Article

When the Light Goes Out: Distribution and Sleeping Habitat Use of Parrotfishes at Night

Marcos Lucena [1], Thiago Costa Mendes [1], César Augusto Marcelino Mendes Cordeiro [1,2], Moysés Cavichiloli Barbosa [1], Jora Batista [3,4], Linda Eggertsen [1,5], Carlos W. Hackradt [4] and Carlos Eduardo Leite Ferreira [1,*]

1   Reef Systems Ecology and Conservation Lab, Universidade Federal Fluminense, Niterói 24020-141, RJ, Brazil; boucasdelucena@hotmail.com (M.L.); tcmendes@gmail.com (T.C.M.); cammcordeiro@gmail.com (C.A.M.M.C.); moysescb@gmail.com (M.C.B.); eggertsen.linda@gmail.com (L.E.)
2   Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes 28013-602, RJ, Brazil
3   Programa de Pós-Graduação em Sistemas Aquáticos Tropicais, Universidade Estadual de Santa Cruz, Ilhéus 45662-900, BA, Brazil; jorabatista@gmail.com
4   Marine Ecology and Conservation Lab, Centre for Environmental Sciences, Universidade Federal do Sul da Bahia, Porto Seguro 45810-000, BA, Brazil; hackradtcw@ufsb.edu.br
5   Hawaiian Institute of Marine Biology, University of Hawai'i at Manoa, Kaneohe, HI 96744, USA
*   Correspondence: carlosferreira@id.uff.br

Abstract: Understanding the diurnal and nocturnal activity of organisms is a key topic in behavioral ecology, with implications for population structure and management strategies. In reef systems, parrotfishes play crucial roles as nominal herbivores, but overfishing has led to population collapses with detrimental effects on reef functions. Parrotfish are good models to study diel rhythms, as they are often easily observed while sleeping at night. We assessed the distribution, sleeping substrate selectivity and sleeping areas of parrotfishes during the night in a subtropical rocky reef of the Southwestern Atlantic. We performed replicated visual censuses (50 × 2 m) at different depths to estimate parrotfish abundance, while quantifying the structural complexity of sleeping sites. Among the seven recorded parrotfish species, we focused on the four most abundant to determine their sleeping habitat selectivity. Active telemetry was used for the two most abundant species to define their sleeping site areas and sleeping hotspots. All four species exhibited a preference for sediment as a sleeping substrate, while avoiding zoanthids. Species distribution was influenced by depth, with *Scarus zelindae* predominantly sleeping in high-complexity substrate at intermediate depths and *Sparisoma tuiupiranga* sleeping in the rock–sand interface at deeper depths. Tagged *Sparisoma axillare* and *Sparisoma frondosum* exhibited similar sleeping areas in terms of size and geographical locations; showing high site fidelity, they returned to the same sleeping sites over consecutive nights. These results represent the first assessment of parrotfish distribution and habitat use at night in the Atlantic. This information is crucial for guiding management actions, particularly in the planning of no-take zones for fishing control and population recovery.

Keywords: nocturnal behavior; reef fish; sleeping site area; sleeping site fidelity

Key Contribution: Parrotfishes in subtropical reefs of the Southwestern Atlantic exhibit high site fidelity for sleeping sites; with different species choosing different reef substrates to sleep along a depth gradient.

1. Introduction

Reef fishes exhibit several behavioral characteristics that influence their population dynamics, distribution patterns and ecological interactions within reef ecosystems, including high site fidelity [1], long-term site attached behavior [2], territoriality [3] and

other complex behaviors [4]. These behaviors shape their affinity and reliance on the reef substrate, further impacting their ecological roles on reefs.

Most reef fish species are diurnal, being mainly active during the day [5]. This period of time is when they carry out most of their critical activities, such as feeding, breeding and several intra- and interspecific interactions (e.g., cleaning and agonistic interactions) [4]. In addition, several species exhibit circadian movements associated with migration, feeding and reproduction, which can have implications for ecosystem dynamics [6,7]. Thus, evaluating the temporal variation of the various activities performed by reef fish throughout day and night is essential to comprehensively understand their functional roles as well as to evaluate their spatial and temporal variability at different scales [8,9]. Ultimately, this information can provide valuable insights into species dynamics and functional ecology, providing critical information to prioritize effective initiatives of conservation and management.

Throughout the daily cycle of activities, species are subjected to diverse threats that vary in types and intensity. Anthropogenic impacts can affect species in a similar way during the day and night [10]. However, local impacts during specific periods can disrupt the circadian rhythms of some species. For example, nocturnal fishing activities in marine environments have been observed to alter the behavior of target species [11]. The escalating pressure of recreational and commercial nocturnal fishing [12], and the use of artificial lights are some of the major threats to nocturnal marine life [11]. Unfortunately, general information on behavior and, more specifically, on habitat use by reef fish at night is scarce [9,13–15], mainly due to logistical difficulties in data acquisition.

Herbivorous reef fishes are considered key species in reef ecosystems due to their comparatively high biomass and their intense grazing activity, which can influence the distribution and composition of the benthic community at various scales [16,17]. Parrotfishes (family Labridae, subfamily Scarinae) are among the most ubiquitous components of fish assemblages in tropical and subtropical reefs [18,19]. Their specialized feeding morphology allows them to graze on both biogenic and non-biogenic substrates in search of microscopic photoautotrophs [20–22], thereby contributing to successional dynamics of epilithic and endolithic biota.

In recent decades, the overexploitation of top predators in reef systems around the world has promoted an increase in the spearfishing of large herbivorous fish, including numerous parrotfish species [19,23–26]. The removal of these large parrotfishes has resulted in the disruption of critical functions and changes in ecosystem dynamics [27–29]. For instance, *Scarus trispinosus*, the largest endemic parrotfish on the Brazilian coast, is now considered functionally extinct in certain regions at its southern limit of distribution due to intensive spearfishing pressure [19,25]. One of the reasons for this is the sleeping behavior of many parrotfish species, which involves resting in exposed substrate rather than seeking shelter, making them particularly vulnerable to night spearfishing activities. Indeed, night spearfishing has been reported as an important driver of population decrease for various parrotfish species around the world [25,26,30–34].

To optimize conservation initiatives focused on parrotfish species, it is crucial to comprehensively understand not only their diurnal behavior and distribution [2,35], but also their habitat use and distribution at night. Night time is when these species are most vulnerable to fishing and studying them during this period will provide crucial information to promote parrotfish conservation [36]. Our objective was to investigate the abundance and spatial distribution patterns of parrotfish species, with a special focus on their fidelity of sleeping site and selectivity for particular reef substrates during nighttime. We worked in subtropical rocky reefs of the Southwestern Atlantic, using a combination of underwater visual census and active acoustic telemetry during nocturnal periods. The obtained information will help managers define areas of high habitat quality for sleeping sites to include those in no-take zones.

2. Methods

2.1. Study Site

The study sites are located within the Marine Extractive Reserve of Arraial do Cabo (Figure 1), which was established in 1997, in the state of Rio de Janeiro, Brazil (22°57′57″ S, 42°01′40″ W). This Extractive Reserve consists of a partially protected area where only local fishermen are allowed to exploit resources. However, no-take zones are absent in this reserve and enforcement is poorly employed, with different sorts of fishing gear being used, including spearfishing [25]. Local reefs consist of shallow granitic rocky shores with depths reaching a maximum of 12 m. Benthic cover is dominated by epilithic algae and zoanthids, with sponges and a few massive and branching coral species [37–39]. The region lacks significant freshwater inputs, with low precipitation (<850 mm year^{-1}, [40]) resulting in good visibility (~8 m) throughout most of the year.
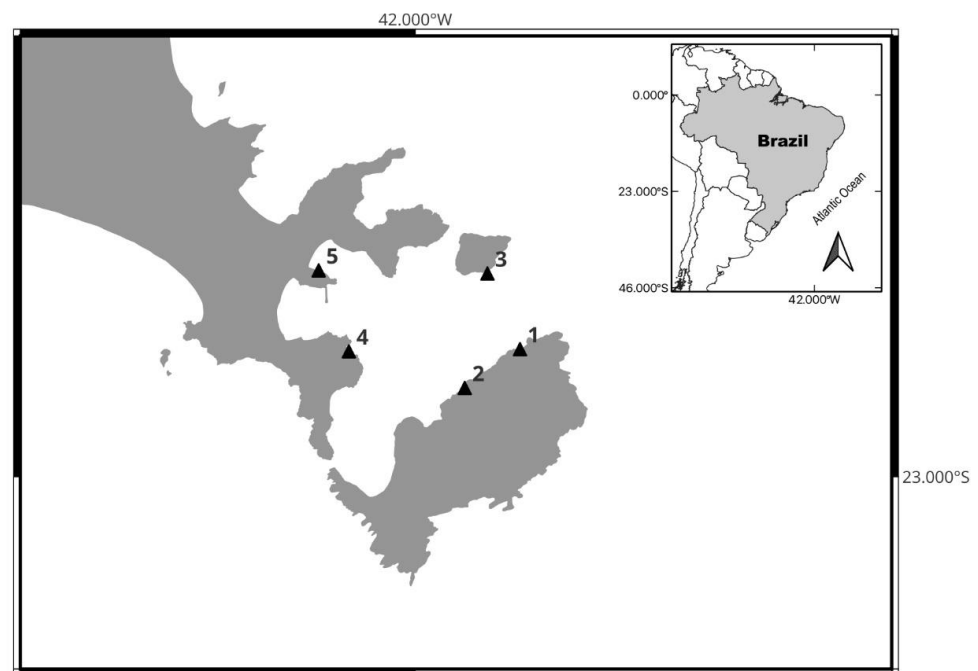

Figure 1. Map of the study area, with the sampling sites. 1 = Anequim, 2 = Pedra Vermelha, 3 = Ilha dos Porcos, 4 = Saco do Gato, 5 = Forno.

2.2. Parrotfish Spatial Distribution at Night

Fieldwork to assess the spatial distribution of parrotfishes at night was conducted over two periods: April to may 2017 and April to may 2018, each lasting 40 days. Nocturnal underwater sampling commenced one hour after sunset and was concluded before 11 pm, encompassing depths ranging from 1.5 to 12 m. We performed 126 underwater visual censuses (UVCs) using replicated strip transects measuring 50 m long and 2 m wide (100 m^2). We surveyed five sites with a minimum of 25 replicated UVCs in each of them (Figure 1). The UVC method consists of identifying, counting and estimating the size (total length in cm) of all parrotfish observed along each transect. We used flashlights with no color filters during surveys, as they have been shown not to influence the assessment of the local reef fish assemblages at night [41]. Additionally, we recorded the depth and topographic complexity in each transect. Three habitats were classified according to their depth strata: shallow (<4 m), slope (4–8 m) and the interface between reef and sand (8–12 m). Topographic complexity was classified in three categories adapted from [37]: high (large boulders and holes > 1 m in size and height), medium (predominance of small boulders and holes < 1 m in size and depth) and low (few and small boulders and holes, <10 cm).

2.3. Sleeping Substrate Selectivity

We conducted an assessment of the sleeping substrate selectivity for the most abundant parrotfish species in the area, namely *Sparisoma axillare* (Steindachner, 1878), *Sparisoma frondosum* (Agassiz, 1831), *Sparisoma tuiupiranga* Gasparini, Joyeux, and Floeter, 2003 and *Scarus zelindae* Moura, Figueiredo, and Sazima, 2001 (Figure 2). We actively searched for sleeping individuals and recorded the type of substrate each was using. We also recorded the substrate availability by assessing the substrate at four points located 90° apart from each other around a center point (i.e., the sleeping parrotfish) and 30 cm away from this central point. Therefore, the substrate just below each individual parrotfish was used to characterize sleeping substrate, while the substrate at the four other points was used to characterize substrate availability. Substrate type was classified into the following categories: *Codium* spp., *Sargassum* spp., *Dictyota* spp., other macroalgae, crustose coralline algae (CCA), epilithic algal matrix (EAM), *Millepora alcicornis*, *Mussismilia hispida*, *Phyllogorgia dilatata*, *Siderastrea stellata*, *Palythoa caribaeorum*, *Tubastraea* spp., *Aplysina* spp. and encrusting sponges. Non-biogenic substrates were classified as sediment or bare rock. Finally, we recorded the use of shelter by each sleeping individual as: low (totally exposed), medium (partially protected by topography) and high (sheltered, protected by topography on more than two sides), and a graphical representation of the data (heatmap) where the individual, topographic and habitat values, contained in a matrix, are represented as colors using the R package pheatmap 1.0.10.

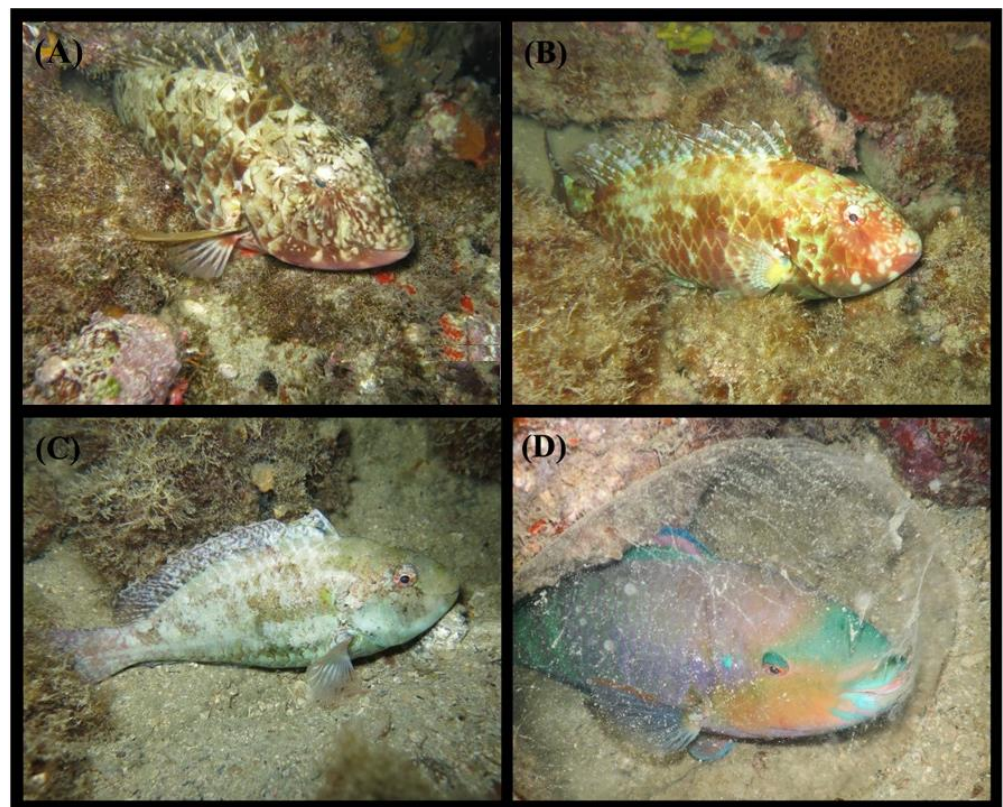**Figure 2.** Examples of the four most abundant parrotfish species during inactivity: (**A**) *Sparisoma axillare* (initial phase); (**B**) *Sparisoma frondosum* (terminal phase); (**C**) *Sparisoma tuiupiranga* (terminal phase); and (**D**) *Scarus zelindae* (terminal phase).

During observations, divers maintained a minimum distance of one meter from the fish to minimize disturbance and avoid awakening the individuals [42].

2.4. Sleeping Site Area and Sleeping Hotspots—Acoustic Telemetry

We used active acoustic telemetry techniques to determine sleeping site area and sleeping hotspot of *S. frondosum* and *S. axillare*. We used these two species as models due to their size suitability for transmitter implantation and their higher abundances in the region [43]. Tracking activities were restricted to nighttime hours when parrotfish were inactive, estimating the sleeping site area over 3–5 consecutive days. We captured individual fish while sleeping by using hand nets and SCUBA diving at nine distinct sites between March 2018 and August 2019. Upon capture, the individuals were brought to the boat and carefully placed on a tray containing seawater for transmitter implantation. The total length (TL) of all individuals was measured to the nearest millimeter. The area between the pelvic fins was sterilized, and a 10 mm incision was made to insert a sterilized transmitter (V9-2H, VEMCO Ltd, Halifax, NS, Canada) in the peritoneal cavity. After surgery, each individual was transferred to a seawater tank for a rehabilitation period of at least 10 min. After this recovery phase, tagged individuals were released by divers in the same location where they were initially collected. No tagging-induced mortality was recorded, and all tagged individuals exhibited normal swimming behavior within 24 h following tagging.

Active tracking was conducted using a multidirectional hydrophone and a calibrated receiver (VH110, VEMCO Ltd, Halifax, NS, Canada) from a 4.8 m inflatable boat. The receiver was able to detect six different frequencies emitted by the transmitters (60, 63, 75, 78, 81 and 84 kHz). Consequently, the maximum number of individuals that could be simultaneously tagged in a single location was limited to six. The battery of each tag lasted for 7–10 days. During the tracking observations, the position of the boat was adjusted to optimize the signal strength, ensuring recording over 80 dB, which indicated that the tagged individuals were within a five-meter range from the boat.

Prior to the first night of tracking, a diver observed the behavior of tagged fish in response to boat noise, specifically searching for signs of escape responses. The presence of the boat did not influence the sleeping behavior of the tagged parrotfish, as they remained stationary during the nocturnal tracking activities. Tracking of each individual started more than 24 h after tagging, allowing time for recovery. Once a tagged fish was detected, continuous tracking was conducted for at least 10 min to confirm its lack of activity. Throughout the following nights, the tagged fish were searched for in all sites until the batteries of the transmitters were depleted. If a tagged fish was not found during the search, we assumed that high structural complexity could have impeded signal reception. All tracking started 60 min after sunset, when it was expected that the parrotfish had already returned to their sleeping sites.

2.5. Data Analysis

Parrotfish density was compared among sites through one-way analysis of variance (ANOVA), followed by a Tukey post-hoc test to determine specific differences among sites. To assess the composition of parrotfish spatial distribution across depth strata, topographic complexity and sites, we used a Permutational Multivariate Analysis of Variance (PERMANOVA; with 999 permutations) based on a Bray–Curtis dissimilarity matrix using density data as the response variable. To visualize the spatial distribution of parrotfish density among sites, we performed a non-metric multidimensional scaling (nMDS) using each UVC as a replicate. PERMANOVA and nMDS were performed with the functions "adonis" and "metaMDS", respectively, with the package "vegan" [44] in the software R (ver. 4.3.2).

The sleeping substrate selectivity of each species was evaluated using Ivlev's electivity index [45,46]. This index is calculated as $E_i = (r_i - p_i)/(r_i + p_i)$, where r_i is the proportion of substrate i used to sleep on and p_i is the availability of the substrate i. The electivity index values vary from -1.0 to $+1.0$, with positive values indicating preference, negative values indicating avoidance and values close to 0 indicating that the use of a given substrate is proportional to its availability. To determine the significance of substrate selectivity, we

calculated the 95% confidence interval benthic category of each parrotfish species. If the 95% CI did not cross zero, we considered the benthic substrate to be statistically significantly considered either positively or negatively by the species. To verify similarities in the use of sleeping substrates among species, we performed a cluster analysis using Euclidean distance with complexity (high, medium and low) and habitat type (interface, slope and shallow) grouped in categories. By clustering the substrates, we could identify patterns of substrate preference or avoidance shared among the different parrotfish species.

To evaluate whether parrotfishes displayed sleeping homing behavior by returning to their capture site after displacement, we estimated the sleeping site area using kernel utilization distribution (KUD) analysis. KUD calculates relative probability of where the fish will be found during a given time [47]. Only individuals recorded on at least two non-consecutive nights were considered in the analyses of sleeping site area. We used the 50% KUD to identify fish sleeping hotspots (i.e., the areas where fish were likely to sleep in 50% of cases) and the 95% KUD to calculate the core area of the animals' sleeping site area. KUDs were calculated for each individual based on the total number of tracking positions. Analyses were performed with the R software and executed with the package "adehabitatHR" [48].

Data on the homoscedasticity of sleeping site areas and sleeping hotspots (95% and 50% KUD, respectively) were assessed with Fisher's F-test ($F_{17,22} = 20.86$, $p > 0.05$; $F_{17,22} = 9.16$, $p > 0.05$). We then used a Student's two-sample *t*-test to check for significant differences in KUD area between parrotfish species. The relationship between sleeping site area (based on 95% KUD) and fish body size (TL) was assessed with a Pearson correlation test as the assumption of normality for parametric correlation evaluations was confirmed by the Shapiro–Wilk normality test.

3. Results

3.1. Composition and Spatial Distribution of Parrotfish at Night

We recorded seven parrotfish species during the UVCs: *Sparisoma axillare*, *Sparisoma frondosum*, *Sparisoma tuiupiranga*, *Sparisoma radians* (Valenciennes, 1840), *Sparisoma amplum* (Ranzani, 1841), *Scarus zelindae* and *Scarus trispinosus* (Valenciennes, 1840). The most abundant species was *S. frondosum* (35% of the total abundance), followed by *S. tuiupiranga* (27%) and *S. axillare* (25%). *Scarus trispinosus* and *S. amplum* were found in less than 1% of transects, corresponding to 0.02% and 0.01% of the total number of recorded individuals, respectively. Among the four most abundant species, the only species that showed significant statistical difference among sites was *S. frondosum*, which was more abundant at Ilha dos Porcos than Saco do Gato (ANOVA, F = 3.292, *p*(>F) = 0.015; Tukey HSD, *p* = 0.006) (Figure 3).
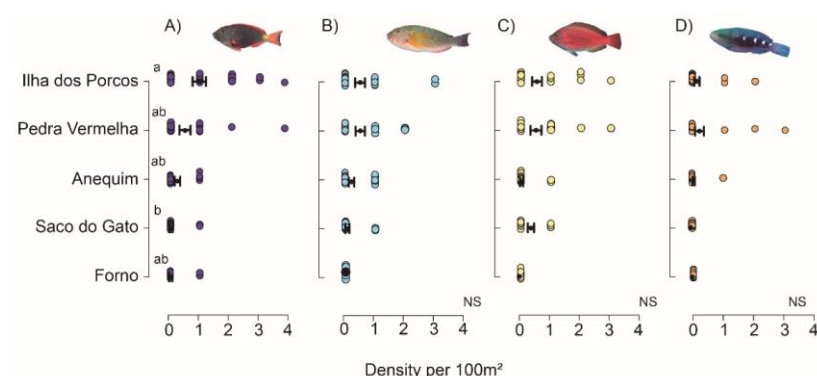

Figure 3. Density (individuals / 100 m²) of the four most abundant parrotfish species on the studied sites: (**A**) *Sparisoma frondosum*; (**B**) *Sparisoma axillare*; (**C**) *Sparisoma tuiupiranga* and (**D**) *Scarus zelindae*. Color dots represent transect values, black dots are mean, bars indicate standard error and letters indicate homogeneous groups from Tukey's HSD test.

Depth was the most important environmental factor influencing the composition and distribution of parrotfish spatial distribution along the rocky reef at night (PERMANOVA, $R^2 = 0.04$, P = 0.03), whereas topographic complexity was not significant ($p > 0.05$) (Table S1). Most species showed higher abundances at intermediate depth, while *Sparisoma tuiupiranga* was significantly more abundant in the deeper strata of the rocky reef (Figure 4).
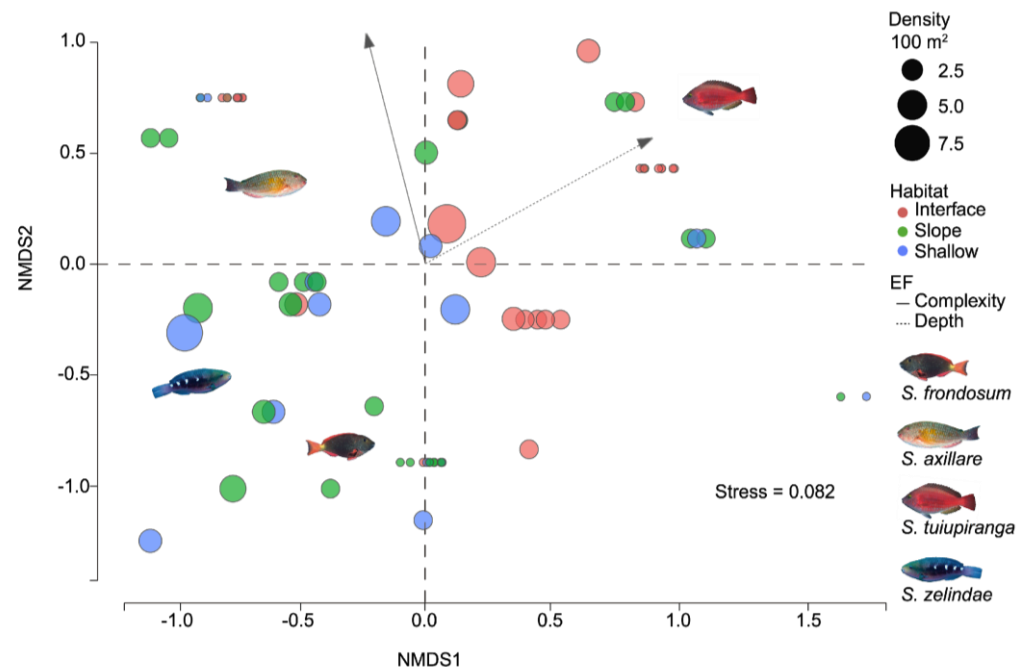

Figure 4. Non-metric multidimensional scaling of parrotfish density (individuals/100 m^2) at night among depth strata (habitat) and reef complexity. Vectors indicate the environmental factors (EFs) of depth and complexity. Fish images are located in the centroid of their position in the multivariate space; size of circles represent total species density, and length of arrows represent the strength of each variable.

3.2. Sleeping Substrate Selectivity

We registered 192 sleeping parrotfish: 54 *S. frondosum*, 63 *S. axillare*, 52 *S. tuiupiranga* and 23 *S. zelindae*. All species used the substrate similarly, selecting sediment as their preferred substrate, and avoiding *Palythoa caribaeorum* (Figure 5). Additionally, *S. axillare* avoided *Millepora alcicornis* and *Siderastrea stellata* (Figure 5B), *S. tuiupiranga* avoided *Sargassum* spp. (Figure 5C) and *S. zelindae* avoided *S. stellata* (Figure 5D).

Sleeping substrate preferences varied among species in terms of topographic complexity and habitat (depth). Both *S. frondosum* and *S. axillare* used all three habitats in similar proportions for sleeping (Figure 5F), with a higher frequency in areas of low and medium structural complexity (Figure 5E). In contrast, *S. zelindae* individuals predominantly selected sleeping areas with high topographic complexity, usually within crevices (Figure 5E). *Sparisoma tuiupiranga* was more frequently observed sleeping on the interface (61.54%), while *S. zelindae* was primarily observed sleeping in the slope (medium depth) (60.87%) (Figure 5F).

3.3. Sleeping Site Area and Sleeping Hotspots—Acoustic Telemetry

We successfully captured and tagged 39 *S. axillare* and 25 *S. frondosum*. However, only 23 *S. axillare* (mean TL = 408 mm; range 312–500 mm) and 18 *S. frondosum* (mean TL = 363 mm; range 310–432 mm) were registered in more than two consecutive nights and were included in the final analyses (Table 1). We found no difference in 95% KUD (t = 1.52, df = 39, *p* = 0.14) nor 50% KUD (t= 1.48, df = 39, *p* = 0.15) between *S. axillare* and *S. frondosum* (Figure 6). The sleeping site area (95% KUD estimates) of *S. axillare* ranged

from 0.14 to 208.8 × 10³ m² with an average of 25.93 ± 10.15 × 10³ m² (mean ± SE), and *S. frondosum* ranged from 0.057 to 70.38 × 10³ m² with an average of 8.15 ± 3.79 × 10³ m² (mean ± SE) (Table 1). There was no relationship between fish size (TL) and sleeping site area for *S. axillare* (*r* = 0.19, *p* = 0.38) or *S. frondosum* (*r* = −0.38, *p* = 0.13).

Figure 5. Sleeping substrate selectivity (Ivlev's index) for (**A**) *Sparisoma frondosum*; (**B**) *Sparisoma axillare*; (**C**) *Sparisoma tuiupiranga* and (**D**) *Scarus zelindae* (Values are means ± 95% confidence interval (CI), red dots mean that CI did not cross zero value). Heatmap of the four most abundant parrotfishes in the study area representing the species distribution by (**E**) topographic complexity (low, medium and high) and distribution by (**F**) habitat (shallow, slope and interface).

Figure 6. Sleeping site area and sleeping hotspots of (**A**) 23 *Sparisoma axillare* and (**B**) 18 *Sparisoma frondosum*, tracked with active acoustic telemetry in Arraial do Cabo. Darker colors represent 95% kernel utilization distributions (KUDs) (sleeping site area) and lighter colors represent 50% KUDs (sleeping hotspots). Non-significant values (NS) are shown between respective KUD values and between species. Data were log-transformed for better visualization.
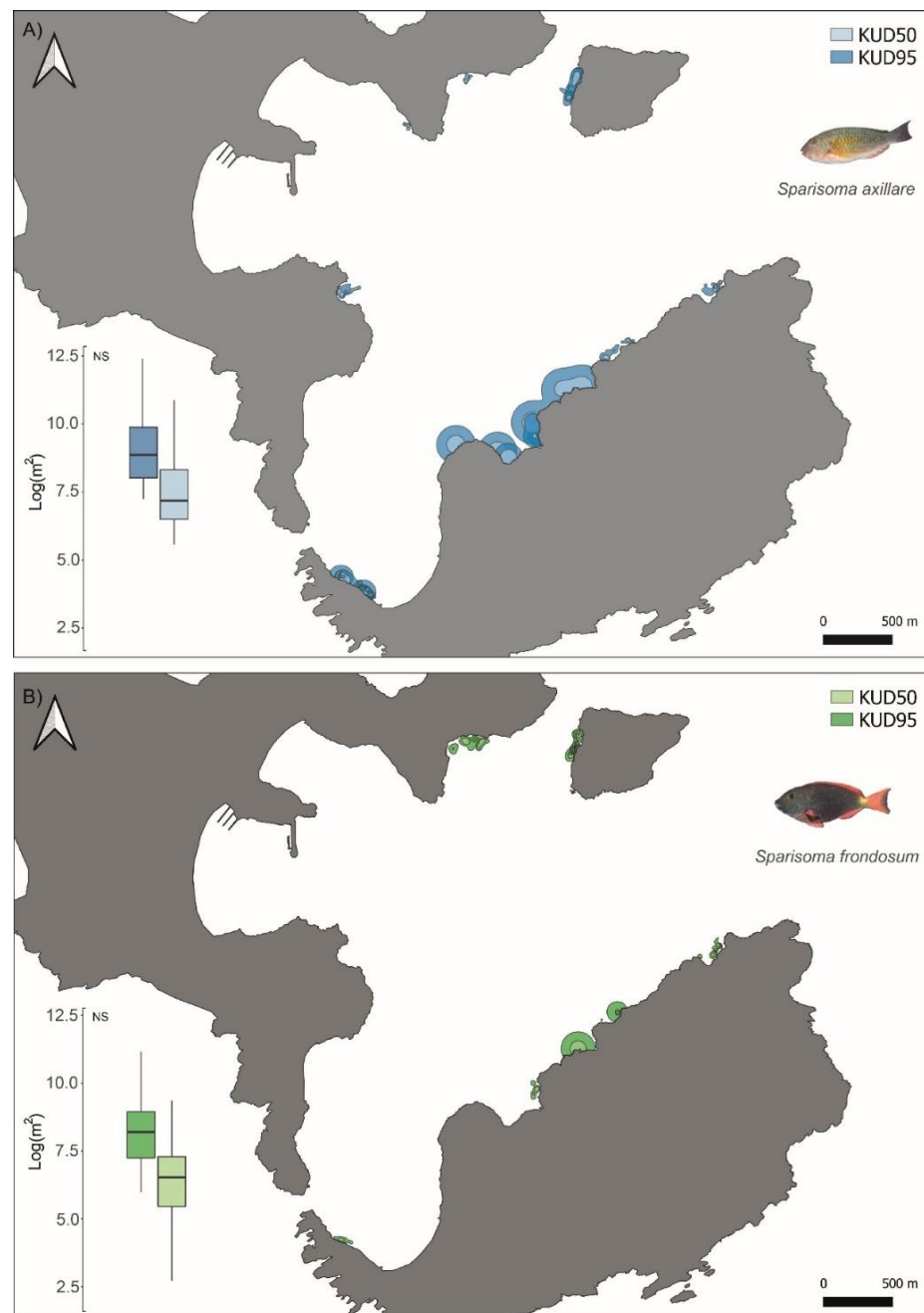
Table 1. Summary of sleeping site areas (KUD 95) and sleeping hotspots (KUD 50) of *Sparisoma axillare* and *Sparisoma frondosum* tagged with a V9-2H continuous transmitter. Values are average ± standard error.

Fish ID	TL (mm)	95% KUD (10^3 m^2)	50% KUD (10^3 m^2)	50:95 UD Ratio
Sparisoma axillare	407.65 ± 43.27	25.93 ± 10.15	5.86 ± 2.56	21.14 ± 0.8
Sparisoma frondosum	363.9 ± 42.9	8.15 ± 3.79	1.45 ± 0.62	19.81 ± 0.83

Sleeping hotspots (50% KUD) represented 21.14 ± 0.8% of the sleeping site area (95% KUD) for *S. axillare* individuals and 19.81 ± 0.83% for *S. frondosum* individuals. These values were calculated as 5.86 ± 2.56 × 10^3 m^2 (mean ± SE) and 1.45 ± 0.62 × 10^3 m^2 for *S. axillare* and *S. frondosum*, respectively (Table 1 and Table S2). Individuals of *S. axillare* (65.22%) showed mainly two cores of sleeping hotspots, while 61.11% of *S. frondosum* had one core sleeping hotspot (Table 1 and Figure 6).

4. Discussion

Our study presents unique findings regarding the distribution and sleeping habits of parrotfishes at night, achieved by combining underwater visual censuses, behavioral observations and acoustic telemetry. There is clear evidence of distinct nocturnal distribution patterns among studied parrotfish species in these reefs, with depth being the primary driver. The four most abundant species consistently select non-biogenic substrates, such as sediment patches, for resting during the night, while avoiding zoanthids. The only *Scarus* species included in the study (*S. zelindae*) was frequently observed sleeping in high-complexity substrates, while the smallest species, *S. tuiupiranga*, was frequently found at the reef–sand interface. The two tagged *Sparisoma* species (*S. frondosum* and *S. axillare*) displayed strong site fidelity to their respective sleeping areas over consecutive nights, exhibiting similar-sized sleeping site areas and sleeping hotspots.

4.1. Composition and Spatial Distribution of Parrotfish at Night

During their life cycle, different parrotfishes explore a diverse set of shallow habitats, from sandy vegetated areas to mangroves and reefs [18,49], feeding on epilithic and endolithic microscope photoautotrophs [20,50]. Several factors can influence the diurnal distribution of parrotfishes, such as algal species composition and benthic cover [51–54], wave action and water temperature [43,51], reef structural complexity [36,55], depth [43,53] and reef zone [55]. In the Caribbean, topographic reef complexity is positively correlated with parrotfish abundance, providing increased niche availability, refuge and food resources [56]. Habitat preferences in parrotfish seem to be established during the settlement and recruitment period [56], but habitat utilization is also influenced by ontogenetic shifts in some species [57,58].

Our results indicate that reef complexity only weakly explained the occurrence and density of parrotfish species during the night. The rocky reefs in our study area mainly consist of rocks and boulders of varying sizes, forming crevices through their arrangement [37]. The presence of milleporids (*Millepora alcicornis*), gorgonians (*Phyllogorgia dilatata*) and sponges can enhance rugosity when present [38]. Although such complexity varies across depth, habitats and sites [43], and influences the dynamics of fish and mobile invertebrates, it had no significant effect on parrotfish distribution during the night, which corroborates findings on parrotfish sleeping sites in a deeper reef gradient in the Red Sea [15]. Apart from *S. zelindae*, which exhibited a preference for sleeping in crevices, the other species showed less selectivity for specific sleeping substrates. Indeed, they remain partially or entirely exposed during the night, rendering them especially vulnerable to spearfishing.

Depth is considered an important factor influencing the structure of reef fish assemblages during the day [59]. In addition, wave exposure influences fish composition through physical disturbances [56], affecting the mobility and foraging behavior of several fish species [60,61]. Although these drivers play an important role in shaping the dynamics of parrotfish during the day [43], they may not necessarily serve as reliable predictors for site and habitat selection during rest periods [15,36]. Previous studies in Arraial do Cabo have shown that parrotfish are absent from areas with stronger upwelling and higher wave surge [43]. In our study, depth influenced the distribution of one parrotfish species, with sleeping *Sparisoma tuiupiranga* being significantly more abundant in the deeper regions. Similarly, *Scarus ovifrons* from Japan use deeper habitats to sleep during the night, habitats different from those used for their usual behavior during the day [62]. Parrotfish species can exhibit niche partitioning during both day and night to avoid potential competition

and seek refuge from predators [2], although such patterns need further geographical comparisons [15].

We did not observe any juvenile parrotfish during our night surveys, due to cryptic behavior of seeking refuge in crevices and holes, which differ from most adults [63,64]. Although there is limited information on the habitat use of juvenile parrotfish in the Southwestern Atlantic [52,65], macroalgae beds are important habitats for juveniles of several reef fish species during the day and it is likely that juvenile parrotfish use them as sleeping habitats [65].

4.2. Sleeping Substrate Selectivity

The presence and availability of suitable sleeping sites have been suggested as factors influencing fish distribution and resulting in differences in assemblage structure [2,66]. Consequently, it would be expected that species would exhibit spatial partitioning, or highly selective behaviors of sleeping habitats, to facilitate coexistence. In the Gulf of Aqaba, some species were indicated to show intraspecific variability in sleeping site selection; however, among the seven species considered, most species exhibited substantial overlap in site characteristics [15]. On the other hand, Nanami et al. (2024) [36] found species-specific significant positive associations with particular architectural characteristics for some parrotfish species in reefs of Okinawa.

Our results, considering only the four most abundant species, indicate some degree of similarity in the selectivity and avoidance of sleeping substrate (interspecific similarity), also suggesting that habitat utilization during the night might not be the major factor driving the coexistence of parrotfish species. Welsh and Bellwood (2012) [2], working in the Great Barrier Reef with only one species (*Chlorurus microrhinos*), suggested niche partitioning as a major strategy employed by parrotfish to avoid potential competition during the day. All four species studied avoided *Palythoa caribaeorum*, potentially due to the presence of abundant mucus and nematocysts present in this zoanthid [67]. In addition, all species used the EAM as a sleeping substrate based on its availability. The EAM is known to harbor a myriad of cryptic invertebrates [68], and may serve as a potential source of ectoparasite contamination (e.g., gnathids and caligids) [69]. Hematophagous gastropods that inhabit coral and rocky environments in tropical, subtropical and temperate seas have been reported to parasitize gobies [70], rabbitfishes [71] and parrotfishes [72,73] during the night. Together, *P. caribaeorum* and EAM represent over 70% of the benthic cover in our study sites [43,74], therefore limiting the availability of other preferred sleeping substrates for parrotfish.

Sparisoma tuiupiranga, the smallest species in the reefs studied (25 cm TL—total length), was frequently observed at the rocky/sand interface, sleeping over sand in close proximity to sponges and gorgonians. This behavior is similar to that reported for its congener, *Sparisoma aurofrenatum*, in the Caribbean [75]. Parrotfish sleeping in open areas could be an alternative to reduce predation risk while providing easier escape from predators (e.g., [76–78]). Further, it is possible that the ability of *S. tuiupiranga* to camouflage within its sleeping habitats contributes to this behavior (Figure 2C).

Scarus zelindae was often registered sleeping in high-complexity substrates such as holes and crevices. This species is the only one among the study species to produce a mucous cocoon [79], which serves as a protective barrier against predators and ectoparasites [33] (Figure 2D). By associating with high-complexity areas, *S. zelindae* mitigate the potential damage effects of water flow on its mucus cocoon [75], as well as reduce their risk of predation [80,81].

4.3. Sleeping Site Area and Sleeping Hotspots

Fidelity for sleeping sites has been widely studied in terrestrial organisms, such as non-human primates, which exhibit a strong avoidance of sleeping sites with a high risk of predation [76,82], plus abundance and distribution of food sources [82]. Parrotfishes on average sleep 13 h a day [2], which means that half of their lives are dedicated to resting in

their preferred sleeping sites. This significant amount of time spent sleeping, coupled with their increased vulnerability to predators and parasites during the night [6,71], underscores the critical importance of finding suitable substrate.

Across tropical and temperate reef systems, researchers have estimated parrotfish home ranges to determine the appropriate size of marine protected areas (MPAs) [2,35,83–87]. The diurnal movement and territorial behavior of parrotfish have been studied using both active and passive acoustic telemetry methods [2,35,83,86–89]. Daytime home ranges estimates varied from 7.83×10^3 m^2 for *Chlorurus microrhinus* in the Great Barrier Reef (active telemetry—[2]) to 124.7×10^3 m^2 for *Sparisoma cretense* in the Mediterranean (passive telemetry—[86]). Moreover, fish in enclosed bays can exhibit different movement patterns compared to those in open coastlines [87], highlighting the need for cautious comparisons between distinct seascapes using different methods.

The diurnal area used by parrotfishes in the subtropical reefs studied (mean 50×10^3 m^2) (Batista et unpublished data) was on average twice the sleeping area of *Sparisoma axillare* (25.93×10^3 m^2) and six times the sleeping area of *Sparisoma frondosum* (8.15×10^3 m^2). There is limited knowledge about the size, location and factors that determine the sleeping area of the majority of parrotfish species [88,89]. In Hawaii, *Scarus rubroviolaceus* was observed to engage in long migrations at dusk, likely related to the search for resting sites [87]. In the mediterranean, *Sparisoma cretense* exhibited a diurnal home range larger than its nocturnal sleeping areas (70.39 to 256.40×10^3 m^2 = diurnal; 30.16 to 92.20×10^3 m^2 = nocturnal), although no significant statistical differences were found [86]. As expected, our results show that parrotfishes in subtropical reefs exhibit comparatively smaller sleeping site areas to their diurnal home range. During the survey period, neither of the tagged species (*S. axillare* and *S. frondosum*) changed their sleeping site areas, although they utilized multiple sleeping hotspots (50% KUD). These findings suggest that benthic community structure and habitat features can operate at a fine scale to determine the selection of sleeping areas in parrotfishes. Parrotfishes tend to sleep in the same general area each night, but might use different hotspots within that area if sufficient preferred habitat features are present [75].

4.4. Management Implications

Our results highlight the importance of studying nocturnal spatial use by fish, particularly for species vulnerable to spearfishing at night such as large parrotfishes [30,31,34]. Given their importance for the maintenance of reef health across various scales [1], parrotfish have been increasingly protected in several countries [90]. While parrotfishes have historically been a common target for fishing in many parts of the world, [28,29,34,90–92], management and conservation of endemic parrotfishes in Brazil are still in development [93]. They became targeted species in Brazil following the declines of top predator populations, especially during the 1980s and 1990s [19,25,94,95]. Today, several Brazilian parrotfish species are highly threatened by fishing activities [95], but the lack of scientific information on temporal fisheries hinders effective management. Among these species, the status of the largest and endemic Brazilian parrotfish, *Scarus trispinosus*, is particularly critical as it is currently classified by the IUCN as endangered with a declining population trend [96]. For the subtropical reefs studied, this species is considered functionally extinct due to intense spearfishing over the past few decades [25]. Indeed, a recent study concluded that *S. trispinosus* is one of the most endangered parrotfish species worldwide due to its slow growth and late sexual maturation [26]. During our surveys, we only recorded two individuals of *S. trispinosus* out of the 192 observed parrotfish individuals.

Currently, the total area of no-take marine protected areas established and effectively enforced along the Brazilian province is insufficient (aprox. 2.5%) to sustain the intense fishing pressure of parrotfish populations, particularly along the Brazilian coast [97]. This is more critical because several disproportionately important areas, which serve as sources for larval supply and replenishment for parrotfish populations, are poorly enforced or lack any protection status at all [26,98]. The establishment of MPAs on areas that effectively

protect the parrotfish species is crucial for the maintenance of their populations and the delivery of their functions on reefs. This is particularly critical in Brazilian waters, as we still lack a thorough understanding of the roles and functions performed by herbivorous fishes compared to those in Caribbean and Indo-Pacific reefs [1,39,99,100].

The data generated by this study may provide new information to explore the possibility of implementing more efficient fishing management tools in the study area, such as no-take zones. Parrotfishes and other species with high economic value have had their populations reduced in recent decades because of overfishing and lack of proper enforcement [19,25,101–103]. Protecting parrotfish populations is critical to maintaining the functioning of reef systems due to the various functions they deliver [1]. However, this group is highly vulnerable to spearfishing during the night [31,104,105], reinforcing the need to join data on home ranges and patterns of population structure [43] to support optimal initiatives of management and conservation. The data herein generated and data on diurnal home range (*S. axillare* and *S. frondosum*, unp. data) are expected to provide valuable support to inform management decisions regarding the establishment of no-take areas, still lacking in the study area, and necessary for the effective protection of populations of those large parrotfish.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes9100370/s1, Table S1: Comparative results of PERMANOVA for parrotfish species composition among depth, complexity and site at Arraial do Cabo. Table S2: Sleeping site area and sleeping hotspots data of 23 *Sparisoma axillare* and 18 *Sparisoma frondosum* tagged with a V9-2H continuous transmitter.

Author Contributions: Conceptualization, M.L. and C.E.L.F.; Methodology, M.L., T.C.M., M.C.B., J.B., C.W.H. and C.E.L.F.; Software, M.L.; Formal analysis, M.L.; Investigation, M.L., T.C.M., M.C.B. and C.E.L.F.; Resources, M.L.; Data curation, M.L.; Writing—original draft, M.L.; Writing—review and editing, M.L., T.C.M., C.A.M.M.C., M.C.B., L.E. and C.E.L.F.; Supervision, T.C.M. and C.E.L.F.; Funding acquisition, C.E.L.F. All authors have read and agreed to the published version of the manuscript.

Institutional Review Board Statement: This study was conducted in accordance with the Research ICMBio permits number 55911-3.

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors on request.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Bonaldo, R.M.; Krajewski, J.P.; Sazima, C.; Sazima, I. Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. *Mar. Biol.* **2006**, *149*, 423–433. [CrossRef]
2. Welsh, J.Q.; Bellwood, D.R. Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): An evaluation using acoustic telemetry. *Coral Reefs* **2012**, *31*, 55–65. [CrossRef]
3. Keeley, E.R. An experimental analysis of territory size in juvenile steelhead trout. *Anim. Behav.* **2000**, *59*, 477–490. [CrossRef]
4. Cantor, M.; Longo, G.O.; Fontoura, L.; Quimbayo, J.P.; Floeter, S.R.; Bender, M.G. Interaction Networks in Tropical Reefs. In *Ecological Networks in the Tropics*; Springer International Publishing: New York, NY, USA, 2018; pp. 141–154.
5. Mouillot, D.; Villéger, S.; Parravicini, V.; Kulbicki, M.; Arias-González, J.E.; Bender, M.; Chabanet, P.; Floeter, S.R.; Friedlander, A.; Vigliola, L.; et al. Functional over-redundancy and high functional vulnerability in global fish faunas on 683 tropical reefs. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 13757–13762. [CrossRef]
6. Helfman, G.S. Fish behaviour by day, night and twilight. In *The Behaviour of Teleost Fishes*; Springer: New York, NY, USA, 1986; pp. 366–387.

7. Nagelkerken, I.; Dorenbosch, M.; Verberk, W.C.E.P.; Cocheret de la Morinière, E.; van der Velde, G. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Mar. Ecol. Prog. Ser.* **2000**, *194*, 55–64. [CrossRef]

8. Brewin, P.E.; Brown, J.; Brickle, P. Diurnal variation of fish and macrobenthic invertebrate community structure in an isolated oceanic island of the South Atlantic. *J. Mar. Biol. Assoc. UK* **2016**, *96*, 737–747. [CrossRef]

9. Hinojosa, I.A.; Zapata-Hernández, G.; Fowles, A.E.; Gaymer, C.F.; Stuart-Smith, R.D. The awakening of invertebrates: The daily dynamics of fishes and mobile invertebrates at Rapa Nui's multiple use marine protected area. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **2020**, *31*, 290–303. [CrossRef]

10. Simpson, S.D.; Jeffs, A.; Montgomery, J.C.; McCauley, R.D.; Meekan, M.G. Nocturnal relocation of adult and juvenile coral reef fishes in response to reef noise. *Coral Reefs* **2008**, *27*, 97–104. [CrossRef]

11. Gaston, K.J. Nighttime ecology: The "nocturnal problem" revisited. *Am. Nat.* **2019**, *193*, 481–502. [CrossRef]

12. Pauly, D.; Zeller, D. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* **2016**, *7*, 10244. [CrossRef]

13. Lecchini, D. Highlighting ontogenetic shifts in habitat use by nocturnal coral reef fish. *C. R. Biol.* **2006**, *329*, 265–270. [CrossRef] [PubMed]

14. Azzurro, E.; Pais, A.; Consoli, P.; Andaloro, F. Evaluating day–night changes in shallow Mediterranean rocky reef fish assemblages by visual census. *Mar. Biol.* **2007**, *151*, 2245–2253. [CrossRef]

15. Pickholtz, R.; Kiflawi, M.; Buba, Y.; Chaikin, S.; Gavriel, T.; Lapid, G.; Lazarus, M.; Malamud, S.; Marom, N.; Marom, S.; et al. Confronting the nocturnal problem in coral reefs: Sleeping site selection and cocoon formation in parrotfishes. *Coral Reefs* **2023**, *42*, 811–825. [CrossRef]

16. Burkepile, D.E.; Hay, M.E. Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* **2011**, *30*, 351–362. [CrossRef]

17. Jessen, C.; Wild, C. Herbivory effects on benthic algal composition and growth on a coral reef flat in the Egyptian Red Sea. *Mar. Ecol. Prog. Ser.* **2013**, *476*, 9–21. [CrossRef]

18. Bonaldo, R.M.; Hoey, A.S.; Bellwood, D.R. The ecosystem roles of parrotfishes on tropical reefs. *Oceanogr. Mar. Biol. Annu. Rev.* **2014**, *52*, 81–132.

19. Floeter, S.R.; Halpern, B.S.; Ferreira, C.E.L. Effects of fishing and protection on Brazilian reef fishes. *Biol. Conserv.* **2006**, *128*, 391–402. [CrossRef]

20. Clements, K.D.; German, D.P.; Piché, J.; Tribollet, A.; Choat, J.H. Integrating ecological roles and trophic diversification on coral reefs: Multiple lines of evidence identify parrotfishes as microphages. *Biol. J. Linn. Soc.* **2017**, *120*, 729–751. [CrossRef]

21. Mendes, T.C.; Ferreira, C.E.L.; Clements, K.D. Discordance between diet analysis and dietary macronutrient content in four nominally herbivorous fishes from the Southwestern Atlantic. *Mar. Biol.* **2018**, *165*, 1–12. [CrossRef]

22. Nicholson, G.M.; Clements, K.D. Resolving resource partitioning in parrotfishes (Scarini) using microhistology of feeding substrata. *Coral Reefs* **2020**, *39*, 1313–1327. [CrossRef]

23. Mumby, P.J.; Dahlgren, C.P.; Harborne, A.R.; Kappel, C.V.; Micheli, F.; Brumbaugh, D.R.; Holmes, K.E.; Mendes, J.M.; Broad, K.; Sanchirico, J.N.; et al. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **2006**, *311*, 98–101. [CrossRef] [PubMed]

24. Edwards, C.B.; Friedlander, A.M.; Green, A.G.; Hardt, M.J.; Sala, E.; Sweatman, H.P.; Williams, I.D.; Zgliczynski, B.; Sandin, S.A.; Smith, J.E. Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. *Proc. R. Soc. B Biol. Sci.* **2013**, *281*, 20131835. [CrossRef] [PubMed]

25. Bender, M.G.; Machado, G.R.; De Azevedo Silva, P.J.; Floeter, S.R.; Monteiro-Netto, C.; Luiz, O.J.; Ferreira, C.E.L. Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the Southwestern Atlantic. *PLoS ONE* **2014**, *9*, e11033. [CrossRef]

26. Roos, N.; Taylor, B.; Carvalho, A.; Longo, G. Demography of the largest and most endangered Brazilian parrotfish, Scarus trispinosus, reveals overfishing. *Endanger. Species Res.* **2020**, *41*, 319–327. [CrossRef]

27. Bellwood, D.R.; Hoey, A.S.; Choat, J.H. Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. *Ecol. Lett.* **2003**, *6*, 281–285. [CrossRef]

28. Bellwood, D.R.; Hoey, A.S.; Hughes, T.P. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proc. R. Soc. B Biol. Sci.* **2012**, *279*, 1621–1629. [CrossRef]

29. Taylor, B.M.; Lindfield, S.J.; Choat, J.H. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography* **2015**, *38*, 520–530. [CrossRef]

30. Aswani, S.; Hamilton, R.J. Integrating indigenous ecological knowledge and customary sea tenure with marine and social science for conservation of bumphead parrotfish (*Bolbometopon muricatum*) in the Roviana Lagoon, Solomon Islands. *Environ. Conserv.* **2004**, *31*, 69–83. [CrossRef]

31. Donaldson, T.J.; Dulvy, N.K. Threatened fishes of the world: *Bolbometopon muricatum* (Valenciennes 1840) (Scaridae). *Environ. Biol. Fishes* **2004**, *70*, 373. [CrossRef]

32. Aswani, S.; Sabetian, A. Implications of Urbanization for Artisanal Parrotfish Fisheries in the Western Solomon Islands. *Conserv. Biol.* **2010**, *24*, 520–530. [CrossRef]

33. Grutter, A.S.; Rumney, J.G.; Sinclair-Taylor, T.; Waldie, P.; Franklin, C.E. Fish mucous cocoons: The "mosquito nets" of the sea. *Biol. Lett.* **2011**, *7*, 292–294. [CrossRef] [PubMed]

34. Taylor, B.M.; Houk, P.; Russ, G.R.; Choat, J.H. Life histories predict vulnerability to overexploitation in parrotfishes. *Coral Reefs* **2014**, *33*, 869–878. [CrossRef]

35. Welsh, J.Q.; Bellwood, D.R. How far do schools of roving herbivores rove? A case study using Scarus rivulatus. *Coral Reefs* **2012**, *31*, 991–1003. [CrossRef]

36. Nanami, A. Nocturnal substrate association of four coral reef fish groups (parrotfishes, surgeonfishes, groupers and butterflyfishes) in relation to substrate architectural characteristics. *PeerJ* **2024**, *12*, e17772. [CrossRef]

37. Ferreira, C.E.L.; Gonçalves, J.E.A.; Coutinho, R. Community structure of fishes and habitat complexity on a tropical rocky shore. *Environ. Biol. Fishes* **2001**, *61*, 353–369. [CrossRef]

38. Rogers, R.; de Oliveira Correal, G.; de Oliveira, T.C.; de Carvalho, L.L.; Mazurek, P.; Barbosa, J.E.F.; Chequer, L.; Domingos, T.F.S.; de Andrade Jandre, K.; Leão, L.S.D.; et al. Coral health rapid assessment in marginal reef sites. *Mar. Biol. Res.* **2014**, *10*, 612–624. [CrossRef]

39. Cordeiro, C.A.M.M.; Harborne, A.R.; Ferreira, C.E.L. The Biophysical Controls of Macroalgal Growth on Subtropical Reefs. *Front. Mar. Sci.* **2020**, *7*, 1–14. [CrossRef]

40. INMET. Instituto Nacional de Meteorologia—INMET (Brazilian Meteorological Institute). 2020. Available online: http://www.inmet.gov.br (accessed on 1 July 2020).

41. Lucena, M.B.; Mendes, T.C.; Barbosa, M.C.; Cordeiro, C.A.M.M.; Eggertsen, L.M.; Ferreira, C.E.L. Does the colors of light matter? Testing different light color in nocturnal underwater visual censuses. *Mar. Environ. Res.* **2021**, *166*, 105261. [CrossRef]

42. Itzkowitz, M.; Ludlow, A.; Haley, M. Territorial boundaries of the male beaugregory damselfish. *J. Fish. Biol.* **2000**, *56*, 1138–1144. [CrossRef]

43. Cordeiro, C.A.M.M.; Mendes, T.C.; Harborne, A.R.; Ferreira, C.E.L. Spatial distribution of nominally herbivorous fishes across environmental gradients on Brazilian rocky reefs. *J. Fish. Biol.* **2016**, *89*, 939–958. [CrossRef]

44. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Ouellette , M.-H.; Cunha, E.R.; Smith, T.; Stier, A.; et al. Vegan: Community Ecology Package. R Package Version 2.5–4. 2019. Available online: https://CRAN.R-project.org/package=vegan (accessed on 17 September 2024).

45. Zar, J.H. *Biostatistical Analysis*, 4th ed.; Prentice Hall: Upper Saddle River, NJ, USA, 1999.

46. Manly, B.F.J.; Thomas, D.L.; Mcdonald, T.L. *Resource Selection by Animals: Statistical Design an Analisys for Field Studies*, 2nd ed.; Springer: New York, NY, USA, 2002; 240p.

47. Worton, B.J. A review of models of home range for animal movement. *Ecol. Modell.* **1987**, *38*, 277–298. [CrossRef]

48. Calenge, C. *Home Range Estimation in R: The adehabitatHR Package*; Office National de la Classeet de la Faunesauvage: Auffargis, France, 2019.

49. Harborne, A.R.; Mumby, P.J.; Micheli, F.; Perry, C.T.; Dahlgren, C.P.; Holmes, K.E.; Brumbaugh, D.R. The Functional Value of Caribbean Coral Reef, Seagrass and Mangrove Habitats to Ecosystem Processes. *Adv. Mar. Biol.* **2006**, *50*, 57–189. [PubMed]

50. Cardozo-Ferreira, G.C.; Ferreira, C.E.L.; Choat, J.H.; Mendes, T.C.; Macieira, R.M.; Rezende, C.E.; Joyeux, J.C.; Clements, K.D. Seasonal variation in diet and isotopic niche of nominally herbivorous fishes in subtropical rocky reefs. *Mar. Ecol. Prog. Ser.* **2023**, *722*, 125–143. [CrossRef]

51. Guidetti, P.; Boero, F. Spatio-temporal variability in abundance of the parrotfish, *Sparisoma cretense*, in SE Apulia (SE Italy, Mediterranean Sea). *Ital. J. Zool.* **2002**, *69*, 229–232. [CrossRef]

52. Feitosa, J.L.L.; Ferreira, B.P. Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs. *Mar. Ecol.* **2014**, *36*, 462–474. [CrossRef]

53. Hernández-Landa, R.C.; Acosta-González, G.; Núñez-Lara, E.; Arias-González, J.E. Spatial distribution of surgeonfish and parrotfish in the north sector of the Mesoamerican Barrier Reef System. *Mar. Ecol.* **2015**, *36*, 432–446. [CrossRef]

54. Carlson, P.M.; Davis, K.; Warner, R.R.; Caselle, J.E. Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. *Mar. Ecol. Prog. Ser.* **2017**, *577*, 165–176. [CrossRef]

55. Roos, N.C.; Pennino, M.G.; Carvalho, A.R.; Longo, G.O. Drivers of abundance and biomass of Brazilian parrotfishes. *Mar. Ecol. Prog. Ser.* **2019**, *623*, 117–130. [CrossRef]

56. Harborne, A.R.; Mumby, P.J. FAQs about Caribbean Parrotfish Management and their Role in Reef Resilience. In *Biology of Parrotfishes*; CRC Press: Boca Raton, FL, USA, 2018.

57. Chen, L.S. Post-settlement diet shift of *Chlorurus sordidus* and *Scarus schlegeli* (Pisces: Scaridae). *Zool. Stud.* **2002**, *41*, 47–58.

58. Smith, K.M.; Quirk-Royal, B.E.; Drake-Lavelle, K.; Childress, M.J. Influences of ontogenetic phase and resource availability on parrotfish foraging preferences in the Florida Keys, FL (USA). *Mar. Ecol. Prog. Ser.* **2018**, *603*, 175–187. [CrossRef]

59. Luiz, O.J.; Mendes, T.C.; Barneche, D.R.; Ferreira, C.G.W.; Noguchi, R.; Villaça, R.C.; Rangel, C.A.; Gasparini, J.L.; Ferreira, C.E.L. Community structure of reef fishes on a remote oceanic island (St Peter and St Paul's Archipelago, equatorial Atlantic): The relative influence of abiotic and biotic variables. *Mar. Freshw. Res.* **2015**, *66*, 739–749. [CrossRef]

60. Fulton, C.J.; Bellwood, D.R. Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnol. Oceanogr.* **2005**, *50*, 255–264. [CrossRef]

61. Mendes, T.C.; Quimbayo, J.P.; Bouth, H.F.; Silva, L.P.S.; Ferreira, C.E.L. The omnivorous triggerfish *Melichthys niger* is a functional herbivore on an isolated Atlantic oceanic island. *J. Fish. Biol.* **2019**, *95*, 812–819. [CrossRef] [PubMed]

62. Gomi, K.; Nakamura, Y.; Kanda, M.; Honda, K.; Nakaoka, M.; Honma, C.; Adachi, M. Diel vertical movements and feeding behaviour of blue humphead parrotfsh *Scarus ovifrons* in a temperate reef of Japan. *J. Fish. Biol.* **2021**, *99*, 131–142. [CrossRef] [PubMed]

63. Williams, D.M.B. Patterns in the distribution of fish communities across the Central Great Barrier Reef. *Coral Reefs* **1982**, *1*, 35–43. [CrossRef]

64. Russ, G. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* **1984**, *20*, 23–34. [CrossRef]

65. Eggertsen, L.; Ferreira, C.E.L.; Fontoura, L.; Kautsky, N.; Gullström, M.; Berkström, C. Seaweed beds support more juvenile reef fish than seagrass beds in a south-western Atlantic tropical seascape. *Estuar. Coast. Shelf Sci.* **2017**, *196*, 97–108. [CrossRef]

66. Almany, G.R. Priority Effects in Coral Reef Fish Communities. *Ecology* **2004**, *84*, 1920–1935. [CrossRef]

67. Hines, D.E.; Pawlik, J.R. Assessing the antipredatory defensive strategies of Caribbean non-scleractinian zoantharians (Cnidaria): Is the sting the only thing? *Mar. Biol.* **2012**, *159*, 389–398. [CrossRef]

68. Kramer, M.J.; Bellwood, D.R.; Bellwood, O. Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. *Coral Reefs* **2012**, *31*, 1007–1015. [CrossRef]

69. Santos, T.R.N.; Sikkel, P.C. Habitat associations of fish-parasitic gnathiid isopods in a shallow reef system in the central Philippines. *Mar. Biodivers.* **2017**, *49*, 83–96. [CrossRef]

70. Modica, M.V.; Lombardo, F.; Franchini, P.; Oliverio, M. The venomous cocktail of the vampire snail *Colubraria reticulata* (Mollusca, Gastropoda). *BMC Genom.* **2015**, *16*, 441. [CrossRef]

71. Oliverio, M.; Modica, M.V. Relationships of the haematophagous marine snail Colubraria (Rachiglossa: Colubrariidae), within the neogastropod phylogenetic framework. *Zool. J. Linn. Soc.* **2010**, *158*, 779–800. [CrossRef]

72. Bouchet, P. A marginellid gastropod parasitizes sleeping fishes. *Bull. Mar. Sci.* **1989**, *45*, 76–84.

73. Bouchet, P.; Perrine, D. More gastropods feeding at night on parrotfishes. *Bull. Mar. Sci.* **1996**, *59*, 224–228.

74. Aued, A.; Smith, F.; Quimbayo, J.P.; Candido, D.V.; Longo, G.O.; Ferreira, C.E.L.; Witman, J.D.; Floeter, S.R.; Segal, B. Large-scale patterns of benthic marine communities in the Brazilian Province Anaide. *PLoS ONE* **2018**, *13*, e0198452. [CrossRef]

75. Dubin, R.; Baker, J. Two types of cover-seeking behavior at sunset by the princess parrotfish, scarus taeniopterus, at barbados, west indies. *Bull. Mar. Sci.* **1982**, *32*, 572–583.

76. Hamilton, W.J. Baboon sleeping site preferences and relationships to primate grouping patterns. *Am. J. Primatol.* **1982**, *3*, 41–53. [CrossRef]

77. Hoey, A.S.; Bellwood, D.R. Suppression of herbivory by macro algal density: A critical feedback on coral reefs? *Ecol. Lett.* **2011**, *14*, 267–273. [CrossRef]

78. Kerry, J.T.; Bellwood, D.R. The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs* **2011**, *31*, 415–424. [CrossRef]

79. Sazima, I.; Ferreira, C.E.L. A cocoon-producing parrotfish in the Southwestern Atlantic. *Coral Reefs* **2006**, *25*, 212. [CrossRef]

80. Hay, M.E. Herbivory, Algal Distribution, and the Maintenance of Between-Habitat Diversity on a Tropical Fringing Reef. *Am. Nat.* **1981**, *118*, 520–540. [CrossRef]

81. Fox, R.J.; Bellwood, D.R. Quantifying herbivory across a coral reef depth gradient. *Mar. Ecol. Prog. Ser.* **2007**, *339*, 49–59. [CrossRef]

82. Albert, A.; Savini, T.; Huynen, M.C. Sleeping site selection and presleep behavior in wild pigtailed macaques. *Am. J. Primatol.* **2011**, *73*, 1222–1230. [CrossRef]

83. Afonso, P.; Fontes, J.; Holland, K.N.; Santos, R.S. Social status determines behaviour and habitat usage in a temperate parrotfish: Implications for marine reserve design. *Mar. Ecol. Prog. Ser.* **2008**, *359*, 215–227. [CrossRef]

84. Garcia, J.; Mourier, J.; Lenfant, P. Spatial behavior of two coral reef fishes within a Caribbean marine protected area. *Mar. Environ. Res.* **2015**, *109*, 41–51. [CrossRef]

85. Garcia, J.; Saragoni, G.; Tessier, A.; Lenfant, P. Herbivorous Reef Fish Movement Ability Estimation in Marine Protected Areas of Martinique (FWI). In Proceedings of the Gulf and Caribbean Fisheries Institute, San Juan, Puerto Rico, 1–5 November 2010; pp. 254–259.

86. La Mesa, G.; Consalvo, I.; Annunziatellis, A.; Canese, S. Movement patterns of the parrotfish *Sparisoma cretense* in a Mediterranean marine protected area. *Mar. Environ. Res.* **2012**, *82*, 59–68. [CrossRef] [PubMed]

87. Howard, K.G.; Claisse, J.T.; Clark, T.B.; Boyle, K.; Parrish, J.D. Home range and movement patterns of the Redlip Parrotfish (*Scarus rubroviolaceus*) in Hawaii. *Mar. Biol.* **2013**, *160*, 1583–1595. [CrossRef]

88. Davis, K.; Carlson, P.M.; Lowe, C.G.; Warner, R.R.; Caselle, J.E. Parrotfish movement patterns vary with spatiotemporal scale. *Mar. Ecol. Prog. Ser.* **2017**, *577*, 149–164. [CrossRef]

89. Chateau, O.; Wantiez, L. Movement patterns of four coral reef fish species in a fragmented habitat in New Caledonia: Implications for the design of marine protected area networks. *ICES J. Mar. Sci.* **2009**, *66*, 50–55. [CrossRef]

90. Comeros-Raynal, M.T.; Choat, J.H.; Polidoro, B.A.; Clements, K.D.; Abesamis, R.; Craig, M.T.; Lazuardi, M.E.; McIlwain, J.; Muljadi, A.; Myers, R.F.; et al. The likelihood of extinction of iconic and dominant herbivores and detritivores of coral reefs: The parrotfishes and surgeonfishes. *PLoS ONE* **2012**, *7*, e39825.

91. Mccauley, D.J.; Young, H.S.; Guevara, R.; Williams, G.J.; Power, E.A.; Dunbar, R.B.; Bird, D.W.; Durham, W.H.; Micheli, F. Positive and Negative Effects of a Threatened Parrotfish on Reef Ecosystems. *Conserv. Biol.* **2014**, *28*, 1312–1321. [CrossRef] [PubMed]

92. Vallès, H.; Gill, D.; Oxenford, H.A. Parrotfish size as a useful indicator of fishing effects in a small Caribbean island. *Coral Reefs* **2015**, *34*, 789–801. [CrossRef]

93. Pinheiro, H.T.; Nunes, J.A.C.C.; Coni, E.O.C.; Almeida, E.C.G.; Sampaio, C.L.S.; Ferreira, C.E.L.; Meirelles, P.M.; Hostim-Silva, M.; Pereira, P.H.C.; Giglio, V.J.; et al. An inverted management strategy for the fishery of endangered marine species. *Front. Mar. Sci.* **2021**, *8*, 604108. [CrossRef]

94. Cunha, E.; Aurélio, R.; Carvalho, A.D.; Araújo, E.D. Exportation of reef fish for human consumption: Long-term analysis using data from Rio Grande do Norte, Brazil. *Bol. Inst. Pesca* **2012**, *38*, 369–378.

95. Pereira, P.H.C.; Ternes, M.L.F.; Nunes, J.A.C.C.; Giglio, V.J. Overexploitation and behavioral changes of the largest South Atlantic parrotfish (*Scarus trispinosus*): Evidence from fishers' knowledge. *Biol. Conserv.* **2021**, *254*, 108940. [CrossRef]

96. Padovani-Ferreira, B.; Floeter, S.; Rocha, L.A.; Ferreira, C.E.; Francini-Filho, R.; Moura, R.; Gaspar, A.L.; Feitosa, C. Scarus trispinosus. The IUCN Red List of Threatened Species 2012: e.T190748A17786694. 2012. Available online: https://www.iucnredlist.org/species/190748/17786694 (accessed on 17 September 2024).

97. Magris, R.A.; Costa, M.D.P.; Ferreira, C.E.L.; Vilar, C.C.; Joyeux, J.C.; Creed, J.C.; Copertino, M.S.; Horta, P.A.; Sumida, P.Y.G.; Francini-Filho, R.B.; et al. A blueprint for securing Brazil's marine biodiversity and supporting the achievement of global conservation goals. *Divers. Distrib.* **2020**, *27*, 198–215. [CrossRef]

98. Endo, C.A.K.; Gherardi, D.F.M.; Pezzi, L.P.; Lima, L.N. Low connectivity compromises the conservation of reef fishes by marine protected areas in the tropical South Atlantic. *Sci. Rep.* **2019**, *9*, 1–11. [CrossRef] [PubMed]

99. Mendes, T.C.; Cordeiro, C.A.M.M.; Ferreira, C.E.L. An experimental evaluation of macroalgal consumption and selectivity by nominally herbivorous fishes on subtropical rocky reefs. *J. Exp. Mar. Biol. Ecol.* **2015**, *417*, 146–152. [CrossRef]

100. Feitosa, J.L.L.; Queiroz-Véras, L.V.M.V.; Maida, M.; Ferreira, B.P. Going further on herbivore fishing: The removal of smaller fishes from algal-dominated reefs. *Mar. Ecol. Prog. Ser.* **2023**, *713*, 117–132. [CrossRef]

101. Fogliarini, C.O.; Ferreira, C.E.L.; Bornholdt, J.; Barbosa, M.C.; Giglio, V.J.; Bender, M.G. Telling the same story: Fishers and landing data reveal changes in fisheries on the Southeastern Brazilian Coast. *PLoS ONE* **2021**, *16*, e0252391. [CrossRef] [PubMed]

102. Eggertsen, L.; Luza, A.; Cordeiro, C.A.M.M.; Dambros, C.; Ferreira, C.E.L.; Floeter, S.R.; Francini-Filho, R.B.; Freire, K.M.F.; Gasalla, M.A.; Giarrizzo, T.; et al. Complexities of reef fisheries in Brazil: A retrospective and functional approach. *Rev. Fish. Biol. Fish.* **2024**, *34*, 511–538. [CrossRef]

103. Fogliarini, C.O.; Giglio, V.J.; Bender, M.G.; Ferreira, C.E.L. Multidecadal fishers' knowledge reveals overexploitation of sharks in southeastern Brazil. *Neotrop. Ichthyol.* **2024**, *22*, e230087. [CrossRef]

104. Pearse, A.R.; Hamilton, R.J.; Choat, J.H.; Pita, J.; Almany, G.; Peterson, N.; Hamilton, G.S.; Peterson, E.E. Giant coral reef fishes display markedly different susceptibility to night spearfishing. *Ecol. Evol.* **2018**, *8*, 10247–10256. [CrossRef]

105. Barbosa, M.C.; Luiz, O.J.; Cordeiro, C.A.; Giglio, V.J.; Ferreira, C.E.L. Fish and spearfsher traits contributing to catch composition. *Fish. Res.* **2021**, *241*, 105988. [CrossRef]