Home Range Characteristics and Diel Patterns in Space Use of Mutton Snapper, *Lutjanus analis*, in St. Thomas, US Virgin Islands

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Abstract

Background: The movement ecology of mutton snapper *Lutjanus analis* is poorly understood despite their ecological and economic importance in the Caribbean. Passive acoustic telemetry was used to determine home ranges of six adult *L. analis*, including diel patterns, in Brewers Bay, St. Thomas, US Virgin Islands. Understanding long-term space use, including site fidelity and habitat usage, is necessary to implement effective and appropriate management actions for a species with extensive space and resource needs.

Results: Individual *L. analis* were tracked over an average period of 316 days (range 125 - 509 days) and showed high site fidelity to relatively small home ranges (mean $\pm$ SD: 0.103 ± 0.028 km², range 0.019 - 0.190 km²) and core use areas with low overlap among individuals. Most home ranges had a habitat composition dominated by seagrass and to a lesser degree, coral reef and/or pavement. Nighttime activity spaces were distinct from but contained within daytime areas.

Conclusions: Mutton snapper showed strong site fidelity to home ranges in Brewers Bay. Two individuals that were absent from the array for more than a few hours were detected at separate arrays at spawning aggregation sites. This study expands upon knowledge of mutton snapper home range characteristics, highlights the importance of maintaining adjacent high-quality habitat types in any spatial management plan, and encourages the adoption of other types of management strategies, particularly for transient-aggregating species.

Background

The movement patterns of animals examined in the context of their surroundings reveal central aspects of their life history and resource needs. Coral reef fish, in particular, live in highly heterogeneous environments, making diel movements between habitat types in order to balance predation risk, foraging benefits, and competition avoidance [1, 2]. The mosaic of habitats inhabited by a fish comprises their home range, an area regularly utilized for feeding and shelter [3]. Analysis of reef fish movement patterns demonstrates direct connectivity across different habitat types for certain reef fish families [4], a life history strategy that promotes survival of the individual and influences overall productivity and reef health in visited areas [5].

Studies using visual surveys have shown that spatial distributions of fish can be predicted by underlying habitat type and condition [6]. This type of assessment is limited, however, in that it is affected by observer presence, usually represents a single time point, and is difficult to link to other environmental variables such as temperature or tidal phase. For general long-term, coarse-scale movement patterns and space utilization analysis, passive acoustic telemetry is a well-suited method [7], which allows the tracking of many fish continuously over a long period of time [8, 9]. This technology can help identify important parameters of fish ecology and life history such as diel changes in space use [1, 4, 10, 11], habitat association [12, 13], site fidelity [14], residence time [15], and seasonal migrations [16].

Members of the coral-reef-associated fish family Lutjanidae have been shown to have high site fidelity and a relatively small home range [4, 12], so their movements should display a strong association with a small area within their home range. Lutjanid abundance is higher in specific edge habitats, such as areas with abundant patch reefs and large amounts of seagrass [6, 17], presumably because the proximity of usable resources signifies higher-quality habitat than structure alone [18]. Lutjanids and Haemulids have been shown to predictably use multiple habitats within a day, performing diel movements between coral reefs, where they shelter during the day, and seagrasses, where they forage at night [1, 4, 19]. Therefore, an individual's home range would be expected to contain a large proportion of each of these habitats, with daytime and nighttime activity spaces dominated by coral reef and seagrass habitats, respectively.

Mutton snapper, *Lutjanus analis* (Cuvier, 1828), are economically important to Caribbean fishers that target nearshore reef fish. In the northern US Virgin Islands, this species comprised an average of 18% by weight of commercial snapper landings between 2011 and 2017 (USVI Department of Planning and Natural Resources, unpublished data). The species is classified as "Near Threatened" by the International Union for Conservation of Nature due to trends of decreasing estimated population sizes throughout its range [20]. This is due, at least in part, to their reproductive strategy of aggregating at predictable times and locations in large groups for spawning. These transient fish spawning aggregations occur after the full moon in March through

July, during which the species is highly vulnerable to fishing [21, 22]. When not aggregating, individuals are solitary and territorial [23], and are found in a wide variety of habitats. This species undergoes ontogenetic shifts in primary habitat association, with juveniles being found mainly in nearshore seagrass beds and adults in coastal or offshore habitats over hard substrate [24]. In the Dry Tortugas, Florida, adults are usually observed over hard bottom, swimming actively along reef edges [25], and are also often observed in these locations in St. Thomas (S. L. Heidmann, pers. obs.).

L. analis are generalist predators, opportunistically feeding mainly on arthropods such as crabs and shrimp, gastropods, and reef fish [26], with individual variability in foraging style to reduce intraspecific competition [23]. It has been shown that *L. analis* have temporal diet variations based on prey availability [27, 28], and therefore the species is ecologically important for top-down control over prey populations. This species is known to be more mobile than some comparably sized benthic-associated grouper species, but retain high site fidelity [25].

With size-at-maturity estimates ranging from 28.0 cm to 52.0 cm [28, 29, 30], *L. analis* are likely to utilize a larger home range size than well-studied smaller species of snapper because of associated increased mobility and resource needs [31, 32], but previous studies of this species have been limited in acoustic receiver array continuity. A long-term tracking study by Farmer and Ault [33] obtained location data from a single mutton snapper for 168 days and estimated its home range size at 7.64 km², but this estimate included two long-distance presumed spawning migrations which were unrepresentative of routine movements. Another study by Feeley et al. [34] identified home range areas, excluding observed spawning migrations, for 13 resident *L. analis* at a mean size of 2.5 km². Both these studies had non-overlapping array coverage over a large area, which may inflate home range estimates. Additionally, these studies contained only a cursory description of home range characteristics and finer-scale movements, which are not currently well-understood in this species.

To quantitatively describe *L. analis* movement patterns, this study used passive acoustic telemetry and spatial analysis tools on an individual level to 1) determine home range characteristics and degree of site fidelity and 2) examine diel, daily, and seasonal changes in space use. Based on characteristics of other snapper species, we hypothesized that *L. analis* display high site fidelity to a home range that is smaller than previous estimates, and that each has a nighttime activity space comprising seagrass beds in which they forage, which is larger than and separate from a coral-reef-dominated daytime activity space.

Methods

Study Site and Acoustic Receiver Array

An array of 43 omnidirectional acoustic receivers (69 kHz; Model VR2W, VEMCO, AMIRIX Systems Inc., Halifax, Nova Scotia) was deployed in Brewers Bay (Fig. 1), on the south side of St. Thomas, US Virgin Islands (USVI). Brewers Bay faces southwest, and is approximately 0.9 km² in area, with depths from 0 to 27 m that increase gradually from northeast to southwest. Temperature is fairly homogenous across Brewers Bay, with a mean annual temperature of 28.6 ± 0.002 °C (mean ± SE, range 25.2–31.8 °C; R. Nemeth unpublished data).

The benthic habitats of the bay were delineated and mapped by digitizing LiDAR bathymetry and both aerial and satellite imagery. This characterization was validated using drop camera imagery, following previous methods used by NOAA [35, 36]. The substrate of the bay is composed of several habitat types, categorized for the purpose of this study as coral reef, seagrass (comprising the native *Thalassia testudinum* and *Syringodium filiforme*, and the invasive *Halophila stipulacea*), sand with scattered coral and rock, artificial, pavement, and other (i.e., bare sand, algae, mud) (Fig. 1).

Range testing was performed in June of 2015 to determine detection probabilities around the bay to account for variability in acoustic transmission across shifting environmental conditions and degrees of habitat complexity [37, 38, 39]. A general detection probability of 70% (based on V9 transmitters) was used to determine spacing of receivers for the final array configuration. For the V13 transmitters used in this study, this resulted in highly overlapping estimated 70% detection ranges, of between 101 and 120 m radius depending on location. This maximized coverage of the bay with a limited number of receivers and provided an overall maximum detection probability of 91% under optimal conditions when a fish was inside overlapping detection ranges [37].

Moorings were placed at depths between 2 m and 27 m and constructed using sand screws and cinder blocks with subsurface buoys, as well as existing no-wake buoys and swim buoys. The body of each receiver was wrapped in electrical tape for easy removal of biofouling that could grow over the hydrophone and affect detection efficiency [40]. Receivers were retrieved, cleaned, data were downloaded into the VUE software [41] and batteries replaced approximately every four months over the duration of the 19-month study. Temperature was recorded every 15 minutes on a subset of the receiver moorings using 22 HOBO Water Temp Pro v2 (Onset Computer Corporation, Bourne, MA), and 5 miniDOT loggers (Precision Measurement Engineering, Vista, CA).

Fish Tagging Methods

Lutjanus analis were caught using Antillean fish traps and hook and line baited with squid at various locations within Brewers Bay. Total length (TL) and fork length (FL) were measured for each captured individual. The sex of each fish was not determined due to a lack of sexual dimorphism in this species. Incidence of barotrauma was minimal, due to the relatively shallow depths of traps and hook and line fishing locations. Fish were implanted with a VEMCO V13 acoustic transmitter (codespace A69-1601; 13 mm diameter, 36 mm long, 6 g; 69 kHz, 147/153 dB, 30–250 s delay, estimated battery life 365–653 days) using surgical insertion, which has a longer retention time than force feeding, and minimizes drag and fouling compared to external attachment [9]. No anesthetic was used in order to minimize handling and recovery time and ensure no additional risk of predation due to aftereffects [42]. Fish were inverted in a tub of aerated seawater to induce tonic immobility. A 1.5 cm incision was made approximately 1 cm from and parallel to the ventral midline. The acoustic transmitter was coated in triple antibiotic ointment and inserted into the peritoneal cavity. The incision was closed using 2–3 chromic gut or silk surgical sutures or staples and covered with triple antibiotic ointment. Fish were observed for at least two minutes to ensure recovery before being released at the surface near their catch location. After release, all individuals swam immediately down and out of sight.

Data Processing

Detections from each fish were examined for insufficient data or abnormal behavioral patterns, such as a sharp decrease in activity or consistent detections only at a couple adjacent receivers over several weeks, which implied transmitter loss, predation, or mortality. In these cases, transmitters were either excluded entirely from analysis due to insufficient detections (i.e. 36029, 45336), or detections were removed after a presumed predation event (i.e. 59271). Detections at separate arrays outside Brewers Bay were noted but, as they represented extraordinary movements, were not included in home range estimations.

All data processing and analyses were performed in the R 3.6 programming language [43] through the RStudio environment [44]. Detection data from the day of tagging as well as the following full day were not used in analyses. Each detection was categorized into daytime, nighttime, and crepuscular activity based on daily sunrise and sunset times [45] with crepuscular considered to be within an hour before or after sunrise or sunset. Detection data from crepuscular periods were used for calculation of home ranges, but not for day/night activity spaces, because detection rates on reefs in the USVI have been shown to drop substantially during crepuscular periods due to increases in ambient noise, potentially obscuring any patterns in activity during these times [38].

To reduce the influence of variable detection rates and false detections resulting from signal collisions, as well as to enhance position estimates, detections were pooled into hourly short-term center of activity (COA) locations. The COA locations of each fish were calculated using the mean-position algorithm described by Simpfendorfer et al. [7], as the arithmetic mean of the latitude and longitude positions of the receivers that recorded each valid detection within each hour. This time period was chosen as it was long enough to expect 5–20 detections per fish even if all tagged fish were near the same receiver at the same time [46], without unduly decreasing data resolution.

Spatial Analysis

Site fidelity was determined by calculating a residence index (RI) within the array for each fish, as the total number of days the fish was detected divided by the number of days between the first and last detections [47]. The RI varied between 0 for no residency and 1.0 for absolute residency. An hourly RI was also calculated to ensure home range estimations were comprehensive and not limited by the extent of the array.

Home ranges were estimated from COA locations using the R package *adehabitatHR* [48] to calculate 95% minimum convex polygons (MCPs) and 95% Brownian Bridge movement models (BBMMs) for each tracked mutton snapper, chosen to illustrate most daily movements and exclude infrequent longer-distance migrations. The same methodology was used to create 50% MCPs, which represent each fish's smaller core use area, and to create 95% MCPs for daytime and nighttime activity spaces. MCPs were computed by creating the smallest convex polygon around 95% of the input data and illustrated the extent of the most common space used by each fish. BBMMs were computed by modeling conditional random walks between successive locations, dependent on the time and distance between each pair of locations and accounting for Brownian motion variance; this method described the expected movement paths of each animal by producing a rasterized map of the probability of occurrence. BBMMs were chosen as a comparison method to the more common MCP (i.e. [7, 8, 33]) as it is less frequently used, but provides more detailed information about space use, including paths between successive relocations, allowing the identification of movement corridors [49].

Because MCPs are heavily influenced by sample size [50], all home ranges and activity spaces were calculated using 2770 randomly selected COAs, the smallest overall sample size. All points were used in calculating BBMMs, as they are less sensitive to sample size and account for paths between consecutive points. Smoothing parameters for BBMMs were calculated using the standard deviation of the distances between relocations (*sig2*, the approximate location error), and a maximum likelihood estimation (*sig1*, the estimated Brownian motion variance). The sizes of MCPs were compared to those of BBMMs using a t-test paired by individual. Degree of territoriality in Brewers Bay was determined using an overlap index (OI) of 50% core use areas, calculated as the total area of polygons overlap divided by the combined area of all polygons, with possible values ranging from 0.0 (no overlap) to 1.0 (100% overlap).

The sizes of daytime and nighttime activity spaces were compared using a one-tailed t-test paired by individual, with the alternative hypothesis that nighttime spaces were larger than daytime ones. To evaluate the degree of spatial segregation between these activity spaces for each individual, an OI was calculated, as well as the distance between center-of-mass centroids of day and night 95% MCPs. Activity levels were compared on an hourly basis across day and night with a t-test paired by individual, using as proxies first the number of detections, then the number of stations receiving detections.

Habitat composition of *L. analis* home ranges and day/night activity spaces was determined by overlaying the 95% MCPs on the benthic habitat map of Brewers Bay and calculating the percent coverage of each habitat type. A habitat selection index (HSI) was used to determine preference or avoidance of each habitat by each fish. The index was calculated by dividing the percent coverage of each habitat in an MCP by the percent coverage of each habitat type available, such that the degree of positive or negative deviation from a neutral value of 1 indicates preference or avoidance [51]. The HSI of each habitat type across all home ranges was tested against the neutral value of 1 with a Mann-Whitney-Wilcoxon test to evaluate selection of that habitat, and differences between daytime and nighttime activity spaces were tested with a paired Mann-Whitney-Wilcoxon test.

To test whether *L. analis* were selecting for specific temperature ranges, a frequency distribution of available temperatures across the entire study period, scaled to a probability density, was compared to a similar distribution of temperatures at which fish were present, using a two-sample Kolmogorov-Smirnov test.

Daily and seasonal changes in space usage were analyzed with two iterations of a repeated measures PERMANOVA using the *adonis* function in the R package *vegan* [52]. Receiver usage composition, defined as presence/absence at each receiver across the array at each time point, was tested over time using the Jaccard index. The longest period of overlapping tracking time for the largest number of fish was used in the test, which was for five fish over seven months from November 2016 through May 2017. During this period, receiver presence composition for each fish was compared across months, using 999 unique permutations to develop a distribution for computing the pseudo-F statistic, then again across 220 days for each fish, compared to a distribution developed with 31 unique permutations.

Results

Eight individual *L. analis* were tagged opportunistically between September 2015 and November 2016. Sizes ranged from 37.5 cm to 69.0 cm TL (Table 1), with a mean of 48.6 ± 3.8 cm TL (mean $\pm$ SEM, same throughout manuscript). The first

detection of any fish in the study was on 12 September 2015, and the last on 8 November 2017. Over the course of the study, at least one individual was detected at 39 of the 43 receivers in the array, with each fish detected at between 0 and 29 receiver stations per day (Fig. 2).

Table 1. Total length (TL), tag date, and summary of tracking data from *Lutjanus analis* tagged in Brewers Bay, St. Thomas, sorted by date tagged. Information sorted by tagging date.

* data excluded from analysis

☒ data after 6/16/16 removed due to suspected predation

Transmitter	TL (cm)	Tag date (mm/dd/yy)	Total no. detections	Date of first detection	Date of last detection	Residence Index (RI)	Hourly Residence Index	Total stations detected	Mean no. stations detected per day
*36029	69	09/10/15	9363	9/12/15	9/29/15	1.0	0.99	17	9.3
☒59271	38.1	02/11/16	26432	2/13/16	6/16/16	1.0	0.92	15	6.1
24797	48	06/16/16	89799	6/18/16	11/8/17	1.0	0.78	32	3.4
*45336	50	08/15/16	168	8/18/16	7/16/17	0.32	0.02	4	0.4
45337	37.5	08/24/16	434939	8/26/16	7/30/17	1.0	1.0	30	20.8
45338	45.6	09/30/16	546511	10/2/16	7/30/17	0.94	0.93	38	15.9
45339	42.5	09/30/16	1093389	10/2/16	11/8/17	1.0	1.0	38	21.8
45334	58.2	11/1/16	475774	11/3/16	6/10/17	1.0	1.0	33	20.3

The six *L. analis* used in analyses were tracked from their date of tagging for as long as possible, resulting in tracking duration ranging between 125 and 509 days (Table 1), with a mean tracking time of 316 ± 55 days. All individuals but one (45338) were detected on the Brewers Bay array every day between their first and last detection in Brewers Bay, which resulted in RI values of 1.0. Individual 45338 had an RI of 0.94, due to two periods of absence from the Brewers Bay array in June and July of 2017, each lasting approximately one week. During these periods, this fish was detected at arrays at the Grammanik Bank and Tampo (Fig. 1), two sites on the edge of the southern Puerto Rican shelf at 15 km and 30 km distance from Brewers Bay, respectively. One additional fish (45334), that was tracked continuously for 220 days in Brewers Bay (RI = 1.0), was also detected at the Tampo array for 12 hours, but never returned to Brewers Bay afterward. Hourly RI values for all individuals were greater than 0.9 except in one case (24797; RI = 0.78) (Table 1).

Both 95% and 50% MCPs showed different home range sizes and locations across tagged fish within Brewers Bay (Fig. 3), with an OI of 0.11 among 50% MCPs. Full 95% MCPs were between 0.019 km^2 and 0.190 km^2 with a mean of $0.103 \pm 0.028 \text{ km}^2$, while 50% core use MCPs were between 0.004 km^2 and 0.064 km^2 with a mean of $0.030 \pm 0.011 \text{ km}^2$ (Table 2). Home range estimation using BBMMs yielded polygons of similar location but different size and shape than MCPs (Fig. 3). 95% BBMMs were between 0.096 km^2 and 0.270 km^2 , with a mean of $0.168 \pm 0.028 \text{ km}^2$, which were significantly larger than 95% MCPs across all individuals ($t_5 = -3.62$, $p = 0.02$).

Table 2

Area and habitat composition of home ranges of tracked *Lutjanus analis*, created using 95% and 50% minimum convex polygons (MCPs) and Brownian bridge movement models (BBMMs). Percent habitat composition was derived from the intersection of MCPs with the benthic habitat map, and categorized as seagrass, coral reef, pavement and other (bare sand, artificial); habitat selection index (HSI) is indicated in parentheses for each habitat type in 95% MCPs.

Transmitter	Level (%)	MCP (km ²)	BBMM (km ²)	Seagrass % (HSI)	Coral Reef % (HSI)	Pavement % (HSI)	Other % (HSI)
24797	95	0.019	0.145	75.1 (1.4)	0 (0)	24.9 (2.8)	0 (0)
	50	0.004	0.019	95.7	0	4.3	0
45334	95	0.126	0.144	91.0 (1.7)	9.0 (1.6)	0 (0)	0 (0)
	50	0.063	0.029	89.6	10.4	0	0
45337	95	0.168	0.320	62.4 (1.2)	19.9 (3.5)	17.7 (2.0)	0 (0)
	50	0.064	0.062	58.2	15.3	26.6	0
45338	95	0.190	0.286	94 (1.7)	6 (1.1)	0 (0)	0 (0)
	50	0.021	0.034	100	0	0	0
45339	95	0.075	0.092	93.8 (1.7)	6.2 (1.1)	0 (0)	0 (0)
	50	0.018	0.019	93.5	6.5	0	0
59271	95	0.040	0.106	89.4 (1.7)	0 (0)	10.6 (1.2)	0 (0)
	50	0.012	0.022	91.4	0	8.6	0

Daytime 95% MCPs were between 0.041 km² and 0.195 km², with a mean of 0.103 ± 0.026 km², while nighttime 95% MCPs were between 0.010 km² and 0.036 km², with a mean of 0.021 ± 0.004 km² (Table 3). Nighttime activity spaces were significantly smaller than daytime activity spaces across all individuals ($t_5 = 3.28$, $p = 0.02$); on average, a nighttime space was 25% of the size of its corresponding daytime space, ranging from 7–42% of the size. Nighttime activity spaces either strongly overlapped or were contained within daytime activity spaces (Fig. 4), resulting in a mean overlap index of 0.20 ± 0.05 (range 0.07 to 0.36; Table 3). Day and night centroid separation distances were between 47 m and 274 m (mean 142 ± 40 m). *L. analis* were detected at more receiver stations per hour during the day than during the night ($t_{1896} = 23.6$, $p < 0.001$) and there were overall more detections per hour during the day than night ($t_{1896} = 5.6$, $p < 0.001$). A Spearman's rank showed a significant correlation between number of receiver stations per hour and number of detections per hour ($\rho = 0.95$, $p < 0.001$).

Table 3

Characteristics of daytime and nighttime activity spaces of tracked *Lutjanus analis*, created using 95% MCPs. Statistics include day to night overlap index, activity space size ratio, centroid separation distance, size (km²), and habitat composition. Percent habitat composition was derived from the benthic habitat map, and categorized as seagrass, coral reef, pavement and other (bare sand, artificial).

Transmitter	Overlap Index	Night:Day Size Ratio	Centroid Separation (m)	Time of Day	Size (km ²)	Seagrass %	Coral Reef %	Pavement %	Other %
24797	0.24	0.24	64	Day	0.041	71.2	0	28.8	0
				Night	0.010	84.3	0	15.7	0
45334	0.09	0.18	257	Day	0.096	89.4	10.6	0	0
				Night	0.017	90.9	9.1	0	0
45337	0.15	0.21	274	Day	0.167	64.4	21.7	13.8	0.1
				Night	0.036	69.8	7.8	22.5	0
45338	0.07	0.07	97	Day	0.195	89.6	9.8	0.6	0
				Night	0.014	100	0	0	0
45339	0.30	0.42	113	Day	0.071	94.1	5.9	0	0
				Night	0.030	93.9	6.1	0	0
59271	0.36	0.36	47	Day	0.049	91.2	0	8.8	0
				Night	0.018	91.7	0	8.3	0

All individuals used a combination of seagrass, reef, and pavement habitats, with no other habitat types appearing in home ranges (Table 2). Benthic cover of 95% MCPs had a mean of 84.3% seagrass, 6.9% reef, and 8.9% pavement; corresponding mean HSI values were 1.6, 1.2, and 1, respectively. HSI values for seagrass were significantly more than an even ratio of 1 ($V = 21$, $p = 0.03$), but were not significantly different from 1 for coral reef ($V = 12$, $p = 0.8$) or pavement ($V = 10.5$, $p = 1$). As for daytime and nighttime activity spaces, each was dominated by seagrass habitats, but most also included some proportion of reef and/or pavement (Table 3). Daytime activity spaces had a mean coverage of 83.3% seagrass, 8.0% reef, and 8.7% pavement, while nighttime activity spaces had a mean coverage of 88.4% seagrass, 3.8% reef, and 7.8% pavement. There was suggestive evidence that seagrass coverage was higher in nighttime spaces than daytime spaces ($V = 1$, $p = 0.06$), but there was no difference for reef ($V = 9$, $p = 0.2$) or pavement ($V = 7$, $p = 0.6$).

There was no evidence that *L. analis* select for specific temperature ranges; instead, tagged individuals utilized available temperatures equitably ($D_{75} = 0.173$, $p = 0.21$). Space use patterns over time showed significant differences across days ($F_{8579} = 27.1$, $p = 0.03$) but not across months ($F_{272} = 1.37$, $p = 0.23$), indicating variability in movement patterns but no apparent seasonal shifts.

Discussion

The six *L. analis* included in analyses showed high site fidelity to Brewers Bay, with home ranges that rarely overlapped, were highly variable in size and location among individuals, and together, covered the majority of Brewers Bay. This result is expected due to the territorial nature of *L. analis*, which defend their home range center [23], although it was not discussed in previous acoustic telemetry studies. Territoriality of home ranges is common in many species of coral reef fish and is usually associated with reproductive behavior of surgeonfish [53], parrotfish [54], and groupers [55, 56], but has also been observed during non-reproductive periods in the dusky grouper, *Epinephelus marginatus* [57], and by damselfish in defense of food resources [58].

All home ranges in this study covered a combination of entirely seagrass, coral reef, and pavement habitats, as expected for a generalist predator like *L. analis*, which frequently feeds in sand, seagrass, and coral rubble near reefs [26]. Home range habitat composition was dominated by seagrass for all individuals, who showed a preference for this habitat beyond its prevalence. The only receivers in the Brewers Bay array without any detections from an individual *L. analis* through the course of the study were the four forming the southernmost row along the airport runway. These receivers were in deep bare sand (23–27 m), an unfavorable habitat type for this species as it provides limited food and structure.

Home Range Characteristics

Five of the six *L. analis* were detected daily, and all had RI values of greater than 0.9. Two individuals (45334, 45338) that departed from Brewers Bay were detected at separate acoustic arrays at known multi-species spawning aggregation sites of Tampo, south of St. John, and the Grammanik Bank, south of St. Thomas. One was only detected at Tampo (45334), and the other (45338) was detected at both sites within the span of a week, before returning to Brewers Bay. These absences followed the full moon during June and July, when peak spawning of *L. analis* is known to occur [21, 59], suggesting that these fish migrated for reproductive purposes. It was interesting to note, however, that nearly all other fish showed an increase in activity at the beginning of spawning season (April) and swam to the receivers on the south side of the airport runway each afternoon for a few hours on days that coincided with full moon periods. These fish were all were of reproductive size (> 28 cm fork length; [30]) and may have spawned nearby their home ranges, as has been shown for dog snapper (*Lutjanus jocu*) [60].

Two fish were tracked during the two Category 5 hurricanes (Irma and Maria) that struck the USVI in September 2017. While detection rates dropped during the storms, these individuals were still present in Brewers Bay, and did not temporarily retreat to deeper water, as sharks, sea turtles, and stingrays have been observed doing before a storm [61, 62].

The average size of 95% MCPs was $0.103 \pm 0.028 \text{ km}^2$ and the average 95% BBMM was $0.168 \pm 0.028 \text{ km}^2$, which were smaller than previous estimates for this species. The 7.64 km^2 estimate from Farmer and Ault [33] included home range, spawning site, and the migration corridor between them; doing so in this study would increase MCP sizes from 0.126 to 18 km^2 (45334) and from 0.190 to 69.7 km^2 (45338). Feeley et al. [34] excluded spawning sites from home range estimates, but still found a home range of a minimum of 1.97 km^2 , larger than any in this study. While array coverage in that study was sparse to cover a larger area than described here and may not be directly comparable, it may be that a different spatial configuration of habitat types in Florida may necessitate a larger home range to access a similar set of resources [63].

There was high variation in the estimated size of home ranges among individuals, and different estimation methods produced significantly differently sized home ranges. MCPs, while easy to calculate, do not take into account the density of usage within them or any indication of directed movement pathways [50]. BBMMs are better at accounting for error in location estimates, and the output is less sensitive to outliers and highlights the densest areas of usage and pathways between them [49]. In this study, BBMMs seemed to provide more precise, and typically larger, estimations of home range than MCPs. For two individuals (45334 and 45337), the BBMM showed two hotspots with a connection between them that were not apparent in the MCPs, portraying movement pathways along reef edges and between patch reefs.

While fish movement patterns were variable from day to day, there were no significant seasonal changes in individual space use patterns across months. Although the time period tested was only seven months and included the coldest water temperatures of the year, there were no apparent temperature associations when considering the entire study period. Since minimum and maximum annual temperatures in Brewers Bay are within 7°C and are fairly spatially homogeneous, temperature variation may not be large enough to warrant a behavioral change, unlike estuaries where temperature is a primary factor affecting fish distribution [64].

Diel Patterns

Tracked fish moved farther from their home range center during the day than at night but showed high overlap of daytime and nighttime spaces in both location and habitat composition, with at least 56% of each nighttime activity space overlapping with the corresponding daytime activity space. There may have been higher usage of seagrass at night, but there was less

differentiation from daytime usage than observed by Hitt et al. [4] in species of a similar trophic group (schoolmaster snapper, *Lutjanus apodus*, and bluestriped grunts, *Haemulon sciurus*), which used larger nighttime activity spaces that were clearly separated from daytime spaces, with a clear shift from high-relief hard substratum habitats to low-relief soft substratum habitats. Hitt et al. actively tracked fish, which allowed for a much finer estimate of space use and had a greater power to detect differences. The 24 h tracking period likely did not encapsulate day-to-day variations [33], therefore, the stark differences between daytime and nighttime activity spaces may become less detectable with the lower spatial resolution and added daily variance present in this study. Alternatively, while *L. analis* and *L. apodus* are closely related, these species may exhibit behavioral variation due to differential predation risk and use of different habitat types to meet dietary needs [65]. Diet studies have suggested that unlike other species of snapper, *L. analis* forage opportunistically throughout the day [26, 27], which would explain the habitat similarity between daytime and nighttime activity spaces. Furthermore, the larger size of the daytime activity space in combination with the low overlap of core use areas suggests a regular patrol of the edges of a territory to defend against competition for valuable resources. Future studies could use a VEMCO Positioning System (VPS) array, which has more accuracy in detection locations, to clarify whether animal behavior or methodology is the source of the discrepancies between these studies.

Conclusions

Despite the small sample size of six *L. analis*, this study presents the most comprehensive home range description to date on this economically important Caribbean reef fish. Home range estimates demonstrate usage of multiple habitat types within a relatively small area by individual adult *L. analis*, with the additional need for offshore spawning sites. Seagrass beds, which are an important food source for snapper and other reef fish, can change quickly in size and coverage with shifting environmental conditions or disturbances [66], and while the effects of natural disasters such as hurricanes cannot be prevented, disturbances from human activity could be limited by prohibiting specific practices, such as anchoring in known seagrass beds and along reef edges. As habitat variability in an area is an important component of its suitability for many species, spatial management efforts should focus on zones with proximity to multiple habitat types [67], including mangroves and seagrasses as well as nearshore and offshore coral reefs, which support coral reef fish across diel movements and ontogenetic stages [24, 63, 65].

Quantifying specific characteristics of *L. analis* movements, including home range size, habitat requirements, and diel movement patterns, are necessary to implement directed management at an appropriate scale. Although *L. analis* are highly mobile during reproductive periods, they show site fidelity to a relatively small home range during all other periods, indicating that effective management of this species should target home ranges and spawning aggregations separately. While small marine protected areas of less than 1 km² placed over reef and seagrass habitats where *L. analis* are known to reside could protect more than 95% of the space usage of a few individuals, many areas have a relatively low or unknown population density, warranting a more effective use of resources. For example, restrictions on bottom gear and seasonal closures of aggregation fishing during reproductive periods, with cooperation from local artisanal fishers, may be better approaches for targeted management of *L. analis* to maintain its ecological and economic benefits.

Declarations

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Ethics Approval

All tagging and tracking methods for *L. analis* presented in this manuscript were approved by the University of the Virgin Islands Institutional Animal Care and Use Committee (IRB #747807-1).

Consent for publication

Not applicable.

Availability of data and materials

The datasets used and/or analyzed during the current study or associated R code are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' Contributions

RSN conceived the idea and secured the funding; RSN, JJ, and SLH designed the methodology; SLH, JJ, and RSN collected the data; SLH and JJ analyzed the data; SLH led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication. All authors read and approved the final manuscript.

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Figures

Figure 1

Map of Brewers Bay, with inset showing location on St. Thomas, USVI, and nearby Lutjanus analis spawning sites at Grammanik Bank and Tampo. Triangles represent locations of 43 VEMCO acoustic receivers, with circles representing 70% detection range (for V13 transmitters; varies by receiver: 101-120 m). Benthic habitat maps were manually digitized by Melissa Kimble (unpublished data).

Figure 2

Activity of tagged *Lutjanus analis*, measured as number of detections per day (upper panel) and number of receiver stations visited per day (middle panel) in Brewers Bay, St. Thomas, USVI, between February 2016 and November 2017. Lower panel shows average temperature (°C) across the bay during the study period. Vertical dashed lines delineate the period used in the PERMANOVA.

Figure 3

Estimated home ranges of six *Lutjanus analis* tracked in Brewers Bay, St. Thomas, USVI, between February 2016 and November 2017. Color denotes probability of occurrence as estimated by Brownian bridge movement models (BBMMs); dashed lines represent 95% minimum convex polygons (MCPs) and solid lines represent core use areas (50% MCPs). Triangle indicates catch and release location for each fish.

Figure 4

Daytime (dotted) and nighttime (dot-dashed) activity spaces for each tracked *Lutjanus analis* in Brewers Bay, St. Thomas, created using 95% minimum convex polygons (MCPs).