REPORT

Mesophotic reef fish assemblages of the remote St. Peter and St. Paul's Archipelago, Mid-Atlantic Ridge, Brazil

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Abstract Mesophotic reef fish assemblages (30–90 m depth) of the small and remote St. Peter and St. Paul's Archipelago (SPSPA), Mid-Atlantic Ridge, Brazil, were characterized using remotely operated vehicles. Ordination analyses identified distinct fish assemblages in the upper (30–50 m) and lower (50–90 m) mesophotic zones, the former characterized by high abundances of species that are also abundant at euphotic reefs (*Caranx lugubris*, *Melichthys niger*, *Stegastes sanctipauli* and *Chromis multilineata*) and the latter dominated by two mesophotic specialists (*Prognathodes obliquus* and *Chromis enchrysur*). Planktivores dominated fish assemblages, particularly in the upper mesophotic zone, possibly due to a

greater availability of zooplankton coming from the colder Equatorial Undercurrent in mesophotic depths of the SPSPA. Turf algae, fleshy macroalgae and scleractinian corals dominated benthic assemblages between 30 and 40 m depth, while bryozoans, black corals and sponges dominated between 40 and 90 m depth. Canonical correspondence analysis explained 74 % of the relationship between environmental characteristics (depth, benthic cover and complexity) and structure of fish assemblages, with depth as the most important independent variable. Juveniles of *Bodianus insularis* and adults of *P. obliquus* and *C. enchrysur* were clearly associated with branching black corals (*Tanacetipathes* spp.), suggesting that black corals play key ecological roles in lower mesophotic reefs

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of the SPSPA. Results from this study add to the global database about mesophotic reef ecosystems (MREs) and provide a baseline for future evaluations of possible anthropogenic and natural disturbances on MREs of the SPSPA.

Keywords Black corals · *Bodianus insularis* · Mesophotic reefs · Oceanic islands · *Prognathodes obliquus* · *Stegastes sanctipauli*

Introduction

The Atlantic coast of Brazil and its oceanic islands are partially isolated from the Caribbean by the Amazon River outflow and from the west coast of Africa by the wide expanse of the Atlantic (Rocha 2003; Floeter et al. 2008). Such geographical isolation leads to relatively high endemism of reef fish (ca. 25 %) and to the classification of the region as the “Brazilian Province” (Floeter et al. 2008). The Brazilian oceanic insular reef fish fauna is an impoverished outpost of the Brazilian Province, encompassing ca. 260 species. The lowest insular endemism (5 %) in Brazil is recorded for the Fernando de Noronha Ridge (Fernando de Noronha Archipelago plus Rocas Atoll), an intermediate level (5.7 %) for the Trindade/Martim Vaz Insular group and the highest insular endemism (9 %) for the St. Peter and St. Paul’s Archipelago (SPSPA) (Floeter and Gasparini 2000; Floeter et al. 2008).

Quantitative information on the structure of euphotic reef fish assemblages (0–30 m depth) is now available for the four Brazilian oceanic sites: Fernando de Noronha Archipelago (Minte-Vera et al. 2008; Krajewski and Floeter 2011), Rocas Atoll (Rosa and Moura 1997; Longo et al. 2015), the SPSPA (Luiz et al. 2015) and the Trindade/Martim Vaz Island group (Pereira-Filho et al. 2011; Pinheiro et al. 2011). Euphotic reefs of the SPSPA harbor an impoverished reef fish fauna in comparison with mainland and other larger Brazilian oceanic islands (Luiz et al. 2015), including four recognized endemic reef fish species (*Choranthias salmopunctatus*, *Prognathodes obliquus*, *Enneanectes smithi* and *Stegastes sanctipauli*) (Lubbock and Edwards 1981; Feitoza et al. 2003; Ferreira et al. 2009; Anderson and Heemstra 2012). The SPSPA is an important site for pelagic fisheries (Vaske-Jr et al. 2006; Hazin et al. 2009), and there is evidence for overfishing in the area despite its isolation (Ferreira et al. 2009). Overfishing is believed to have caused the local population extinction of the Galapagos shark *Carcharhinus galapagensis* and sharp decreases in the abundance of other shark species (Luiz and Edwards 2011).

Mesophotic reef ecosystems (MREs) occur in tropical and subtropical regions in depths ranging between 30 and

150 m. They are considered as extensions of shallow reef communities, but at the same time harbor unique biodiversity and ecological characteristics (Hinderstein et al. 2010; Harris et al. 2013; Kane et al. 2014). Although MREs are not immune to local and global disturbances (Bak et al. 2005; Menza et al. 2007; Lesser and Slattery 2011), they may be less susceptible than shallow and highly threatened reefs, thus possibly functioning as refuges (the “deep reef refugia” hypothesis; Lesser et al. 2009; Bongaerts et al. 2010). Despite their importance, MREs remain poorly studied due to logistical challenges, with gaps in knowledge of community composition, depth range of taxa and other basic biological and ecological aspects (Lesser et al. 2009; Kahng et al. 2010, 2014). Until recently, there were few studies focusing on southwest Atlantic MREs, with the exceptions of one for the northeast Brazilian coast (Feitoza et al. 2005) and another for the Trindade/Martim Vaz Island group (Pereira-Filho et al. 2011). More recently, three other studies have been published: one focusing on benthic assemblages of the euphotic (0–30 m depth) and the upper mesophotic (30–60 m) zones of the SPSPA (Magalhães et al. 2015); a study assessing microbial, benthic and fish assemblages of mesophotic reefs of the Vitória-Trindade seamount chain (VTC; Meirelles et al. 2015); and an analysis of the fish biodiversity associated with the VTC (Pinheiro et al. 2015).

This study provides the first quantitative assessment of mesophotic reef fish assemblages of the SPSPA. Sampling was performed at 30–90 m depth, with the following main goals: (1) to describe depth variation in abundance and trophic structure of fish assemblages; (2) to evaluate the relative influence of depth, benthic cover and complexity on the structure of fish assemblages; and (3) to discuss the similarities/differences between mesophotic reef fish assemblages of the SPSPA and those from other locations in the Atlantic and other geographical regions.

Materials and methods

Study area

The SPSPA is a small group of five islets and rocks (total emerged area ~15,000 m²) located in the central equatorial Atlantic Ocean, just above the Mid-Atlantic Ridge and about 1000 km off the northeastern Brazilian coast (Fig. 1) (Edwards and Lubbock 1983a, b; Feitoza et al. 2003). The SPSPA is influenced by the surface South Equatorial Current, which flows westwards, as well as by the Equatorial Undercurrent, which flows eastwards below the surface, at depths of 40–150 m. The area of reefs <100 m depth is about 0.5 km² (Edwards and Lubbock 1983a, b). Shallow rocky reefs of the SPSPA are covered mainly by

Fig. 1 Map showing: **a** location of the St. Peter and St. Paul's Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean and **b** detail of the SPSPA showing the study area (light gray)

the zoanthid *Palythoa caribaeorum* and algae of the genera *Bryopsis*, *Caulerpa* and *Dictyota*. In depths >30 m, the most common organisms are the scleractinian corals *Madracis decactis* and *Scolymia wellsi*, crustose calcareous algae and bryozoans. Sponges and branching black corals of the genus *Tanacetipathes* are dominant in depths >40 m (Edwards and Lubbock 1983a, b; Magalhães et al. 2015).

Sampling procedures

Sampling was performed during four expeditions between September 2010 and June 2011, totaling 60 d of field-work. Fish and benthic assemblages were assessed using video footage obtained using two remote-operated vehicles (ROV; VideoRay Explorer and Seabotix LBV150S2, both equipped with light and laser scale). Samples were composed of 5 min continuous footage covering a circular area with ~4 m radius. The ROV was maintained as stationary as possible in the center of each sampling unit, and a full rotation was performed for counting fish species. A total of 46 samples were obtained across a 30–90 m depth gradient, with the following sampling sizes per 10 m depth stratum: 30–40 m ($n = 18$), 40–50 m ($n = 11$), 50–60 m ($n = 6$), 60–70 m ($n = 5$), 70–80 m ($n = 3$), 80–90 m ($n = 3$).

Relative cover of benthic organisms was quantified from 30 still frames per ROV sample (i.e., one frame every 10 s). Images were taken about 50 cm from the bottom and as perpendicular to the substrate as possible. The Coral Point Count with Excel extensions (CPCe)

software was used for image analysis (Kohler and Gill 2006), with ten randomly distributed points used per frame (totaling 300 points per sample unit). The following categories were used in the benthic cover characterizations: bare rock; branching black corals (*Tanacetipathes* spp.); *Caulerpa* spp.; crustose calcareous algae; fleshy macroalgae (other than *Caulerpa* spp.); bryozoans; hydrozoans; live scleractinian corals; sediment; sponges; turf algae; and zoanthids. General habitat features recorded here were similar to those previously recorded for the SPSPA (Edwards and Lubbock 1983b), and a comprehensive analysis with greater taxonomic resolution is given by Magalhães et al. (2015).

Benthic complexity was visually estimated from ROV video samples by assigning values from 1 to 3 to each frame (i.e., 15 measurements per sample). Samples with no crevices and a smooth surface received a value of 1; samples with few crevices and small rocks received a value of 2; samples containing many crevices and rocks, as well as three-dimensional organisms (e.g., branching sponges and black corals), received a value of 3. Results obtained may be considered as a reliable metric considering the gross resolution applied (Wilson et al. 2007).

Preliminary sampling revealed that juveniles of *Bodianus insularis* and the two mesophotic specialists, *Chromis enchrysurus* and *Prognathes obliquus*, were clearly associated with branching black corals in the mesophotic zone. Thus, the absolute number of black coral colonies per sample, as well as the identity and abundance of fishes within branches of each colony, was recorded.

Due to logistical limitations with operation of the ROVs, only one site on the northeast coast of the SPSPA was sampled. The northeast portion of the archipelago is almost permanently sheltered from the strong waves and currents that act in the other portions of the SPSPA. Despite the lack of site replication, the small area of the SPSPA allowed for the assessment of about 15 % of the total perimeter of the archipelago (see Fig. 1).

Data analyses

Quantitative analyses used data for species with ≥ 0.1 % of total fish abundance and frequency of occurrence in more than five samples (except for the analyses of trophic groups, for which all species were taken into account). The 12 species retained for analyses belong to seven families and represented 97.4 % of total fish abundance recorded. Fish species were classified according to their predominant diet in one of the following trophic categories: omnivores; piscivores; predators on benthic invertebrates; or territorial herbivores (Feitoza et al. 2003; Francini-Filho and Moura 2008; Krajewski and Floeter 2011; Pinheiro et al. 2011, Luiz et al. 2015) (Table 1).

Non-metric multidimensional scaling (MDS) ordination was used to summarize spatial similarities (Bray–Curtis) according to benthic cover and fish abundance. Analyses of similarities (ANOSIM) were applied to evaluate possible significant differences between depth strata. Linear correlations (Spearman) were used to investigate the relationship between benthic cover/fish abundance and the MDS axes. Only categories/species with correlation > 0.3 were included in the final solution, and results were illustrated as superimposed vectors in the MDS diagrams (Clarke and Warwick 1994).

The relationship between depth and abundance of the 12 most abundant fish species (see Table 1) was explored using generalized additive models (GAM). Models were built using the Gaussian distribution, an identity link and cubic regression splines (Hastie and Tibshirani 1990). Variance explained by each model (pseudo-r-squared) was estimated as $1 - (\text{residual deviance}/\text{null deviance})$ (Swartzman et al. 1992).

Canonical correspondence analysis (CCA) (ter Braak 1996) was used to evaluate the relative influence of habitat characteristics (depth, benthic cover and complexity) on the structure of fish assemblages. A forward selection procedure was used to include only the most important independent variables, i.e., those that increased the explanatory power of the model. Only significant variables, as defined by a Monte Carlo permutation test (999 permutations), were included in the final solution.

All analyses were carried out in R (version 3.1.2; R Core Development Team 2014; available at <http://www.R-project.org>).

Results

A total of 19 species belonging to 12 families were recorded (~ 35 % of the reef fish species pool known for the SPSPA) (Feitoza et al. 2003; Floeter et al. 2008; Luiz et al. 2015). The five most abundant species were *Chromis multilineata* (29.0 % of total fish abundance), *Melichthys niger* (24.3 %), *Caranx lugubris* (19.5 %), *Stegastes sanctipauli* (7.8 %) and *P. obliquus* (3.1 %) (Table 1). The two-dimensional MDS ordination diagram and ANOSIM (Global $R = 0.52$, $p = 0.01$) showed that distinct fish assemblages were associated with two different zones (i.e., no differences between depth strata within each zone): one at 30–50 m depth and another at 50–90 m depth, hereafter called upper (UMZ) and lower (LMZ) mesophotic zones, respectively. Most typical species of the UMZ (highest values of Spearman correlation considering the first two axes of the MDS) were *C. lugubris* (0.61), *M. niger* (0.57), *S. sanctipauli* (0.45) and *Chromis multilineata* (0.37), while the most typical species of the LMZ were *P. obliquus* (-0.72) and *C. enchrysur* (-0.68) (Fig. 2a).

Fish abundance varied significantly by depth for seven species. *Bodianus insularis*, *C. multilineata*, *Halichoeres radiatus*, *M. niger* and *S. sanctipauli* showed the highest abundances in the UMZ (Fig. 3c, f, g, i, l). *Chromis enchrysur* and *P. obliquus* were nearly absent from the UMZ and increased sharply in abundance from 60 m depth onwards (Fig. 3e, k). Twenty individuals of *B. insularis* (35.2 % of total number of individuals recorded for this species) were < 20 cm total length (TL), all of them restricted to depths between 40 and 70 m depth.

Planktivores dominated mesophotic fish assemblages (33.1 % of total fish abundance), followed by omnivores (29.6 %), piscivores (20.6 %), predators on benthic invertebrates (9.0 %) and territorial herbivores (7.8 %). The abundance of predators on benthic invertebrates increased sharply from 50 m depth onwards (Fig. 4a), a pattern largely driven by a single species (*P. obliquus*). Abundance of omnivores, planktivores and territorial herbivores was highest in the UMZ (Fig. 4b, d, e). No significant trend in abundance according to depth was recorded for piscivores (Fig. 4c).

The two-dimensional MDS ordination diagram and ANOSIM (Global $R = 0.65$, $p = 0.01$) identified three distinct benthic assemblages associated with the following depth strata: 30–40 m (dominated by *Caulerpa* spp., other fleshy macroalgae, scleractinians and turf algae), 50–60 m (dominated by bryozoans and bare rock) and 40–50 m plus all remaining strata between 60 and 90 m (dominated by bryozoans, black corals and sponges). However, the MDS plot indicated a clear distinction between samples from the UMZ and LMZ (Fig. 2b).

Table 1 Reef fish species recorded on mesophotic reefs (30–90 m depth) of the St. Peter and St. Paul's Archipelago and their respective trophic groups

Family	Species	N	FO	Trophic group
Pomacentridae	<i>Chromis multilineata</i>	591	23	Planktivore
Balistidae	<i>Melichthys niger</i>	495	28	Omnivore
Carangidae	<i>Caranx lugubris</i>	398	20	Piscivore
Pomacentridae	<i>Stegastes sanctipauli</i>	160	20	Territorial herbivore
Chaetodontidae	<i>Prognathodes obliquus</i>	64	13	Invertebrate feeder
Pomacentridae	<i>Abudefduf saxatilis</i>	61	14	Omnivore
Labridae	<i>Bodianus insularis</i>	57	23	Invertebrate feeder
Balistidae	<i>Canthidermis sufflamen</i>	41	9	Planktivore
Labridae	<i>Halichoeres radiatus</i>	41	17	Invertebrate feeder
Holocentridae	<i>Myripristis jacobus</i>	31	10	Planktivore
Pomacanthidae	<i>Holacanthus ciliaris</i>	24	20	Omnivore
Pomacentridae	<i>Chromis enchrysur</i>	20	15	Planktivore
Muraenidae	<i>Muraena pavonina</i>	16	11	Piscivore
Pomacanthidae	<i>Pomacanthus paru</i>	11	7	Omnivore
Chaetodontidae	<i>Chaetodon striatus</i>	9	4	Invertebrate feeder
Aulostomidae	<i>Aulostomus strigosus</i>	6	3	Piscivore
Serranidae	<i>Rypticus saponaceus</i>	6	6	Piscivore
Labrisomidae	<i>Malacoctenus</i> sp.	3	2	Invertebrate feeder
Blenniidae	<i>Ophioblennius trinitatis</i>	1	1	Territorial herbivore

N, total number of individuals recorded; FO, frequency of occurrence in samples. Species arranged according to abundance. Bold denotes species retained for quantitative analyses (see text)

Depth, turf algae, sponges, black corals, crustose calcareous algae and scleractinians were, in decreasing order (i.e., order of entrance in the model), the most important variables affecting the structure of fish assemblages. The first two axes explained 74 % of the relationship between environmental characteristics and fish assemblage structure. There were unnoticeable differences in the structure of fish assemblages within the UMZ and a clear depth gradient from 50 m depth downwards (Fig. 5a). Nine species were associated with the UMZ, which was dominated by turf and crustose calcareous algae between 30 and 40 m and by scleractinian corals between 40 and 50 m. *Abudefduf saxatilis* was associated with the 50–60 m depth stratum, which was characterized by low coral cover and intermediate values for all other independent variables. *Chromis enchrysur* was associated with the 60–70 m depth stratum and *P. obliquus* with reefs deeper than 70 m, both of these latter species were clearly influenced by the abundance of black corals and sponges (Fig. 5a, b).

Abundance of black corals (total $n = 141$ colonies) increased sharply with depth, with up to 15 colonies recorded per sample ($\sim 50 \text{ m}^2$) at depths $\geq 70 \text{ m}$ (Fig. 6). Seven reef fish species were recorded seeking refuge within branches of black coral colonies: *P. obliquus* (37 individuals; 24.6 % of total number of colonies occupied), juveniles of *B. insularis* (12; 6.5 %), *C. enchrysur* (8; 6.5 %), *S. sanctipauli* (4; 3.3 %), *C. multilineata* (3; 2.4 %) and *Holacanthus ciliaris* (1; 0.8 %).

Discussion

Assessments of mesophotic reefs of highly geographically isolated oceanic locations, such as the SPSPA, are still rare, due mainly to logistical challenges (Wagner et al. 2014; Magalhães et al. 2015; Meirelles et al. 2015). Euphotic reefs of the SPSPA are characterized by the lowest reef fish species richness among all tropical oceanic archipelagos (~ 55 species; Feitoza et al. 2003; Luiz et al. 2015). They are marked by the absence/rarity of snappers (Lutjanidae), groupers (Epinephelidae), surgeonfishes (Acanthuridae) and parrotfishes (Scarinae) (Feitoza et al. 2003; Luiz et al. 2015), all of them relatively common in the other three Brazilian oceanic islands (Rosa and Moura 1997; Krajewski and Floeter 2011; Pereira-Filho et al. 2011; Pinheiro et al. 2011) and along the Brazilian coast (e.g., Floeter et al. 2007; Francini-Filho and Moura 2008). Mesophotic reef fish assemblages of the SPSPA are even more depauperate, with only 19 species recorded in this study. In contrast, a total of 32 species were recorded in mesophotic reefs of the VTC (Meirelles et al. 2015; Pinheiro et al. 2015), while 28 species were recorded in the mesophotic zone of the Trindade Island, Brazil (Pereira-Filho et al. 2011; Pinheiro et al. 2015). The UMZ (30–50 m depth) of the SPSPA may be considered as an extension of the euphotic zone, as three species (*C. multilineata*, *M. niger* and *S. sanctipauli*) were among the four most abundant species in both zones (see Table 1 in Luiz et al. 2015; Table 1). The LMZ was

Fig. 2 Multidimensional scaling (MDS) of: **a** fish assemblages and **b** benthic assemblages, both based on Bray–Curtis similarities. Colored polygons indicate groups of samples with no significant differences ($p > 0.05$) as defined by analyses of similarities (ANOSIM). Colored dots indicate samples from different depth strata

dominated by *C. enchrysur* and *P. obliquus*, the former absent from euphotic reefs and the latter rarely sighted in the shallows (Luiz et al. 2015).

Depth was the most important variable influencing the structure of euphotic (Luiz et al. 2015) and mesophotic (this study) reef fish assemblages of the SPSPA. The influence of depth in reef fish assemblages is well known and may be explained by changes in light, water temperature, current regimes and food availability (e.g., McGehee 1994; Brokovich et al. 2008; Pereira-Filho et al. 2011; Fitzpatrick et al. 2012). Such changes may explain the sharp shift in the structure of fish assemblages at 50 m depth in the SPSPA, although more data are needed to formally test this hypothesis. Similarly, a unique and specialized reef community was identified in the lower mesophotic zone (60–100 m depth) of Curaçao, southern Caribbean (Bongaerts et al. 2015). Fish assemblages in the UMZ were influenced mainly by cover of turf algae, crustose calcareous algae and scleractinian corals, which

may be explained by habitat preferences of the different species. For example, turf algae represent an important food source for *M. niger* and *S. sanctipauli* (Feitoza et al. 2003; Luiz et al. 2015).

Fish assemblages in the LMZ were influenced mainly by black corals and sponges. Colonies of black corals recorded here (*Tanacetipathes* spp.) were relatively large (up to 1.2 m in height) and with branching morphologies. The tridimensional habitat provided by black corals was clearly used as shelter by *C. enchrysur*, *P. obliquus* and juveniles of *B. insularis*. *Prognathodes obliquus*, which is endemic to the SPSPA, was also recorded grazing over black coral colonies [see Boland and Parrish (2005) for similar observations on *Forcipiger flavissimus* in Hawaii]. Reef fish species recorded within black corals in the mesophotic zone in Hawaii include *Aulostomus chinensis*, *Canthigaster jactator*, *Centropyge potteri*, *Dascyllus albisella*, *Forcipiger flavissimus* and *Oxycirrhites typus*, this latter considered a nearly obligate black coral dweller (Boland and Parrish 2005). These results highlight the key roles played by black corals in the mesophotic zone of the SPSPA and elsewhere.

The dominance of planktivores and low abundance of herbivores in mesophotic reefs of the SPSPA were expected, as similar patterns were recorded in previous studies focusing on MREs of other regions (e.g., Colin et al. 1986; Dennis and Bright 1988; Garcia-Sais 2010; Bryan et al. 2013; Bejarano et al. 2014). Greater abundances of herbivores in euphotic reefs dominated by photosynthetic algae are a widely recognized pattern (Choat 1991), and herbivores are indeed scarce at mesophotic habitats (Colin 1974; Brokovich et al. 2010; Kahng et al. 2010). The predominance of planktivores in mesophotic reefs may be explained by the fact that their food supply is not directly influenced by light and generally more abundant in the relatively cold waters of mesophotic depths. Garcia-Sais (2010) explained the high abundance of planktivores (particularly *Chromis cyanea*) in the upper limit of the mesophotic zone of Isla Desecheo, Puerto Rico, by the high availability of zooplankton arriving from the shelf edge. Variations in wind regime have been suggested to induce surfacing of the Equatorial Undercurrent in the SPSPA (Bowen 1966). During this study, abrupt drops in temperature of up to 5 °C were recorded in depths of 30–40 m. Therefore, high zooplankton availability coming from the colder Equatorial Undercurrent is a plausible explanation for the dominance of planktivores in mesophotic reefs of the SPSPA. *Chromis multilineata* was by far the most important species driving this pattern in depths up to 50 m, while *C. enchrysur* was the most abundant planktivorous fish from 50 m down. In fact, the genus *Chromis* includes the few pomacentrid species known to

Fig. 3 Relationship between abundance and depth for different fish species as defined by generalized additive models. **a** *Abudefduf saxatilis*; **b** *Caranx lugubris*; **c** *Canthidermis sufflamen*; **d** *Bodianus insularis*; **e** *Chromis enchrysurus*; **f** *Chromis multilineatus*; **g** *Halichoeres radiatus*; **h** *Holacanthus ciliaris*; **i** *Melichthys niger*; **j** *Myripristis jacobus*; **k** *Prognathodes obliquus*; **l** *Stegastes sanctipauli*. 95 % confidence limits are shown in gray. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns—not significant

occur in mesophotic habitats, a pattern largely attributed to their diet based on zooplankton (Pyle et al. 2008).

Ontogenetic shifts in habitat use often occur in reef fish in ways to maximize foraging, reproduction and/or protection against predation (Dahlgren and Eggleston 2000). Ontogenetic trends along depth gradients have previously been recorded for reef fish, with juveniles generally concentrated at shallower depths (Colin 1974; Nagelkerken et al. 2000; Moura et al. 2011). However, there is growing evidence for the existence of mesophotic nurseries for some reef fish species (Brokovich et al. 2007). Twenty of the 57 individuals of *B. insularis* recorded here (35.2 %) were <20 cm TL, all of them restricted to depths of 40–70 m, while only individuals >20 cm TL were sighted in the euphotic zone (authors' pers. obs.). Several species of *Bodianus* are recognized as having juveniles mostly or

exclusively associated with mesophotic habitats (Lobel 1981; Randall and Chen 1985; Sazima et al. 2010). Mesophotic reefs were also recognized as important nurseries for *Genicanthus caudovittatus* (Pomacanthidae) in the Gulf of Aqaba, Red Sea (Brokovich et al. 2007), and for *Clepticus parrae* (Labridae) and *Chromis insolata* (Pomacentridae) in Isla Desecheo, Puerto Rico (Garcia-Sais 2010).

Mesophotic reefs are generally considered to be less susceptible to local and global disturbances, such as overfishing, pollution and climate change, than euphotic reefs. Thus, they may act as refuges and sources of propagules for shallow threatened reefs (the “deep reef refugia” hypothesis; Lesser et al. 2009; Bongaerts et al. 2010). The level of connectivity between euphotic and mesophotic zones (via larval dispersal or juvenile/adult

Fig. 3 continued

migration) is a central question regarding the mesophotic refuge hypothesis, with most benefits expected for species inhabiting both zones and with high levels of demographic/genetic connectivity (Slattery et al. 2011; Tenggardjaja et al. 2014; Papastamatiou et al. 2015). Data from this study, together with previously published data (Feitoza et al. 2003, Luiz et al. 2015), indicate that most reef fish species occurring in the SPSPA (>80 % of all species) have a broad bathymetric distribution including both euphotic and mesophotic reefs. However, fish species nearly exclusively or exclusively associated with euphotic reefs, such as *Ophioblennius trinitatis*, *Malacoctenus* sp., *Kyphosus* spp. and *Cantherhines macrocerus* (Luiz et al. 2015), may be more susceptible to local extinction in the event of extreme events affecting euphotic reefs, such as

storms and habitat degradation due to global changes (Fitzpatrick et al. 2012). However, it is important to note that the abundance of relatively small fishes such as *O. trinitatis* and *Malacoctenus* sp. may have been underestimated by the ROVs.

This study adds to the knowledge about Brazilian MREs (Feitoza et al. 2005; Pereira-Filho et al. 2011; Magalhães et al. 2015) and to the global database, as it includes novel information from a small and highly isolated site. Given the paucity of studies about MREs in the Atlantic and elsewhere, we hope that our data support future attempts for making broader generalizations about MREs (e.g., Lesser et al. 2009; Kahng et al. 2010, 2014) and serve as a baseline for future evaluations of possible anthropogenic and natural disturbances on MREs of the SPSPA.

Fig. 4 Relationship between fish trophic groups and depth as defined by generalized additive models. 95 % confidence limits are shown in gray. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns—not significant. Fish trophic groups: **a** invertebrate feeders, **b** omnivores, **c** piscivores, **d** planktivores and **e** territorial herbivores

Fig. 5 Canonical correspondence analysis (CCA) plot showing: **a** relationship between independent variables (arrows) and samples from different depth strata (colored dots); and **b** distribution of fish species (gray dots) in the two-dimensional ordination space

Fig. 6 Relationship between black coral abundance and depth as defined by generalized additive models. 95 % confidence limits are shown in gray, *** $p < 0.001$

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