Coarse- and fine-scale acoustic telemetry elucidates movement patterns and temporal variability in individual territories for a key coastal mesopredator

Sarah L. Becker ⓘ · John T. Finn · Ashleigh J. Novak ·
Andy J. Danylchuk · Clayton G. Pollock ·
Zandy Hillis-Starr · Ian Lundgren · Adrian Jordaan

Abstract Great barracuda (*Sphyraena barracuda*) are a high trophic level predator that uses a wide variety of habitats globally throughout tropical and subtropical waters. Despite the important top-down pressure this species likely exerts on fish communities within its foraging territories, the specifics of spatial ecology remain relatively unknown. This study tracked 17 great barracuda throughout Buck Island Reef National Monument, a marine-protected area located in St. Croix, U.S. Virgin Islands (17.786944° N, − 64.620556° W) from July 2014 to May 2016. Broad- and fine-scale acoustic telemetry was used to examine individual variability and study population patterns in residency, site fidelity, territoriality, and complexity of spatial use within home ranges. Network analysis of broad-scale data revealed spatial and temporal differentiation among the population in location of core use areas and showed that these areas contained multiple unique receiver groups or communities, a product of spatial or temporal variation within core activity spaces. Results from the fine-scale positioning system reinforced spatial and temporal partitioning in core use areas between individuals, indicating territorial behaviors, and showed evidence for both resident and transient movements. Preliminary fine-scale analysis also suggested diel variation in location of activity spaces. Although ubiquitous throughout all shallow water habitats, detection patterns for the study population appear to be influenced by high residency, territoriality, spatial partitioning, and diel variation. Understanding the complexities of individual space use is fundamental to ecologically founded and effective area-based spatial management frameworks at community scales.

Keywords Acoustic telemetry · Great barracuda · Individuality · Network analysis · Territoriality · VEMCO Positioning System

S. L. Becker (✉) · J. T. Finn · A. J. Novak ·
A. J. Danylchuk · A. Jordaan (✉)
Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA 01003-9285, USA
e-mail: sarah.becker3@gmail.com
e-mail: ajordaan@eco.umass.edu

C. G. Pollock · Z. Hillis-Starr
National Park Service, Buck Island Reef National Monument, Christiansted, St. Croix, VI 008020-4611, USA

I. Lundgren
NOAA Fisheries, Office of Habitat Conservation, Habitat Protection Division, Silver Spring, MD 20910-3282, USA

Introduction

Successful application of spatial management approaches for marine species requires providing adequate protection of often spatially distinct and temporally variable activity spaces. To receive full benefits, target species home ranges must be contained within reserve boundaries. Mobile species whose whole range cannot be protected are at risk during movements outside the protected area (Dunton et al. 2015). Movements among distinct spatial areas for different life history needs are common in order to access spawning grounds, nursery

areas, shelter from predators, and foraging locations (Burke 1995; Mumby et al. 2004; Meyer et al. 2007; Domeier and Nasby-Lucas 2008; Luo et al. 2009; Kimirei et al. 2011). Acoustic telemetry is valuable for tracking movements of nearshore marine species, allowing for long-term data sets on residency and migration (Heupel et al. 2006; Hussey et al. 2015). Quantifying movement patterns can show spatial and temporal variation in habitat use and also reveal connectivity among habitat types and management areas. Increased understanding of home-range size, residency, and site fidelity can improve assessments of marine protected area (MPA) efficacy and lead to improvements in future planning (Meyer et al. 2007; Afonso et al. 2009; Augé et al. 2013; Letessier and Bouchet 2015; Aspillaga et al. 2016).

Great barracuda *Sphyraena barracuda* display genetic and behavioral traits that closely resemble reef-associated fish, but others indicate they are capable of large pelagic movements, thus occupying a middle ground between these two distinct movement behaviors (Daly-Engel et al. 2012). As large, high trophic level predators, barracuda could exert a significant influence on fish community structure within their foraging locations (Blaber 1982; Kadison et al. 2010). Adults have been documented using all nearshore habitats types in tropical and subtropical waters globally, but the specifics of habitat use and spatial ecology remain relatively unknown (De Sylva 1963; Blaber 1982; Kadison et al. 2010). Great barracuda are believed to aggregate to spawn during summer months, but to date, no aggregation locations or behaviors have been documented (De Sylva 1963; Blaber 1982; Domeier and Colin 1997; Kadison et al. 2010). One of the few studies that investigated habitat use by this species indicated seasonal variation in certain habitats but also demonstrated large spans of time in which habitat use appeared random (Faunce and Serafy 2008). The first tracking study conducted for adult great barracuda showed high individual variability in habitat use, residency, and site fidelity; however, the ecological functions that drive adult movement patterns remain unknown (O'Toole et al. 2011). Becker et al. (2016) utilized the same dataset analyzed for this study and found that individuals occupy small core use areas, undergo larger sporadic movements, and demonstrate little benthic habitat preference in location of core use areas. A spatial use strategy employing ubiquitously dispersed core areas with sporadic transient movements leads to questions regarding territoriality

and conspecific overlap, habitat use within home ranges, and implications for spatial management (Aspillaga et al. 2016).

Quantifying fine-scale movements within home ranges can identify spatial differentiation within high-use areas for different ecological functions and improve understanding of area and habitat requirements for target species (Pittman et al. 2014). Variability in movement patterns, residency, and site fidelity to high-use areas has been demonstrated for a number of marine species, driven by factors ranging from habitat and environmental conditions to population dynamics and life history of conspecifics and prey species. Season and water temperature are common drivers of shifts in movement patterns and activity space location, with migratory species such as Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* moving between coastal hotspots of abundance cued by temperature changes (Melnychuk et al. 2016). Other temperate species such as striped bass *Morone saxatilis* have shown seasonal and temperature-related fluctuations in residency and activity space (Hollema et al. 2017), while elephant seals *Mirounga leonine* have shown behavioral variation in movements associated with water temperature (Bestley et al. 2013). Both tropical and temperate species such as sand tiger sharks *Carcharias taurus* and white sharks *Carcharodon carcharias* also demonstrate temporal and seasonally driven shifts in activity space via movements to and from nursery and foraging grounds (Domeier and Nasby-Lucas 2008; Kneebone et al. 2012). Numerous reef fish demonstrate diel shifts in habitat use and movement patterns, seeking shelter within reef structures and resting during the day, then foraging in adjacent seagrass and reef flats at night (Burke 1995) when visual predators may be less active (Bosiger and McCormick 2014).

In addition to temporally variable environmental conditions, spatial variables such as habitat type often drive shifts in movement patterns: blacktip sharks *Carcharhinus melanopterus* have been shown to switch from fast, linear movements to slow, meandering swimming depending on benthic habitat (Papastamatiou et al. 2009). Prey availability is another strong driver of the spatial ecology and movements of marine predators. Optimal foraging strategies—switching between linear movements when prey is abundant and meandering random walk patterns when prey is sparse—have been well documented to explain changing movement patterns in marine predators (Humphries et al. 2010), though species-specific traits and individual variability

still influence the expression of these patterns. Grey seals *Halichoerus grypus*, for example, display three distinct movement modes, and only some individuals display meandering search tactics (Austin et al. 2004). Changes in behavior such as from foraging to rest also manifest in changes in movement rate and patterns as well as in habitat use. Additionally, there is evidence that habitat complexity influences the dynamics of foraging and competition, with implications for the spatial dynamics of predators (Almany 2004).

Food abundance and conspecific density often influence home-range size and territorial behaviors. Many species decrease home-range size, modify site fidelity, and increase territoriality in order to mitigate the negative impact of high competition for food on fitness or reproductive output (Hixon 1980; Ostfeld 1990). The reef fish beaugregory *Eupomacentrus leucostictus* demonstrates density-dependent changes in home-range size, with females benefiting from a "food maximizing" strategy and expanding home ranges in times of low food abundance, while male home ranges remain the same (Ebersole 1980). More territoriality literature exists for terrestrial predator species. For example, transient versus resident behaviors have been hypothesized for coyotes *Canis latrans* to facilitate an evolutionary trade-off in which subpopulations maximize dispersal over individual fecundity in order to minimize competition for resources at the population scale (Hinton et al. 2015). Black bears *Ursus americanus*, black-backed jackals *Canis mesomelas*, and hyenas *Crocuta crocuta* have all been shown to display variations in territoriality and home-range size in order to maximize fitness and reproduction (Powell 1987; Boydston et al. 2003; Humphries et al. 2016). While few specifics are known about great barracuda reproductive ecology and the implications of competition on fecundity, territoriality could indicate a response to high competition for resources to maximize individual fitness. Movement patterns within home ranges, residency, and site fidelity could provide additional information on population-level spatial partitioning. To examine movement patterns and habitat use within home ranges, assess evidence for territoriality, and identify high-use areas and movement corridors throughout the study population, we used acoustic telemetry to track great barracuda (*n* = 17) within Buck Island Reef National Monument (BIRNM) off the northeast shore of St. Croix, U.S. Virgin Islands, from July 2014 to May 2016. Both broad- and fine-scale tracking were conducted as

independent but complimentary studies investigating spatial and temporal variability in movement patterns for individual fish, as well as among the full study population. Home range areas were modeled using network analysis community metrics in order to identify groups of receivers sharing common detection histories, thereby dividing the array into spatial use categories for individual fish. These results were summarized across the study population and mapped to associate use patterns with benthic habitat. A VEMCO Positioning System (VPS) was incorporated into the array to validate patterns suggested by the broad-scale analysis with preliminary fine-scale visualizations of movement patterns and intraspecies interactions.

Materials and methods

Study area

BIRNM, located off the Northeast corner of St. Croix, USVI (17.786944° N, − 64.620556° W), contains a shelf habitat composed of a patchy mosaic of shallow ecosystems, including linear reef to the south of Buck Island and patch reefs to the north and east of the island, which create shelter for calm lagoon habitats (Fig. 1). Extensive seagrass beds and sand flats are found to the south and west of the island, while the northern reach of the reserve contains patch reefs, colonized pavement, and a steep drop-off towards a deep oceanic trench (Costa et al. 2012). The National Park Service (NPS) manages the MPA and maintains an acoustic telemetry network that consists of a broad-scale array of receivers dispersed throughout the shallow water habitats of the reserve, as well as a VPS located on the western edge of the Buck Island shelf. BIRNM is bordered by East End Marine Park (EEMP), a multiuse marine reserve managed by the territorial government, to the east and south, and unprotected waters to the west and north. In 2001, BIRNM's boundaries were expanded 5-fold to its current size19,000 acres (~ 7689 ha) and its designation was switched from multiuse to a no-take reserve.

Broad-scale array design

The broad-scale portion of this study used passive tracking with fixed, autonomous omnidirectional acoustic receivers (VR2W 69 kHz VEMCO Inc., Nova Scotia, Canada). At the time of the broad-scale study, 52

acoustic receivers were anchored semi-permanently throughout shallow water habitats spanning approximately 10 km^2 (Fig. 1). Receivers were suspended 2–3 m above the seafloor and remained in place for the duration of the study, across all seasons. Sites were chosen based on habitat type and distance to nearest receiver in order to minimize overlapping detection ranges and provide coverage for all benthic habitat types. Receivers were attached to the bottom using sand screws (1 m long with 15-cm diameter blades) in soft sandy areas, and cement blocks in hard bottom habitats as anchors from which moorings constructed of polypro line and 20-cm diameter foam floats were tethered. Range testing was conducted by Selby et al. (2016) on 19 receivers across the 52-receiver array, encompassing all habitat types in a representative sample of environmental conditions. Fixed delay tags were submerged at various intervals in each cardinal direction for these test receivers and used to model detection probabilities given a range of environmental conditions. Mean detection probabilities at 100 m were 58.2% and dropped to 26.0% at 200 m. These low detection ranges are due primarily to high rugosity reef habitat (Selby et al. 2016).

VEMCO Positioning System array design

A VPS was nested within the larger acoustic array (Fig. 1) in June 2015 to examine fine-scale movement patterns of fish. The VPS was predominantly deployed over seagrass and colonized hardbottom habitats on the western edge of the shelf drop-off in order to monitor diel movements on and off the shelf by smaller reef fish as part of a separate study. While the broad-scale array provides presence or absence data within the area of coverage of an individual receiver, the VPS generates unique positions of transmissions. The VPS consisted of 28 closely spaced (~ 100 m) receivers (VR2W 69 kHz VEMCO Inc., Nova Scotia, Canada) with overlapping detection ranges which allowed individual fish positions to be triangulated with a high level of accuracy based on differences in transmission arrival times at three or more receivers (Espinoza et al. 2011). Receivers were deployed between 7- and 18-m (mean 9.4 m) depth by cement anchors or sand screws tethering receivers 2–3 m above the seafloor. Synchronization tags or "sync tags" (VEMCO model V16-4x, 69 kHz) programmed with a nominal delay of 600 s (range 500–700 s) were collocated with each VPS receiver to correct for time

drift of the internal receiver clocks. Three additional stationary reference tags were placed at intermediate points within the center of the VPS array (Fig. 1).

Barracuda capture and tagging

Great barracuda (*n* = 35; Becker et al. 2016) were captured by trolling throughout the study site at 8 knots using artificial lures and 2 9/0 circle hooks (O'Toole et al. 2011; Becker et al. 2016). Tagging was only conducted on fish deemed healthy enough to support an acoustic transmitter; those with hook damage or other injuries were not tagged (Becker et al. 2016). VEMCO V16 (16-mm diameter by 54-mm length, dry weight 8.1 g, 3650 days (~ 10 year) battery life) and V13 (13-mm diameter by 36-mm length, dry weight 6 g, 1299 days (~ 3.5 years) battery life) transmitters were used, depending on the size class of the tag recipient (range 61–107 cm). All tagged great barracuda were adults or sub-adults, and all tags were appropriate to the size of the organisms and did not increase mortality following tagging. Sex was not determined at tagging as there are minimal external indicators of sex in great barracuda (De Sylva 1963). Transmitters were programmed to ping at random once every 60–180 s. After capture, fish were placed in a Tupperware tote (108 × 54.3 × 45.7 cm) containing seawater and a 10 g/L concentration of MS222 was added slowly to the water until the fish showed slowed gill movement and loss of equilibrium representative of stage 4 anesthesia (O'Toole et al. 2011; FAU IACUC Guidelines 2014). While fish were held in a supine position with gills submerged, tags disinfected with 70% isopropyl alcohol were surgically implanted into the body cavity just off the central mid-line between the pelvic and anal fins. The surgical incision was made with no. 10 blade carbon steel sterile disposable scalpels and was closed with 2–3 interrupted sutures using Ethicon polydioxanone monofilament sterile absorbable FS-1, 24-mm reverse cutting needle sutures (Model PDS*II). Halfway through the surgery, fresh seawater was added to dilute the anesthetic and begin to bring the fish out of anesthesia. Once total and fork length measurements were taken, fish were placed in ambient seawater, either in a separate tote, in a mesh pen (122 × 183 cm, 2.5-cm mesh size) anchored within the calm lagoon habitat, or held manually facing into the current over the side of the boat, depending on fish size, until normal swimming patterns returned at which point they were released back into the study area from which they were
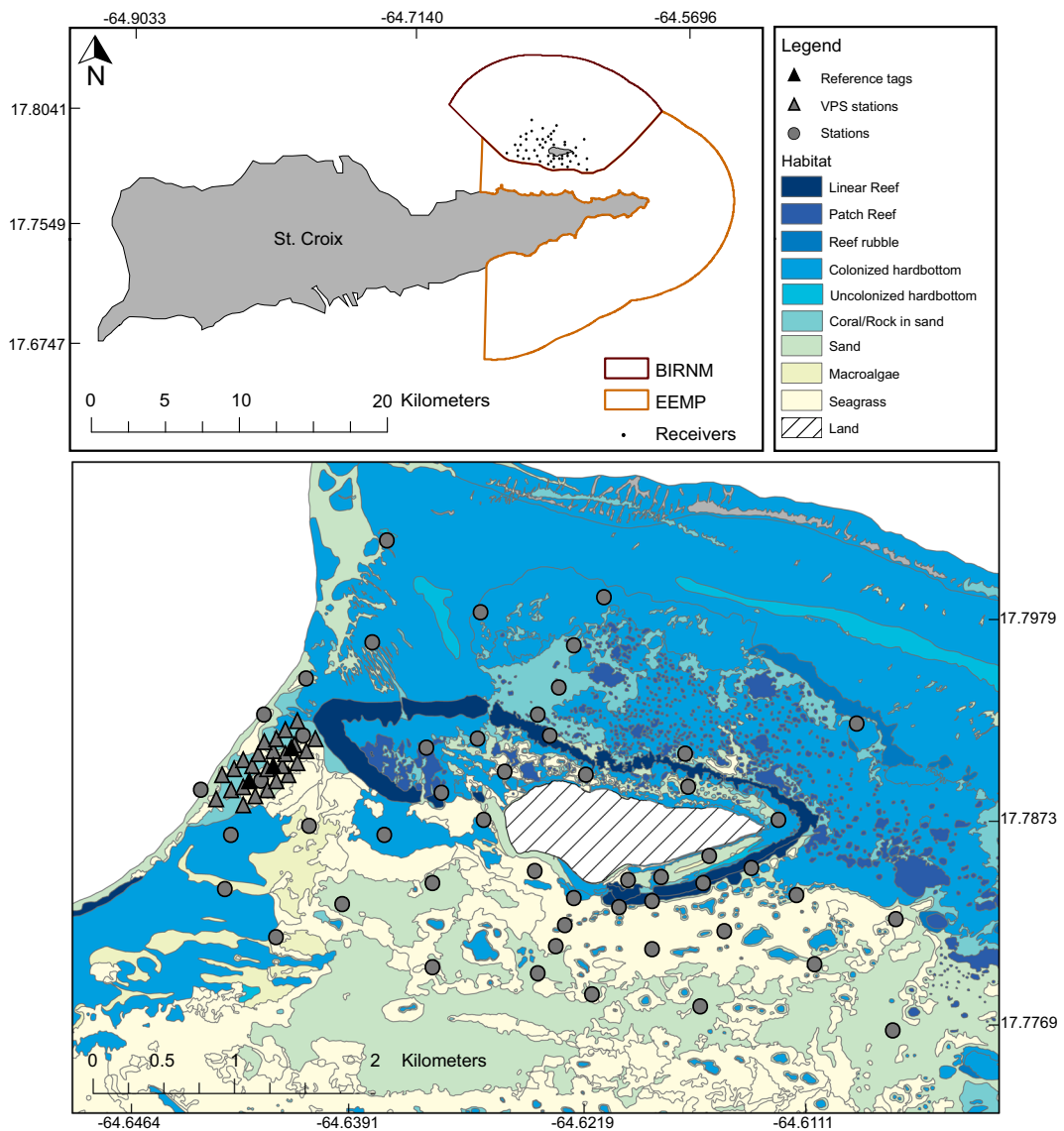
Fig. 1 Location of Buck Island Reef National Monument (BIRNM), adjacent East End Marine Park (EEMP) acoustic receivers, and adjacent protected areas in relation to the island of St. Croix are shown in the upper panel. The lower panel shows the location of receiver stations, VPS stations, and reference tag stations within the shallow water region of BIRNM surrounding Buck Island and in relation to benthic habitat coverage. NOAA Biogeography Branch generated the benthic habitat shapefiles

captured (Friedlander and Monaco 2007; O'Toole et al. 2011; Becker et al. 2016). No more than four fish were tagged at each capture site in order to ensure that tagged animals were distributed throughout the array and to minimize tag collisions. All sampling and tagging techniques were approved by IACUC no. 2013-0031 (University of Massachusetts Amherst) and NPS study no. BUIS-00058 and research collect permit nos. BUIS-2013-SCI-0003 and BUIS-2014-SCI-0006 (Becker et al. 2016).

Broad-scale data management

A year of data spanning July 2014–July 2015 (available via the Dryad Data Repository at datadryad.org) was filtered in R version 3.2.2 (R Core Team 2015) and VUE (VEMCO Inc., Halifax, NS) to remove false detections due to tag collisions, echoes, and simultaneous detections. We filtered out any detection that occurred < 55 s after a previous detection from the same tag, based on our tags' 60–180-s ping rate. This assumes

accuracy of the first detection and classifies the second detection as false and requiring removal. A cutoff of 3 weeks of consecutive detection at one receiver was set to filter out mortality events or shed tags. These filtering procedures removed three of the 35 tagged fish from the dataset and left 32 great barracuda detected within the array within the study period. Based on results from Becker et al. (2016) that indicate low detection frequencies can lead to spurious interpretation of results, we rejected any dataset showing less than 5% of possible detections. This filtering left a total of 17 out of 32 great barracuda for use in this study (Table 1).

VEMCO Positioning System data management

All downloaded data collected from the VPS between June 2015 and May 2016 were post-processed by VEMCO. Two-dimensional positions were derived from the raw detection data using a set of positioning algorithms that weight the average location of a transmission detected on three or more receivers and favor the position with lowest error sensitivity (Espinoza et al. 2011; Meckley et al. 2014; Roy et al. 2014). Positions for both sync tags and animal-implanted tags have an associated unit-less error or confidence value derived from the calculation, termed horizontal positioning error (HPE). Sync and reference tags also have measured error in meters (HPEm) based on the known location of the tag in the array (Smith 2013). If there is a strong statistical relationship between HPE and HPEm, then derived animal positions can be used with greater confidence (Meckley et al. 2014). Therefore, prior to any analyses, a HPE cutoff value was assigned 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). In order to determine the appropriate cutoff value, we binned calculated reference and sync tag positions (1-m increments up to 25 m) based on ranges of HPE values and calculated a twice the distance root mean squared (2DRMS) statistic. Using the relationship between 2DRMS and average HPE value for each bin, we constructed linear models with a desired 5-m accuracy (our selected goal) to designate HPE cutoff values. For a 95% confidence in 5-m accuracy, the 2DRMS equation deemed that tag positions with an HPE value of > 7.5 should be excluded from analyses, as they were estimated to have an actual positioning error greater than 5 m. In general, a lower HPE threshold was warranted due to

the system being particularly noisy (Selby et al. 2016) and the desire to have more precise estimates for positions that would allow for more reliable ecological conclusions and to avoid the risk of over filtering the data.

Broad-scale tracking analysis

Previous network analysis of the movement patterns for great barracuda in BIRNM has shown coarse partitioning of activity space into highly used core areas to which individuals have high site fidelity and general use areas with infrequent but repetitive use patterns (Becker et al. 2016). We have extended this analysis of individual fish networks in order to look for patterns across the study population. Using the igraph package (Csardi and Nepusz 2006), we generated networks for individual fish with receivers as nodes and movements between them as edges weighted by the number of movements connecting each receiver pair. These networks were used to generate centrality rankings for receivers, based on centrality degree, or the number of edges connected to a single node including self-loops (Ledee et al. 2015). We summed the centrality rankings of individual fish for each receiver in order to identify common patterns across the array network regarding high-use areas for the study population and mapped these cumulative centrality rankings in relation to benthic habitat type.

Building off previous work using network analysis to identify commonalities between network nodes (Finn et al. 2014), we used similar methods to identify receiver groups displaying common properties for individual fish. We refer to these receiver groups henceforth as "spatial communities," defined as groups of nodes that have a stronger relationship to one another than to the rest of the nodes in the network. There are several algorithms used to determine how to divide network relationships into community groups, many of which were tested for usefulness in analysis of acoustic telemetry array network models by Finn et al. (2014). Using the movement matrices generated to develop the centrality rankings, we applied the fast-greedy algorithm to test for differentiation between receivers within an individual fish's network. Fast-greedy works by hierarchically dividing receivers into groups, based on similar patterns of connections to other receivers, and provides as output a list of communities based on these traits (Clauset et al. 2004; Newman and Girvan 2004). In order to determine the category and significance of these

Table 1 Dataset summary for all tags analyzed. Morphometric and detection history summaries include tag ID (Tag), fork length (FL), total number of detections (Detections), remaining number of detections after filtering processes (Detections > 55), the ratio of observed over expected detection, based on tag ping rates (Obs/exp), and the number of days each tag was detected in the array over the year-long study period (Days heard)

Tag	FL (cm)	Detections	Detections > 55	Obs/exp	Days heard
173	84.5	19144	13572	5.160848734	117
24550	97	27585	24433	9.290820595	364
24554	61	15706	13282	5.050574188	364
24556	85	51448	44037	16.74537988	364
24776	84.5	182495	152752	58.08502548	364
24779	92	31506	31106	11.82827591	348
24780	90.5	43067	39693	15.09354324	363
24784	90.5	250055	224179	85.24564606	364
24785	79.5	191770	174354	66.29933835	364
26793	101.5	163087	73399	27.91048749	364
26796	63	39963	19178	7.292569777	364
26797	96	175140	77435	29.44520496	270
26798	89	102271	50343	19.14328086	361
26799	71	82509	51276	19.49806069	364
26800	97	221287	106074	40.33538672	364
26801	107	115956	57774	21.96897102	364
26802	103	152258	32225	12.25378356	332

community designations, we assessed each node (receiver) within the community for the number of in-degree links (links to nodes within the community group) and out-degree links (links to nodes outside the group). Wilcoxon rank sum tests were employed to test for significance of each group by indicating whether the community has significantly more links within, which indicated a positive community. Conversely, a group of receivers that demonstrate significantly greater connections to receivers outside their community is an anti-community (Finn et al. 2014). Positive communities can be thought of as destinations within a total activity space. They could be a resident territory or a feeding or spawning ground where a fish travels to and remains long enough to generate frequent connections between receivers within that space (Finn et al. 2014). Anti-communities represent groups of receivers that have more connections to receivers outside their community than within it. These communities can be thought of as transit hubs or places that a fish frequently passes through to get to another destination, and are indicative of movement corridors (Finn et al. 2014).

Communities were plotted as spatially referenced graphs with edges weighted by number of movements between nodes and with nodes weighted by numbers of connecting edges. These plots demonstrate along what lines spatially proximate receivers are being divided among communities and make direct comparisons with spatial variables such as benthic habitat type more intuitive. They also give a visual representation of movement patterns, as edges laid out in this context begin to approximate direction and area of movements within the array. For example, great barracuda with high residency to a small core area will result in a community pattern resembling spokes on a wheel, while a highly mobile roaming predator would result in large repeated loops or a tangled web of lines (Finn et al. 2014). Cumulative maps were made that summarize station values for significant communities for all analyzed fish, divided into positive communities and anti-communities. For community membership maps, any receiver present in a positive significant community was assigned a value of 1, an anti-community member received a value of − 1, and no significant membership a value of zero. These community membership scores for each tag were then summed by station. Cumulative membership scores defined commonly used positive communities (high positive value), highly used anti-communities (negative

value), or areas with neutral use due to lack of use or variable use among individuals.

Fine-scale tracking analysis

A limited amount of initial data from the VPS was available for a preliminary analysis of fine-scale movement patterns of great barracuda ($n = 5$) in order to guide future research. To examine temporal movement variations at a finer spatial resolution, filtered positions for each individual fish were binned by diel stage as day, night, or crepuscular (1 h before sunrise and 1 h before sunset). Sun ephemerides calculations with approximately 1-min accuracy were performed in the R package maptools with the associated algorithms supplied by NOAA (Bivand et al. 2017). Diel positions for the three great barracuda (Tags 24785, 26799, and 26801) with the most robust position histories were plotted using the ggplot2 package (Wickham 2009) to illustrate potential diel patterns in spatial use within the VPS array. To investigate any patterns of distinct space use between individual fish within the VPS array, positions for barracuda were illustrated using the ggplot2 package (Wickham 2009) on the daily scale, which allowed for a visual comparison of variation in fine-scale movement patterns. Two consecutive days in early February and late April 2016 were ultimately chosen as target days for comparison since they contained the greatest number of tagged barracuda present and provided the best opportunity to compare fine-scale movement patterns of individual fish.

Results

Broad-scale network centrality ranking and spatial community plots

Tracking of the study population ($n = 17$) yielded > 1,000,000 filtered detections within the array (Table 1). Detection histories were predominantly consistent throughout the study period for all individuals and did not show any consistent seasonal patterns, with fish detected on average 341 days per year (median = 364 days per year). Individual fish consistently utilized home ranges dispersed across all benthic habitats as well as making occasional larger forays into the rest of the array (Becker et al. 2016). The fast-greedy algorithm separated the array into 5.82 (± 2.35) mean communities

per fish when results for individual fish were summarized across the study population (Table 2). Once significance testing was conducted, the average number of significant communities per fish was 1.65 (± 0.61). The majority of significant communities were positive, with more connections to receivers within the community than outside of it. Although in the minority, there were several significant anti-communities as well, one each for Tags 26796, 26793, and 24556. Significant communities had on average greater numbers of receivers with higher ratios of in versus out connections than non-significant communities. Positive communities and anti-communities occurred with similar frequency before significance testing was conducted (mean of 2.65 positive versus 2.71 anti), but significant communities were much more frequently positive than anti (25 versus 3; Table 2).

Significant communities included more receivers on average than the core use areas previously defined by network analysis (Becker et al. 2016), possibly because these earlier methods were looking only at network centrality degree rather than the more nuanced hierarchical model employed by the fast-greedy algorithm. Additionally, the fast-greedy algorithm frequently identified two significant communities, in addition to the presence of a third non-specific pattern of movement rather than dividing the use areas into two groups of core and general use areas (Becker et al. 2016). Spatial community plots for individual fish (Fig. 2) show spatially proximate groups of receivers that correspond both with intensity of use, shown by weight of receiver nodes, and with broad benthic habitat zones. Cumulative maps show higher centrality values and positive community membership across linear reef and seagrass (Fig. 3), with positive communities more closely associated with seagrass areas adjacent to reefs and colonized pavement. Anti-community sums highlight two open areas adjacent to highly rugose linear reef within BIRNM (Fig. 3). However, numbers even for these sites are low, with no more than two fish indicating these areas as an anti-community. Positive communities on the other hand, showed values as high as 11 out of 17 individual fish (Fig. 3).

Fine-scale diel variation and comparison of movement patterns

For a period of approximately 1 year (June 2015 to May 2016; 348 days), the VPS calculated a total of

Table 2 Fast-greedy summary statistics for each tagged great barracuda. For both total communities and significant communities (identified from Wilcoxon tests), the number of communities, mean number of receivers per community, mean in connections per community, and mean out connections per community are reported. The total positive, anti-, and neutral communities are listed for general communities, while the mean p values for community significance testing and the percent significant communities that were positive are reported for significant communities

Communities of receivers								Significant communities of receivers					
Tag	No.	Receivers	In	Out	Pos	Anti	NA	No.	Receivers	In	Out	p value	%Pos
26802	6	4.67	21	5	4	1	1	2	9.5	51	6.5	0.001	100
26801	7	5.14	30.9	24.6	3	3	1	2	8	63	15	0.018	100
26800	5	8.4	43.2	23.2	3	2	0	2	13.5	78	27	0.0044	100
26799	8	5.5	32.3	17	3	5	0	2	15.5	106	20.5	> 0.001	100
26798	4	7.5	35.5	8.5	2	1	1	1	23	118	13	> 0.001	100
26797	5	5.8	31.2	14.4	2	2	1	2	11	67	15	0.0012	100
26796	11	4.36	19.1	20.9	4	6	0	2	10	42	27	0.011	50
26793	5	10.4	80.4	68.4	2	3	0	2	15.5	118	70.5	0.014	50
24785	5	6	28.8	14.4	1	3	1	1	22	118	20	> 0.001	100
24784	5	5.4	27.2	16	2	3	0	2	11	60	16.5	0.0019	100
24780	6	4.17	17.7	7	4	2	0	2	10	47	11.5	0.003	100
24779	4	3.5	16	7.5	3	1	0	1	9	48	12	0.0012	100
24776	2	4.5	14	4	1	0	1	1	7	24	4	0.0037	100
24556	10	3.6	13.8	18.4	3	7	0	3	7	28.7	20.7	0.014	66
24554	8	3.88	17.5	20.5	2	6	0	1	11	60	18	> 0.001	100
24550	5	4.2	14.4	8.4	4	1	0	1	8	28	10	0.022	100
173	3	2.67	8.7	3.33	2	0	1	1	4	16	3	0.02	100
Mean	5.8	5.3	26.6	16.6	2.7	2.7	0.4	1.7	11.5	63.1	18.3	0.01	92.1

157,924 positions for thirteen great barracuda (Table 3), and of those, number of positions per fish ranged from 1 position (Tag 24555) to 141,957 positions (Tag 24785). The sync tags performed quite well in the system, with 95.8% of transmissions logged on three or more receivers indicating reliability in representative estimates of animal positions. A minimum of 100 filtered positions was used as a cutoff to ensure that any ecological inferences made from these data were better supported. Therefore, out of the thirteen fish that were detected in the VPS, only five passed our cutoff value (Table 3). Collectively, the five great barracuda generated 125,018 positions, which represented 79.3% retained from the unfiltered positions. The five selected fish had a wide range in number of retained positions (108–121,855 ± 24,216.7; Table 3).

The preliminary results from these five fish indicate diel variation in activity space and individual variation in movement patterns with some fish were more active within the VPS at night while others were more active in the VPS during the day. Activity was defined by the numbers of retained positions during day, night, and crepuscular time periods (Table 3). While some overlap in diel use areas occurred, all five fish analyzed demonstrated spatial differentiation in daytime versus nighttime activity space, though areas were not completely distinct and there were no clear patterns in crepuscular movements (Fig. 4). Daily plots of great barracuda positions showed large individual variation in detection patterns (Fig. 5). All four plots, regardless of day or month, showed Tag 24785 with by far the most positions. Tag 26799 was also present in every plot, but with far fewer positions. Other great barracuda were present sporadically, with few positions generated on each day of presence. Tag 24785 dominated the central portions of the VPS, while Tag 26799 was only detected in the southwest portion of the VPS. There was limited spatial overlap between observed great barracuda. Where overlap did occur, it was predominantly along the edges of Tag 24785's use area. Tag 24785 had positions that were
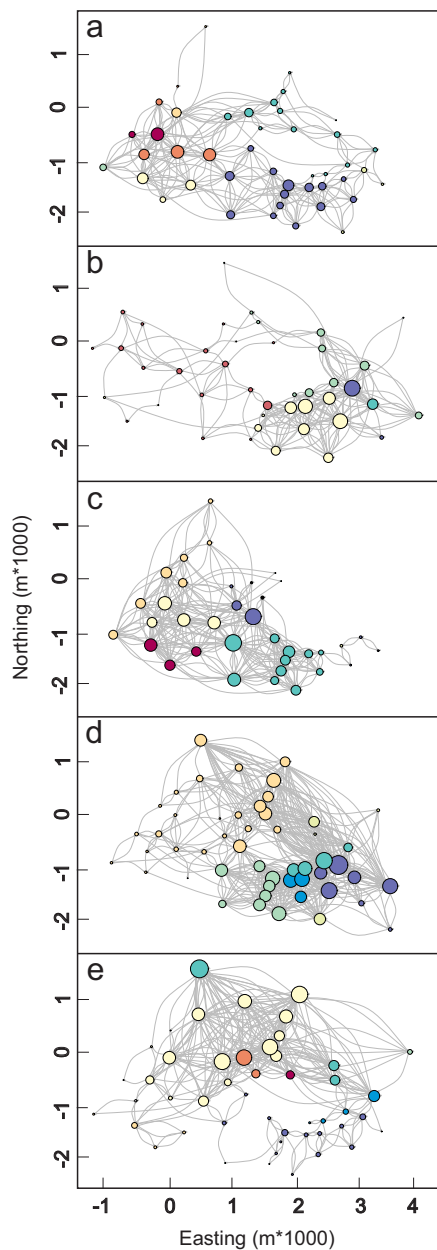
Fig. 2 Spatial referenced plots show spatially proximate acoustic receiver groups that display unique use patterns. Each panel illustrates several unique use groups per fish. Tags 24778 (**a**), 24779 (**b**), 24785 (**c**), 26799 (**d**), and 26801 (**e**) show spatial community maps for 5 example fish of the 17 modeled. Circles (nodes) represent receivers sized according to network centrality value, with larger circles representing increased centrality. Community groups within each panel are designated by color, with like shades indicating shared community membership

highly concentrated, indicating repeated use of the same resident space, while individuals with fewer positions

showed movements that appeared more sparse and transitory (Fig. 5).

Discussion

As a population, BIRNM great barracuda appear to be generalists using all habitat types, with individual variation in habitat use based largely on the location of core use areas. Though present in all habitats and generalists on the population level, spatial differentiation in movement patterns that corresponded to benthic habitat changes was present within individual home ranges. Individuals showed consistent residency patterns within high-use activity spaces throughout the year, with little seasonal variation. Though they made sporadic forays outside of these territories, they always returned to core use areas, displaying high site fidelity. These broad movements showed no temporal synchrony across the population and little overlap into other great barracuda territories. Where spatial overlap occurred, it tended to be on the edge of a different individual's activity space as a transitory movement with low likelihood of temporal overlap, indicating territoriality. While broad patterns of high and low use areas remain for individual fish (Becker et al. 2016), receiver communities show more complex movement patterns within home ranges. Fine-scale analysis of movements showed preliminary evidence of diel variation within individual activity spaces, while broad-scale analysis showed a rough correspondence between receiver community groups and benthic habitat boundaries.

Documenting habitat associations of marine species is a vital tool for marine spatial planning, as benthic habitats are often used to predict species distributions (Leslie et al. 2003; Halpern et al. 2008). Great barracuda have been documented in all coastal subtropical and tropical waters (De Sylva 1963), and previous studies have shown mixed results regarding habitat preference (Faunce and Serafy 2008; O'Toole et al. 2011). Similarly, the equal distribution of high centrality receivers throughout the array at the population level showed little indication of preference for a specific benthic habitat type for this study population. However, community membership analysis showed that spatial differentiation in movement patterns within each individual's home range corresponded with broad habitat zones, with community membership partitions for individuals often occurring along habitat transitions, even between spatially
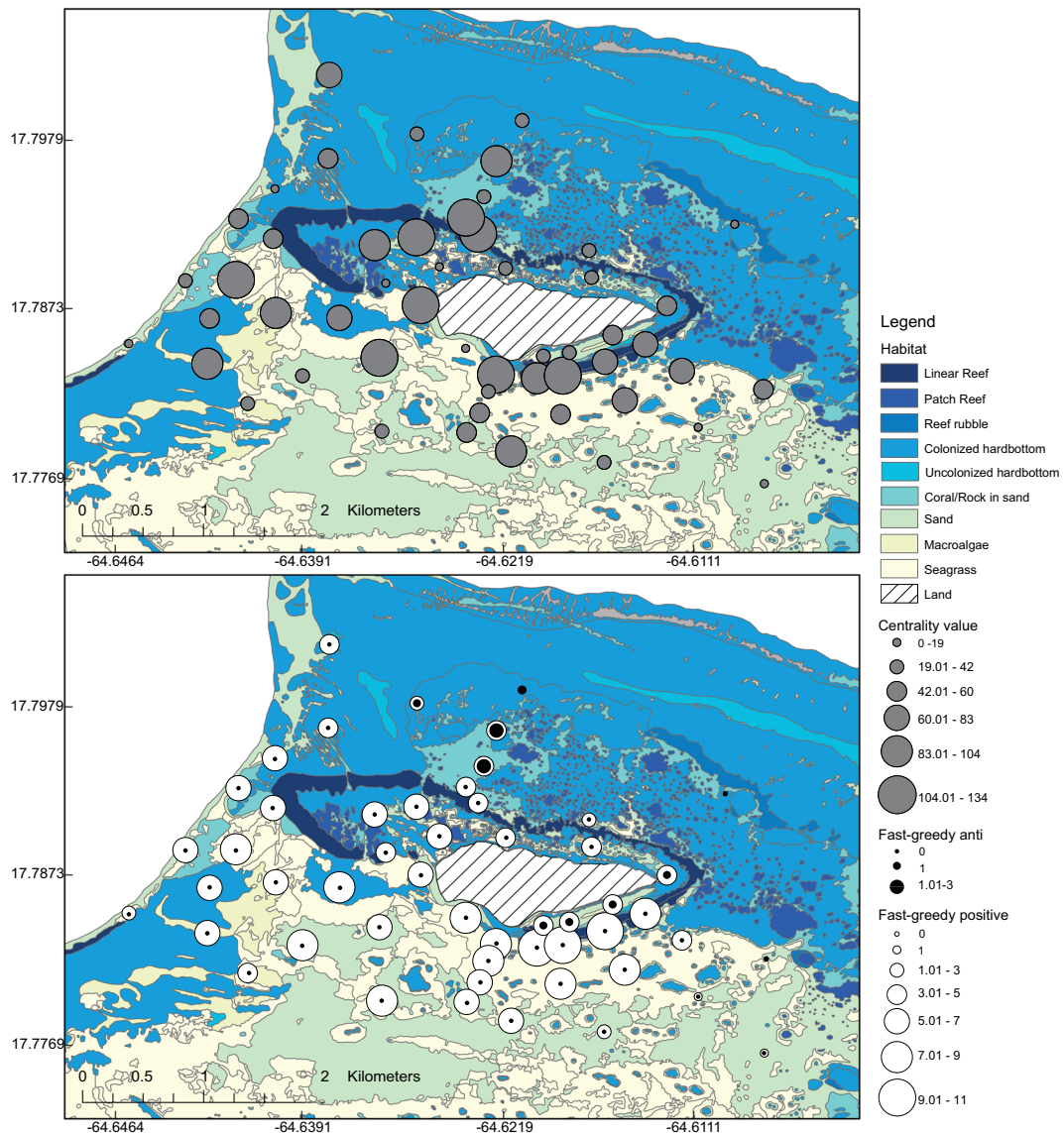
Fig. 3 The upper panels show receiver stations weighted by centrality values summed across the study population. The lower panel shows receiver stations weighted by presence in a significant positive or anti-community across the study population as determined by the fast-greedy algorithm. Centrality score is shown in grey circles, positive communities in white circles, and anti-communities in black circles. Both networks are mapped over benthic habitat type (NOAA Biogeography Branch)

proximate receivers, which is consistent with research documenting changes in movement patterns of other large marine predators over different habitat types (Kneebone et al. 2012). The two significant anti-communities both occurred in open areas adjacent to highly rugose linear reefs. One was found in the northern part of the array in an area shown to have poor detection ranges (Selby et al. 2016). Therefore, this area may naturally generate sporadic detection histories that could give appearance of a movement corridor due to

frequent missed detections. The other anti-community, on the south side of the island within a shallow lagoon, has been shown to have adequate detection range, providing greater confidence that the area is a movement corridor between the lagoon and other reefs. Though population-level patterns were slight, they also correspond with benthic habitat. Receivers located within reef and seagrass habitat showed the highest rates of positive community membership and centrality. These habitats, known for their high fish biomass and diversity

Table 3 Total number and filtered number of positions generated for all great barracuda within the VEMCO Positioning System (VPS). Asterisks indicate fish that had over 100 positions kept for analyses based on having an estimated positioning error of > 5 m. Number of days, nights, and crepuscular positions are also shown

Tag	Original positions	Filtered positions	Percent retained	Day positions	Night positions	Crepuscular positions
26801*	1237	444	35.9	444	0	0
26800	4	0	0.0	–	–	–
26799*	13,983	2443	17.5	811	1552	80
26796	94	4	4.3	–	–	–
26793	28	18	64.3	–	–	–
24785*	141,957	121,855	85.8	65,807	47,241	8807
24784	4	3	75.0	–	–	–
24780	8	4	50.0	–	–	–
24779*	342	168	49.1	168	0	0
24778*	151	108	71.5	107	1	0
24556	16	14	87.5	–	–	–
24555	1	0	0.0	–	–	–
24554	99	24	25.5	–	–	–

(Moberg and Folke 1999; Grober-Dunsmore et al. 2007), could function as prime hunting grounds for this population, resulting in unique movement patterns in these areas and therefore high rates of significant community membership.

Additional research quantifying these unique movements is required in order to determine the drivers of this variability, but some initial conclusions can be drawn from the presence of multiple significant positive communities. Positive communities represent destinations or core use areas (Finn et al. 2014). Animals that showed high residency and high differentiation in habitat use would have movement patterns that generated a greater number of significant positive communities, while highly mobile species' networks would be dominated by anti-communities (Finn et al. 2014). Multiple positive spatial communities within the activity spaces of individual great barracuda suggest the presence of
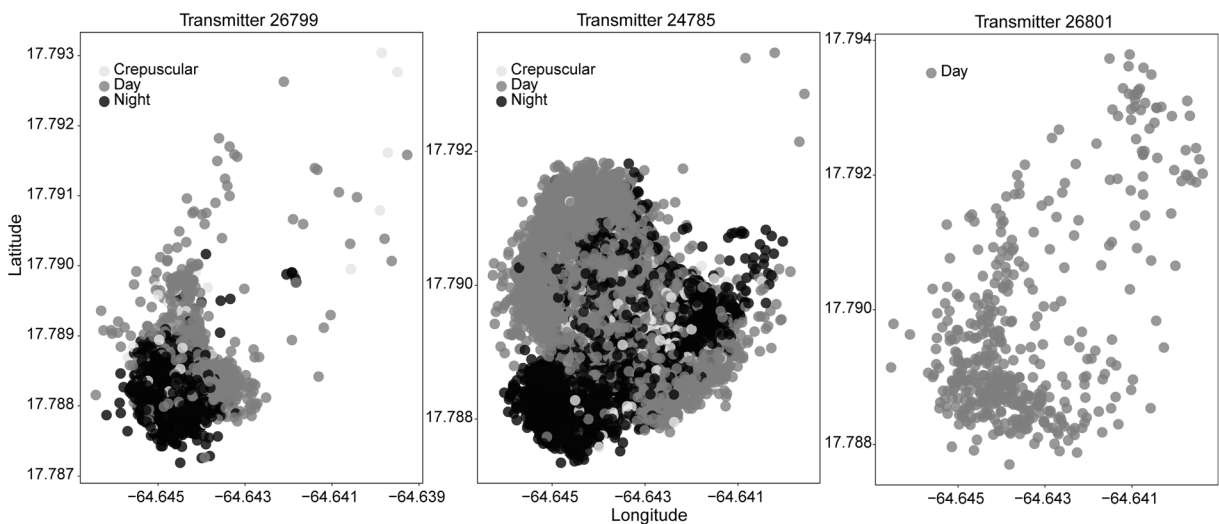

Fig. 4 VEMCO Positioning System (VPS) position locations for three great barracuda (Tags 26799, 24785, and 26801) binned by day, night, or crepuscular hours across the duration of the fine-scale tracking period (June 2015–May 2016). Crepuscular detections are shown in light grey, daytime detections are shown in dark grey, and nighttime detections are shown in black. There is slight deviation in latitude values between each panel

Fig. 5 VEMCO Positioning System (VPS) detections of five individual barracuda on two consecutive days in February (top) and April 2016 (bottom). Note the slight variation in latitude and longitude between each panel. Unique tags are distinguished by shape and color, consistent between panels. Detections are dominated by one barracuda (Tag 24785) and there is little overlap in detection locations between individuals, except around the edges of Tag 24785's territory
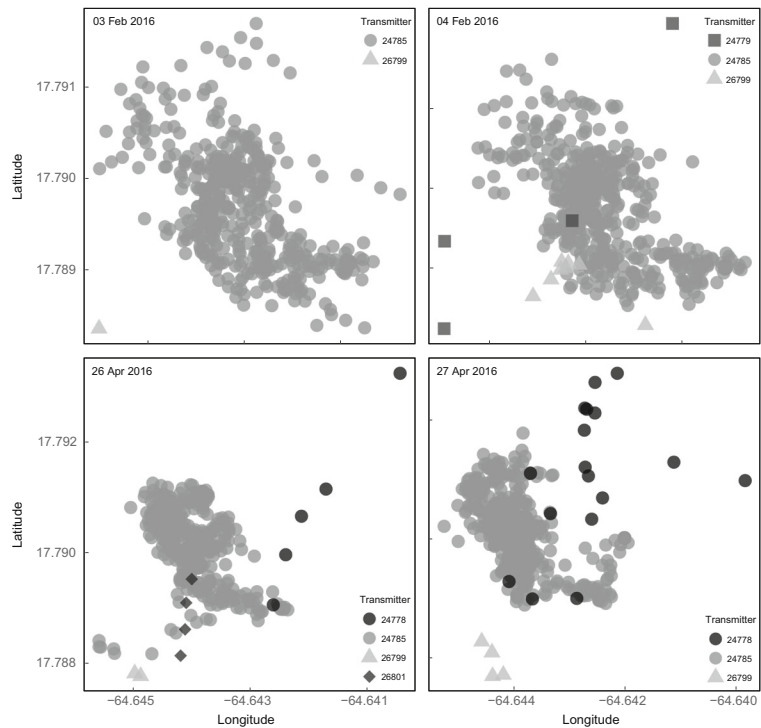
multiple unique use areas within the overall activity space but does not indicate the high differentiation expected of an animal with highly specific habitat preferences (Finn et al. 2014). A rough correspondence with benthic habitat boundaries indicates that movements may shift in reaction to habitat (Papastamatiou et al. 2009) but does not demonstrate a strong habitat bias. One explanation could be a change in foraging behaviors in different habitat types (Persson and Greenberg 1990; Austin et al. 2006) or the use of different areas of the home range for rest versus foraging (Papastamatiou et al. 2015). In addition, temporal differentiation in movements could exist, consistent with seasonal patterns shown in previous studies (Faunce and Serafy 2008) or with diel variation that could be expected from a visual predator such as a great barracuda (James and Heck 1994). The lack of temporal synchrony means that a population-level seasonal migration like a spawning aggregation (De Sylva 1963; Blaber 1982; Kadison et al. 2010) is not shown by the study population but does not rule out seasonal environmental drivers such as weather that have been documented to influence juvenile great barracuda habitat use (Faunce and Serafy 2008) and drive large movements outside of home ranges (Aspillaga et al. 2016). Fine-scale tracking shows evidence for diel portioning of activity spaces, although

these spaces were not entirely distinct, and is consistent with previous research showing shifts in habitat use during midday periods by great barracuda (O'Toole et al. 2010). Diel variation in movement patterns could be driven by changes in foraging behavior, shifts from foraging to rest, or light availability impacting hunting (James and Heck 1994; Papastamatiou et al. 2015).

In addition to the presence of multiple significant positive communities indicating differentiation of use within multiple core areas, anti-communities and low centrality receivers demonstrate that transient movements occur outside the high-use areas. The presence of anti-communities, even though most were not statistically significant, indicates that while not frequent enough to generate a significant number of links between receivers, mobile and resident movement patterns were commonly displayed within the study population. The infrequency of significant anti-communities, however, indicates that these individuals are predominantly resident within their home range, with larger exploratory movements occurring less frequently. Detections patterns suggesting resident and transient movement modes are present in both fine- and broad-scale arrays. The existence of these two separate movement categories is reinforced by the sporadic and infrequent movements shown outside of core use areas (Becker et al. 2016).

These patterns of residence and potential for high mobility are consistent with genetic and tracking studies indicating characteristics of great barracuda are common to both reef-associated as well as pelagic species (O'Toole et al. 2011; Daly-Engel et al. 2012). Previous tracking studies provide support for the presence of both resident and transient behaviors (O'Toole et al. 2011). However, our results indicate that many individuals demonstrate both movement behaviors rather than indicating behavioral subpopulations (O'Toole et al. 2011). While more research would be needed to identify drivers of movement behaviors, there is strong evidence for switches between linear and random walk movement modes during foraging based on prey availability and density for other marine predators (Humphries et al. 2010; Benoit-Bird et al. 2013) as well as evidence of weather events driving large movements of otherwise resident fish (Aspillaga et al. 2016).

The even dispersal of core use areas among all habitat types for individuals shown by broad-scale analysis indicates that great barracuda prioritize unique, individual activity spaces over preferential habitat types, a population-level spatial differentiation common in territorial animals (Ostfeld 1990). Fine-scale tracking reinforced evidence from the broad-scale array, and in combination, these results suggest that great barracuda in BIRNM display territoriality within their core use areas. Little spatial overlap was seen in heavily used areas of an individual's activity space. Existing overlap does not appear to overlap temporally, with the bulk of detections occurring at core use area edges, at different times of day, or as a rapid movement of one great barracuda through the core use area of another. The large decrease in retained positions for non-resident fish indicates that generated positions were occurring on the edge of the dominant territory and beyond the capability of the VPS to accurately triangulate a position (Smith 2013). High conspecific density could drive territoriality (Hixon 1980), which is often a mechanism for mitigating intraspecific competition for resources and maximizing fitness or fecundity (Powell 1987; Hinton et al. 2015). The even dispersal of home ranges with little overlap displayed by the study population resembles individual-level spatial niche partitioning, potentially to avoid competition for resources (Ostfeld 1990).

Though providing valuable data on a little-studied, ecologically important coastal predator, there are some inherent limitations to our study that could be built upon with future research. The fine-scale analysis presented here is preliminary. As more data from the VPS becomes available, allowing for more rigorous analyses, further work following up on the initial results presented here could better test theories of diel variation and movement behaviors. The bulk of detections occur within core use areas, but transition movements are less likely to be as thoroughly detected by the broad-scale array, potentially skewing the dataset towards resident movements. However, these missed detections are less likely within the VPS, with its more thorough coverage, and the detection patterns seen there support the interpretation of transient movements outside of core use areas as sporadic. More research is needed to quantify the differences between significant communities and test drivers of these patterns. In particular, it would be beneficial to incorporate the influence of prey distributions on the differentiation seen between movement types. Multiple species across all trophic levels are tagged within BIRNM and a larger multispecies study on interspecies interactions could further illuminate the roles of predation, competition, and community dynamics on movement patterns. Many of the barracuda used in this study were monitored with 10-year tags, and continuing to assess their movements will help to determine whether territories remain static throughout the adult life of barracuda or whether individuals shift to more preferential habitats as they increase in size.

Increased understanding of the spatial ecology of marine species within MPAs is vital for determining the ecological impact of reserves as well as assessing their management efficacy. Residency, site fidelity, and home range are important parameters for quantifying movement patterns within a spatial management framework (Augé et al. 2013) and, in combination with benthic habitat associations and inter and intraspecies interactions, illuminate ecological and trophic influence of target species (Crowder and Norse 2008). Fine-scale tracking and quantifying complex movement patterns can identify locations of ecologically vital areas (Augé et al. 2013). Great barracuda in the study population demonstrated high site fidelity, territoriality, and diel variation in activity space, and showed high residency to core areas in addition to infrequent transient movements. The population-level spatial partitioning of core use areas shows an even distribution of great barracuda throughout the array and benthic habitat types, but with individuals showing differentiation in use patterns within their territories. The territoriality demonstrated within the study population illustrates high intraspecific

competition and could indicate spatial partitioning to allocate resources. While more research is needed to determine specific ecological drivers of movements, increased knowledge of the fine-scale spatial ecology of this predator provides insight into its ecological influence on prey and conspecific populations through top-down pressure and competition with other sympatric predators.

Compliance with ethical standards

References

Afonso P, Fontes J, Holland KN, Santos RS (2009) Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design. Mar Ecol Prog Ser 381:272–286. https://doi.org/10.3354/meps07946

Almany GR (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages. Oikos 106:275–284

Aspillaga E, Bartumeus F, Linares C, Starr RM, López-Sanz À, Díaz D, Zabala M, Hereu B (2016) Ordinary and extraordinary movement behavior of small resident fish within a Mediterranean marine protected area. PLoS One 11(7): e0159813. https://doi.org/10.1371/journal.pone.0159813

Augé AA, Chilvers BL, Moore AB, Davis LS (2013) Importance of studying foraging site fidelity for spatial conservation measures in a mobile predator. Anim Conserv 17:61–71. https://doi.org/10.1111/acv.12056

Austin D, Bowen WD, McMillan JI (2004) Intraspecific variation in movement patterns: modeling individual behavior in a large marine predator. Oikos 105:15–30

Austin D, Bowen WD, McMillan JI, Iverson SJ (2006) Linking movement, diving, and habitat to foraging success in a large marine predator. Ecology 87(12):3095–3108. https://doi.org/10.1890/0012-9658(2006)87[3095:LMDAHT]2.0.CO;2

Becker SL, Finn JT, Danulchuk AJ, Pollock CG, Hillis-Starr Z, Lundgren I, Jordaan A (2016) Influence of detection history and analytic tools on quantifying sparial ecology of a predatory fish in a marine protected area. Mar Ecol Prog Ser 562: 147–161. https://doi.org/10.3354/meps11962

Benoit-Bird KJ, Battaile BC, Heppell SA, Hoover B, Irons D, Jones N, Kuletz KJ, Nordstrom CA, Paredes R, Suryan RM, Waluk CM, Trites AW (2013) Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS One 8(1):e53348. https://doi.org/10.1371/journal.pone.0053348

Bestley S, Jonsen ID, Hindell MA, Guinet C, Charrassin J-B (2013) Integrative modeling of animal movement: incorporating in situ habitat and behavioral information for a migratory marine predator. Proc R Soc B 280:20122262. https://doi.org/10.1098/rspb.2012.2262

Bivand R Lewin-Koh N, Pebesma E, Archer E, Baddeley A, Bearman N, Bibiko H, Brey S, Callahan J, Carrillo G (2017) Package 'maptools': tools for reading and handling spatial objects: v. 0.9-2. Comprehensive R Archive Network

Blaber SJM (1982) The ecology of *Sphyraena barracuda* (Osteichthyes: Perciformes) in the Kosi system with notes on the Sphyraenidae of the other Natal estuaries. S Afr J Zool:17–14

Bosiger YJ, McCormick MI (2014) Temporal links in daily activity patterns between coral reef predators and their prey. PLoS One 9(10):e111723. https://doi.org/10.1371/journal.pone.0111723

Boydston EE, Kapheim KM, Szykman M, Holekamp KE (2003) Individual variation in space use by female spotted hyenas. Journ of Mam 84(3): 1006-1018. doi. https://doi.org/10.1644/BOS-038

Burke NC (1995) Nocturnal foraging habits of French and bluestriped grunts, *Haemulon flavolineatum* and H. sciuru, at Tobacco Caye, Belize. Environ Biol Fish 42(4):365–374

Clauset A, Newman MEJ, Moore C (2004) Finding community structure in very large networks. Phys Rev E 70. https://doi.org/10.1101/PhysRevE.70.066111

Costa BM, Tormey S, Battista TA (2012) Benthic habitats of Buck Island Reef National Monument. Tech Memo NOS NCCOS 142. NOAA, Silver Spring, MD

Crowder L, Norse E (2008) Essential ecological insights for marine ecosystem-based management and marine spatial planning. Mar Policy 32(5):772–778. https://doi.org/10.1016/j.marpol.2008.03.012

Csardi & Nepusz (2006) The igraph software package for complex network research. InterJournal, Complex Systems 1695. http://igraph.org. Accessed May 2015

Daly-Engel TS, Randall JE, Bowen BW (2012) Is the Great Barracuda (*Sphyraena barracuda*) a reef fish or a pelagic

fish? The phylogeographic perspective. Mar Biol 159:975–985. https://doi.org/10.1007/s00227-012-1878-9

De Sylva DP (1963) Systematics and life history of the great barracuda, *Sphyraena barracuda*. University of Miami Press, Coral Gables

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci 60:698–726

Domeier ML, Nasby-Lucas N (2008) Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. Mar Ecol Prog Ser 370:221–237. https://doi.org/10.3354/meps07628

Dunton KJ, Jordaan A, Conover DO, McKown KA, Bonacci L, Frisk MG (2015) Marine distribution and habitat-use of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) leads to fisheries interactions and bycatch. Mar Coast Fish 7(1):18–32

Ebersole JP (1980) Food density and territory size: an alternative model and a test on the reef fish *Eupomacentrus leucostictus*. Am Nat 115:492–509

Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res 108(2):364–371

Faunce CH, Serafy JE (2008) Selective use of mangrove shoreline by snappers, grunts, and great barracuda. Mar Ecol Prog Ser 356:153–162. https://doi.org/10.3354/meps07231

Finn JT, Brownscombe JW, Haak CR, Cooke SJ, Cormier R, Gagne T, Danylchuk AJ (2014) Applying network methods to acoustic telemetry data: modeling movements of tropical marine fishes. Ecol Model 293:139–149

Friedlander A, Monaco M (2007) Acoustic tracking of reef fishes to elucidate habitat utilization patterns and residence times inside and outside marine protected areas around the Island of St. John, USVI. Tech Memo NOS NCCOS 63. NOAA/NOS/NCCOS/CCMA-Biogeography Branch, Silver Spring, MD

Grober-Dunsmore R, Frazer TK, Lindberg WJ, Beets J (2007) Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. Coral Reefs 26:201–216

Halpern BS, McLoed KL, Rosenberg AA, Crowder LB (2008) Managing for cumulative impacts in ecosystem-based management through ocean zoning. Ocean Coast Manag 51(3):203–211

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnet-head sharks, *Sphyrna tiburo*, in a large Florida estuary. Eviron Biol Fish 76(1):47–67. https://doi.org/10.1007/s10641-006-9007-6

Hinton JW, van Manen FT, Chamberlain MJ (2015) Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS One 10(7):e0132203. https://doi.org/10.1371/journal.pone.0132203

Hixon MA (1980) Food production and competitor density as the determinants of feeding territory size. Am Nat 115:510–530

Hollema HM, Kneebone J, McCormick SD, Skomal GB, Danylchuk AJ (2017) Movement patterns of striped bass (*Morone saxatilis*) in a tidal coastal embayment in New England. Fish Res 187:168–177

Humphries NE, Queiroz N, Dyer JRM, Pade NG, Musyl MK, Schaefer KM, Fuller DW, Brunnschweiler JM, Doyle TK, Houghton JDR, Hays GC, Jones CS, Noble LR, Wearmouth VJ, Southall EJ, Sims DW (2010) Environmental context explains Levy and Brownian movement patterns of marine predators. Naure 465:1066–1069. https://doi.org/10.1038/nature09116

Humphries BD, Ramesh T, Hill TR, Downs CT (2016) Habitat use and home range of black-backed jackals (*Canis mesomelas*) on farmlands in the midlands of KwaZulu-Natal, South Africa. Afr Zool 51(1):37–45

Hussey NE, Kessel ST, Aarestrup CSJ, Cowley PD, Fisk AT, Harcourt RG, Holland KM, Iverson SJ, Kocik JF, Flemming JEM, Whoriskey FG (2015) Aquatic animal telemetry: a panoramic window into the underwater world. Science 348. https://doi.org/10.1126/science.1255642

James PL, Heck KLJ (1994) The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. J Exp Mar Biol Ecol 176(2):187–200. https://doi.org/10.1016/0022-0981(94)90184-8

Kadison E, Alessandro EK, Davis GO, Hood PB (2010) Age, growth, and reproductive patterns of the great barracuda, *Sphyraena barracuda*, from the Florida Keys. Bull Mar Sci 86:773–784. https://doi.org/10.5343/bms.2009.1070

Kimirei IA, Nagelkerken I, Griffioen B, Wagner C, Mgaya YD (2011) Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. Estuar Coast Shelf Sci 92:47–58

Kneebone J, Chisholm J, Skomal GB (2012) Seasonal residency, habitat use, and site fidelity of juvenile sand tiger sharks *Carcharias Taurus* in a Massachusetts estuary. Mar Ecol Prog Ser 471:165–181. https://doi.org/10.3354/meps09989

Ledee EJI, Heupel MR, Tobin AJ, Knip DM, Simpfendorfer CA (2015) A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species. Anim Behav 103:17–28

Leslie H, Ruckelshaus M, Ball IR, Andelman S, Possingham HP (2003) Using siting algorithms in the design of marine reserve networks. Ecol Appl 13(1):S185–S198

Letessier TB, Bouchet PJ, Meeuwig (2015) Sampling mobile oceanic fishes and sharks: implications for fisheries and conservation planning. Biol Rev doi: https://doi.org/10.1111/brv.12246

Luo J, Serafy JE, Sponaugle S, Teare PB, Kieckbusch D (2009) Movement of gray snapper *Lutjanus griseus* among subtropical seagrass, mangrove, and coral reef habitats. Mar Ecol Prog Ser 380:255–269

Meckley TD, Holbrook CM, Wagner C, Binder TR (2014) An approach for filtering hyperbolically positioned underwater acoustic telemetry data with position precision estimates. Anim Biotelemetry 2:7

Melnychuk MC, Dunton KJ, Jordaan A, McJown KA, Frisk MG (2016) Informing conservation strategies for the endangered Atlantic sturgeon using acoustic telemetry and multi-state mark-recapture models. J Appl Ecol 54:914–925

Meyer CG, Papastamatiou YP, Holland KN (2007) Seasonal, diel, and tidal movements of green jobfish (*Aprion virescens*, *Lutjanidae*) at remote Hawaiian atolls: implications for marine protected area design. Mar Biol 151:2133–2143

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29:215–233

Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC et al (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533–536

Newman MEJ, Girvan M (2004) Finding and evaluating community structure in networks. Phys Rev E 69. https://doi.org/10.1103/PhysRevE.69.026113

O'Toole AC, Murchie KJ, Pullen C, Hanson KC, Suski CD, Danylchuk AJ, Cooke SJ (2010) Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. Mar Freshw Res 61:1446–1456

O'Toole AC, Danylchuk AJ, Goldberg TL, Suski CD, Phillipp DP, Brooks E, Cooke SJ (2011) Spatial ecology and residency patterns of adult great barracuda (*Sphyraena barracuda*) in coastal waters of The Bahamas. Mar Biol 158:2227–2237

Ostfeld RS (1990) The ecology of territoriality in small mammals. Trends Ecol Evol 5(12):4110415

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90(4):996–1008

Papastamatiou YP, Watanabe YY, Bradley D, Dee LE, Weng K, Lowe CG, Caselle JE (2015) Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? PLoS One 10(6):e0127807. https://doi.org/10.1371/journal.pone.0127807

Persson L, Greenberg LA (1990) Optimal foraging and habitat shift in perch (*Perca fluviatilis*) in a resource gradient. Ecology 71(5):1699–1713. https://doi.org/10.2307/1937579

Pittman SJ, Monaco ME, Friedlander AM, Legare B, Nemeth RS, Kendall MS, Poti M, Clarl RD, Wedding LM, Caldow C (2014) Fish with chips: tracking reef fish movements to evaluate size and connectivity of Caribbean Marine Protected Areas. PLoS One 9(5):e96028

Powell RA (1987) Black bear home range overlap in North Carolina and the concept of home range applied to black bears. International Association for Bear Research and Management. http://www.jstor.org/stable/3872630

Roy R, Beguin J, Argillier C, Tissot L, Smith F, Smedbol S, De-Oliveira E (2014) Testing the VEMCO Positioning System: spatial distribution of the probability of location and the positioning error in a reservoir. Anim Biotelemetry 2:1

Selby TH, Hart KM, Fujisaki I, Smith BJ, Pollock CJ, Hillis-Starr Z, Lundgren I, Oli MK (2016) Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. Ecol Evol 6:4823–4835

Smith F:Understanding HPE in the VPS Telemetry System. VEMCO Tutorials; 2013. http://VEMCO.com/wp-content/uploads/2013/09/ understanding-hpe-vps.pdf. Accessed May 2016

Wickham H. 2009. ggplot2: Elegant Graphics for Data Analysis (Use R) Springer, New York