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# Scale of Biotelemetry Data Influences Ecological Interpretations of Space and Habitat Use in Yellowtail Snapper

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## Abstract

As opposed to passive, broad-scale acoustic telemetry arrays, acoustic positioning systems generate high-resolution animal locations that provide information on long-term, fine-scale movement patterns and habitat preferences. However, limited comparisons have been made between more common broad-scale acoustic data and fine-scale positioning data and it is unknown whether differences exist in ecological inferences gained or lost between using either array configuration over the other. Broad-scale movement and habitat use information was collected for eight Yellowtail Snapper *Ocyurus chrysurus* tagged within an array of 78 stationary acoustic receivers deployed in Buck Island Reef National Monument, a marine protected area located northeast of St. Croix, U.S. Virgin Islands. An additional 25 receivers were nested within the larger array as a VEMCO Positioning System and were used to assess fine-scale habitat use for five of the eight tagged fish. Broad-scale results inferred from network analysis revealed that all individuals had core use receivers along the shallow shelf break situated west of Buck Island, preferring an area that was coarsely characterized by sand and seagrass benthic habitats. Fine-scale results using Euclidean distance analysis (EDA) suggested fish positions occurred randomly or independent of benthic habitat type. Further exploration of positioning data suggested that there were two contingents or groups of fish displaying unique movement patterns within the fine-scale positioning array. Individuality in space and habitat use was thus masked when using an EDA approach at the study population level, as it was also missed during broad-scale analyses. Discrepancies between broad- and fine-scale habitat inferences suggest that positioning systems are necessary for interpreting habitat use in complex coral reef ecosystems. Nested positioning systems appear to add substantial information that is not obtainable using broad-scale data alone, and caution is necessary in inferring habitat use when only coarse-scale location data are available.

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Acoustic telemetry has proven to be a valuable tool for quantifying broad-scale movement patterns of marine species across a wide range of environments (Hussey et al. 2015; Lennox et al. 2017). The most common application of broad-scale acoustic telemetry operates by logging detections on multiple stationary acoustic receivers, which are deployed as regular or irregular grid systems without overlapping detection ranges (Heupel et al. 2006). Passive array designs using fixed receivers only provide coarse detection data (presence or inferred absences) and a general understanding of where acoustically tagged animals are located within a receiver's detection range. Thus, these designs often lack high-resolution positioning information (Espinoza et al. 2011) that may be necessary to infer more subtle movement patterns as well as to substantiate broad-scale ecological inferences. Nevertheless, broad-scale telemetry data have provided previously unattainable information and have been used extensively to quantify residency and site fidelity (Currey et al. 2014; Afonso et al. 2016), habitat use (Farmer and Ault 2011), territoriality (Becker et al. 2016, 2020), and large-scale movements and migrations (Griffin et al. 2018) across a myriad of marine fishes.

Given the coarse resolution of broad-scale telemetry data, new technologies, such as acoustic positioning systems, have been developed and tested to be able to collect reliable data on long-term, fine-scale movement patterns (Espinoza et al. 2011; Binder et al. 2016). Positioning systems employ a closely spaced grid of acoustic receivers with overlapping detection ranges to estimate an animal's location (up to 1–2-m resolution), providing continuous records of positions and thus inferred detailed movement patterns (Espinoza et al. 2011). Previous studies have used positioning systems to identify habitat use and partitioning (Furey et al. 2013; Dance and Rooker 2015; Moulton et al. 2017), to characterize diel and aggregation behaviors (Dean et al. 2014), and more recently to understand how predation risk influences daily movement, space use, and foraging activities of prey species (Rooker et al. 2018).

However, comparison of ecological inferences between traditional broad-scale data and fine-scale positioning data has been limited and remains an important consideration in the development of acoustic arrays based on specific ecological questions. Both broad- and fine-scale telemetry approaches have the potential to resolve specific information gaps regarding species' long-term movement patterns as well as individual differences in movement and spatial use behavior. Accurate documentation of changes in area and habitat use, which may vary with ontogeny or within certain life stages (i.e., habitat generalists), is essential for understanding ecological connectivity within a seascape (Rooker et al. 2018). Connectivity facilitated through movement is central in structuring the functions of an ecosystem, as it enables optimal foraging opportunities and

transfer of nutrients, affects areas used for reproductive events, and influences gene flow (Boström et al. 2011). Capturing the complexity of space use by marine species, especially identifying areas and habitats that are used disproportionately compared to their availability, is necessary for informing appropriate scales of spatial management, such as marine protected areas (MPAs).

Despite the obvious importance of studying animal movement, it is often difficult to distinguish whether movements are linked to environmental cues or driven by individual behavioral differences. Individual movement specialization remains understudied for most marine fishes (Boström et al. 2011; Furey et al. 2013; Spiegel et al. 2017), and integration of fine-scale telemetry systems could provide new insights into individual behaviors in a near real-time context. This incorporation of personality-based individual differences in movement could reshape our existing understanding of population and community dynamics as well as resource selection, partitioning, competition, and the coexistence of species (Bolnick et al. 2003; Allgeier et al. 2017; Jolles et al. 2017). Studying behavior in wild marine fishes presents a challenge, but fine-scale telemetry data provide a unique opportunity to identify how movement patterns and habitat use differ or remain consistent among individuals across varying spatial and temporal scales (Harrison et al. 2015).

The Yellowtail Snapper *Ocyurus chrysurus* is a common yet data-deficient (Lindeman et al. 2016) reef fish that is found throughout the tropical and subtropical waters of the western Atlantic Ocean (Cummings 2004). Since this species occupies a wide geographic distribution and is often observed swimming well above the substrate, presumably independent of benthic habitat type, it is often thought to be both a habitat and a foraging generalist (McClellan and Cummings 1998; Muller et al. 2003), although a few broad-scale telemetry studies have observed specific population-level habitat preferences (Farmer and Ault 2011, 2017; Herbig et al. 2019). Characterizing and comparing broad- and fine-scale movement patterns are necessary to understand the ecological role occupied by Yellowtail Snapper within an ecosystem. Therefore, the main objectives of this study were to (1) characterize broad- and fine-scale movement patterns and habitat use of Yellowtail Snapper and (2) identify potential discrepancies between ecological inferences of habitat use that were analyzed at two spatial scales (i.e., broad- and fine-scale telemetry data).

## METHODS

### Study Area and Array Design

Buck Island Reef National Monument (BIRNM) is a no-take MPA located 1.5 km northeast of St. Croix, U.S.

Virgin Islands, and is managed by the U.S. National Park Service (NPS; Pittman et al. 2008). The BIRNM was established in 1961 as a mixed-use area, in part to preserve fringing reef habitat that surrounds an uninhabited island (Buck Island) from the southwest to the northeast, creating a continuous lagoon habitat. In 2001, the original boundaries were expanded to 77 km<sup>2</sup> and new regulations were simultaneously implemented, restricting all extractive activities within BIRNM boundaries (Pittman et al. 2008).

For the broad-scale telemetry array, 78 acoustic receivers (VR2W, 69 kHz; VEMCO, Inc., Bedford, Nova Scotia) were deployed as fixed stations (depth of receivers: mean = 44.5 m; range = 7–116 m) within BIRNM as part of a large collaborative acoustic network (Figure 1). Twenty-five additional omnidirectional receivers were nested inside the larger acoustic array as a VEMCO Positioning System (VPS), installed in June 2015 (Figure 1). The VPS receivers were deployed approximately 100 m apart and at depths between 7 and 18 m (mean = 9.4 m). Three receivers in the broad-scale array were also part of the VPS array (total VPS receivers = 28), where detections were used for broad-scale analyses and were sent to VEMCO to calculate fine-scale positions. Each VPS receiver was co-located with a synchronization (“sync”) tag (VEMCO Model V16-4x, 69 kHz; nominal delay = 600 s; range = 500–700 s) to synchronize clocks among receivers, estimate the speed of sound, assess temporal array performance, and measure positioning error. In addition, three reference tags (VEMCO Model V16-4x, 69 kHz; nominal delay as listed above) were deployed at fixed locations within the VPS array (Figure 1).

All receivers were anchored with either sand screws (0.91 m long; 15-cm-diameter blades) or cement blocks depending on the underlying habitat type (Becker et al. 2016). Data from the entire array were downloaded biannually via scuba and free diving by NPS employees, collaborators, and volunteers. A variety of benthic habitat types characterizes the seascape within BIRNM; they are distributed throughout the shallow shelf area in a patchy mosaic pattern (Pittman et al. 2008). Each habitat type, along with other environmental and array design factors, affects the ability of receivers to detect transmission signals from tagged fish. Range testing for a subset of receivers in the broad-scale array determined an average detection probability of 50% at approximately 125 m (Selby et al. 2016). However, the effective detection range extends upwards of 200 m in homogeneous sand and low-rugosity hard-bottom benthic habitat types (Selby et al. 2016), which make up a large portion of the habitat where the VPS was deployed.

### Fish Capture and Tagging

Yellowtail Snapper were caught inside BIRNM by trolling during the daytime and dusk hours using an artificial

lure and one 6/0 circle hook and by bottom jigging at night around a full moon event. Upon capture, fish were visually assessed to ensure that they were in a suitable condition for tagging (i.e., no gut hooking or hook damage). If requirements were met, individuals received a surgically implanted coded transmitter (VEMCO Model V9, 69 kHz; 9-mm diameter; approximate battery life = 632 d). Each transmitter was preprogrammed with a varying dominant delay ping rate between 50 and 130 s (mean = 90 s) that reduced the risk of tag collisions. In addition, all tags had a 2-week interval involving a quicker ping rate between 15 and 45 s (mean = 30 s) to maximize detection probability; this 2-week interval was set to start at 30, 120, 210, or 300 d postactivation. The 2-week period with the quicker ping rate had no significant influence on broad- or fine-scale data analyses (refer to Supplement S.1 available separately online for further information).

Prior to tag implantation, fish were placed into a 100-L container of ambient seawater and a diluted stock solution (10 g/L) of tricaine methanesulfonate (MS-222) was slowly added to induce stage 4 anesthesia (O’Toole et al. 2011; Becker et al. 2016). Once an individual displayed a slowing of gill movement and a loss of equilibrium, it was placed on the padded surface of a tote; a tube was gently placed into the mouth so that a continuous stream of the seawater containing MS-222 was lightly pumped over the gills. Halfway through the surgery, fresh seawater was added to initiate recovery. Each transmitter was disinfected with 70% isopropyl alcohol prior to being inserted anteriorly into the abdominal cavity through a small incision off the central midline between the pelvic and anal fins. The incision was closed with two to three simple interrupted sutures (Ethicon PDS II polydioxanone monofilament sterile absorbable sutures; Ethicon FS-1 24-mm reverse cutting needle; Ethicon, Somerville, New Jersey), and all surgeries lasted approximately 8 min. A small fin clip was sampled from the anal fin of each tagged fish for future genetic and stable isotope analysis, and FL was measured to the nearest centimeter. All individual fish were placed into a stationary floating net-pen to allow for recovery prior to release (mean recovery time = 34.8 min). Once individuals displayed normal swimming behavior, they were released either within 200 m of the capture location or in shallow, calmer water near West Beach off Buck Island (~2 km from the capture location) to reduce potential predation events (the red “x” on each figure in Supplement S.2 shows the release location).

### Broad-Scale Data Processing and Analyses

Detection data that were collected between the end of May 2015 and mid-April 2017 (693 d) were used for broad-scale analyses. Data recovered from all receivers were corrected for time drift and then filtered for detections that occurred less than 15 s apart, based on the

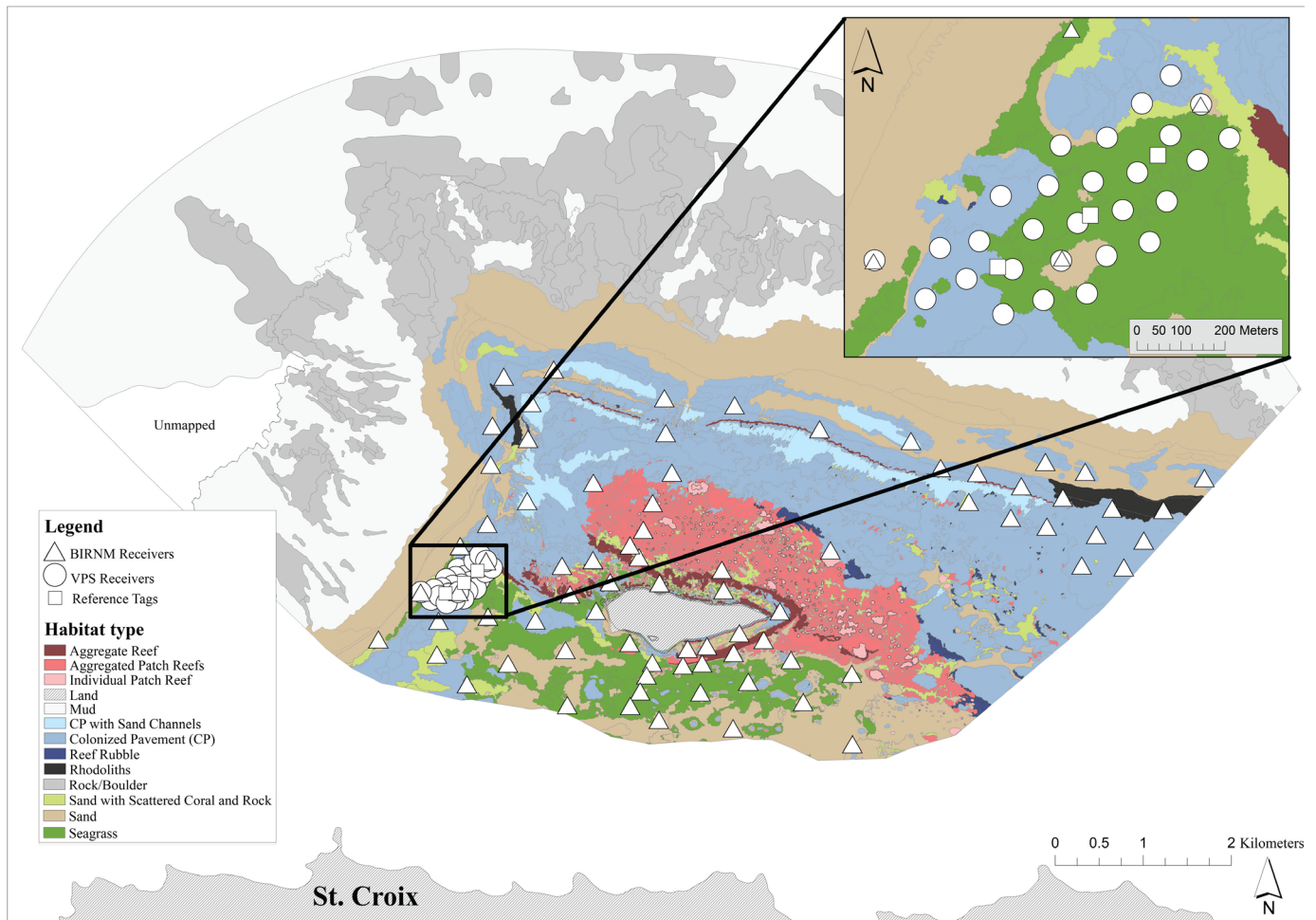


FIGURE 1. Locations of receivers ( $n = 78$ ; white triangles) in the broad-scale array inside Buck Island Reef National Monument (BIRNM) northeast of St. Croix, U.S. Virgin Islands. The inset shows the locations of the VEMCO Positioning System (VPS) receivers (white circles) and three reference tags (white squares) nested within the broad-scale array. Note that three broad-scale receivers were used in the VPS (denoted by white triangles inside white circles in the inset). Benthic habitat shapefiles were obtained from Costa et al. (2012).

higher tag ping rate during the 2-week interval described above. Pings that occurred less than 15 s apart were assumed to be spurious and were attributed to echoes or simultaneous detections and were removed. Fish that were recorded on receivers for less than 3 d and fish that had fewer than 1,000 detections were also removed; both criteria were used as cutoffs to ensure that the analyses were not influenced by fish that either died or quickly emigrated from the array after tagging. The number of detections recorded over the duration of the study has the potential to influence ecological inferences (Becker et al. 2016). Therefore, the two cutoffs were employed to reduce the potential for inaccurate interpretation of the data. All data processing and analyses were conducted in R version 3.3.3 (R Core Team 2017) unless otherwise stated.

*Network analysis.*—To examine broad-scale use and highly visited areas of BIRNM by Yellowtail Snapper,

network analysis (as described by Finn et al. 2014) was implemented using the *igraph* package (Csardi and Nepusz 2006). Briefly, network analysis was used to create individual spatial graphs, where stationary receivers were treated as network nodes, and node size was weighted according to the number of detections recorded at that location. Movement between nodes was represented by edges that were weighted by the amount of movement between two receivers. All receivers were placed in their actual ( $x, y$ ) locations to facilitate interpretation of the extent of space use within BIRNM boundaries. Edge arrows were used to indicate directed movement pathways, with self-loop arrows representing detections occurring consecutively at the same receiver (Finn et al. 2014). In addition, the *ggnetworkmap* function in the *GGally* package (Schloerke et al. 2014) and the *ggmap* package (Kahle and Wickham 2013) were

used to geographically plot individual fish movements in a network.

To test whether observed individuals exhibited nonrandom movements, 10,000 random networks were generated using a bootstrap approach. Each new sequence of movements was based on the number of filtered detections retained for an individual fish and allowed the individual to be detected at any receiver ( $n = 78$  BIRNM stations) throughout the sequence (i.e., a link rearrangement). A to-from matrix was constructed from the new random sequence, creating a weighted movement list and thus a new random movement graph (i.e., random network). Network-level metrics (degree, betweenness, and closeness) were calculated for each new random movement graph ( $n = 10,000$ ) to test against the original observed movement graph metrics using a one-sample Wilcoxon's signed rank test ( $\alpha = 0.05$ ).

Core use receivers (CURs) within individual spatial networks were identified to define highly visited areas with the *igraph* package (Csardi and Nepusz 2006) following the methodology of Becker et al. (2016) and Novak et al. (2020). Centrality metrics based on degree value were used to rank the receivers in an individual's network, with receivers within the top 50% identified as CURs. Centrality degree most closely aligns with other utilization density techniques that estimate frequency of use; therefore, the degree metric (rather than betweenness and closeness centrality metrics) was used to identify CURs for individual networks. Network methods were used as an alternative approach to identify highly visited areas (see Becker et al. [2016] for a comparison of network analysis, kernel utilization density, and dynamic Brownian bridge movement models), as they provide a more holistic representation of individual space use and give more weight to movement corridors (Jacoby and Freeman 2016).

*Habitat classification and connectivity.*—Each receiver ( $n = 78$ ) in the broad-scale BIRNM array was assigned a habitat type by NPS employees based on the underlying habitat where the receiver was installed. However, given the complex mosaic of interwoven habitat types distributed within BIRNM (Figure 1), a more accurate habitat assignment was needed for informing broad-scale habitat use and comparing with the fine-scale habitat analysis.

Therefore, initial habitats assigned to broad-scale receivers by NPS employees were reassigned a new habitat type in a two-step process based on (1) the 125-m average 50% detection range of receivers in BIRNM and (2) range testing results for specific benthic habitat types (Selby et al. 2016). Reassignments were completed in ArcGIS version 10.5, and benthic habitat shapefiles were obtained from Costa et al. (2012). These same shapefiles and thus habitat types were also used in interpreting fine-scale

habitat preference. In the first step, receivers were assigned a new habitat type based on the habitat type with the highest percent coverage in a 125-m buffer around the receiver. The second step used the new habitat type receiver assignments (based on step 1) and reassigned the receiver a new, and final, habitat type using the specific benthic habitat type detection ranges (homogeneous sand: 213.4 m; low-rugosity hard bottom: 123.9 m; mixed hard bottom with sand channels: 83.7 m; high-rugosity reef: 30.7 m; Selby et al. 2016) as opposed to using the 125-m average detection range (used in step 1). All receivers in the broad-scale BIRNM array were reassigned the habitat type with the highest percent coverage (step 2), and these final assignments were used to infer broad-scale habitat preference using modified circular plots.

Circular plots (also known as connectivity plots) were constructed using the *circos.trackPlotRegion* function from the *circlize* package (Gu et al. 2014). A to-from matrix of individual movements between each receiver/habitat was constructed and used to visualize the large number of incoming and outgoing movements (Espinoza et al. 2015). The movement path is indicated by an arrowhead, and the number of movements between the two receivers/habitats is represented by the width of the arrow at its base.

### Fine-Scale Data Processing and Analyses

All detection data that were downloaded from June 2015 to May 2016 (342 d) were processed by VEMCO. Two-dimensional positions were derived from raw detection data using a set of hyperbolic positioning algorithms that weight the average locations of a transmission detected on three or more receivers and favor the position with the lowest error sensitivity (Espinoza et al. 2011; Meckley et al. 2014; Roy et al. 2014; Binder et al. 2016). Positions for both sync tags and animal-implanted tags have an associated unitless error or confidence value, termed horizontal positioning error (HPE), which is derived from the calculation. Sync and reference tags also have measured error (HPEm) based on the known location of the tag in the array. A strong statistical relationship between HPE and HPEm suggests that the derived animal positions can be used with greater confidence (Meckley et al. 2014). Therefore, prior to any analyses, an HPE cutoff value was selected by examining the relationship between HPE and HPEm from the sync and reference tags with methods adapted from Smith (2013) and Meckley et al. (2014). Derived fish positions with an HPE value greater than 7.5 were excluded from analyses based on obtaining 95% confidence in positions having 5-m or better accuracy. This low HPE threshold (5 m) was selected as the cutoff value due to the system being particularly noisy (Selby et al. 2016). More precise estimates for positions allowed for robust and reliable ecological

conclusions to be drawn while also avoiding the risk of overfiltering the data.

To assess fine-scale temporal movement patterns, filtered positions for individual fish were binned by diel period as either day, night, dawn (1 h before sunrise), or dusk (1 h after sunset). Sun ephemerides calculations with an accuracy of approximately 1 min were made using the *maptools* package (Bivand and Lewin-Koh 2017). To ensure accurate diel inferences for fish positions, *t*-tests were used to examine for differences between daytime and nighttime estimated positions for each of the three reference tags. Dawn and dusk reference tag positions were not compared, as these time periods were short and for fish they appeared to represent a transition between two relatively consistent movement behaviors occurring during the day and at night.

*Euclidean distance analysis.*—Habitat use in the VPS was analyzed in ArcGIS version 10.5 using a Euclidean distance analysis (EDA; Conner and Plowman 2001; Conner et al. 2003; Furey et al. 2013; Dance and Rooker 2015; Moulton et al. 2017). This approach is based on measuring the Euclidean distance from animal locations to habitat features (Conner et al. 2003) and was selected over other techniques because it minimizes habitat misclassification due to positioning error. Euclidean distance analysis also reflects the fact that surrounding habitats have an opportunity to influence an animal's space use and thus positions (Conner et al. 2003). Another benefit to EDA is that individuals are used as the sampling unit; thus, it does not require error modeling. This distance-based approach evaluates habitat use through simulation of random points as the expected distances to each habitat type (i.e., the null distribution). If an individual's use of a habitat is random, then the distance between animal locations should be the same as the distance from the random points to a given habitat type.

Filtered positions for Yellowtail Snapper used for fine-scale analyses were bounded by a minimum convex polygon delineating the habitat and area available for EDA. One-thousand random points were generated using the "generate random numbers" tool within the minimum convex polygon boundary (Moulton et al. 2017). Distances between each random point and each distinct habitat type (benthic habitat map obtained from Costa et al. [2012]) were calculated using the "generate near table" tool and then were averaged to create a vector of mean distances to each habitat type (Furey et al. 2013). Similar methods were used to calculate the average distance from the estimated animal positions to each habitat type (Conner and Plowman 2001). Euclidean distance analysis ratios were then calculated for each unique individual  $\times$  habitat combination by dividing the mean distance of an individual's positions to a habitat type by the mean distance of the random points to the respective habitat type. If habitat

use was random, then this ratio would be 1.0; if habitat use was nonrandom, then the ratio would be either greater than 1.0 (indicating relative avoidance) or less than 1.0 (indicating relative preference). Multivariate ANOVA (MANOVA) was used to determine whether EDA ratios differed significantly from a vector of 1s, equal to the number of habitats investigated (Conner et al. 2003).

## RESULTS

### Broad-Scale Analyses

Over two tagging trips (end of May or beginning of June 2015 and January 2016), acoustic transmitters were successfully implanted in 15 Yellowtail Snapper. From the aforementioned cutoffs, only 10 fish met the requirements with sufficient detection histories. Upon inspection of the fine-scale positioning data, we identified two additional fish (tags 19674 and 19676) as having either died or shed their tags within the VPS array; therefore, those fish were not used in any analyses.

The remaining fish ( $n=8$ ) were used for broad-scale analyses and accumulated a total of 151,173 filtered detections (Table 1). Number of individual detections ranged from 2,716 to 69,460, with an average  $\pm$  SE of  $18,896.6 \pm 7,712.8$  (Table 1). The eight fish ranged in size from 23.5 to 35.5 cm FL (mean  $\pm$  SD =  $29.4 \pm 4.26$  cm FL). All Yellowtail Snapper that were monitored in this study exceeded 19.7 cm FL and were considered mature (Muller et al. 2003).

*Network analysis.*—Observed network metrics for each individual fish were all significantly different than random ( $P < 0.001$ ). Therefore, all networks were considered nonrandom and included in subsequent analyses. Individual spatial networks revealed that Yellowtail Snapper frequently occupied spaces near their respective tagging locations (Figure 2; Supplement S.2). All fish had CURs along the shallow shelf break on the west side of Buck Island. This observation could be an artifact of tagging location, as most fish in this study were caught and tagged in this area. Fish that were released off West Beach quickly returned to the approximate location of capture. There is some evidence to suggest that the western shelf break inside BIRNM may be important for Yellowtail Snapper caught in other locations, such as the one fish (tag 19664) that was caught and released on the southeast side of Buck Island (Figure 2B); that individual had two CURs on the western shelf break.

The number of CURs identified varied between individual Yellowtail Snapper (mean = 4.75; range = 3–9; Table 1). Among the eight fish, there was a total of 16 CURs. There were some fish that had CURs exclusively in their own networks. No specific receiver was identified as a CUR in all Yellowtail Snapper networks; however,

TABLE 1. Data set summary for the eight Yellowtail Snapper that were retained for broad-scale analyses. Tagging date, specific tag delays, FL, number of filtered detections, total days present (at least two filtered detections were recorded during a day) within the Buck Island Reef National Monument receiver array, and number of core use receivers (CURs) are reported. Tag delay indicates when the 2-week interval of a quicker transmission rate began (d after tag activation).

Tag ID	Tagging date	Tag delay (d)	FL (cm)	Number of filtered detections	Total days present	CURs
19661	May 25, 2015	30	29.0	5,798	576	4
19668	May 26, 2015	120	29.5	13,411	282	5
19671	Jun 3, 2015	210	30.0	4,053	201	4
19672	Jun 3, 2015	210	23.5	69,460	477	9
19677	Jun 4, 2015	300	23.5	11,092	468	3
19664	Jan 21, 2016	30	35.5	2,716	94	4
19670	Jan 22, 2016	120	31.0	24,112	360	5
19679	Jan 22, 2016	300	33.5	20,531	124	4

individuals shared between 2 and 6 CURs (mean = 2.38; median = 1).

*Habitat classification and connectivity.*—The first step in reassigning new habitat types to the receivers had a 56.4% agreement with the habitats that were originally assigned by NPS employees, and habitat-specific detection ranges (step 2) showed a slightly improved agreement of 59%. There was overall high agreement between steps 1 and 2 (88.5%), suggesting that assigning different-sized buffers to receivers did not make a large difference in classifying habitat type.

Using the final habitat type assigned by habitat-specific detection ranges, connectivity plots showed the majority of Yellowtail Snapper moving between sand and seagrass habitats, although there was some individual variation present (Figure 3). Connections to colonized pavement were also observed. Many of the large circle sectors—each a receiver within the broad-scale array—in each individual connectivity plot were identified as CURs by network analysis.

### Fine-Scale Analyses

From July 2015 to May 2016, a total of 69,814 unfiltered positions were generated for all eight Yellowtail Snapper (Table 2). After positions with HPE values greater than 7.5 were removed, only five fish (of eight) had the number of filtered positions (>100) needed to ensure that ecological inferences were well supported. Collectively, the five fish that were retained for fine-scale analyses generated 59,131 filtered positions (individual range = 108–30,950; Table 2).

There were no significant differences between the numbers of daytime and nighttime reference tag positions ( $t$ -test, reference tag 1:  $t = 0.21$ ,  $df = 21$ ,  $P = 0.84$ ; reference tag 2:  $t = 0.19$ ,  $df = 22$ ,  $P = 0.85$ ; reference tag 3:  $t = -1.42$ ,  $df = 20$ ,  $P = 0.17$ ). Three Yellowtail Snapper, including the two with the highest number of positions (tags 19670 and 19679) had more positions at night compared to daytime hours, and both showed repetitive,

concentrated positions at night, each in one specific area of the VPS (Supplement S.3). Crepuscular (dawn and dusk periods combined) hours showed no clear pattern and presumably represented the period when individuals transitioned between broader daytime movements and concentrated nocturnal behavior.

*Euclidean distance analysis.*—Analysis of EDA ratios indicated random habitat use among the five Yellowtail Snapper (MANOVA:  $P = 0.8486$ ). Further exploration of the positioning data indicated spatial partitioning between two distinct groups of fish (Figure 4). Individual EDA ratios varied in proximity to habitat types, but ratios were very similar among members of the same group (Table 3). For example, the group of two fish (tags 19671 and 19679) occupying the northern part of the VPS were never detected in the southern portion. As a result, the EDA ratios for each distinct habitat were very similar between these two fish. The second group of fish (tags 19668, 19670, and 19672) used the opposite area of the VPS array, with all positions occurring in the southern portion and never in the northern part. These three fish also had similar EDA ratios for each habitat type.

### DISCUSSION

The spatial scale of biotelemetry data influenced the interpretation of habitat use for Yellowtail Snapper. Broad-scale habitat connectivity plots suggested frequent use of receivers dominated by sand and seagrass habitats. If fine-scale positioning data had not been available, sand and seagrass would have been interpreted as important habitats for the study population of Yellowtail Snapper in BIRNM. Fine-scale EDA results suggested that fish moved independent of habitat type (i.e., no significant preference for sand or seagrass habitats); therefore, other variables, such as capture location and perhaps proximity to the shelf break, inferred from the large number of CURs occurring along this area, were more likely stronger influences in structuring space use.

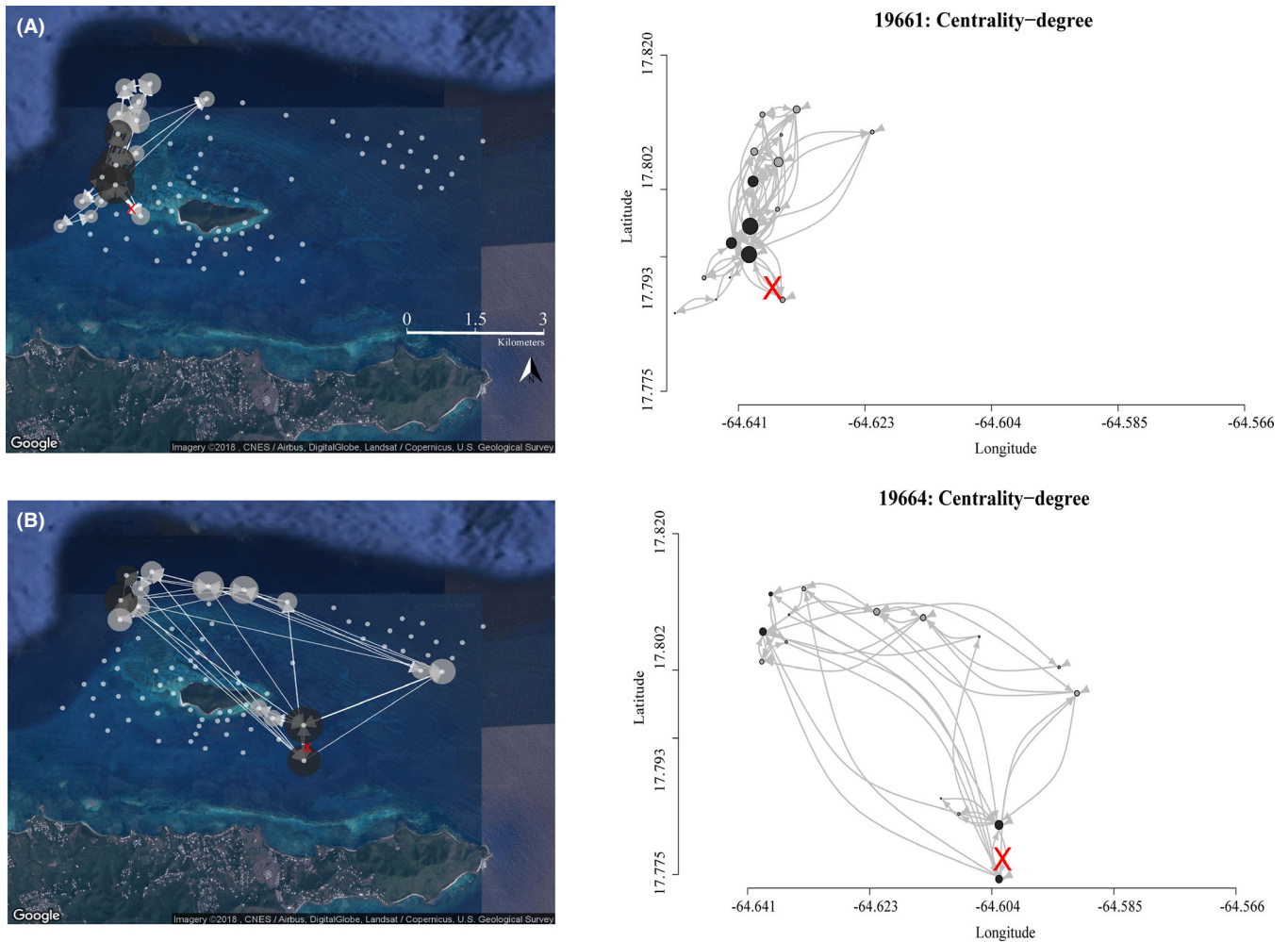


FIGURE 2. Individual spatial networks showing examples of connectivity and space use by two Yellowtail Snapper in Buck Island Reef National Monument: (A) tag ID 19661 and (B) tag ID 19664. The left two plots show visited receivers (white nodes with dark-gray and light-gray halos) with directed movement pathways (white lines). Receivers that the fish did not visit but had the potential to visit are shown as gray nodes without a halo. Core use receivers (CURs) are represented by white nodes with dark-gray halos. Gray lines connecting nodes are directed movement pathways. Dark-gray nodes represent CURs, and light-gray nodes represent visited receivers (note that this type of plot does not show the non-visited receivers). In all plots, the thickness of movement pathways reflects more frequent use. Node size corresponds with amount of detections, with larger nodes indicating higher use. The red “X” in all panels is the release location.

Here, a nested positioning system was necessary to infer that Yellowtail Snapper in BIRNM did not display habitat selection behavior at the study population level. Fine-scale receiver arrays should therefore be used as a tool to complement broad-scale arrays where possible, especially for identifying habitat use in complex coral reef ecosystems.

Broad-scale habitat preferences for sand and seagrass contrasted with fine-scale EDA results as well as previous underwater visual surveys in BIRNM, which documented that adult Yellowtail Snapper occupied all major habitat types (Pittman et al. 2008). Other studies have reported that Yellowtail Snapper preferentially use sandy areas near offshore reefs (Muller et al. 2003), contiguous low-relief reef structures (Farmer and Ault 2011, 2017), and reef

edges (Herbig et al. 2019). When taken together, these studies indicate that the Yellowtail Snapper is a habitat generalist, with certain populations potentially displaying location-specific habitat preferences. It is possible that despite reassigning habitat types to broad-scale receivers based on the highest percent habitat coverage within the receiver’s detection range, the final receiver habitat assignments were still too coarse and not truly representative, thus providing misinformed broad-scale habitat preferences (i.e., sand and seagrass habitats). This further illustrates the need for (1) integrating fine-scale positioning systems to more accurately infer habitat use and (2) devising compatible methodology to better estimate habitat preference for broad-scale arrays.



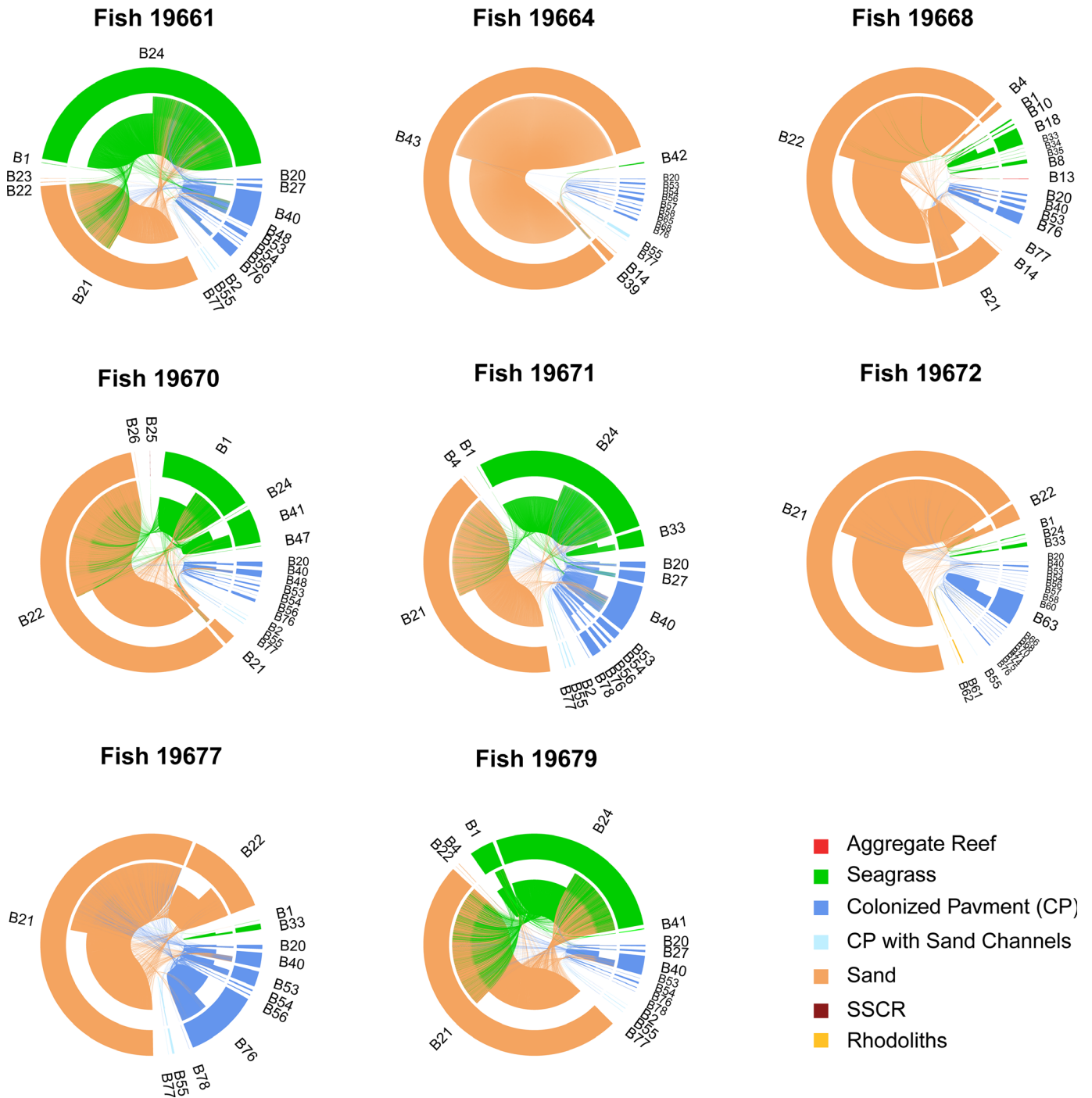


FIGURE 3. Habitat connectivity plots for the eight Yellowtail Snapper that were used for broad-scale analyses (SSCR = sand with scattered coral and rock). Receiver habitat types are from the second reassignment step (see Methods) and are based on habitat-specific detection ranges of individual receivers. Each sector of each circle plot represents an individual receiver (e.g., B21) visited by that fish. Movements between receivers are shown by each thin line connecting the sectors. Movements, or detections, occurring sequentially at the same receiver are represented by the inside arrow being closer to the outside part of the sector.

The Yellowtail Snapper is a semi-pelagic and transient species in reef ecosystems and is often observed swimming well above the substrate (Muller et al. 2003), frequently

moving moderate distances (Farmer and Ault 2011). In contrast, certain Yellowtail Snapper populations have been observed to display high site fidelity (Watson et al.

TABLE 2. Total number and filtered number of fine-scale positions generated by the VEMCO Positioning System for eight Yellowtail Snapper (filtering involved removal of positions with horizontal positioning error >7.5; percent retained is given in parentheses). Numbers of filtered diel positions for the five fish (>100 filtered positions) that were kept for fine-scale analyses (denoted by asterisks) are given.

Tag ID	First position	Last position	Total number of positions	Number of filtered positions (% retained)	Day positions	Crepuscular positions	Night positions
19661	Jun 4, 2015	Jul 7, 2015	184	17 (9.2)			
19668*	Jul 25, 2015	Nov 1, 2015	138	108 (78.3)	81	1	26
19671*	Jun 8, 2015	May 2, 2016	628	528 (84.1)	29	7	492
19672*	Sep 27, 2015	Feb 17, 2016	212	176 (83.0)	166	2	8
19677	Apr 27, 2016	May 1, 2016	24	3 (12.5)			
19664			0	0			
19670*	Jan 23, 2016	May 11, 2016	30,217	27,369 (90.6)	10,514	1,915	14,940
19679*	Jan 23, 2016	May 11, 2016	38,411	30,950 (80.6)	10,956	3,013	16,981

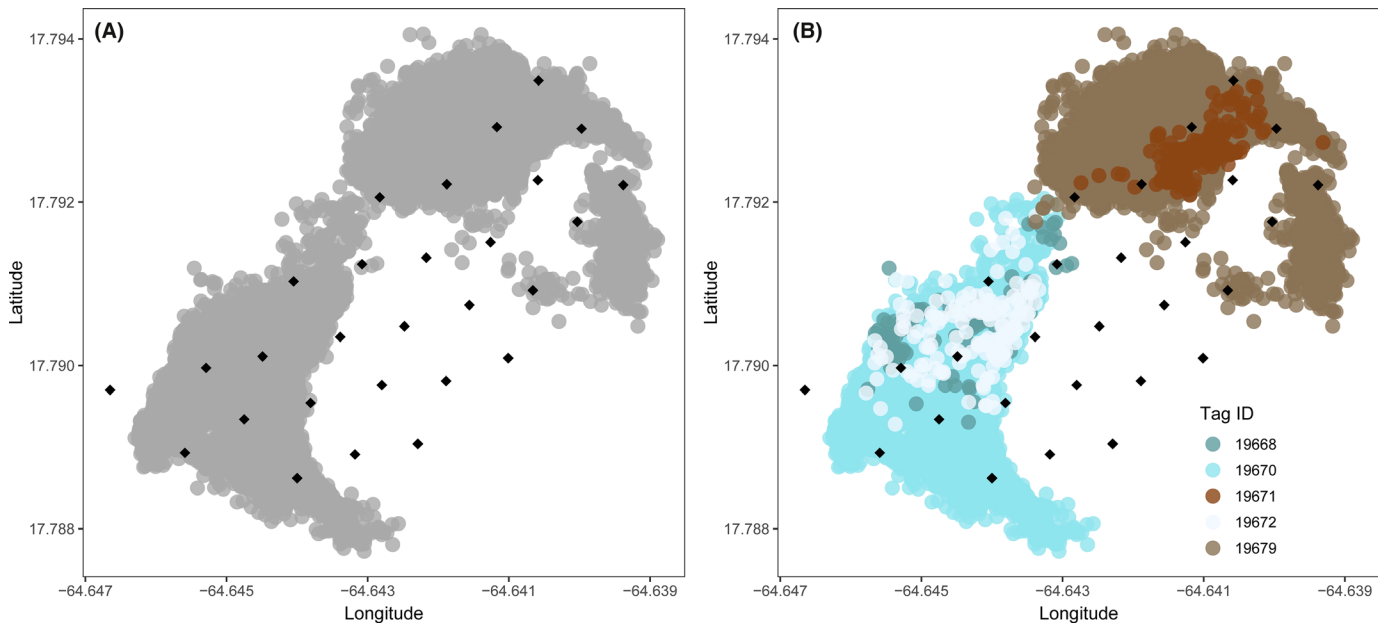


FIGURE 4. (A) Filtered  $x, y$  positions plotted for the five Yellowtail Snapper that were retained for fine-scale analyses and (B) the same positions but with individual fish designated by colors. Black diamonds represent the VPS receivers.

2002; Lindholm 2004; Lindholm et al. 2005), which was supported in this study with almost all CURs clustered along the shelf break. Shelf edges are considered unique areas that support high biodiversity and value (Sih et al. 2017). The shelf break in BIRNM likely provides the necessary resources to support a substantial density of Yellowtail Snapper (Pittman et al. 2008), although other factors may also contribute to this observation. For some smaller reef fish, swimming ability and water current strength were useful threshold indicators in determining movement and connectivity across a seascape (Caldwell and Gergel 2013). Yellowtail Snapper in the Dry Tortugas, Florida, showed a preference for low-relief,

contiguous reef habitats (Farmer and Ault 2011, 2017); as rugosity and patchiness may be important factors in structuring habitat use. Categorizing the extent of vertical relief could be a valuable explanatory variable for analyzing certain species' fine-scale habitat use. It is also possible the importance of edge habitat is missing from our analyses, as some species prefer the boundaries between two disparate habitat types (Dance and Rooker 2015). Future research should move toward developing standardization for an edge habitat category, which could represent an important habitat for Yellowtail Snapper. Essentially, new habitat combinations (e.g., seagrass-colonized pavement or sand-seagrass) could represent specific combinations of

TABLE 3. Individual and mean Euclidean distance analysis (EDA) habitat type ratios for five Yellowtail Snapper that were tracked with the VEMCO Positioning System and used for the fine-scale analysis (CP = colonized pavement; SSCR = sand with scattered coral and rock). An EDA ratio equal to 1.0 indicates random habitat use, a ratio greater than 1.0 indicates relative avoidance, and a ratio less than 1.0 indicates relative preference. Mean EDA ratios were calculated as the distances from Yellowtail Snapper positions divided by the distances from 1,000 random positions to each habitat type. Mean EDA ratios show that habitat use was occurring randomly (multivariate ANOVA:  $P = 0.8486$ ).

Tag ID	Habitat type				
	CP	SSCR	Reef rubble	Sand	Seagrass
Group 1					
19668	1.060	1.112	0.329	0.845	0.898
19670	1.120	1.192	0.341	0.869	0.902
19672	1.044	1.109	0.322	0.822	0.861
Group 2					
19671	0.624	0.596	1.315	0.865	0.948
19679	0.587	0.547	1.314	0.907	1.000
Overall mean	0.887	0.911	0.724	0.862	0.922

preferred habitats. The combination and structure of all interwoven habitat patches in BIRNM likely influenced the movement patterns of Yellowtail Snapper at both spatial scales (Boström et al. 2011) as well as unexplained factors, such as depth, water currents, and proximity to the shelf break. Given that the sample sizes for our broad- and fine-scale analyses were small, additional fish caught throughout BIRNM would strengthen the ecological inferences derived from the present study.

This study provides the first fine-scale telemetry data available for Yellowtail Snapper and highlights new ecological insights into long-term habitat partitioning and connectivity, diel patterns, and individual behaviors. Positioning data revealed two groups of Yellowtail Snapper using the area within the VPS in consistent ways. Individual fish within each group had similar EDA ratios for specific benthic habitat types, most likely because the general locations of the positions overlapped in space. Yellowtail Snapper positions clearly showed evidence of individual niche partitioning between two contingents (see Secor [1999] for the contingent hypothesis), or groups of individuals moving in consistent patterns. Habitat partitioning within the VPS array has been documented for other sympatric reef fishes in BIRNM (Becker et al. 2020; A.J.N., unpublished data). The small sample size and VPS data facilitated this realization; however, for other studies that generalize across many individuals and that lack fine-scale positioning data, the idea that habitat use varies at the individual level may be overlooked in order to

complete analyses and make inferences at the population level. Results of EDA are likely realistic in that the population does not prefer or avoid certain habitats (i.e., the species is a habitat generalist; Muller et al. 2003), but individuals may preferentially select or avoid certain habitats that can vary in space and time.

Reef fish display highly complex diel patterns in movement, with some being more active during different periods of the day (Hitt et al. 2011). Environmental factors, including predation threat and optimal foraging opportunity, likely play a dominant role in structuring diel behaviors (Rooker et al. 2018). For Yellowtail Snapper in BIRNM, fine-scale data showed no clear population-level diel trend in activity, with three fish accumulating more positions at night and two accumulating more daytime positions. The three fish with the most positioning data (tags 19670, 19671, and 19679) had more positions at night that were tightly clustered over colonized pavement. There is some evidence from broad-scale movement studies that Yellowtail Snapper are more likely to be detected during the day (Lindholm et al. 2005; Farmer and Ault 2011; Herbig et al. 2019). However, Herbig et al. (2019) noted that missed nighttime detections could be attributed to Yellowtail Snapper remaining close to the reef floor, thereby inhibiting the chance of detection with a broad-scale receiver array design. Concentrated nighttime positions likely demonstrate resting behavior close to the seafloor, with the VPS able to capture this behavior better than previous broad-scale studies. The Yellowtail Snapper with the lowest number of positions (tags 19668 and 19672) may have displayed similar resting behavior at night in a location outside of the VPS array and as a result were more active in the VPS during daytime exploratory movements. Beginning around dawn and throughout most of the day, all Yellowtail Snapper were considerably more active in the VPS, exhibiting wider-ranging movements across habitat types (A.J.N., unpublished data). To illuminate potential reasons for the differences in daytime and nighttime movement patterns, a trajectory analysis (McLean et al. 2014) can be applied to the positioning data to identify feeding, resting, or other clear behaviors.

The researcher's choice of analytical tools for use in evaluating biotelemetry data will ultimately influence the results upon which spatial management decisions depend (Becker et al. 2016). When designing spatial management areas, it is important to consider both (1) high-use areas in conjunction with corridors of frequent movement and (2) larger space use (Lea et al. 2016). Accurately characterizing habitat use is also important for spatial management decisions that may designate protected areas around essential habitats (Green et al. 2015; Weeks et al. 2017). Interpretation of broad-scale habitat preference across studies is likely imprecise, especially in

complex environments that are dominated by patchy and interwoven habitat configurations, such as coral reefs. We recommend that the scale of the question should guide the tools used to arrive at the appropriate answer. For example, if a researcher is interested in movement connectivity or the efficacy of an MPA (i.e., time spent within or outside protection), then broad-scale telemetry with a strategic array configuration is appropriate (Espinoza et al. 2015; Kendall et al. 2017). If the researcher is interested in habitat selection, diel movements, or intraspecific interactions, then a positioning system—also deployed in a strategic manner—is preferable (Furey et al. 2013). In the present study, broad-scale analyses misinterpreted habitat selection processes, whereas the fine-scale positioning system was able to accurately characterize fine-scale habitat use and also highlighted individual patterns in habitat selection.

As telemetry technologies continue to evolve, so do the techniques that are essential for extracting relevant and compatible information for users and managers. Furthermore, analytical tools must be standardized (Heupel et al. 2006) and critically evaluated (Becker et al. 2016). When analyzing movement data at two different spatial scales, different conclusions and inferences can be drawn that depend upon the choice of analytical method. Here, we demonstrated that the results of fine-scale habitat analyses greatly enhanced ecological inferences extracted from broad-scale data; these findings act as a reminder to be cognizant of the scope and capacity of the different array configurations and what questions should be asked at each scale. Our study offers support for the need to integrate fine-scale positioning systems with broad-scale arrays when interested in understanding habitat use and individual behaviors—information that is otherwise not easily obtainable from broad-scale telemetry data alone.

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## SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.