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Reef fish structure and distribution in a south-western Atlantic Ocean tropical island

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The community structure of the reef fish fauna of Trindade Island, a volcanic oceanic island located 1160 km off the coast of Brazil, is described based on intensive visual censuses. Seventy-six species were encountered in 252 censuses, with mean \pm s.e. of 99 ± 3 individuals and 15.7 ± 0.3 species 40 m^{-2} transect. The average fish biomass, calculated from length-class estimation, was $22.1 \text{ kg } 40 \text{ m}^{-2}$ transect. The species contributing most to biomass were, in decreasing order, *Melichthys niger*, *Cephalopholis fulva*, *Kyphosus* spp., *Holocentrus adscensionis*, *Sparisoma amplum*, *Sparisoma axillare*, *Acanthurus bahianus* and *Epinephelus adscensionis*. Carnivorous fishes were the largest trophic group in terms of biomass, followed by omnivores and roving herbivores. The two predominant types of reef habitat, fringing reefs built by coralline algae and rocky reefs made of volcanic boulders, showed significant differences in the biomass and the abundance of the trophic guilds. Within each habitat type, significant differences in species richness, density and biomass were detected among crest, slope and interface zones. Although similar in overall species composition to coastal reefs in Brazil, the fish fauna of Trindade Island shares certain characteristics, such as a high abundance of planktivores, with other Brazilian oceanic islands. Despite comparatively high fish biomass, including the macro-carnivorous species habitually targeted by fisheries, signs of overfishing were evident. These findings highlight the urgency for a conservation initiative for this isolated, unique and vulnerable reef system.

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Key words: biogeography; Brazil; conservation; species richness; Trindade Island; trophic guilds.

INTRODUCTION

An accurate description of the community structure is essential baseline information to evaluate both natural and anthropogenic effects on vulnerable habitats, such as coral reefs (Connell *et al.*, 2004; Paddock *et al.*, 2009). In the face of increasing loss of biodiversity and ecological function in the marine environment, there is increasing urgency to obtain baseline descriptions of the structure of communities before further changes occur (Mora, 2008; Sandin *et al.*, 2008).

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For tropical reef fishes in particular, there have been a number of studies evaluating the patterns of species richness, density and biomass at different scales, both in the Caribbean (Lara & Gonzalez, 1998; Newman *et al.*, 2006; Dorenbosch *et al.*, 2007; Grober-Dunsmore *et al.*, 2007) and in the Indo-West Pacific Ocean (Gust, 2002; Galzin *et al.*, 2006; Tuya *et al.*, 2009). These regions are well-known centres of high zoological diversity with high rates of endemism (Hughes *et al.*, 2002; Floeter *et al.*, 2008; Bellwood & Meyer, 2009). Similarly, the fish communities on temperate reefs have been well studied, especially in the Mediterranean Sea (García-Charton & Pérez-Ruzafa, 2001; Ordines *et al.*, 2005; Pais *et al.*, 2007) and in New Zealand (Anderson & Millar, 2004; Pande & Gardner, 2009). In comparison, however, little is known about the reef fish community structure of the south-western Atlantic Ocean reefs (Ferreira *et al.*, 2004).

Brazilian reefs are generally included in the tropical Atlantic Ocean region, but have some unique features (Maida & Ferreira, 1997; Ferreira *et al.*, 2004) that qualify them as belonging to a distinct biogeographic province (Floeter *et al.*, 2001, 2008). Isolated from the Caribbean Sea by mostly semi-permeable geographic barriers (Joyeux *et al.*, 2001; Rocha, 2003; Floeter *et al.*, 2008), the relatively small area of Brazilian reefs [$<5\%$ of the total area of western Atlantic Ocean reefs (Moura, 2000)] harbours a significant proportion of endemic reef fish species (Floeter & Gasparini, 2000; Moura & Sazima, 2000).

Along the Brazilian coastline of 7000 km, there are only four sets of oceanic islands: the St Paul's Rocks ($0^{\circ} 55' N$; $29^{\circ} 21' W$), Fernando de Noronha Island ($3^{\circ} 54' S$; $32^{\circ} 25' W$), Atol das Rocas ($3^{\circ} 50' S$; $33^{\circ} 49' W$) and the island complex of Trindade ($20^{\circ} 30' S$; $29^{\circ} 20' W$) and Martin Vaz Archipelago ($20^{\circ} 30' S$; $28^{\circ} 52' W$). These tiny islands are responsible for 23% of the reef fishes endemic to the Brazilian Province (Floeter *et al.*, 2008). All islands are considered vulnerable, which makes them a high priority for conservation efforts in the region (Moura, 2000). Nevertheless, there is a dearth of quantitative data on their reef fish assemblages other than one survey at Atol das Rocas (Rosa & Moura, 1997) and another at Fernando de Noronha (Krajewski & Floeter, 2011). Quantitative data for St Paul's Rocks are still being processed (Ferreira *et al.*, 2009).

Trindade Island, along with the Martin Vaz Archipelago, comprises the most isolated island complex off the Brazilian coast (Gasparini & Floeter, 2001). Despite the distance from the mainland, the reef fish assemblages of Trindade Island show greater similarities to those of coastal habitats than to those of other Brazilian oceanic islands (Rocha & Rosa, 2001; Floeter *et al.*, 2008; Krajewski & Floeter, 2011). This phenomenon could be related to a connecting submarine ridge, the Vitória-Trindade Chain (Gasparini & Floeter, 2001). The fish fauna of Trindade Island, however, is still taxonomically unresolved (Pinheiro *et al.*, 2009) and the recent discovery of endemic species of non-Atlantic Ocean origin raises new questions about its zoogeographic affinities (Rocha *et al.*, 2010).

Reef fish communities generally exist as metapopulations shaped by both pre- and post-recruitment processes (Mora & Sale, 2002; Sale, 2004). The processes of colonization and maintenance of marine populations at isolated islands have been a major topic of debate in ecology and biogeography (Robertson, 2001; Vermeij, 2004). A variety of environmental factors determines local assemblages, primarily habitat complexity (Dominici-Arosemena & Wolff, 2006; Tuya *et al.*, 2009), depth (Brokovich *et al.*, 2008; González-Sansón *et al.*, 2009), wave exposure (Fulton *et al.*,

2005; Jordaan, 2010), fishing pressure (Pet-Soede *et al.*, 2001; Friedlander & DeMartini, 2002; Tittensor *et al.*, 2009) and even pollution gradients (Guidetti *et al.*, 2003).

Oceanic islands typically present reef systems heavily influenced by wave surge and strong currents, which in turn favour the occurrence and abundance of planktivores (Hamner *et al.*, 1988; Friedlander *et al.*, 2003; Ferreira *et al.*, 2004). A few isolated oceanic islands have maintained a high abundance of large carnivores and roving herbivores (Friedlander & DeMartini, 2002; Sandin *et al.*, 2008) that are typically reduced in more degraded coastal areas (Dulvy *et al.*, 2004; Knowlton & Jackson, 2008; Pinheiro *et al.*, 2010a).

Along the Brazilian coast, reef environments are under the deleterious influence of a sharp increase in coastal urbanization (Leão *et al.*, 2003; Leão & Kikuchi, 2005). Overfishing is, however, probably the most widespread and important factor altering reef function and structure (Ferreira & Gonçalves, 1999; Floeter *et al.*, 2006; Francini-Filho & Moura, 2008). Although most Brazilian oceanic islands (*i.e.* Noronha, Atol da Rocas and St Paul's Rocks, but not Trindade nor Martin Vaz) have some degree of legal protection established by the national conservation unit programme (SNUC) (ICMBio, 2007), commercial and recreational fishing is often permitted and negative fishing effects have been detected (Ferreira *et al.*, 2009; Pinheiro *et al.*, 2010b).

This paper assesses for the first time the general patterns of the reef fish community structure of Trindade Island and compares fish biomass, abundance and richness of the two predominant reef types, fringing coralline algae reefs and rocky volcanic reefs, at various depths along the vertical profile. The three questions raised were (1) Are there differences in fish biomass, density and richness between dominant reef types. (2) Are there differences in fish biomass, density and richness among crest, slope and interface zones of the same profile. (3) What are the species or trophic groups that drive these differences?

MATERIALS AND METHODS

STUDY AREA

Trindade Island (20° 30' S; 29° 20' W) is located 1160 km (620 nautical miles) off the coast of the state of Espírito Santo, south-eastern Brazil (Fig. 1). The island is volcanic, *c.* 3–3.5 million years old (Alves, 1998), and constitutes, with the Martin Vaz Archipelago, the eastern end of the Vitória-Trindade submarine ridge. Although the island has an emergent landmass area of only 9.28 km², it is surrounded by 32 km² of shallow (0–50 m depth) platform (Gasparini & Floeter, 2001).

The climate is oceanic tropical, with an average air temperature of 25° C. February is the hottest month (with mean air temperature up to 30° C) and August the coolest (down to 17° C) (Castro, 2011). During the sampling period (April to June 2009), mean water temperature was 26° C and underwater visibility varied from 15 to 50 m.

The main feature of the Trindade Island seascape is a large, flat fringing reef of encrusting coralline algae distributed along almost the entire island shore. The reef crest is in the surf zone (3–6 m deep), extends tens of metres from the island volcanic rocky shores and sandy beaches and has relatively high structural complexity. As depth increases seaward, there is a wide reef slope beyond the reef crest. The slope comprises habitats varying in structural complexity and ends at the interface, *i.e.* the zone between reef and non-consolidated substrata. The slope and interface zones attain depths varying between 6 and 35 m.

In some locations, the fringing reef is replaced by rocky reefs made of volcanic boulders. The blocks provide high structural complexity and encrusting coralline algae, although the

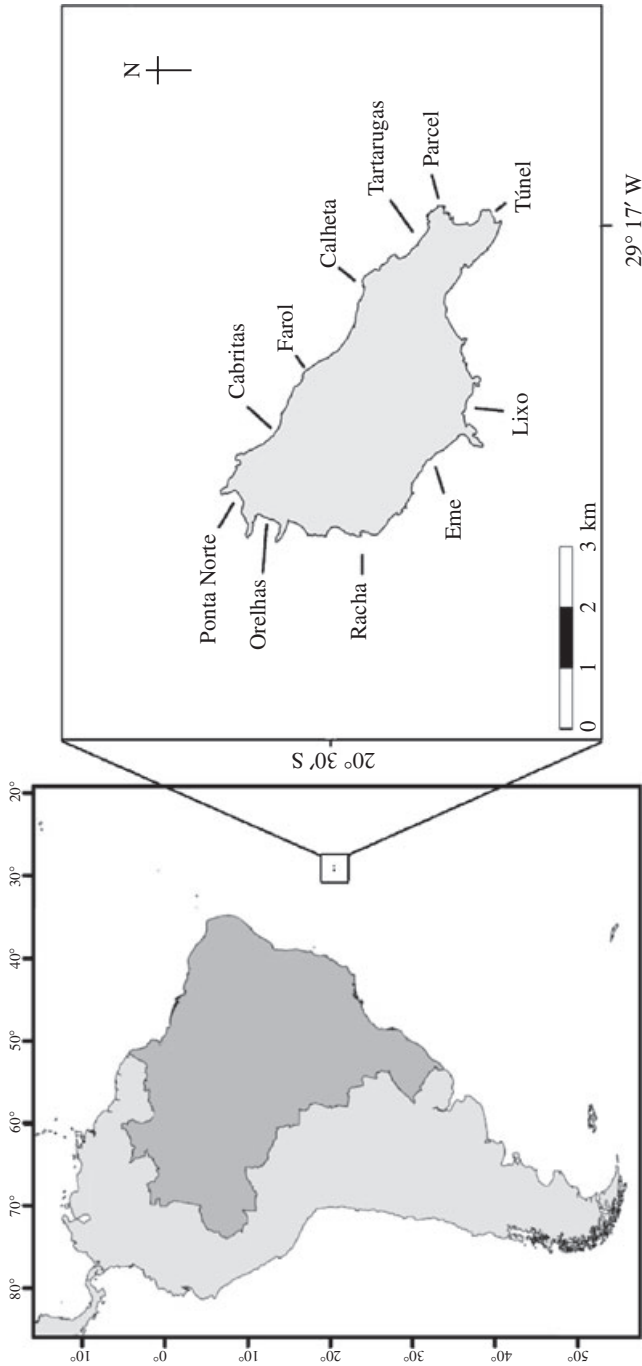


FIG. 1. Trindade Island, off the central coast of Brazil. The sites sampled are shown.

dominant component of the living benthos is not the main reef builder. While crest, slope and interface zones apply to the rocky reefs, the slope is generally steeper and reaches deep interface habitats (to 46 m) in comparatively shorter distances than in fringing reefs.

Fish assemblages were surveyed at 11 sites around Trindade Island (Fig. 1) between 13 April and 26 June 2009. Orelhas (average depth 7 m), Tartarugas (8 m), Cabritas (10 m), Ponta Norte (10 m) and Eme (11 m) are primarily fringing reef habitats, whereas Farol (9 m), Ponta da Calheta (16 m), Racha (28 m) and Túnel (29 m) are mostly rocky reefs. Lixo (10 m) and Parcel (11 m) have both reef habitats. Depth varied among sites, with Túnel being the deepest at 46 m maximum. The shallowest transect surveyed at each site was typically around 3 m deep.

SAMPLING PROCEDURE

Fishes were counted using strip transects ($n = 252$) measuring 20×2 m, following a procedure commonly utilized along the Brazilian coast (Ferreira *et al.*, 2004; Floeter *et al.*, 2007). Two to three visits were conducted at each site. The censuses were distributed in each zone (crest, slope and interface zones) at both rocky and fringing reefs (if present). The number of transects ranged from two to 20 per zone per site with an average of 8.4 transects per zone within each of 11 sites. Along each transect the number of individuals of each species was tallied and the total length (L_T) of each fish was estimated by eye and classified into 10 cm classes (with the first class further divided into 0–5 and 5–10 cm classes).

The topographic complexity of the substrata within each transect was classified as: high (large boulders and holes >1 m in size and depth, respectively), average (predominance of small boulders and holes <1 m in size and depth, respectively) and low complexity (few and small benthic organisms and predominance of epiphytic algae) (Pinheiro, 2010).

Five randomly selected photo-quadrats (25×25 cm) were photographed along 86 transects, sampling all zones of each site. The benthos was categorized as sponges, macroalgae, turf algae, crustose coralline algae or sand and rubble. The Coral Point Count Programme (CPCe) (Kohler & Gill, 2006) was used to calculate the relative benthic coverage of the benthos categories.

DATA ANALYSES

Fish biomass was estimated using L_T and mass (M) relationships from Froese & Pauly (2009). When no relationship was available for a species, an average for the genus was applied (Froese & Pauly, 2009). Trophic guilds were classified mostly following Randall (1967) and Ferreira *et al.* (2004) and comprised carnivores (CA), territorial herbivores (TH), roving herbivores (RH), mobile invertebrate feeders (MIF), sessile invertebrate feeders (SIF), omnivores (OM), piscivores (PI) and planktivores (PL). Some recent taxonomic revisions were adopted, *i.e.* Epinephelidae form part of Serranidae and Scarinae subsumed in Labridae (Westneat & Alfaro, 2005; Craig & Hastings, 2007; Smith & Craig, 2007).

A multidimensional scaling (MDS) analysis was performed to explore the similarities among sites considering fish biomass data. Comparisons of fish biomass, density, richness and trophic guilds between rocky and fringing reef environments ($n = 245$ without the Racha censuses) were performed utilizing a Mann–Whitney (MW) U -test (Zar, 1999). Finally, Kruskal–Wallis (KW) tests were performed to compare fish biomass, density, richness, total and for each trophic guild, among reef zones (crest, middle slope and interface) of both reef environments ($n = 12, 51$ and 45 , respectively, and d.f. = 2 for rocky reefs; $n = 43, 64$ and 37 , respectively, and d.f. = 2 for fringing reefs) (Zar, 1999).

RESULTS

COMPOSITION AND GENERAL PATTERNS OF ABUNDANCE

Seventy-six fish species were counted in the census, including 27 invertebrate feeders (MIF), 13 carnivores (CA) and 10 piscivores (PI). The most speciose family

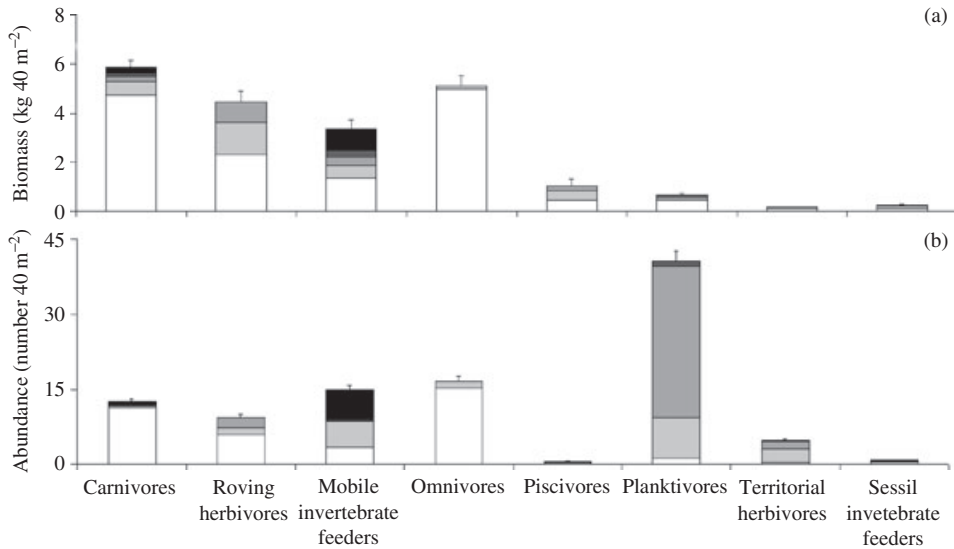


FIG. 2. General patterns of mean \pm S.E. (a) biomass and (b) density of fish trophic guilds at Trindade Island. For each trophic guild, component taxa are listed from bottom (open bars, \square) to top (darker bars, either \square or \blacksquare or \blacksquare) depending on the number of component taxa). Carnivores: *Cephalopholis fulva*, *Epinephelus adscensionis*, *Ginglymostoma cirratum*, *Gymnothorax moringa* and others; roving herbivores: *Kyphosus* spp., *Sparisoma* spp. and *Acanthurus* spp.; mobile invertebrate feeders: Holocentridae, Labridae, *Anisotremus surinamensis*, Balistidae and others; omnivores: *Melichthys niger*, *Abudefduf saxatilis* and others; piscivores: Serranidae, Carangidae, *Sphyrna barracuda* and others; planktivores: *Myripristis jacobus*, *Chromis multilineata*, *Thalassoma noronhanum*, *Cephalopholis furcifer* and others; territorial herbivores: *Microspathodon chrysurus*, *Stegastes fuscus trinidadensis*, Blenniidae and *Stegastes pictus*; sessile invertebrate feeders: *Cantherhines macrocerus*, *Holacanthus tricolor*, Chaetodontidae and *Canthigaster figueiredoi*.

was Labridae (10 species), followed by Epinephelidae (six), Pomacentridae (five) and Carangidae (five). The most speciose genera were *Halichoeres* (four), *Caranx* (three) and *Sparisoma* (three). Hybrids of *Cephalopholis fulva* (L. 1758) and *Cephalopholis furcifer* (Valenciennes 1828) were frequent. Six endemic species, *Halichoeres rubrovirens* Rocha, Pinheiro & Gasparini 2010, *Sparisoma rocha* Pinheiro, Gasparini & Sazima 2010, *Malacoctenus bruno* Guimarães, Nunan & Gasparini 2010, *Hypleurochilus* sp., *Entomacrodus* sp. and *Elacatinus pridisi* Guimarães, Gasparini & Rocha 2004 (the first three recently described), and one endemic sub-species (*Stegastes fuscus trinidadensis* Gasparini, Moura & Sazima 1999) were recorded.

Mean \pm S.E. fish abundance at Trindade was 98.7 ± 3.0 individuals 40 m^{-2} with 15.7 ± 0.3 species 40 m^{-2} , representing an estimated biomass of $21.6 \pm 1.0 \text{ kg } 40 \text{ m}^{-2}$. Epinephelidae accounted for the highest biomass followed by Balistidae, Kyphosidae, Labridae and Holocentridae (Table I). The trophic groups with the greatest biomass were carnivores, primarily due to the high abundance of *C. fulva*, omnivores [mainly *Melichthys niger* (Bloch 1786)] and roving herbivores (*Kyphosus* spp.) (Fig. 2).

The most individuals counted were from the family Labridae, followed by Balistidae, Epinephelidae, Pomacentridae and Holocentridae. The most abundant species was *Thalassoma noronhanum* (Boulenger 1890), followed by *M. niger*, *C. fulva*,

TABLE I. Mean \pm S.E. biomass, abundance and frequency of occurrence (%F) of fish species of Trindade Island, Brazil

Family & species	Mean estimated mass (g)	Biomass (g 40 m ⁻²)	Abundance (n 40 m ⁻²)	%F
Ginglymostomatidae				
<i>Ginglymostoma cirratum</i>	15880.1	189.1 \pm 134.6	0.01 \pm 0.01	0.8
Muraenidae				
<i>Echidna catenata</i>	961.3	7.6 \pm 6.4	0.01 \pm 0.01	0.8
<i>Enchelycore nigricans</i>	212.5	0.8 \pm 0.8	<0.01	0.4
<i>Gymnothorax miliaris</i>	259.7	1.0 \pm 1.0	<0.01	0.4
<i>Gymnothorax moringa</i>	3194.4	164.8 \pm 49.7	0.05 \pm 0.01	5.2
Ophichthidae				
<i>Myrichthys breviceps</i>	2000.0	47.6 \pm 19.2	0.02 \pm 0.01	2.4
Clupeidae				
<i>Harengula jaguana</i>				0.4
Synodontidae				
<i>Synodus synodus</i>	7.1	0.2 \pm 0.1	0.03 \pm 0.01	2.8
Belonidae				
<i>Platybelone argalus</i>	304.7	1.2 \pm 1.2	0.06 \pm 0.06	0.4
Holocentridae				
<i>Holocentrus adscensionis</i>	409.5	1386 \pm 297.2	3.38 \pm 0.67	57.1
<i>Myripristis jacobus</i>	392.0	486.9 \pm 72.6	1.24 \pm 0.18	29.4
<i>Sargocentron bullisi</i>	156.4	8.1 \pm 3.0	0.05 \pm 0.02	4.4
Scorpaenidae				
<i>Scorpaena plumieri</i>	872.7	3.5 \pm 3.5	<0.01	0.4
Dactylopteridae				
<i>Dactylopterus volitans</i>	470.7	1.9 \pm 1.9	<0.01	0.4
Epinephelidae				
<i>Cephalopholis fulva</i>	440.0	5065.6 \pm 245.3	11.51 \pm 0.51	95.6
<i>Cephalopholis furcifer</i>	45.3	43.3 \pm 12.5	0.96 \pm 0.35	11.5
<i>C. fulva</i> \times <i>C. furcifer</i> hybrid	53.0	0.2 \pm 0.2	<0.01	0.4
<i>Epinephelus adscensionis</i>	2073.3	575.9 \pm 123.4	0.28 \pm 0.05	15.9
<i>Mycteroperca interstitialis</i>	5590.3	288.4 \pm 120.4	0.05 \pm 0.02	3.2
<i>Mycteroperca venenosa</i>	28677.2	227.6 \pm 177.8	0.01 \pm 0.01	0.8
<i>Rypticus saponaceus</i>	251.1	44.8 \pm 9.1	0.18 \pm 0.04	14.3
Opisthognathidae				
<i>Opisthognathus</i> aff. <i>aurifrons</i>	5.0	0.3 \pm 0.2	0.05 \pm 0.03	2.0
Priacanthidae				
<i>Heteropriacanthus cruentatus</i>	464.9	36.9 \pm 15.0	0.08 \pm 0.03	4.0
Apogonidae				
<i>Apogon americanus</i>	4.8	0.1 \pm 0.1	0.03 \pm 0.01	2.0
Malacanthidae				
<i>Malacanthus plumieri</i>	251.4	89.8 \pm 19.1	0.36 \pm 0.08	15.1
Carangidae				
<i>Caranx crysos</i>	202.2	13.6 \pm 9.1	0.07 \pm 0.04	1.2
<i>Caranx latus</i>	3585.0	42.7 \pm 31.7	0.01 \pm 0.01	0.8
<i>Caranx lugubris</i>	640.6	89.0 \pm 21.8	0.14 \pm 0.03	8.3
<i>Carangoides ruber</i>	641.8	99.3 \pm 35.8	0.15 \pm 0.05	4.8
<i>Seriola rivoliana</i>	2481.1	167.4 \pm 77.5	0.07 \pm 0.03	2.4

TABLE I. Continued

Family & species	Mean estimated mass (g)	Biomass (g 40 m ⁻²)	Abundance (n 40 m ⁻²)	%F
Haemulidae				
<i>Anisotremus surinamensis</i>	2817.3	341.1 ± 129.4	0.12 ± 0.04	4.4
Sparidae				
<i>Diplodus argenteus</i>	309.6	22.1 ± 9.3	0.07 ± 0.03	3.2
Mullidae				
<i>Mulloidichthys martinicus</i>	530.3	252.5 ± 106.5	0.48 ± 0.18	6.3
<i>Pseudupeneus maculatus</i>	277.9	191.9 ± 25.0	0.69 ± 0.08	32.9
Kyphosidae				
<i>Kyphosus</i> spp.	746.1	2448.6 ± 421.6	3.28 ± 0.57	33.7
Chaetodontidae				
<i>Chaetodon striatus</i>	109.5	33.4 ± 5.7	0.31 ± 0.05	13.5
<i>Prognathodes brasiliensis</i>	60.0	4.8 ± 2.0	0.08 ± 0.03	4.0
Pomacanthidae				
<i>Holacanthus tricolor</i>	399.5	111.0 ± 15.9	0.28 ± 0.04	21.0
Cirrhitidae				
<i>Amblycirrhitus pinos</i>	2.6	<0.1	0.01 ± 0.01	0.8
Pomacentridae				
<i>Abudefduf saxatilis</i>	114.4	157.1 ± 23.3	1.33 ± 0.14	38.5
<i>Chromis multilineata</i>	13.2	108.7 ± 16.1	8.26 ± 0.79	44.8
<i>Microspathodon chrysurus</i>	289.3	102.2 ± 18.2	0.35 ± 0.06	19.0
<i>Stegastes pictus</i>	1.6	0.3 ± 0.1	0.17 ± 0.04	9.5
<i>Stegastes fuscus trinidadensis</i>	20.7	56.0 ± 6.7	2.71 ± 0.22	61.5
Labridae				
<i>Bodianus pulchellus</i>	190.5	3.0 ± 1.8	0.02 ± 0.01	1.6
<i>Bodianus rufus</i>	558.9	113.1 ± 20.7	0.20 ± 0.03	15.1
<i>Halichoeres brasiliensis</i>	575.0	317.2 ± 46.7	0.55 ± 0.07	33.3
<i>Halichoeres penrosei</i>	13.1	46.7 ± 5.8	3.56 ± 0.34	46.4
<i>Halichoeres poeyi</i>	12.1	10.1 ± 1.8	0.84 ± 0.12	29.8
<i>Halichoeres rubrovirens</i>	107.3	34.5 ± 6.2	0.33 ± 0.06	18.3
<i>Sparisoma amplum</i>	2117.6	739.5 ± 145.4	0.35 ± 0.06	17.9
<i>Sparisoma axillare</i>	1203.1	663.6 ± 122.3	0.55 ± 0.08	27.4
<i>Sparisoma rocha</i>	436.2	15.6 ± 6.2	0.04 ± 0.01	2.8
<i>Thalassoma noronhanum</i>	1.6	49.1 ± 3.6	30.33 ± 2.01	92.5
Labrisomidae				
<i>Labrisomus nuchipinnis</i>	48.7	0.6 ± 0.4	0.01 ± 0.01	0.8
<i>Malacoctenus brunoii</i>	0.1	0.6 ± 0.1	4.12 ± 0.36	55.2
Blenniidae				
<i>Hypoleurochilus</i> sp.	0.2	<0.1	<0.01	0.4
<i>Entomacrodus</i> sp.	0.1	<0.1	0.07 ± 0.03	2.8
<i>Ophioblennius trinitatis</i>	3.8	5.9 ± 1.1	1.53 ± 0.27	27.8
Callionymidae				
<i>Callionymus bairdi</i>	0.4	<0.1	<0.01	0.4
Gobiidae				
<i>Coryphopterus thrinx</i>	0.3	0.1 (<0.1)	0.32 ± 0.09	8.3
<i>Elacatinus pridisi</i>	0.1	<0.1	0.12 ± 0.03	5.2
<i>Gnatholepis thompsoni</i>	0.1	<0.1	0.29 ± 0.10	6.0

TABLE I. Continued

Family & species	Mean estimated mass (g)	Biomass (g 40 m ⁻²)	Abundance (n 40 m ⁻²)	%F
Acanthuridae				
<i>Acanthurus bahianus</i>	329.8	586.0 ± 51.0	1.80 ± 0.16	57.9
<i>Acanthurus coeruleus</i>	883.8	277.3 ± 44.9	0.32 ± 0.05	17.5
Sphyraenidae				
<i>Sphyraena barracuda</i>	2960.6	188.0 ± 85.5	0.06 ± 0.03	3.6
Balistidae				
<i>Balistes vetula</i>	807.9	112.2 ± 22.5	0.14 ± 0.03	11.9
<i>Canthidermis sufflamen</i>	2418.8	201.6 ± 63.7	0.08 ± 0.02	6.0
<i>Melichthys niger</i>	334.9	5121.3 ± 455.7	15.29 ± 1.36	95.2
Monacanthidae				
<i>Aluterus scriptus</i>	140.8	2.4 ± 1.1	0.02 ± 0.01	2.0
<i>Cantherhines macrocerus</i>	586.0	111.6 ± 20.1	0.19 ± 0.03	13.9
<i>Cantherhines pullus</i>	247.7	5.9 ± 3.0	0.02 ± 0.01	2.4
Ostraciidae				
<i>Acanthostracion polygonius</i>	718.7	16.3 ± 7.3	0.02 ± 0.01	2.0
<i>Acanthostracion quadricornis</i>	255.0	2.0 ± 1.4	0.01 ± 0.01	0.8
Tetraodontidae				
<i>Canthigaster figueiredoi</i>	7.0	0.3 ± 0.1	0.04 ± 0.01	3.2
<i>Sphoeroides spengleri</i>	42.9	1.7 ± 0.7	0.04 ± 0.01	4.0
Diodontidae				
<i>Diodon holacanthus</i>	782.1	62.1 ± 13.5	0.08 ± 0.02	7.9

Chromis multilineata (Guichenot 1853) and *M. brunoi* (Table I). Planktivores were the most common trophic group, followed by the omnivores (due to the abundance of *T. noronhanum* and *M. niger*, respectively) (Fig. 2). Each of the three species *C. fulva*, *M. niger* and *T. noronhanum* occurred in >90% of the censuses (Table I).

DISTRIBUTION PATTERNS

The most distinct site was Racha, a small, isolated and vertical pinnacle and islet located on the eastern side of Trindade (Fig. 3). Rocky reefs (excluding Racha) had abundance and diversity of species similar to those of fringing reefs (MW, $Z = -0.899$, $P > 0.05$ for abundance and $Z = -1.718$, $P > 0.05$ for diversity), but higher biomass (MW, $Z = -2.868$, $P < 0.01$). Rocky reefs showed significantly higher biomass of mobile invertebrate feeders and piscivores, whereas fringing reefs exhibited higher biomass of carnivores, roving herbivores and omnivores. The relative density of the trophic guilds was mostly similar, but planktivores were more abundant on fringing reefs and sessile invertebrate feeders and piscivores more abundant on rocky reefs (Fig. 4).

Rocky reef topographic complexity decreased with depth and turf algae dominated all three depth zones. Macroalgae and turf algae covers, however, decreased with depth as crustose coralline algae and soft bottom (sand and rubble) cover increased. Overall, fringing reefs were topographically less complex than rocky reefs albeit

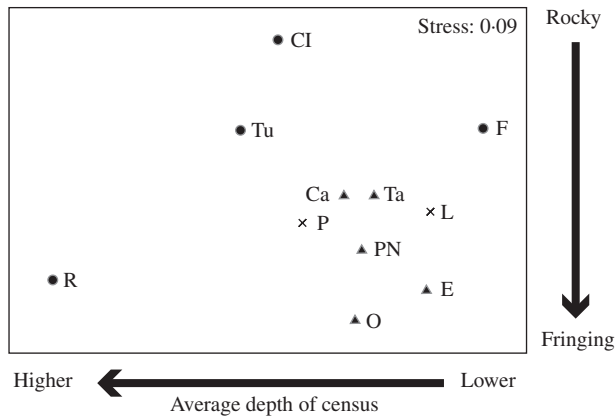


FIG. 3. Multidimensional scaling analysis considering reef fish biomass of all sites sampled in Trindade: rocky reef (▲); fringing reef (●); both reef types present (×); Tu, Túnel; P, Parcel; Ta, Tartarugas; CI, Calheta; F, Farol; Ca, Cabritas; PN, Ponta Norte; O, Orelhas; R, Racha; E, Eme; L, Lixo (see Fig. 1).

their complexity also decreased with depth; macroalgae and soft bottom cover were proportionally higher than in rocky reefs (Fig. 5).

On rocky reefs, fish densities were significantly higher at the crest and slope (KW, d.f. = 2, $P < 0.01$) and species richness peaked in the slope zone (KW, d.f. = 2, $P < 0.05$), although biomass did not vary significantly among zones (KW, d.f. = 2, $P > 0.05$). The density of all guilds other than carnivores (KW, d.f. = 2, $P > 0.05$) and piscivores (KW, d.f. = 2, $P > 0.05$) differed among zones with mobile invertebrate feeders most abundant near the interface (KW, d.f. = 2, $P < 0.001$), planktivores (mainly *Myripristis jacobus* Cuvier 1829) most abundant at the slope (KW, d.f. = 2, $P < 0.01$) and interface zones and territorial (KW, d.f. = 2, $P < 0.001$) and roving herbivores (KW, d.f. = 2, $P < 0.01$) most abundant at the crest and least abundant at the interface (Fig. 6). As a guild, RH comprised different species dominating different zones: *Kyphosus* spp. dominant at the crest, *Acanthurus* spp. the slope and *Sparisoma* spp. the interface. Sessile invertebrate feeders were most abundant on the slope (KW, d.f. = 2, $P < 0.01$), where *Cantherhines macrocerus* (Hollard 1853) was the most abundant species (Fig. 6). The spongivorous (SIF) angelfish, *Holacanthus tricolor* (Bloch 1795), was found at similar densities in all zones. The guild of carnivorous fishes, comprising mainly *C. fulva* and *Epinephelus adscensionis* (Osbeck 1765), was common in all zones (Fig. 6).

In contrast, on fringing reefs the density and biomass of fishes were significantly higher at the crest (both KW, d.f. = 2, $P < 0.001$), while species richness did not vary significantly among zones (KW, d.f. = 2, $P > 0.05$). The density of territorial herbivores (KW, d.f. = 2, $P < 0.001$), roving herbivores (KW, d.f. = 2, $P < 0.001$) and omnivores (KW, d.f. = 2, $P < 0.001$) decreased with depth. The dominant species of these guilds were the same as on rocky reefs and showed similar patterns of distribution with regard to depth (Fig. 7). The remaining trophic groups did not vary significantly with depth (MIF KW, d.f. = 2, $P > 0.05$; SIF KW, d.f. = 2, $P > 0.05$; CA KW, d.f. = 2, $P > 0.05$; PI KW, d.f. = 2, $P > 0.05$; PL KW, d.f. = 2, $P > 0.05$) (Fig. 7).

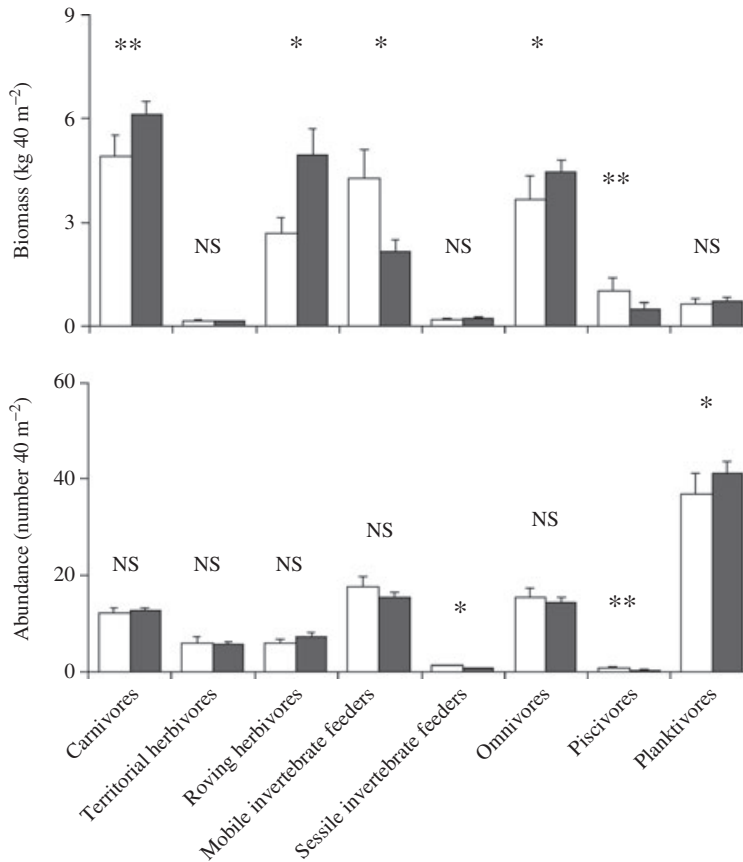


FIG. 4. Biomass (mean + S.E.) and abundance (mean + S.E.) of trophic guilds on rocky (□) and fringing (■) reefs at Trindade Island. *P*-value results from Mann–Whitney *U*-tests (**P* < 0.01; ***P* < 0.001; NS, non-significant).

DISCUSSION

The fish community of Trindade Island is habitually considered to have more affinity with the Brazilian coast than with other Brazilian oceanic islands (Rocha & Rosa, 2001). The continental shelf and the island are linked by the Vitória–Trindade submarine ridge (Gasparini & Floeter, 2001) and the seamounts are supposed to have provided stepping stones usable by colonizing species at 60–250 km intervals, in particular during lowered sea levels in periods of intense glaciation (Floeter & Gasparini, 2000; Joyeux *et al.*, 2001; Floeter *et al.*, 2008).

The trophic structure of the fish assemblage at Trindade Island, however, parallels structures observed at other Atlantic oceanic islands through the dominance of planktivores (Rosa & Moura, 1997; Krajewski & Floeter, 2011). In particular, Trindade shares with Fernando de Noronha and Atol das Rocas a similar pattern of dominance of the planktivores *C. multilineata* and *T. noronhanum*. While *C. multilineata* is abundant all along the Brazilian coast, *T. noronhanum* is only a prominent component of the reef fish assemblage on the north-east coast. Trindade Island is the southernmost

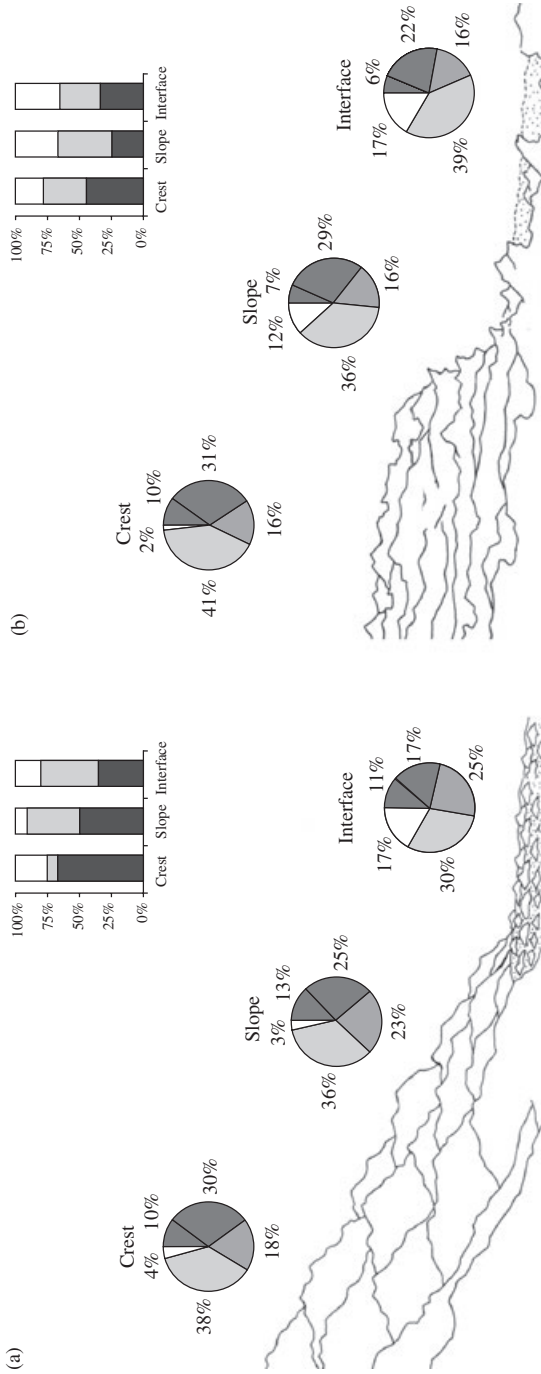


FIG. 5. Diagram showing the profiles of (a) rocky and (b) fringing reefs of Trindade Island, off Brazil. Pie graphs show the composition of the benthic cover of each reef zone following the sequence sponges (■), macroalgae (■), crustose coralline algae (■), turf algae (□), sand and rubble (□). The substratum structural complexity of each zone is shown in bar graphs as high (■), average (□) or low (□).

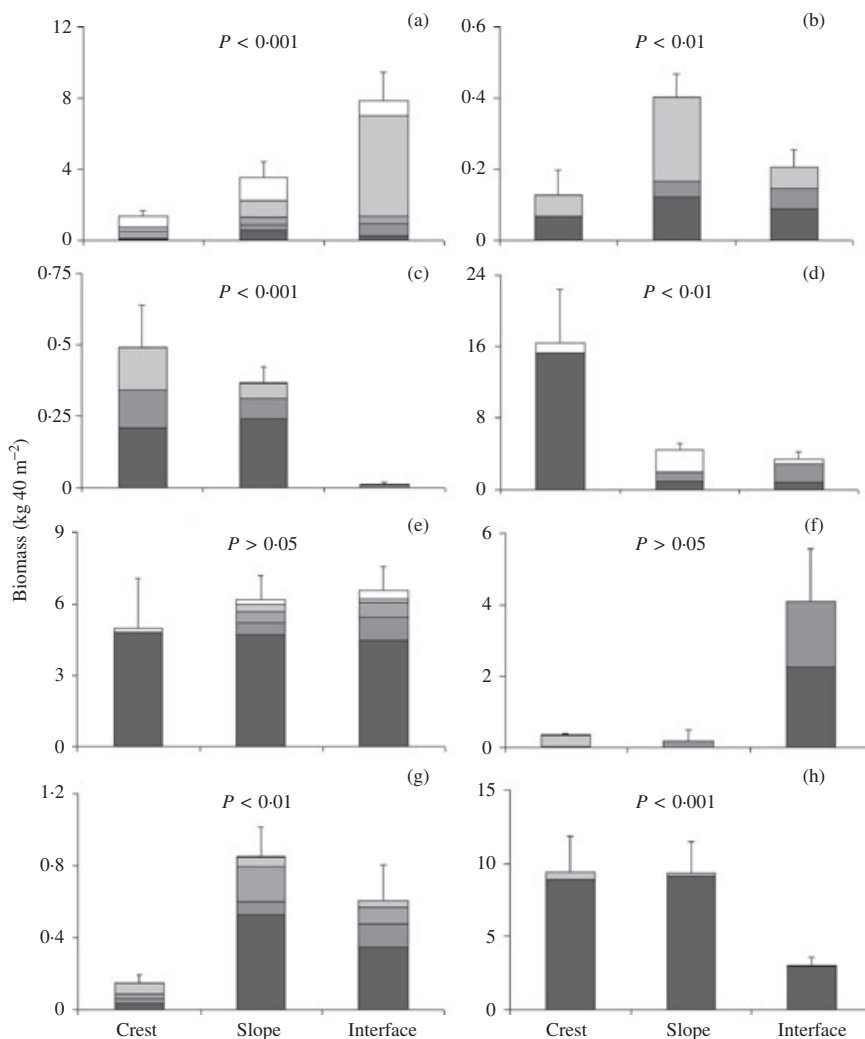


FIG. 6. Comparative biomass (mean + S.E.) of reef fish trophic guilds on distinct zones of rocky reefs at Trindade Island. *P*-value results from Kruskal–Wallis tests. For each trophic guild, component taxa are listed from bottom (■) or (■) or (■) or (□) depending on the number of component taxa): (a) mobile invertebrate feeders: *Anisotremus surinamensis*, Balistidae, Labridae, Holocentridae and others, (b) sessile invertebrate feeders: *Holacanthus tricolor*, Chaetodontidae, *Cantherhines macrocerus* and *Canthigaster figuereidoi*, (c) territorial herbivores: *Microspathodon chrysurus*, *Stegastes fuscus trindadensis*, Blenniidae and *Stegastes pictus*, (d) roving herbivores: *Kyphosus* spp., *Sparisoma* spp. and *Acanthurus* spp., (e) carnivores: *Cephalopholis fulva*, *Epinephelus adscensionis*, *Ginglymostoma cirratum*, *Gymnothorax moringa* and others, (f) piscivores: Serranidae, Carangidae, *Sphyrna barracuda* and others, (g) planktivores: *Myripristis jacobus*, *Cephalopholis furcifer*, *Chromis multilineata*, *Thalassoma noronhanum* and others and (h) omnivores: *Melichthys niger*, *Abudefduf saxatilis* and others.

site where the species is abundant. At the same latitude on the coast *T. noronhanum* is present, but not abundant (Floeter *et al.*, 2007). Furthermore, it only occurs on subtropical rocky reefs as a vagrant. While this species exhibits high trophic plasticity, acting not only as a planktivore but also as an invertivore and a detritivore (Sazima

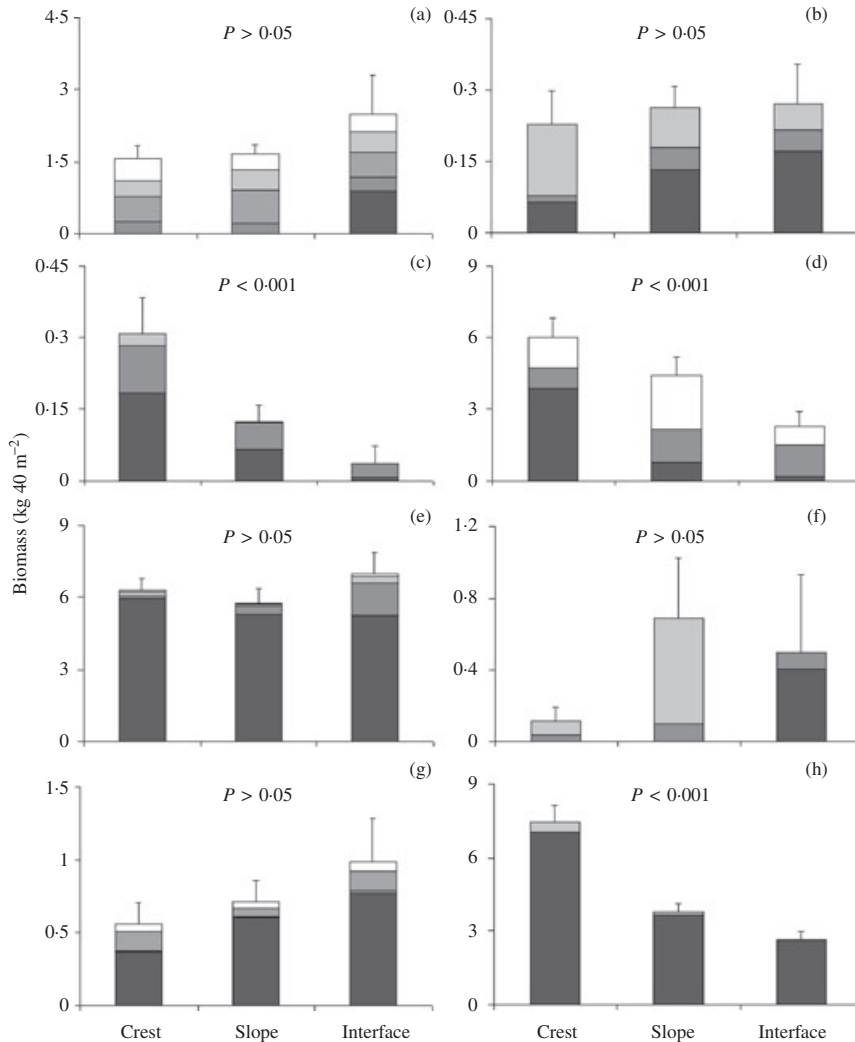


FIG. 7. Comparative biomass (mean + s.e.) of reef fish trophic guilds on distinct zones of fringing reefs at Trindade Island. P -value results from Kruskal–Wallis tests. For each trophic guild, component taxa are listed from bottom (■) to top (■) or (□) depending on the number of component taxa). (a) Mobile invertebrate feeders: *Anisotremus surinamensis*, Balistidae, Labridae, Holocentridae and others, (b) sessile invertebrate feeders: *Holacanthus tricolor*, Chaetodontidae, *Cantherhines macrocerus* and *Canthigaster figueiredoi*, (c) territorial herbivores: *Microspathodon chrysurus*, *Stegastes fuscus trinidadensis*, Blenniidae, and *Stegastes pictus*, (d) roving herbivores: *Kyphosus* spp., *Sparisoma* spp. and *Acanthurus* spp., (e) carnivores: *Cephalopholis fulva*, *Epinephelus adscensionis*, *Gymnothorax moringa* and others, (f) piscivores: Serranidae, Carangidae, *Sphyrnaena barracuda* and others, (g) planktivores: *Myripristis jacobus*, *Cephalopholis furcifer*, *Chromis multilineata* and *Thalassoma noronhanum* and (h) omnivores: *Melichthys niger*, *Abudefduf saxatilis* and others.

et al., 2005), other unknown attributes beyond diet plasticity make it a dominant species in oceanic islands, but not on coastal reefs (Krajewski & Floeter, 2011). In contrast, on the small and highly isolated St Paul's Rocks, despite the presence of *T. noronhanum*, *C. multilineata* alone is the dominant planktivore (Ferreira *et al.*, 2009).

Omnivores and mobile invertebrate feeders were two other dominant trophic groups in Trindade Island. As in Fernando de Noronha and St Paul's Rocks, the pattern of high abundance of omnivores is maintained by *M. niger* and *Abudefduf saxatilis* (L. 1758) (Ferreira *et al.*, 2009; Krajewski & Floeter, 2011). Both *M. niger* and *A. saxatilis* have been considered omnivores as they can feed on plankton as well as on turf algae depending on circumstances (Ferreira *et al.*, 2004). Unfortunately, changes in diet and feeding behaviour at various spatial and temporal scales for these species have never been explored in detail. Thus, it is conceivable that the pattern of dominance of planktivores and herbivores claimed for Atol das Rocas (Ferreira *et al.*, 2004) would also persist in the other Brazilian oceanic islands.

The genus *Haemulon* is the prevailing mobile invertebrate feeder on the Brazilian coast (Floeter *et al.*, 2001; Ferreira *et al.*, 2004), Fernando de Noronha (Krajewski & Floeter, 2011) and Atol das Rocas (Rosa & Moura, 1997). In contrast, the genus remains unrecorded at Trindade (Gasparini & Floeter, 2001; Pinheiro *et al.*, 2009) and St Paul's Rocks (Ferreira *et al.*, 2009). Both Trindade and St Paul's Rocks lie *c.* 1000 km from the mainland, whereas Fernando de Noronha and Atol das Rocas are located 350 km from the mainland. Two *Haemulon* species [*H. chrysargyreum* Günther 1859 and *H. parra* (Desmarest 1823)] are abundant in the latter locales (Floeter *et al.*, 2008; Krajewski & Floeter, 2011). A similar pattern is observed in the tropical eastern Pacific Ocean (TEP): *Haemulon* does not occur in the most isolated Clipperton Atoll (*c.* 1000 km from the mainland) nor in islands at shortest distances from the mainland (*c.* 450 km), like Cocos and Revillagigedo (Allen & Robertson, 1994). Two species of *Haemulon*, however, are found in the Galapagos Archipelago. This archipelago lies far from the mainland (*c.* 1000 km), but contrasting with the other TEP insular systems, it presents a larger shallow area and a higher diversity of habitats (Allen & Robertson, 1994). The genus *Haemulon* has a pelagic larval duration of *c.* 15–18 days (Houde, 1989; Purcell *et al.*, 2006), which is relatively short to accomplish large oceanic dispersal (Floeter *et al.*, 2008). Probable potential factors limiting the dispersal and the successful establishment of these fishes in isolated reef system are distance and habitat availability, as most species are associated with soft bottoms where they feed at night (Rocha *et al.*, 2008).

When biomass instead of abundance is considered, the community structure characteristics change dramatically because planktivores are mostly small-sized fishes, while carnivores, a trophic group that contributes moderately to building the abundance pattern, and omnivores are larger species. Within carnivores, the medium-sized predator (L_T mean = 30 cm) *C. fulva* was the most abundant species. Medium-sized *M. niger* and small-sized *A. saxatilis* are the species that most contribute to the high biomass of omnivores. The high biomass of roving herbivores in Trindade Island was mostly due to *Kyphosus* spp., in contrast to Fernando de Noronha where scarids and acanthurids form the bulk of biomass (Krajewski & Floeter, 2011).

SPATIAL DISTRIBUTION

Fringing reefs are dominated by crustose coralline algae with low coral cover provided by only three massive forms (Gasparini & Floeter, 2001). Albeit the rocky reefs are comparatively more complex than the fringing reefs, they did not show higher density and diversity of fishes. This fact is in contradiction to previous studies

that showed higher values in more complex habitats (Chabanet *et al.*, 1997; Lara & Gonzalez, 1998; Almany, 2004; Gratwicke & Speight, 2005). In Trindade Island, the main differences between rocky and fringing reefs are typically indicated by differences in the relative abundance and biomass of trophic groups as well as by the distribution of guilds among zones.

The abrupt declivity typical of the rocky reef profile at Trindade Island may contribute to the differences among zones in community characteristics (abundance and biomass) and in distribution of trophic guilds in a manner similar to that found for tropical coral reefs (Wedding & Friedlander, 2008) and for Mediterranean Sea temperate rocky reefs (La Mesa *et al.*, 2004). Changes in depth over a relatively small area provide different conditions of temperature, light and wave action, which directly influence the benthic community and the food supply (Willis & Anderson, 2003), with fish distribution patterns resulting from selection and fidelity to specific habitats (Ferreira *et al.*, 2001; Floeter *et al.*, 2007; Medeiros *et al.*, 2010).

Fringing reefs showed important differences in biomass, density and richness among crest, slope and interface zones, but few trophic groups showed differences in species abundance between these zones. Fringing reefs, which are the most extensive reef profile in the shallow areas of Trindade Island, show only slight variations of depth, a feature that may contribute to the relative uniformity of their communities.

The differences in community trophic structure found among depth zones are a pattern prevalent in reefs (Ferreira *et al.*, 2001; Gust, 2002; Pinheiro, 2010; Simon, 2010). It is caused mainly by omnivorous and herbivorous fishes. These exert a great influence on communities of shallower habitats, where they are most abundant, due to the effect of herbivory, on benthic substrata. On Trindade Island reefs, as elsewhere, macroalgae and turf algae have higher cover and productivity in the shallower zones and cover and productivity decrease with depth. Because the distribution of species and trophic groups is closely related to food availability (Nagelkerken *et al.*, 2001; Ferreira *et al.*, 2004; Francini-Filho & Moura, 2008), herbivores such as territorial damselfishes, *Kyphosus* spp. and *M. niger*, were mostly found in the habitats where the occurrence and growth of the macro and turf algae consumed by them were favourable. On the other hand, crustose coralline algae showed a pattern opposite to that of soft algae, with higher cover in deep areas. This feature may contribute to the maintenance of scarids (excavator and scraper species; Ferreira & Gonçalves, 2006) in these deep areas.

CONSERVATION ISSUES

Oceanic islands are by definition isolated and lightly populated and are expected to be more likely to remain in pristine condition (Friedlander & DeMartini, 2002; Stevenson *et al.*, 2007; Sandin *et al.*, 2008; Stallings, 2009). This expectation has been denied, however, for at least the last five decades, as industrial fishing and advances in fishing and navigation technology have opened up the last frontiers of the oceans (Myers & Worm, 2003; Ward & Myers, 2005; Baum & Worm, 2009). Recent collapses of shallow and deep-sea marine stocks have been documented (Roberts, 2002; Myers & Worm, 2003; Devine *et al.*, 2006; Tittensor *et al.*, 2009). Overall, population declines have confirmed that some characteristics of the life cycles of exploited species, such as slow growth, late maturity, high site fidelity and complex

social structure, make certain organisms more highly vulnerable to extirpation (Dulvy *et al.*, 2003; Reynolds *et al.*, 2005; García *et al.*, 2007).

The visual censuses and >200 h of underwater observations revealed a relatively low abundance of large top predators including sharks, barracudas, groupers and jacks. Similar scenarios have been detected in St Paul's Rocks and Fernando de Noronha (Ferreira *et al.*, 2009; Krajewski & Floeter, 2011); in both cases, overfishing was pointed out as the cause for the recent (30–40 years) declines observed in apex predator occurrence. The biomass of macro-carnivores (carnivores plus piscivores; a rough index of fishing pressure) at Trindade, however, was three-fold that observed at Fernando de Noronha ($181 v. 52 \text{ g m}^{-2}$), a Marine National Park with reasonable enforcement of fishing regulations (fishing is permitted in all areas deeper than 50 m and in some shallower areas). Macro-carnivores accounted for 33.6 and 22.6% of total fish biomass at Trindade and Fernando de Noronha, respectively. In comparison, the reported biomass of macro-carnivores in no-take areas in the Caribbean was much higher in proportion (ranging from 50 to 70% of total fish biomass), if not in biomass *per se* ($108\text{--}308 \text{ g m}^{-2}$; Newman *et al.*, 2006; Knowlton & Jackson, 2008). On remote, presumably pristine islands in the Pacific Ocean, biomass of macro-carnivores ranged from 31 to 85% of total fish biomass ($130\text{--}850 \text{ g m}^{-2}$) (Knowlton & Jackson, 2008; Sandin *et al.*, 2008).

Although direct comparisons of different reef communities are only indicative, it appears that all Brazilian oceanic islands, including Trindade Island, have been affected by fishing. In Trindade, as in Fernando de Noronha, the biomass of macro-carnivores is made up of medium-sized epinephelids, such as *C. fulva*, *E. adscensionis* and, to a lesser degree, *Mycteroperca interstitialis* (Poey 1860), while large epinephelids are rare. Pinheiro *et al.* (2010b) reported the presence of a longline fishing fleet operating in the shallow waters of Trindade. Similar activities have been reported to occur around the Trindade and Martin Vaz insular complex and the Vitória–Trindade submarine chain for the last 15 years (Martins *et al.*, 2005). Fishermen interviews indicated that *Mycteroperca venenosa* (L. 1758) is rapidly disappearing from the catches in the region (Pinheiro *et al.*, 2010b) and that the fleet has not yet moved to target smaller species (in particular *C. fulva*); these are mostly used as bait after being caught as by-catch.

All Brazilian oceanic islands harbour military or research facilities. In theory, this should enhance protection of natural resources in general and fishing resources in particular. Such presence has, however, not proved to be an impediment to overfishing. Both St Paul's Rocks and Trindade are part of a national programme funded by Brazilian agencies (www.mar.mil.br/secirm/trindade.htm) with the aim of developing research and maintaining research teams full-time on both islands. Fishing activities are not, however, prohibited and pelagic fishing around St Paul's Rocks is heavily subsidized by the Brazilian Navy for fishing boats to provide economic transport for researchers to and from the archipelago. In addition, Pinheiro & Gasparini (2011) reported that spearfishing by military personnel at Trindade Island is intensive and is likely to continue unabated in the foreseeable future. The high incidence of parrotfishes among the catches clearly indicates that top predators are not as abundant as expected (Pinheiro & Gasparini, 2011).

It is often a hard task to build a suggestive scenario for pristine conditions of natural systems since the exploitation of living resources rewrites the background after each scene. These shifting baselines are commonly encountered worldwide

(Pinnegar & Engelhard, 2008). Oceanic islands, truly isolated marine laboratories, have remained good examples of pristine, or almost-pristine, systems to model and decipher human effects on the marine realm. The oceanic islands of Brazil are important hot spots of endemism and biodiversity that are still poorly known and highly vulnerable to continued exploitation. It is critical that these small remaining elements of the rich Brazilian biodiversity are preserved and protected. Only by preserving such patrimony will it be possible in the near future to understand what humankind has really lost.

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