



# Use of acoustic telemetry to evaluate fish movement, habitat use, and protection effectiveness of a coral reef no-take zone (NTZ) in Brazil

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**ABSTRACT:** Movement is a key factor that shapes the distribution and structure of fish populations and influences the extent of the benefits provided by conservation and management measures, such as the implementation of marine no-take zones (NTZs). We used visual surveys and acoustic telemetry to investigate density and movement of 2 Brazilian endemic and highly targeted reef fish species inside and outside a coral reef NTZ, and subsequently inferred the effectiveness of the NTZ for protecting these species. To do so, visual surveys were performed on protected and unprotected reefs between 2016 and 2017. Moreover, 20 gray parrotfish *Sparisoma axillare* and 9 Brazilian snapper *Lutjanus alexandrei* were tagged with acoustic transmitters and passively monitored from December 2016 to October 2017. For both species, fish densities were significantly higher within the NTZ. Also, both species presented a high residence index over the short term, indicating they were full-time residents of the monitored area until detections were permanently lost. The absence of detections may indicate relocation to deeper reefs, predation, or fishing mortality when fish left the NTZ. Home ranges were small (0.10 to 0.45 km<sup>2</sup>), and both species presented spatially segregated subgroups within the populations. On average, the percentage of the home ranges within the NTZ was 88% for *S. axillare* and 95% for *L. alexandrei*. The results showed that small NTZs that are important to part of the life cycle of a target species are an effective measure to conserve reef fish populations, and also highlight the importance of fisheries management outside NTZs.

**KEY WORDS:** Acoustic monitoring · Marine protected area · *Sparisoma axillare* · *Lutjanus alexandrei* · Parrotfish · Snapper · Home range · Spatial ecology · Reserve effect

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## 1. INTRODUCTION

The creation of marine no-take zones (NTZs) has been considered one of the most effective tools in restoring and preserving biodiversity in coral reef environments (Halpern & Warner 2003, Lester et al.

2009, Edgar et al. 2014). Since the establishment of the first NTZs on coral reefs, a large body of evidence has shown that these protected areas are effective in increasing fish size, abundance, and biomass (Polunin & Roberts 1993, Gell & Roberts 2003, Halpern 2003), recovering populations of endangered species (Afonso

et al. 2011, Anderson et al. 2014), restoring the complexity of ecosystems through reestablishment of trophic cascades (Harborne et al. 2008, Leleu et al. 2012), and promoting an overall increase in resilience and complexity within their boundaries (Micheli et al. 2012, Barnett & Baskett 2015).

Effectiveness of NTZs for rebuilding and conserving fish populations is inherently linked to the movement of fishes that they are intended to safeguard (Green et al. 2015). Reef fishes have complex social systems that evolve during their life cycles, connecting habitats and ecosystems through movements and migrations (Jones et al. 2010, Kimirei et al. 2013). Fish movements and resulting changes in habitat use often occur at different spatial and temporal scales, and these dispersive behaviors are influenced by a variety of biological and ecological processes including ontogeny (Dahlgren & Eggleston 2000), reproduction (Afonso et al. 2008, Rhodes et al. 2012), competition (Abesamis & Russ 2005), predation (Bosiger & McCormick 2014, Rooker et al. 2018), and resource availability (Meyer et al. 2000).

Because habitat use and movement may vary considerably among species, the benefits of marine protected areas (MPAs) are species specific, and understanding the timing and degree of movements displayed by species of interest is needed to predict the value of these conservation measures (Green et al. 2015). If NTZs are relatively small in area or unrepresentative of essential habitats, regular movements of species may not be totally encompassed, and individuals will be constantly exposed to a potential risk of fishing mortality, thus compromising the ability of the protected area to promote fish growth and survival within its limits (Kramer & Chapman 1999, Halpern & Warner 2003). On the other hand, one of the main benefits expected from NTZs is their ability to enhance fishery yields and biodiversity outside their boundaries through spillover (Gell & Roberts 2003, Di Lorenzo et al. 2016). In this context, knowledge on short- and long-term movement and habitat-utilization patterns of fish is a key element to the design, management, and evaluation of NTZs in coral reef environments.

Passive acoustic telemetry allows the continuous and simultaneous tracking of individuals within a monitored area over different time scales (Topping et al. 2005, Heupel et al. 2006), and the approach has been commonly used to assess the effectiveness of NTZs (Lea et al. 2016, Di Franco et al. 2018, Lippi et al. 2021) by evaluating different aspects of fish movement ecology including site fidelity (Abecasis & Erzini 2008, Meyer et al. 2010, Harasti et al. 2015),

residency (March et al. 2011, Abecasis et al. 2013), home range size (Topping & Szedlmayer 2011, Villegas-Ríos et al. 2013, Garcia et al. 2014), habitat preference (Alós et al. 2011, Marshall et al. 2011, Rooker et al. 2018), mortality events (Khan et al. 2016, Tickler et al. 2019), and reproductive and ontogenetic migrations (Rhodes et al. 2012, Huijbers et al. 2015, Nanami et al. 2018).

In the present study, we used visual surveys and passive acoustic telemetry to characterize the habitat use and movement of 2 endemic and highly targeted fish species within a coral reef NTZ in Brazil: gray parrotfish *Sparisoma axillare* (Steindachner, 1878) (Labridae: Scarini) and Brazilian snapper *Lutjanus alexandrei* Moura & Lindeman, 2007 (Lutjanidae). The primary goals of this study were to estimate residency, movement patterns, and home range of *S. axillare* and *L. alexandrei* to assess the effectiveness of the current NTZ for protecting these species.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The monitored area was located on the Tamandaré coral reef complex off the coast of Pernambuco state, in northeastern Brazil (8° 44' S, 35° 6' W), and included the main reef formations inside and around a 2.7 km<sup>2</sup> well-enforced NTZ established in 1999 (Fig. 1). The NTZ is situated within the larger multiple-use Coral Coast MPA (established in 1997) and is also the core of the marine area of the Municipal Natural Park of Tamandaré Fort (established in 2003). About 30% of the NTZ area is covered by coral reef formations, which are mostly located on its north side and are contiguous to the reefs outside the NTZ.

Four distinct reef areas comprise the seascape within the NTZ: (1) scattered patch reefs, (2) aggregated patch reefs, (3) single-unit reef, and (4) barrier reef. Scattered patch reefs are surrounded by broad sand areas at depths of ~1–3 m, while aggregated patch reefs are clustered and separated by narrow sand corridors distributed over a deeper area (up to 8 m) with reefs shallower towards the north and outside the NTZ. In both scattered and aggregated patch reef areas, reefs are also surrounded by seagrass and algae beds. Single-unit reef is characterized by a high complexity and relatively isolated structure, with depth ranging from 4 to 12 m. Reef top is exposed during low tide and overhanging

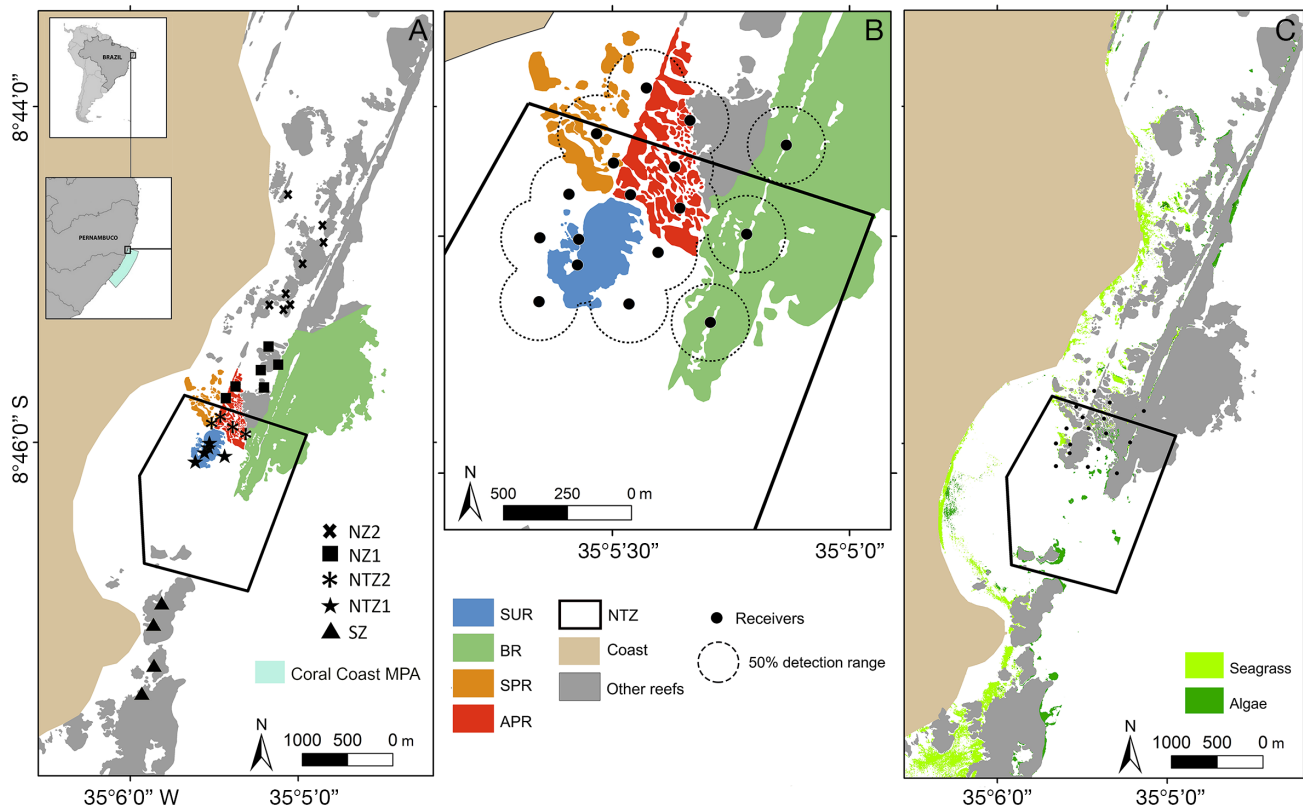


Fig. 1. Study area in the Tamandaré coral reef complex off the northeast coast of Brazil. (A) Locations of the Coral Coast marine protected area (MPA), the no-take zone, and sites where the fish surveys were conducted in the different reef zones: South zone (SZ), No-take zones 1 and 2 (NTZ1, NTZ2), North zones 1 and 2 (NZ1, NZ2). (B) Locations of the acoustic receivers and 50% detection range (150 m). Panels A and B also highlight the different reef areas where fish were collected/released (SUR: single-unit reef; BR: barrier reef; SPR: scattered patch reefs; APR: aggregated patch reefs). (C) Locations of seagrass beds and algae patches in the study area

ledges shade the systems of interconnected caves. Barrier reef consists of an elongated reef formation subjected to stronger wave action. Depth ranges from 3 to 6 m. Eastward, beyond the last line of receivers, depth increases continuously up to 8 m.

## 2.2. Study species and fisheries

*Sparisoma axillare* has a widespread distribution along the Brazilian coast, from Maranhão (northeastern Brazil) to Santa Catarina (southern Brazil), also including the oceanic islands (Moura et al. 2001). The species is commonly found from shallow coastal reefs and seagrass beds to deeper reefs at depths of up to 54 m (Moura et al. 2001, Feitoza et al. 2005). Current data of landings from the artisanal fisheries in the study area show that *S. axillare* is the most representative species in spear and hook-and-line fisheries in the coastal reefs of Tamandaré (Silveira 2018). The species is also an important target for the

bottom trap fisheries along the Pernambuco continental shelf (Ribeiro 2004).

*Lutjanus alexandrei* is restricted to northeastern Brazil (from Maranhão to Bahia) and is absent from oceanic islands (Moura & Lindeman 2007). The species undergoes ontogenetic migrations from estuarine/mangrove areas to reefs at depths greater than 50 m (Moura & Lindeman 2007, Aschenbrenner et al. 2016a,b). It is worth noting that the species has only recently been described (Moura & Lindeman 2007), and records of the species had been misidentified as *L. jocu* and/or as the Caribbean species *L. griseus* and *L. apodus* up to that date (Moura & Lindeman 2007). Brazil is lacking official landing statistics since 2008 (Freire et al. 2021), and therefore such misidentifications are incorporated in the available records for the Lutjanidae fisheries. *L. alexandrei* is captured by different gears (line, gillnet, and bottom traps) from both small-scale and commercial reef fisheries of northeastern Brazil, where it is part of the Lutjanidae complex (Ribeiro 2004, Frédou et al. 2006).

### 2.3. Reef fish surveys

Visual surveys using belt transects of 100 m<sup>2</sup> (5 m wide by 20 m long) were used to compare fish density and size composition for the 2 target species. During surveys, *S. axillare* and *L. alexandrei* individuals were identified and counted, and total length (TL, cm) was estimated and recorded by trained observers. A minimum of 4 replicate transects were surveyed at each site during low tides, with no sampling taking place when underwater visibility was lower than 4 m. Surveyed sites were randomly chosen within 5 different reef areas, always along reef crests. A total of 314 transects were surveyed during 2 consecutive dry seasons (January to April 2016 and September 2016 to March 2017). Visual surveys conducted within the NTZ corresponded to the single-unit reef area (NTZ1 = 98 transects) and patch-reef area (protected portions of scattered patch reefs and aggregated patch-reef areas, NTZ2 = 32 transects). Surveys outside the NTZ were performed on the reefs located beyond the southern (SZ = 48 transects) and northern (NZ1 = 74 and NZ2 = 62 transects) borders of the NTZ (Fig. 1).

### 2.4. Acoustic monitoring system

From December 2016 to August 2018, an array of 17 omnidirectional acoustic receivers (VR2W-69kHz, VEMCO) were used to monitor the movements and habitat use by tagged *S. axillare* and *L. alexandrei* individuals (Fig. 1). Preliminary range tests conducted inside the NTZ demonstrated that, in addition to distance between receivers and transmitters, tide level also had a negative effect on detection probability. A minimum detection rate of 50% was obtained for transmitters at 150 m distance from the receiver during preliminary trials, and therefore this range was used as a guideline to design the array. At 300 m, average detection probability dropped to below 5% during high tide hours (V. M. Giacalone et al. preprint, doi:10.13140/RG.2.2.35735.57768).

In most cases, receiver positioning allowed for overlapping detection ranges, and the total area covered by the array was approximately 1 km<sup>2</sup>, including more than 80% of the reef area within the NTZ and the reef formations adjacent to its northern border. To identify fish movement to unprotected areas, 3 receivers were placed outside the NTZ, on the reef continuum beyond its northern boundary. Depth inside the monitored area ranged from 1 to 12 m.

As reef tops may be exposed (or just below the surface) during low tide, receivers were placed over the

sandy bottom around the reefs, moored in a PVC pipe attached to a concrete base to ensure vertical positioning and avoid dragging. Data downloads, battery checks, and clearing of fouling organisms took place every 1–2 mo. One receiver located at the southernmost part of the barrier reef (Fig. 1) was lost in the 2017 winter due to severe sea conditions.

### 2.5. Fish collection and tagging

From December 2016 to May 2017, 20 *S. axillare* and 9 *L. alexandrei* were caught and tagged. All fish were caught inside the NTZ (Fig. 1). To reduce possible school influence on parrotfish behavior (Welsh & Bellwood 2012a) and better represent the local population, collections of *S. axillare* were equally distributed among the 4 reef areas: single-unit reef (n = 5), scattered patch reefs (n = 5), aggregated patch reefs (n = 5), and barrier reef (n = 5). For *L. alexandrei*, fish were captured in the single-unit reef (n = 5), scattered patch reefs (n = 3), and aggregated patch reefs (n = 1).

Individuals were caught with hand nets by SCUBA divers at night when fish were either 'sleeping' (*S. axillare*) and/or with reduced flight capability (*L. alexandrei*). This way, impact was minimized, as only individuals from the target species and with a desirable body size (*S. axillare* >24 cm TL and *L. alexandrei* >19 cm TL) were caught. This collection method also reduced the disturbance to the local fish community and the risk of injury caused by fishing gears. Individuals were transported to a research facility on land and kept in 1000 l holding tanks with direct seawater and monitored for 24 h prior to tag implantation. *S. axillare* were implanted with individually coded V9-4L acoustic transmitters (30 to 90 s delay, 476 d expected lifetime, 4.5 g tag weight, VEMCO) while *L. alexandrei* were implanted with V8-4L acoustic transmitters (30 to 90 s delay, 150 d expected lifetime, 2.1 g tag weight, VEMCO). Prior to surgery, fish were transferred to a smaller tank and anesthetized in a 0.04 ml l<sup>-1</sup> seawater and eugenol solution (Pastor et al. 2009, Lee et al. 2015, Honda et al. 2016, 2017), weighed (total weight, nearest g), and measured (TL, nearest mm). Individuals were then placed in a 'V' shaped bed, and scales were plucked from the ventral midline to expose the tag-insertion area. Transmitters were cleaned in povidone-iodine to prevent infection (Abecasis et al. 2009, Ferguson et al. 2013) and then surgically inserted into the peritoneal cavity through a 1.5–2.0 cm incision, which was closed with 2 stitches of absorbable 4/0 monofilament suture. Direct seawater flow was maintained

through the gills by a water pump allowing fish to breathe normally throughout the procedure. After surgery, individuals were returned to the holding tanks and observed for a 24 h period prior to release. Releases occurred the following morning, at the capture site of each individual. All tagged *S. axillare* were initial-phase females, with a mean ( $\pm$ SD) size of  $26.5 \pm 2.3$  cm TL (24.2–33 cm) and weight of  $296.3 \pm 73.5$  g (Table 1). Sex of *L. alexandrei* was not determined, and mean size and weight were  $22.5 \pm 2.3$  cm TL (19.5 to 25.2 cm) and  $186.3 \pm 60.3$  g (Table 2). For all individuals, the tag-to-body weight relationship never exceeded 2% ( $\bar{x} = 1.49 \pm 0.14\%$  CI, range = 0.83–1.95%) of fish total weight in air, as recommended by the manufacturer of the transmitters.

## 2.6. Data analysis

Fish density and TL were compared among reef sites using the non-parametric Kruskal-Wallis and post hoc Dunn's pairwise ranked tests. For the purpose of fish density analyses, *S. axillare* were divided in 2 size categories:  $\leq 20$  and  $> 20$  cm, as followed by the Reef Check protocol (Ferreira et al. 2018); *L. alexandrei* had a single size category.

For the acoustic telemetry data, prior to statistical analysis, spurious detections (i.e. any detection from a single fish occurring alone within a 24 h period) were removed to prevent any false-positive detections (March et al. 2011, Harasti et al. 2015). Detections obtained within the first 24 h post-release were also excluded from all individuals to avoid potentially negative effects of the tagging procedure on fish behavior (Honda et al. 2016). To identify groups of individuals with distinct spatial occupation patterns within each species, the relative number of detections on each receiver was calculated for each fish. Proportions were then arcsine-square root transformed (Meyer et al. 2010, Topping & Szedlmayer 2011) and a similarity matrix among fish was built for each species based on the Bray-Curtis similarity index. Statistically distinct spatial groups were then identified through hierarchical cluster analysis followed by a SIMPROF procedure (Clarke & Gorley 2006). Differences in TL were tested among spatial groups for each species using ANOVA and Student's *t*-test.

Permanence within the monitored area was quantified for each fish by 2 indices (Abecasis et al. 2013, 2015, Özgül et al. 2019): (1) a residency index expressed as the number of days an individual was actually detected ( $D_D$ ) divided by the detection period of the individual (number of days between

release and the last detection,  $D_P$ ) and (2) a weighted residency index calculated as:

$$\text{Weighted residency index} = \frac{D_D}{D_{\max}} \times \left( \frac{D_P}{D_{\max}} \right) \quad (1)$$

where  $D_{\max}$  is the maximum number of possible monitoring days for each species based on estimate battery life (*S. axillare* V9 lifetime = 476 d; *L. alexandrei* V8 lifetime = 150 d). The end of study date was considered as  $D_{\max}$  when the removal of the receiver array occurred before the expected lifetime of the transmitter was over. For both indices, values range from 0 (no residency) to 1 (permanent residency).

To estimate the extent of space used by each individual, centers of activity (COAs) were first calculated for each fish at 60 min intervals (Simpfendorfer et al. 2002). This method uses the weighted means of the number of detections registered by each receiver to provide estimated hourly fish positions (mean latitude and longitude). The nonparametric kernel utilization distribution (KUD) was then used to calculate home range (defined as 95% KUD) and core range (defined as 50% KUD) areas, based on the COA estimates over the entire detection period of the individual. KUDs were estimated based on bivariate fixed kernels (Worton 1989) over a  $25 \times 25$  m cell grid and a fixed bandwidth smoothing factor (*h*) of 150 m (corresponding to the 50% detection probability range). As observed during diurnal and nocturnal dives in the monitored reefs, both species are highly reef attached and the use of bare sand/mud areas is limited to the immediate reef vicinity. Therefore, the entire 95 and 50% KUD areas were considered an overestimation of the actual space used by both species. To produce more reliable home range and core range estimates, the surrounding sand-covered areas located more than 50 m away from any reef formation were excluded from the initially calculated 95 and 50% KUDs. The selection of an area of interest reduced the home range and core range areas of *S. axillare* by  $25.1 \pm 10.6\%$  CI and  $21.2 \pm 10.4\%$  CI, respectively. For *L. alexandrei*, home range and core range areas were reduced by  $34.0 \pm 13.6\%$  CI and  $24.9 \pm 16.3\%$  CI, respectively. The majority of seagrass and macroalgae patches present in the monitored area were included within the 50 m limit range. Finally, individual home range and core range areas were overlapped with the NTZ boundary to assess the percentage of home range and core range areas located inside the NTZ.

To investigate space-use sharing between the different spatial groups within species, mean home range



Table 1. Summary of the monitoring data for tagged *Sparisoma axillare* (n = 20) in the coastal reefs of the Tamandaré coral reef complex. Total length (TL, cm), capture/release areas and spatial groups (SPR: scattered patch reefs; APR: aggregated patch reefs; BR: barrier reef; SUR: single-unit reef), detection period (D<sub>p</sub>), days detected (D<sub>d</sub>), weighted residency index (I<sub>WR</sub>), residency index (I<sub>R</sub>), number of centers of activity (COAs), percentage of home range located inside the no-take zone (NTZ) (%HR<sub>in</sub>), and percentage of core range located inside the NTZ (%CR<sub>in</sub>). Dashes (–) indicate no detection; NA: not available

| Fish ID                 | TL (cm) | Date released (d/mo/yr) | Capture/<br>release areas | Spatial<br>groups | No. of<br>detections | D <sub>p</sub> | D <sub>d</sub> | I <sub>WR</sub> | I <sub>R</sub> |             | COAs | Home range (km <sup>2</sup> ) |                    | Core range (km <sup>2</sup> ) |                    |
|-------------------------|---------|-------------------------|---------------------------|-------------------|----------------------|----------------|----------------|-----------------|----------------|-------------|------|-------------------------------|--------------------|-------------------------------|--------------------|
|                         |         |                         |                           |                   |                      |                |                |                 | All            | Outside NTZ |      | All                           | % HR <sub>in</sub> | All                           | % CR <sub>in</sub> |
| SPAAXI #01              | 26.2    | 13/12/2016              | SUR                       | SUR               | 13002                | 51             | 51             | 0.01            | 1.00           | –           | 837  | 0.10                          | 100                | 0.02                          | 100                |
| SPAAXI #02 <sup>a</sup> | 26.1    | 13/12/2016              | SUR                       | NA                | 87                   | 01             | 01             | NA              | NA             | NA          | NA   | NA                            | NA                 | NA                            | NA                 |
| SPAAXI #03              | 25.5    | 12/01/2017              | SUR                       | SUR               | 4091                 | 18             | 18             | 0.001           | 1.00           | –           | 314  | 0.14                          | 100                | 0.04                          | 100                |
| SPAAXI #04              | 25.0    | 12/01/2017              | SPR                       | NA                | 1252                 | 25             | 25             | 0.003           | 1.00           | –           | 212  | 0.44                          | 98.9               | 0.11                          | 100                |
| SPAAXI #05 <sup>a</sup> | 31.5    | 14/01/2017              | SUR                       | NA                | 34234                | 480            | 325            | NA              | NA             | NA          | NA   | NA                            | NA                 | NA                            | NA                 |
| SPAAXI #06              | 25.0    | 14/01/2017              | SPR                       | SPR               | 733                  | 23             | 23             | 0.002           | 1.00           | 0.13        | 111  | 0.34                          | 86.8               | 0.07                          | 99.7               |
| SPAAXI #07              | 27.7    | 14/01/2017              | SPR                       | SPR               | 942                  | 17             | 17             | 0.001           | 1.00           | 0.18        | 117  | 0.42                          | 85.1               | 0.07                          | 97.2               |
| SPAAXI #08              | 33.0    | 20/01/2017              | BR                        | BR                | 437                  | 107            | 62             | 0.03            | 0.58           | 0.07        | 158  | 0.40                          | 80.8               | 0.07                          | 100                |
| SPAAXI #09              | 27.0    | 20/01/2017              | BR                        | BR                | 63                   | 26             | 20             | 0.002           | 0.77           | –           | 37   | 0.25                          | 100                | 0.07                          | 100                |
| SPAAXI #10              | 25.4    | 20/01/2017              | BR                        | BR                | 490                  | 55             | 50             | 0.01            | 0.91           | –           | 217  | 0.18                          | 100                | 0.05                          | 100                |
| SPAAXI #11              | 27.5    | 20/01/2017              | BR                        | BR                | 125                  | 91             | 39             | 0.02            | 0.43           | –           | 65   | 0.16                          | 100                | 0.04                          | 100                |
| SPAAXI #12 <sup>a</sup> | 25.0    | 20/01/2017              | BR                        | NA                | 19                   | 06             | 04             | NA              | NA             | NA          | NA   | NA                            | NA                 | NA                            | NA                 |
| SPAAXI #13              | 25.2    | 26/01/2017              | APR                       | APR               | 180                  | 56             | 39             | 0.01            | 0.70           | –           | 86   | 0.28                          | 82.9               | 0.07                          | 100                |
| SPAAXI #14 <sup>a</sup> | 29.0    | 26/01/2017              | APR                       | NA                | 484                  | 03             | 02             | NA              | NA             | NA          | NA   | NA                            | NA                 | NA                            | NA                 |
| SPAAXI #15              | 25.0    | 30/03/2017              | SPR                       | SPR               | 7190                 | 58             | 58             | 0.02            | 1.00           | 0.26        | 840  | 0.22                          | 72.1               | 0.05                          | 97.9               |
| SPAAXI #16              | 24.5    | 30/03/2017              | SPR                       | SPR               | 12353                | 180            | 34             | 0.03            | 0.18           | 0.01        | 377  | 0.21                          | 78.7               | 0.05                          | 99.9               |
| SPAAXI #17              | 26.8    | 30/03/2017              | SUR                       | SUR               | 13821                | 38             | 38             | 0.01            | 1.00           | –           | 555  | 0.19                          | 100                | 0.06                          | 100                |
| SPAAXI #18              | 24.3    | 28/04/2017              | APR                       | APR               | 3017                 | 159            | 151            | 0.14            | 0.95           | 0.03        | 711  | 0.31                          | 84.1               | 0.06                          | 100                |
| SPAAXI #19              | 25.6    | 28/04/2017              | APR                       | SPR               | 717                  | 28             | 25             | 0.004           | 0.89           | 0.61        | 136  | 0.45                          | 58.8               | 0.10                          | 49.0               |
| SPAAXI #20              | 24.2    | 28/04/2017              | APR                       | APR               | 866                  | 187            | 134            | 0.15            | 0.71           | 0.01        | 355  | 0.34                          | 86.6               | 0.07                          | 100                |

<sup>a</sup>Fish that prematurely left the array, lost the tag, or died

Table 2. Summary of the monitoring data for tagged *Lutjanus alexandrei* (n = 9) in the coastal reefs of the Tamandaré coral reef complex. Abbreviations as in Table 1

| Fish ID    | TL (cm) | Date released (d/mo/yr) | Capture/<br>release areas | Spatial<br>groups | No. of<br>detections | D <sub>p</sub> | D <sub>d</sub> | I <sub>WR</sub> | I <sub>R</sub> |             | COAs | Home range (km <sup>2</sup> ) |                    | Core range (km <sup>2</sup> ) |                    |
|------------|---------|-------------------------|---------------------------|-------------------|----------------------|----------------|----------------|-----------------|----------------|-------------|------|-------------------------------|--------------------|-------------------------------|--------------------|
|            |         |                         |                           |                   |                      |                |                |                 | All            | Outside NTZ |      | All                           | % HR <sub>in</sub> | All                           | % CR <sub>in</sub> |
| LUTALE #01 | 24.0    | 13/12/2016              | SUR                       | SUR               | 3122                 | 24             | 24             | 0.03            | 1.00           | –           | 276  | 0.15                          | 100                | 0.05                          | 100                |
| LUTALE #02 | 21.5    | 13/12/2016              | SUR                       | SUR               | 29810                | 152            | 146            | 0.99            | 0.96           | –           | 1400 | 0.19                          | 100                | 0.06                          | 100                |
| LUTALE #03 | 24.5    | 12/01/2017              | SUR                       | SUR               | 14154                | 135            | 135            | 0.81            | 1.00           | –           | 1801 | 0.15                          | 100                | 0.03                          | 100                |
| LUTALE #04 | 25.2    | 12/01/2017              | SPR                       | SPR               | 3261                 | 127            | 119            | 0.67            | 0.93           | –           | 1066 | 0.40                          | 86.2               | 0.08                          | 100                |
| LUTALE #05 | 23.1    | 12/01/2017              | SPR                       | SUR               | 1893                 | 19             | 17             | 0.01            | 0.89           | –           | 113  | 0.26                          | 100                | 0.07                          | 100                |
| LUTALE #06 | 24.5    | 14/01/2017              | SPR                       | SPR               | 39736                | 143            | 143            | 0.91            | 1.00           | 0.74        | 2139 | 0.27                          | 74.2               | 0.05                          | 99.2               |
| LUTALE #07 | 19.5    | 30/03/2017              | SUR                       | SUR               | 45837                | 150            | 150            | 1.00            | 1.00           | –           | 2345 | 0.15                          | 100                | 0.05                          | 100                |
| LUTALE #08 | 20.4    | 28/04/2017              | APR                       | SPR               | 2032                 | 107            | 94             | 0.45            | 0.88           | –           | 582  | 0.19                          | 96.9               | 0.04                          | 100                |
| LUTALE #09 | 19.5    | 05/05/2017              | SUR                       | SUR               | 885                  | 16             | 16             | 0.01            | 1.00           | –           | 126  | 0.12                          | 100                | 0.03                          | 100                |

and mean core range areas were calculated for each spatial group based on the total number of COAs estimated for all fish from the group. Estimates of mean home range and core range followed the same procedures used to calculate individual KUDs. An overlap index (OI) was then calculated for each spatial group as:

$$OI = OV_{(KUD_i, KUD_{i+1})} \div (KUD_i + KUD_{i+1}) \quad (2)$$

where  $OV_{(KUD_i, KUD_{i+1})}$  is the overlap area between the mean home range or core range areas of 2 spatial groups, and  $(KUD_i + KUD_{i+1})$  is the combination of the mean home range or core range areas of 2 spatial groups. Values range from 0 (no overlap, groups are spatially segregated) to 1 (mean home range or core range are completely overlapped and groups show no spatial segregation).

KUD analyses were performed using the 'Home Range Tools' extension for ArcGIS (Rodgers et al. 2015). Selection of KUD areas of interest, overlap between home range and core range areas and NTZ boundary, as well as the overlapped and combined mean home range and core range areas were obtained using geoprocessing tools on ArcGIS 10.4. Differences in residency index, weighted residency index, and home range and core range areas between species and among spatial groups were assessed using ANOVA and Student's *t*-test (or the non-parametric Kruskal-Wallis and Mann-Whitney *U*-test when parametric assumptions were not met). Also, Spearman's rank correlations were used to investigate if fish TL was significantly correlated with residency index, weighted residency index, home range, and core range. Analyses were conducted in Statistica v. 8.0 (Statsoft) and PRIMER v. 6.1 (Clarke & Gorley 2006). Significance was tested at  $\alpha = 0.05$ .

## 2.7. Ethics statement

This research was approved by the Ethics Committee and Animal Use of the Federal University of Pernambuco (CEUA-UFPE Number: 23076.007810/2015-01) and Chico Mendes Institute for Biodiversity Conservation (ICMBIO – Sisbio License: 45992).

## 3. RESULTS

### 3.1. Reef fish surveys

Fish densities for both species were significantly higher inside the Tamandaré NTZ, with *Sparisoma*

*axillare* >20 cm forming large roving schools along reef crests and *Lutjanus alexandrei* aggregating in large numbers to rest inside caves. Outliers and extreme outliers indicate the occurrence of those schools, which for *S. axillare* could include up to 70 individuals (Fig. 2). Densities were significantly higher in NTZ1 (corresponding to the single-unit reef area) for *S. axillare* >20 cm (Kruskal-Wallis  $H = 36.2$ ,  $p < 0.001$ ) and for *L. alexandrei* ( $H = 39.8$ ,  $p < 0.001$ ), and in NTZ2 (corresponding to scattered patch reefs and aggregated patch reefs) for smaller *S. axillare*  $\leq 20$  cm ( $H = 37.5$ ,  $p < 0.001$ ) (Fig. 2). For *S. axillare*, fish TL was also significantly higher in NTZ1 ( $H = 36.2$ ,  $p < 0.001$ ), whereas larger *L. alexandrei* were observed in NZ2 ( $H = 16.5$ ,  $p < 0.01$ ) (Fig. 2).

### 3.2. Acoustic telemetry

The tagging and monitoring data of the 20 *S. axillare* and 9 *L. alexandrei* individuals are summarized in Tables 1 & 2, respectively. Three *S. axillare* were detected for a short period of  $\leq 6$  d (ID nos. SPAAXI #02, #12 and #14). One *S. axillare* (SPAAXI #05) was assumed to be dead a few days after tagging in a detectable location in the array, as this fish was continuously being detected by only 1 receiver and detection ceased only after the estimated lifespan of the transmitter was over. Therefore, these 4 *S. axillare* individuals were excluded from all subsequent analyses. Only 1 fish (SPAAXI #11) seemed to have its monitoring discontinued following receiver loss, as this fish was being recorded exclusively by this receiver and ceased to be detected only 3 d before the last date of download. Two other *S. axillare* individuals were constantly being detected by this receiver while it was still in place; however for both fish, detection ceased more than 40 d prior to receiver loss. The remaining 16 *S. axillare* and all 9 *L. alexandrei* were monitored for 16 to 187 d, from December 2016 to October 2017 (Fig. 3A,B).

Even with a shorter transmitter battery lifespan, *L. alexandrei* had a higher number of detections per fish ( $\bar{x} = 15637 \pm 18018$  SD) and longer detection period ( $97 \pm 59.5$  d) than *S. axillare* ( $3705 \pm 5002$  detections and  $70 \pm 58.3$  d), although individual variation within each species was high (Tables 1 & 2). Based on the relative number of detections for each fish at each receiver, hierarchical cluster analysis followed by a SIMPROF procedure revealed 4 significantly distinct clusters for *S. axillare*: barrier reef, scattered patch reefs, aggregate patch reefs, and single-unit reef spatial groups (Fig. 3C), and 2 significantly distinct clus-

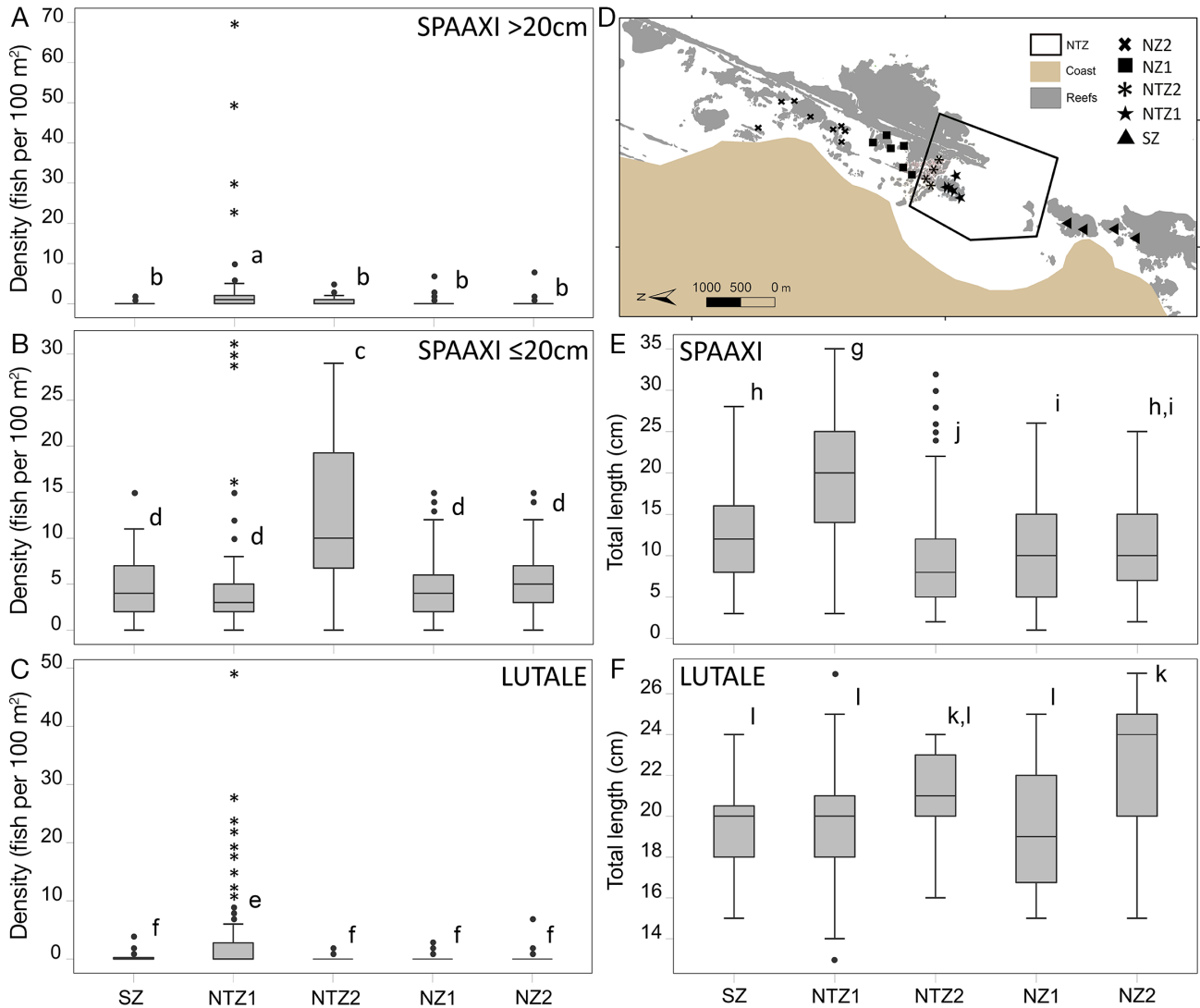


Fig. 2. Fish density (left column) and total length (right column) of *Sparisoma axillare* (SPAAXI) and *Lutjanus alexandrei* (LUTALE) obtained by the visual surveys performed in the Tamandaré coral reef complex. For density estimates, *S. axillare* was divided in 2 size categories (>20 and ≤20 cm total length). Letters above error bars (a–l) indicate the results of Dunn's pairwise ranked tests. Solid line within the box indicates the median, box represents the interquartile range (lower = 25<sup>th</sup> percentile, upper = 75<sup>th</sup> percentile), whiskers extend to the largest value within 1.5× the interquartile range, outliers outside this range are represented by black dots, and extreme outliers (values beyond 3× the interquartile range) are represented by asterisks. The top-right panel shows the location of the surveyed site (abbreviations as in Fig. 1)

ters for *L. alexandrei*: scattered patch reefs and single-unit reef spatial groups (Fig. 3D), which corresponded to groups of individuals with distinct spatial occupation patterns. For both species, spatial groups were mostly composed of the individuals captured in the same reef area (corresponding to 94% of *S. axillare* and 78% of *L. alexandrei* individuals). Only 1 *S. axillare* (SPAAXI #19, Fig. 3C) and 2 *L. alexandrei* (ID nos. LUTALE #05 and #08, Fig. 3D) had more detections on reef areas other than their original capture locations. Fish SPAAXI #04 was not included in any spatial group. Neither species showed significant dif-

ferences in fish TL among spatial groups (*S. axillare*: ANOVA,  $F = 2.39$ ,  $p = 0.12$ ; *L. alexandrei*: Student's *t*-test,  $t = 0.82$ ,  $p = 0.44$ ).

On average, *S. axillare* individuals were detected on  $11 \pm 9.7\%$  SD of the maximum number of monitoring days (lifetime of V9 = 476 d, or end of the study), resulting in low weighted residency index values for the species ( $0.03 \pm 0.05$ ) (Table 1, Fig. 3A). For *L. alexandrei*, weighted residency index values were considerably higher ( $0.54 \pm 0.42$ ) as fish remained in the monitoring area for  $62.5 \pm 39\%$  of the maximum number of monitoring days (expected lifetime of V8 =



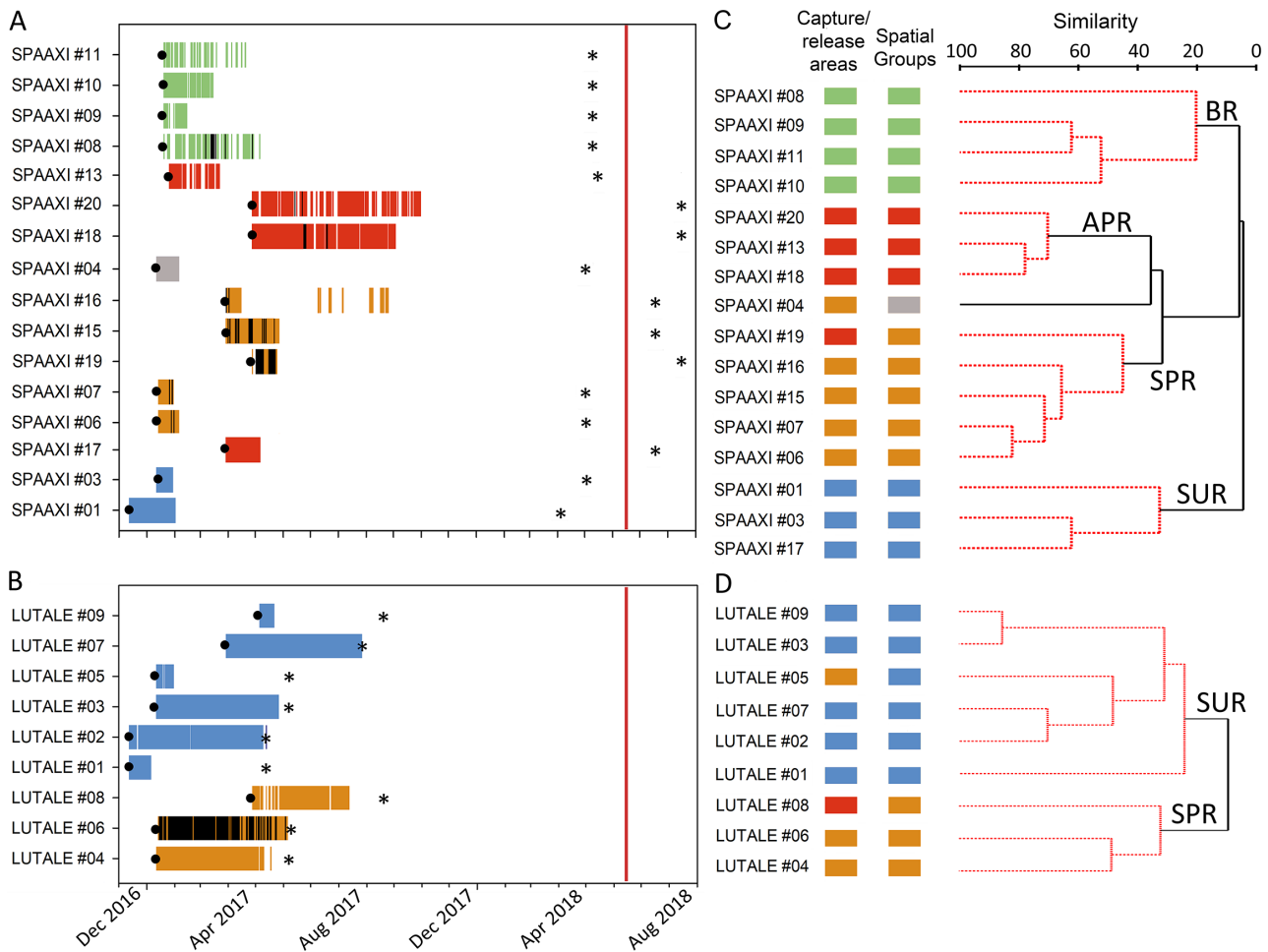


Fig. 3. (A,B) Detection plots of fish daily presence–absence at the monitored area and (C,D) hierarchical cluster analysis followed by a SIMPROF procedure indicating the formation of significantly distinct groups of fish with distinct spatial occupation patterns (red dotted lines) for tagged *Sparisoma axillare* (SPAAXI; A,C) and *Lutjanus alexandrei* (LUTALE; B,D) in the Tanageré coral reef complex. Original capture/release areas and fish spatial groups formed after clustering with correspondent colors: barrier reef (BR, green), aggregate patch reefs (APR, red), sparse patch reefs (SPR, orange), and single-unit reef (SUR, blue). Fish SPAAXI #04 (gray) was not included in any group. Fish release dates (black circles), days with detections outside the no-take zone (black bars), estimated lifetime of transmitters (465 d for *S. axillare* V9 and 150 d for *L. alexandrei* V8) (asterisks), and removal of receiver array (end of study, vertical red line) are also shown

150 d) (Table 2, Fig. 3B). For both species, no significant differences in weighted residency index were observed among fish groups (*S. axillare*: Kruskal-Wallis,  $H = 4.04$ ,  $p = 0.25$ ; *L. alexandrei*: Mann-Whitney,  $U = 8$ ,  $p = 0.90$ ). Both species had high residency index values (*S. axillare*:  $0.82 \pm 0.24$ ; *L. alexandrei*:  $0.96 \pm 0.05$ ) (Tables 1 & 2), with no significant difference between them (Mann-Whitney,  $U = 52$ ,  $p = 0.24$ ). For *S. axillare*, higher residency index values were observed for the single-unit reef (residency index = 1 for all fish), followed by scattered patch reef ( $0.82 \pm 0.35$ ) and aggregated patch reef ( $0.79 \pm 0.14$ ) groups, whereas lower values were obtained for the barrier reef group ( $0.67 \pm 0.21$ ). Significant differences in residency index were ob-

served for *S. axillare* between single-unit reef and barrier reef groups (Mann-Whitney,  $U = 0$ ,  $p = 0.02$ ) and between single-unit reef and aggregated patch reef groups (Mann-Whitney,  $U = 0$ ,  $p = 0.03$ ). For *L. alexandrei*, no statistical difference was found between the 2 groups (Mann-Whitney,  $U = 5$ ,  $p = 0.30$ ). No correlations were found between fish TL and weighted residency index (Spearman rank correlation; *S. axillare*,  $r_s = -0.02$ ,  $p = 0.93$  and *L. alexandrei*,  $r_s = -0.01$ ,  $p = 0.97$ ) or residency index (Spearman rank correlation; *S. axillare*,  $r_s = -0.42$ ,  $p = 0.10$  and *L. alexandrei*,  $r_s = 0.07$ ,  $p = 0.85$ ).

The estimated home range (95% KUD) areas ranged from 0.10 to 0.45 km<sup>2</sup> ( $\bar{x} = 0.28 \pm 0.11$  km<sup>2</sup> SD) for *S. axillare* (Table 1) and from 0.12 to 0.40 km<sup>2</sup>

( $0.21 \pm 0.09 \text{ km}^2$ ) for *L. alexandrei* (Table 2). Regarding the core range (50% KUD) estimates, areas ranged from 0.02 to 0.11  $\text{km}^2$  ( $0.06 \pm 0.02 \text{ km}^2$ ) for *S. axillare* (Table 1) and from 0.03 to 0.08  $\text{km}^2$  ( $0.05 \pm 0.02 \text{ km}^2$ ) for *L. alexandrei* (Table 2). Both home range and core range sizes did not differ significantly between species (Student's *t*-test,  $t = 1.48$ ,  $p = 0.15$  and  $t = 1.31$ ,  $p = 0.20$ , respectively) or among spatial groups within each species (Table 3). For *S. axillare*, no correlations were found between fish TL and home range or core range size (Fig. 4A). For *L. alexandrei*, the influence of fish TL on home range and core range sizes was also not significant (Fig. 4B).

Nine individuals were recorded outside the NTZ, but only 3 of them (all from the scattered patch reef group) left the protected area on a regular basis: SPAAXI #15 (26% of monitoring period), SPAAXI #19 (61%), and LUTALE #06 (74%) (Tables 1 & 2, Fig. 3A,B). SPAAXI #19 also had the highest number of detections outside the NTZ (65% of all detections). All *S. axillare* and *L. alexandrei* from single-unit reef groups were never detected outside the NTZ. Regarding the percentage of fish home range and core range located inside the NTZ (%HR<sub>in</sub> and %CR<sub>in</sub>, respectively), most *S. axillare* individuals (except for SPAAXI #19) and all *L. alexandrei* had a %HR<sub>in</sub> higher than 70% (*S. axillare*:  $\bar{x} = 88.4 \pm 6\%$  CI; *L. alexandrei*:  $95.2 \pm 4.5\%$ ) and a %CR<sub>in</sub> over 95% (*S. axillare*:  $96.5 \pm 6.2\%$ ; *L. alexandrei*:  $99.9 \pm 0.1\%$ ) (Tables 1 & 2). No significant differences between species were observed for both %HR<sub>in</sub> (Mann-Whitney,  $U = 45$ ,  $p = 0.16$ ) and %CR<sub>in</sub> (Mann-Whitney,  $U = 52$ ,  $p = 0.24$ ). For *S. axillare*, all fish from the single-unit reef spatial group had their home ranges located entirely inside the NTZ, whereas 1 fish from barrier reef (%HR<sub>in</sub> =  $95.2 \pm 9.4\%$ ) and all fish from scattered patch reefs (%HR<sub>in</sub> =  $76.3 \pm 9.9\%$ ) and aggregated patch reefs (%HR<sub>in</sub> =  $84.5 \pm 2.1\%$ ) had part of their home ranges outside the NTZ

(Fig. 5A). Similarly, all *L. alexandrei* from the single-unit reef group used only areas inside the NTZ, while all fish from scattered patch reefs (%HR<sub>in</sub> =  $85.7 \pm 12.9\%$ ) had part of their home ranges beyond the NTZ boundary (Fig. 5B). Significant differences in %HR<sub>in</sub> were observed among *S. axillare* spatial groups (Kruskal-Wallis,  $H = 7.8$ ,  $p = 0.04$ ), specifically between single-unit reef and scattered patch reefs (Mann-Whitney pairwise,  $U = 0$ ,  $p > 0.03$ ). For *L. alexandrei*, a significant difference in %HR<sub>in</sub> was also found between single-unit reef and scattered patch reefs groups (Mann-Whitney pairwise,  $U = 0$ ,  $p > 0.03$ ). Regarding the %CR<sub>in</sub>, only 5 *S. axillare* (all from scattered patch reefs group, %CR<sub>in</sub> =  $88.8 \pm 19.5\%$ ) and 1 *L. alexandrei* (also from scattered patch reefs group, %HR<sub>in</sub> =  $99.7 \pm 0.4\%$ ) had part of their core ranges outside the NTZ.

In general, fish from the different spatial groups used their respective capture/release reef areas more intensively (Fig. 6A,B). Therefore, low overlap index (OI) values were observed among the mean home range areas of the spatial groups for both *S. axillare* ( $\bar{x} = 0.14 \pm 0.16 \text{ SD}$ ) and *L. alexandrei* (OI = 0.22) (Fig. 6C,D). A moderate overlap (OI = 0.44) was only observed between *S. axillare* from scattered patch reefs and aggregated patch reefs. For both species, fish from the different spatial groups used completely distinct mean core range areas resulting in no overlap (Fig. 6A,B).

#### 4. DISCUSSION

Positive effects of NTZs for fish communities, characterized by increased fish density and larger body size within the protected area, have been well documented worldwide (Halpern 2003, Lester et al. 2009, Malcolm et al. 2018, Gilchrist et al. 2020) and in Brazil (Floeter et al. 2006, Anderson et al. 2014, 2020).

Table 3. Mean  $\pm$  SD home range and core range areas ( $\text{km}^2$ ) for *Sparisoma axillare* and *Lutjanus alexandrei* spatial groups (SUR: single-unit reef; SPR: scattered patch reefs; APR: aggregated patch reefs; BR: barrier reef). Results of ANOVA and Student's *t*-test are shown

| Source                       | SUR             | SPR             | APR             | BR              | ANOVA |          |      |
|------------------------------|-----------------|-----------------|-----------------|-----------------|-------|----------|------|
|                              |                 |                 |                 |                 | df    | F        | p    |
| <i>Sparisoma axillare</i>    |                 |                 |                 |                 |       |          |      |
| Home range                   | $0.14 \pm 0.04$ | $0.33 \pm 0.11$ | $0.31 \pm 0.03$ | $0.25 \pm 0.11$ | 3     | 2.92     | 0.08 |
| Core range                   | $0.04 \pm 0.02$ | $0.07 \pm 0.02$ | $0.07 \pm 0.01$ | $0.05 \pm 0.01$ | 3     | 1.84     | 0.19 |
| — Student's <i>t</i> -test — |                 |                 |                 |                 |       |          |      |
| <i>Lutjanus alexandrei</i>   |                 |                 |                 |                 |       |          |      |
| Home range                   | $0.17 \pm 0.05$ | $0.29 \pm 0.10$ |                 |                 | df    | <i>t</i> | p    |
| Core range                   | $0.05 \pm 0.02$ | $0.06 \pm 0.02$ |                 |                 | 7     | 2.30     | 0.06 |
|                              |                 |                 |                 |                 | 7     | 0.91     | 0.39 |

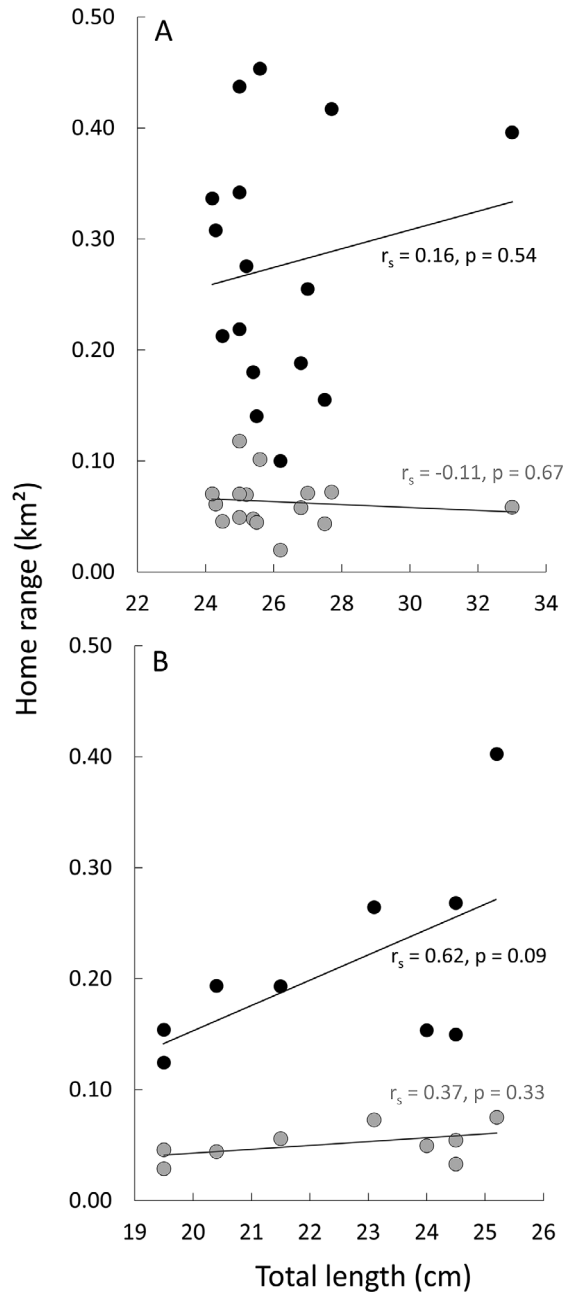


Fig. 4. Spearman rank correlation between total length and home range (black circles and font color) and core range (grey circles and font color) sizes for (A) *Sparisoma axillare* and (B) *Lutjanus alexandrei* in the Tamandaré coral reef complex

Our results also revealed a positive effect on fish density and size within the Tamandaré NTZ for both gray parrotfish *Sparisoma axillare* and Brazilian snapper *Lutjanus alexandrei*, corroborating previous studies in the area (Ferreira & Maida 2007). *S. axillare* >20 cm and *L. alexandrei* showed markedly higher densities in the single-unit reef area. In this area, *L. alexandrei* often aggregate to rest in caves

located underneath reef crests, forming large groups. Indeed, this behavior has been previously described to be a characteristic of many reef fishes that seek shelter and school for protection (McClanahan et al. 2007, Beck et al. 2014). Larger *S. axillare* (>20 cm) formed roving schools that could include up to around 70 individuals. This schooling behavioral strategy, efficient to avoid predators and competitors, makes those schools a target to fisheries, and as a consequence, they tend to shrink in numbers in heavily fished areas (Sadovy & Domeier 2005, Hamilton et al. 2016, Guerra et al. 2020). The presence of large schools in the Tamandaré NTZ shows a positive effect of the protection inside the NTZ.

Smaller *S. axillare* ( $\leq 20$  cm), by contrast, were more abundant in the patch reef areas (scattered patch reefs and aggregated patch reefs) of the NTZ, indicating a preference for this shallower habitat that is continuous inside to outside the NTZ. This area is less complex than the single-unit reef area, but has closely spaced shelter, and is less populated by larger fish, including predators, optimizing safe foraging. In addition, this area includes seagrass and algal beds, which are important as nursery areas for *S. axillare* (Feitosa & Ferreira 2015, Eggertsen et al. 2017). The observed size distribution of *S. axillare* indicates that recruitment occurs in the area, and that the patch reef areas are the preferred sites. For *L. alexandrei*, very few individuals smaller than 15 cm were observed, an expected pattern since the species has been shown to spend its first years in estuarine/mangrove areas, moving to reefs during their third or fourth year of life (Aschenbrenner et al. 2016a,b).

Despite the low weighted residency index values for *S. axillare* and some *L. alexandrei* individuals, nearly all tagged individuals showed a high residency index over the short term, indicating that both species were full-time residents in the monitored area until detections were permanently lost. Comparable detection periods were observed for the Mediterranean parrotfish *S. cretense* in a similar sized marine reserve (0.83 km<sup>2</sup>) in the Mediterranean (La Mesa et al. 2012) and for the stoplight parrotfish *S. viride* and schoolmaster *L. apodus* in a relatively larger (9.56 km<sup>2</sup>) Caribbean marine reserve (Garcia et al. 2015). However, long-term studies have shown high residency of up to 937 d for *S. cretense* (Afonso et al. 2008) and up to 363 to 1096 d for other *Lutjanus* species in natural and artificial habitats (Tin-Han et al. 2014, Huijbers et al. 2015, Williams-Grove & Szedlmayer 2016).

A decline in the number of detected fish throughout the monitoring period is usually observed in

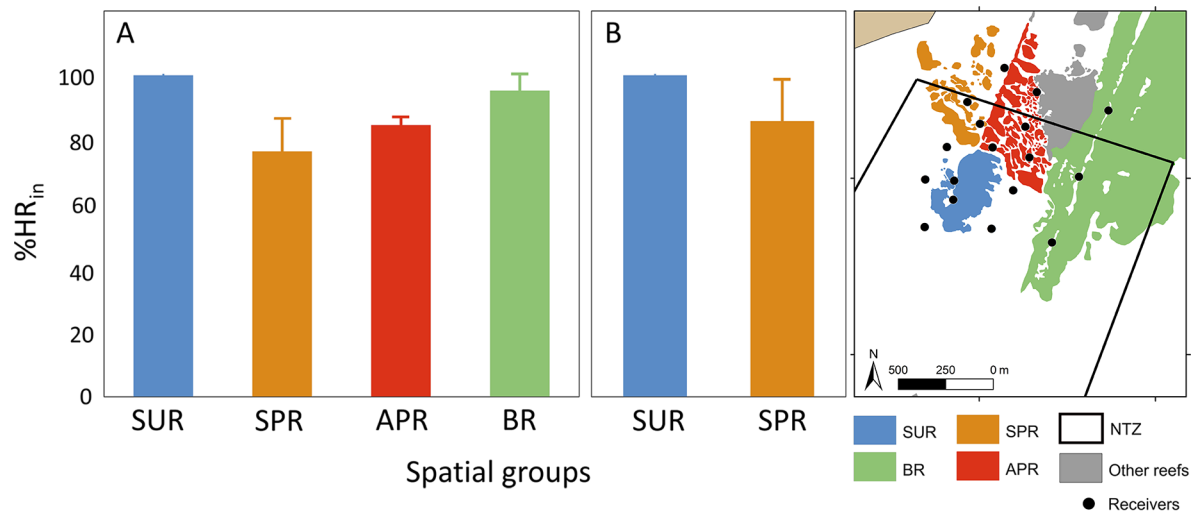


Fig. 5. Mean percentage of home range areas located inside the Tamandaré no-take zone (NTZ) (%HR<sub>in</sub>) for (A) *Sparisoma axillare* and (B) *Lutjanus alexandrei* spatial groups: single-unit reef (SUR), scattered patch reefs (SPR), aggregated patch reefs (APR), and barrier reef (BR). Error bars indicate 95% confidence interval. Map on the right highlights the location of the different reef areas that correspond to each of the spatial groups

acoustic telemetry studies (TinHan et al. 2014, Garcia et al. 2015, Wolfe & Lowe 2015), which can be mostly explained by natural mortality (e.g. predation), fishing mortality, and movement beyond the detection range of receivers (Khan et al. 2016, Brownscombe et al. 2019). Another possibility is that detection loss of tagged fish may be due to a transmitter malfunction or premature failure of the battery; however, equipment failure was not addressed as a relevant reason for detection loss in studies using similar equipment (Afonso et al. 2016, Khan et al. 2016). Moreover, in our study, transmitters used on 2 *L. alexandrei* and the one used on SPAAXI #05 were detected throughout their entire estimated battery lifetime. For the 3 *S. axillare* with noticeably short detection periods (SPAAXI #02, #12, #14) and for SPAAXI #05 (assumed to be dead a few days after release) mortality as a consequence of the tagging procedure should also be considered (Khan et al. 2016, Brownscombe et al. 2019).

Predation mortality is an expected effect of NTZs, as the initial increase in the abundance of prey attracts and even sustains populations of larger predators (Russ & Alcalá 1996, Steneck 1998). On the Tamandaré coral reef complex, large predators such as goliath grouper *Epinephelus itajara*, green moray eel *Gymnothorax funebris*, cubera snapper *L. cyanopterus*, and great barracuda *Sphyraena barracuda* are commonly seen inside the NTZ, as are signs of predation attempts on the resident prey fishes (B. P. Ferreira & D. L. Lippi pers. obs.). Seven parrotfish (SPAAXI #02, #03, #07, #13, #14, #16, #17) had their

last detections while sheltering at night. Since parrotfishes are strictly diurnal (Hobson 1975), it seems unlikely that these individuals would have left the monitoring area undetected during the night, and thus predation seems to be a reasonable explanation for fish disappearance in the present study.

Illegal fishing can also be a reason for detection loss in acoustic telemetry studies conducted inside NTZs, especially for areas with limited enforcement, such as large and remotely located NTZs (TinHan et al. 2014, Tickler et al. 2019). Although illegal fishing can also be a reason for detection loss in acoustic telemetry studies, fishing mortality inside the Tamandaré NTZ is unlikely as the area is relatively small, with well-defined boundaries and located close to the shore in front of the research facility. Such characteristics make the Tamandaré NTZ a fully enforced area that is easily monitored from both boat and land. However, fishing is allowed at the immediate vicinity of the NTZ, so mortality by fisheries would be expected to occur as a consequence of spillover or even due to short displacements to the open area. Those species are important fish targets, and *S. axillare* is one of the main species caught by both spear and hook-and-line fishing in the region (Silveira 2018). *S. axillare* and *L. alexandrei* individuals (mostly from scattered patch reefs and aggregated patch reefs) were detected outside the NTZ and had part of their home range and core range beyond its northern border, indicating a potential for fish spillover through those areas (Afonso et al. 2008, La Mesa et al. 2012). Our results thus suggest that

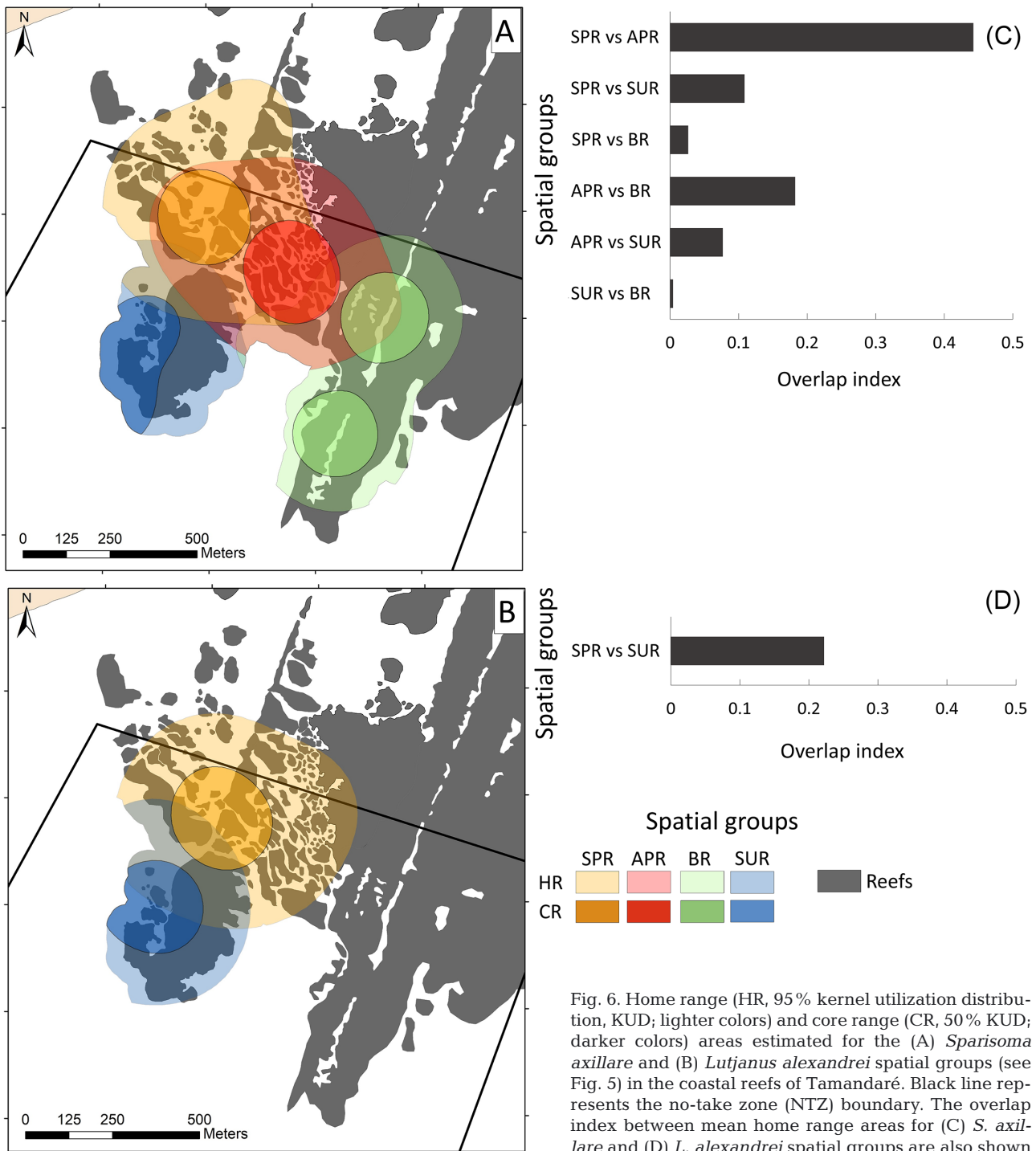


Fig. 6. Home range (HR, 95% kernel utilization distribution, KUD; lighter colors) and core range (CR, 50% KUD; darker colors) areas estimated for the (A) *Sparisoma axillare* and (B) *Lutjanus alexandrei* spatial groups (see Fig. 5) in the coastal reefs of Tamandaré. Black line represents the no-take zone (NTZ) boundary. The overlap index between mean home range areas for (C) *S. axillare* and (D) *L. alexandrei* spatial groups are also shown

fishing mortality is likely to occur at the unprotected reefs contiguous to the scattered and aggregated patch reef areas.

Emigration to areas outside the detection range of the receivers is also likely related to movements toward the deeper reefs beyond the last line of receivers in the barrier reef area. Snappers in Brazil

commonly perform ontogenetic migrations from shallow coastal to deeper reef areas (Frédou & Ferreira 2005, Aschenbrenner & Ferreira 2015). Like many snappers, *L. alexandrei* migrate from estuarine/mangrove areas to coastal reefs (Aschenbrenner et al. 2016a,b), a movement that continues gradually to deeper areas as the species is observed up to



depths of 50 m at sizes larger than 33 cm TL (Moura & Lindeman 2007, Fernandes et al. 2012). Therefore, the NTZ in the Tamandaré coral reef complex may act as a stepping stone during the ontogenetic migration. Individuals are likely to remain in the NTZ for a few years, as indicated by the increased densities inside the NTZ, with marked abundance of intermediate sizes (around 20 cm). This results in a buildup of abundance and biomass inside the NTZ, with expected spillover to nearby reefs, but mainly to deeper areas as individuals mature.

Snappers are known to perform reproductive migrations from home sites to aggregation sites during well-defined spawning seasons (Biggs & Nemeth 2016). The length at first sexual maturity for *L. alexandrei* is estimated around 20 cm TL, and the species has a clear spawning season (from November to March, with a peak in February) during which fish may aggregate, as indicated by an increase in fisheries landings for the species in the same period (Fernandes et al. 2012). In the present study, the monitoring period of 6 adult sized *L. alexandrei* (size range from 21.5 to 25.2 cm TL) overlapped with their spawning season. The loss of detections observed for 2 of those individuals (LUTALE #01 and #05, both with markedly short weighted residency indices) occurred during the spawning season and could be related to reproductive migrations to aggregation sites outside the NTZ, as suggested for *L. apodus* in Martinique (Garcia et al. 2014).

For *S. axillare*, the time of residency in the NTZ also seems to be sufficient for a significant reduction in mortality, resulting in an increase in both density and size. The formation of large schools, frequently observed in the single-unit reef area, is also a positive sign of recovery, since schooling behavior may be directly affected by fishing mortality (Guerra et al. 2020). Those schools were formed exclusively by initial-phase females, as shallow reef areas in Tamandaré are occupied mainly by this phase. Terminal-phase males are most likely present in the deeper areas of the barrier reef (B. P. Ferreira pers. obs.), where visual surveys were not conducted during this study due to limiting conditions (i.e. low visibility caused by stronger current and wave action). It is thus expected that ontogenetic and reproductive movements to deeper areas are likely to occur.

Several parrotfish species have complex social systems (van Rooij et al. 1996, Mumby & Wabnitz 2002), and movement patterns related to social interactions and reproductive behavior may play an important role in space used by individuals (Afonso et al. 2008). Size at maturation for female *S. axillare* is estimated at 25 cm TL, and reproduction is protracted and

occurs over the entire year (D. Veras unpubl. data). Therefore, most tagged individuals were mature females, and migrations associated with reproduction might be an important factor determining movements and residency times of this species in shallow reef areas. Nine *S. axillare* were last detected during daylight hours by the receivers on barrier reef or by the receiver located at the easternmost part of the aggregated patch reef area, which could indicate a permanent relocation to the unmonitored deeper reefs inside or outside the NTZ. Also, the lower residency index registered for aggregated patch reef and barrier reef fish might be related to frequent short-term displacements to the deeper portions of the barrier reef area beyond the monitoring ranges of the receivers. Such movements could possibly lead to low survival rates due to spillover movements in deeper areas. Indeed, the unmonitored deeper portion of the barrier reef area contiguous to the NTZ is recognized by local fishermen as a major fishing ground for larger parrotfish (>20 cm).

Acoustic telemetry is recognized as an effective tool for examining fish movements and habitat use at a variety of marine environments, as well as to assess the effectiveness of NTZs for protecting different species (Di Franco et al. 2018). However, acoustic telemetry is still relatively expensive, and the number of available acoustic receivers determines the spatial extent of the monitored area. Moreover, in morphologically complex high-relief habitats such as coral reefs, the detection range of receivers will be affected by the existence of physical barriers to signal propagation (Welsh et al. 2012, Selby et al. 2016). In the present study, the capability to detect cross-boundary movements and the extent of fish displacements at unprotected areas might have been limited by the low number of receivers deployed outside the NTZ that resulted in gaps in acoustic coverage, particularly in deeper areas. Similarly, possible relocations towards deeper reefs may have been undetected due to the non-overlapping listening ranges of the last line of receivers in the barrier reef area. Therefore, an expansion of the acoustic array to areas outside the NTZ as well as to deeper reef areas within the NTZ are necessary to better understand the extent of spill-over and cross-shelf movements performed by *S. axillare* and *L. alexandrei*, as well as the identification of the pathways utilized during those movements.

Both *S. axillare* and *L. alexandrei* used small home range and core range areas usually corresponding to the fish capture locations. Moreover, although relatively small, reefs within the Tamandaré NTZ were

shown to harbor spatially segregated subgroups of individuals for both species. The use of distinct reef areas by groups of fish has been shown for other reef fish species (Egli & Babcock 2004, Hammerschlag-Peyer & Layman 2010, Pillans et al. 2017). Site-attached species may benefit from the continued use of small home range and core range areas by the prompt access to resources (e.g. food and shelter) within a familiar reef area (Kramer & Chapman 1999). Additionally, low overlapping space use among fish subgroups may reduce intraspecific competition and therefore improve the overall fitness of the population (Welsh & Bellwood 2012b).

The mean home range size of *S. axillare* was comparable to the home range estimated for *S. cretense* (La Mesa et al. 2012), but approximately 6 to 30 times greater than previously reported for parrotfish species using acoustic telemetry (Afonso et al. 2008, Welsh & Bellwood 2012b, Garcia et al. 2014, Davis et al. 2017). Mean home range for *L. alexandrei* was equivalent to that estimated for *L. apodus* (Garcia et al. 2014) and red snapper *L. campechanus* (Froehlich et al. 2019), although about 6 to 50 times greater than that observed in other studies on *Lutjanus* species (Hammerschlag-Peyer & Layman 2010, Hitt et al. 2011a, Topping & Szedlmayer 2011). Such differences in home range sizes might be related to specific environmental and ecological features of the different studied sites and to species-specific requirements and behavior (Zeller 1997). However, it could also be a consequence of the different methods used to detect the acoustic signals and the duration of the monitoring period. A common characteristic of the above-mentioned studies with markedly smaller home range estimates was the utilization of active acoustic tracking instead of a multi-receiver passive monitoring array as used in the present study. During the active tracking, acoustic signals are detected by a hydrophone connected to a receiver on the surface and fish position fixes are recorded using a GPS as fish are individually tracked for short durations (from 1 to several days) (Brownscombe et al. 2019). Therefore, this method identifies fine-scale movement patterns over limited time intervals which may not encompass the entire activity space and consequently provides underestimated home ranges. On the other hand, our home range estimates with passive monitoring acoustic arrays are related to the detection ranges of the receivers and are then subject to a higher level of uncertainty. In the present study, such uncertainties were incorporated into the calculation of the utilization distributions (KUD<sub>95</sub> and KUD<sub>50</sub>) as a kernel bandwidth of 150 m (correspond-

ing to the 50% detection probability range) and, therefore, may have resulted in overestimated home ranges. It is also noteworthy that the implementation of the Vemco Positioning System to obtain fine-scale acoustic telemetry data would highly benefit future work in the region by providing more precise home range estimates.

Low variability in home range and core range sizes was observed among individuals within each species. For *S. axillare*, both home range and core range were not correlated with fish length, as previously observed for *S. cretense* (Afonso et al. 2008) and steephead parrotfish *Chlorurus microrhinos* (Welsh & Bellwood 2012b). For adult populations of *S. cretense*, home range size seemed to be related to individual type of social behavior (i.e. schooling fish or territorial fish) instead of body length (Afonso et al. 2008). On the other hand, positive relationships between fish length and home range size have been reported for snappers such as *L. campechanus* (Topping & Szedlmayer 2011, Piraino & Szedlmayer 2014, Froehlich et al. 2019) and checkered snapper *L. decussatus* (Nanami & Yamada 2008), which might be attributed to an increase in resource requirements of larger individuals (Wakeman et al. 1979, Kramer & Chapman 1999). However, other studies on snappers have found no influence of body length on home range size (Hammerschlag-Peyer & Layman 2010, Hitt et al. 2011a), suggesting that other factors including competition (Jones 2005), individual learning and behavior (Parsons et al. 2003, Brown & Laland 2003), and seascape structure (Hitt et al. 2011b, Pittman et al. 2014) likely determine home range variability within populations. The lack of statistical significance in the results reported here are likely to have been influenced by the small number of tagged fish, which is a recurrent issue in acoustic telemetry studies (Luo et al. 2009, Hammerschlag-Peyer & Layman 2010). Moreover, for both species, the minimum fish sizes suitable for tagging was limited by the transmitter sizes in order to not exceed the 2% tag to body mass threshold, and thus tagging was biased toward larger individuals. Further investigation on a higher number of individuals comprising a broader size scale (including juvenile and/or sub-adult individuals present in the NTZ) would provide a better understanding of how home range and core range sizes vary within *S. axillare* and *L. alexandrei* populations inhabiting the shallow coastal reefs of Tamandaré.

This study was the first to investigate movements and habitat use of teleost coral reef fishes by means of acoustic telemetry in Brazil and provides invaluable insights on the efficiency and functioning of the

NTZ established in the coastal reefs of Tamandaré. The effect of the Tamandaré NTZ in terms of increasing fish density and size was shown; however, our findings also highlight the importance of fisheries management outside the NTZ where fishing pressure is high (Silveira 2018) and capable of promoting a rapid decline in *S. axillare* and *L. alexandrei* populations. In addition, due to ontogenetic migrations, protection for areas that shelter older life stages of both species is necessary to maintain healthy stocks capable of continuing to sustain high fishing pressure. Protection of larger areas in order to encompass the reef continuum seems to be necessary, although the implementation of large NTZs or an increase in the size of existing NTZs is not an easy task. Recent work has highlighted the need to protect spawning areas (França et al. 2021) and deeper habitats (Eduardo et al. 2018) on Brazilian coral reef complexes. The establishment of more NTZs along the northeastern coast of Brazil is part of the management plan of the large Coral Coast MPA; this study indicates the importance of considering both isolation and connectivity in the design of new protected areas, as well as the relevance of including a heterogeneity of reef habitats.

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