



Home range and movement patterns of parrotfish in subtropical reefs of the Southwestern Atlantic

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Parrotfish are considered a key functional group on reefs, yet little information exists on home ranges of this group. We estimated short-term home ranges of two species of parrotfish (*Sparisoma axillare* and *S. frondosum*) on subtropical rocky reefs in Arraial do Cabo, Brazil, using active acoustic telemetry. We tagged 39 *S. axillare* and 25 *S. frondosum* and monitored them for 6.4 ± 0.35 days. Both species showed high residency during monitoring and relatively small home ranges of $30,600 \text{ m}^2 \pm 3,000 \text{ SE}$ for *S. axillare* and $31,200 \text{ m}^2 \pm 4,000$ for *S. frondosum* (Minimum Convex Polygon). Home range size increased with size of fish and was dependent on life phase for *S. axillare*, but not for *S. frondosum*. The relatively small home range sizes compared to other species and the same species in other locations may be related to high productivity and resource availability locally. The high residency and small home ranges observed here indicate that, at least under the short-term and site-specific conditions of Arraial do Cabo, small Marine Protected Areas could offer conservation benefits for *S. axillare* and *S. frondosum*, although broader and longer-term studies are needed to confirm this across their range.

Keywords: Home range, *Sparisoma axillare*, *Sparisoma frondosum*, Telemetry, Marine protected areas.

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Os peixes-papagaio são considerados um grupo funcional chave nos recifes, mas há pouca informação sobre as áreas de vida desse grupo. Estimamos as áreas de vida de curto prazo de duas espécies de peixes-papagaio (*Sparisoma axillare* e *S. frondosum*) em recifes rochosos subtropicais em Arraial do Cabo, Brasil, usando telemetria acústica. Marcamos 39 *S. axillare* e 25 *S. frondosum* e os monitoramos por $6,4 \pm 0,35$ dias. Ambas as espécies mostraram alta residência durante o monitoramento e áreas de vida relativamente pequenas de $30.600 \text{ m}^2 \pm 3.000$ SE para *S. axillare* e $31.200 \text{ m}^2 \pm 4.000$ para *S. frondosum* (Polígono Convexo Mínimo). O tamanho da área de vida aumentou com o tamanho do peixe e foi dependente da fase de vida para *S. axillare*, mas não para *S. frondosum*. Os tamanhos relativamente pequenos de áreas de vida comparados a outras espécies e às mesmas espécies em outros locais podem estar relacionados à alta produtividade e disponibilidade de recursos localmente. Sugerimos que os peixes-papagaio são plásticos no uso espacial e que a disponibilidade de recursos e o comportamento social moldam as áreas de vida dos peixes-papagaio. A alta residência e as pequenas áreas de vida indicam que mesmo pequenas Áreas Marinhas Protegidas devem funcionar bem como ferramentas de conservação para *S. axillare* e *S. frondosum*.

Palavras-chave: Área de vida, Áreas protegidas marinhas, *Sparisoma axillare*, *Sparisoma frondosum*, Telemetria.

INTRODUCTION

The study of animal home range can be defined as the spatial representation of the area needed for survival and reproduction, and is a classical issue in terrestrial (Seaman, Powell 1996; Bellis *et al.*, 2004; Börger *et al.*, 2008) and marine ecology (Kramer, Chapman, 1999). On reefs, movements of a given fish species are influenced by environmental drivers such as topography, resource availability, habitat quality and general seascape features (Pittman *et al.*, 2007; van Lier *et al.*, 2018; Streit *et al.*, 2021). Interactions between biotic processes (*e.g.*, predation) and habitat characteristics further shape fish behavior and distribution; for example, high reef rugosity is attractive for a majority of species of reef fish while most species will avoid crossing larger areas of bare sand, especially where predators are abundant (Chateau, Wantiez, 2009). At the individual level, size and maturity determine social status and intensity of intra- and inter-specific interactions, thus further shaping spatial movement patterns (Bruggemann *et al.*, 1994; Rooij *et al.*, 1996; Feitosa *et al.*, 2021). The combined characteristics of habitats, species and individuals thus act in conjunction as drivers, governing home range and patterns of movement behavior of fishes (Mumby, Wabnitz, 2002; Lowe *et al.*, 2003).

Parrotfish (Labridae: Scarinae) is an iconic functional group on reef ecosystems, mediating coral-algae interactions and taking part in nutrient cycling, sediment transport and bioerosion (Bonaldo *et al.*, 2014; Morgan, Kench, 2016). Size of territory and home range in parrotfish have been suggested to be influenced by a range of factors such as social structure, fish size, seascape characteristics (complexity, reef area, coastal morphology), local population density, interspecific competition and local benthic

productivity, (Rooij *et al.*, 1996; Howard *et al.*, 2013; Catano *et al.*, 2015; Carlson *et al.*, 2017; Davis *et al.*, 2017). Home range also depends on life stage of parrotfishes (Howard *et al.*, 2013). Most parrotfish species are protogynous hermaphrodites, with an initial phase (IP) as females and then changing sex to terminal phase males (TP) with a distinct coloration (Hoey, Bonaldo, 2018). It is common for terminal phase (TP) individuals of the majority of species to maintain a harem of initial phase (IP) fish, while defending their territory from other TP males (Rooij *et al.*, 1996; Howard *et al.*, 2013). For the species where this behavior occurs, territories are hypothesized to be defended to protect food resources and secure mating success of the TP males (Bruggemann *et al.*, 1994; Rooij *et al.*, 1996). However, different social structures may occur, also in harem species, such as dominant IP fish defending territories (Buckman, Ogden, 1973), or smaller males managing to fertilize eggs (*i.e.*, sperm competition), resulting in that it is not always advantageous for large females to transform into TP males (Muñoz, Warner, 2003, 2004). As food resources (*e.g.*, patches of high quality high-quality turf or endolithic algae) are not evenly distributed in reef seascapes, maintaining a territory with high-quality resources of food to maximize energy outcomes of foraging is an expected strategy (Bruggemann *et al.*, 1994).

Much of the parrotfish conservation initiatives which have spread worldwide sustain that, based on their important functional roles as herbivores, the higher their biomass, the better to improve reef resilience (Nyström, Folke, 2001; Adam *et al.*, 2011). As different functional herbivores, parrotfishes are roving microphages (Clements *et al.*, 2016), targeting cyanobacteria and other protein-rich autotrophic epilithic or endolithic microorganisms, while spending the majority of their daily activity feeding, often foraging in groups of complex social structures (Bruggemann *et al.*, 1994; Afonso *et al.*, 2008a). Due to their relatively small home ranges and high site fidelity, Marine Protected Areas (MPAs) have been suggested as an effective tool for parrotfish conservation and stock management (Afonso *et al.*, 2008b; La Mesa *et al.*, 2012; Howard *et al.*, 2013; Lippi *et al.*, 2022). The available knowledge on patterns of parrotfish movement behavior is mostly based on tropical species (*e.g.*, Howard *et al.*, 2013; Davis *et al.*, 2017; Lippi *et al.*, 2022), with a few cases from temperate reef systems (*e.g.*, Afonso *et al.*, 2008b). Despite their ecological uniqueness, functional roles, as well as importance as fishery targets, there is still little information on home ranges of parrotfishes, with marginal subtropical reef systems yet to be explored (Cordeiro *et al.*, 2016). This information is critical to support the optimal design of MPAs in order to be effective and meet management objectives (Sale *et al.*, 2005; Chateau, Wantiez, 2009; Di Franco *et al.*, 2018).

The southwestern Atlantic reefs are characterized by low coral cover comparative to Caribbean reefs, and with high dominance of turfs and macroalgae (Aued *et al.*, 2018). Ten species of parrotfish occur in the southwestern Atlantic, of which the genus *Sparisoma* is the most diverse, with the majority of species being endemic (Moura *et al.*, 2001). They are functionally important mainly as scrapers, with only two species being classified as excavators (*Scarus trispinosus* and *Sparisoma amplum*) (Ferreira, Gonçalves, 2006; Francini-Filho *et al.*, 2010). The larger species are important targets for the artisanal and recreational fishery in several regions in Brazil (Roos *et al.*, 2016; Queiroz-Véras *et al.*, 2025). Lack of effective management has unfortunately led to substantially decreases in population of the larger species during the last decades with unknown consequences for reef ecosystem function (Bender *et al.*, 2014; Roos *et al.*, 2020; Eggertsen *et al.*, 2024).

The gray parrotfish *Sparisoma axillare* and the Agassiz's parrotfish *Sparisoma frondosum* are two of the larger and most abundant endemic species, both with a broad distribution from subtropical to tropical reefs (00°25'S to 27°20'S), including the oceanic islands. They occur on both biogenic and rocky reefs with a depth distribution of about 1 to 40 m (Pinheiro *et al.*, 2018). Both species are listed as Vulnerable (VU) by the Brazilian official list of threatened species in the decree MMA N° 445/2014 (MMA, 2014). While these two species are threatened by intense fishing and protected only by a few no-take zones (2.5% of the Brazilian EEZ; Magris *et al.*, 2020), almost nothing is known about their movement patterns and home range. However, a recent study confirmed high site fidelity for *S. axillare* on tropical reefs at the Northeastern Brazilian coast (Lippi *et al.*, 2022). Home range sizes may however differ between tropical and subtropical environments due to different metabolic/energetic demands in different temperature regimes (Scott *et al.*, 2017, 2019) and differences in resource distribution.

Despite the two species being similar in size and occurring in the same habitat, behavioral differences exist that may result in distinct home ranges. Terminal phase *S. axillare* displays territorial behavior such as patrolling of territories while no such behavior has been recorded for *S. frondosum* TP males (Bonaldo *et al.*, 2006). Most *S. axillare* TP males are larger than the IP individuals, while this relationship is not so evident for *S. frondosum* where TPs are similar, or even smaller than IP fish (CELF, unpub. data).

We evaluated short-term home range and movement patterns for *S. axillare* and *S. frondosum* using active acoustic telemetry in subtropical rocky reefs on the Brazilian southeastern coast. The primary aim of the study was to establish home range size of the two species, to provide information on spatial patterns linked to social structure and size of parrotfish, and ultimately, giving support as baseline information for parrotfish management and conservation initiatives. We hypothesized that: 1) home range would not differ between the two species; 2) home range would be influenced by seascape variables (depth and coastal morphology) and fish size; and, 3) size of territory would differ between TP and IP individuals of *S. axillare* but not between TP and IP individuals of *S. frondosum* due to a more territorial behavior by the former.

MATERIAL AND METHODS

Study area. This study was performed on subtropical reefs in Arraial do Cabo (22°57'S 41°01'W), on the southeastern Brazilian coast, in Rio de Janeiro State. The region consists of an isthmus and four islands (Fig. 1), surrounded by rocky shores and sand beaches. The region was declared a marine extractive reserve in 1997, where only traditional fishers are allowed to exploit marine resources. However, no-take areas are absent and general enforcement is limited. Small-scale upwelling processes often occur in the region because of the prevailing winds (north-easterlies) and coastal morphology, where upwelling water is characterized by temperatures below 20°C (originating from the South Atlantic Central Water mass). It is worth noting that there is no significant freshwater input (*i.e.*, rivers) within a 40 km radius. The region is located in a micro tidal regime with semi-diurnal tides fluctuating between 1 and 0.06–0.025 m in maximum tides (the Brazilian Navy, Castro *et al.*, 2018). The benthic community is dominated by the epilithic algal matrix but also includes a variety of sponges, macroalgae, zoanthids,

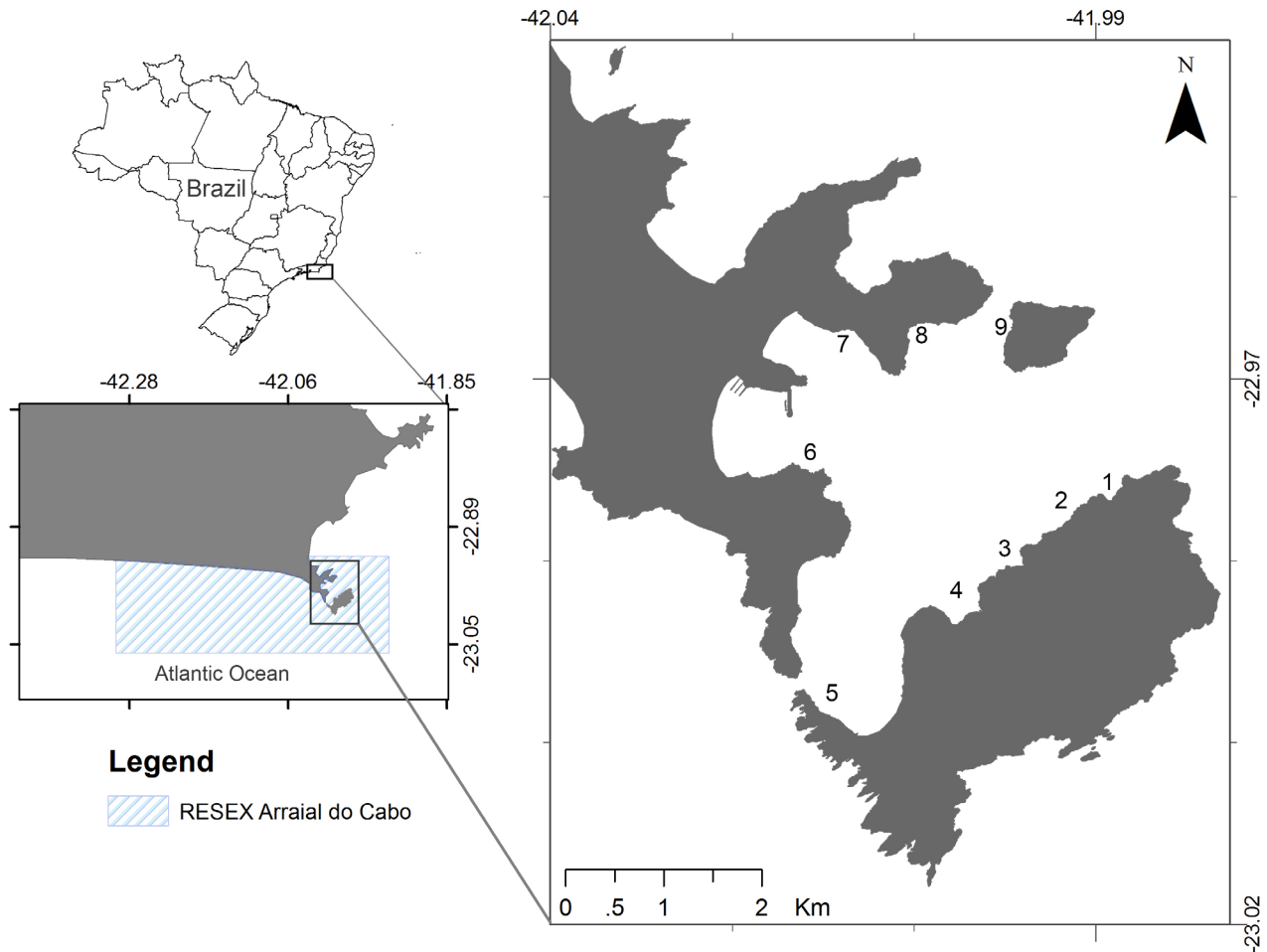


FIGURE 1 | Map of the study area, with the capture and tracking sites of *Sparisoma axillare* and *Sparisoma frondosum* with active telemetry. 1 = Anequim (coastal complexity - $cc = 0.30$), 2 = Abobrinha ($cc = 0.23$), 3 = Pedra Vermelha ($cc = 0.43$), 4 = Maramutá ($cc = 0.41$), 5 = Boqueirão ($cc = 0.04$), 6 = Saco de gato ($cc = 0.42$), 7 = Praia do Forno ($cc = 0.10$), 8 = Cardeiros ($cc = 0.29$), and 9 = Ilha dos Porcos ($cc = 0.12$). The blue box in the small map (lower right) indicates the limits of the Arraial do Cabo Marine Extractive Reserve (RESEX).

gorgonians, hydrocorals and some massive stony corals (Ferreira *et al.*, 2001; Cordeiro *et al.*, 2014). The east side where the study was performed is protected from the upwelling by coastal morphology and possesses subtropical characteristics with water temperatures averaging 22–24°C (Ferreira *et al.*, 1998). Narrow rocky reefs line the islands, with sand covering the area between the islands and the isthmus. Movement patterns of *S. axillare* and *S. frondosum* were studied at nine sites on the east side of the peninsula (e.g., where subtropical conditions prevail) (Fig. 1). Parrotfishes occur only on the rocky reefs on the east side (Cordeiro *et al.*, 2016), and we therefore expected the fish to have their entire home ranges within the study area. The nine sites were chosen to maximize spatial cover OF the study area with similar depth, benthic composition and extension of the reef habitat (Cordeiro *et al.*, 2014), and where the two study species are abundant (Cordeiro *et al.*, 2016). The identification of the species *S. axillare* and *S. frondosum* was based on the descriptions by Moura *et al.* (2001). Voucher specimens of these species are deposited in the collections mentioned in Moura *et al.* (2001).

Range test. We performed a detection range test of the acoustic receivers to evaluate signal detection at different gain settings (6–48). At gain 6, detections were obtained up to approximately 150 m from the transmitter, whereas at gains 24 and 48, the maximum detection distance increased to about 220 m. At gains 6 and 24, the highest number of detections and strongest signal strengths occurred at zero distance from the transmitter. At gain 48, the number of detections decreased with increasing distance from the transmitter (Fig. S1), accompanied by a less pronounced decline in signal strength compared to the other gain settings (Fig. S1). These results indicate that the highest detection rates and strongest signal strengths at gains 6 and 24 are achieved at shorter distances from the transmitter, whereas monitoring at gain 48 can be conducted over greater distances. To minimize false detections, signal intensities below 60 dB were excluded from the analyses, as such low values are more likely to represent noise rather than true detections.

Tagging and tracking. Field work was realized in March, November and December 2018, and in August in 2019. Movement patterns of fish were studied using active telemetry tracking. Active tracking allows for higher spatial resolution compared to passive monitoring, and also the possibility to search for fish over large spatial areas, although it is more labour-intensive. Fish were captured at night with a net bag and SCUBA, when fish were sleeping. Captured fish were brought to the boat, where total and fork length were measured. Fish were placed in a surgery tray with seawater (Fig. S2). A continuous acoustic tag (V9, 1000 milliseconds) was surgically implanted in the peritoneal cavity through a small incision between the pelvic and anal fins. The area of surgery and the tag was disinfected and the incision was closed with cyanoacrylate adhesive, since the muscle tissue of parrotfish is very soft and sutures may rupture their tissue. After the surgery, fish were placed in a large plastic container with seawater to recover, and then released by a diver at the same spot where it was captured. At each capture site, six individuals were tagged at the same occasion. In total, 39 *S. axillare* and 25 *S. frondosum* were captured, tagged and released (Tab. 1). No mortality was observed related to the surgery.

Monitoring was performed from a 4.8 m inflatable boat, using a unidirectional or a multidirectional hydrophone (VEMCO VH110 and VH165, respectively) and an acoustic receiver (VEMCO 100VR). No difference in detection rate was found between the two different types of hydrophones. The tags emit pings on six frequencies (60, 63, 75, 78, 81 and 84 kHz), resulting in a maximum number of six fish that can be tagged at one site at the same time. Each individual fish was tracked for 10 min per day during the lifetime of the tag (on average 10 days $\pm$ 0.23 SE), with tracking periods evenly distributed during mornings and afternoons to account for spatial variability due to diurnal patterns. The first active tracking started 24 h after the tagging to allow fish to recover. Due to the micro-tidal nature of tides in the study area, tides were not considered to influence movement patterns of the fish. The hydrophones were handheld from the boat and the tracking was conducted by searching for tagged fish while slowly following the reef at the tagging sites. When detected, an effort was made to follow the fish as close as possible (e.g., stay within the strongest signal possible > 90dB; < 5 m distance). All detections lower than 60dB (> 100 m distance from the hydrophone indicated by the range test performed pre-tagging) were excluded from the data analyses.

Coastal complexity was used as a proxy for reef area because local rocky reefs are narrow stripes following the coastal contour, thus more complex contours are likely to bear larger reef areas. This variable was then calculated similarly to the chain-and-tape method widely applied for substrate complexity (English *et al.*, 1997). In this case, the linear coastal contour (C) of each site was measured in Google Earth Pro software (Google Earth Pro 9.159.0.0 WebAssembly), as well as the straight distance between natural limits of each site (L). Thus, coastal complexity was calculated as $1 - (L/C)$, with values ranging from 0 to 1, where values close to 1 value indicate larger complexity (see Fig 1).

Statistical analysis. An occurrence index was calculated for all tagged individuals using the number of days when the individual was detected divided by the total number of days the individual was monitored. Differences in fish total length between the two species and between IP and TP individuals were tested with one-way ANOVA. All independent variables were tested for normality and homoscedasticity before analysis and, in case, those criteria were not met (KUD 50 and KUD 95), variables were log- (base 10) or square root-transformed to achieve normality. Functions *shapiro.test* and *levene.test* from the *stats* and *car* packages were applied for testing normality and homoscedasticity, consequently.

The acoustic telemetry data was used to determine home range using two methods: minimum convex polygons (MCPs) and kernel utilization distributions (KUD). The MCP determines home range based on the peripheral detections of each individual, while kernel distribution calculates relative probability of where the fish will be found during a given time (Worton, 1987). Home range was determined as KUD 95% and core use area as KUD 50% (Afonso *et al.*, 2008a), calculated using least-square cross validation (LSCV) smoothing parameter (Seaman, Powell, 1996). The MCPs and KUDs were calculated in the *adehabitatHR* package (Calenge, 2006) in R. When MCPs or KUDs overlapped land, area on land was manually excluded from home ranges in QGIS.

To test if home range area was dependent on size or life phase of fish (IP or TP), home range area was modeled separately for each species using linear mixed-effect models (LMMs) with the *lme4* package (Bates *et al.*, 2015) in R (v. 4.0.0). We tested *a priori* differences in species size using ANOVA applied to total length and using species, life phase and the interaction of these as fixed factors. Species were analyzed separately because of ecological and behavioral characteristics of species, as well as previously known size differences (tested here) that could influence measured variables. Fish size, life phase and coastal contour were applied as fixed factors to the models, and site was included as a random factor in the models to account for any non-measured or non-replicable habitat variability. Linear models were also applied to KUD 95 and 50 relationships with fish size, life phase and coastal contour using the function “*lmer*” from the “*lme4*” package (Bates *et al.*, 2015). The KUDs were log transformed, and MCP was square-root transformed to comply with model premises and normality was tested with the Shapiro-Wilks test. All models were initially built including a random term, the fixed effects of the independent variables and the interaction between size and life phase. Whenever interactions were non-significant, final models were rerun without the interaction term. P-values from models output were extracted using the “*Anova*” function from the “*car*” package (Fox, Weisberg, 2019).

Relative contribution of independent variables was extracted by partitioning the R^2 values of each model using the function “partR2” from the “partR2” package (Stoffel *et al.*, 2021), and the random variance relative contribution was extracted from the total residual variance using the functions “VarCorr” and “get_variance_residual” from packages “lme4” and “insight” (Lüdtke *et al.*, 2019), respectively.

Species movement was extrapolated from the total length of individual trajectories during the 10 min monitoring, calculated using the function “as.ltraj” from “adehabitatLT” package (Calenge, 2006). Trajectories were calculated as type II, in which sequential detections are defined as points of the trajectories and the total length is based on the sum of the geographical distances between each sequential detection for each individual per surveyed day. Original coordinates were projected to the metric system (*i.e.*, UTM, EPSG 32724) using the “spTransform” function from the “rgdal” package (Bivand *et al.*, 2022).

We applied generalized linear models (GLM) using Gamma distribution (log link) to model association of daily fish trajectory with fish size, life phase stage and coastal complexity. Models did not converge using sites as a random factor, thus site was not included in the final models. To account for any seasonal variation in daily trajectories, we included a ‘time of the year’ (combination of year and month) random factor in the models. We applied the *glmmTMB* function from the homonymous package (Brooks *et al.*, 2017).

To investigate if any territorial behavior could be detected, overlap in home range core use (KUD 50) between individual fish was calculated in QGIS (v. 3.4). For *S. axillare*, this resulted in 10 TP, 15 IP and 26 fish for the IP/TP overlap. For *S. frondosum*, four TP, 10 IP and 11 IP/TP were tagged at the same occasion and site and used in the overlap calculations.

RESULTS

Each of the 64 fish were monitored 2–11 days (6.4 ± 0.35 SE), which resulted in a total of 3860 min (Tab. S3). Total length of fish varied between 374.6 and 405.6 mm for *S. axillare* and 369.6 and 409.7 mm for *S. frondosum* (Tabs. 1, S4). Significant size differences (TL) between *S. axillare* and *S. frondosum* were observed (ANOVA; F-value 1, 60 = 12.1, $p < 0.01$), and also between phases (IPs and TPs) (F-value 1, 60 = 11.2, $p < 0.01$) which were more evident for *S. axillare* (Tab. 1).

Movement and home range size. Home range for the tagged fish varied with the MCPs ranging between 2,100 and 83,400 m² for *S. axillare* averaging 30,600 m² $\pm$ 3,000 SE and between 1,800 and 77,500 m² for *S. frondosum*, averaging 31,200 m² $\pm$ 4,000 SE (Tab. 1, Figs. S4, S5, S6). Home ranges estimated with kernel distribution (KUD 95%) ranged between 500 and 20,250 m² for *S. axillare* and between 1,200 and 358,800 m² for *S. frondosum* (Tab. 1; Fig. 2; Figs. S4, S5, S6) with an average of 50,500 m² $\pm$ 10,000 and 46,100 m² $\pm$ 10,000 for the former and latter, respectively. The largest home ranges were recorded for terminal phase (TP) individuals of both species.

The core areas followed the same patterns, with TP individuals using the largest recorded areas, and the IPs the smallest (Tab. S3; Fig. 2), with an average of 10500 m² $\pm$ 2000 SE for *S. axillare* and 10,400 m² $\pm$ 3,000 SE for *S. frondosum*. The largest MCPs

TABLE 1 | Number of tagged fish (N), phase (IP = Initial phase, TP = Terminal phase), total length (TL), mean home range ($\pm$ SE) and mean trajectory length ($\pm$ SE) for each species and phase.

Species	N	Phase	Mean TL (mm)	Mean KUD 95% (m ²)	Trajectory length (m)
<i>S. axillare</i>	25	IP	389.0 $\pm$ 7.5	50600 $\pm$ 8900	455 $\pm$ 326
<i>S. axillare</i>	14	TP	438.6 $\pm$ 13.6	56400 $\pm$ 16500	452 $\pm$ 287
<i>S. frondosum</i>	18	IP	363.4 $\pm$ 9.0	34000 $\pm$ 11100	417 $\pm$ 271
<i>S. frondosum</i>	7	TP	372 $\pm$ 15.9	62000 $\pm$ 45900	526 $\pm$ 324

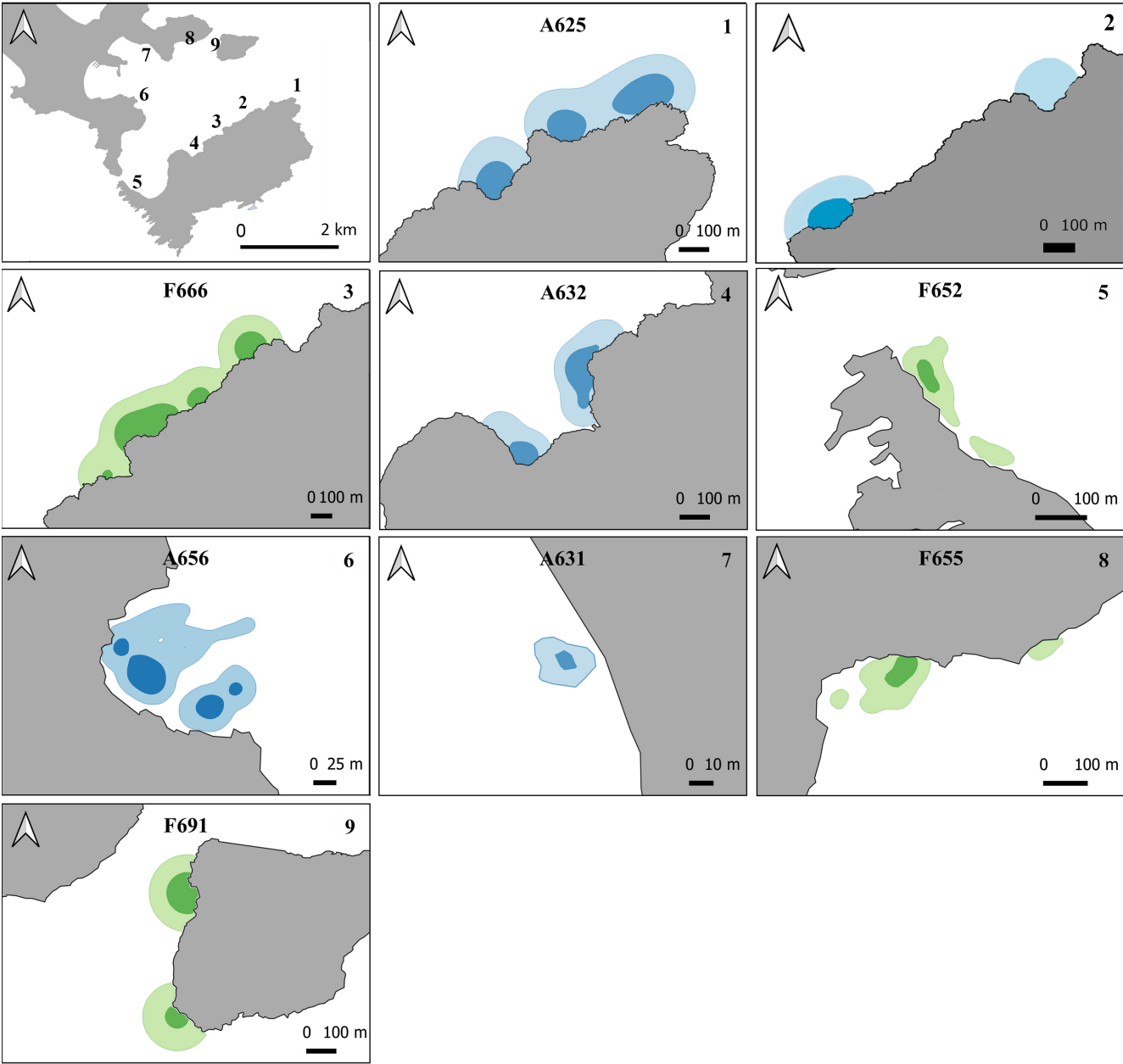


FIGURE 2 | Examples of home ranges (KUD 95) and core areas (KUD 50) for randomly selected individuals of tagged *Sparisoma axillare* (blue) and *S. frondosum* (green) at each site. Darker shades represent core areas for each species, and lighter shades home ranges. The codes represent the individual code for each fish, and the number in the right corner the site number. Note that the scale is not the same for all sites.

for *S. axillare* were located at site 1, 2, 3 and 4, while the largest home range and core area were located at site 1, 2 and 5 (Fig. 3). Only one individual was tagged at site 7. Regarding *S. frondosum*, the largest MCPs, home ranges and core areas were all detected at site 3 (Fig. 3). The longest movement detected for *S. axillare* from the caption site was 715 m (A 623), and for *S. frondosum* 749 m (F 666). All movements were always recorded along the rocky reef (Fig. 4).

MCP values for both species were not related to any of the tested variables (Tab. 2). Home range of *S. axillare* (KUD 95) was positively associated with individual fish size (Tab. 2; Fig. 5) and size explained 7.1% of the variance of the linear model (total variance explained by the model was 15.9%). Between-site variation contributed 50.1% of total variation for *S. axillare* data indicating considerable variability in samples among sites. Contrastingly, home range of *S. frondosum* (KUD 95) was positively associated with coastal complexity (Tab. 2), which explained 18.1% of total variance of the linear model (total variance explained by the model 20.1%). Random factors (fish size and life phase) showed a low contribution to the total variance (3.1%) of the *S. frondosum* model. Regarding daily linear distances, *S. axillare* tended to rove comparatively larger distances at sites with more complex coasts irrespective of individual size or life phase (table x). Daily movements of *S. frondosum* were not related to any of the tested variables ($p > 0.05$). Variance associated with the random factor time of the year was $< 0.01\%$ for both *S. axillare* and *S. frondosum*, indicating an absence of temporal variation during the sampling period.

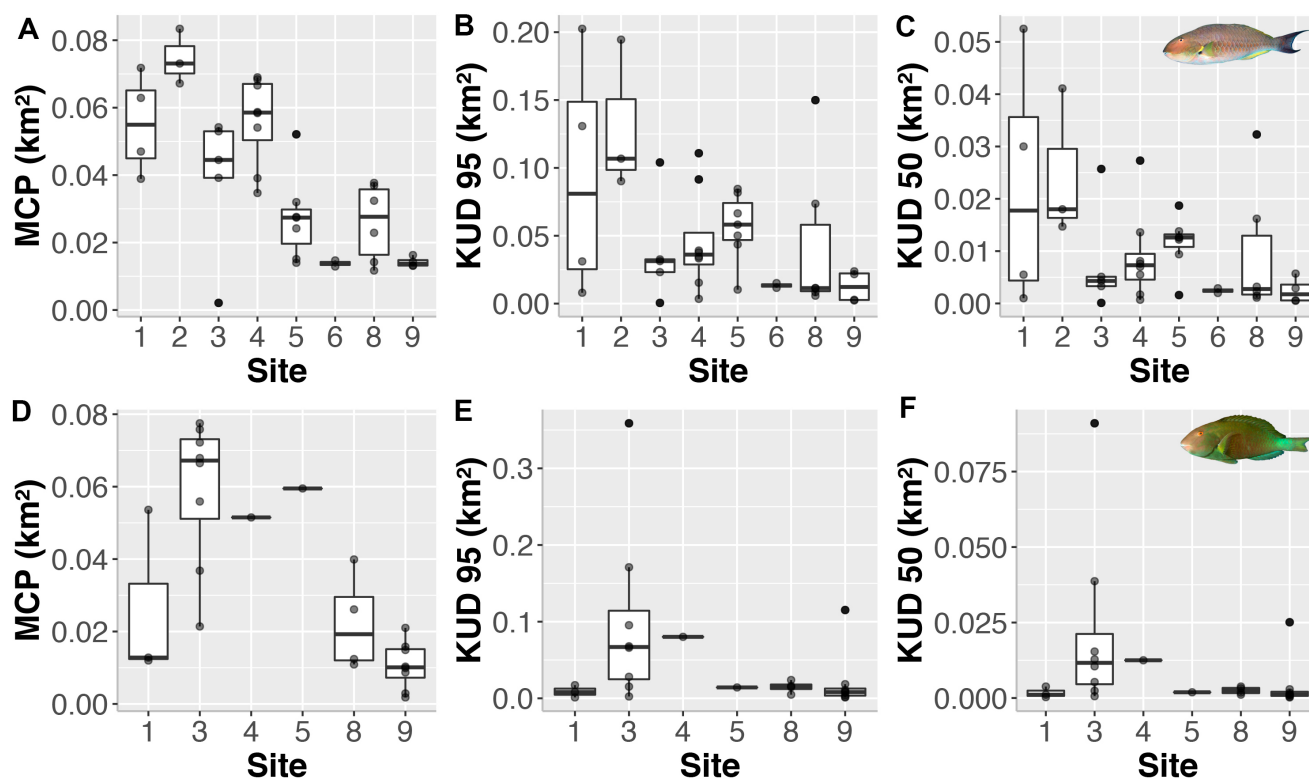


FIGURE 3 | Comparative home range size and core use of *Sparisoma axillare* (A-C) and *S. frondosum* (D-F). Horizontal lines represent median, boxes 25 and 75% percentiles and the dots are outliers. The numbers on the x-axis represent each site where fish was captured as in Fig. 1.

TABLE 2 | Summary of linear mixed effect models applied for *Sparisoma axillare* and *Sparisoma frondosum* probabilistic home range (KUD 95), probabilistic core use (KUD 50) and maximum home range (MCP) variables using acoustic telemetry in Arraial do Cabo (RJ), Brazil. Log – logarithmic transformation of variables (natural base), sqrt – square root transformation of variables, CI – confidence interval of model intercept.

Species	Variable		Fixed Effects				Random Effects	
			Intercept	Coastal Complexity	Life phase	Total length		
<i>Sparisoma axillare</i> (N = 39)	log(KUD 95)	Estimates	-8.79	1.65	-0.05	0.01	Site	1.04 (51%)
		CI	[-12.49, -5.09]	[-4.04, 7.34]	[-0.99, 0.88]	[0.00, 0.02]	Residual	1.02 (49%)
		t-value	-4.84	0.59	-0.12	2.64	N	9
		p-value	<0.001	0.559	0.908	0.013	Marginal R ² / Conditional R ²	0.159 / 0.584
	log(KUD 50)	Estimates	-10.88	1.11	-0.21	0.01	Site	0.74 (37%)
		CI	[-14.82, -6.95]	[-4.04, 6.27]	[-1.24, 0.81]	[0.00, 0.02]	Residual	1.27 (63%)
		t-value	-5.62	0.44	-0.42	2.76	N	9
		p-value	<0.001	0.663	0.678	0.009	Marginal R ² / Conditional R ²	0.168 / 0.474
	sqrt(MCP)	Estimates	0.11	0.19	0.00	0.00	Site	0.00 (67%)
		CI	[-0.05, 0.28]	[-0.12, 0.50]	[-0.04, 0.04]	[-0.00, 0.00]	Residual	0.00 (33%)
		t-value	1.42	1.26	0.08	0.12	N	9
		p-value	0.165	0.218	0.940	0.907	Marginal R ² / Conditional R ²	0.133 / 0.712
<i>Sparisoma frondosum</i> (N = 25)	log(KUD 95)	Estimates	-7.41	5.38	-0.11	0.01	Site	0.06 (3%)
		CI	[-13.53, -1.28]	[0.47, 10.28]	[-1.45, 1.23]	[-0.01, 0.02]	Residual	2.01 (97%)
		t-value	-2.53	2.29	-0.17	0.68	N	6
		p-value	0.020	0.033	0.865	0.508	Marginal R ² / Conditional R ²	0.205 / 0.229
	log(KUD 50)	Estimates	-8.82	5.66	-0.16	0.00	Site	0.06 (3%)
		CI	[-14.93, -2.72]	[0.81, 10.50]	[-1.50, 1.17]	[-0.01, 0.02]	Residual	2.00 (97%)
		t-value	-3.02	2.44	-0.26	0.54	N	6
		p-value	0.007	0.024	0.801	0.595	Marginal R ² / Conditional R ²	0.225 / 0.246
	sqrt(MCP)	Estimates	0.06	0.21	0.01	-0.00	Site	0.00 (0.3%)
		CI	[-0.21, 0.33]	[0.01, 0.41]	[-0.05, 0.07]	[0.00, 0.00]	Residual	0.00 (99.7%)
		t-value	0.48	2.18	0.39	-0.41	N	6
		p-value	0.639	0.042	0.700	0.689	Marginal R ² / Conditional R ²	0.195 / 0.198

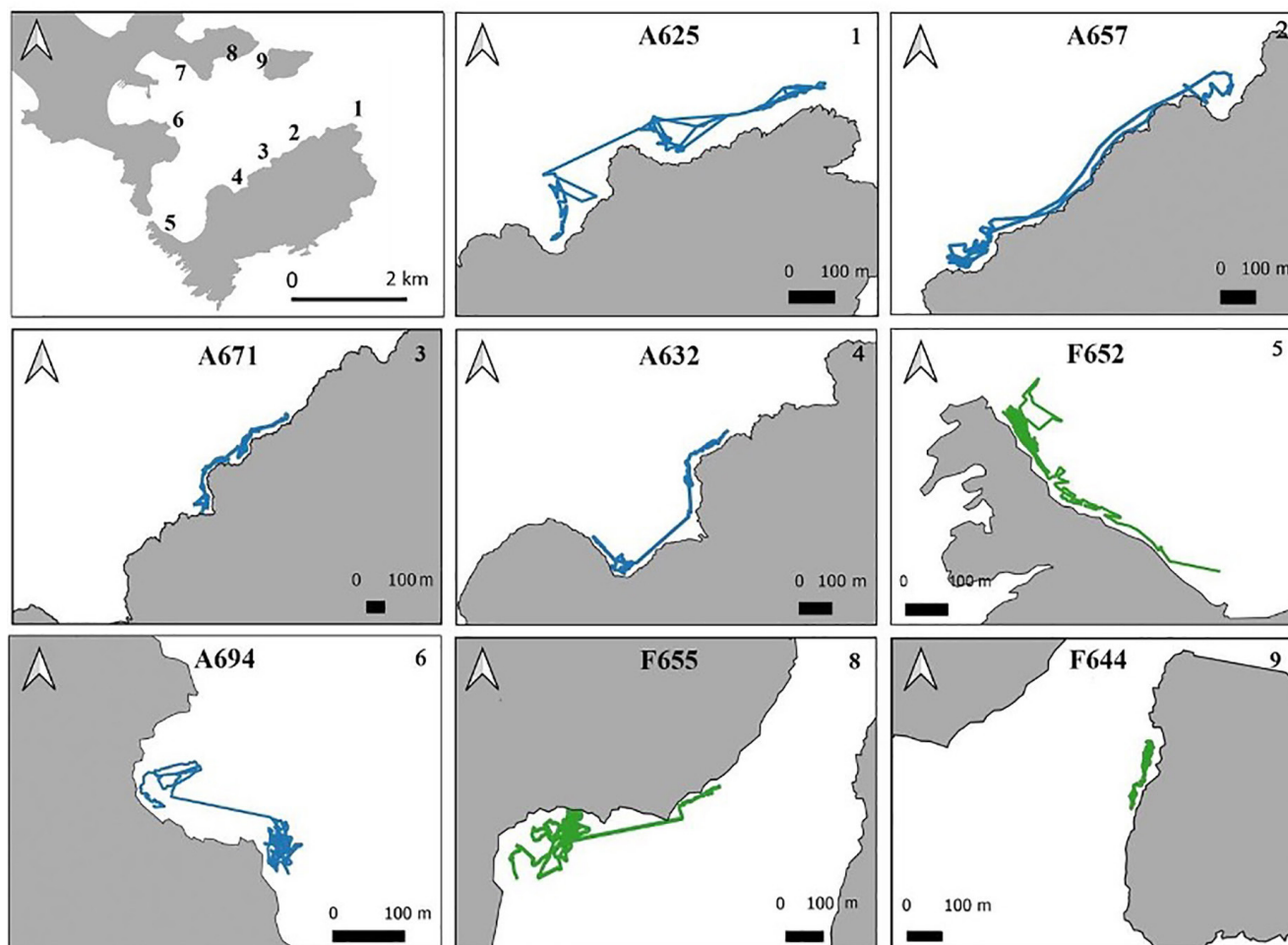


FIGURE 4 | Examples of movement patterns of *Sparisoma axillare* (blue) and *S. frondosum* (green) at the studied sites (1–9).

Site fidelity/habitat utilization. All tagged fish were detected along the rocky reef (*i.e.*, on hard substrate), at the same stretch of coast or island where they were tagged. Occurrence index was $70.1 \pm \text{SE } 2.6$ for *S. axillare* and $61.5 \pm \text{SE } 4.7$ for *S. frondosum*, with values ranging from 25 to 100 for the former and 25 to 90.9 for the latter (Tabs. 1, S1). No individual was ever detected in a location where it would have had to cross the open sand areas to reach the other islands or peninsulas on the isthmus.

Overlap in homerange. *Sparisoma frondosum* showed a lower % of overlap in core home range (KUD 50) of all life stages except terminal phase compared to *S. axillare*. While overlap in core home range was similar for all life phases of the former, overlap was very low (0.34% of core use areas (KUD 50%) between terminal phase individuals of *S. axillare* (Tab. 3).

TABLE 3 | Overlap in home range between initial (I) phase, initial and terminal (T) phase and terminal phase fish of the two studied species. Overlap in home range is calculated as % of Kernel Utilization Distribution 50% and shown $\pm$ standard error

Species	Phase	KUD 50 (%)
<i>Sparisoma axillare</i>	I/I	5.53 $\pm$ 0.037
	I/T	2.91 $\pm$ 0.013
	T/T	0.34 $\pm$ 0.001
<i>Sparisoma frondosum</i>	I/I	1.54 $\pm$ 0.007
	I/T	2.50 $\pm$ 0.014
	T/T	19.57 $\pm$ 0.131

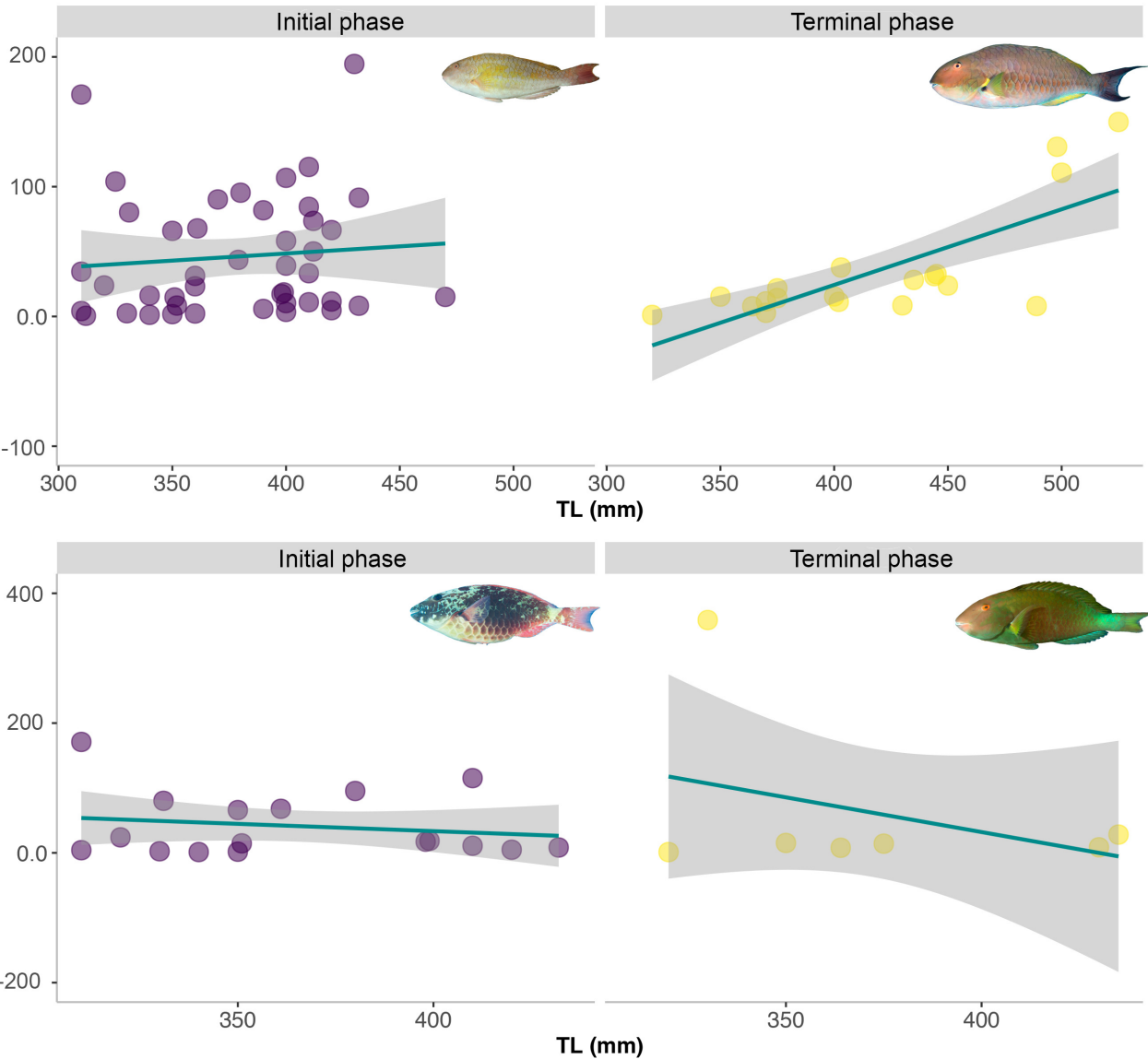


FIGURE 5 | Comparative relationship between home range and total length (TL) for *Sparisoma axillare* (upper panels) and *S. frondosum* (lower panels) with a fitted line. Shaded areas represent confidence intervals, and each dot the home range of an individual fish.

DISCUSSION

The present study provides critical information on home ranges for the endemic and abundant *S. axillare* and *S. frondosum* in the Southwestern Atlantic. Our data show that on a short time scale, site fidelity is high for the two studied species. This is consistent with other home range studies of parrotfish in the tropical Atlantic and Pacific (e.g., Howard *et al.*, 2013; Davis *et al.*, 2017; Lippi *et al.*, 2022). No individual was ever detected on the cooler upwelling side of the islands or isthmus in accordance with previous observation studies (Cordeiro *et al.*, 2016), confirming that temperature is an important factor for spatial use. Further, sandy areas seem to function as barriers, maintaining low movement connectivity among adults between reefs on the coast and islands, with fishes moving only along and over the rocky reef substrate. This behavior has been recorded for several species of reef fish (Lowe *et al.*, 2003; Berkström *et al.*, 2020) and has implications for the placement of MPAs and conservation strategies (Di Franco *et al.*, 2018). Visual observations in the area confirm that the two species spend most of their time along the reef and seldom venture out on the sand, as most of the area lacks patches of seagrass, macroalgae beds or rubble habitats that would serve as stepping stones or alternative habitats (Ferreira *et al.*, 2001; Cordeiro *et al.*, 2016; Lucena *et al.*, 2024).

Since fish habitat is restricted to the rather narrow (average 30 m in length from the surface to the sand interface (Ferreira *et al.*, 2001) and shallow (average 10 m deep) rocky substrates, home range of large parrotfishes as *S. axillare* and *S. frondosum* comprise mainly longitudinal movements.

Our results support that fish size does not necessarily seem to be a primary factor in driving size of home ranges for parrotfish. In a study by La Mesa *et al.* (2012), *Sparisoma cretense*, who inhabit temperate to subtropical reefs, sustained comparatively larger home ranges than the individuals in our study, despite being smaller (max size of tagged individuals 29.8 cm; La Mesa *et al.*, 2012). For the Pacific species *Chlorurus microrhinus* (max length 70 cm; Welsh, Bellwood, 2012; Howard *et al.*, 2013), considerably smaller home ranges than the fish in our study have been recorded. Although most TP fish in our study had larger home ranges compared to IP fish, home range was not statistically influenced by size or life phase for *S. frondosum*, as hypothesized, and was only weakly influenced by size for *S. axillare*. Home and core ranges of *S. axillare* were one order of magnitude smaller in Arraial do Cabo compared to the same species on tropical coral reefs in the state of Pernambuco (Lippi *et al.*, 2022), despite that most of the fish in our study were larger and included TP individuals. Although we used active instead of passive telemetry, limiting direct comparability with previous studies, our results nevertheless indicate that *S. axillare* in Arraial do Cabo occupies substantially smaller home ranges than conspecifics on tropical reefs.

Similarly to home range, daily trajectory was positively associated with size for *S. axillare*, but not for *S. frondosum*. Longer forays of up to 400 m from tagging sites have been observed for *S. rubroviolaceus* on reefs in Hawai'i (Howard *et al.*, 2013) and over 500 m for *C. microrhinus* at the Palmyra atoll (Davis *et al.*, 2017), comparable to the movements in the present study (< 700 m).

Coastal complexity was positively associated with the linear movements of *S. axillare* and with the home range of *S. frondosum*. Previous studies have documented differences in parrotfish movements between more open coasts and small bays (Howard *et al.*,

2013). Although our models explained only a modest proportion of the variance, this is consistent with the expectation that home range is shaped by multiple interacting factors beyond those measured here. For instance, in harem-forming species, characteristics such as harem size (*i.e.*, number of IP females) have been suggested as potential drivers of home range (Howard *et al.*, 2013), but these aspects were not quantified in our study. Other unmeasured variables such as local resource availability, fine-scale habitat heterogeneity, interactions with territorial damselfish, and temperature (Francini-Filho *et al.*, 2010; Catano *et al.*, 2015; Davis *et al.*, 2017) may also play a role. Evaluating these factors would require detailed, in-water behavioral observations and is therefore beyond the scope of the present study but would provide valuable avenues for future research.

A possible explanation to the smaller home ranges found in this study compared to home ranges of *S. axillare* on tropical reefs may be high resource availability due to the localized upwelling. The subtropical reefs of Arraial do Cabo are constantly influenced by upwelling events (Cardozo-Ferreira *et al.*, 2023), resulting in food resources being comparatively N-enriched (Cardozo-Ferreira *et al.*, 2026). Turf biomass is two-fold (70 to 280 gcm⁻²; Ferreira *et al.*, 1998) the values reported for the Great Barrier Reef (Klumpp *et al.*, 1987; Russ, 1987; Klumpp, McKinnon, 1992) or for Caribbean reefs (Lobel, 1980; Carpenter, 1985, 1988). Local upwelling certainly contributes to these high values of algae biomass and primary productivity (Lanari, Coutinho, 2014), suggesting that smaller home ranges may be sufficient to meet energetic needs compared to locations where upwelling is absent (*e.g.*, Lippi *et al.*, 2022). Micro components of the diet of *S. axillare* include beyond detritus also green filamentous algae, cyanobacteria, diatoms and micro-invertebrates (Cardozo-Ferreira *et al.*, 2023), all present in abundance in turf algae. Including nutrient content in studies of home ranges and comparisons of fish movement among geographic regions could be a useful approach in further studies to better explain spatial patterns (see for example Catano *et al.*, 2015).

Core use areas may among other factors also be influenced by competition because parrotfish often use distinct sites for sleeping and migrate daily to their diurnal foraging areas (Davis *et al.*, 2017; Lucena *et al.*, 2024). Consistent with previous studies (*e.g.*, Welsh, Bellwood, 2012; Davis *et al.*, 2017), small core use areas were also confirmed in this study, with most individuals showing one or two core use areas on the reef. The spatial pattern of core utilization has previously been linked to optimal foraging behavior for parrotfish (Welsh, Bellwood, 2012; Yarlett *et al.*, 2020). Parrotfish can be highly selective when feeding, and preferred resources may be patchily distributed or according to habitat and depth, with implications for their distribution on a local scale (Bruggemann *et al.*, 1994; Clements *et al.*, 2016; Carlson *et al.*, 2017). At all study sites, the reef slope is rather steep (> 20 degrees of inclination) with few plateaus, which means that depth is only constant at a very narrow range. *Sparisoma axillare* prefer shallow areas of the reef (1–5 m) while *S. frondosum* have a more even distribution, although with higher biomass at the deeper parts of the reef slope (10–15 m) (Cordeiro *et al.*, 2016). The methodology used in our study does unfortunately not allow for the detection of movement patterns at this fine spatial scale.

Social behavior is an important factor influencing distribution patterns of parrotfish (Buckman, Ogden, 1973; Afonso *et al.*, 2008a,b; Feitosa *et al.*, 2021). In our study, IP and TP fish showed considerable overlap of home range areas, while on tropical coral reefs of Pernambuco, on the Brazilian northeastern coast, they show some level

of niche segregation (Lippi *et al.*, 2022). The seascape in our study lacks deeper reefs, thus confining all individuals to a max depth of < 15 m. However, TP individuals of *S. axillare* had significantly larger home ranges than IP fish. This may be an effect of both social behavior and size. Despite that TPs of this species have been shown to display territorial behavior (Bonaldo *et al.*, 2006), large fishes are also more prone to rove large areas. The larger overlap in home range by TP *Sparisoma frondosum* corroborates previous observations of lack of territorial patrolling (Bonaldo *et al.*, 2006), but a larger sample size is needed to confirm these patterns, as they were highly variable.

In conclusion, short-term home range estimates indicate that the studied species utilize rather small areas (on the order of a few hundred meters – 1,000 m in length), which would fit in manageable no-take zones and possibly be effective to protect their main habitats in Arraial do Cabo. Within the Arraial do Cabo MPA, the restricted-use zone (ZURE) located between our sites 2 and 3 measures approximately 1,000 × 200 m, fitting this description. In this zone, both fishing and tourism is prohibited. Interestingly, this zone coincided with the highest number of parrotfish detections in our study. While our data were not designed to evaluate the effectiveness of specific management measures, this pattern may indicate that even relatively small, well-delimited areas can provide benefits to parrotfish populations when adequately enforced. Since all larger species of parrotfish in the study area have been severely affected by spearfishing, with the largest, green beaked parrotfish (*Scarus trispinosus*), being considered functional extinct (Bender *et al.*, 2014), these results are potential good news for local efforts on parrotfish conservation. The entire MPA banned parrotfish harvest since 2019 (MMA, 2019), but to our knowledge there has been no systematic assessment of compliance or enforcement effectiveness of this ban. Such evaluations would be crucial to determine whether these strategies are achieving their intended conservation outcomes. Both studied species were restricted to narrow rocky reef habitats, which increases the concerns about habitat conservation, but potentially facilitates the establishment of conservation efforts. Geographical placement would be dependent on the objective of protected areas, *i.e.*, if promoting spill-over would be important.

Our findings indicate that a combination of size, life phase and seascape features primarily shape home range size and movement behavior in the present study. Larger individuals of *S. axillare* exhibited larger home ranges, which is likely important for the social organization of harem-forming species and should be taken into consideration when designing no-take areas. This study provides the first home range estimations of these two species in Brazilian subtropical reefs, but long-term monitoring would be advisable to understand if individuals relocate over broader temporal scales, as documented for tropical species of parrotfish elsewhere (Chateau, Wantiez, 2009; Davis *et al.*, 2017). Integrating nutritional ecology with detailed feeding observations, as suggested by previous studies (*e.g.*, Carlson *et al.*, 2017), would also improve our understanding of resource partitioning and spatial use within this functional group. Such complementary approaches will be essential for refining management strategies and predicting how parrotfishes will respond to ongoing environmental change. Finally, to further enhance our understanding of spatial use by *S. axillare* and *S. frondosum*, future studies should explore the influence of resource availability and agonistic interactions on their movement and home range dynamics.

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ETHICAL STATEMENT

Fish tagging and field work was approved by Collection Licenses of the Brazilian Sistema de Autorização e Informação em Biodiversidade (SISBIO) number 55911–4.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author, upon reasonable request.

AI STATEMENT

The authors did not use any AI-assisted technologies in the creation of this manuscript or its figures.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

Supplementary material S1

Supplementary material S2

Supplementary material S3

Supplementary material S4

Supplementary material S5

Supplementary material S6

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