebrate Feeder	–	–	–	18	0.20 ± 0.54	4.38
HAEMULIDAE	<i>Haemulon aurolineatum</i>	Mobile invertebrate Feeder	–	–	–	2	0.02 ± 0.14	0.49
Holocentridae	<i>Holocentrus adsensionis</i>	Mobile invertebrate Feeder	11	0.12 ± 0.41	2.97	12	0.13 ± 0.45	2.92
KYPHOSIDAE	<i>Kyphosus sectatrix</i>	Roving Herbivore	8	0.08 ± 0.35	2.16	14	0.15 ± 0.57	3.41
LABRIDAE	<i>Halichoeres poeyi</i>	Mobile invertebrate Feeder	23	0.25 ± 0.53	6.22	31	0.34 ± 0.75	7.54
LABRISOMIDAE	<i>Labrisomus nuchipinnis</i>	Carnivore	19	0.21 ± 0.52	5.14	29	0.32 ± 0.63	7.06
MONACANTHIDAE	<i>Stephanolepis hispidus</i>	Omnivore	47	0.52 ± 0.90	12.70	28	0.31 ± 0.53	6.81
MULIIDAE	<i>Pseudupeneus maculatus</i>	Mobile invertebrate Feeder	8	0.08 ± 0.38	2.16	13	0.14 ± 0.41	3.16
OPHICHTHIDAE	<i>Myrichthys ocellatus</i>	Carnivore	–	–	–	3	0.03 ± 0.18	0.73
	<i>Holacanthus ciliaris</i>	Omnivore	–	–	–	3	0.03 ± 0.18	0.73
POMACANTHIDAE	<i>Holacanthus tricolor</i>	Omnivore	2	0.02 ± 0.14	0.54	–	–	0.00
	<i>Pomacanthus paru</i>	Omnivore	8	0.08 ± 0.32	2.16	–	–	0.00
POMACENTRIDAE	<i>Abudefduf saxatilis</i>	Omnivore	9	0.1 ± 0.36	2.43	17	0.18 ± 0.57	4.14
	<i>Stegastes fuscus</i>	Territorial Herbivore	70	0.77 ± 0.94	18.92	83	0.92 ± 1.03	20.19
	<i>Stegastes pictus</i>	Mobile invertebrate Feeder	16	0.17 ± 0.46	4.32	12	0.13 ± 0.40	2.92
	<i>Stegastes variabilis</i>	Territorial Herbivore	1	0.01 ± 0.10	0.27	3	0.03 ± 0.18	0.73
SCARIDAE	<i>Cryptotomus roseus</i>	Roving Herbivore	13	0.14 ± 0.57	3.51	–	–	–
	<i>Sparisoma axillare</i>	Roving Herbivore	10	0.11 ± 0.48	2.70	–	–	–
	<i>Sparisoma frondosum</i>	Roving Herbivore	–	–	–	15	0.16 ± 0.56	3.65
SCIAENIDAE	<i>Pareques acuminatus</i>	Mobile invertebrate Feeder	7	0.07 ± 0.31	1.89	8	0.08 ± 0.35	1.95
SCORPAENIDAE	<i>Scorpaena isthmensis</i>	Piscivore	–	–	–	5	0.05 ± 0.23	1.22
SERRANIDE	<i>Mycteroperca acutirostris</i>	Piscivore	–	–	–	3	0.03 ± 0.18	0.73
	<i>Rypticus bistrispinus</i>	Mobile invertebrate Feeder	4	0.04 ± 0.25	1.08	–	–	–
	<i>Serranus baldwini</i>	Mobile invertebrate Feeder	18	0.20 ± 0.54	4.86	16	0.17 ± 0.46	3.89
SPARIDAE	<i>Diplodus argenteus</i>	Omnivore	–	–	–	8	0.08 ± 0.35	1.95
SYNODONTIDAE	<i>Synodus saurus</i>	Piscivore	4	0.04 ± 0.20	1.08	–	–	–
TETRAODONTIDAE	<i>Canthigaster figueiredoi</i>	Sessile Invertebrate Feeder	8	0.08 ± 0.32	2.16	6	0.06 ± 0.29	1.46
TOTAL			370			411		

all samples. Differences were observed for density on shallow within samples 1 and 3 whereas a similar pattern of abundance was observed above density and richness of intermediate zone on samples 2 and 3 (Fig. 2).

On ID patches, 411 fishes belonging to 29 species were recorded (Table I). A similar pattern observed for OD was repeated in ID patches, with sample 1 showing highest density and richness per census but without significant differences within depths. On sample 2 no differences were evidenced to density while richness ex-

hibited differences only to shallow and interface depths. Sample 3 density and richness presented the same pattern, with differences only to interface. Differences in densities were observed only on intermediate zone, which presented a similarity pattern within samples 2 and 3. This similarity was also observed to shallow and intermediate in richness (Fig. 3).

Considering most abundant fishes, no significant differences were observed within samples for *Stegastes fuscus*, *Labrisomus nuchipinnis* and *Parablennius*

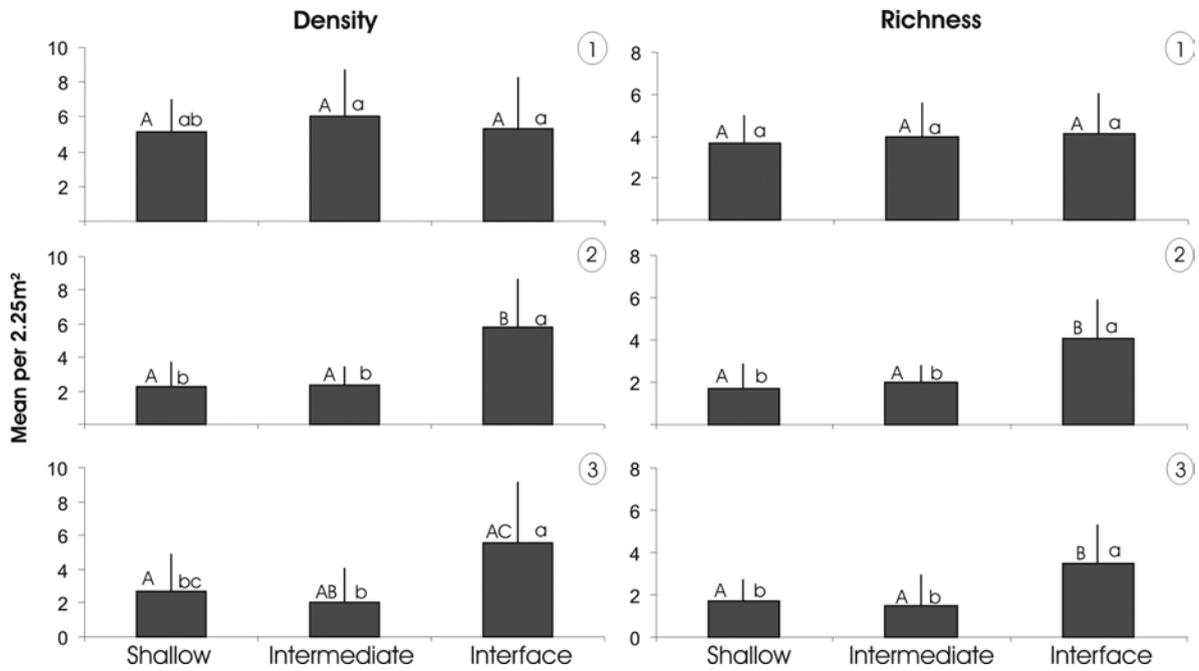


Fig. 2 – Means of density and richness of all species sighted in OD patches at Maramutá reefs. Numbers in circle indicates samples (period); letters above bars indicates homogeneous groups formed by Tukey results. Capital letters refers to comparison depth on the same time while minuscule letters refers to comparison depth on different period.

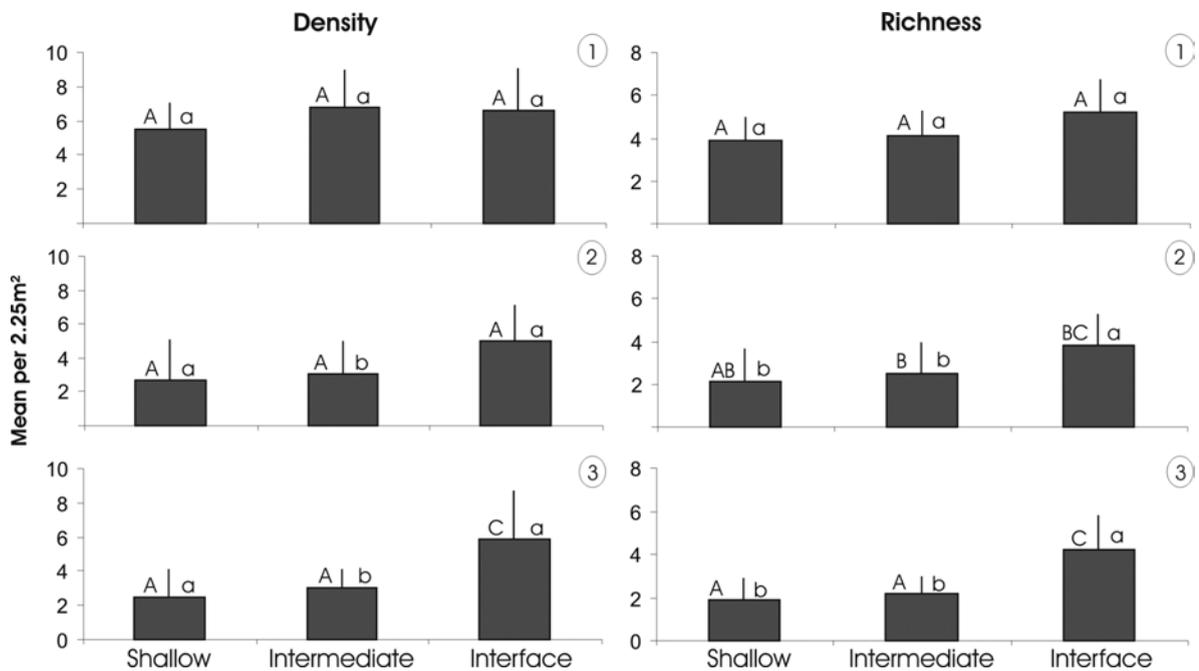


Fig. 3 – Means of density and richness of all species sighted in ID patches at Maramutá reefs. Numbers in circle indicates samples (period); letters above bars indicates homogeneous groups formed by SNK results. Capital letters refers to comparison depth on the same time while minuscule letters refers to comparison depth on different period.

pilicornis. Only *Halichoeres poeyi*, *L. nuchipinnis* and *Serranus baldwini* did not presented differences within depths among samples (Fig. 4). To these most representative species, interface was the only depth with no significant differences within samples (Fig. 4).

Most abundant fishes recorded in all bathymetric zones at ID patches, were analyzed and no significant differences were observed within samples for *Abudefduf saxatilis*, *Halichoeres poeyi* and *Stephanolepis hispidus*. These three species and *Elacatinus figaro* were the only without differences among depths. *Stegastes fuscus* and *Labrisomus nuchipinnis* showed differences among depths only on sample 1 (Fig. 5).

BENTHIC COMMUNITY AND COMPLEXITY

Benthic community of OD patches were represented mainly by articulate coralline algae which were widely distributed and was the most abundant organism in all depths; on shallow areas, urchins, especially *Echinometra lucunter*, colonies of *Millepora alcicornis* and macroalgae were the most representative organisms. On intermediate zone, articulate coralline algae, dominated by *Amphiroa* and *Jania* plus sparse colonies of *Palythoa caribaeorum* were the most conspicuous organisms, whereas on interface *Phyllogorgia dilatata* and *Siderastrea stellata* were typically abundant (Table II). Intermediate zone presented highest values of complexity index among depths (Table II).

On shallow zone of ID patches, benthic organisms were represented mainly by articulate coralline algae, coralline crusts and *Millepora alcicornis* colonies. Intermediate zone presented large colonies of *Palythoa caribaeorum* covering most of this zone. Articulate coralline algae and green sponges were the other organisms with high percent cover registered for this zone. On interface, *Phyllogorgia dilatata*, articulate coralline algae and green sponge were the most abundant organisms (Table II). On these patches, shallow and intermediate zone presented similar values of complexity index (Table II).

FISH AND BENTHIC ORGANISMS VERTICAL DISTRIBUTION

The mean abundance of the top ten most abundant fish species of all samples and the most important benthic variables are represented by points and arrows in the

CCA ordination diagram for the two study areas (OD and ID patches). The fish species and habitat variables jointly reflected the species distribution along each depth zone.

In OD ordination, calcareous crust, articulate coralline algae and urchins, were the most important benthic variables describing the shallow zone. The most abundant fishes in this zone included *Stegastes fuscus*, *Stephanolepis hispidus*, *Labrisomus nuchipinnis* and *Parablennius pilicornis*. The axis 1 clearly represents a depth gradient with shallow environments on the left side and deepest on the right end (Fig. 6). Articulate coralline algae showed a distribution associated with axis 2, which was responsible for the dispersing of points in the vertical position. Fishes with high mobility, as *Halichoeres poeyi* and roving herbivores *Acanthurus chirurgus* and *Acanthurus bahianus* did not present a well defined pattern and seems to have an ample distribution along rocky shore. Covering of *Palythoa caribaeorum* and *Phyllogorgia dilatata* were the most important variables influencing the distribution of *Serranus baldwini*, *Coryphopterus glaucofraenum* and *Stegastes pictus*, typical species that inhabit interface zone (Fig. 6).

On ID patches, coralline crusts and urchins were the most representative organisms of shallow zones. The most abundant fishes in this zone were *Abudefduf saxatilis* and *Kyphosus sectatrix*. *Stegastes fuscus*, *Stephanolepis hispidus*, *Labrisomus nuchipinnis* and *Emblemaropsis signifera* presented higher abundance on shallow/intermediate depth zones, which were dominated by *Palythoa caribaeorum*. Also in this zone, but more related to axis 2 and on opposite distribution to *P. caribaeorum*, articulate coralline algae presented high cover. *Halichoeres poeyi* and *Sparisoma frondosum* did not present a well defined pattern of distribution, which was expected based on their high vertical mobility. Otherwise, on deeper zones it can be clearly observed the gorgonian *Phyllogorgia dilatata* as the major benthic organism, probably influencing the presence of small fishes (Fig. 7).

COMPARISON AMONG OD/ID PATCHES

Nine species were exclusively detected in OD patches, whereas twelve species were detected only in ID patches (Table I). Transects on different depth zones on OD and ID patches, showed that interface zone in ID had highest

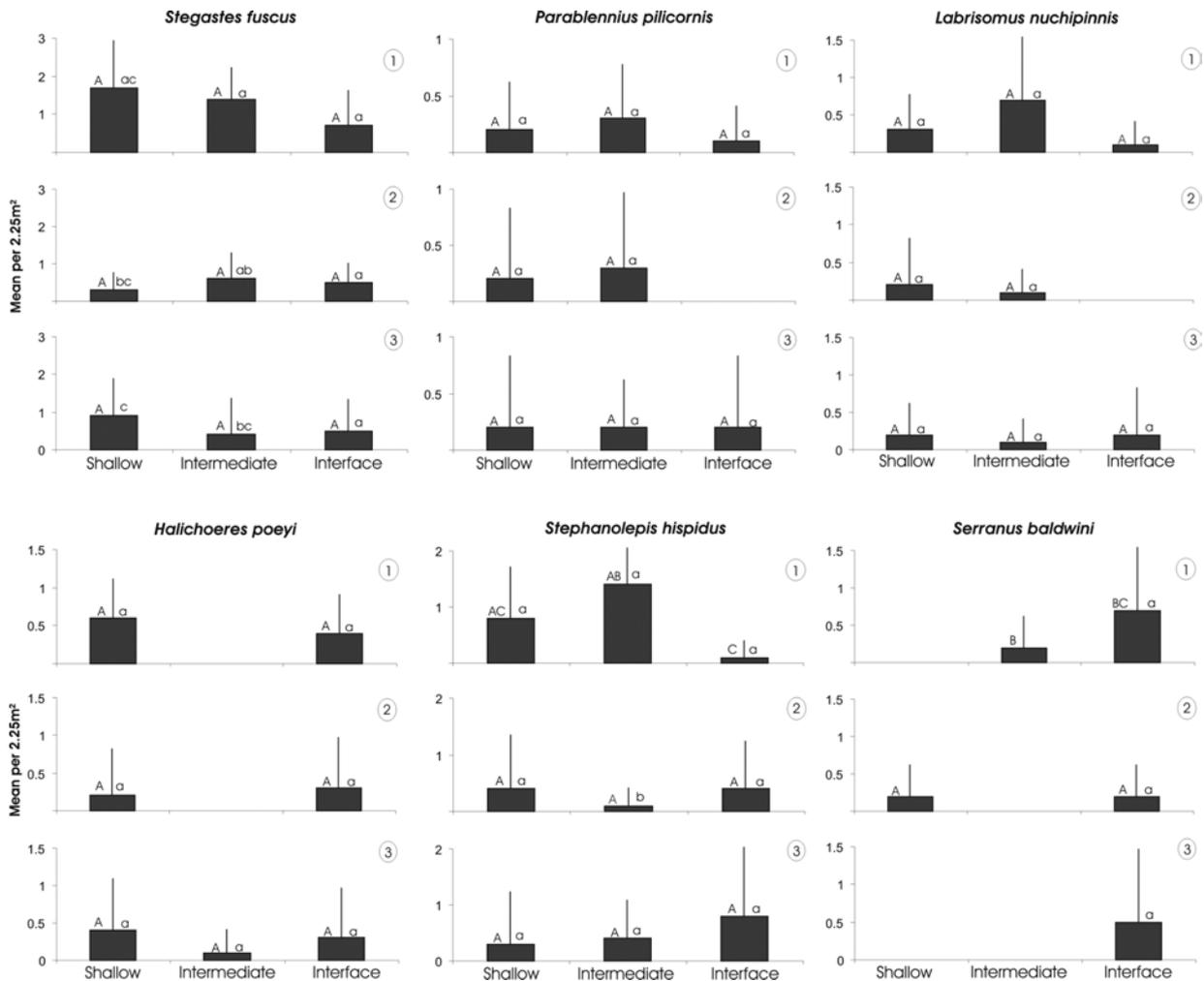


Fig. 4 – Means of density of most representative species sighted in OD patches at Maramutá reefs. Numbers in circle indicates samples (period); letters above bars indicates homogeneous groups from SNK test. Capital letters refers to comparisons depth on the same time while minuscule letters refers to comparisons depth on different period.

richness and density whereas OD shallow zone present lowest species richness and density per census (Table II).

Trophic guilds on OD patches exhibited a similar pattern of abundance within samples, with exception to omnivores and mobile invertebrate feeders guilds with distinct composition concerning to sample 1 and sample 3, respectively. In most of guilds, depths differing from a pattern shallow/intermediate to interface, exception were noted only to carnivores, piscivores and sessile invertebrate feeders whose presented similar abundance within depths. In ID patches, omnivores, piscivores and territorial herbivores densities were similar among samples whereas mobile invertebrate feeders, omnivores, pisci-

vores and sessile invertebrate feeders didn't present differences among depths (Figs. 8, 9, 10).

Mobile invertebrate feeders were the most representative trophic guild in all depth zones above on OD and ID patches. Cluster analysis formed groups which evidenced highest similarity within samples 2 and 3 in all depth zones for both zones (Figs. 8, 9, 10). On shallow depth, beyond mobile invertebrate feeders, omnivores and territorial herbivores were the most abundant guilds and no particular differences were observed among OD and ID patches (Fig. 8).

On intermediate depth zones, differences among OD and ID patches were evidenced by cluster analysis

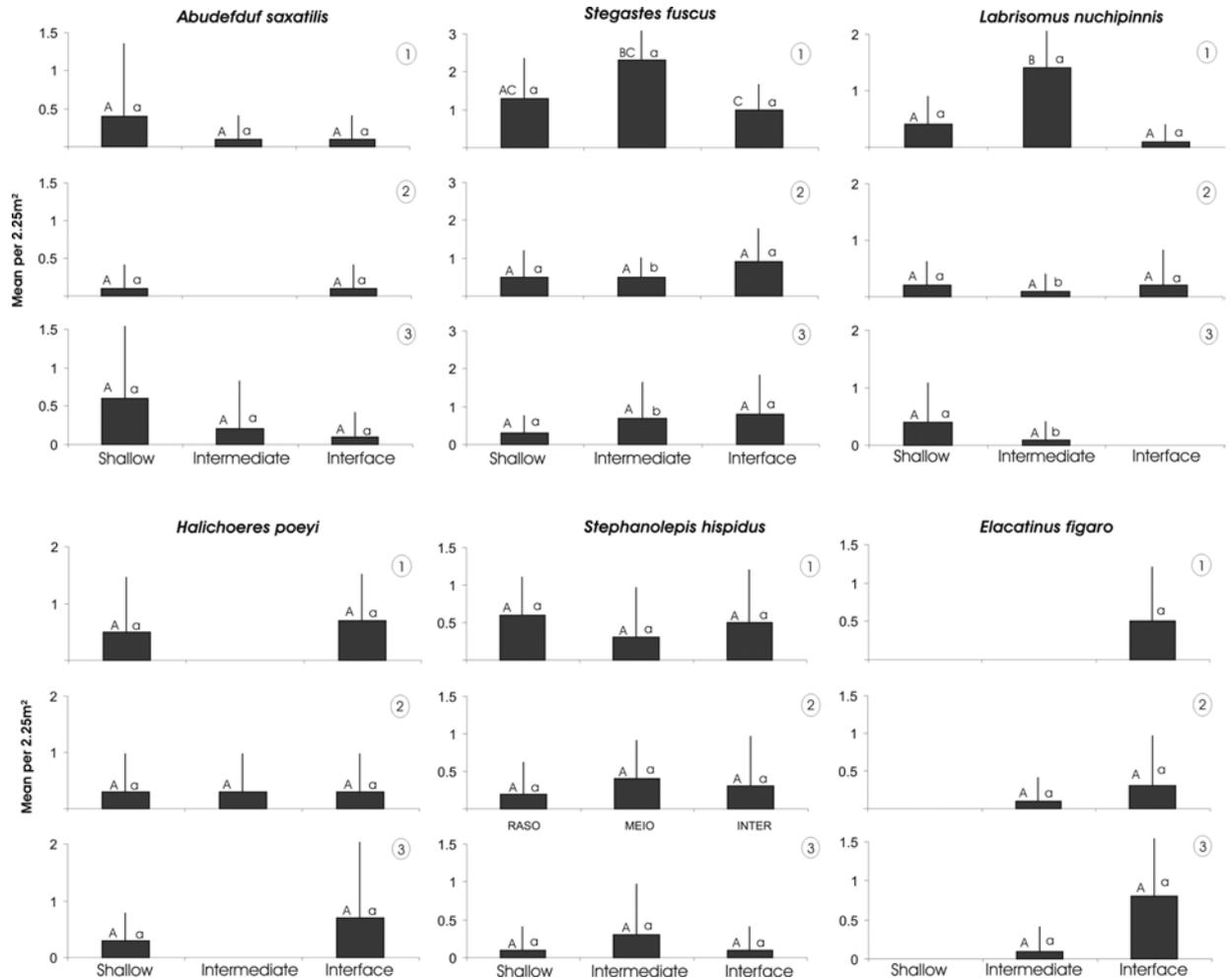


Fig. 5 – Means of density of most representative species sighted in ID patches at Maramutá reefs. Numbers in circle indicates samples (period); letters above bars indicates homogeneous groups from SNK test. Capital letters refers to comparisons depth on the same time while minuscule letters refers to comparisons depth on different period.

arrange, which classified, (except for sample 1), OD and ID in distinct groups. To sample 1 group, major difference between OD and ID was the higher representative of omnivores on OD patches. The principal distinction observed within samples was the higher presence of carnivores and roving herbivores in sample 1 whereas in samples 2 and 3, the major difference was the presence of piscivores guild only on OD patches (Fig. 9).

On interface depth zones, cluster analysis distinguished OD and ID patches in all samples. The highest similarity was noted within samples 2 and 3 to ID patches and in this depth zone, sample 1 follow the same pattern observed for the others and presented, into ID

patches, most similarity with samples 2 and 3 than to sample 1 OD patches. Essential difference between OD and ID was the presence of sessile invertebrate feeders on ID and the most representative abundance of roving herbivores on OD patches. Despite mentioned before, in this depth zone, mobile invertebrate feeders reached expressive abundance when compared to the other guilds (Fig. 10).

Benthic communities assessed on shallow zones reveals similarities between composition of major groups (eg. urchins, *Millepora alcicornis* and encrusting calcareous algae) both in OD and ID patches; but with significant differences in abundance to yellow sponges, macro-

TABLE II
 Summary (mean \pm SD) of fish density and richness; complexity index and % cover of benthic composition on depths, plus the one way ANOVA results of comparisons among studied patches on Maramutá reefs.

	Shallow			Intermediate			Interface			p		
	OD	ID	F	p	OD	ID	F	p	OD		ID	F
Fish density per census	3.33 \pm 2.25	3.56 \pm 2.29	0.21	0.69	3.43 \pm 2.75	4.31 \pm 2.49	1.61	0.21	5.56 \pm 3.05	5.83 \pm 2.47	0.21	0.71
Fish species richness per census	2.36 \pm 1.50	2.63 \pm 1.51	0.18	0.49	2.51 \pm 1.70	2.93 \pm 1.41	0.15	0.28	3.91 \pm 1.84	4.41 \pm 1.61	1.17	0.27
Complexity index	1.53 \pm 0.17	1.57 \pm 0.16	0.15	0.69	1.66 \pm 0.27	1.59 \pm 0.34	0.25	0.62	1.29 \pm 0.15	1.30 \pm 0.14	0.02	0.86
% cover of bare rock	4.28 \pm 6.51	0.45 \pm 1.17	8.18	0.01*	7.24 \pm 8.08	—	15.93	0.01*	1.20 \pm 3.83	1.36 \pm 4.07	0.04	0.85
% cover of coralline crust algae	7.93 \pm 8.39	11.81 \pm 8.14	3.17	0.08	12.75 \pm 11.87	0.50 \pm 1.22	6.09	0.02*	3.06 \pm 4.99	3.63 \pm 3.97	0.46	0.50
% cover of articulate coralline algae	27.44 \pm 15.56	39.54 \pm 13.42	3.57	0.07	40.28 \pm 20.86	9.50 \pm 11.91	47.57	0.01*	34.40 \pm 19.19	20.15 \pm 20.73	4.28	0.04*
% cover of green sponge	0.31 \pm 1.45	0.91 \pm 1.83	0.09	0.77	4.49 \pm 6.56	5.15 \pm 3.30	8.52	0.01*	3.20 \pm 1.10	10.91 \pm 13.18	7.18	0.01*
% cover of macroalgae	7.14 \pm 8.31	—	14.90	0.01*	—	2.50 \pm 3.56	13.76	0.01*	3.46 \pm 3.81	—	6.08	0.02*
% cover of <i>Millepora alcicornis</i>	10.95 \pm 9.37	8.78 \pm 11.15	1.24	0.27	—	—	1.15	0.01	3.60 \pm 10.53	4.09 \pm 11.17	0.32	0.58
% cover of orange sponge	4.60 \pm 6.01	5.91 \pm 6.25	0.43	0.51	5.36 \pm 7.50	0.66 \pm 1.36	7.56	0.01*	0.40 \pm 1.46	4.24 \pm 8.85	4.83	0.03*
% cover of other organisms	3.80 \pm 4.86	5.30 \pm 8.64	0.05	0.82	4.49 \pm 7.75	0.66 \pm 1.74	14.44	0.01*	—	—	—	—
% cover of <i>Palythoa caribaeorum</i>	6.98 \pm 8.22	5.61 \pm 9.83	1.83	0.18	10.43 \pm 10.31	77.33 \pm 9.94	399.71	0.01*	8.26 \pm 11.67	9.54 \pm 14.95	0.05	0.83
% cover of <i>Phyllogorgia dilatata</i>	1.42 \pm 2.25	0.75 \pm 2.03	0.89	0.35	3.76 \pm 4.85	—	12.00	0.01*	20.80 \pm 14.60	23.33 \pm 17.72	0.07	0.80
% cover of <i>Siderastrea stellata</i>	—	—	—	—	—	—	—	—	1.33 \pm 4.81	1.81 \pm 5.11	0.15	0.70
% cover of urchins	14.12 \pm 8.74	14.39 \pm 7.79	0.01	0.91	4.34 \pm 6.46	0.83 \pm 2.62	5.15	0.03*	3.33 \pm 6.66	2.27 \pm 5.18	0.21	0.65
% cover of yellow sponge	0.79 \pm 1.79	1.96 \pm 2.84	4.12	0.04*	2.02 \pm 3.98	—	4.11	0.04*	2.40 \pm 3.57	4.54 \pm 8.13	1.14	0.29

*Indicates significant difference.

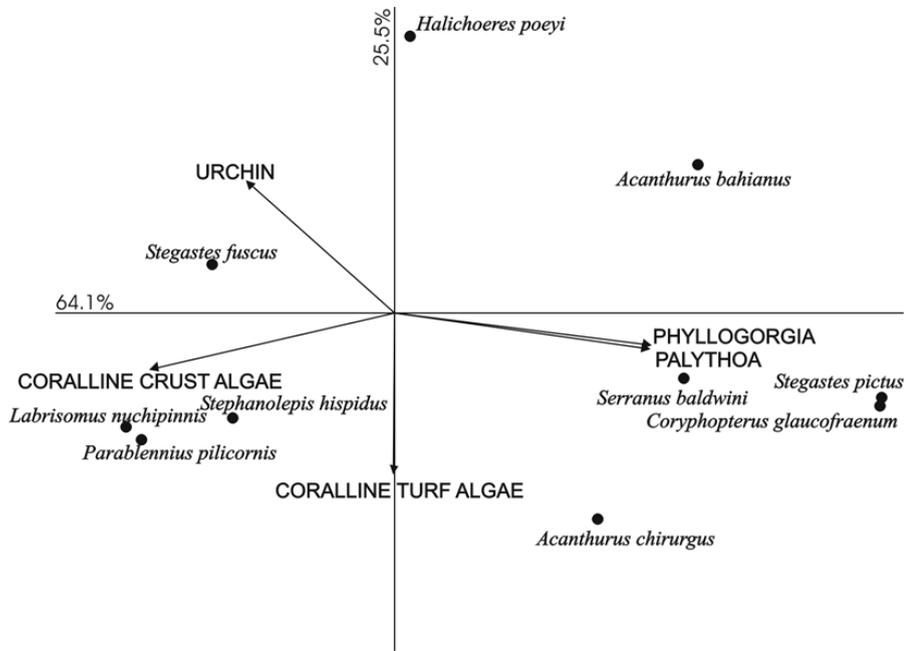


Fig. 6 – Canonical correspondence analysis of fish abundance and benthic organisms obtained from transects on OD patches of Maramutá reefs.

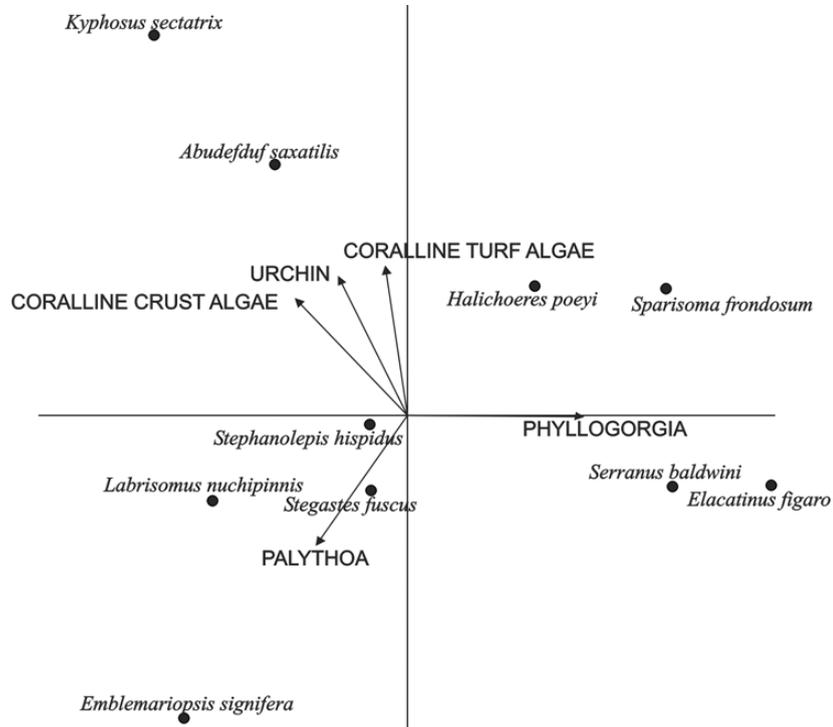


Fig. 7 – Canonical correspondence analysis of fish abundance and benthic organisms obtained from transects on ID patches of Maramutá reefs.

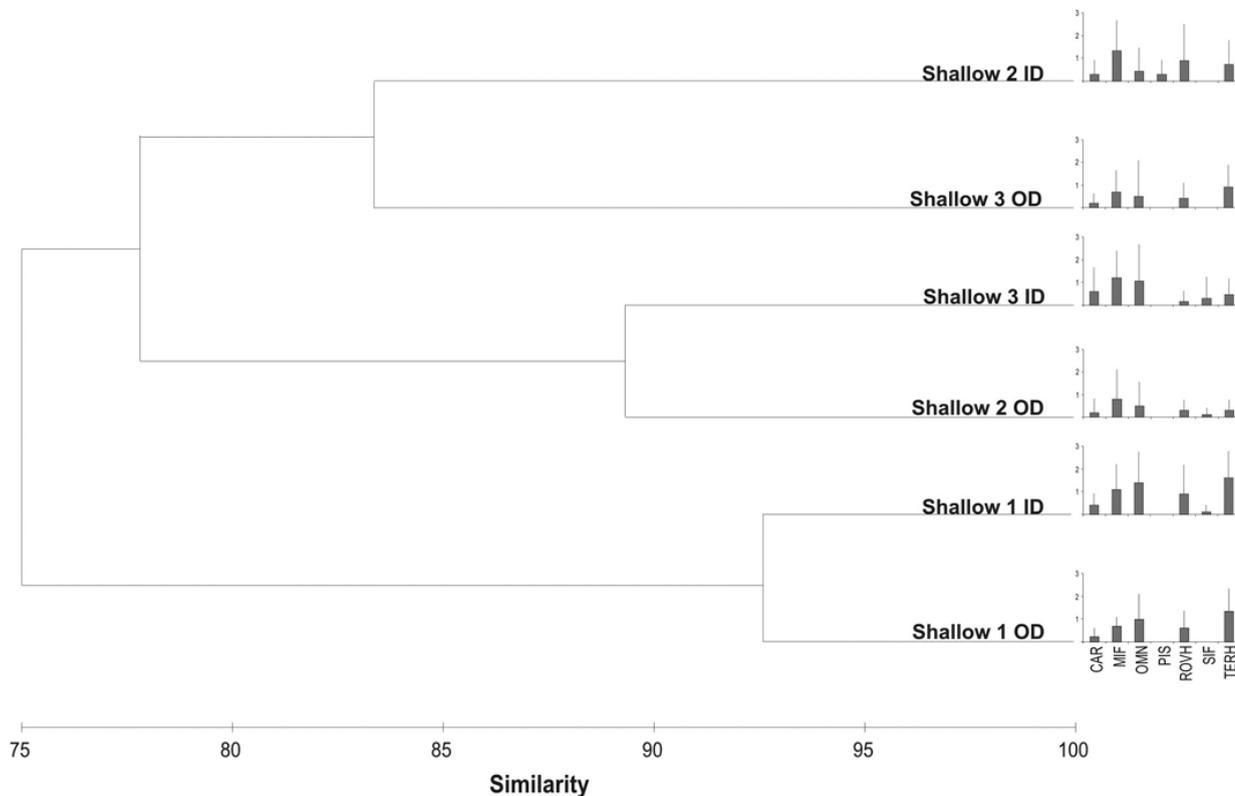


Fig. 8 – Similarity cluster analysis of trophic guilds among OD and ID patches on shallow zones of Maramutá reefs. CAR = carnivore; MIF = Microinvertebrate feeder; OMN = Omnivore; PIS = Piscivore; ROVH = Roving Herbivore; SIF = Sessile Invertebrate feeder; TERH = Territorial Herbivore.

algae and bare rock among patches (Table II). Contrasting to shallow zone, at intermediate depths all benthic groups were significantly different within OD and ID, and a clear pattern of higher diversity on OD was observed (Table II). In the interface zone, four major groups: articulate coralline algae; *Phyllogorgia dilatata*; *P. caribaeorum* and green sponge, presented higher abundance than other organisms both in OD and ID. Nevertheless, in this zone, articulate coralline algae, orange and green sponge groups and macroalgae significantly differed among OD and ID patches (Table II).

A similar pattern was observed to OD and ID, with intermediate zone presenting the highest and interface zone the lowest values of complexity index. Despite these values, no significant difference within OD and ID were observed when complexities of depth zones were tested. However, while in OD interface presented significant difference than other depths, in ID patches this difference was observed between shallow and interface (Table II).

DISCUSSION

The subtropical reef systems of the Brazilian coast are still among the less investigated in the world. Which factors lead to the dominance of *P. caribaeorum* is still not understood. As observed from other studies, *P. caribaeorum* dominated rocky shores throughout an extensive area of the Brazilian coast (Villaça and Pitombo 1997, Castro et al. 1999, Ferreira et al. 2001, Oigman-Pszczol et al. 2004). These reports indicate its presence from the Northeastern (Pérez et al. 2005) to the Southeastern coast (Boscolo and Silveira 2005), including oceanic islands (Edwards and Lubbock 1983, Gasparini and Floeter 2001), and there is always a relationship with the depth gradient, something about 2 to 8 meters, and also with a weak/intermediate hydrodynamic regime. Despite a wide distribution, its dominance over reef fish communities were not investigated until now.

Our results corroborate previous results about the existence of another major abundant component which

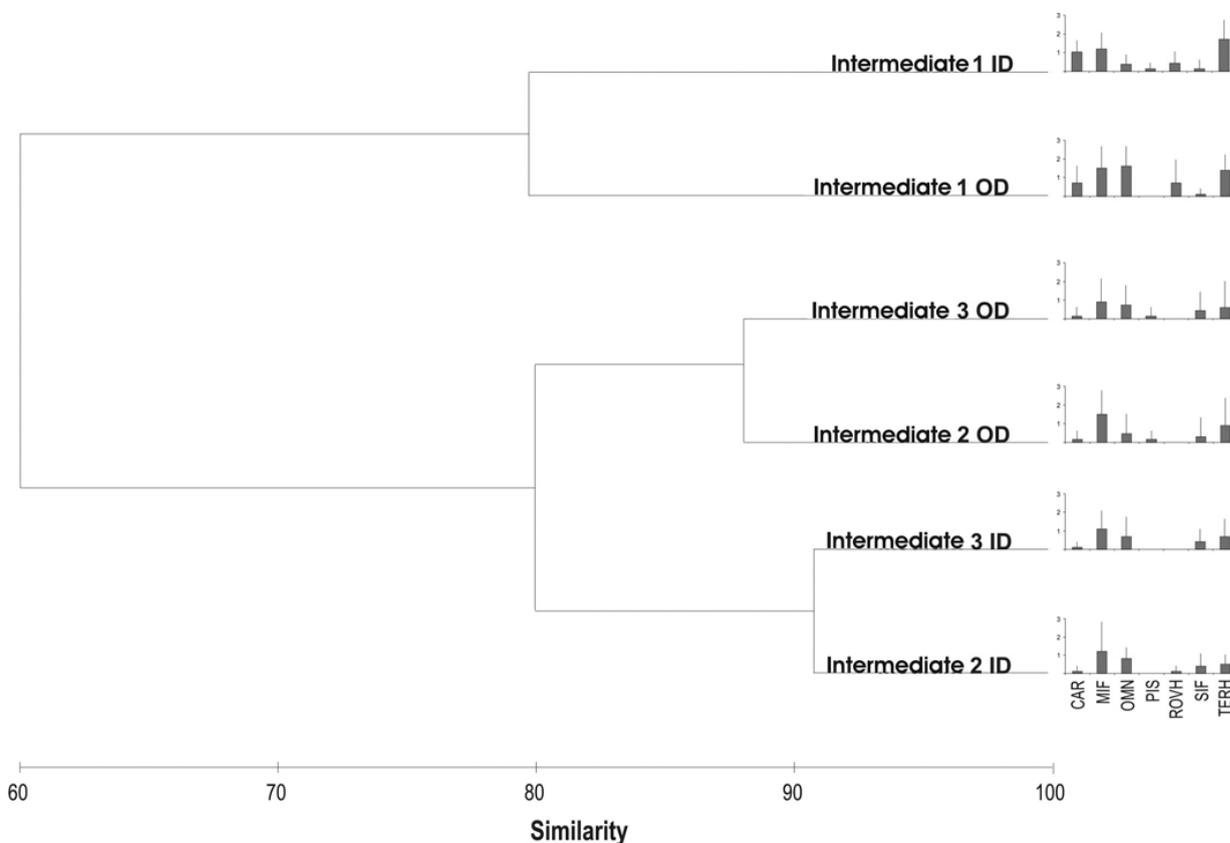


Fig. 9 – Similarity cluster analysis of trophic guilds among OD and ID patches on intermediate zones of Maramutá reefs. CAR = carnivore; MIF = Microinvertebrate feeder; OMN = Omnivore; PIS = Piscivore; ROVH = Roving Herbivore; SIF = Sessile Invertebrate feeder; TERH = Territorial Herbivore.

also dominates large portions of the reef substratum on the study site, together with *Palythoa*, the epilithic algal community (EAC) (Ferreira et al. 1998a, b, 2001). The EAC in the study site and in rock shores of Arraial do Cabo in general was dominated by red articulate coralline algae (*Amphiroa* and *Jania*), and red and green filamentous (*Ceramium*, *Polysiphonia*, *Cladophora*). While EAC community presented high cover in all depth zones, high cover of *P. caribaeorum* was restricted to shallow/intermediate zones.

Different patterns on benthic composition were found between OD and ID patches, demonstrating that spatially discrete factors may be acting on each patch. On intermediate depth zones of ID patches were observed a “strangle” of benthic communities distribution, shaped by *P. caribaeorum* massive presence. In OD patches, despite the huge covering of articulate coralline algae, the meager presence of *P. caribaeorum* may provide

sufficient space to the growth and an increase in richness of benthic organisms.

Temporal distinctions within samples were mainly configured by higher densities and richness on sample 1 than the other samples. Nevertheless, reef fish communities between studied patches were similar, both in terms of species composition and vertical distribution. Considering only the most site-attached fishes, which was the most frequent and abundant species, data showed that ID sustains higher diversity and abundance of fishes than OD. It could be considered an unexpected result, as the initial hypothesis assumed that additional space on the substratum provided by low cover of *P. caribaeorum* could increase diversity of food and available shelter, consequently increasing fish richness and abundance. Actually, results suggested that benthic composition differ significantly among patches, but not complexity. So, food availability (i.e. benthic cover of the

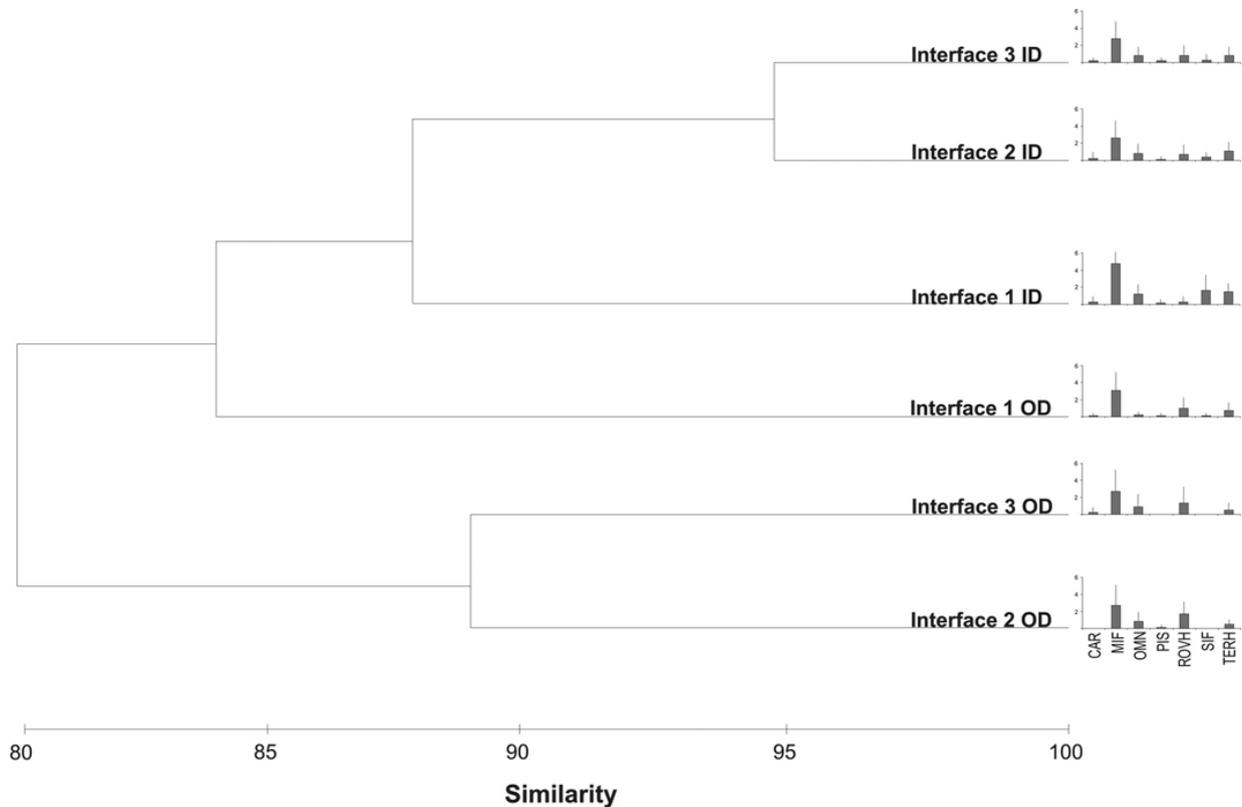


Fig. 10 – Similarity cluster analysis of trophic guilds among OD and ID patches on interface zones of Maramutá reefs. CAR = carnivore; MIF = Microinvertebrate feeder; OMN = Omnivore; PIS = Piscivore; ROVH = Roving Herbivore; SIF = Sessile Invertebrate feeder; TERH = Territorial Herbivore.

preferred resource) could be considered as a major force structuring reef fish community on this study. The utilization of resources are in fact determined by swimming ability and associated feeding performance that influenced the abundance of fishes in particular zonation on reef habitats.

Rugosity was the only variable used to express the complexity in this study. Many studies have described positive correlations between fish species richness and substrate rugosity (Risk 1972, Luckhurst and Luckhurst 1978). One of the explanations for an increasing in fish number at areas with more rugosity was additional refuge from predators (Gratwicke and Speight 2005). Nevertheless, the studied reefs were considered severely overfished for typical predators (eg. Serranids, lutjanids and carangids) (Ferreira et al. 2001, Floeter et al. 2007), thus the role of complexity as prey refuge may become less consistent. This fact could explain in part, the overall presence of small body size of fishes (author

pers. obs.) and the weak correspondence of fish abundance and complexity. Actually, the complexity index attained by the chain link method, widely used for other reef systems, was not useful for describing and compares patches as demonstrated by analysis among OD and ID patches reefs. Luckhurst and Luckhurst (1978) suggested that reefs with a variety of hole sizes would offer shelter to species across a range of body sizes, and that this would increase available niche space and number of species. Ferreira et al. (2001) assessed complexity by counts and estimative of size holes in rocky reef, but no effectiveness were reached as the results do not revealed significant differences between studied sites. Other types of complexity measures capable to detect clear differences and scales still should be developed or can be used in combination to assess micro scale rugosity distinctions on rocky reefs systems.

The data herein produced showed that reef fish assemblage presented a typical vertical distribution along

the rocky shore, common to both patches. This pattern is highly correlated with patterns of vertical distribution of benthic organisms and it seems to be determined by factors such as feeding habits and behavior, refuge from predation and social interactions (Ferreira et al. 2001). Fish richness and density increased toward depth zones, from shallow to interface. This pattern may be related to the target fish assessed in this study, those most sedentary and site-attached species (eg. *Stegastes fuscus* in intermediate and *Elacatinus figaro* in interface zones). A great number of species that were frequently observed forming schools while foraging in the water column in shallow zones (eg. *Diplodus argenteus* and *Abudefduf saxatilis*) were not well detected in the plots of visual census. Some species, like *Halichoeres poeyi* and *Chaetodon striatus*, which forage on mobile and sessile invertebrates respectively, find their food in different parts of the rocky shore, as these invertebrates are associated with different kinds of substratum. This pattern is also observed for roving herbivores, like *Acanthurus bahianus* and *Sparisoma frondosum*, which possess high mobility. The interface, the deeper zone, was mostly characterized by high cover of *Phyllogorgia dilatata* and the higher values of fish richness and density. Fishes occurring in this habitat were the gobiids, *Coryphopterus glaucofraenum*, highly associated with soft bottom, and the cleaner fish *Elacatinus figaro*. Typical fossorial feeders like *Dactylopterus volitans* and *Pseudupeneus maculatus* were also commonly sighted in this zone.

Considering only species which exclusively occurred on each patch, nine in OD and twelve in ID, we observed roving herbivores to be more abundant in OD and sessile invertebrate feeders in ID. This difference may be attributed to availability of preferred food resources within each patch. Despite some studies have found no relationship between the abundance of herbivorous fishes and algae cover (Wellington and Victor 1985, Chabanet et al. 1997), the absence of *P. caribaeorum* on OD provide more space for algal growth which potentially benefits herbivores. Other important factor explaining the comparative higher abundance of roving herbivorous fishes at OD were the lower density of *Stegastes fuscus* territories in these patches. Actually, as described elsewhere, damselfishes may have a great influence on benthic communities and exert a fundamental role in the

community structure of reef fishes (Choat 1991, Ceccarelli et al. 2006). In the present study *S. fuscus* seems to especially influence the feeding behavior of scarids and acanthurids, who reached their highest abundance in territorial herbivores low densities areas. *Stegastes fuscus* sustains the highest densities within all fishes sighted, both on OD and ID patches, especially on shallow and intermediate depth zones, where its main food item, the EAC, reaches its highest diversity and biomass (Ferreira et al. 1998a), as these algae are directly dependent of sunlight. Territories defended by this species are largely distributed at shallow zones in most of sheltered reefs of Arraial do Cabo and seem to be among the most productive and competitive areas due to the intense and active territorial behavior promoted by this species against a great variety of herbivorous fishes (Ferreira et al. 1998a, b).

ID patches seems to provide best conditions to sessile invertebrate feeders (mainly chaetodontids) which notably could forage also on polyps. Chaetodontids are well known by their associations with corals, especially the Pacific species (Cadoret et al. 1999, Bouchon-Navaro 1986, Roberts and Ormond 1987, Fowler 1990, Cox 1994). However *C. striatus* is a much more non selective feeder, although observed to feed on diverse polyps and probably mucus, their diet is more ample than that (Bonaldo et al. 2005). Coral mucus is known to be high proteic (Brown and Bythell 2005) and mucus from *Palythoa* is reported to be tasteful by a great variety of fishes (Fukui et al. 1987, Kodama et al. 1989, Nogushi et al. 1987), invertebrates (Gleibs et al. 1995, Gleibs and Mebs 1999) and also turtles (Stampar et al. 2007).

Despite the recognizable differences in densities and richness of reef fishes among OD and ID patches, the results herein indicate effects of *P. caribaeorum* benthic dominance only for site-attached species, analyzed in small scale habitat and on a limited temporal period. The data raised should be considered as evidence that these specific areas might be fundamental in the local rocky reef dynamic, influencing space limitation and structuring neighborhood benthic and reef fish assemblages. Further experimental works including large spatial and temporal scales are essential to understand the dynamics of those subtropical rock shores.

ACKNOWLEDGMENTS

Thanks are due to Carlos Gustavo Ferreira and Carlos Rangel for help on field work and to the colleagues of Marine Biology Department of Universidade Federal Fluminense for comments and suggestions. Thanks are also due to Carol Ferreira for all infrastructure and logistic support along fieldwork. The authors are thankful to logistic support from Instituto de Estudos do Mar Almirante Paulo Moreira (IEAPM) (Brazilian Navy). The financial support for this study has in part been provided by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ).

RESUMO

Este estudo visou testar a influência de *Palythoa caribaeorum*, um zoantídeo amplamente distribuído no Atlântico, na estruturação da comunidade de peixes recifais associados a um costão rochoso de uma região subtropical. A densidade, a riqueza e a distribuição vertical de peixes recifais em áreas previamente selecionadas com e sem a dominância de *Palythoa caribaeorum* foram comparadas através de censos visuais estacionários em três períodos distintos de tempo. Os peixes foram agrupados em guildas tróficas a fim de evidenciar diferenças nos usos dos recursos nas diferentes áreas analisadas. Foram analisados também índices de complexidade estrutural através do método da corrente e os percentuais de cobertura bentônica através de fotos quadracts replicados. Foram registradas trinta e oito espécies de peixes recifais de vinte e cinco famílias diferentes. A comunidade de peixes entre as áreas estudadas foi similar tanto em composição de espécies quanto em distribuição vertical. Considerando apenas as espécies mais associadas ao substrato, que foram as mais frequentes e abundantes, os dados mostraram que as áreas com dominância de *P. caribaeorum* sustentam maior diversidade e abundância do que as áreas sem a dominância de *P. caribaeorum*. Foram encontradas ainda diferenças significativas na composição bentônica entre os diferentes tratamentos estudados, mas não foram verificadas diferenças entre a complexidade estrutural entre estas áreas. No entanto, os resultados sugerem que as áreas com dominância de *P. caribaeorum* podem desempenhar papel importante na limitação de espaços, estruturando as comunidades bentônicas e, conseqüentemente, afetando a comunidade de peixes recifais.

Palavras-chave: cobertura bentônica, complexidade de habitat, comunidade de peixes recifais, recifes costeiros, zoantídeo.

REFERENCES

- ABURTO-OROPEZA O AND BALART E. 2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Mar Ecol* 22: 283–305.
- ACOSTA A. 2001. Disease in Zoanthids: dynamics in space and time. *Hydrobiol* 460: 113–130.
- ACOSTA A, SAMMARCO LF AND DUARTE G. 2005. New fission processes in the zoanthid *Palythoa caribaeorum*: Description and quantitative aspects. *Bull Mar Sci* 76: 1–26.
- ALMANY GR. 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141: 105–113.
- BAK RPM, TERMAAT RM AND DEKKER R. 1982. Complexity of coral interactions: influence of time, location of interaction and epifauna. *Mar Biol* 69: 215–222.
- BELL JD AND GALZIN R. 1984. Influence of live coral cover on coral reef fish communities. *Mar Ecol Progress Series* 15: 265–274.
- BELL SS, MCCOY ED AND MUSHINSKY HR. 1991. Habitat structure: the physical arrangement of objects in space. London: Chapman and Hall, 130 p.
- BEUKERS JS AND JONES GP. 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114: 50–59.
- BONALDO RM, KRAJEWSKI JP AND SAZIMA I. 2005. Meals for two: foraging activity of the butterflyfish *Chaetodon striatus* (perciformes) in southeast Brazil. *Braz J Biol* 65: 211–215.
- BOSCOLO HK AND SILVEIRA FL. 2005. Reproductive biology of *Palythoa caribaeorum* and *Protopalmythoa variabilis* (Cnidaria, Anthozoa, Zoanthidea) from the southeastern coast of Brazil. *Braz J Biol* 65: 29–41.
- BOUCHON-NAVARO Y. 1986. Partitioning of food and space resources by chaetodontid fishes on coral reefs. *J Exp Mar Biol Ecol* 103: 21–40.
- BOUCHON-NAVARO Y AND BOUCHON C. 1989. Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea). *Environ Biol Fishes* 25: 47–60.
- BOZEC YM, DOLÉDEC S AND KULBICKI M. 2005. An analysis of fish-habitat associations on disturbed coral reefs: chaetodontid fishes in New Caledonia. *J Fish Biol* 66: 966–982.
- BROWN BE AND BYTHELL JC. 2005. Perspectives on mucus secretion in reef corals. *Mar Ecol Progress Series* 296: 291–309.

- CADORET L, ADJEROUD M AND TSUCHIYA M. 1999. Spatial distribution of chaetodontid fish in coral reefs of the Ryukyu Islands, Southern Japan. *J Mar Biol Assoc UK* 79: 725–735.
- CALEY MJ AND JOHN J. 1996. Refuge availability structures assemblages of tropical reef fishes. *J Anim Ecol* 65: 414–428.
- CARLON DB AND OLSON RR. 1993. Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals. *J Exp Mar Biol Ecol* 173: 247–263.
- CARPENTER KE, MICLAT RI, ALBALADEJO VD AND CORPUZ VT. 1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proceedings of the 4th International Coral Reef Symposium*, p. 497–502.
- CASTRO CB, ECHEVERRYA CA, PIRES DO, MASCARENHAS BJ AND FREITAS SG. 1995. Distribuição de Cnidaria e Equinodermata no infralitoral de costões rochosos de Arraial do Cabo, Rio de Janeiro, Brasil. *Rev Brasil Biol* 55: 471–480.
- CASTRO CB, ECHEVERRYA CA, PIRES DO AND FONSECA CG. 1999. Distribuição de bentos (Cnidaria e Echinodermata) em costões rochosos da Baía da Ilha Grande, Rio de Janeiro, Brasil. *Oecologia Brasiliensis*. In: SILVA SHG AND LAVRADO HP (Eds), *Ecologia dos Ambientes Costeiros do Estado do Rio de Janeiro. Série Oecologia Brasiliensis 7*, PPGE-UFRJ, Rio de Janeiro, Brasil, p. 179–193.
- CECCARELLI DM, HUGHES TP AND MCCOOK LJ. 2006. Impacts of simulated overfishing on the territoriality of coral reef damselfish. *Mar Ecol Progress Series* 309: 255–262.
- CHABANET P, RALAMBONDRAINY H, AMANIEU M, FAURE G AND GALZIN R. 1997. Relationships between coral reef substrata and fish. *Coral Reefs* 16: 93–102.
- CHENEY KL AND CÔTÉ IM. 2003. Habitat choice in adult longfin damselfish: territory characteristics and relocation times. *J Exp Mar Biol Ecol* 287: 1–12.
- CHOAT JH. 1991. The biology of herbivorous fishes on coral reefs. In: SALE PF (Ed), *The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego, p. 120–155.
- CLARKE KR. 1993. Non-parametric multivariate analysis of changes in community structure. *Aust J Ecol* 18: 117–143.
- COOKE WJ. 1976. Reproduction, growth and some tolerances of *Zoanthus pacificus* and *Palythoa vestitus* in Kaneohe Bay, Hawaii. In: MACKIE GO (Ed), *Coelenterate ecology and behavior*. Plenum Press, NY, p. 281–288.
- COX EF. 1994. Resource use by corallivorous butterflyfishes (Chaetodontidae) in Hawaii. *Bull Mar Sci* 54: 535–545.
- EDWARDS A AND LUBBOCK R. 1983. The ecology of Saint Paul's Rocks (Equatorial Atlantic). *J Zool London* 200: 51–69.
- ESTON VR, MIGOTTO A, OLIVEIRA FILHO EC, RODRIGUES SA AND FREITAS JC. 1986. Vertical distribution of benthic marine organisms on rocky coasts of the Fernando de Noronha Archipelago (Brazil). *Bol Inst Oceanogr* 34: 37–53.
- FERREIRA CEL, PERET AC AND COUTINHO R. 1998a. Seasonal grazing rates and food processing by tropical herbivorous fishes. *J Fish Biol* 53: 222–235.
- FERREIRA CEL, GONÇALVES JEA, COUTINHO R AND PERET AC. 1998b. Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. *J Exp Mar Biol Ecol* 229: 241–264.
- FERREIRA CEL, GONÇALVES JEA AND COUTINHO R. 2001. Community structure of fishes and habitat complexity on a tropical rocky shore. *Environ Biol Fish* 61: 353–369.
- FERREIRA CEL, FLOETER SR, GASPARINI JL, JOYEUX JC AND FERREIRA BP. 2004. Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *J Biogeogr* 31: 1093–1106.
- FLOETER SR, GUIMARÃES RZP, ROCHA LA, FERREIRA CEL, RANGEL CA AND GASPARINI JL. 2001. Geographic variation in reef fish assemblages along the Brazilian coast. *Global Ecol Biogeogr* 10: 423–431.
- FLOETER SR, KROHLING W, GASPARINI JL, FERREIRA CEL AND ZALMON IR. 2007. Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. *Environ Biol Fish* 78: 147–160.
- FOWLER AJ. 1990. Spacial and temporal patterns of distribution and abundance of Chaetodontidae fishes at One Three Reef southern GBR. *Mar Ecol Progress Series* 64: 39–53.
- FUKUI M, MURATA M, INOUE A, GAWEL M AND YASUMOTO T. 1987. Occurrence of palytoxin in the trigger fish *Melichthys vidua*. *Toxicon* 25: 1121–1124.
- GASPARINI JL AND FLOETER SR. 2001. The shore fishes of Trindade Island, Western South Atlantic. *J. Nat Hist* 35: 1639–1656.
- GLEIBS S AND MEBS D. 1999. Distribution and sequestration of palytoxin in coral reef animals. *Toxicon* 37: 1521–1527.

- GLEIBS S, MEBS D AND WERDING B. 1995. Studies on the origin and distribution of palytoxin in a Caribbean coral reef. *Toxicon* 33: 1531–1537.
- GRATWICKE B AND SPEIGHT MR. 2005. The relationship between species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol* 6: 650–667.
- GUIMARAENS MA AND COUTINHO R. 1996. Spatial and temporal variation of benthic marine algae at Cabo Frio upwelling region, Rio de Janeiro, Brazil. *Aquatic Bot* 52: 283–299.
- HARMELIN JG. 1990. Ichthyofaune des fonds rocheux de Méditerranée: structure du peuplement du coralligène de l'île de Port-Cros (Parc National, France). *Mesogee* 50: 23–30.
- HAYWICK DW AND MUELLER EM. 1997. Sediment retention in encrusting *Palythoa* spp. – a biological twist to a geological process. *Coral Reefs* 16: 39–46.
- HIXON MA AND BROSTOFF WN. 1982. Differential fish grazing and benthic community structure on Hawaiian reefs. In: CAILLIET GM AND SIMENSTAD CA (Eds), *Fish Food Habits Studies*, University of Washington Sea Grant Program, Washington, p. 249–257.
- HIXON MA AND BROSTOFF WN. 1983. Damselfish as keystone species in reverse: Intermediate disturbance and diversity of reef algae. *Science* 220: 511–513.
- HIXON MA AND MENGE BA. 1991. Species diversity: prey refuges modify the interactive effects of predation and competition. *Theor Popul Biol* 39: 178–200.
- JONES GP. 1986. Food availability affects growth in a coral reef fish. *Oecologia* 70: 136–139.
- JONES GP, FERRELL DJ AND SALE PF. 1991. Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. In: SALE PF (Ed), *The ecology of fishes on coral reefs*. Academic Press, San Diego, p. 156–179.
- KEMP DW, COOK CB, LAJEUNESSE TC AND BROOKS WR. 2006. A comparison of the thermal bleaching responses of the zoanthid *Palythoa caribaeorum* from three geographically different regions in south Florida. *J Exp Mar Biol Ecol* 335: 266–276.
- KEMPF M. 1970. Notes on the benthic biometry of the N-NE Brazilian shelf. *Mar Biol* 5: 213–224.
- KLUMPP DW, MCKINNON AD AND MUNDY CN. 1988. Motile cryptofauna of a coral reef: abundance distribution and trophic potential. *Mar Ecol Progress Series* 45: 95–108.
- KODAMA AM, HOKAMA Y, YASUMOTO T, FUKUI M, MANEA SJ AND SUTHERLAND N. 1989. Clinical and laboratory findings implicating palytoxin as a cause of ciguatera poisoning due to *Decapterus macrosoma* (mackerel). *Toxicon* 27: 1051–1053.
- KOHLER KE AND GILL SM. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32: 1259–1269.
- LANA PC, CAMARGO MG, BROGIM RA AND ISAAC VJ. 1996. Os Bentos da Costa Brasileira: Avaliação crítica e levantamento bibliográfico (1858–1996). Revizee. MMA/CIRM/FEMAR, Rio de Janeiro, Brasil, 431 p.
- LANG J. 1973. Interspecific aggression by scleractinian coral 2: why the race is not always to the swift. *Bull Mar Sci* 23: 260–279.
- LEÃO ZMAN. 1996. The coral reefs of Bahia: morphology, distribution and the major environmental impacts. *An Acad Bras Cienc* 68: 439–452.
- LEWIS AR. 1997. Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Mar Ecol Progress Series* 161: 37–50.
- LOBEL PS. 1980. Herbivory by damselfishes and their role in coral reef community ecology. *Bull Mar Sci* 30: 273–289.
- LUCKHURST BE AND LUCKHURST K. 1978. Analysis of the influence of the substrate variables on coral reef fish communities. *Mar Biol* 49: 317–323.
- MAIDA M AND FERREIRA BP. 1997. Coral reefs of Brazil: overview and field guide. *Proceedings 8th International Coral Reef Symposium*, p. 263–274.
- MEBS D. 1998. Occurrence and sequestration of toxins in food chains. *Toxicon* 36: 1519–1522.
- MCCLANAHAN TR. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13: 231–241.
- MOORE RE AND SCHEUER PJ. 1971. Palytoxin: a new marine toxin from a coelenterate. *Science* 172: 495–498.
- MOYER RP, RIEGL B, BANKS K AND DODGE RE. 2003. Spatial patterns and ecology of benthic communities on a high-latitude South Florida (Broward County, USA) reef system. *Coral Reefs* 22: 447–464.
- MUELLER E AND HAYWICK DW. 1995. Sediment assimilation and calcification by the Western Atlantic reef zoanthid, *Palythoa caribaeorum*. *Bull Inst Océanographique* 14: 89–100.
- MUNDAY PL. 2002. Does variability determine geographical-scale abundances of coral-dwelling fishes? *Coral Reefs* 21: 105–116.

- MURDOCH WW AND OATEN A. 1975. Predation and population stability. *Adv Ecol Res* 9: 125–132.
- NOGUSHI T, HWANG DF, ARAKAWA O, DAIGO K, SATO S, OZAKI H, KAWAI N, ITO M AND HASHIMOTO K. 1987. Palytoxin is the causative agent in the parrotfish poisoning. In: GOPALAKRISHNAKONE P AND TAN CK (Eds), *Progress in Venom and Toxin Research*. Nat Univ Singapore, p. 325–335.
- OIGMAN-PSZCZOL S, FIGUEIREDO MAO AND CREED JC. 2004. Distribution of Benthic communities on the tropical rocky subtidal of Armação dos Búzios, Southeastern Brazil. *Mar Ecol* 25: 173–190.
- ORNELLAS A AND COUTINHO R. 1998. Spatial and temporal patterns of distribution and abundance of a tropical fish assemblage in a seasonal sargassum bed, Cabo Frio Island, Brazil. *J Fish Biol* 53: 198–208.
- PÉREZ CD, VILA-NOVA DA AND SANTOS AM. 2005. Associated community with the zoanthid *Palythoa caribaeorum* (Duchassaing and Michelotti, 1860) from littoral of Pernambuco, Brazil. *Hydrobiol* 548: 207–215.
- REIS RP AND YONESHIGUE-VALENTIN Y. 1998. Variação espaço-temporal de populações de *Hypnea musciformis* (Rhodophyta, Gigartinales) na Baía de Sepetiba e Armação dos Búzios, RJ, Brasil. *Acta Bot Bras* 12: 465–483.
- RISK MJ. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res Bull* 153: 1–6.
- ROBERTS CM AND ORMOND RFG. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Progress Series* 41: 1–8.
- ROSA RS AND MOURA RL. 1997. Visual assessment of reef fish community structure in the Atol das Rocas Biological Reserve, off northeastern Brazil. *Proceedings 8th International Coral Reef Symposium*, p. 983–986.
- SALE PF AND DYBDAHL S. 1975. Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* 56: 1343–1355.
- SANO M, SHIMIZU M AND NOSE Y. 1984. Changes in structure of coral reef fish communities by destruction of hermatypic corals – observational and experimental views. *Pac Sci* 38: 51–79.
- SEBENS KP. 1982. Intertidal distribution of zoanthids on the Caribbean coast of Panama: effects of predation and desiccation. *Bull Mar Sci* 32: 316–335.
- SHEPPARD CRC. 1982. Coral populations on reef slopes and their major controls. *Mar Ecol Progress Series* 7: 83–115.
- SHIMA JS. 2001. Recruitment of a coral reef fish: roles of settlement, habitat, and postsettlement losses. *Ecology* 82: 2190–2199.
- SHIMA JS AND OSENBERG CW. 2003. Cryptic density dependence: effects of covariation between density and site quality in reef fish. *Ecology* 84: 46–52.
- SOROKIN YI. 1991. Biomass, metabolic rates and feeding of some common reef zoantharians and octocorals. *Aus J Mar Freshwat Res* 42: 729–741.
- SOROKIN YI. 1995. *Coral reef ecology*. Ecological Studies. Springer-Verlag, Berlin, 465 p.
- STAMPAR S, SILVA PF AND LUIZ JR O. 2007. Predation on the zoanthid *Palythoa caribaeorum* by a hawksbill turtle in Southeastern Brazil. *Marine Turtle Newsletter* 117: 3–5.
- STEPHEN JD, LARSON RJ AND PONDELLA DJ. 2006. Rocky reefs and kelp beds, p. 227–252. In: ALLEN LG, PONDELLA DJ AND HORN MH (Eds), *The Ecology of Marine Fishes: California and Adjacent Waters*. University of California Press, Berkeley, p. 227–252.
- SUCHANEK TH AND GREEN DJ. 1981. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix reefs, U.S. Virgin Islands. *Proceedings 4th International Coral Reef Symposium*, p. 679–684.
- SYMS C AND JONES GP. 2000. Disturbance, habitat structure and the dynamics of a coral-reef fish community. *Ecology* 81: 2714–2729.
- TER BRAAK CJF AND VERDONSCHOT PFM. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat Sci* 57: 255–289.
- UNDERWOOD AJ. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, 504 p.
- USAMI M, SATAKE M, ISHIDA S, INOUE A, KAU Y AND YASUMOTO T. 1995. Palytoxin analogs from the dinoflagellate *Ostreopsis siamensis*. *J Am Chem Soc* 117: 5389–5390.
- VILLAÇA R AND PITOMBO FB. 1997. Benthic communities of shallow-water reefs of Abrolhos, Brazil. *Rev Bras Oceanogr* 45: 35–43.
- WELLINGTON GM AND VICTOR BC. 1985. El Nino mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* 68: 15–19.
- ZAR JH. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, 662 p.
- ZELLER DC. 1988. Short-term effects of territoriality of a tropical damselfish experimental exclusion of large fishes on invertebrates in algal turfs. *Mar Ecol Progress Series* 44: 85–93.