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REEF FISH AND BENTHIC ASSEMBLAGES OF THE TRINDADE AND MARTIN VAZ ISLAND GROUP, SOUTHWESTERN ATLANTIC

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ABSTRACT

The Trindade and Martin Vaz island group (TMVIG) is located at about 1,120 km off the Brazilian coast. Despite its importance, highlighted by the presence of several endemic fish species, the TMVIG lacks detailed information on the structure of fish and benthic assemblages. Presented here is the first quantitative assessment of reef fish and benthic assemblages of the TMVIG in a depth gradient ranging from 5 to 45 m. Additional qualitative information on reef assemblages between 45 and 100 m was obtained using advanced gas diving techniques (TRIMIX) and a remotely operated vehicle (ROV). Similarly to other Brazilian oceanic islands, the TMVIG possesses depauperated fish and benthic assemblages, possibly due to its isolation and small size in comparison to the mainland. Depth was the most important factor affecting the structure of fish assemblages, with the density of most fish species declining with depth. Deep reefs (> 45 m) were characterized by the presence of extensive rhodolith beds and rocky reefs sparsely covered with crustose coralline algae, black coral (*Cirripathes* sp.) and a few massive or plate-like reef corals. Part-time or obligatory planktivorous fishes (e.g. *Cephalopholis furcifer* and *Clepticus brasiliensis*) also dominated deep reefs. Similar characteristics were recorded in mesophotic reef ecosystems across the Western Atlantic. Evidence of overfishing (obtained here and in other recent studies), the presence of four endemic and restricted range fish species, as well as the increase in number of new (and still undescribed) endemic taxa, indicates that the adoption of precautionary conservation measures are urgently needed in order to maintain the fragile and unique ecosystems of the TMVIG.

RESUMO

O conjunto insular de Trindade e Martin Vaz (CITMV) está localizado a aproximadamente 1.120 km da costa brasileira. Apesar de sua importância, salientada pela presença de diversas espécies endêmicas de peixes, não existem informações detalhadas sobre as assembléias de peixes e bentos do CITMV. É apresentada aqui a primeira caracterização quantitativa das assembléias de peixes e bentos do CITMV em um gradiente de profundidade entre 5 e 45 m. Informações qualitativas adicionais sobre assembléias recifais entre 45 e 100 m foram obtidas utilizando-se técnicas avançadas de mergulho (TRIMIX) e um veículo de operação remota (VOR). Assim como outras ilhas oceânicas brasileiras, a CITMV possui assembléias depauperadas de peixes e bentos, possivelmente devido ao seu isolamento e pequeno tamanho em comparação ao continente. A profundidade foi o fator que mais afetou a estrutura das assembléias de peixes, com a densidade da maioria das espécies declinando com o aumento da profundidade. Os recifes profundos (> 45 m) foram caracterizados pela presença de bancos extensivos de rodolitos e recifes rochosos esparsamente cobertos por algas coralináceas incrustantes, corais negros (*Cirripathes* sp.) e alguns corais massivos e em de forma de placa. Peixes parcialmente ou obrigatoriamente planctívoros (e.g. *Cephalopholis furcifer* and *Clepticus brasiliensis*) também dominaram em recifes profundos. Características similares foram registradas para recifes mesofóticos ao longo do Atlântico Ocidental. Evidências de sobrepesca (obtidas aqui e em outros estudos recentes), a presença de quatro espécies de peixes endêmicas e com distribuição restrita, e o aumento no número de espécies novas ainda não descritas, indicam que a adoção de medidas de conservação baseadas no princípio da precaução é urgentemente necessária para garantir a manutenção dos ecossistemas frágeis e únicos do CITMV.

Descriptors: Oceanic islands, Brazil, Reef fish, Benthic assemblages, Habitat characteristics, Mesophotic reefs.
Descritores: Ilhas oceânicas, Brasil, Peixes recifais, Assembléias bentônicas, Características do hábitat, Recifes mesofóticos.

INTRODUCTION

Oceanic islands typically harbor low species richness and a high proportion of endemic reef fish and benthic species owing to their extreme isolation and relatively restricted shallow water zones (WHITTAKER; FERNANDEZ-PALACIOS, 2007). This high endemism relative to that found in mainland coastal areas makes them priority areas for biodiversity conservation (ALLEN, 2008; FLOETER et al., 2008; KIER et al., 2009). Despite a wealth of qualitative information from Brazilian oceanic islands (e.g. GASPARINI; FLOETER, 2001; FLOETER et al., 2008), there are few quantitative data, either spatial or temporal (but see ROSA; MOURA, 1997; FRANCINI-FILHO et al. 2000; MINTE-VERA et al., 2008), thus precluding the evaluation of their conservation status and the implementation of effective conservation and management measures.

The Vitória-Trindade Chain (VTC) comprises a series of eight seamounts that terminates with a group of emergent islands (hereafter called Trindade and Martin Vaz island group) at its easternmost end, about 1,120 km off the Brazilian coast. The marine biodiversity of Trindade Island is remarkably low; it is considered one of the poorest among tropical islands in the world (FLOETER et al., 2008). Only 129 species of reef fishes (PINHEIRO et al., 2009), 132 species of marine algae (NASSAR, 1994; YONESHIGUE-VALENTIN et al., 2005; VILLAÇA et al., 2006) and 26 species of sponges (MORAES et al., 2006) had previously been recorded on the island.

Logistical issues and the remoteness of Trindade have limited previous studies to qualitative sampling (e.g. NASSAR, 1994; GASPARINI; FLOETER, 2001; PINHEIRO et al., 2009). In addition, most benthic assessments were restricted to the intertidal zone and based on single-day samplings (PEDRINI el al., 1989; NASSAR, 1994), while reef fish assessments used only snorkeling and were thus limited to depths of up to 20 m (GASPARINI; FLOETER, 2001). The most recent benthic survey, carried out during a large-scale Brazilian EEZ assessment (LAVRADO, 2006), included only a few dredging stations at depths between 30 and 300 m around the island (YONESHIGUE-VALENTIN et al., 2006). Until now, there has only been one qualitative assessment of reef fish from Martin Vaz Island (PINHEIRO et al., 2009), with no additional data (quantitative or qualitative) on the marine biota of this island. Recent reviews indicate that the marine biota of the Trindade and Martin Vaz island group (TMVIG) is the least known among the Brazilian oceanic islands (ALVES; CASTRO, 2006).

This study is the first quantitative assessment of reef fish and benthic assemblages of the TMVIG for depths ranging between 5 and 45 m. Additional qualitative information on reef fish and benthic assemblages between 45 and 100 m is provided.

METHODS

Study area

The areas of the two main islands in the TMVIG (20°30'S, 29°20'W; Fig. 1) are approximately 10 and 0.5 km^2, respectively, with narrow insular shelves, extending about 3 km from the shore and composed of heterogeneous subvolcanic structures and pyroclastic deposits (MARQUES et al., 1999). The littoral zone is comprised of about 2.5 km of beaches and 14 km of narrow (<1 km) and steep (30-90º) rocky shores. The sublittoral hard bottom is composed of boulders ranging up to several hundred meters in diameter interspersed with patches of sandy/calcareous algae rubble, as well as large uniform rock expanses. The VTC originated from the mantle plume activity along the Vitória-Trindade/Hotspur Fracture Zone which, after erosional events, created eight seamounts with flattened tops at depths of about 50 m (ALVES et al., 2006). The VTC is mainly under the influence of the Brazilian Current (BC), characterized by warm (>20ºC SST), relatively saline (36 psu) and oligotrophic waters (SILVEIRA et al., 2000).

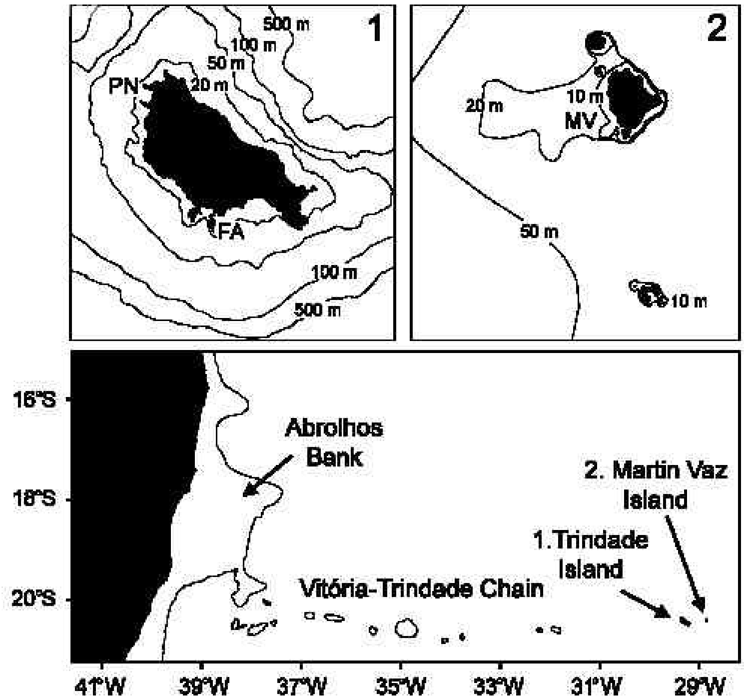

Fig. 1. Map of the eastern Brazilian coast showing the Vitória-Trindade Chain and the Trindade and Martin Vaz island group. Study sites: A) Enseada dos Farilhões (FA), B) Ponta do Noroeste (PN) and C) Martin Vaz Island (MV).

Field Procedures

Surveys were conducted at two sites in Trindade (Ponta Noroeste, PN, and Enseada dos Farilhões, FA) and one site in Martin Vaz (MV) (Fig. 1), between March 16 and 26, 2009. At each site, benthic assemblages were sampled using photoquadrats according to Francini-Filho et al. (2008, 2010). Ten quadrants of 0.7 m2 were randomly placed along two 50 m transects parallel to the coast at each site, one at 10 m and another at 20 m depth. An additional deeper transect (at about 45 m depth, which represents the limit of hard bottom) was sampled at FA, along which three quadrants were obtained. Each quadrant was subdivided into fifteen smaller (0.33 x 0.20 m) frames. Thus, each quadrant (sample) was composed of a mosaic of 15 digital images. Benthic percentage cover was estimated with the Coral Point Count with Excel Extension software (CPCe) (KOHLER; GILL, 2006). Fifteen randomly located points were generated per photograph, thus totaling 225 points per quadrant. Organisms immediately below each point were identified to the most precise taxonomic level possible. Quantitative analyses were performed considering the ten following major benthic categories: abiotic (subdivided into bare rock and sand), crustose coralline algae (subdivided into Peyssonelia sp. and others, the latter including mainly Hydrolithon onkodes, Lithophyllum prototypum, Phymatolithon masonianum, Spongites sp.), corals (mainly Siderastrea sp., Montastrea cavernosa and the Brazilian endemic Mussismilia hispida), fleshy macroalgae (cf. STENECK; DETHIER, 2004), octocorals, sponges (subdivided according to color), turf algae (subdivided into: Jania plus Amphiroa plus other small filamentous algae, and the cyanobacteria Lyngbya sp.), and stoloniferous algae (Caulerpa verticilata and C. pusilla). Reference samples of benthic organisms are deposited at both the Jardim Botânico do Rio de Janeiro (JBRJ) and the Instituto de Botânica de São Paulo (IBt-SP).

Reef fish density was assessed using a stationary visual census (n = 10 per depth strata), following the procedures of MINTE-VERA et al. (2008). Fish counts were carried out at the same sites and depth strata as the benthic sampling with the use of conventional SCUBA. Reference specimens were collected with spears and hand-nets and are deposited at the Museu de Zoologia, Universidade de São Paulo (MZUSP).

Qualitative observations on deep reefs (45-100 m depth) were carried out using advanced mixed gas diving techniques (TRIMIX; n = 4 dives) and a remotely operated Seabotix® LBV 150S2 vehicle (ROV) equipped with a color video camera and a pair of scaling lasers 5 cm apart (n = 20 operations).

Data Analysis

Calculations were performed for: 1) the 20 most abundant benthic taxa, 2) all major benthic categories, 3) the 20 most abundant reef fish species, and 4) total fish density. Density of large-sized carnivorous fishes (a group particularly susceptible to overfishing; RUSS; ALCALA, 1998) was calculated to allow comparisons with those of protected areas within Brazil, in accordance with fish classification based on data taken from the literature (FRANCINI-FILHO; MOURA, 2008; PINHEIRO; GASPARINI, In press) (see Table 1).

Table 1**.** Reef fish species recorded at Trindade (TR) and Martin Vaz (MV) Islands. Plus sign denotes presence.

FAMILY / SPECIES	TR	MV
Ginglymostomatidae		
Ginglymostoma cirratum[c]	+	
Carcharhinidae		
Carcharhinus perezi[c]		+
Synodontidae		
Synodus synodus	+	
Muraenidae		
Gymnothorax miliaris	+	
Gymnothorax moringa	+	+
Ophichthidae		
Myrichthis breviceps	+	+
Holocentridae		
Holocentrus adscensionis[b]	+	+
Sargocentron bullisi[b]	+	
Scorpaenidae		
Scorpaena plumier	+	
Sphyraenidae		
Sphyraena barracuda[c]		+
Serranidae		
Cephalopholis fulva[b]	+	+
Cephalopholis furcifer[b]	+	
Epinephelus adscensionis[c]	+	+
Mycteroperca bonaci[c]	+	
Mycteroperca venenosa[b, c]	+	
Rypticus saponaceus	+	
Apogonidae		
Apogon americanus	+	
Astrapogon stellatus	+	
Phaeoptyx pigmentaria	+	
Malacanthidae		
Malacanthus plumieri[b]	+	
Cirrhitidae		
Amblycirrhitus pinos	+	
Carangidae		
Carangoides crysos[c]	+	
Carangoides ruber[c]	+	
Caranx lugubris[BC]	+	+
Seriola rivoliana[c]		
Haemulidae		
Anisotremus surinamensis	+	
Sparidae		
Diplodus argenteus	+	+
Mullidae		
Pseudupeneus maculatus	+	
Mulloidichthys martinicus[b]	+	
Chaetodontidae		
Chaetodon striatus	+	
Prognathodes brasiliensis[b]	+	+
Pomacanthidae		
Centropigy aurantonotus	+	
Holacanthus tricolor[b]	+	
Kyphosidae		
Kyphosus sectator	+	+
Pomacentridae		
Abudefduf saxatilis	+	+
Chromis flavicauda[b]	+	
Chromis jubauna[a,b]	+	
Chromis multilineata	+	+
Microspathodon chrysurus	+	+
Stegastes pictus[b]	+	+
Stegastes fuscus trindadensis	+	+
Labridae		
Bodianus pulchellus[b]	+	
Bodianus rufus	+	
Clepticus brasiliensis[b]	+	
Halichoeres brasiliensis	+	+
Halichoeres rubrovirens	+	+
Halichoeres poeyi	+	+
Thalassoma noronhanum	+	+
Scaridae		
Sparisoma amplum	+	
Sparisoma axillare	+	
Trypterygiidae		
Enneanectes sp.	+	
Labrisomidae		
Labrisomus nuchipinnis	+	+
Malacoctenus brunoi	+	+
Bleniidae		
Entomacrodus sp.	+	
Hypleurochilus sp.	+	+
Ophioblennius trinitatis	+	+
Scartella poiti	+	+
Gobiesocidae		
Arcos sp.	+	
Gobiidae		
Coryphopterus sp.	+	
Elacatinus pridisi	+	+
Acanthuridae		
Acanthurus bahianus	+	+
Acanthurus coeruleus	+	+
Balistidae		
Balistes vetula	+	+
Canthidermis sufflamen[b]	+	+
Melichthys niger	+	+
Monacanthidae		
Aluterus scriptus	+	
Cantherhines macrocerus	+	+
Cantherhines pullus	+	+
Tetraodontidae		
Canthigaster figueiredoi	+	
Sphoeroides spengleri	+	+
Diodontidae		
Diodon holacanthus	+	
Diodon hystrix	+	
Ostraciida		
Acanthostracion polygonius[a]	+	

[a]New record for the TMVIG; [b]Species only recorded or particularly abundant on deep reefs (> 60 m); [c]Large carnivorous fishes targeted by fisheries.

Two-way analysis of variance (ANOVA) was used to evaluate differences in benthic coverage and fish density between sites and depths. The deeper transect at the FA site was excluded from the ANOVA due to lack of sampling in a similar depth stratum at the other sites. Normality and homoscedasticity were improved by converting percentage values of benthic cover to arcsin√X and fish density estimates to log (x+1). *Post-hoc* comparisons were performed using the Tukey test (ZAR, 1999). Linear regression was used to evaluate the relationship between depth and total fish density, with both variables previously converted to log (x+1). Samples from the deeper strata at the FA site were included in this latter analysis.

Non-metric multidimensional scaling (nMDS) was used to summarize similarities (Bray-Curtis) in benthic and fish assemblage structures between sites and depths, and a two-way analysis of similarity (ANOSIM) was performed to evaluate significant differences among sites (CLARKE; WARWICK, 1994). A fourth root transformation was performed prior to the analyses in order to avoid the excessive weight of numerically dominant species (CLARKE; WARWICK, 1994). Canonical correspondence analysis (CCA) (TER BRAAK, 1996) was used to evaluate the influence of habitat characteristics (i.e. benthic coverage and depth) on the structure of fish assemblages.

Results

Fish Assemblages

A total of 73 species of fish belonging to 33 families were recorded (Table 1), representing about 67% of the known reef fish species pool of the TMVIG (GASPARINI; FLOETER, 2001; PINHEIRO et al., 2009). Total fish density varied significantly between sites, with the highest values recorded at the MV and PN sites, respectively. Total fish density declined with depth (linear regression: $F = 23.3$; $P < 0.001$; $R = -0.54$), the same pattern being recorded for all fish species for which significant between-depth strata differences were recorded (see *post-hoc* comparisons in Table 3). The twenty most abundant fish species are shown in Figure 2. Four species (*Cephalopholis fulva*, *Chromis multilineata*, *Halichoeres rubrovirens* and *Stegastes fuscus trindadensis*) were more abundant at the MV or at the MV plus PN sites, while three species (*Abudefduf saxatilis*, *Acanthurus bahianus* and *Malacoctenus brunoi*) were more abundant at the PN or at the PN plus FA sites. There were no differences in density of large carnivorous fishes between sites and depth strata, with the overall density value (i.e., of all sites pooled) estimated at 0.03 ± 0.01 individuals.m^{-2}. No other significant differences between sites and/or depth strata were recorded (Fig. 2; Table 3). The structure of fish assemblages differed significantly between both sites ($R = 0.25$; $P = 0.001$) and depth strata ($R = 0.56$; $P = 0.001$; Figure 4a), with a stronger difference (i.e., higher R values) recorded for the latter.

Qualitative observations on deep reefs (>60 m) showed that 16 species were dominant (see Table 1). Part-time or obligatory planktivorous fishes (*Cephalopholis furcifer*, *Mulloidichthys martinicus*, *Chromis flavicauda*, *Chromis jubauna* and *Clepticus brasiliensis*) were particularly abundant in deeper areas. Fishes were mostly associated with prominent and complex bottom features (e.g. *Malacanthus plumieri* nests composed of piles of rhodoliths and rock expanses covered mainly by black corals near the break of the narrow insular shelf; see below).

Benthic Assemblages

A total of 51 benthic taxa were recorded. The three new records of corals and 11 new records of macroalgae for the TMVIG are worth noting (Table 2). In addition, the crustose coralline algae, *Lithophyllum prototypum* (Martin Vaz Island, 20°28’05’’S, 28°51’28’’W, GM Amado-Filho, 22.III.2009, RB 498282), represents a new record for the entire South Atlantic Ocean.

Sand was the dominant type of benthic cover, followed by *Caulerpa verticillata*, crustose coraline algae (excluding *Peyssonelia sp.*), *Dictyota mertensii* and *Canistrocarpus cervicornis*. The other common benthic organisms are shown in Figure 3. The benthic cover of two reef corals (*Mussismilia hispida* and *Siderastrea* sp.), the stoloniferous algae *Caulerpa pusilla* and the cyanobacteria *Lyngbya* sp., was greater at the MV site. Four taxa (*Peyssonelia* sp., *Canistrocarpus cervicornis*, green sponges, and *Jania* plus *Amphiroa* turf) dominated at the FA site, while two fleshy macroalgal species (*Dictyota ciliolata* and *D. mertensii*) were more abundant at the PN site (Fig. 3; Table 4). No other significant differences between sites and/or depth strata were recorded. Similarly to fish assemblages, the structure of benthic assemblages differed significantly between the two sites ($R = 0.86$; $P = 0.001$) and depth strata ($R = 0.57$; $P = 0.001$; Fig. 4b), with a stronger effect of the former, as indicated by the higher R value.

The shallow benthic realm was replaced by a deep reef assemblage at about 45 m, this latter comprised of a mosaic of small sandy patches and rhodolith pavement. From 80 to 90 m depth, the rhodolith pavement was substituted by a narrow steep rocky reef (~35º), which marks the end of the insular shelf. These deep rocky reefs were sparsely covered with crustose coralline algae, colonies of the black coral *Cirripathes* sp., as well as the plate-like and massive reef corals *Agaricia* cf. *fragilis*, *Montastrea cavernosa* and *Scolymia wellsi* (see Table 2).

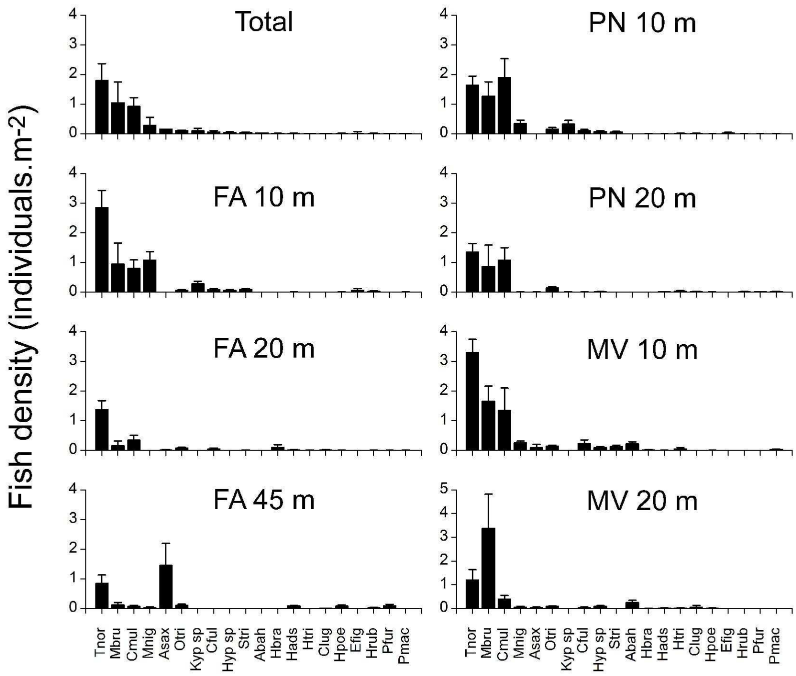

Fig. 2. Density (mean + SE) of the 20 most abundant fish species FA - Enseada dos Farilhões, PN - Ponta do Noroeste and MV - Martin Vaz. Numbers denote depth strata. Note differences in scale of y axes. Abbreviations of species names: genus indicated by first capital letter and specific epithet by following letters (except for species identified to genus level only, for which the first three letters of genus name were used; see full names in Table 1).

Table 2. Benthic reef organisms recorded at Trindade (TR) and Martin Vaz (MV) Islands. Plus sign denotes presence.

Taxa	TR	MV	Taxa	TR	MV
Cyanobacteria			Rhodophyta (cont.)		
Lyngbya sp.	+	+	*Ceramium* spp.	+	+
Chlorophyta			*Champia parvula* [a]	+	+
Anadyomene saldanhae	+	+	*Dasya brasiliensis* [a]	+	
Anadyomene stellata	+		*Heterosiphonia crassipes* [a]	+	
Bryopsis pennata	+	+	*Herposiphonia secunda f. tenella*	+	
Caulerpa kempfii		+	*Hydrolithon onkodes* [a]	+	
Caulerpa mexicana	+		*Lithophyllum prototypum* [c]	+	+
Caulerpa pusilla	+	+	*Phymatolithon masonianum* [a]	+	
Caulerpa verticillata	+	+	*Peyssonelia sp.*	+	
Dictyosphaeria sp.	+		*Polysiphonia* spp.	+	
Halimeda discoidea	+		*Jania adhaerens*	+	+
Neomeris sp.	+		*Spongites* sp.[a]	+	
Rhipilia tomentosa	+		Octocorals		
Udotea flabellum	+		*Plexaurela regia*	+	
Ochrophyta			Scleractinians		
Canistrocarpus cervicornis	+	+	*Agaricia* cf. *fragilis*[b]	+	
Dictyopteris delicatula	+		*Favia gravida*	+	+
Dictyopteris plagiogramma	+		*Favia leptophyla*	+	+
Dictyota ciliolata [a]	+	+	*Montastrea cavernosa*[b]	+	
Dictyota mertensii	+	+	*Mussismilia hispida*	+	+
Dictyota pulchella [a]	+		*Scolymia wellsi*[b]	+	
Feldmannia indica [a]	+		*Siderastrea* sp.	+	
Lobophora variegata	+	+	Black corals (Antipatharia)		
Padina gymnospora	+		*Cirripathes* sp.[b]	+	
Rhodophyta			Sponges	+	+
Amphiroa beauvoisii [a]	+		Green Sponge	+	+
Asparagopsis taxiformis	+		Brown Sponge	+	+
Botryocladia pyriformis	+	+	Yellow Sponge	+	+
Centroceras clavulatum	+		Orange Sponge	+	+

[a]New record for the TMVIG; [b]Species only recorded or particularly abundant on deep reefs (> 60 m); [c]New record for the South Atlantic Ocean.

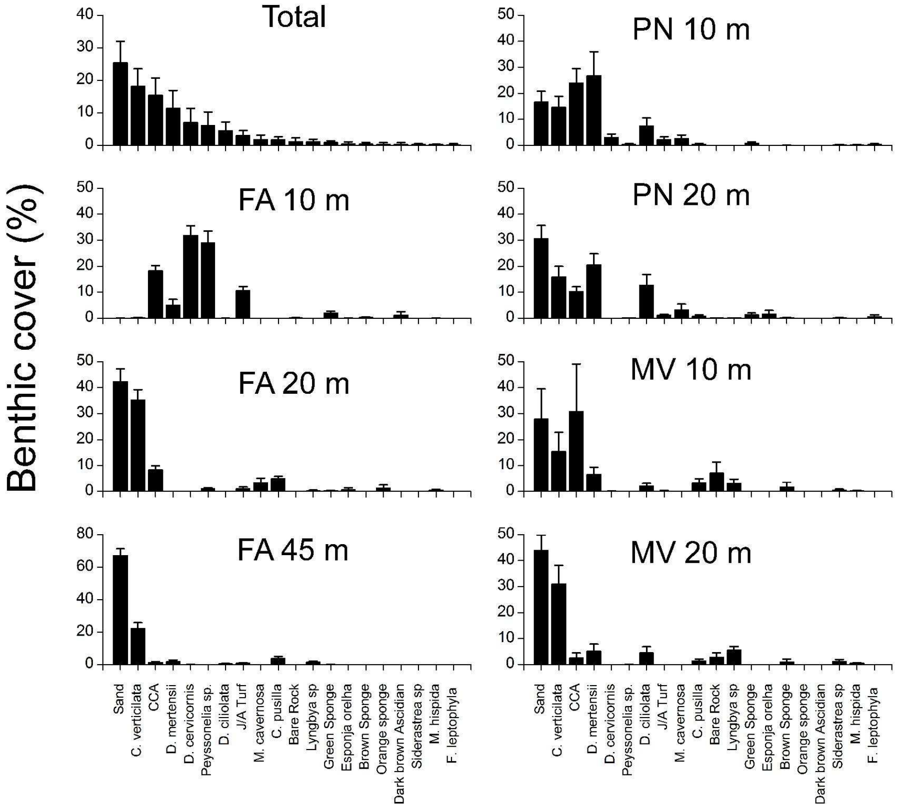

Fig. 3. Benthic cover (mean + SE) of the 20 most abundant organisms (relative cover > 1%). FA - Enseada dos Farilhões, PN -Ponta do Noroeste and MV - Martin Vaz. Numbers denote depth strata. Note differences in scale of y axes.

Table 3. Two-way analysis of variance (ANOVA) testing differences in fish density among sites and depths and Tukey post-hoc comparisons. Df - degrees of freedom. Depth strata: S - shallow (10 m) and I - intermediate (20 m). Sampling sites: FA - Enseada dos Farilhões, PN - Ponta do Noroeste and MV - Martin Vaz. Ns - not significant.

Fish species	**Site (df = 2)**		**Depth (df = 1)**		**Site x depth (df = 2)**		**Tukey post-hoc**	
	F	**p**	**F**	**p**	**F**	**p**	**Site**	**Depth**
Abudefduf saxatilis	3.37	*	14.88	***	3.03	ns	PN = FA > FA = MV	S > I
Acanthurus bahianus	3.47	*	1.69	ns	5.70	**	FA = PN > PN = MV	ns
Caranx lugubris	0.86	ns	0.44	ns	1.37	ns	ns	ns
Cephalopholis fulva	3.52	*	0.87	ns	0.30	ns	PN = MV > MV = FA	ns
Chromis multilineata	5.57	**	0.23	ns	1.14	ns	MV = PN > PN = FA	ns
Elacatinus pridisi	1.70	ns	0.02	ns	1.34	ns	ns	ns
Halichoeres brasiliensis	1.43	ns	0.58	ns	7.73	**	ns	ns
Halichoeres rubrovirens	40.58	***	0.12	ns	0.09	ns	MV > PN = FA	ns
Halichoeres poeyi	0.64	ns	3.36	ns	1.18	ns	ns	ns
Holacanthus tricolor	0.02	ns	1.71	ns	0.06	ns	ns	ns
Holocentrus adscensionis	0.04	ns	1.66	ns	0.18	ns	ns	ns
Hypleurochillus sp.	0.36	ns	1.20	ns	0.36	ns	ns	ns
Kyphosus sectator	1.03	ns	9.61	**	1.26	ns	ns	S > I
Malacoctenus brunoi	5.46	**	40.04	***	6.73	**	FA > MV = PN	S > I
Melichthys Níger	2.74	ns	3.76	ns	0.05	ns	ns	ns
Ophioblennius trinitatis	1.35	ns	31.83	***	1.10	ns	ns	S > I
Cephalopholis furcifer	2.59	ns	0.05	ns	0.65	ns	ns	ns
Pseudupneneus maculatus	2.08	ns	2.19	ns	0.54	ns	ns	ns
Stegastes trindadensis	3.50	*	4.93	*	0.83	ns	MV = PN > PN = FA	S > I
Thalassoma noronhanum	1.18	ns	12.22	**	2.05	ns	ns	S > I
Total fish density	3.43	***	15.21	***	1.64	ns	MV = PN > PN = FA	S > I
Large carnivores	0.79	ns	0.73	ns	1.72	ns	ns	ns

* $P<0.05$, ** $P<0.01$, *** $P<0.001$ and ns - not significant.

Table 4. Two-way analysis of variance (ANOVA) testing differences in benthic cover among sites and depths and Tukey post-hoc comparisons. Df - degrees of freedom. Depth strata: S - shallow (10 m) and I - intermediate (20 m). Sampling sites: FA - Enseada dos Farilhões, PN - Ponta do Noroeste and MV - Martin Vaz. Ns - not significant.

Benthic category / species	Site (df = 2)		Depth (df = 1)		Site x depth (df = 2)		Tukey post-hoc	
	F	p	F	p	F	p	Site	Depth
Ascidian								
Dark-brown Ascidian	0.83	ns	0.71	ns	0.83	ns	ns	ns
Coral								
Montastrea cavernosa	2.51	ns	1.33	ns	0.78	ns	ns	ns
Mussismilia híspida	4.49	*	1.74	ns	4.89	*	MV > FA > PN	ns
Siderastrea sp.	7.19	***	0.92	ns	0.61	ns	MV > PN > FA	ns
Favia leptophyla	1.59	ns	0.08	ns	0.09	ns	ns	ns
Total	1.23	ns	2.11	ns	0.66	ns	ns	ns
Crustose Coralline Algae								
Peyssonelia sp.	82.77	***	41.94	***	46.24	***	FA > PN > MV	S > I
Other	0.94	ns	15.21	***	1	ns	ns	S > I
Total	2.71	ns	29.36	***	2.5	ns	ns	S > I
Fleshy macroalgae								
Canistrocarpus cervicornis	43.64	***	77.53	***	43.68	***	FA > PN > MV	S > I
Dictyota ciliolata	18.57	***	1.84	ns	0.72	ns	PN > MV > FA	ns
Dictyota mertensii	14.95	***	1.41	ns	1.17	ns	PN > MV > FA	ns
Total	7.59	**	5.92	*	5.25	**	PN > FA = MV	S > I
Sponge								
Green Sponge	8.26	***	1.77	ns	6.22	**	FA = PN > MV	ns
Brown Sponge	1.94	ns	0.38	ns	0.34	ns	ns	ns
Yellow Sponge	0.73	ns	1.89	ns	0.84	ns	ns	ns
Orange Sponge	1.11	ns	0.95	ns	1.11	ns	ns	ns
Total	0.31	ns	0.24	ns	1.1	ns	ns	ns
Stoloniferous Algae								
Caulerpa verticillata	2.28	ns	37.57	***	14.71	***	ns	I > S
Caulerpapusilla	5.02	**	10.33	***	14.97	***	MV > FA > PN	I > S
Total	2.16	ns	26.24	***	11.97	***	ns	I > S
Turf								
Jania plus *Amphiroa*	28.21	***	24.25	***	14.73	***	FA > PN > MV	S > I
Lyngbya sp.	39.45	***	7.39	**	1.6	ns	MV > PN = FA	I > S
Total	9.15	***	8.52	**	13.66	***	FA > PN = MV	S > I
Abiotic								
Bare Rock	11.43	***	2.71	ns	2.12	ns	MV > FA = PN	ns
Sand	3.89	*	32.26	***	5.43	**	MV > FA = PN	I > S
Total	8.75	***	34.79	***	7.35	**	MV > FA = PN	I > S

* P<0.05, ** P<0.01, *** P<0.001 and ns - not significant.

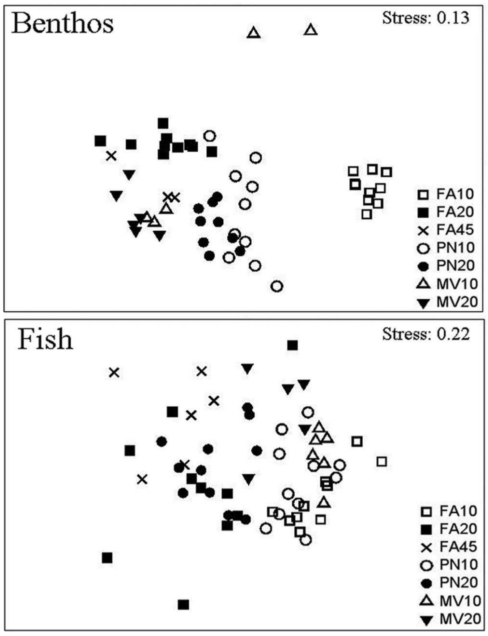

Fig. 4. Non-metric multi-dimensional scaling (nMDS) ordination based on Bray-Curtis similarities. A) Fish assemblages and B) benthic assemblages. FA - Enseada dos Farilhões, PN -Ponta do Noroeste and MV - Martin Vaz. Numbers denote depth strata.

Influence of Depth and Benthic Cover on Fish Assemblages

Results from the CCA showed that depth was the main predictor of fish assemblage structure, followed by cover of crustose coralline algae, turf algae, ascidians, sand, fleshy macroalgae and sponges, successively. The first two axes explained 79.4% of the relationship between habitat characteristics and fish assemblage structure. Most of the fish species were associated with shallow benthic communities, characterized by crustose coralline algae, fleshy macroalgae and sponges. Four species (*Cephalopholis furcifer*, *Holacanthus tricolor*, *Holocentrus adscensionis* and *Pseudopeneus maculatus*) were associated with deep reefs (i.e., the 45 m depth stratum at the FA site), where stoloniferous algae and sand patches covered the rocky bottom (Fig. 5). This latter result corroborates the qualitative observations on fish assemblages of deep reefs (see above).

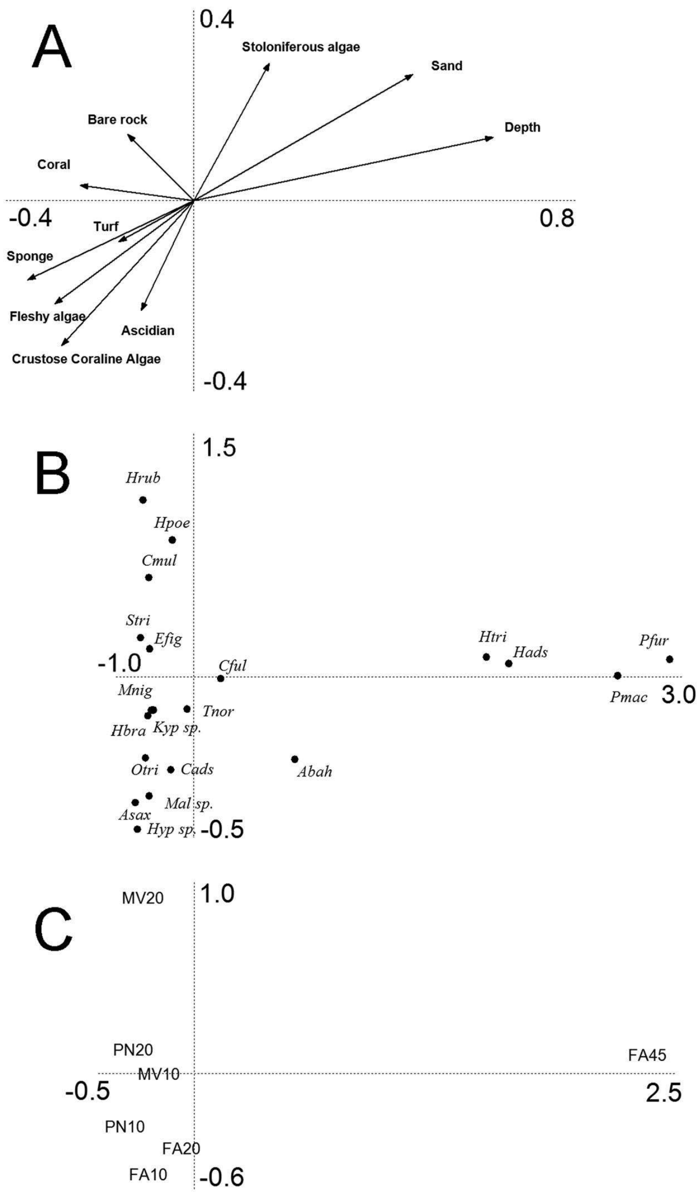

Fig. 5. Canonical correspondence analysis plot showing (A) habitat characteristics, (B) fish species and (C) sampling sites. FA - Enseada dos Farilhões, PN -Ponta do Noroeste and MV - Martin Vaz. Numbers denote depth strata. Abbreviations of species names: genus indicated by first capital letter and specific epithet by following letters (except for species identified to genus level only, for which the first three letters of genus name were used; see full names in Table 1).

Discussion

Similarly to the other three Brazilian oceanic islands (i.e., Atol das Rocas, Fernando de Noronha and St. Paul's Rocks), the TMVIG possesses poor fish and benthic assemblages. In fact, the relatively small size and isolation from the mainland are the two most important and widely recognized factors leading to lower species richness among oceanic islands (SANDIN et al., 2008).

Despite the biological connectivity between the TMVIG and mainland (i.e., the eastern Brazilian coast), facilitated by the seamounts of the Vitória-Trindade Chain which work as a series of "stepping stones" (PINHEIRO et al., 2009), the structure of fish assemblages of the TMVIG is more closely similar to those of Atol das Rocas and Fernando de Noronha (ROSA; MOURA, 1997; FRANCINI-FILHO et al., 2000) than to those of the mainland. For these three oceanic islands, three fish species (*Talassoma noronhanum*, *Chromis multilineata* and *Abudefduf saxatilis*) dominate the assemblages, with *C. fulva* and *M. niger* also featuring as conspicuous elements. In addition, benthic assemblages of all Brazilian oceanic islands are dominated by macroalgae (fleshy and crustose), with sparse patches of other benthic organisms (especially sponges and a few coral species). Thus, other than the possibility of periodic colonization from a main but remote source (the mainland), the maintenance of these isolated populations may rely primarily on their ability to maintain viable populations in small isolated oceanic habitats. Exceptions to this pattern are the reef coral *Favia leptophylla* and the Brazilian wrasse *Halichoeres brasiliensis*. *Favia leptophylla* was previously considered endemic to the eastern Brazilian coast (LEÃO et al., 2003), but it is now known to occur in the TMVIG as well, possibly because of the connection promoted by the VTC. *Halichoeres brasiliensis* is common in the mainland (e.g. FRANCINI-FILHO; MOURA, 2008) and the TMVIG, but is absent from the other Brazilian oceanic islands, again corroborating the hypothesis of greater connectivity between mainland and the TMVIG through the VTC.

Depth, as expected, was the most important environmental variable affecting the structure of fish assemblages (see FRANCINI-FILHO; MOURA, 2008, for similar results). The influence of depth may occur via the alteration of physical variables (e.g., pressure, salinity and luminosity) or through the modification of benthic assemblages, this latter serving as shelter and/or food for fish. The shallow portion of the TMVIG is dominated by fleshy macroalgae and crustose coraline algae, a pattern possibly related to high irradiance levels promoted by the sediment-free and oligotrophic oceanic waters, and by the scarcity of specialized herbivores such as parrotfishes (family Scaridae) (FRANCINI-FILHO et al. 2010). Densities of *Sparisoma amplum* and *Sparisoma axillare* were relatively low in the TMVIG. The abundant *Acanthurus bahianus*, *Kyphosus sectator* and *Melichthys niger* were frequently recorded feeding upon turf and macroalgae. Despite a significant spatial variation in turf and macroalgae cover (the former dominating the shallowest strata of the FA site and the latter most abundant throughout the entire depth gradient of the PN site), no similar spatial variation in the density of the above-mentioned fishes (see Table 3) was detected. Detailed studies are still needed in order to better understand the possible role of herbivorous fishes in mediating competition between algae and other benthic organisms in the TMVIG.

Similarly to herbivores, most fish species showed little between-sites spatial variation, despite marked differences in benthic cover (see Tables 3 and 4). Exceptions to this pattern include *Halichoeres rubrovirens*, *Chromis multilineata* and *Stegastes fuscus trindadensis*, all of them most abundant at the same site (Martin Vaz) in which coral cover was relatively higher. The positive relationship between coral cover and reef fish abundance/species diversity is widely recognized (e.g. BELL; GALZIN, 1984), but again additional studies are needed in order to better understand the relationship between fish abundance and coral cover in the TMVIG.

The direct observations undertaken here with advanced mixed gas diving (TRIMIX) and ROV operations in the mesophotic reef ecosystems of the TMVIG are the first of their kind in Brazil. The results obtained indicate that the mesophotic reef ecosystems of the TMVIG are similar to those in other portions of the world, particularly in the Caribbean, where planktivorous fishes, black corals and plate-like/massive coral species dominate (KAHNG et al., 2010). The large rhodolith beds that separate the deepest portion of the shallow rocky reef (at about 45 m depth) from the deep rocky reefs at the insular shelf break (at about 80-90 m) may play an important role in the connectivity between these shallow and deep zones, mainly by providing corridors of complex habitat. In this regard, the nests of *Malacanthus plumieri*, which are formed by mounds of living rhodoliths, may be of particular importance.

Most colonies of the Brazilian endemic reef coral *Mussismilia hispida* were bleached, diseased or partially dead at the time of the sampling. The same situation was observed in the Fernando de Noronha Archipelago, off northeastern Brazil, in November 2009 (authors' pers. obs.). The causes of the decline in the vitality of *M. hispida* on these two Brazilian oceanic islands are still unknown, but an increase in sea surface temperature and infection by pathogenic bacteria cannot be disregarded, as both factors have negatively affected the health of corals (including *M. hispida*) in eastern Brazil (FRANCINI-FILHO et al., 2008; ALVES-JR et al., 2010).

Signs of overfishing in the TMVIG are suggested by the relatively low density of large carnivorous fishes (0.03 ± 0.01 individuals.m-2) such as *Epinephelus adscensionis* and *Sphyraena barracuda*. Comparative values for this same group in the fully-protected area of the Abrolhos Archipelago, Eastern Brazil, are 0.05 ± 0.02 individuals.m-2 (authors' unpub. data). Additional weight is lent to this hypothesis by the sighting of only two sharks during the entire expedition (a *Ginglymostoma cirratum* individual in Trindade and a *Charcharhinus perezi* in Martin Vaz). Recent studies show that the TMVIG is an appreciated fishing ground, with *Caranx lugubris*, *Cephalopholis fulva* and *Epinephelus adscensionis* figuring among the most important target species for the hook and line fishery (PINHEIRO; GASPARINI, in press). Besides evidence of overfishing, the TMVIG possess five endemic and restricted range fish species (*Elacatinus pridisi*, *Halichoeres rubrovirens*, *Scartella poiti*, *Sparisoma rocha* and *Stegastes fuscus trindadensis*), as well as at least three new, but still undescribed reef fish species (PINHEIRO et al., 2009; C.A. RANGEL, pers. comm.). Considering the evidence of overfishing and the fragility and uniqueness of the ecosystems of isolated oceanic islands (ALLEN, 2008), there is a clear need to implement precautionary conservation measures, most importantly the establishment of a permanent no-take zone encompassing the entire TMVIG.

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