

Trophic role of demersal mesopredators on rocky reefs in an equatorial Atlantic Ocean island

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Summary

The decrease in the number of sharks around Saint Peter and Saint Paul Archipelago (SPSPA) may impact food web structure. We investigated trophic relationships in the shallow rocky reefs of the SPSPA using stable isotopes and stomach contents with a particular focus on three abundant mesopredators: *Caranx lugubris*, *Enchelycore nigricans* and *Muraena pavonina*. Food web structure was described using samples of the most abundant basal resources, fishes and invertebrates, which were collected in April and October 2012. Individuals of the three focal species ($n = 138$: *C. lugubris*, $n = 56$; *E. nigricans*, $n = 18$; *M. pavonina*, $n = 64$) were collected during four expeditions to SPSPA (April and October of 2011 and 2012). Results suggest that this shallow water food web is supported by trophic pathways originating from benthic resources. Stable isotope data suggest potential competitive interactions between the whitespot moray and the other two mesopredators. Conversely, stomach content data suggest little niche overlap in the three focal species, but these data must be interpreted carefully because of the small sample sizes and restricted temporal sampling windows. All three mesopredators have a significant, albeit weak, relationship between body size and $\delta^{15}\text{N}$, suggesting ontogenetic diet shifts. These data contribute baseline information to assess shifts in food web structure that may stem from top predator decline in this unique ecosystem.

1 | INTRODUCTION

Food web studies depict the exchange of matter among organisms within an ecosystem, including the energy flow from basal resources to top predators (Polis & Winemiller, 1996). Fishing is a major agent of disturbance in marine ecosystems (Pauly et al., 2002) and can fundamentally alter the structure of food webs (Friedlander & DeMartini, 2002; Heithaus, Frid, Wirsing, & Worm, 2008). The magnitude of these effects are dependent on the number and function of the species lost (Dunne, Williams, & Martinez, 2002), with the trends amplified in less diverse ecosystems such as rocky reefs (McClanahan, Polunin, & Done, 2002; Pace, Cole, Carpenter, & Kitchell, 1999). Changes in trophic interactions due to fishing impacts are often mediated by mesopredators

(Ritchie & Johnson, 2009). There is limited information on the habitat use and feeding ecology for many of these mesopredators, which limits our ability to understand the mechanisms underlying ecological responses (Ajemian & Powers, 2011; Chase & Leibold, 2003).

Saint Peter and Saint Paul Archipelago (also known as St Paul's Rocks, hereafter abbreviated as SPSPA), a remote group of barren islets in the equatorial Atlantic Ocean, is a unique ecosystem. These islands have limited areas of shallow habitat (<50 m deep), and they support ~60 fish species of which ~9% are endemic (Ferreira et al., 2009; Floeter et al., 2008; Robertson, 2001). It has been hypothesized that a decrease in shark population sizes around the archipelago could impact food web structure, which might be most evident within the mesopredator community (Luiz & Edwards, 2011). In surveys from 1979, the whitespot

moray (*Muraena pavorina* Richardson, 1845) was common and usually found in holes and crevices (Lubbock & Edwards, 1981), similar to observations from the Atol das Rocas Biological Reserve, another Brazilian oceanic island (Véras & Tolotti, 2011). Currently in the SPSPA whitespot moray is one of the most abundant in rocky reef habitat species (Ferreira et al., 2009; Pinheiro, Leite, & Castello, 2011) and, uncharacteristically for moray eels, is often observed swimming away from the shelter during daylight hours (Luiz-Jr, 2005). This behavior might occur because they can spend more time foraging, or foraging over larger areas, with shark predation risk lower (Heithaus et al., 2008). Such shifts raise concerns on the status of small fishes upon which these mesopredators prey, particularly endemic species (Luiz & Edwards, 2011). For instance, the small endemic basslet *Choranthias salmopunctatus* (Anderson & Heemstra, 2012) was once common on rocky surfaces below 30 m (Lubbock & Edwards, 1981), but is now rare (Luiz-Jr, Joyeux, & Gasparini, 2007).

We used stable isotope and direct diet analyses to examine the food web structure in the SPSPA. First, we characterized general aspects of trophic structure using isotope analyses of the most common basal resource pools, invertebrates and fishes. Second, we chose three of the most abundant mesopredators (black jack *Caranx lugubris* Poey, 1860; mulatto conger *Enchelycore nigricans* Bonnaterre, 1788, and the whitespot moray) for a more focused study using stomach contents and isotope analyses. Specifically, we investigated resource use across size classes, as well as the niche width and overlap of these mesopredators. We provide a baseline view of food web structure in this system that can be used to develop more detailed studies on this unique ecosystem.

2 | MATERIALS AND METHODS

2.1 | Study area

Along 8,500 km of Brazilian coastline there are four sets of oceanic islands (Fig.1); these islands shelter 23% of the reef fishes endemic

to the Brazilian Province (Floeter et al., 2008). The archipelago lies ~1,000 km from the Brazilian coast and 1,890 km southwest of Senegal, West Africa. SPSPA (0°55' N and 29°21' W) and has a unique geophysical scenario, made up of a small group of 10 islets and rocky points that rise from the deep ocean (Macedo-Soares, Freire, & Muelbert, 2012). Commercial fishing began in the area in 1956, and since 1988 a commercial fishing fleet from Brazil has been operating continuously in SPSPA (Oliveira, Evangelista, & Ferreira, 1997; Vaske Jr et al., 2010). Significant declines in shark populations have occurred, including local extirpation of the Galapagos shark (*Carcharhinus galapagensis* Snodgrass and Heller, 1905) (Luiz & Edwards, 2011; Oliveira et al., 1997), formerly an important predator of benthic fishes (Froese & Pauly, 2015; Wetherbee, Crow, & Lowe, 1996).

SPSPA is characterized by a rocky reef habitat where most of the shallow subtidal zone is dominated by soft coral *Palythoa caribeorum* (Duchassaing and Michelotti, 1860) and algae *Caulerpa racemosa* (Agardh, 1873). Hermatipic corals (*Madracis decactis* Lyman, 1859 and *Scolymia wellsii* Laborel, 1967) appear at ~30 m, which is the *C. racemosa* distribution limit (Feitoza, Rocha, & Luiz-Júnior, 2003). A small bay of maximum 35 m depth is ringed by three of the major islets. Other reef habitat consists almost entirely of nearly vertical cliffs extending to >60 m depths.

2.2 | Methods

We took two different approaches to examine aspects of food web structure in SPSPA. First, we used stable isotope data to provide a general overview of trophic structure. In April and October 2012, we collected samples of the most abundant basal resources, including brown algae, green filamentous algae and *C. racemosa*. Particulate organic matter (POM) samples were obtained by pumping seawater (10 L) through the 50 mm GF/C filter. Zooplankton was obtained from horizontal tows using a conical-cylindrical plankton net with 300 µm

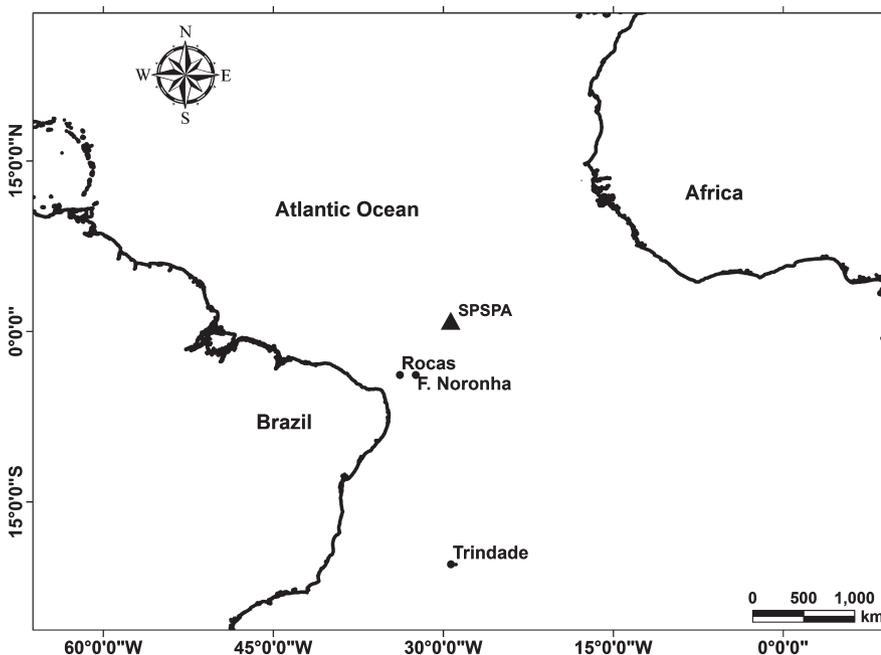


FIGURE 1 Location of Saint Peter and Saint Paul Archipelago (SPSPA) and three other Brazilian oceanic islands: Atol das Rocas (Rocas), Fernando de Noronha Archipelago (F. Noronha) and Trindade and Martim Vaz Archipelago (Trindade)

mesh size. Abundant fishes and invertebrates were collected with a hand net (see Table 1 for complete species list).

Second, using spearguns and traps, individuals of the three focal species ($n = 138$: black jack, $n = 56$; mulatto conger, $n = 18$; whitespot moray, $n = 64$) were collected during four expeditions to SPSPA (April and October of 2011 and 2012). Whitespot moray is the most abundant benthic predator in SPSPA, with restricted distribution in northeastern Brazil and the oceanic islands (Fernando de Noronha Archipelago, Trindade and Martins Vaz Archipelago, Atol das Rocas, and SPSPA) and Ascension Island (Froese & Pauly, 2015; Pinheiro et al., 2011; Vaske Jr et al., 2005). Mulatto conger is another abundant moray eel in SPSPA, and is distributed across tropical areas of the Atlantic and Pacific oceans (Froese & Pauly, 2015). Black jack has a circumtropical range (Froese & Pauly, 2015), and is the second most abundant demersal predator in SPSPA (Pinheiro et al., 2011).

Immediately after collection, fish were measured (total length in cm), weighed (g), and their stomachs and intestines removed and preserved in 10% formalin. The stomachs were dissected in the laboratory, and the food items sorted and identified to the lowest possible taxonomic level. Data were organized by numeric percentage (NP %) of individuals of a prey category relative to total prey number for each species, as well as frequency of occurrence (FO) of a prey item by species. Due to a relatively small sample size and the absence of volumetric data, we focused our interpretation on FO (Baker, Buckland, & Sheaves, 2014). Muscle tissue was removed from the dorsal region of specimens (total $n = 104$: black jack, $n = 43$; mulatto conger, $n = 16$;

whitespot moray, $n = 45$) and frozen for subsequent stable isotope analysis.

Samples were dried at 60°C for 48 hr and ground to a fine powder with a mortar and pestle. Sub-samples were loaded in tin capsules (Costech, Valencia, CA) and sent to the Analytical Chemistry Laboratory, Institute of Ecology at the University of Georgia for determination of stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Standards for carbon were from PeeDee Belemnite and nitrogen from air. Analytical precision was 0.08 for carbon and 0.02 for nitrogen (SD for replicates of laboratory standards).

2.3 | Data analysis

One-way ANOVA and Tukey *post hoc* tests were used to compare mean $\delta^{13}\text{C}$ values among species. Homogeneity of variance was confirmed using the Levene's test. The $\delta^{15}\text{N}$ data did not meet requirements for parametric tests, thus differences among species were assessed using a nonparametric Kruskal–Wallis test, followed by the Wilcoxon test (Zar, 1999). Linear models were used to analyze the relationship between total length and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each of the three focal species, in order to infer potential ontogenetic trophic changes.

We also quantified three niche aspects: isotopic niche position, niche overlap and niche width. These metrics are commonly used to infer the trophic role of consumers, and may help predict particular situations where competitive interactions might be manifest.

TABLE 1 Mean ($\pm SD$) size, sample size (N) and isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of muscle tissue removed from specimens collected in 2011 and 2012, Saint Peter and Saint Paul Archipelago. Trophic groups in first column based on literature sources (Ferreira, Gonçalves and Coutinho, 2001)

Trophic group	Scientific name	N	Total length (cm)	Nitrogen (δ^{15})	Carbon (δ^{13})
Invertebrate predator	<i>Octopus insularis</i> ^a (Leite & Haimovici, 2008)	2	13.1 and 10.1	9.9 and 10.6	-12.1 and -15.5
	<i>Panulirus echinatus</i> (Smith, 1869)	4	16.2 \pm 1.9	9.8 \pm 0.9	-15.4 \pm 0.4
	<i>Plagusia depressa</i> (Fabricius, 1775)	2	2.4 and 4.7	8.8 and 9.3	-7.2 and -13.3
Zooplanktivore	<i>Chromis multilineata</i> (Guichenot, 1853)	4	11.9 \pm 0.6	8.8 \pm 0.6	-17.7 \pm 0.1
	<i>Cypselurus cyanopterus</i> (Valenciennes, 1847)	4	29.3 \pm 3.8	9.4 \pm 0.3	-17.3 \pm 0.2
	<i>Myripristis jacobus</i> (Cuvier, 1829)	6	18.9 \pm 0.7	9.8 \pm 0.4	-17.3 \pm 0.2
Roving herbivore	<i>Kyphosus sectatrix</i> (Linnaeus, 1758)	3	43.4 \pm 5.1	10.9 \pm 0.7	-13.3 \pm 1.6
Territorial herbivore	<i>Ophioblennius trinitatis</i> Miranda Ribeiro, 1919	2	6.0 and 6.4	7.5 and 7.9	-17.0 and -17.1
	<i>Stegastes sanctipauli</i> Lubbock & Edwards, 1981	6	8.5 \pm 1.0	11.5 \pm 0.9	-14.5 \pm 1.2
Omnivore	<i>Abudefduf saxatilis</i> (Linnaeus, 1758)	4	13.4 \pm 5.1	9.7 \pm 0.6	-16.6 \pm 1.1
	<i>Canthidermis sufflamen</i> (Mitchill, 1815)	2	39.1 and 39.2	9.1 and 9.7	-16.5 and 16.6
	<i>Melichthys niger</i> (Bloch, 1786)	4	27.9 \pm 6.7	9.7 \pm 0.5	-16.9 \pm 0.3
Mobile invertebrate feeder	<i>Halichoeres radiatus</i> (Linnaeus, 1758)	4	31.2 \pm 1.2	10.6 \pm 0.2	-15.4 \pm 1.1
Carnivore	<i>Caranx crysos</i> (Mitchill, 1815)	3	35.8 \pm 5.1	10.2 \pm 0.9	-17.7 \pm 0.2
	<i>Caranx lugubris</i> Poey, 1860	43	36.1 \pm 12.2	10.0 \pm 0.9	-17.2 \pm 0.3
	<i>Enchelycore nigricans</i> (Bonnaterre, 1788)	16	82.1 \pm 8.9	11.5 \pm 0.4	-15.8 \pm 0.3
	<i>Lutjanus jocu</i> (Bloch & Schneider, 1801)	2	81.1 and 99.2	11.5 and 11.9	-16.7 and -15.1
	<i>Muraena pavonina</i> Richardson, 1845	45	61.9 \pm 11.1	11.0 \pm 0.5	-16.4 \pm 0.3
	<i>Seriola rivoliana</i> Valenciennes, 1833	2	41.7 and 49.9	9.4 and 9.6	-15.9 \pm 0.2

^aOctopus dorsal mantle length.

Potential differences among species in mean position within isotopic space were analyzed following Turner, Collyer, and Krabbenhoft (2010), where nested linear models and residual permutation procedures (RPP) were used to generate and compare measures of central tendency for each species. When the Euclidean distance between two groups was significantly >0 , then the mean isotopic niche position was considered to be different. p -values from RPP were compared to those obtained using the parametric Hotelling's T^2 test statistic. Hotelling's T^2 is a multivariate analogue of the univariate t test that is suited for the comparison of population mean vectors. Niche overlap was assessed using the percentage of individuals that were encompassed by other species' convex hulls (i.e. the area of the smallest convex polygon that contains all individuals of a group in a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; Layman, Arrington, Montaña, & Post, 2007). Convex hulls are a niche width metric that encompass variation in niche position among all individuals in a sample (Layman et al., 2012). We also calculated a second niche width measure using a Bayesian approach based on multivariate ellipse-based metrics (Jackson, Inger, Parnell, & Bearhop, 2011). The analysis generates standard ellipse areas (SEA_B), which are bivariate equivalents to standard deviations in univariate analysis, and represent the core isotopic niche of that species (Layman et al., 2012). These analyses were calculated following methods from Jackson et al. (2011) and the R package SIAR (Parnell, Inger, Bearhop, & Jackson, 2010).

In addition, the numeric percentage (NP %) of prey in the gut contents of the three focal species was compared with a chi-square test. Unidentifiable stomach content items were excluded in the analysis. All tests were performed in R, version 3.0.1 (R Core Team, 2014).

3 | RESULTS

The POM stable isotopes values ($\delta^{13}\text{C} = -21.12\text{‰} - \delta^{15}\text{N} = 1.81\text{‰}$) and zooplankton (copepods: $\delta^{13}\text{C} = -20.99\text{‰} - \delta^{15}\text{N} = 5.56\text{‰}$ and chaetognatha: $\delta^{13}\text{C} = -20.41\text{‰} - \delta^{15}\text{N} = 6.14\text{‰}$) were depleted relative to most consumers (Table 2; Fig. 2). The most enriched $\delta^{15}\text{N}$ values were for predators, including dog snapper (*Lutjanus jocu* Bloch and Schneider, 1801; 11.7‰) and mulatto conger (11.5‰), whereas the most depleted values occurred in the benthic herbivore redlip blenny (*Ophioblennius trinitatis* Miranda Ribeiro, 1919; 7.7‰), planktivorous brown chromis (*Chromis multilineata* Guichenot, 1853; 8.8‰) and tidal spray crab (*Plagusia depressa* Fabricius, 1775; 8.8‰). For $\delta^{13}\text{C}$, the most enriched values were found in tidal spray crab (-12.5‰) and Bermuda sea chub (*Kyphosus sectatrix* Linnaeus, 1758; -13.3‰), and most depleted in brown chromis (-17.7‰), blue runner (*Caranx crysos*

TABLE 2 Linear model of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures with total length for *Caranx lugubris*, *Enchelycore nigricans* and *Muraena pavonina* collected in 2011 and 2012, Saint Peter and Saint Paul Archipelago. Significant values are in bold.

Species	Stable isotope	Slope	y intercept	R ²	p
<i>Caranx lugubris</i>	$\delta^{13}\text{C}$	0.008	-17.47	.11	.027
	$\delta^{15}\text{N}$	0.04	8.71	.23	.001
<i>Enchelycore nigricans</i>	$\delta^{13}\text{C}$	0.009	-16.59	.01	.296
	$\delta^{15}\text{N}$	0.032	8.91	.36	.008
<i>Muraena pavonina</i>	$\delta^{13}\text{C}$	0.005	-16.75	.03	.166
	$\delta^{15}\text{N}$	0.024	9.54	.23	.0001

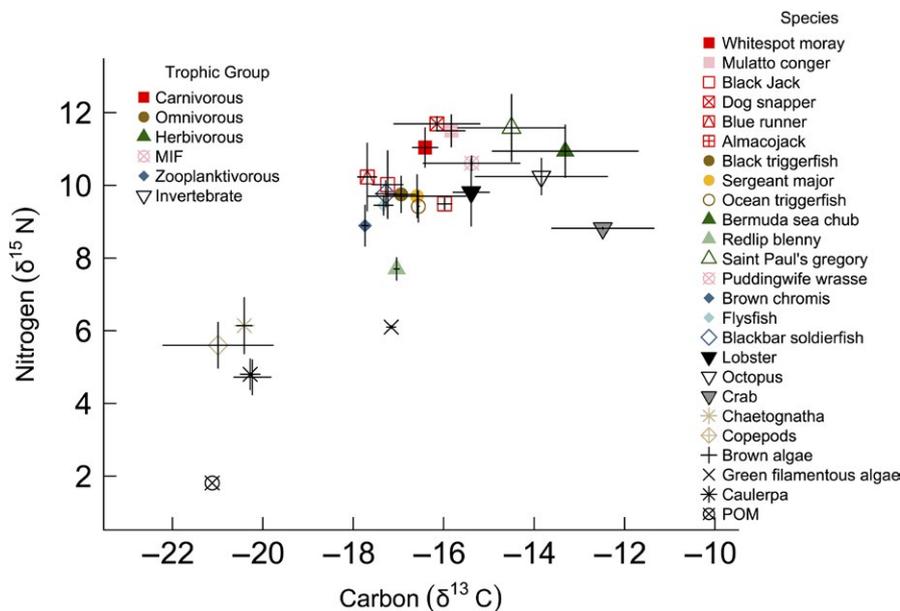


FIGURE 2 Stable isotopes values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of particulate organic matter (POM) and demersal organisms collected in 2011 and 2012 around Saint Peter and Saint Paul Archipelago. Dots = means; bars = standard deviations. MIF = Mobile invertebrate feeders

Mitchill, 1815; -17.7%) and black jack (-17.2%). The endemic Saint Paul's gregory (*Stegastes sanctipauli* Lubbock & Edwards, 1981) had relatively enriched values for $\delta^{13}\text{C}$ (-14.5%) and $\delta^{15}\text{N}$ (11.5%).

Mean $\delta^{13}\text{C}$ values \pm SD differed among the three predators (ANOVA: $d.f = 2$; $F = 282.2$; $p < .001$), with significant differences for all three pairwise species comparisons (Tukey test: all $p < .001$). Mean $\delta^{15}\text{N}$ values \pm SD also differed among species (Kruskal–Wallis: $H = 39.44$; $d.f = 2$; $p < .001$), with all three pairwise species comparisons significant (Wilcoxon test: all $p < .01$).

Niche positions were different for the three predator species: between moray and mulatto conger (distance = 0.74; $p < .002$; Hotelling's $T^2 = 41.74$; $p < .02$), mulatto conger and black jack (distance = 2.1; $p < .002$; Hotelling's $T^2 = 172.16$; $p < .001$) and whitespot moray and black jack (distance = 13.11; $p < .002$; Hotelling's $T^2 = 169.7$; $p < .001$). There was no isotopic niche overlap between mulatto conger and black jack; moderate overlap was found between the other pairs of species, with whitespot moray overlapping with 51% of the niche space (using the convex hull niche area) of mulatto conger and 47% of black jack (Fig. 3). Niche width for black jack was significantly greater than for whitespot moray ($p < .02$); there was no difference between black jack and mulatto conger ($p = .1$), or between the two moray eel species ($p = .2$). There was a significant positive linear relationship between total length and $\delta^{15}\text{N}$ for the three predators, although R^2 values were relatively low (black jack, $R^2 = .23$; mulatto conger, $R^2 = .36$; whitespot moray, $R^2 = .23$).

Black jack preyed primarily on small pelagic crustaceans (Table 3, size range: 1–2.5 cm) and small fishes, including flying fish (Family

Exocoetidae), blackbar soldierfish (*Myripristis jacobus* Cuvier, 1829), brown chromis and sergeant-major (*Abudefduf saxatilis* Linnaeus, 1758). Whitespot moray diet consisted mainly of small crabs, small fishes such as redlip blenny and flying fish, and polychaetes. Mulatto conger preyed upon small crabs and small fishes (e.g. sergeant-major). Numeric percentage of prey found in the gut contents varied between the two moray eel species ($X^2 = 21.03$; $d.f = 2$; $p = .03$), black jack and mulatto conger ($X^2 = 48.19$; $d.f = 2$; $p = .0001$) and black jack and whitespot moray ($X^2 = 44.91$; $d.f = 2$; $p = .0001$).

4 | DISCUSSION

The relatively depleted $\delta^{13}\text{C}$ of POM and zooplankton (copepods and chaetognaths) in relation to most consumer species, suggests that species in this shallow water food web are supported by trophic pathways largely originating from benthic resources (Layman et al., 2012). Most reef fish species have relatively similar $\delta^{13}\text{C}$ values (i.e. a range of $<5\%$), which suggests either a limited number of basal resources support this food web or the resources on which the organisms depend have similar isotopic signatures. As would be expected, predators (e.g. dog snapper, moray eels) had relatively high $\delta^{15}\text{N}$ values, but surprisingly, some fish assumed *a priori* to be herbivorous (Bermuda sea chub and Saint Paul's gregory) were also positioned relatively high along the $\delta^{15}\text{N}$ -axis. The latter could be because these species consume resources besides primary producers, or that direct inference regarding relative trophic level is confounded by subtle differences

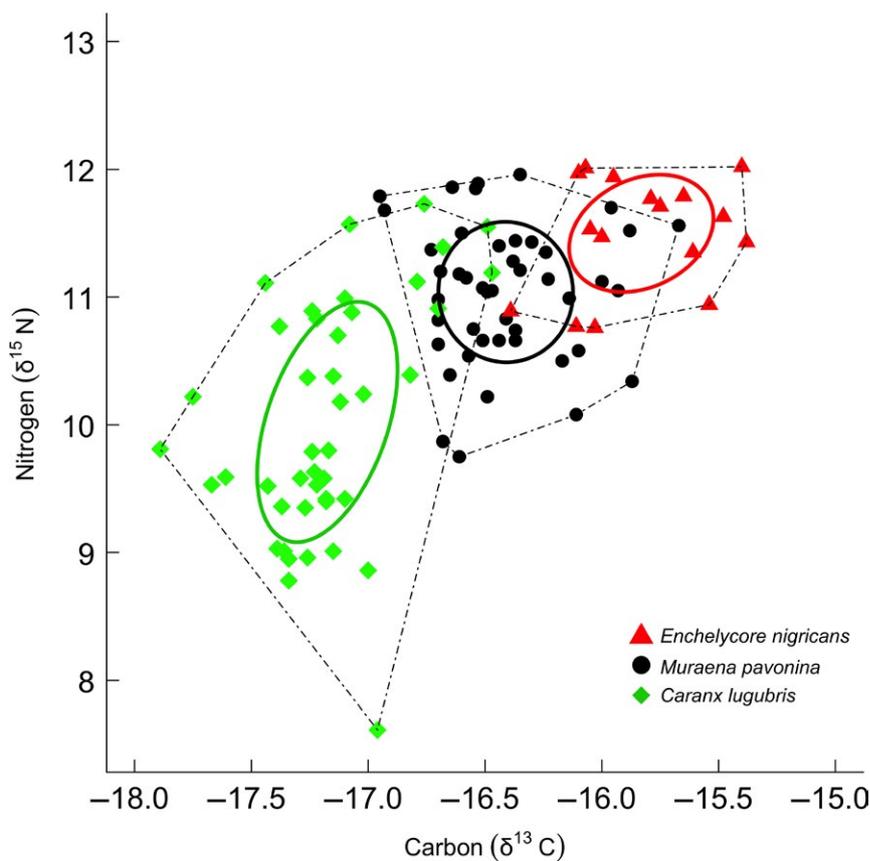


FIGURE 3 Isotopic niche width of *Caranx lugubris*, *Enchelycore nigricans* and *Muraena pavonina*, Saint Peter and Saint Paul Archipelago. Each data point = stable isotopes values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for one individual. Dashed lines = convex hull representation of total niche width. Solid lines: standard ellipse areas (SEA_B), a representation of the core isotopic niche

TABLE 3 Stomach content data from *Caranx lugubris*, *Enchelycore nigricans* and *Muraena pavonina* collected in 2011 and 2012, Saint Peter and Saint Paul Archipelago

Prey	<i>Caranx lugubris</i> (N = 56)		<i>Enchelycore nigricans</i> (N = 18)		<i>Muraena pavonina</i> (N = 64)	
	NP %	FO	NP %	FO	NP %	FO
Invertebrates						
Crabs	0	0	13	6	19	11
Polychaete	0	0	0	0	15	9
Small pelagic crustaceans	75	25	0	0	0	0
Vertebrates						
<i>Myripristis jacobus</i>	1	4	0	0	0	0
<i>Chromis multilineata</i>	1	4	0	0	0	0
<i>Cypselurus cyanopterus</i>	1	4	0	0	4	3
<i>Ophioblennius trinitatis</i>	0	0	0	0	2	2
<i>Abudefduf saxatilis</i>	1	2	25	11	0	0
Unidentified fish	10	30	12	6	17	13
Unidentified	11	48	50	38	43	38
Empty stomachs (%)	33		55		48	

Sample size (N), numeric percentage (NP %) of prey items and frequency of occurrence (FO) for each prey type. NP % calculated excluding individuals with empty stomachs.

in isotopic baselines among food resources. More refined sampling of basal resource pools and direct diet information is needed to further elucidate the trophic roles of these species.

Variations in isotopic niche positions of the three focal species is driven by variation along both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ axes, each of which suggests different aspects of the trophic roles of these species (Layman et al., 2012). Moray eels are typically assumed to be primarily benthic feeders (Randall, 1967; Young & Winn, 2003), but the recent shift of whitespot moray to forage openly during the day might result in the consumption of more pelagic prey (e.g. flying fishes), which would be consistent with the depleted $\delta^{13}\text{C}$ relative to mulatto conger. The $\delta^{13}\text{C}$ values were more depleted for black jack than for moray eels. Black jack is an active benthic-pelagic species (Froese & Pauly, 2015) that may utilize prey which rely more on pelagic resource pools, consistent with their relatively depleted $\delta^{13}\text{C}$ values. Black jack niche width is also significantly greater than whitespot moray and mulatto conger. Since it is the most mobile of the three focal predators (Froese & Pauly, 2015), it may be able to take advantage of alternative food resources that the eels cannot (Randall, 1967).

Whitespot moray had a moderate overlap in isotopic niche with the other two species (51% of the niche space of mulatto conger and

47% of the black jack niche based on convex hull measures). These data, as well as the fact that the whitespot moray is the most abundant mesopredator (Pinheiro et al., 2011), suggest that there might be some competitive interactions with the other two mesopredators. Conversely, stomach content data suggest little diet overlap for the three focus species. However, these diet data should be interpreted carefully because of the relatively small sample sizes, restricted temporal sampling windows, and absence of volumetric data. Furthermore, there was a high incidence of empty stomachs, making inferences difficult.

There were slight differences in $\delta^{15}\text{N}$, perhaps suggesting differences in trophic position among species. However, these data should be interpreted cautiously for three reasons. First, the magnitude of the $\delta^{15}\text{N}$ differences was small, with mean values among species varying <1.5‰. Second, we lacked the refined baseline values for basal resource pools that could be used to calculate more accurate trophic position estimates. Third, we found trends in $\delta^{15}\text{N}$ variation through ontogeny, with individuals of the three focal species apparently having higher trophic positions at larger sizes. Such intraspecific variation in trophic niche suggests that different size/age classes may play very different roles within the food web (e.g. Woodward & Hildrew, 2002).

This study provides the first food web insights, using stable isotopes analyses and direct diet information, into this ecosystem in these equatorial Atlantic islands. Detecting changes in trophic interactions when a predator is depleted is a formidable challenge, in part because of the complexity of marine food webs (Steneck, 1998). Yet our data provide the basis for some intriguing hypotheses regarding the interactions of carnivorous mesopredators in this rocky reef system. An important future direction would be to develop a more detailed stable isotope data set, complemented by stomach content analyses of other common species in the system. Further, behavioral observations of the mesopredators would reveal direct information on feeding strategies, which also would help interpret isotope data. Such information on the trophic structure would be an important step for developing long-term management and conservation plans for this understudied and threatened ecosystem.

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REFERENCES

- Ajemian, M. J., & Powers, S. P. (2011). Habitat-specific feeding by cownose rays (*Rhinoptera bonasus*) of the northern Gulf of Mexico. *Environmental Biology of Fishes*, 95, 79–97.
- Anderson, W. D., & Heemstra, P. C. (2012). Review of Atlantic and eastern Pacific anthiine fishes (Teleostei: Perciformes: Serranidae), with descriptions of two genera. *Transactions of the American Philosophical Society*, 102, 1–173.
- Baker, R., Buckland, A., & Sheaves, M. (2014). Fish gut content analysis: Robust measures of diet composition. *Fish and Fisheries*, 15, 170–177.
- Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. Chicago: University of Chicago Press, 216 pp. (ISBN: 0226101797)
- Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, 5, 558–567.
- Feitoza, B., Rocha, L., & Luiz-Júnior, O. (2003). Reef fishes of St. Paul's Rocks: New records and notes on biology and zoogeography. *Journal of Ichthyology and Aquatic Biology*, 7, 61–82.
- Ferreira, C. E. L., Gonçalves, J. E., & Coutinho, R. (2001). Community structure of fishes and habitat complexity on a tropical rocky shore. *Environment Biology of Fishes*, 61, 353–369.
- Ferreira, C. E. L., Luiz, O. J., Feitoza, B. M., Ferreira, C. G. W., Noguchi, R., Gasparini, J. L., Joyeux, J., Godoy, E. A. S., Rangel, C. A., Rocha, L. A., Floeter, S. R., & Carvalho-Filho, A. (2009). Peixes recifais: Síntese do atual conhecimento. In: D. Viana, F. Hazin & M. Souza (Eds.), *Arquipélago de São Pedro e São Paulo: 10 anos de estação científica* (pp 244–250). Brasília: SECIRM.
- Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J., Smith-Vaniz, W. F., Wirtz, P., Edwards, A. J., Barreiros, J. P., Ferreira, C. E. L., Gasparini, J. L., Brito, A., Falcón, J. M., Bowen, B. W., & Bernardi, G. (2008). Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, 35, 22–47.
- Friedlander, A., & DeMartini, E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. *Marine Ecology Progress Series*, 230, 253–264.
- Froese, R., & Pauly, D. (2015). *Fishbase 2015*. World Wide Web electronic publication. Retrieved from <http://www.fishbase.org>. (accessed on 5 December 2015)
- Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, 23, 202–210.
- Jackson, A., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80, 595–602.
- Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M., & Bearhop, S. (2012). Applying stable isotopes to examine food-web structure: An overview of analytical tools. *Biological Reviews of the Cambridge Philosophical Society*, 87, 545–562.
- Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotopes ratios provide for community-wide measures of trophic structure? *Ecology*, 88, 42–48.
- Lubbock, R., & Edwards, A. (1981). The fishes of Saint Paul's Rocks. *Journal of Fish Biology*, 18, 135–157.
- Luiz, O. J., & Edwards, A. J. (2011). Extinction of a shark population in the Archipelago of Saint Paul's Rocks (equatorial Atlantic) inferred from the historical record. *Biological Conservation*, 144, 2873–2881.
- Luiz-Jr, O. (2005). Unusual behaviour of moray eels on an isolated tropical island (St. Paul's Rocks, Brazil). *Coral Reefs*, 24, 501.
- Luiz-Jr, O., Joyeux, J., & Gasparini, J. L. (2007). Rediscovery of *Anthias salmopunctatus* Lubbock & Edwards, 1981, with comments on its natural history and conservation. *Journal of Fish Biology*, 70, 1283–1286.
- Macedo-Soares, L., Freire, A. S., & Muelbert, J. (2012). Small-scale spatial and temporal variability of larval fish assemblages at an isolated oceanic island. *Marine Ecology Progress Series*, 444, 207–222.
- McClanahan, T., Polunin, N., & Done, T. (2002). Ecological states and the resilience of coral reefs. *Conservation Ecology*, 6, 1–28.
- Oliveira, G. M., Evangelista, J., & Ferreira, B. P. (1997). Considerações sobre a biologia e a pesca no Arquipélago dos Penedos de São Pedro e São Paulo. *Boletim Técnico Científico Do CEPENE*, 5, 31–52.
- Pace, M. L., Cole, J. J., Carpenter, S. R., & Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution*, 14, 483–488.
- Parnell, A. C., Inger, R., Bearhop, S., & Jackson, A. (2010). Source partitioning using stable isotopes: Coping with too much variation. *PLoS ONE*, 5, e9672.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R. R., Walters, C. J., Watson, R., & Zeller, D. (2002). Towards sustainability in world fisheries. *Nature*, 418, 689–695.
- Pinheiro, I. E. G., Leite, T. S., & Castello, J. P. (2011). Distribuição dos predadores de topo associados ao sistema demersal bentônico raso do Arquipélago São Pedro e São Paulo: Estação chuvosa. In: *Congresso Latino-Americanos de ciências do mar* (pp. 29–31). Balneário Camburiu.
- Polis, G. A., & Winemiller, K. O. (1996). *Food webs: Integration of patterns and dynamics* (p. 472). New York: Chapman and Hall.
- R Core Team (2014). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>. (accessed on 15 October 2014)
- Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, 5, 665–847.
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998.
- Robertson, D. R. (2001). Population maintenance among tropical reef fishes: Inferences from small-island endemics. *Proceedings of the National Academy of Sciences*, 98, 5667–5670.
- Steneck, R. S. (1998). Human influences on coastal ecosystems: Does overfishing create trophic cascades?. *Trends in Ecology & Evolution*, 13, 429–430.
- Turner, T. F., Collyer, M. L., & Krabbenhoft, T. J. (2010). A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology*, 91, 2227–2233.
- Vaske Jr, T., Lessa, R. P., Nobrega, M., Montealegre-Quijano, S., Marcante Santana, F., & Bezerra, J. L. (2005). A checklist of fishes from Saint Peter and Saint Paul Archipelago, Brazil. *Journal of Applied Ichthyology*, 21, 75–79.
- Vaske Jr, T., Nóbrega, M., Lessa, R., Hazin, F. H. V., Santana, F. M., Ribeiro, A. C., Pereira, A. A., & Andrade, C. (2010). Pesca. In: T. Vaske Jr, R. Lessa, M. Nóbrega, F.D. Amaral, S. O'Brien & F. Costa (Eds.), *Arquipélago de São Pedro e São Paulo: Histórico e recursos naturais* (pp. 181–188). Fortaleza: UFC/NAVE/LABOMAR. 242pp.
- Véras, D., & Tolotti, M. (2011). *Guia para identificação de peixes do Atol das Rocas*. Recife.
- Wetherbee, B. M., Crow, G. L., & Lowe, C. G. (1996). Biology of the Galapagos shark, *Carcharhinus galapagensis*, in Hawai'i. *Environmental Biology of Fishes*, 45, 299–310.
- Woodward, G., & Hildrew, A. G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology*, 71, 1063–1074.
- Young, R. F., & Winn, H. E. (2003). Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. *Copeia*, 2003, 44–55.
- Zar, J. H. (1999). *Bioestatistical analysis*, 4th edn. New Jersey: Prentice Hall. 663 pp.