

Influence of detection history and analytic tools on quantifying spatial ecology of a predatory fish in a marine protected area

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ABSTRACT: As marine protected areas expand globally, filling data gaps regarding the spatial ecology of marine species has become increasingly important. Acoustic telemetry aims to provide this vital information through generating datasets that can be used to reveal complex movement patterns. The effects of analytic method choice and study design on results must be rigorously analyzed to validate the accuracy of ecological interpretations. We assessed the role of analytic method choice on ecological conclusions derived from an acoustic telemetry array at Buck Island Reef National Monument, USVI. Core use area estimates of great barracuda *Sphyraena barracuda* (n = 32) generated with 3 methods were compared, and the impact of variation in detection history on the ability to interpret results was modeled. Kernel utilization densities, dynamic Brownian bridge movement models, and network analysis indicated high site fidelity paired with less frequent broad exploratory movements. The first 2 methods both identified high use areas, whereas network methods placed higher emphasis on movement corridors and links between core and peripheral use areas. Generalized linear models showed that detection history impacted home range area estimates and confounded the ability to determine ecological relationships. As marine protected areas increase in relevance, it is important that methods to evaluate their effectiveness do not miss complex spatial-temporal patterns and that areas vital to ecological processes are considered alongside areas of highest use. Including network methods in routine spatial assessments may help reveal fish movement patterns previously hidden by using conventional home range analyses.

KEY WORDS: Acoustic telemetry · Home range · Marine protected areas · Great barracuda · *Sphyraena barracuda* · Analytical tools

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INTRODUCTION

In recent decades, fisheries management has shifted from single-species stock management towards adopting ecosystem-based principles (Pikitch et al. 2004), with increasing emphasis on spatial frameworks such as the creation of marine protected areas (MPAs; Pauly et al. 2002, Airame et al. 2003, Douvère 2008). While the increase in MPA estab-

lishment in the last decade (Spalding et al. 2013) is broadly seen as a conservation success (Allison et al. 1998, Lester et al. 2009, Cressey 2011), the actual net benefits that MPAs have on the ecosystems and human populations within and surrounding them is variable (Claudet et al. 2010, De Santo 2013, Edgar et al. 2014). Recent studies have shown a global trend of MPA failure, often caused by insufficient overlap in MPA area and target species range. Even

where planning aligns with ecological needs, success is contingent on compliance with restrictions and sufficient enforcement (Edgar et al. 2014, Klein et al. 2015). Large-scale assessments of MPA efficacy evaluate home ranges modeled as static core use areas (Pressey et al. 2007). However, dynamic movement patterns vary in relation to habitat use, population dynamics, species interactions, and physical environmental variables, as well as in relation to temporal scales ranging from life-span ontogenetic shifts (Polis et al. 1997, Mumby et al. 2004, Kimirei et al. 2011) to diel foraging migrations (Burke 1995, Meyer et al. 2007, Luo et al. 2009). In order to benefit mobile species whose home ranges cannot be fully protected, MPAs can still aid conservation goals by protecting essential ecological functions such as spawning or feeding (Runge et al. 2014, Pérez-Jorge et al. 2015), assuming no other fisheries management tools that could reduce fishing effort are employed. In many cases, more refined analysis of movement data can provide managers with the information needed to maximize the overlap of target species' shifting habitat needs throughout their life cycles (Bolger et al. 2008, Buler & Moore 2011, Runge et al. 2014).

Cumulative research on MPA efficacy has shown that when implemented correctly, reducing fishing pressure typically leads to increased fish abundance (Allison et al. 1998, Murawski et al. 2000, Roberts et al. 2001, Pauly et al. 2002, Halpern 2003, Lester et al. 2009). However, guidance on correct implementation has received less attention. Quantitative assessments are required to determine whether decreased fishing pressure in designated zones results in healthier ecosystems (Heupel et al. 2006b, Farmer & Ault 2011). Trophic dynamics, fish assemblage structure, and the history and type of harvest in a region may all impact how an ecosystem recovers after fishing pressure is reduced or eliminated (Murawski et al. 2005, McClanahan et al. 2007, Lester et al. 2009, Claudet et al. 2010). In addition, geographic and socioeconomic factors also play a huge role in the success of MPAs (Murawski et al. 2005, Suuronen et al. 2010, Edgar et al. 2014). In some cases, closing of non-relevant areas will lead to greater concentration of fishing effort in adjacent habitats (Murawski et al. 2005, Suuronen et al. 2010). If target habitats are misidentified, or if spatial closures are based on political feasibility rather than ecological research, managers run the risk of merely shifting or even intensifying fishing pressure while simultaneously 'meeting' conservation goals by increasing the percent of space under protection (Suuronen et al. 2010).

Gathering the information needed to manage MPAs requires building a nuanced understanding not just of the target area or habitat type, but also of the interrelationships between species, adjacent habitats, and regional networks of ecosystems and metapopulations (Crowder & Norse 2008). This can be a very complex task and may not initially be realistic in a management decision-making timeline (Tallis et al. 2010). Metrics that summarize spatial use, such as home range utilization distributions or area estimates, can be used to approximate cumulative activity space of an individual or population (Kie et al. 2010). These metrics can be very useful as a planning tool, but must be applied carefully so that broad summaries are not excluding nuances in habitat use vital to a target species' life history (Powell 2000, Kie et al. 2010). This is especially true for highly mobile species, given that spatial closures are used to target areas of specific ecological relevance, rather than cover entire home ranges (Buler & Moore 2011, Runge et al. 2014). Additionally, even for species whose movement patterns are well represented by traditional home range estimators, many marine species that MPAs seek to conserve currently lack comprehensive home range estimates.

Tracking of movements using telemetry is valuable in quantifying habitat use within and between habitat types, allowing for long-term data sets on residency and migration patterns (Heupel et al. 2006a, Hussey et al. 2015). Terrestrial telemetry has traditionally used kernel utilization density (KUD) estimation to predict core activity space using telemetry data (Kie et al. 2010, Jacoby et al. 2012a). Terrestrial data often utilize technologies such as GPS collars, which produce a large number of highly accurate and unique positions (Hedger et al. 2008, Ledee et al. 2015). Acoustic telemetry is a relatively new method that is rapidly increasing in popularity (Cooke 2008, Hussey et al. 2015). In contrast to other forms of telemetry, these arrays generate data that are spatially limited to the range of the acoustic receiver, and datasets take the form of repeated detections at the location of the receiver rather than the animal. Methods for analyzing the often vast quantities of data from the marine environment are still developing (Heupel et al. 2006b, Ledee et al. 2015). Estimates of activity space are ultimately as coarse as the spatial scale of the array design, or alternately, use this coarse scale data to make broad interpolations through density estimation methods such as a KUD (Hedger et al. 2008, Ledee et al. 2015). While KUDs can provide valuable data, there is concern that these interpolation

methods may be less accurate for broad-scale acoustic telemetry (Hedger et al. 2008).

By incorporating temporal sequences of detections into analysis rather than analyzing only the aggregated data points, dynamic Brownian bridge movement models (DBBMMs) are an alternate utilization density method to KUD that takes movements between receivers as the input, interpolates intermediate points between these 2 detections, and then bases density estimates off of the interpolated points (Horne et al. 2007).

Network analysis takes a completely different approach from utilization density estimators (KUD and DBBMM) by quantifying relationships between points, referred to as nodes, and connections between those points, referred to as edges, within interconnected networks (Jacoby et al. 2012a,b, Finn et al. 2014). It has been used for analyzing neural networks, social networks, and increasingly, spatial networks. The format is well suited to the interconnected nature of individual receivers that comprise a broad-scale acoustic array, but its potential has only recently begun to be explored.

As activity space estimates often have direct repercussions for management decisions, it is important to understand whether and under what conditions there are variations in the estimates produced by disparate analytical methods. We sought to investigate how detection frequency and methodological choice influenced estimates of core activity space of great barracuda *Sphyraena barracuda* tagged with transmitters within an extensive broad-scale, passive acoustic telemetry receiver array deployed at Buck Island Reef National Monument (BIRNM), a marine protected area in the US Virgin Islands. The objective for this study was to generate activity space estimates for great barracuda within BIRNM using telemetry datasets generated from 1 yr of tracking. In order to provide a more robust evaluation of activity space estimates, we compared 3 estimation methods and investigated the effect that methodological choice had on the resulting area estimates. Specifically, we aimed to compare home range estimates from 2 utilization density methods (KUD and DBBMM) as well as from central activity spaces indicated by network analysis. In addition to the methodological comparison, we used generalized linear models (GLMs) to assess how variation in detection frequency (referred to throughout this paper as 'detection history') for individual great barracuda influenced activity space estimates and the ability to detect body size as an ecological driver of home range. All utilized methods and comparisons were

taken into account in order to generate home range estimates for individual fish as well as to provide summaries across the study population.

MATERIALS AND METHODS

Study site and array design

BIRNM is an MPA managed by the US National Park Service (NPS). The monument is located on the northeastern shelf off the island of St. Croix (Fig. 1), USVI. In 2001, management shifted from restricted recreational take to no-take and the original park boundaries were expanded 5-fold to over 19 000 acres (~7689 ha). BIRNM is bordered to the east and south by St. Croix East End Marine Park, a mixed use MPA managed by the territorial government. To date, no studies have quantified fish species home ranges, habitat use, and connectivity among habitat structures within and adjacent to the park. BIRNM is composed of a shelf habitat containing both shallow- and deeper-water habitats bordered to the north and west by a steep drop-off towards an oceanic trench. An extensive linear reef runs parallel to the coast from the southeast to the northeast coastline, creating a contiguous lagoon habitat. High rugosity linear and patch reefs are interspersed with colonized hard bottom and spur and groove reef to the north and west of the island. Sandy flats and seagrass occur to the south and west. Habitat types are highly interwoven in a patchy mosaic pattern (Costa et al. 2012).

We used presence/absence data derived from passive detection of tagged barracuda using a broad-scale, non-overlapping array of fixed, autonomous acoustic receivers (VR2W 69 kHz, VEMCO) deployed as part of a multi-partner collaborative research effort. A total of 52 acoustic receivers were anchored semi-permanently throughout the shallow water habitats of the monument. Anchors included cement blocks in hard-bottom habitats and 3 foot (91 cm) long sand screws with 6 inch (15 cm) diameter blades in soft-bottom habitats. Sites were chosen based on proximity to other receivers, with the intention of avoiding overlapping ranges and providing equal coverage among the various benthic habitats (Fig. 2). Range of detection of an acoustic signal by a fixed receiver can be influenced by bottom structure, depth, and numerous other environmental factors such as suspended particulate matter, background noise, currents, turbidity, wave height, and weather and can vary from several meters to upwards of 100 m, depending on placement and con-

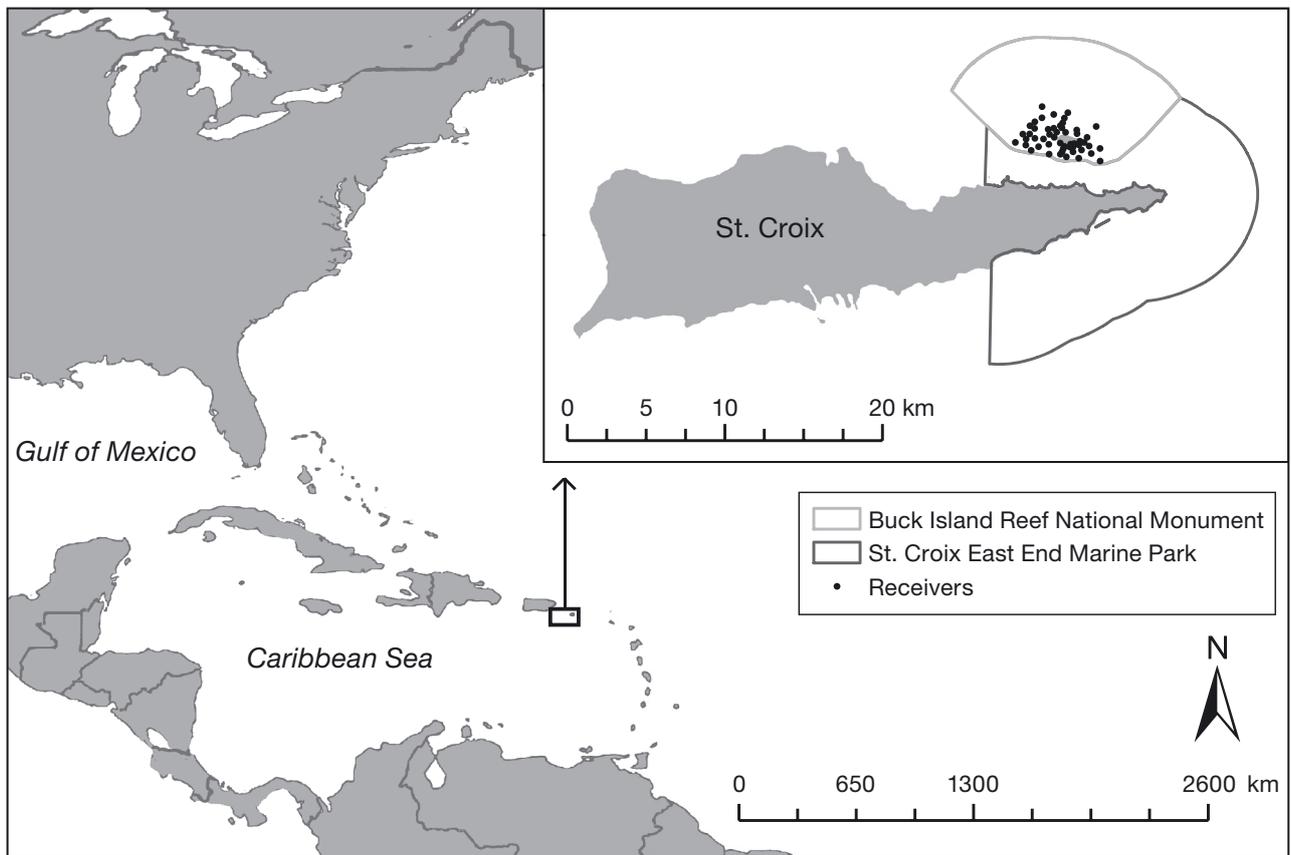


Fig. 1. Location of St. Croix (US Virgin Islands) within the Caribbean. Inset shows the location of Buck Island Reef National Monument (BIRNM) and adjacent protected areas in relation to St. Croix

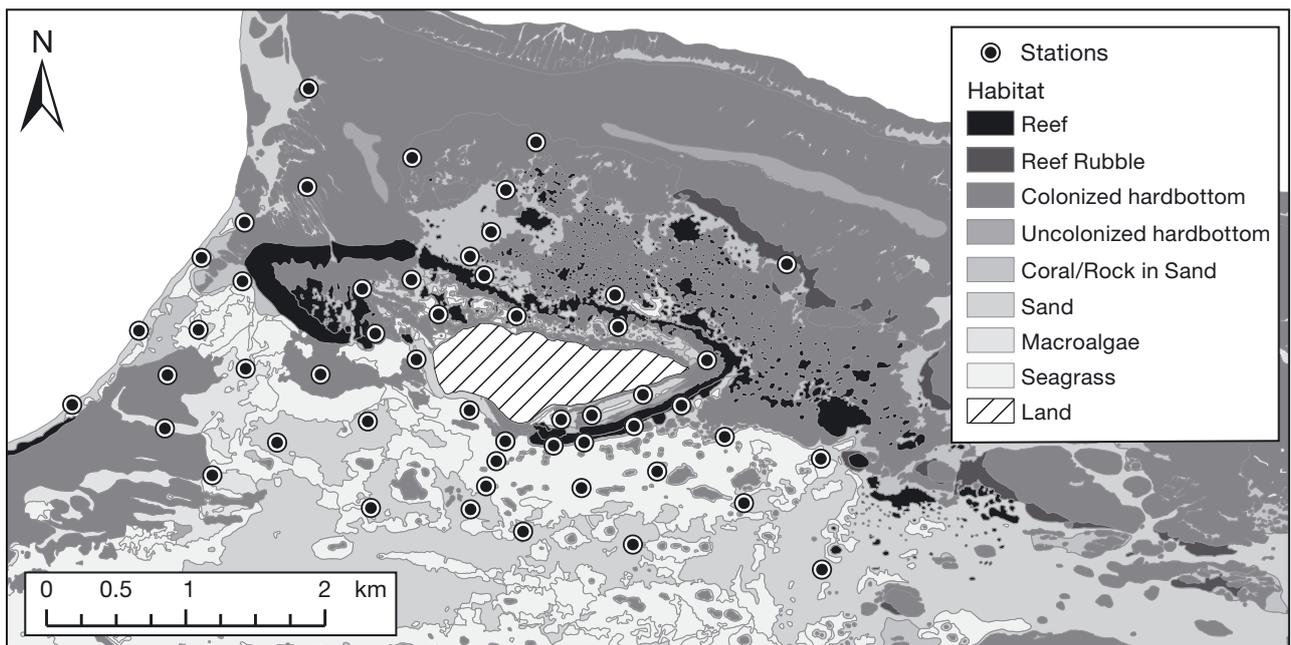


Fig. 2. Location of receiver stations within the shallow water section of Buck Island Reef National Monument (BIRNM). Benthic habitat shapefiles were generated by NOAA Biogeography Branch. Deeper water habitats outside the areas mapped by NOAA are shown here in white.

ditions (Kessel et al. 2014). Range testing was conducted on the BIRNM array to calculate maximum detection range and the average range of 50% detectability was 125 m (Selby et al. 2016).

Barracuda capture and tagging

Great barracuda were captured by trolling at 8 knots with medium action 10–50 lb (4.5–23 kg) recreational fishing gear and artificial lures rigged with brightly colored plastic 1 inch (2.54 cm) diameter tubing and two 9/0 circle hooks (O'Toole et al. 2011). Fishing effort was calculated by timing trolling and recording gear type and number of hooks. All capture sites were marked with a GPS waypoint. Upon capture, the fish were evaluated visually, looking for hook damage, other recent injuries, normal swimming, and ability to maintain equilibrium in order to determine whether health was adequate to support a tag.

Depending on size class (range 61–107 cm), barracuda ($n = 35$) were tagged with either a V16 (16 × 54 mm, 8.1 g) or V13 (13 × 36 mm, 6 g) standard VEMCO acoustic transmitter programmed to ping randomly between 60 and 180 s for the duration of the battery life, ranging from 1299 d for V13 to 3650 d for V16. Fish selected for tagging were placed into a 204.4 l Rubbermaid tote (108 × 54.3 × 45.7 cm) filled with seawater. The anesthetic MS222 diluted to a 10 g l⁻¹ concentration stock solution was slowly added to the tote to induce stage 4 anesthesia (O'Toole et al. 2011, FAU IACUC 2014). Fish were deemed sufficiently dosed for surgeries at the onset of slowing of gill movement and loss of full equilibrium. Anesthetized fish were held in a supine position with gills submerged while an incision was cut with a no. 10 blade carbon steel sterile disposable scalpel just off the central mid-line between the pelvic and anal fins. Acoustic tags disinfected with 70% isopropyl alcohol were then surgically implanted into the body cavity. Incisions were closed with Ethicon polydioxanone monofilament sterile absorbable FS-1, 24 mm reverse cutting needle sutures (Model PDS*II), using 2 to 3 simple interrupted sutures. Halfway through the surgery, fresh seawater was added to the cooler to dilute the anesthetic and begin the recovery process. Total length and fork length were measured. Time of day and length of the procedure were recorded for all aspects of the capture and surgery. Fish were allowed to recover and were monitored in ambient seawater until normal swimming patterns were observed before being released back into the study area from which they were captured (Friedlander & Monaco

2007, O'Toole et al. 2011). Small fish were recovered in a floating mesh pen (4 × 6 foot [122 × 183 cm], 2.5 cm mesh size) to isolate them from predators, while fish too large for the pen (and less at risk for predation) were lowered over the side of the boat and held facing into the current until they were strong enough to swim normally. No more than 4 fish from a given capture site were tagged on a single tagging trip to ensure adequate distribution of tagged animals throughout the array and across habitat types and to avoid tag collisions. All capture and tagging methods were approved under IACUC no. 2013-0031 (University of Massachusetts Amherst). All work within the monument was approved by NPS under study no. BUIS-00058 and individual research collection permit nos. BUIS-2013-SCI_0003 and BUIS-2014-SCI-0006.

Data management, filtering, and analyses

Acoustic data were filtered in R version 3.2.2 (R Core Team 2015) and VUE (VEMCO) software to remove false detections caused by tag collisions and interference from background noise. Biologically unlikely movement patterns that would indicate the death of a tagged fish or another event that would invalidate data from that transmitter were also removed. Any fish that recorded more than 3 consecutive weeks of transmissions at a single receiver was presumed to have died or shed its tag in the vicinity of that receiver.

For all analyses, the same dataset was used, spanning from July 2014 to July 2015, providing a full year of data after the last fish in this study was tagged. We calculated the time between each detection, and removed any detections that occurred less than 55 s apart. The nominal delay in transmission was set to vary randomly between 60 and 180 s. We allowed detections that strayed 5 s or less in order not to falsely remove detections that could be real and due to clock drift or tag irregularities. Short ping rates due to echoes or simultaneous detections were considered not to be representative of actual barracuda location data. All analysis was conducted in R version 3.2.2 (R Core Team 2015). Once filtering was conducted and study year selected, 32 of the original 35 tagged fish remained for analysis. Additional information is provided in Supplement 1 at www.int-res.com/articles/suppl/m562p147_supp/. Supplement 1A lists fork length, number of raw detections, number of filtered detections, observed to expected detection ratio, and number of days heard for each fish included in this dataset, and Supplement 1B contains a residency plot that graphs detections over time.

Utilization density home range estimations

KUD estimates were conducted for all 32 fish present in the dataset spanning July 2014 to July 2015. Grid size was set to approximately 50×50 m, and the smoothing parameter was set at 125 m, which corresponds to the average 50 % contour for receiver detection range in this array. We standardized the area over which the utilization distribution was calculated to include the entire array. In order to allow the KUD to run on acoustic telemetry data without encountering errors due to the lack of variance that occurs if all relocations were sited at the receiver station, each data point was randomly assigned a location within the 50 % cut-off in detection range for that receiver (125 m).

A DBBMM framework differs from KUD, which uses single point location data, by employing movements between 2 locations as the data input. We created movement matrices in which each line of data indicates a movement between 2 receivers and used this as the model input. All models were run using the move package (Kranstauber & Smolla 2015). DBBMM interpolates intermediate points between detections and generates a density surface based on these. We set the interpolation time to be 120 s, to replicate the average ping rate, and set the location error to be 125 m, based on the average receiver detection range.

For both utilization density methods, we calculated contour lines representing where on the density surface 50 % and 95 % of density probabilities occurred. We then calculated the area falling within each of these contour lines in order to generate core and general use area estimates, which we later used to compare these 2 utilization density methods, as well as to compare utilization density methods to network analysis.

Network analysis

Network analysis uses different metrics to assess the association between nodes, i.e. points in a network, and edges, i.e. the connections between those nodes. Recently, this method has begun to be used to analyze broad-scale acoustic telemetry arrays (Jacob et al. 2012a, Finn et al. 2014, Ledee et al. 2015). We created networks of receivers for each fish, with each node representing an individual receiver and each edge a movement of the fish from one receiver to another. We used the igraph package (Csárdi & Nepusz 2006) to assign centrality to metrics for each node in each individual fish array (Ledee et al. 2015). We assessed centrality based on degree. This metric

represents the number of edges connected to a single node, including self-loops, when a fish was detected consecutive times at the same receiver. Centrality degree should, therefore, be broadly comparable to utilization density methods estimating frequency of use. We used degree ranks to create spatially referenced plots in order to visualize activity spaces for individual fish. Code, data (for one example fish), and source files needed to generate KUD and DBBMM utilization distributions, as well as network centrality plots are included in Supplement 2 at www.int-res.com/articles/suppl/m562p147_supp/.

Model comparisons

In addition to using utilization density to define home range areas, we followed the methods of Ledee et al. (2015) by using 50 % contours to define core use receivers (CURs) to compare utilization density estimation methods with network analysis. The 50 % area was used to look at core areas, since for many of the fish, the 95 % areas lay outside the array, leading to greater confidence in the 50 % estimates for model comparison. For network analysis, degree metrics were used to assign CURs for each fish. Receivers were rank ordered by degree value, and all receivers that fell below the 50 % were identified. Numbers of CURs were compared to numbers of receivers that fell within the utilization density-generated 50 % contour lines in order to compare overlap between approaches. The differences to Ledee et al. (2015) were adding the analysis using DBBMM and eliminating comparison to minimum convex polygon, which is essentially reflected in the full number of receivers identified in the network analyses.

Normality tests indicated non-normally distributed data. Additionally, detection data indicates movements from one receiver to another, which automatically violates the assumption of independence of data. Therefore, permutation randomization tests without replacement were used to test for significant differences between results of the various methods. Area estimates at both 50 % and 95 % contour areas were tested against each other. CURs identified by KUD and DBBMM were tested against CURs identified by network analysis.

Impact of variation in detection history on activity space estimates

Several GLMs were created to assess drivers of home range size and centrality ranking generated by

the comparison methods. The models examined how home range estimates generated by each method were influenced by fork length, as well as by mean number of detections per week. Fish size has been shown to be a driver of home range size (Kramer & Chapman 1999). Mean weekly detections were highly variable for individual great barracuda. We included mean weekly detections as a predictor variable in the model to examine to what degree the data variations as opposed to barracuda ecology were influencing patterns. The GLMs tested these 2 covariates and their interaction for each of the 3 methods. For the first 2 models (DBBMM core area and KUD core area estimates) we used the gamma distribution with a log link because the data for these models was in the form of positive real numbers, and for the last (network analysis CUR estimates) we used the Poisson distribution with a log link, as the number of CURs was in the form of count data. For all models, the predictor variables include fish fork length, average number of detections per week, and the interaction between length and detections. Conditional plots generated using the R package VisReg were used to more closely examine the relationship between body size and detection history within the interaction term (Breheny & Burchett 2015).

RESULTS

Activity space estimation

Filtered detections ranged from 251 to 224 179, with corresponding observed/expected values of 0.1 to 85.25% (Supplement 1A). While individual great barracuda had detections on many or all receivers, both utilization distribution methods (KUD and DBBMM) showed steep distribution surfaces dominated by relatively small activity spaces (Table 1).

The 50% home range estimates were very small for both utilization distribution models, between 0.1 to 0.2 km² for each method. The 95% home range areas were much larger for both estimates and were more variable across the 2 methods compared to 50% estimates. Supplements 1C–1E contain all plots generated across all 3 methods.

KUDs showed a mean of 1.39 km², and DBBMM showed more than twice that, with a mean of 3.69 km². Results from the CUR analysis for both utilization density methods as well as centrality degree network analysis showed comparable numbers for KUD and DBBMM, but noticeably larger numbers of core receivers as defined by network analysis (Table 1). For these estimates, CUR generated by KUD and DBBMM again appeared to be fairly similar, albeit slightly greater for DBBMM. However, estimates were much larger for CUR estimates generated using network analysis.

Methods comparison

Visual comparison of plots from KUD, DBBMM, and network analysis indicated agreement across methods in predicting location and size of home range territories for our study population. All methods showed broad use of the array by individuals, with general use areas encompassing large swaths of multiple receivers and core use areas distributed across all habitat types that overlapped spatially with the territories of neighboring barracuda (Fig. 3).

Results from the randomization permutation tests validated the trends shown by the summary statistics of utilization density and CUR comparisons (Table 2). There was no significant difference between estimates at the 50% utilization density, but a significant difference was observed at 95%. Plotting observed versus expected detection ratios against area esti-

Table 1. Summary statistics for estimation of home range and activity space of great barracuda *Sphyræna barracuda*. Home range area estimates include core (50%) and general (95%) area estimates for both kernel utilization density (KUD) and dynamic Brownian bridge movement model (DBBMM). Core use estimates include the number of core use receivers (CURs) generated by KUD, DBBMM, and network analysis (NA). All estimates used to generate these summary statistics can be found in Supplement 1F, and the figures used to calculate these estimates in Supplements 1C–1E at www.int-res.com/articles/suppl/m562p147_supp/

| | Home range area estimates (km ²) | | | | Core use estimates (no. receivers) | | |
|--------|--|----------|--------|----------|------------------------------------|-----------|--------|
| | KUD 50 | DBBMM 50 | KUD 95 | DBBMM 95 | CUR KUD | CUR DBBMM | CUR NA |
| Mean | 0.21 | 0.2 | 1.39 | 3.69 | 2.31 | 3.03 | 6.81 |
| Median | 0.13 | 0.15 | 0.94 | 1.37 | 1.5 | 2 | 7 |

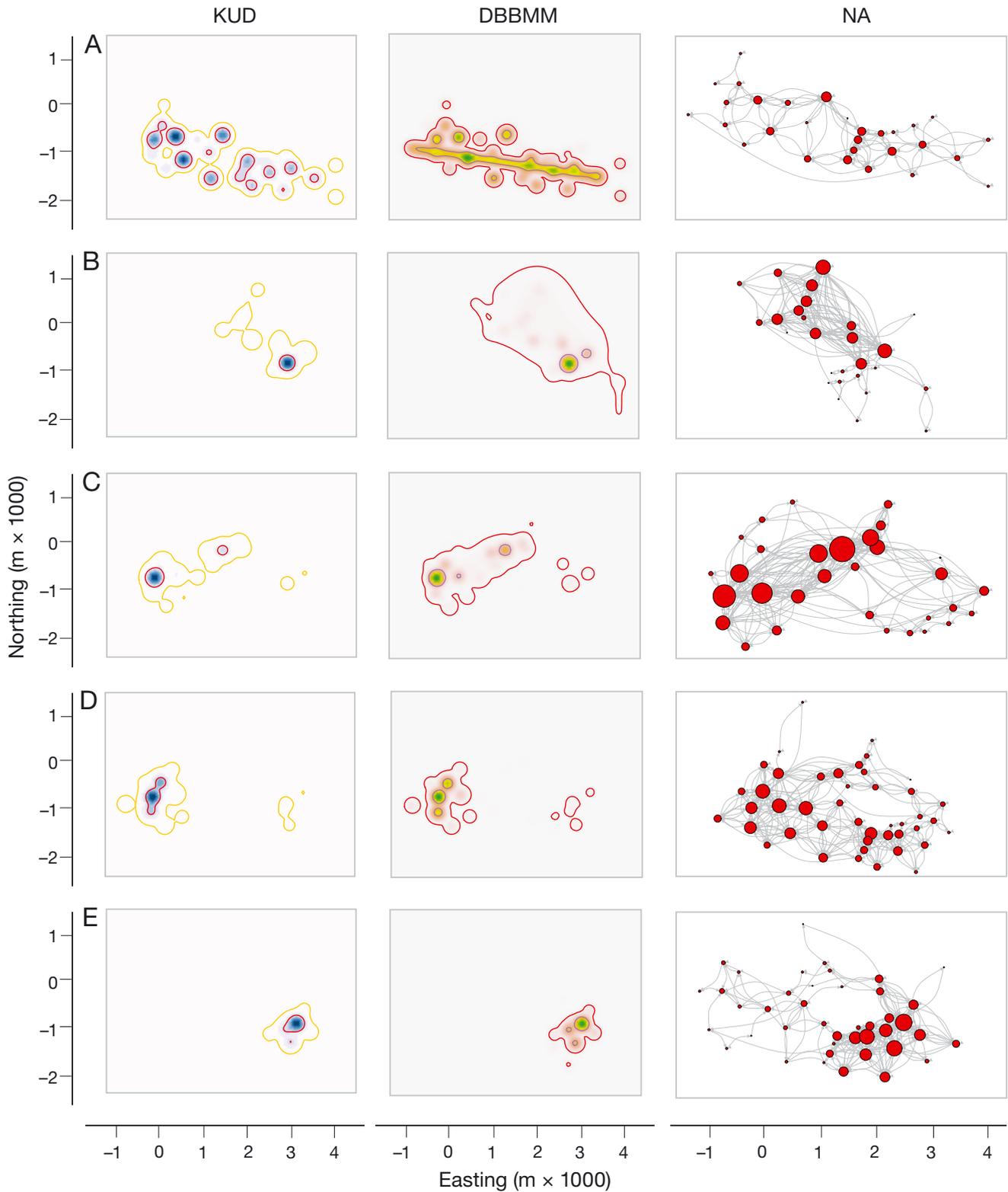


Fig. 3. Comparison between 3 different methods of estimation of activity space for 5 example great barracuda *Sphyraena barracuda*. (A) Tag 24551, 812 detections; (B) Tag 24555, 7645 detections; (C) Tag 24554, 13 282 detections; (D) Tag 26799, 51 276 detections; (E) Tag 26800, 106 074 detections. Methods compared are kernel utilization densities (KUD), dynamic Brownian bridge movement models (DBBMM), and network analysis (NA). Contour lines at the 50% and 95% density estimates were plotted for KUD and DBBMM, shown in yellow (95%) and red (50%) for KUD, and red (95%) and lilac (50%) for DBBMM

Table 2. Significance tests between kernel utilization density (KUD) and dynamic Brownian bridge movement model (DBBMM) for great barracuda *Sphyraena barracuda* at the 50th percentile (core home range), 95th percentile (general home range), as well as between the number of core use receivers (CURs) generated by each method. CUR tests were conducted between KUD and DBBMM, KUD and network analysis (NA), and DBBMM and NA. Significance was determined using permutation tests without replacement. Significant values are highlighted in **bold**

| Test | p |
|-------------------|------------------|
| KUD_50:DBBMM_50 | 0.904 |
| KUD_95:DBBMM_95 | 0.0091 |
| KUD_CUR:DBBMM_CUR | 0.999 |
| KUD_CUR: NA_CUR | <0.001 |
| DBBMM_CUR:NA_CUR | <0.001 |

mates for both utilization distribution methods showed a pattern of decreasing area estimates with increasing detection histories (Fig. 4). The difference between estimates by the 2 utilization distribution methods, as well as the overall variability in estimated area, both decreased with increasing detection histories (Fig. 4). When examined more closely by plotting KUD and DBBMM results against each other, and then looking at the residuals for the 2 utilization distribution methods against mean detections per week, it was apparent that as detection histories increased, residuals decreased (Fig. 5). Therefore, as detection histories increased, the difference in area estimates between KUD and DBBMM decreased.

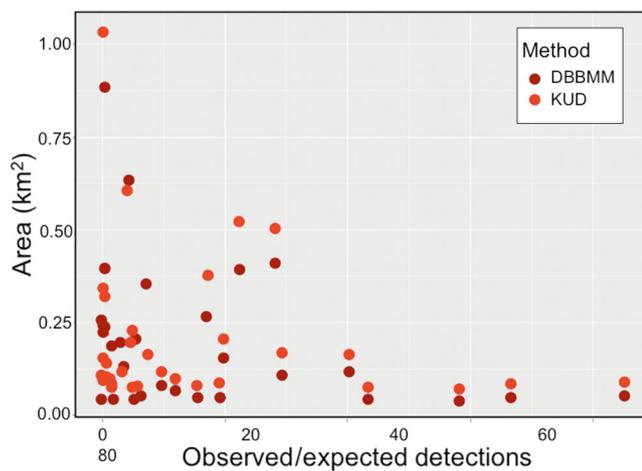


Fig. 4. Core use area estimates for great barracuda *Sphyraena barracuda* by dynamic Brownian bridge movement models (DBBMM) and kernel utilization densities (KUD) plotted against observed/expected detections ratio

GLMs

There were variations among the 3 models regarding which variables were significant but agreement as to whether relationships between model parameters and core use area estimates (the dependent variable) were positive or negative (Table 2). The model with KUD as the dependent variable showed no significant predictor variables, in contrast to the DBBMM, despite there being no significant difference between these 2 methods in the randomization tests. CUR also had a significant relationship between detection history strength and home range size. This model also showed the interaction between detection history and body size as significant, warranting closer examination of this relationship. All models showed negative relationships for the detection history variable. As detection histories increased, home range size decreased. Fork length showed a negative relationship across all models, although none found this variable significant on its own.

When plotted separately in conditional plots with fixed detection history values, the interaction of fork length and detections per week was positive across all models, and significant for the CUR model (Table 3). Detection history strength initially clouded the relationship, but when strong detection histories were observed, a strong positive relationship between fork length and home range size existed (Fig. 6). This relationship was shown by the randomization testing to be significant just for CUR, but the trend of a positive relationship between body size and home range for high detection history individuals was shown across all models, but was hidden by the numbers of individuals with low detection histories that did not display this relationship.

DISCUSSION

Utilization distribution methods indicated that great barracuda within our study are predominantly using small, overlapping territories at the detection scale of the acoustic array. Individual fish had unique core areas of use and they frequently returned to these areas after not being continuously detected. Of the 32 observed fish, 27 individuals were detected on a large number of receivers, but the majority of their detections occurred on a much smaller subset of receivers. Our study revealed that great barracuda in BIRNM display high site fidelity to small core use areas, but periodically demonstrate broad movements throughout surrounding areas.

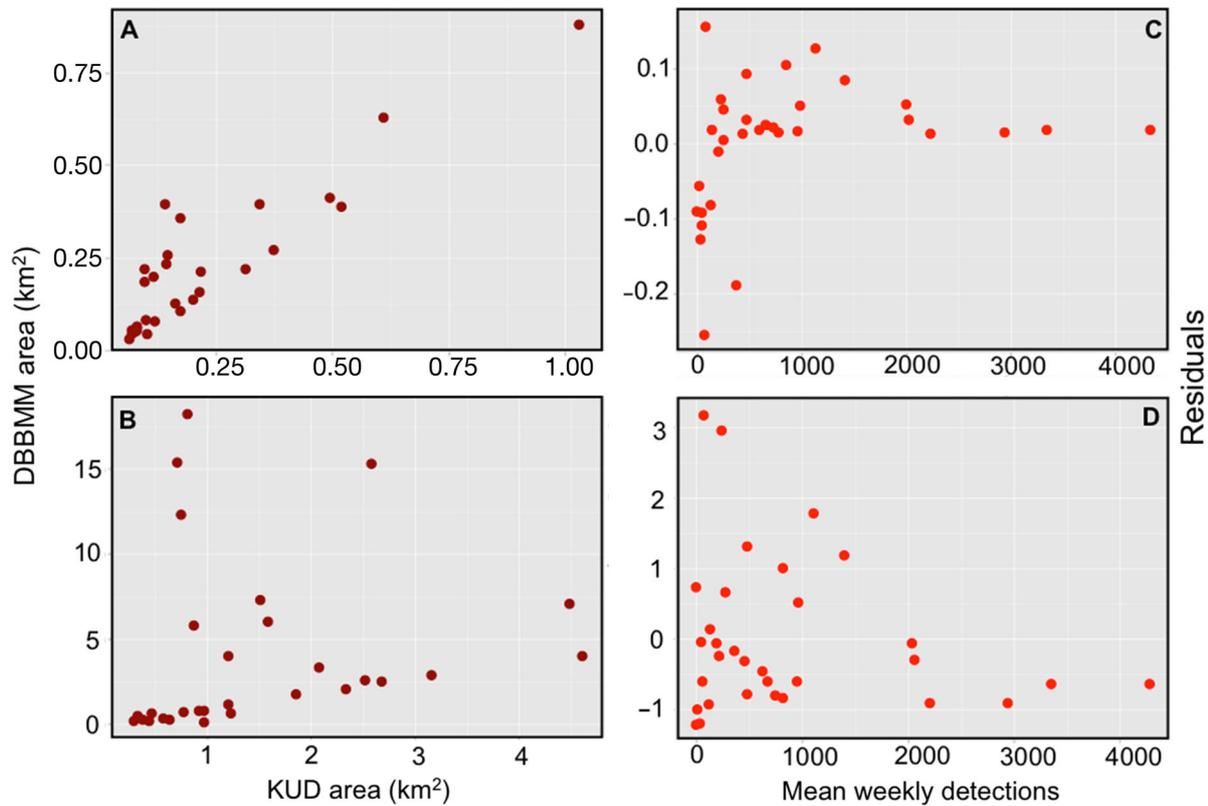


Fig. 5. Kernel utilization densities (KUD) and dynamic Brownian bridge movement model (DBBMM) area estimates for great barracuda *Sphyraena barracuda*, for (A) 50th and (B) 95th percentiles, plotted in maroon. Residuals of linear regressions run on each scatterplot, plotted against mean weekly detections for (C) 50th and (D) 95th percentile area estimates are shown in red

Activity space estimation and method comparison

The 2 utilization distribution methods used in our study predicted very similar values using 50 % area estimates, but showed significantly different results at the 95 % level, with DBBMM predicting values with an average twice as high as the KUD. Comparison of utilization density plots and area estimates showed that a handful of fish have 95 % DBBMM

predictions many times the size of the KUD estimates. Individual fish that show the highest discrepancies are those with comparatively weak detection histories and drive the divergence in 95 % estimates for the 2 methods. While functioning very similarly when detection histories were high, DBBMM estimated larger areas compared to KUD when detection histories were low. Since DBBMM used movements between receivers to interpolate intermediary points

Table 3. Outputs from 3 generalized linear models examining influence of mean weekly detection rates (dets wk⁻¹), body size (fork length, FL), and the interaction between these 2 terms on core use area estimates for great barracuda *Sphyraena barracuda* generated by kernel utilization density (KUD), dynamic Brownian bridge movement model (DBBMM), and network analysis (NA) centrality-degree ranking of core use receivers (CURs). KUD and DBBMM generate area estimates at the 50th percentile contour of density plots, and CUR generates the number of receivers in the top 50th percentile for centrality-degree rankings. For KUD and DBBMM, a gamma distribution with a log link was used, whereas a Poisson distribution with a log link was used for the CUR model. Values are estimates (± SE). Significance levels: *p < 0.05, **p < 0.005, ***p < 0.0005

| | KUD | DBBMM | NA |
|----------------------------|---------------------|---------------------|-----------------------|
| Intercept | -0.74 (±1.342) | -0.30 (±1.19) | 2.44 (±0.61)*** |
| Dets wk ⁻¹ | -0.0024 (±0.002) | -0.0028 (±0.0013)* | -0.002 (±0.0007)* |
| FL | -0.0078 (±0.016) | -0.012 (±0.014) | -0.0069 (±0.0071) |
| Dets wk ⁻¹ : FL | 0.000025 (±0.00002) | 0.000027 (±0.00002) | 0.000019 (±0.000008)* |

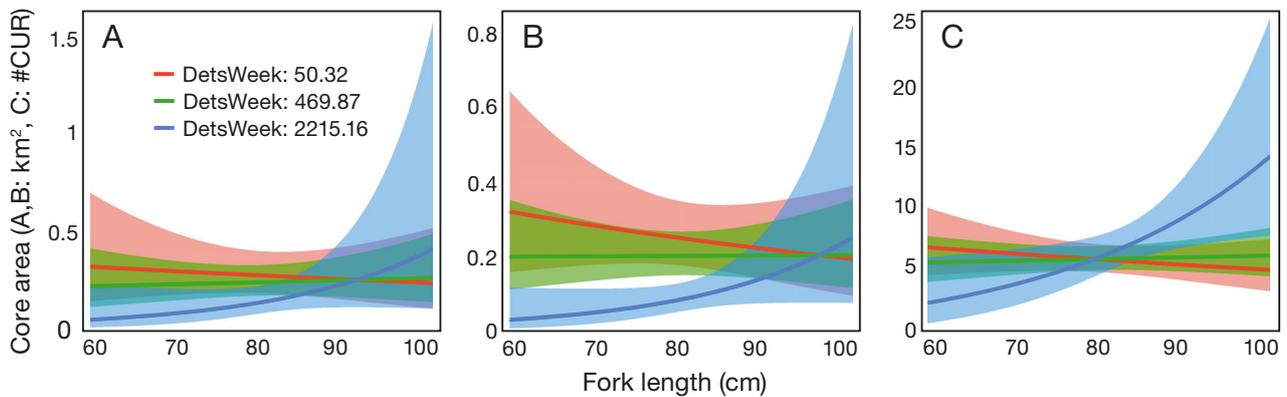


Fig. 6. Relationship between great barracuda *Sphyræna barracuda* fork length and core activity space, with detection history segregated by weekly detection rates for each of the 3 generalized linear models. (A) Kernel utilization densities (KUD) core area estimates; (B) dynamic Brownian bridge movement model (DBBMM) core area estimate as the dependent variable; and (C) number of core use receivers (CURs) as the dependent variable in network analysis. The relationship is plotted separately for 3 fixed values of detection history (detections per week, DetsWeek), with low, moderate, and high values shown in red, green, and blue, respectively. An alternative plot, included in Supplement 1G (at www.int-res.com/articles/suppl/m562p147_supp/), visualizes core area plotted against detections per week

(Horne et al. 2007), distribution surfaces for fish with fewer detections were based on a higher ratio of interpolated intermediary points versus true detections, resulting in the apparent emphasis on large-scale movements.

The number of CURs predicted by both utilization distributions were similar, but network analysis using the centrality degree metric predicted significantly more CURs; therefore, utilization distribution methods estimated significantly smaller central activity spaces than network analysis. Since location input data from broad-scale acoustic telemetry for utilization distributions, especially KUD, are limited, these methods magnify the effect of high value receivers, concentrating density estimates. Utilization distribution methods, while useful for showing high-use areas, are limited in identifying less frequently used areas, at least for a fish displaying periodic movements, like great barracuda. Less commonly used spaces may still be vital to an animal's ecology; many species demonstrate periodic use of vital spawning, nursery, and feeding grounds that might be outside their typical resident territory (Burke 1995, Meyer et al. 2007, Nemeth et al. 2007, Starr et al. 2007, Luo et al. 2009). Network analysis ranked receiver use metrics in relation to other receivers rather than interpolating across intermediate areas, and thus appeared to be quantifying receivers as more highly valuable to an animal's activity space than utilization densities. These findings indicate that the method of choice can significantly impact estimates of core area use.

Variability in detection history on ecological interpretations

GLMs were employed to look at the effects of strength of detection history and fish size on core activity space estimates, and to evaluate the impact of the interaction between these 2 predictor variables. The results were varied across the 3 models, but trends that support a negative relationship between strength of detection history and home range size were consistent across all models and significant in 2 of the 3 models. When detection histories were more consistent, predicted home range size was smaller. Greater detection histories identified fish whose resident activity space was captured within the array and therefore the bulk of detections was detected within small, frequently used territories. The lowest mean weekly detections identified individuals for which the acoustic array only overlapped with infrequent use areas. Thus, area estimates were based on widely spread movements indicating a large core use area, when in reality, the core resident territory lay outside the array.

Fork length was not a significant predictor across any of the models, even though previous research indicated that body size can influence home range size for reef associated fish species (Kramer & Chapman 1999). The interaction between fork length and detection history was only significant when CURs were defined in network analysis, where estimates indicated that this interaction was not a driver of home range size. However, when the regression rela-

tionships were evaluated at different mean weekly detections, there was a positive relationship between fork length and home range size for fish with strong detection histories across all models. While a relationship exists for great barracuda with stronger detection histories, this trend is masked in the full dataset. Thus, detection histories in the study not only influenced predictions of home range size, but also the interpretation of the role of body size. These results indicate that it is important to examine how variation in the strength of detection histories within a given dataset might contribute to erroneous ecological conclusions.

Management implications

Estimates of movement patterns are implemented widely to inform planning decisions regarding spatial management of marine and aquatic ecosystems (Kie et al. 2010). The methods comparison results indicate that method choice can influence the size of predicted core activity areas and can affect the ability of researchers to detect ecologically valuable but infrequently used activity spaces such as spawning grounds or feeding areas (Burke 1995, Meyer et al. 2007, Nemeth et al. 2007, Starr et al. 2007, Luo et al. 2009), and identify important ecological relationships. Great barracuda in this study appeared to be territorial and showed strong site fidelity rather than having highly dispersed movements, indicating individuals whose core use area during the 1 yr study period is completely encompassed within the acoustic array and thus the MPA. Utilization density methods (KUD and DBBMM) strongly highlight these core use areas but miss complexities, thus leading to the risk of failing to identify movement corridors or peripheral areas of use. Network analysis ranks these core areas as highly central as well, but also displays wide-ranging forays outside core areas, identifying significantly greater numbers of receivers as having high centrality than shown by both utilization distribution methods.

For the conservation of mobile predators, the effectiveness of MPAs may lie in their ability to protect specific ecologically valuable areas, rather than attempting to cover large and unpredictable home ranges (Hooker et al. 2011, Runge et al. 2014). Defining ecologically valuable areas is often contingent on the ability to analyze detections generated in less frequently used areas, rather than only high-use areas (Burke 1995, Meyer et al. 2007, Nemeth et al. 2007, Starr et al. 2007, Luo et al. 2009). The great barra-

cuda in this study appear to occupy a middle ground between residency and mobility, given their high site fidelity paired with larger-ranging movements, proving to be an informative species on which to compare how these methods summarize activity space. Variability between methods will likely be highly dependent on the movement patterns and life history of the study species. The discrepancies between the complexities of movement patterns shown by utilization distributions versus network analysis demonstrate the potential of network analysis in identifying movement corridors and peripheral use areas (Ledee et al. 2015). More analysis is needed to understand the ecological function of these movement patterns, but as MPAs become more widely applied as a conservation tool for mobile as well as resident species, it is increasingly important to develop tools to identify ecologically vital areas rather than only closing off areas with the highest density of use (Hooker et al. 2011).

Detection histories have the potential to greatly influence the interpretation of results. It is intuitive that poor detection histories may lead to spurious results, and many studies have corrected for this by rejecting fish whose datasets are not robust enough for analysis (Ledee et al. 2015). There is currently no *a priori* method for determining what constitutes a sufficient detection history, something that will vary by species, array design, and specific research question. The relationship shown in the data between detection histories and home range size demonstrates the importance in determining a specific cut-off point based on individual data prior to analysis. Without taking detection histories into account, it would appear that some of the fish inconsistently use much larger areas than others. For this dataset, it seems that the fish whose home ranges appear much larger and infrequent are individuals whose core home range lies outside the array. So while these animals were indeed intermittently resident and transient to the array, this interpretation indicates that the patterns seen in our site are consistent across the study population and not indicative of behaviorally unique sub-groups. There was an additional impact of variable detection histories on identifying ecological patterns, in this case the relationship between fish size and home range size. Failure to account for detection histories risks misidentifying patterns as being of ecological origin. We anticipate varied results if the same approaches are applied to other study species, geographic areas, and array configurations, as much of the noise in telemetry data is highly dependent on these study-specific factors.

However, the presence of these patterns within this study demonstrate the importance of careful analysis regarding the impact of methodological choice and detection history as a critical part of the process of analysis of acoustic telemetry data.

While we are confident of the general findings, a suite of methods are available to estimate home range and quantify movement patterns using acoustic telemetry data. The use of autocorrelation-adjusted KUD analyses offers an opportunity to reduce the weight from a series of detections in a common location, although in a study of black bears this would only inflate the size of the home range by 8% (Katajisto & Moilanen 2006). Exploring how resampling and other adjustments for autocorrelation influence the home range of different species, and in relation to the detection history, would aid in understanding the potential applicability moving forward. Mechanistic approaches, such as state-space models, are emerging as promising tools with which to analyze tracking data (Alós et al. 2016). While these methods are complex and computationally intense and offer promise towards elucidating details of an animal's ecology, they may be prohibitive to use in some situations. Identification of individuals with sufficient detections for full analyses and other preliminary data explorations will still require an appreciation of the detection histories. Additionally, to appropriately parameterize aspects of these models, some preliminary data on species' behavioral ecology and the detection probability of the acoustic receivers are required (Patterson et al. 2008, Alós et al. 2016). Brownian bridge approaches used in this study required far more computation time than either other method (KUD or network analysis), but with location error of the acoustic array, provided nearly identical results as KUD. Network analysis provides an additional approach that does not include assumptions that are automatically violated by tracking data and which is computationally non-intensive and rapid to perform. As it does not require specifying habitat preferences, environmental requirements, or known behaviors, it is a useful method in analyzing the movements of an understudied species with limited existing movement data, such as great barracuda. Once preliminary assessments of movements have been identified in these little-studied species, incorporation of these findings into a state-space model or simulation study would be a widely beneficial future step in continuing to better understand the multi-species efficacy of BIRNM.

While useful in identifying core use areas, utilization distribution methods are less well suited to iden-

tifying movement corridors and peripheral use areas from acoustic telemetry datasets. Network analysis shows potential in filling this missing link. Sporadic use or rapid movements through larger areas may generate fewer detections than resident behavior, but repeated use provides ecological information about the movements of a mobile species that can inform management. Analyses that disregard patterns based on less frequent detections ignore a vital asset of acoustic telemetry data: the ability to use temporal relationships in the data to tease apart drivers for observed movements. As MPAs are created with the conservation of mobile species in mind, it is important to identify movement corridors among ecologically valuable territories. Regardless of method choice, variability in detection histories heavily influenced home range area results, and confounded the ability to determine the influence of the ecological parameter of fork length in this study. As tools to analyze acoustic telemetry continue to be fine-tuned, it is important to move towards standard approaches for linking fish movements, developing array designs, and integrating findings into spatial management frameworks.

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