Article

Ecological Links between Pelagic and Mesophotic Reef Fishes in an Oceanic Archipelago of the Equatorial Atlantic Ocean

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Abstract: Geographic isolation, a relatively low species richness and high endemism make oceanic islands excellent natural laboratories for ecological and evolutionary studies. Here we used Baited Remote Underwater stereo-Video systems (stereo-BRUVS) to investigate the taxonomic, trophic and size structures of fish assemblages from pelagic and mesophotic reef ecosystems in the smallest archipelago of the equatorial Atlantic Ocean, the Saint Peter and Saint Paul's Archipelago (SPSPA). The occurrence of steep reef walls favors studies on the ecological connections between pelagic and reef ecosystems. We performed five pelagic stereo-BRUVS deployments and fourteen benthic stereo-BRUVS deployments, totaling 1440 min of footage. We recorded 14 species from eight families in the pelagic ecosystem, with Carangidae and Balistidae as the most diverse families. The most abundant species were *Elagatis bipinnulata* (Quoy and Gaimard, 1825), *Melichthys niger* (Bloch, 1786), and *Caranx crysos* (Mitchill, 1815), which together accounted for over 75% of the total relative abundance. The carnivores were the most diverse and abundant trophic group. On the mesophotic reefs, 41 taxa were recorded, with carnivores and planktivores being the most diverse, whereas omnivores were the most abundant. Here, the most abundant species were *M. niger*, *Azurina multilineata*, *Chromis vanbebberae*, *Seriola rivoliana*, *Caranx lugubris* and *Stegastes sanctipauli*. Nine species were recorded in both ecosystems, with *Melichthys niger*, *Caranx lugubris* and *S. rivoliana* being the main species linking them (i.e., occurring in both). These species are known to forage in both pelagic and mesophotic reef ecosystems, and thus represent potential ecological links between them. Such links combined with the endangered status of some species, suggest the need for an integrated management strategy in this remote archipelago.

Keywords: Brazilian province; conservation; ecology; ecosystems linking; energy flux; oceanic island

1. Introduction

Oceanic islands are widely considered as natural laboratories for ecological and evolutionary studies [1]. The combination of intrinsic characteristics such as high geographic isolation, relatively low species richness and high endemism allow the understanding of ecological and evolutionary processes and patterns in these iconic model systems [2,3].

Significant advances in the understanding of biogeographic and evolutionary processes, such as colonization and speciation, in reef fishes from oceanic islands have occurred in the past few years (e.g., [2,4–9]), placing them as key systems for conservation. Ecological characteristics of oceanic reef fish communities have also been extensively studied, especially their bathymetric variation and association with benthic substrate (e.g., [10–13]). Moreover, information about the anthropogenic impacts (e.g., fishing pressure and litter pollution) on the fish assemblages of these remote systems has increased [14–17], raising concerns on species conservation [18,19]. However, ecological studies of pelagic fish assemblages are relatively more challenging and are mostly based on fisheries data. The large spatial scale of the environment and the heterogeneous distribution of pelagic species, make consistent and accurate sampling complex [20–22], especially with classical non-extractive techniques, such as underwater visual census.Ecological connectivity and energy transfer driven by animal movements between habitats and ecosystems are important processes influencing community structure and productivity [23–25]. For instance, marine animals from tiny (e.g., krill) [26] to large sizes (e.g., seals and whales) [27] are known for playing important functional roles in nutrient transport from deep to shallow areas, incrementing the local primary productivity and influencing the carbon sink. Likewise, seabirds can be an important component where their feces fertilize reefs adjacent to their colonies [24]. Many studies using different techniques, such as acoustic telemetry and stable isotope analyses, have shown that predatory fish are important trophic links, acting directly on nutrient cycling as they make regular and periodic foraging movements between pelagic and reef ecosystems (e.g., [25,28–30]). However, the knowledge on the community connections between mesophotic reef and adjacent pelagic ecosystems is still scarce (but see [31]). The relative greater proximity between reefs and the surrounding oceanic pelagic environment, as well as the occurrence of highly mobile and transitory fish species, make oceanic islands appropriate ecological models in such investigations.

The oceanic Saint Peter and Saint Paul's Archipelago (SPSPA), in the equatorial Atlantic Ocean, presents great ecological importance, due to its high fish biomass [6,32] and endemism on shallow (0–30 m depth) and mesophotic reefs (31–150 m), despite a general low species richness [33]. Many pelagic fishes use the SPSPA, including species of high commercial interest (e.g., tuna and wahoo) [34,35] and species globally or locally threatened with extinction (e.g., whales and Galapagos sharks) [36,37]. However, although the shallow reef ichthyofauna is relatively well studied [11,38–40], the mesophotic reef fish need more attention as only limited information about their biodiversity [33,38] and ecology [41,42] is currently available. Similarly, the pelagic fish assemblage has not been studied through standardized fishery-independent data (but see [32]), making it difficult to quantitatively assess the ecological connections between these ecosystems. The extremely steep local geomorphology results in a great proximity between the oceanic pelagic and reef ecosystems, facilitating studies on their interaction and connectivity.

Baited remote underwater video systems (BRUVS) allow standardized non-extractive sampling in both pelagic and reef ecosystems, in addition to allowing new records [17,33,43,44]. The BRUVS may also detect elusive species [37,45] hardly recorded by other non-extractive techniques such as visual census and remotely operated vehicles [46–51]. Therefore, here we used pelagic and benthic stereo-BRUVS to investigate the taxonomic and trophic structure of pelagic and mesophotic reef fish assemblages at the small and isolated Saint Peter and Saint Paul's Archipelago. The main goal of this work was to analyze the variation in abundance, diversity, and size structure of the fish assemblages, along the depth gradient and between the pelagic and mesophotic ecosystems, identifying species co-occurrence (i.e., ecological linkages) between these ecosystems in an oceanic archipelago of the equatorial Atlantic Ocean.

2. Materials and Methods

2.1. Study Area

The remote Saint Peter and Saint Paul's Archipelago (SPSPA; Figure 1) is located on the Mid-Atlantic Ridge, in the equatorial Atlantic Ocean, about 1010 km from the Northeastern Brazilian coast (00°55′ N; 29°21′ W). This is one of the smallest and most isolated oceanic tropical archipelagos in the world, composed of a small group of islets and rocks. Totaling an emerged area of ca. 15,000 m^2, there are only about 0.5 km^2 of reefs shallower than 100 m depth [11,14,41]. Shallow rocky reefs (≤30 depth) are mostly found around a small bay, mainly covered by the zoanthid *Palythoa caribaeorum*, the fleshy algae *Caulerpa racemosa* and *Bryopsis* spp., and crustose coralline algae [52]. The mesophotic reef ecosystem has sharp relief and steep walls, covered by crustose coralline algae, bryozoans, and scleractinian corals (e.g., *Madracis decactis* and *Scolymia wellsii*) down to around 40 m depth, while sponges and branching black corals (*Tanacetipathes* sp.) dominate deeper zones down to ca. 100 m [33,41,52]. The surface South Equatorial Current, flowing westwards, and the Equatorial Undercurrent, flowing eastwards at depths between 40 and 150 m, directly influence the area [53,54]. The interaction of these currents with the local topography results in a complex hydrodynamic system, which can favor the occurrence of up- and down-welling currents, influence the reef assemblages and attract many species from the pelagic ecosystem [33].

Until recently, this archipelago was part of the multiple-use Marine Protected Area (MPA) of Fernando de Noronha-Rocas-São Pedro and São Paulo Environmental Protected Area [55]. In March 2018, a large MPA including two categories of protected areas was created around the SPSPA: a multiple-use and a no-take area (Figure 1). The no-take area is nested within the multiple-use MPA, however most of the archipelago is part of the latter see [18,19].
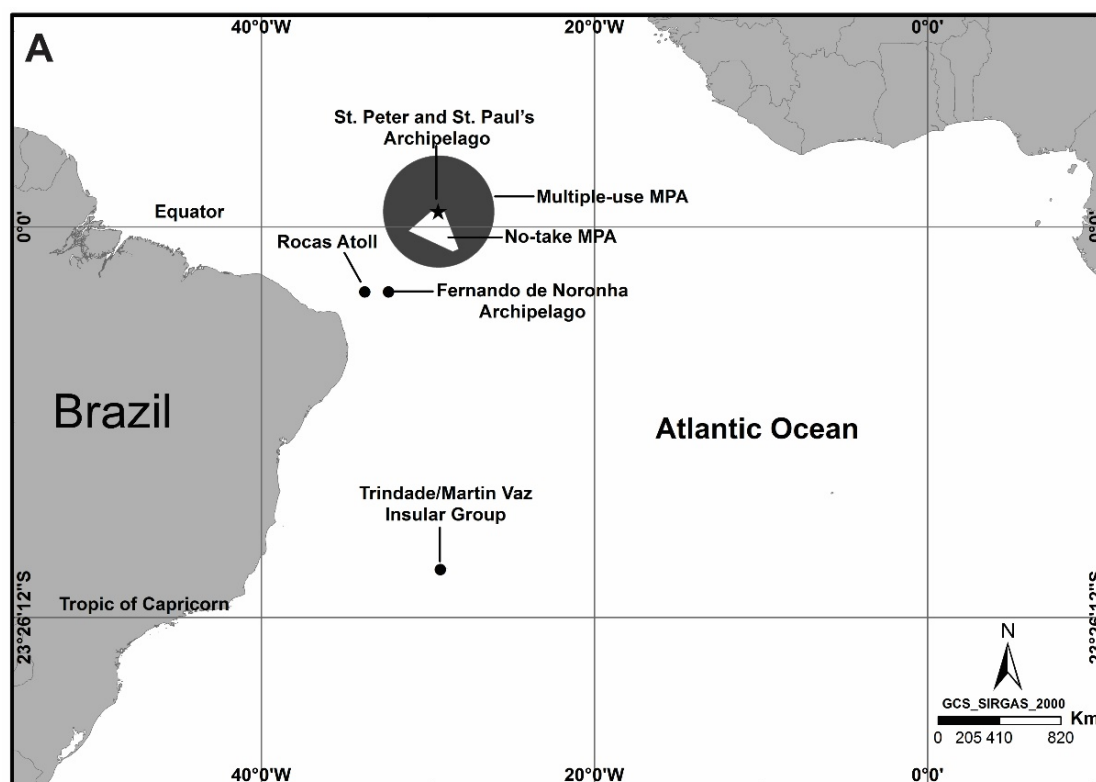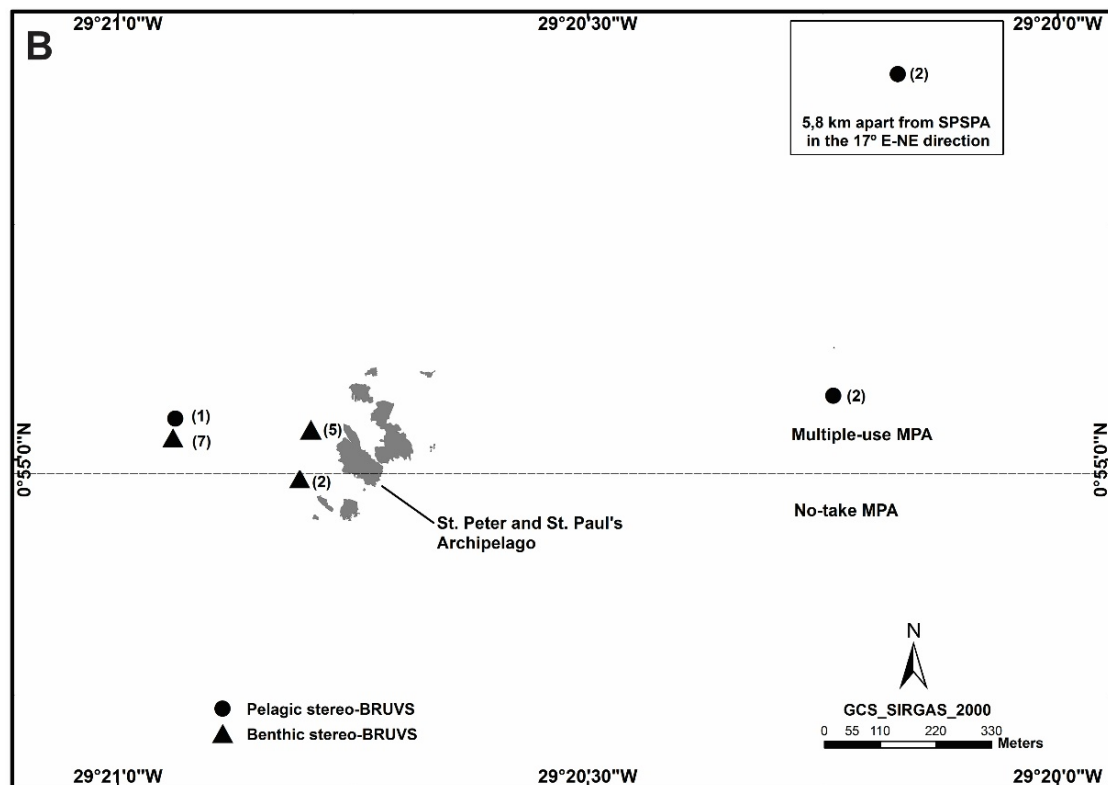

Figure 1. *Cont.*

Figure 1. Study area showing the location of Saint Peter and Saint Paul's Archipelago in the Atlantic Ocean, the multiple-use (dark gray circle) and no-take (white polygon) marine protected areas, and the other Brazilian oceanic islands (**A**), and the pelagic (dark dots) and benthic (dark triangles) stereo-BRUVS deployment sites (**B**). The number of deployments on each site is in parentheses and the dashed gray line indicates the border between multiple-use (above) and no-take (below) marine protected areas.

2.2. Sampling Procedures

Both pelagic and benthic stereo-BRUVS consisted of a metal bar with two GoPro Hero 3+ Silver video cameras in housings capable of sampling up to 100 m deep, positioned approximately 500 mm apart and inwardly converging at 5 degrees (Figure S1). A 1.2 m bait arm with a bait bag at the end was fixed in the center of the metal bar. For the benthic stereo-BRUVS, the metal bar was enclosed inside a metal frame with weights at the base. For the pelagic stereo-BRUVS, no frame was used and weights were hanging directly on the metal bar.

During a two weeks expedition to SPSPA in September 2018, we performed five day-time (8–16 h) pelagic stereo-BRUVS deployments between 20 and 30 m depth, and fourteen benthic stereo-BRUVS deployments between 30 and 84 m depth. All the BRUVS setups were equipped with a depth gauge to assess the depth in each deployment. Due to strong local currents, both the pelagic and the benthic stereo-BRUVS were attached to mooring buoys situated less than 1 km from the Archipelago, with deployments varying between 50 to 800 m from archipelago; one exception was located about 5.8 km away (Figure 1). Simultaneous deployments had a minimum distance of 250 m from each other. Pelagic deployments were at least 50 m above the reefs. Benthic deployments lasted 60 min and were baited with 500 g of crushed false herring *Harengula clupeola* (Cuvier, 1829), while pelagic deployments lasted 120 min and were baited with 1 kg of the same bait. Due to the sparse and heterogeneous nature of pelagic fish assemblages, an increased soak time is required for an adequate characterization [21,56].

2.3. Video Analysis

All fishes were identified to the lowest possible taxonomic level and the relative abundance of each species in both pelagic and mesophotic deployments was recorded as MaxN, i.e., the maximum number of individuals of a given species present in a single frame [57]. During the MaxN moment of each species, we measured the total length for species with lobe, lanceolate and/or rhomboid fins, and the fork length for fish with forked fins. All measurements had precision of ≤1 cm, according to the distance (≤5 m) and angle (≤45°) of the cameras. The lengths of two large (>1 m) *Mobula tarapacana* (Philippi, 1892) recorded in the pelagic system were visually estimated based on objects or fishes of known size in the video (e.g., [58]). Video analysis was carried out in the EventMeasure software (www.seagis.com.au, accessed on 30 March 2022).

2.4. Data Analysis

Species were classified into trophic groups as carnivores, mobile invertebrate feeders, sessile invertebrate feeders, planktivores, omnivores, territorial herbivores or roving herbivores (according to [59]). Variations in the taxonomic and trophic structure of the mesophotic reef fish assemblages along the depth gradient were examined using principal coordinate analysis (PCO), based on Bray–Curtis similarity matrix calculated from square root transformed MaxN data and Spearman's correlation overlaid vectors. Similarity Percentages (SIMPER) one-way analysis was conducted to evaluate each species contribution to the overall assemblage, and separately for the pelagic and mesophotic assemblages. These analyses were run in PRIMER version 6.1.13 and PERMANOVA+ version 1.0.3 software. The species contributions based on the SIMPER analysis are presented using an Alluvial diagram. For both taxonomic and trophic structures of the mesophotic reef fish assemblages, generalized additive models (GAM) using Gaussian distribution and identity link were performed to analyze the correlation between PCO axes (response variables) and depth of deployment (predictor variable). The GAMs can be used as a semi-parametric regression technique for exploring relationships, having greater flexibility for drawing out the long-term non-linear trends than chain or linear methods [60]. This makes GAMs one of the most common and well-developed statistical tools for providing a nonlinear approach for fitting ecological responses to the predictor variables [61–63]. The influence of depth of deployment on species richness, total relative abundance (TMaxN—the sum of all species MaxN for deployment) and relative abundance (MaxN) of the six most abundant species and trophic groups of the mesophotic reef fish assemblages, were also explored using GAMs with Poisson distribution and log link [64]. The GAMs were run in the R software using the package mgcv [65,66].

3. Results

3.1. Pelagic Fish Assemblages

In the pelagic system, we recorded 14 species belonging to eight families (Table S1). The most diverse families were Carangidae and Balistidae with four and three species, respectively. The most abundant species were *Elagatis bipinnulata* (Quoy and Gaimard, 1825), *Melichthys niger* (Bloch, 1786), and *Caranx crysos* (Mitchill, 1815), which together accounted for over 75% of the total relative abundance. Carnivores were the most diverse trophic group, represented by nine species, followed by planktivores with three species, and omnivores with one (Figure 2; Table S1). Carnivores were also the most abundant trophic group, represented mainly by *E. bipinnulata* and *C. crysos*, which accounted for over 60% of the total relative abundance. The carnivores *Acanthocybium solandri* (Cuvier, 1832), *Carcharhinus falciformis* (Müller and Henle, 1839), *E. bipinnulata*, and *Thunnus albacares* (Bonnaterre, 1788), and the planktivore *Mobula tarapacana* (Philippi, 1892), were the largest species (TL > 100 cm) recorded. Medium-sized (40 < TL < 101 cm) specimens were represented by the carnivores *C. crysos*, *Caranx lugubris* Poey, 1860, *Coryphaena hippurus* Linnaeus, 1758, *E. bipinnulata*, *Seriola rivoliana* Valenciennes, 1833 and *Sphyraena barracuda* (Edwards, 1771), and the planktivores *Canthidermis maculata* (Bloch, 1786) and *Canthidermis*

sufflamen (Mitchill, 1815). The smallest species (TL ≤ 40 cm) were small specimens of *C. crysos*, *C. lugubris*, *S. rivoliana* (carnivores), *C. maculata*, *C. sufflamen* (planktivores), and the highly abundant omnivore *M. niger*.
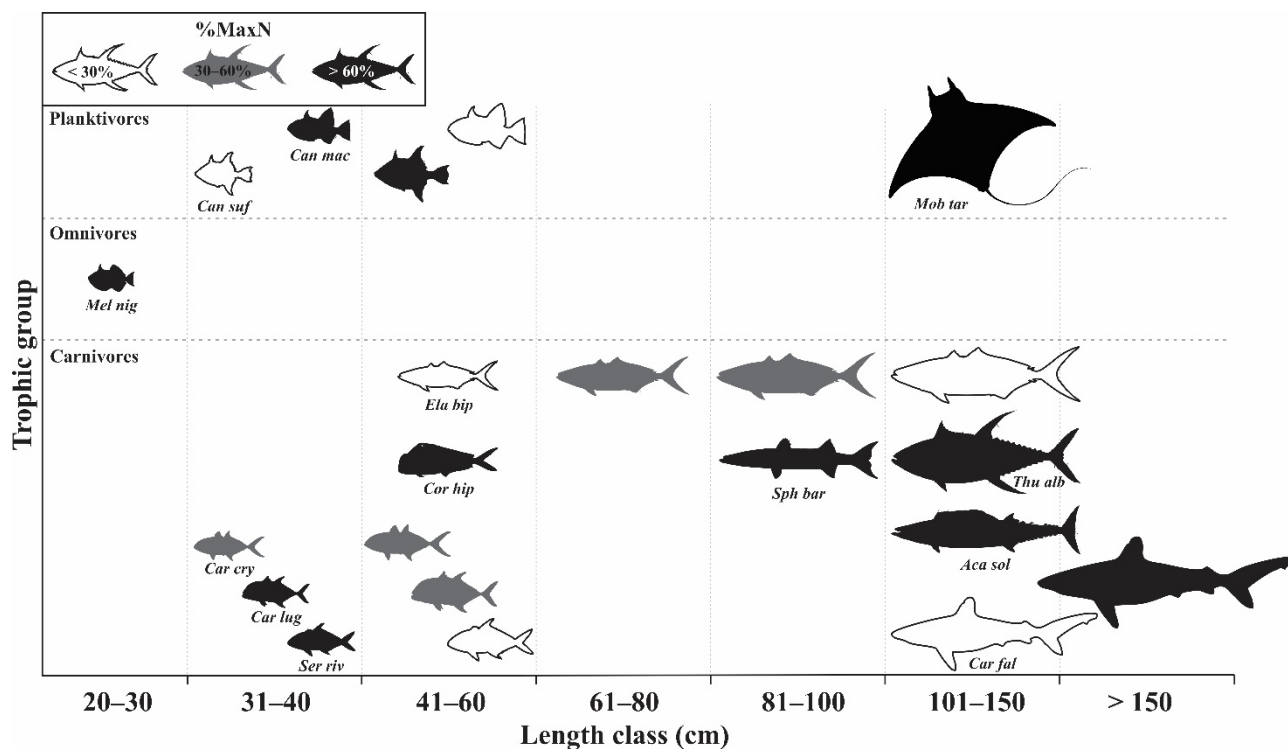

Figure 2. Percentage of total relative abundance (%TMaxN) by length class and trophic group of the fish species recorded in the pelagic environment of SPSPA. Aca sol: *Acanthocybium solandri*; Can mac: *Canthidermis maculata*; Can suf: *Canthidermis sufflamen*; Car cry: *Caranx crysos*; Car lug: *Caranx lugubris*; Car fal: *Carcharhinus falciformis*; Cor hip: *Coryphaena hippurus*; Ela bip: *Elagatis bipinnulata*; Mel nig: *Melichthys niger*; Sph bar: *Sphyraena barracuda*; Mob tar: *Mobula tarapacana*; Ser riv: *Seriola rivoliana*; Thu alb: *Thunnus albacares*.

3.2. Mesophotic Reef Fish Assemblages

On the mesophotic reef system, we recorded 41 taxa belonging to 19 families (Table S2). Specimens of *Kyphosus* spp. and *Enchelycore* cf. *nycturanus* Smith, 2002 could not be identified to the species level. The most diverse families were Muraenidae (five taxa), Balistidae, Carangidae, and Pomacentridae (four species each). The most abundant species, based on the total (sum of MaxN) and mean (mean MaxN ± SD) relative abundance of each species per deployment were *M. niger* with 808 individuals (57.7 ± 23.6), *Azurina multilineata* (Guichenot, 1853) with 209 individuals (14.9 ± 17.9), *Chromis vanbebberae* McFarland, Baldwin, Robertson, Rocha and Tornabene, 2020 with 123 individuals (8.8 ± 16.0), *S. rivoliana* with 90 individuals (6.4 ± 12.1), *C. lugubris* with 85 individuals (6.1 ± 8.7) and *Stegastes sanctipauli* Lubbock and Edwards, 1981 with 53 individuals (3.8 ± 5.6). We also recorded two sharks, one *Carcharhinus galapagensis* (Snodgrass and Heller, 1905) and one *C. falciformis* (see [36]). Carnivores (16 species from 8 families) and planktivores (7 species from 6 families) were the most diverse trophic groups. Omnivores, represented mainly by *M. niger*, was the most abundant trophic group on the mesophotic reefs, accounting for ca. 50% of the total fish abundance. Planktivores and carnivores represented about 21% and 18%, respectively. All other trophic groups represented less than 5% of the total abundance each.

There were no clear taxonomic or trophic patterns of fish assemblage structure by depth (Figure 3A,B; Tables S3 and S4). Deployments segregated into two groups not related to depth (PCO1 axis; Figure 3A). One group (on the left) was associated with species considered of shallow affinities (i.e., species relatively more abundant in the shallower

areas of the reef), such as *Abudefduf saxatilis* (Linnaeus, 1758), *A. multilineata*, *S. sanctipauli* and *Halichoeres radiatus* (Linnaeus, 1758). The other group (on the right) was correlated to demersal mesophotic specialists such as *C. vanbebberae* and *Prognathodes obliquus* (Lubbock and Edwards, 1980), along with the benthopelagic species *S. rivoliana*, *C. lugubris*, *B. capriscus* and *Cantherhines macrocerus* (Hollard, 1853). The single sample most related to *M. tarapacana* and with high abundance of *Kyphosus* spp. stands isolated at the top of the plot (Figure 3A). In the trophic structure plot (Figure 3B), the first axis separated the same sample dominated by roving herbivores (i.e., *Kyphosus* spp.) from all others. The second axis partially separated samples associated with carnivores and mobile invertebrate feeders (below) from those associated with planktivores and sessile invertebrate feeders (in the middle), and those associated with omnivores and territorial herbivores (above).
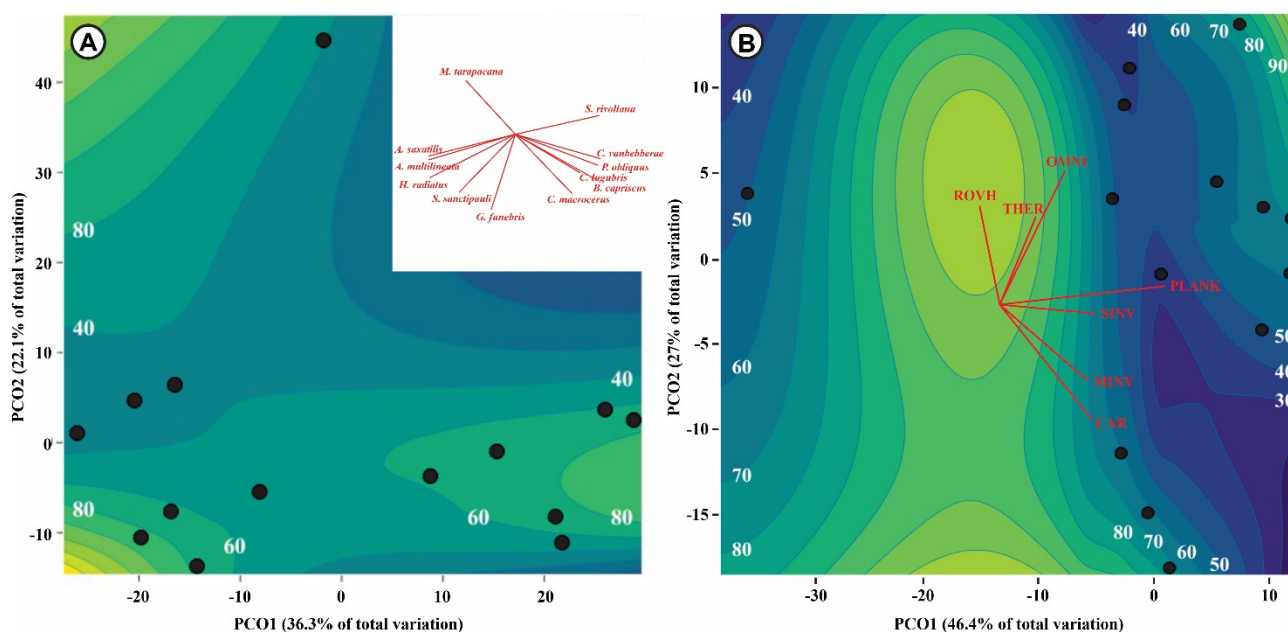

Figure 3. Principal coordinate analysis plots based on the relative abundance of (**A**) species and (**B**) trophic groups. Species with Spearman correlations > 0.65 and the trophic groups are overlaid with their respective vectors. Each dot represents a BRUVS deployment. White numbers indicate the depth gradient.

     Species richness and TMaxN of the mesophotic reef fish assemblages varied significantly with depth, as well as MaxN of the most abundant species except *C. vanbebberae* (Figure 4). Species richness and TMaxN showed a strong increase along the depth gradient. *Seriola rivoliana*, *C. lugubris* and *S. sanctipauli*, in contrast, showed a moderate increase in MaxN, while *A. multilineata* presented a bimodal distribution, with lower MaxN in the intermediate depth zone. The distribution of trophic groups also showed significant variation with depth (Figure 5). Carnivores, mobile and sessile invertebrate feeders and, to a lesser extent, territorial herbivores, increased in abundance along the mesophotic depth gradient. Planktivores showed an evident bimodal depth distribution, while omnivores did not show a clear pattern of bathymetric distribution (Figure 5).
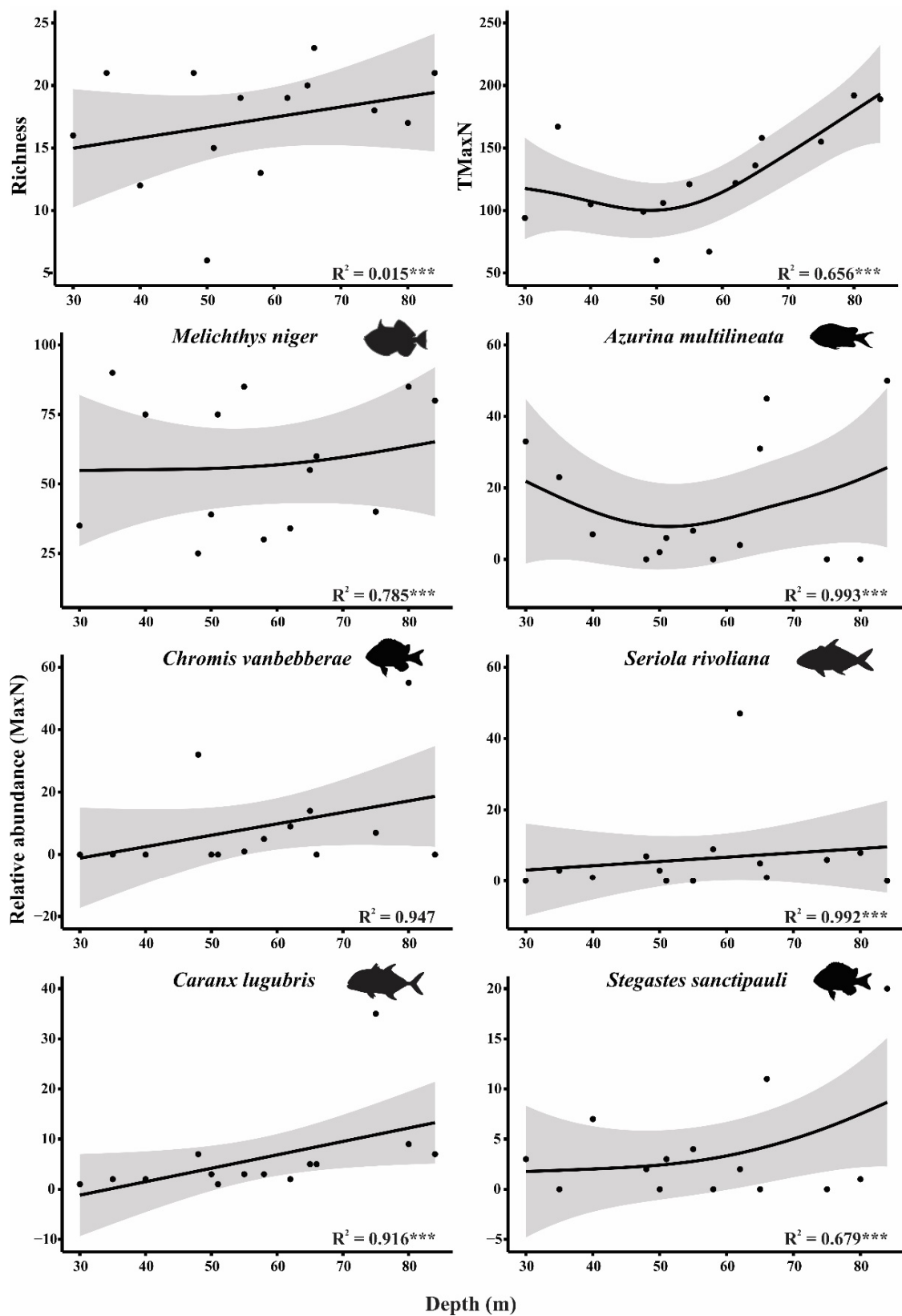
Figure 4. Relationship between species richness, total relative abundance (TMaxN) and relative abundance (MaxN) of the six most abundant species and depth according to the generalized additive models. Each dot represents a BRUVS deployment. 95% confidence limits are shown in gray. *** *p* < 0.001.
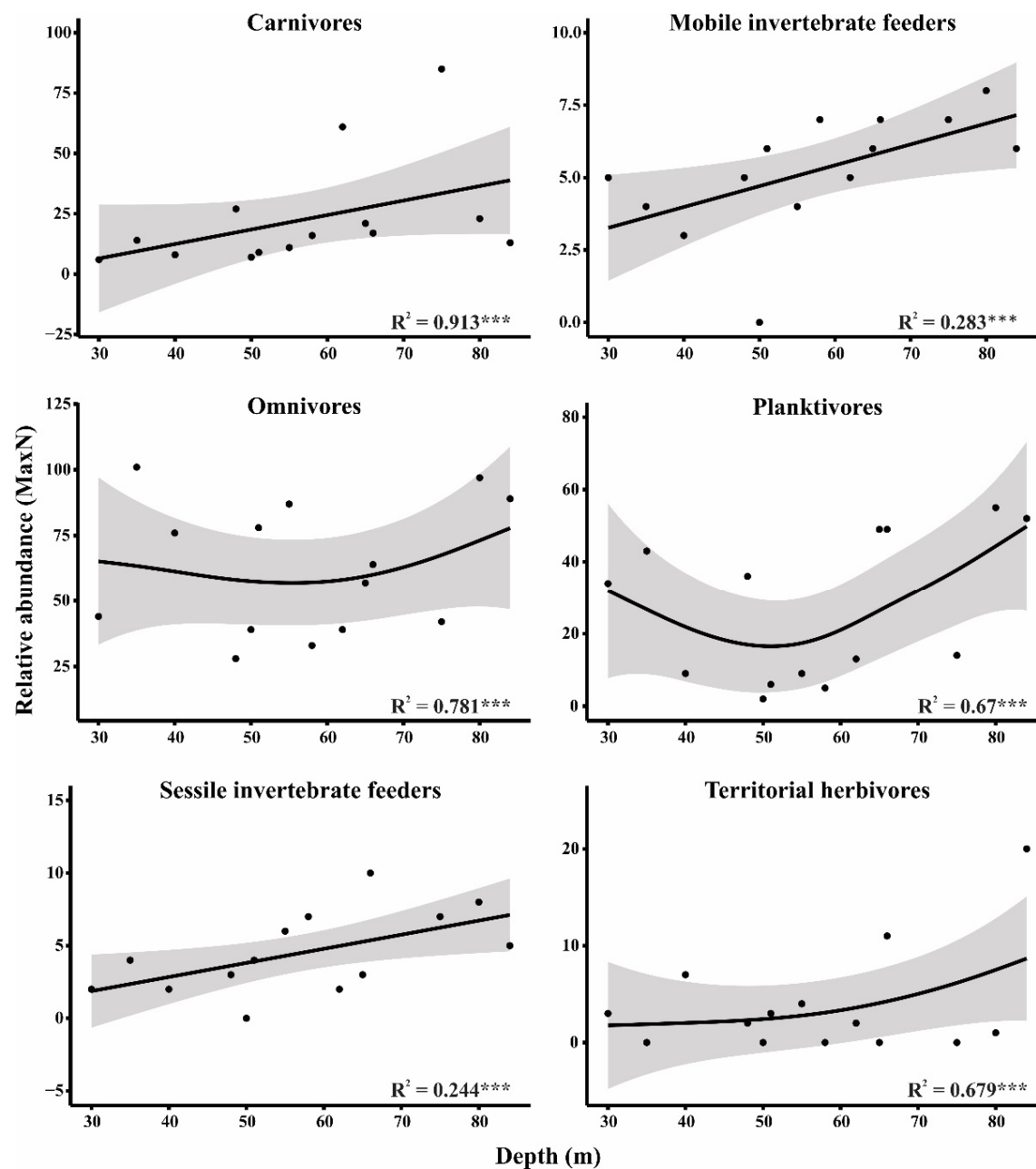
Figure 5. Relationship between relative abundance (MaxN) of the trophic groups and depth according to the generalized additive models. Each dot represents a BRUVS deployment. 95% confidence limits are shown in gray. *** $p < 0.001$.

3.3. Ecosystems' Connections

Overall, 46 taxa were recorded in the SPSPA (Figure 6). Nine fish species from six families and three trophic groups were recorded in both ecosystems, contributing 40.1% for the overall assemblage similarity (SIMPER analysis; Table S5). *Melichthys niger*, *C. lugubris* and *S. rivoliana* presented the greatest individual contributions for the overall assemblage, with 19.4%, 9.4% and 6.6%, respectively (Table S5). The nine link species contributed 33.8% for the within pelagic assemblages' similarity and 34.4% for the within mesophotic reef assemblages' similarity (Figure 6).
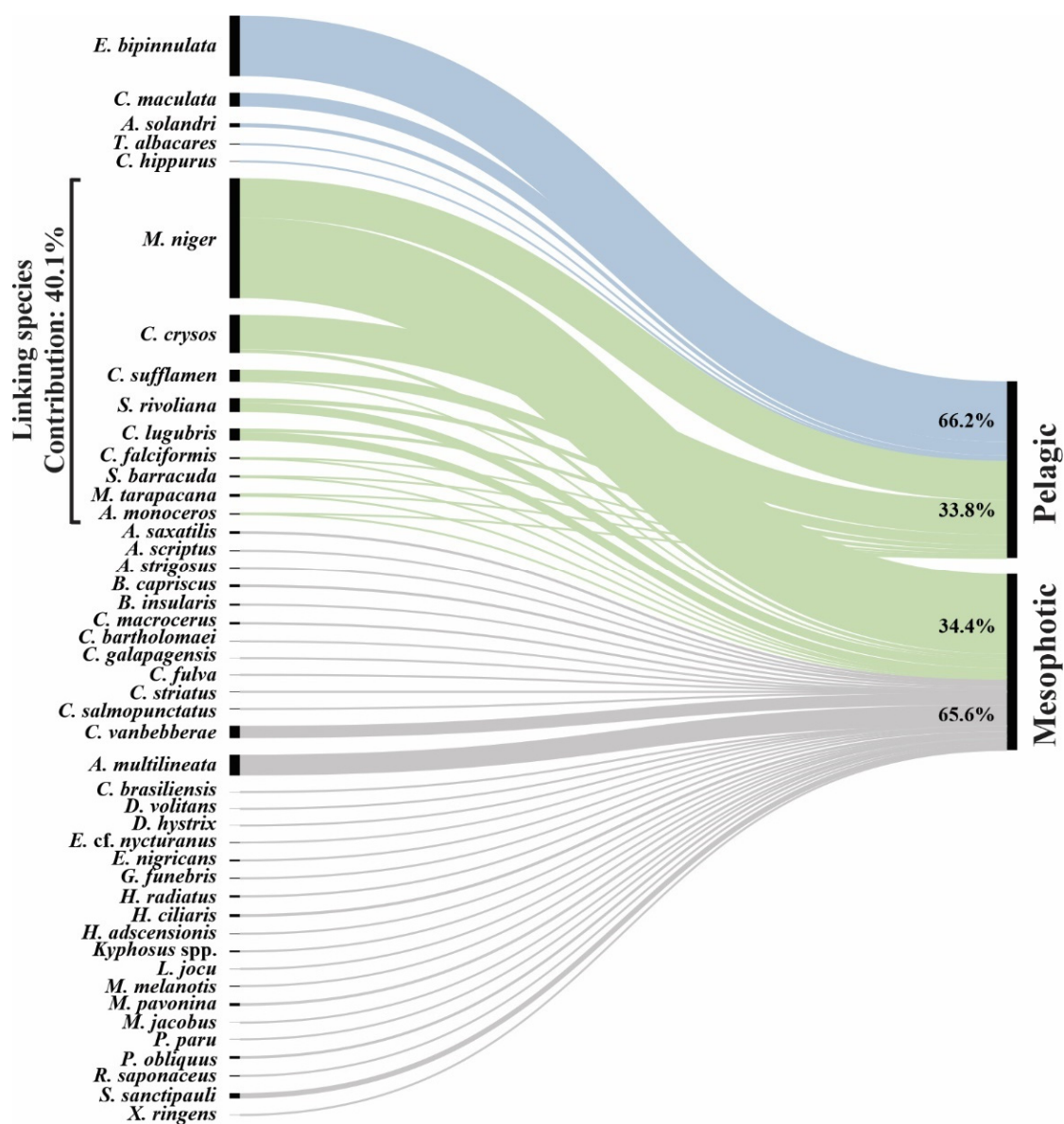
Figure 6. Alluvial plot based on the %MaxN of the species showing the contributions of the link species (green) to the pelagic (blue) and mesophotic reef (gray) fish assemblages.

4. Discussion

This study reinforces that the BRUVS efficiently provide fast and robust estimates of abundance, diversity and size structure of fish assemblages, allowing us to increase our understanding of ecological connectivity between pelagic and reef ecosystems. Such information is crucial to understanding nutrient flux along the trophic web in these unique oceanic reefs, where we still have poorly knowledge about the relative contribution of pelagic and benthic production to maintain local biomass [67]. This information is also important for managers and researchers to detect assemblage shifts in response to multiple threats, such as overfishing and climate change [68,69]. Our data also revealed that, although the pelagic and mesophotic reef fish assemblages are independently structured, taxonomic and functional aspects link both ecosystems into a single ecological perspective. However, we acknowledge that MaxN is a conservative measure used to avoid the repeated counting of individuals, tending to underestimate abundance, particularly in the case of schooling fish [70,71]. Besides that, bait plume behavior must be considered as an important drive resulting in specific fish structure patterns [72]. These factors were considered in

our study, and made our findings regarding ecosystem connectivity robust. Nevertheless, further field surveys and techniques, such as with isotopic approaches, could contribute to a deeper understand about ecosystems connectivity in SPSPA.

4.1. Pelagic Assemblages

Our work is one of the first fishery-independent ecological assessments of the pelagic fish assemblages in the southwestern Atlantic (but see [54]) and also explores community-level ecological connections between pelagic and mesophotic reef ecosystems. Despite the challenges to study pelagic fish assemblages [20,72–74], the BRUVS are standing out as an efficient technique, presenting relatively fast deployment time, enabling many replications, and covering a large area, combined with a high capacity to record predators [37,73]. As most pelagic species are elusive meso (e.g., barracudas, tuna and wahoo) and large predators (e.g., sharks), BRUVS are well suited to conduct surveys in marine protected areas as a non-extractive technique [20,74,75].

Despite the relatively limited sampling effort, our study recorded about 25% of pelagic fish species known from the SPSPA, including new records [33]. Although researchers have previously investigated pelagic fishes in the SPSPA, their studies focused mainly on the trophic ecology of fisheries resources (e.g., [76–78]), where the assemblage structure was characterized through analyses of commercial fishing data (e.g., [34,35]). Fishery-dependent data is biased due to gear catchability and size-selectivity [79,80]. In SPSPA, for instance, commercial fishing data show that mesopredators (e.g., tuna and wahoo) dominate the pelagic assemblage [34,35], whereas our study disclosed a greater variety of trophic levels.

Despite a decade-long ban on shark and longline fishing close to the SPSPA [81], there being allowed only hook and line fishing of pelagic species (e.g., wahoo, tuna and carangids), shark species richness and abundance remain low. At least 10 species of pelagic sharks have been recorded in the area, including *C. galapagensis*. This species that was very abundant a few decades ago [14] and, despite signs of its recovery [82], our data suggest that it is still extremely rare nowadays [33,37]. Managing longline fishing in the SPSPA protection zone is an important step to restore local populations of sharks and other predators and to achieve the conservation goals pursued by the creation of the MPA in the archipelago.

4.2. Mesophotic Reef Assemblages

The SPSPA reef fish fauna has been considered one of the poorest globally due to the remoteness and small size of the archipelago [33]. However, in comparison to previous studies on the fish assemblage structure of shallow and mesophotic reefs of the SPSPA [52,83], our study recorded a greater diversity of species (~20% and 53% more species, respectively), including recent new records in [32]. Such a difference could be related to the use of different sampling techniques and effort. For example, Luiz et al. [52] performed underwater visual censuses (UVCs), conducting 213 belt transects between 0 and 30 m depth. On their side, Rosa et al. [41] analyzed 230 min of footage acquired by remotely operated vehicle (ROV) between 30 and 90 m depth. Finally, we used 840 min of BRUVS footage between 30 and 84 m depth. The use of UVCs and ROV can cause avoidance behavior in some fish species, varying according to the size, intensity of noise and light emitted by the equipment and the divers. In contrast, the BRUVS attract carnivores and a great variety of fishes (e.g., planktivores and omnivores), including rare and endangered species [48,49]. Therefore, the BRUVS are well suited for biodiversity assessments and ecological studies in remote sites, especially where researchers have limited expedition time and restricted logistic resources.

Unexpectedly, we did not find the fish assemblages to be clearly structured according to the depth gradient, as detected in the same archipelago [41] and in other mesophotic reef ecosystems elsewhere [83–87]. However, the structure we found was greatly driven by species with shallow and mesophotic affinities. Strong up- and down-welling events were recorded between 50 and 100 m, switching drastically the temperature in a matter of minutes,

and influencing the movement of fishes along the reef wall (HT Pinheiro and LA Rocha, pers. obs.). Such occasional oceanographic processes increase connectivity between shallow and mesophotic reef habitats, in addition to providing nutrients and rich plankton to local fish and benthic assemblages [88]. Mesophotic specialists possibly take advantage of cold ascendant currents that occur in the region [89] to briefly rise up and use resources more common in shallower reefs, such as turf, crustose calcareous algae and scleractinian corals [41]. According to Nunes et al. [42], *P. obliquus* has a bathymetric distribution coincident with the temperature stratification, showing greatest abundances in deep (>60 m) and cold (14–18 °C) waters, but with regular sightings at 40 m depth. Similarly, *C. vanbebberae* is also a mesophotic species associated with cold waters that can occur at depths of up to 10 m [90] under the right temperature conditions. Quick variation in temperature has also been observed in mesophotic reefs of Hawaii [91] and could drive the ephemeral occurrence of both assemblages at the same depth range. As shallow reefs are limited in the SPSPA, competition for territory and other resources (e.g., food and shelter) might be intense and should influence the expansion of species of shallow waters affinity, such as *S. sanctipauli*, to mesophotic reefs. However, ontogeny and plasticity might play important roles. Based on the ecology of other species of *Stegastes* [92–94], adults of *S. sanctipauli* are territorial herbivores, favoring a distribution concentrated to shallow reefs due to the higher abundance of turf and other algae [41,52], while juveniles are omnivores/invertivores, which makes them more capable to migrate and inhabit deeper reefs.

4.3. Ecosystems Connections

The high number of species linking (i.e., co-occurring) pelagic and mesophotic reefs (~40% of the overall assemblages' similarity; Figure 6) supports the hypothesis of ecological connectivity between these ecosystems. In contrast to previous studies that showed fish predators as important links between coral reefs and the pelagic environment [22,29], our study showed community-level links mainly driven by an omnivore species. The abundant *M. niger*, however, is considered a functional herbivore in the SPSPA that transfers nutrients from the benthic primary production to higher trophic levels [95], through daily transitions between pelagic and reef systems. The enrichment of the pelagic ecosystem by nutrients from *M. niger* (and other link species) feces could contribute to the primary productivity. The process is similar to the "whale pump", in which marine mammals that feed at depth release fecal plumes near the surface, enhancing local primary productivity [27]. On the other hand, *M. niger* also feeds on zooplankton in the pelagic system [95,96], thus possibly transferring pelagic nutrients back to the reefs, by providing extra fertilization for the primary producers or by serving as prey. In fact, pelagic subsidies can make a substantial contribution to reef fish productivity [67], which would contribute to the high reef fish abundance and biomass found in the SPSPA, despite its remoteness and small area [6,32].

Maximum size and high mobility are key attributes that allow reef fish to colonize distant reefs [97], as well as make them important link among different habitats. Some large and highly mobile predators also perform constant migrations between pelagic and reef ecosystems, thus influencing the energy flux and dynamics in both systems [25,30]. However, due to the current low abundance of large predators recorded in the SPSPA, this important trophic link may have been replaced by mesopredators that are still abundant in the region. For instance, in SPSPA, *C. lugubris* feeds mainly on pelagic prey (e.g., small crustaceans and flying fish), as well as reef fish such as *Myripristis jacobus* Cuvier, 1829, *A. multilineata* and *A. saxatilis* [98]. Similarly, carangid species such as *C. crysos* and *S. rivoliana*, which are common in the SPSPA, have a diet based mainly on pelagic fish, but can also prey on a wide variety of demersal/reef fishes such as labrids, serranids, sparids, mullids and even gobies [96,99,100]. Even exclusive pelagic species also opportunistically prey on fish and other reef organisms in SPSPA, including resident reef predators [76–78]. Therefore, our findings hint at important connections between ecosystems and, consequently, point out ecological processes occurring through different species and trophic pathways (i.e., herbivory, planktivory, piscivory). Despite sustaining a low diversity reef

fish assemblage, these fish-mediated nutrient processes probably are critical to sustain the high biomass and the highly productive reef assemblages [101] of isolated reefs, even surrounded by oligotrophic oceanic waters.

5. Conclusions

The ecological connections between pelagic and mesophotic reef ecosystems inferred here based on species co-occurrences, as well as the endangered status of species found in both environments, suggest the need for an ecosystem integrated management strategy. The effectiveness of the very large MPA created in 2018, which includes only a tiny fraction of the SPSPA as a no-take zone [18,19], needs to be continuously evaluated, assessing the recovery of threatened species, such as the Galapagos shark, and further increasing knowledge on ecosystem connectivity presented here. This research shows the importance of protecting not only the fragile and unique reef ecosystem, but also the pelagic environment around the SPSPA. As fishing activities around the archipelago are affecting fish diversity and ecological processes [85], stricter fishing restrictions are suggested as the best alternative for biodiversity conservation and maintenance of critical ecological processes, to help the system resilience.

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