



Estimating Space Use of Mobile Fishes in a Large Marine Protected Area With Methodological Considerations in Acoustic Array Design

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Marine protected areas (MPAs) have become an increasingly important tool to protect and conserve marine resources. However, there remains much debate about how effective MPAs are, especially in terms of their ability to protect mobile marine species such as teleost and chondrichthyan fishes. We used satellite and acoustic tags to assess the ability of a large oceanic MPA, the British Indian Ocean Territory MPA (BIOT MPA), to protect seven species of pelagic and reef-associated teleost and chondrichthyan fishes. We satellite-tagged 26 animals from six species (Blue Marlin, Reef Mantas, Sailfish, Silky Sharks, Silvertip Sharks, and Yellowfin Tuna), producing 2,735 days of movement data. We also acoustically tagged 121 sharks from two species (Grey Reef and Silvertip Sharks), which were monitored for up to 40 months across a large acoustic receiver array spanning the MPA. We found that the activity spaces of all satellite-tagged animals, including pelagic species, were much smaller than the area of the BIOT MPA, even taking into account errors associated with position estimates. Estimates of space use of acoustically tagged sharks, based on dynamic Brownian Bridge Movement Models (dBBMM), were also much smaller than the size of the MPA. However, we found important limitations when using dBBMM and demonstrate its sensitivity to both study duration and array design. We found that Grey Reef Sharks should be monitored for at least 1 year and Silvertip Sharks for 2 years before their activity space can be effectively estimated. We also demonstrate the potentially important role that intraspecific variability in spatial ecology may play in influencing the ability of MPAs to effectively protect populations of mobile species. Overall, our results suggest that, with effective enforcement, MPAs on the scale of the BIOT MPA potentially offer protection

to a variety of pelagic and reef species with a range of spatial ecologies. We suggest that animals need to be tagged across seasons, years, and ontogenetic stages, in order to fully characterize their spatial ecology, which is fundamental to developing and implementing effective MPAs to conserve the full life history of target species.

Keywords: spatial ecology, marine protected areas, coral reef, acoustic tag, satellite telemetry, conservation

INTRODUCTION

The need to effectively manage marine resources and ecosystems in the face of increasing human exploitation and climate change is one of the pressing conservation issues of our time. Marine protected areas (MPAs), areas where extractive activities are restricted or prohibited, have become an important tool to help resource managers conserve and protect marine ecosystems and resources. While the ability of MPAs to protect marine species will depend on many factors, including the location of the MPAs, the spatial ecology of species of interest, and the level of enforcement, MPAs have the potential to provide protection to many marine taxa, including mobile species such as sharks (Edgar et al., 2014; Ward-Paige, 2017; White et al., 2017; Speed et al., 2018). Due to their known and perceived conservation benefits, the number of MPAs has increased dramatically over the past five decades (Worm, 2017). The total area protected is accelerating even more rapidly, in particular due to an emphasis in recent years on the creation of very large MPAs, which typically encompass hundreds of thousands of square kilometers of remote, oceanic habitat, often enclosing entire reef or island systems (e.g., Phoenix Islands Protected Area, Pacific Remote Islands Marine National Monument, Rapa Nui Marine Park, and Pitcairn Islands Marine Reserve) (Letessier et al., 2017).

However, despite their increasing implementation, much remains unclear about how to best design MPAs to achieve specified goals, particularly that of protecting mobile marine taxa of management and conservation interest, which includes many teleost and chondrichthyan fishes (Sibert et al., 2012; Kaplan et al., 2014; Boerder et al., 2017). The movement patterns of mobile fishes can be complex and highly variable within and across species, with some transient species wandering over large areas (Meyer et al., 2009; O'Toole et al., 2011; Ferreira et al., 2015), while others exhibit various migration strategies (Block et al., 2011; Jaine et al., 2014) or ontogenetic shifts in habitat or space use (Dahlgren and Eggleston, 2000; Carlisle et al., 2015). Movement dynamics are a key consideration when planning spatial protection for these species. At the extremes, transient or highly migratory species (e.g., pelagic fishes and sharks) may not be amenable to full protection by even the largest MPA, whereas highly resident species (e.g., small reef fish) can be protected by MPAs at the scale of single reefs (Mumby et al., 2006; Mee et al., 2017), if there is appropriate enforcement of the MPA. Nevertheless, even for highly mobile species, appropriately designed MPAs have the capacity to protect key habitats that fulfill important ecological or life history needs for a species, such as reproduction or foraging (Runge et al., 2014; Hays et al., 2019).

While it is critical to fully describe the spatial ecology of taxa of conservation and management interest in order

to design effective MPAs, accurately quantifying the activity space of mobile teleost and chondrichthyan fishes remains challenging due to technological and logistical issues associated with accurately characterizing the movements and distributions of marine fishes. The use of electronic tags is one of the most common approaches to study their movements and spatial ecology (Arnold and Dewar, 2001; Block et al., 2011; Hussey et al., 2015). While advances in electronic tag technologies over the last several decades have greatly improved our understanding of the spatial ecology of fishes, each design has different limitations in terms of its capacity to describe the movements of fishes. Importantly, these technologies often have substantial error associated with positional estimates, though this varies across tag technologies (Teo et al., 2004; Kessel et al., 2014). This is particularly true in the case tags that use light-based geolocation to reconstruct tracks of tagged animals. This approach can have errors in latitude and longitude in excess of several degrees (Teo et al., 2004; Winship et al., 2012), which, depending upon the scale of the error and the size of the MPA, can bias inferences regarding the degree of protection provided by an MPA. On the other extreme, acoustic monitoring approaches can provide fine scale estimates of space use, but only provide information when tagged animals are within range of an acoustic receiver. One method to estimate space use from acoustic data is the use of Brownian Bridge models, which generate probability distributions for animal locations between successive detections based on conditional random walks between locations (Horne et al., 2007). This approach is increasingly being used to estimate patterns of space use from acoustic receiver arrays (Pagès et al., 2013; Becker et al., 2016; Acolas et al., 2017; Oh et al., 2017), though it is known to be sensitive to irregular detection records or large temporal gaps in detections (Horne et al., 2007; Pagès et al., 2013), which are common in acoustic tag data. One approach to mitigate these limitations is to use a combination of tagging technologies to evaluate the degree of protection conferred on mobile taxa by existing MPAs (Weng et al., 2005; Meyer et al., 2010; Carlisle et al., 2011; Papastamatiou et al., 2015; Drymon and Wells, 2017).

The British Indian Ocean Territory MPA (BIOT MPA) is one of the largest no-take MPAs in the world. Established in 2010, the BIOT MPA contains the islands and atolls of the Chagos Archipelago and extends out to the 200 nautical mile (nm) exclusive economic zone (EEZ), bringing the total MPA area to ~640,000 km² (Figure 1). The only resident human population in the BIOT MPA is based on Diego Garcia, in the south east of the MPA, where approximately 3,000 individuals support a joint United Kingdom–United States military base. Its remote location and low population density means that the MPA is relatively free from local anthropogenic effects (Sheppard et al., 2012)

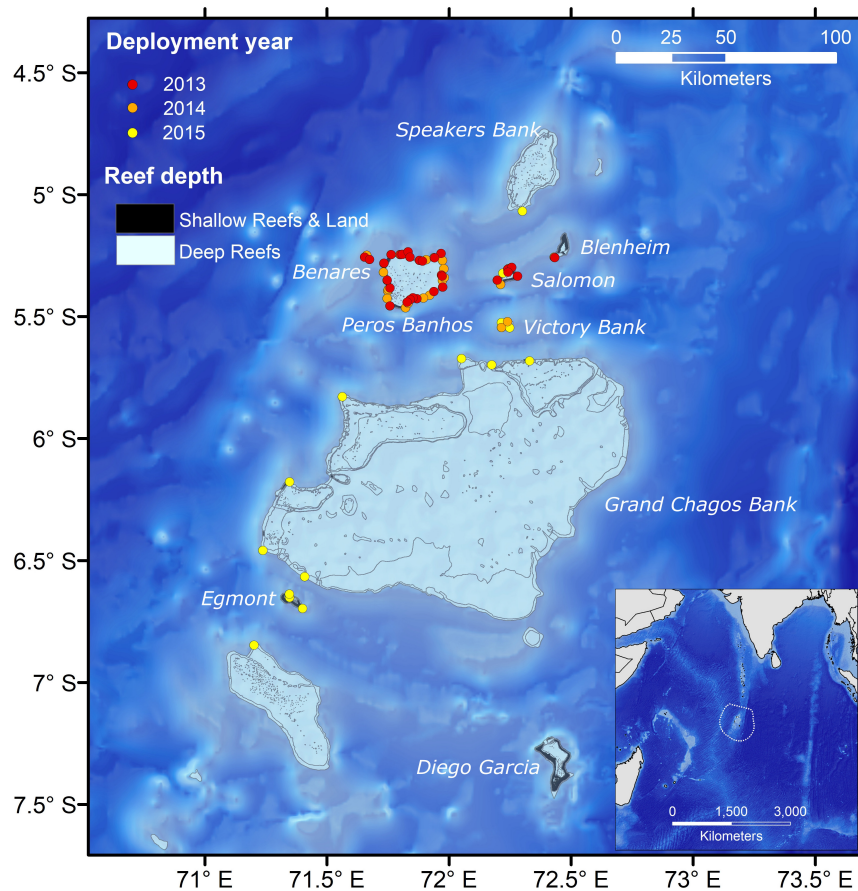


FIGURE 1 | Acoustic array in the BIOT MPA showing year of deployment for acoustic receivers. The inset shows the location of the BIOT MPA with the extent of the MPA being shown by the dotted line. Shallow reefs are $< \sim 20$ m, deep reefs are ~ 100 to 20 m in depth. Gray lines show contours of major submerged features. Note that there is little land in the archipelago.

and therefore boasts a relatively high reef fish biomass (Graham et al., 2013) and abundance of top predators (Graham and McClanahan, 2013). However, the MPA has been targeted by illegal, unreported and unregulated fishing (IUU) (IOTC-2015-WPEB11-48), predominantly by vessels from India and Sri Lanka fishing for sharks (Graham et al., 2010), a problem that continues to be a significant management concern (Ferretti et al., 2018; Tickler et al., 2019).

Since 2013, a research program has been working to better understand the ecology of the MPA, sponsored by the Bertarelli Programme in Marine Science¹ and supported by the United Kingdom Foreign and Commonwealth Office and British Indian Ocean Territory Administration. As part of this program, a variety of species of sharks and predatory fishes have been tagged with satellite and acoustic tags. These tags have not only provided information on the species' fine-scale spatial and temporal ecology, but also allowed us to investigate the ability of the BIOT MPA to effectively protect a range of pelagic and reef-associated teleost and chondrichthyan fishes. In this paper we estimate the activity space of seven mobile reef

and pelagic species in the BIOT MPA using a combination of electronic tag technologies, and present a preliminary assessment of the potential effectiveness of this MPA for their protection. We also describe several factors that influence the ability of electronic tags to fully describe the spatial ecology of mobile marine species, including choice of electronic tagging technology, study duration and, in the case of acoustic tagging, the design of the acoustic receiver array.

MATERIALS AND METHODS

Between 2013 and 2016, seven species of teleost and chondrichthyan fishes were tagged in the BIOT MPA with pop-up archival transmitting satellite tags (MiniPAT models 247A and 348A, Wildlife Computers, Redmond, WA United States), acoustic tags (VR16 coded tags, 69 kHz, transmission interval 30–90 s, Vemco, Halifax, Nova Scotia, Canada), or both. Pelagic species were tagged opportunistically and included Blue Marlin (*Makaira nigricans*), Sailfish (*Istiophorus platypterus*), Silky Sharks (*Carcharhinus falciformis*), and Yellowfin Tuna (*Thunnus albacares*). Reef species included Grey Reef Sharks

¹<https://marinescience.fondation-bertarelli.org/>

(*Carcharhinus amblyrhynchos*), Reef Mantas (*Manta alfredi*), and Silvertip Sharks (*Carcharhinus albimarginatus*). All sharks were caught from small boats using hand lines with barbless circle hooks. Billfish and tunas were caught on lures, with billfish tagged in the water alongside the boat. Reef Mantas were all tagged in the water by free divers. Except for larger sharks (>~1.5 m) which were kept in the water, all other animals were brought onto the boat and restrained, a seawater hose inserted into their mouth to irrigate the gills, and a wet cloth placed over their eyes. Once restrained, the animals were measured, tagged, and had tissue samples collected for genetic and stable isotope analyses.

Externally attached satellite tags were leadered with ~15 cm of 180 kg monofilament (Moimoi, Kobe, Japan), covered with a layer of Spectra and shrink wrap, and attached to a titanium dart. External tags were embedded in the dorsal musculature below the dorsal fin in sharks and fishes and off the midline of the posterior disc in Reef Mantas. For sharks, acoustic tags were implanted intraperitoneally through a small incision (~2–3 cm) just off the midline of their abdomen. Total handling time was generally less than 5 min. All procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) under permit APLAC-10765.

Satellite Tag Analysis

MiniPATs recorded temperature, depth, and light data for the duration of the tag deployments and detached after a user defined period of time and transmitted summaries of archived data sets to orbiting Argos receivers. Light data from MiniPATs were processed using the manufacturer's software (Wildlife Computers DAP Processor 3.0) and geolocations estimated following Teo et al. (2004). A Bayesian state space model (SSM) was used to generate the most probable track while quantifying the uncertainty associated with each daily position (Block et al., 2011; Winship et al., 2012). We saved the full posterior distribution of daily location estimates (20,000 estimates of position for each day) from the SSM for all tags for use in further analysis.

We used the Geospatial Modeling Environment version 0.7.3.0 (Beyer, 2012) to estimate 50% (core activity space) and 95% (total activity space) kernel utilization distributions (KUDs) for satellite tag tracks. To incorporate SSM model error into analysis of space use, we calculated KUDs for both the SSM track and the full posterior distribution of estimated positions used to generate the most probable SSM track (hereafter PD positions) (**Supplementary Figure S1**). The KUDs for the SSM tracks represent the least conservative (smallest) estimate of space use of the tagged animals, while the PD KUDs take into account SSM model error and represent the most conservative (largest) estimate of space use. For each tag we also calculated the proportion of the full dataset of PD positions that were inside the boundary of the BIOT MPA.

We analyzed the SSM tracks to investigate how long animals spent in areas of a given scale using residence time analysis (Barraquand and Benhamou, 2008), which is an extension of first passage time analysis (Johnson et al., 1992). Residence time analysis estimates the time an animal spends within a circle of a given radius centered on a given location, including travel time to and from that location. The animal is not considered to have left

the circle until it has spent more than a user defined maximum time threshold outside the circle, which we set to 1 day. We used that threshold because it would provide the most conservative (lowest) estimate of time spent in an area of a given radius, and would reduce the risk of overestimating duration of residency. Residence time analysis was implemented in R (version 3.4) using the package 'adehabitat' version 1.8.18 (Calenge, 2006).

Acoustic Receiver Array

An array of acoustic receivers, primarily comprised of VR2W receivers (Vemco Inc., Nova Scotia, Canada), was deployed around the BIOT MPA starting in 2013 and then expanded during 2014 and 2015 (**Figure 1**). VR2W acoustic receivers were attached to a subsurface mooring consisting of an anchor, three meters of polypropylene line, and a float. Due to permitting and diving regulations, receivers were predominantly placed on the fore reefs of the atolls between 15 and 20 m depth. The northern atolls (Benares Shoal, Peros Banhos, Salomon, Victory Bank) had the highest density of receivers as they were the geographic focus of the study, which over time expanded to cover a broader area of the archipelago. In 2013, 20 VR2W receivers were deployed around Peros Banhos, five at Salomon Atoll and three at Benares Shoals and Blenheim Reef. In subsequent years the array in the northern atolls was further expanded while the broader array was also extended to other areas of the archipelago. In 2014 and 2015, 36 additional VR2W units were added (22 in 2014; 14 in 2015) to include Victory Bank, Great Chagos Bank, Egmont Island, and Speakers Bank. Two VR4 Global units were also deployed in 2013 and four VR4 Underwater Monitors in 2014. Receivers were downloaded and serviced annually.

Acoustic Tag Analysis

Monthly KUDs were estimated for the acoustic tag data using a dynamic Brownian Bridge Movement Model (dBBMM) (Kranstauber et al., 2012) implemented in R statistical software version 3.3.1 using the package 'move' (Kranstauber et al., 2013). The dBBMM is an extension of the Brownian Bridge Movement Model (BBMM) which approximates the movement between consecutive data points using a conditional random walk, taking into account the distance and elapsed time between consecutive data points (Horne et al., 2007). A key parameter of this framework estimated from the data is the variance of Brownian motion (σ^2_m), which defines the animal's mobility along a path. Whereas the BBMM uses a constant σ^2_m along the entire movement path, the dBBMM allows the σ^2_m to vary along the path based on estimates within a sliding window providing a more precise estimate of the KUD by incorporating behavioral changes in the estimate of σ^2_m (Kranstauber et al., 2012). For each month of an animal's detection data, a 95% KUD was estimated using the dBBMM. Individual monthly polygons, starting with the first month of data, were incrementally overlaid and a union operation performed in order to investigate how the cumulative space (i.e., total area of the union at each time step) use increased over time.

The cumulative space use of individual animals over time changed following a sigmoid curve. We modeled this process to estimate total space use for each species and understand how monitoring time affects estimates of space use. We applied

non-linear mixed effect models to the monthly dBBMM KUD estimates. The non-linear model was a sigmoid model with three parameters

$$y(x) = \frac{\phi_1}{1 + e^{[(\phi_2 - x)/\phi_3]}}$$

where ϕ_1 is the asymptote, ϕ_2 is x at $\phi_1/2$ and ϕ_3 is a scale parameter. Initially, we tested a random effect (shark ID) for the three parameters. The analysis suggested that the inter-individual variation of ϕ_2 and ϕ_3 was marginal, and significant only on ϕ_1 , especially for Silvertip Sharks. Therefore, we eventually left the random effect only on $\phi_{1j[i]}$

$$\phi_{1j} \sim N(\mu_{\phi_3}, \sigma_{\phi_3}^2)$$

For $j = 1, \dots, J$, where J are individual sharks. Additionally, we tested whether the individual variation on the curve asymptote could be explained by changes in the size of the array, expressed by the minimum convex polygon (MCP) of the array receiver locations at any time in the study period (see section “Acoustic Receiver Array”), but the effect was not significant (**Supplementary Tables S1, S2**), so array size did not influence estimated patterns of space use. Before fitting the models we removed the individuals with less than five months of observations ($n = 33$ Grey Reefs and 21 Silvertips) and sharks with activity spaces greater than 800 km² (two Grey Reefs) as these emerged as outliers compared to all other individuals in the dataset. This left 26 Grey Reefs and 33 Silvertips for further analyses.

We used the duration of gaps in acoustic detection to estimate whether a shark could have left the BIOT MPA assuming a straight-line movement from location of the last detection before the gap toward the MPA boundary and then back to the location of the first detection after the gap. The distance from the center of the MPA to the boundary was ~450 km. Time intervals between consecutive detection events were combined with mean cruising swim speeds of both species (Ryan et al., 2015) to calculate the maximum distance an individual could have traveled. This was compared with the minimum round-trip distance from the starting point to the nearest part of the MPA boundary to the finish point. Where the computed swim distance exceeded the boundary round trip distance, it was determined that the shark theoretically could have left the MPA. The number and total time for all such events was summed by individual and species and compared with total monitoring period and total number of movement events.

Array Design Modeling

The ability of acoustic monitoring to describe the distribution of an acoustically tagged animal will be determined by how the spatial ecology of the animal overlaps with the acoustic array, hence array design fundamentally constrains the types of observations and questions that acoustic monitoring can be used to address (Clements et al., 2005; Heupel et al., 2006). Optimally, something is known about the spatial ecology of the species of interest which can guide the array design. However, often there is no *a priori* information on the patterns of space use of a

species of interest to guide array design, as obtaining that type of information is often a goal of these types of studies. Furthermore, once the data are collected from an acoustic receiver array, rarely are there any sensitivity analyses conducted to understand how array design might have influenced the results.

To investigate the effect of array design on different analyses of acoustic tag data (residency indices, gaps in detection, and dBBMM estimates), we investigated two aspects of receiver placement: receiver location (i.e., array size relative to tagging location), and array density (i.e., distance between adjacent receivers), by subsampling our existing dataset. For these analyses we used data from the densest part of the BIOT array in the northern atolls and banks at Peros Banhos, Benares Shoal, Salomon Atoll, and Victory Bank. Detection data for 2014 and 2015 were used, but only data from array elements present in the 2014 season were retained since all array elements deployed in 2014 were used over both years, providing a consistent baseline for our analyses. Shark tags with fewer than 30 days of detections were excluded ($n = 39$).

To investigate the effect of receiver distance relative to shark tagging location, a matrix of distances between shark tagging locations and receivers was produced using the function `dist()` in the package ‘*vegan*’. We used a Euclidean distance measure calculated on the matrix of individual shark tagging and receiver locations, and the mean residency index (days detected per total days monitored) of each shark at receivers 5, 10, 15, 20... 70 km from their tagging location was calculated, as well as a weighted average per species. The number of individual sharks of each species detected at increasing distances from their tagging location was also calculated. The probability of detecting a shark at different radii from tagging location was then modeled using a generalized linear model with a logit link function, with ‘successes’ being the number of tags of a species detected at a given distance and ‘failures’ the number of undetected tags based on the total tags for that species. An interaction between species, as a factor, and tagging location-receiver distance was used to test the hypothesis that Silvertip Sharks range further, on average, than Grey Reef Sharks.

To model the effect of array density on detection metrics (residency indices, gaps in detection), we filtered the detection data based on subsets of the existing receiver array. Subsets of receivers from the northern array were selected based on a minimum threshold distance between adjacent receivers, which was varied from 0 to a maximum of 20 km. At spacing greater than 20 km between receivers, the simulated arrays had too few elements to produce data that could be usefully analyzed. To generate the sub-arrays, a matrix of array distances was calculated using the function `dist()` in the package ‘*vegan*’ with a Euclidean distance measure as above. For each threshold distance, a random starting node in the array was chosen and the distance to the remaining receivers tested iteratively. On each iteration an additional receiver was added only if it was at least the threshold distance from all receivers previously selected. This process was repeated until no further receivers could be added to the subsampled array. The subsampling was repeated 1,000 times for each distance step, with duplicate sub-arrays discarded. This process generated a group of receiver sub-arrays that was

comprised only of receivers that were above a given threshold distance from each other. The raw detection data were filtered based on the subsampled arrays and the observed residency index and mean time interval between pairs of consecutive detections was calculated for each individual shark. Median and IQR of these metrics were then calculated for each array spacing.

We investigated the potential effect of array density on observed activity space using data from a Silvertip with a high overall residency, long monitoring period, and relatively high mobility (visiting 18 receivers). Sub-setting this shark's detection data for smaller/less dense arrays provides a reasonable indication of the effect of reduced receiver coverage on estimates of activity space. For each distance step, ten subsets of the array were randomly generated and used the distance based method described above, subject to the additional condition that they contained at least two of the receivers visited by the shark (the dBMM model requires at least two different locations in the data to make a UD estimate). The 95% KUD using the dBMM implementation described above was calculated for each iteration, and the mean and CI for each distance step plotted against array spacing.

We also evaluated the potential effect that the size of the array, in terms of receiver coverage relative to tagging location, had on dBMM 95% KUD estimates. We used data from nine Silvertip Sharks with relatively high residency (>33% of days) and which were detected at 8 or more receivers, in order to have enough data to model, and sequentially added data from receivers in order of their distance from a shark's tagging location. For each array iteration, we estimated the 95% KUD using dBMM as described above. Although we attempted the same analysis with Grey Reef Sharks, their high level of residency to often a single receiver made the analysis uninformative, and hence we analyzed data for Silvertip Sharks only.

RESULTS

Satellite Tagging

Twenty-six MiniPATs were deployed on six species in the BIOT MPA (Blue Marlin, Reef Mantas, Sailfish, Silky Shark, Silvertip Shark, and Yellowfin Tuna) between 2013 and 2016. (Figure 2 and Table 1). Tags transmitted time series and summarized data sets of temperature, depth, and light to the Argos system. However, here we only report on patterns of horizontal space use in tagged animals. Deployment lengths ranged from 7 to 269 days (median 104.5, 23–180 days interquartile range, IQR).

Activity Space From Satellite Tags

Overall, activity spaces (50 and 95% KUDs) of the SSM tracks of tagged animals were much smaller than those estimated from the PD positions, and all KUDs were all much smaller than the area of the BIOT MPA (Table 1). All but one of the tagged animals remained within the BIOT MPA for the duration of the tag deployments (up to 269 days), even taking into account model error (Figure 2 and Table 1). The median of all 95% KUDs of PD positions, the most conservative (largest) estimate of activity space, was 8.1% (6.6–11.3% IQR) the size of the MPA, whereas

for the 50% KUDs of PD positions it was 1.9% (1.6–2.2% IQR) (Table 1). A Silky Shark (6913001) was the only animal observed leaving the BIOT MPA. Over the course of the 86 days track, it remained in the vicinity of the archipelago for ~2 months before making a directed easterly movement to about 83°E, where it remained for several weeks. This shark had the largest activity space of any tagged animal, with a 95% KUD of the SSM track being 199,706 km² (~32% size of the BIOT MPA) and the 95% KUD of the PD positions being 433,086 km² (~69% size of the BIOT MPA). The other Silky Shark, which remained within the BIOT MPA around the archipelago for 269 days, used a much smaller area with 95% KUDs that were ~20–30% the size of its conspecific.

Based on the SSM tracks, Silvertip Sharks generally had larger activity spaces, about three times larger, than Reef Mantas. They also had much more variability in KUD estimates than Reef Mantas, which had narrower interquartile ranges for both 50 and 95% KUDs. Two Silvertip Sharks (3913008 and 3913010) had the longest tracks of the reef-associated species (Table 1). These two animals appeared to move across much of the archipelago, while the others all generally remained around the northern atolls, where they were tagged (Figure 2 and Table 1). However, the tag attached to Silvertip Shark 3913008, which had the longest track and largest KUD, detached several km from the original tagging location. Reef Manta 5216006 was the only reef species that appeared to make an extended (~2 months, ~100 km offshore) pelagic excursion away from the archipelago though it returned to its tagging location (Egmont) prior to its tag detaching. Even considering uncertainty around the SSM tracks, based on distance between tagging location and pop-up location, Silvertip Sharks and Reef Mantas were moving between atolls, islands, and other features of the archipelago which are generally separated by distances < 20–40 km. This is supported by data from a Silvertip Shark that was double tagged with both acoustic and satellite tags. The animal was detected frequently on the receivers while the satellite tag was attached, allowing the mean daily position obtained by acoustic detections to be compared directly with the estimated SSM positions. The difference between daily SSM positions and the mean daily location derived from acoustic detections differed by less than 0.25 degrees of longitude or latitude, approximately 25 km at the latitude of the BIOT MPA (Supplementary Figure S2). This provides some evidence that our SSM positions were relatively accurate, and also suggests that the double tagged shark was moving within a relatively tight radius of the reefs, even when not detected by receivers.

Residence time analysis suggested that reef-associated species and some pelagic species exhibit a high degree of residency in areas much smaller than the size of the BIOT MPA (Figure 3), which is consistent with activity space estimates for pelagic and reef species. Reef Mantas exhibited the highest degree of residency, spending extended periods of time in areas with radii 5–25% that of the MPA. Silvertip Sharks were generally less resident (spent less time) in areas of a given radius relative to Reef Mantas, exhibiting wider ranging, more directed movements. Sailfish were the most residential pelagic fish, spending extended periods of time in areas much smaller than the BIOT MPA.

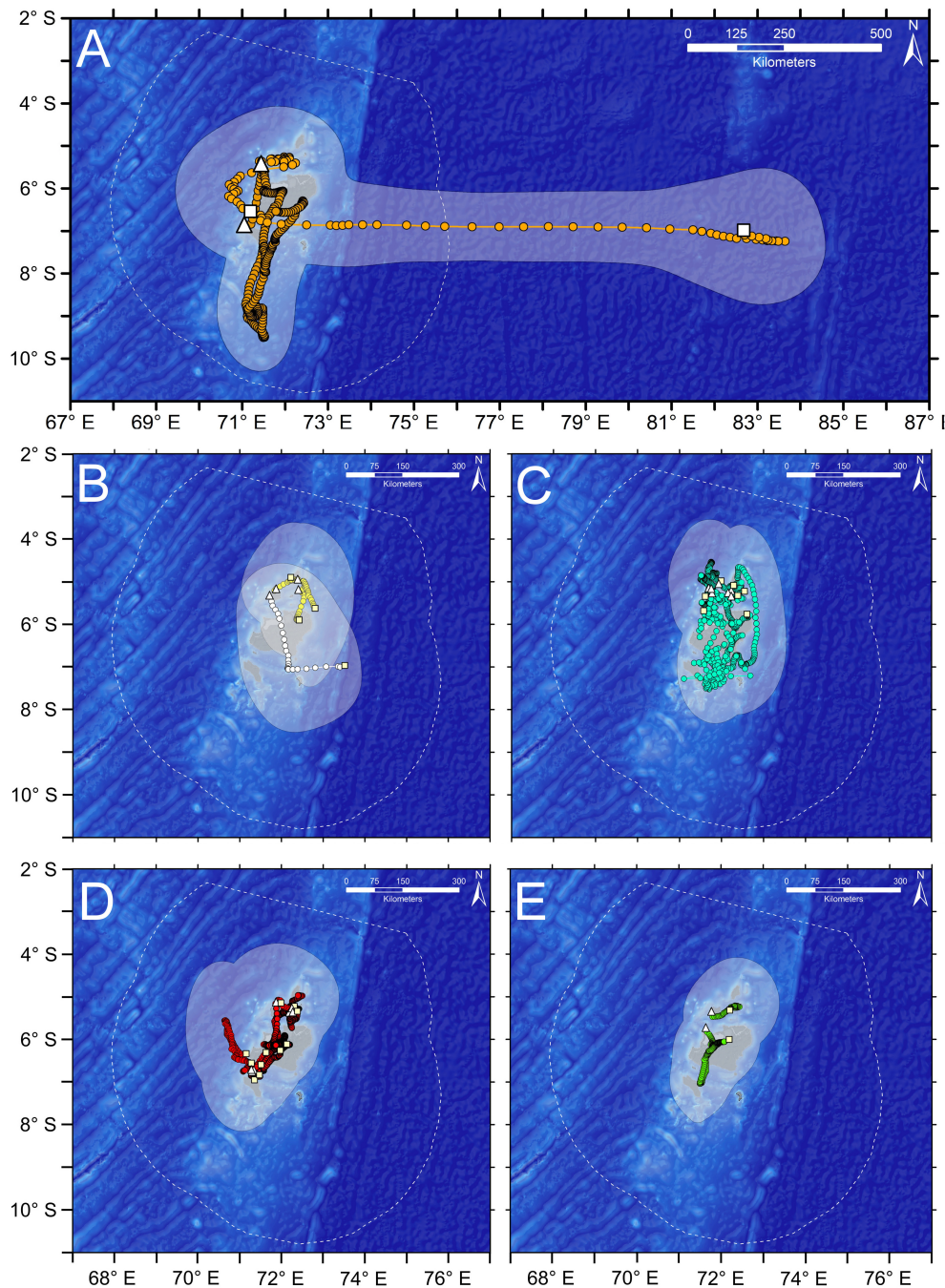


FIGURE 2 | State space model tracks, and 95% KUD (shaded polygon) of full posterior distribution of estimated positions from SSM model for satellite-tagged pelagic fishes and elasmobranchs in BIOT MPA. Tagging location is indicated with the white triangle, pop-up position with white square. Boundary of the BIOT MPA is shown with the dotted white line. **(A)** Silky Sharks (SKY, $n = 2$), **(B)** Blue Marlin (BLM, white, $n = 1$) and Yellowfin Tuna (YFT, yellow, $n = 3$), **(C)** Silvertip Sharks (STP, $n = 7$), **(D)** Reef Mantas (MAN, $n = 11$), and **(E)** Sailfish (SAI, $n = 2$).

Yellowfin Tuna and Blue Marlin exhibited directed movements and were less resident although animals were only tracked for very short periods of time (<26 days). The two Silky Sharks showed completely different patterns, with one spending ~200 days in an area with a radius ~80% the size of the MPA and the other being the only animal to be observed leaving the BIOT

MPA, having very low residency across all spatial scales. While caution should be used when interpreting these results as they are based on modeled tracks, we believe that the relative differences in residency patterns are generally valid, as even modeled tracks are able to distinguish between directed movements and more residential behaviors.

TABLE 1 | Activity space of fishes and elasmobranchs tagged with satellite tags (miniPATs) in BIOT MPA.

Sp.	ID	Date	Size (cm)	Sex	Track length (km)	Pop-off distance (km)	Track duration (days)	Prog. duration (days)	Tr. 50% KUD (km ²)	Tr. 95% KUD (km ²)	PD. 50% KUD (km ²)	PD. 95% KUD (km ²)	Tr. 50% % MPA	Tr. 95% KUD % MPA	PD. 50% KUD % MPA	PD. 95% KUD % MPA
YFT	1113005	3/15/2013	100	U	75	73	12	180	224	890	12,583	55,476	0.04	0.14	2.00	8.81
YFT	1113006	3/15/2013	99	U	112	58	26	180	200	1,023	12,912	76,711	0.03	0.16	2.05	12.18
YFT	1113007	3/15/2013	108	U	177	40	14	180	339	1,739	10,331	41,680	0.05	0.28	1.64	6.62
BLM	5516002	4/16/2016	U	U	409	303	23	180	6,750	28,773	26,686	114,012	2.29	0.42	4.24	18.11
SKY	6913001	2/12/2013	194	U	2350	1152	86	180	49,669	199,706	77,930	433,086	7.89	31.71	12.38	68.78
SKY	6913002	3/21/2013	195	F	1488	43	269	270	11,248	38,641	34,532	120,256	1.79	6.14	5.48	19.10
SAI	7013007	3/19/2013	225	U	414	44	184	180	643	3,121	10,232	52,838	0.10	0.50	1.62	8.39
SAI	7016001	3/24/2016	220	U	126	41	50	180	141	667	11,551	51,361	0.02	0.11	1.83	8.16
STP	3913008	2/12/2013	155	U	3113	4	180	180	9,037	35,191	13,058	62,386	1.44	5.59	2.07	9.91
STP	3913010	3/16/2013	134	M	567	111	105	270	6,648	24,884	23,438	94,191	1.06	3.95	3.72	14.96
STP	3913014	3/12/2013	134	U	291	87	116	180	733	2,879	12,728	50,632	0.12	0.46	2.02	8.04
STP	3913033	3/22/2013	124	U	267	4	104	180	761	2,864	12,711	52,600	0.12	0.45	2.02	8.35
STP	3914008	3/24/2014	161	F	178	298	121	120	178	734	7,706	28,647	0.03	0.12	1.22	4.55
STP	3914016	3/25/2014	133	F	196	59	108	180	183	691	9,213	36,759	0.03	0.11	1.46	5.84
STP	3914018	3/27/2014	150	F	204	58	101	180	686	3,287	12,528	49,465	0.11	0.52	1.99	7.86
MAN	5213001	2/13/2013	290	U	549	15	180	180	1,090	4,761	9,964	41,618	0.17	0.76	1.58	6.61
MAN	5214001	3/30/2014	250*	U	45	28	7	180	11	53	10,552	47,721	0.00	0.01	1.68	7.58
MAN	5214002	3/30/2014	250*	U	88	89	7	120	105	398	10,372	45,698	0.02	0.06	1.65	7.26
MAN	5215003	3/25/2015	250*	U	171	76	157	180	74	440	7,910	30,329	0.01	0.07	1.26	4.82
MAN	5215014	3/29/2015	250*	U	103	4	14	180	323	1,097	14,149	74,177	0.05	0.17	2.25	11.78
MAN	5216006	3/29/2016	250*	F	369	28	89	240	1,090	3,807	18,285	77,110	0.17	0.60	2.90	12.25
MAN	5216007	3/29/2016	250*	U	103	50	17	180	23	152	11,751	53,965	0.00	0.02	1.87	8.57
MAN	5216008	3/29/2016	250*	U	249	22	149	180	306	955	9,088	34,985	0.05	0.15	1.44	5.56
MAN	5216017	4/14/2016	250*	F	466	4	254	270	1,597	5,738	13,747	49,719	0.25	0.91	2.18	7.90
MAN	5216018	4/15/2016	250*	U	262	6	180	180	281	1,140	9,099	35,830	0.04	0.18	1.44	5.69
MAN	5216025	2/16/2016	250*	F	145	92	182	180	16	170	7,458	27,951	0.00	0.03	1.18	4.44

Size is TL for sharks, DW for mantas, and CFL for teleosts. Area of each tag's 50% (core activity space) and 95% (total activity space) kernel utilization distributions (KUDs) are shown for modeled SSM tracks (Tr) as well as for full posterior distribution (PD.) of estimated positions from SSM model. KUD % MPA columns show the (%) of the different KUDs relative to the area of the BIOT MPA (~630,000 km²). YFT, Yellowfin Tuna; BLM, Blue Marlin; SKY, Silky Shark; SAI, Sailfish; STP, Silvertip Shark; MAN, Reef Manta. * Estimated DW.

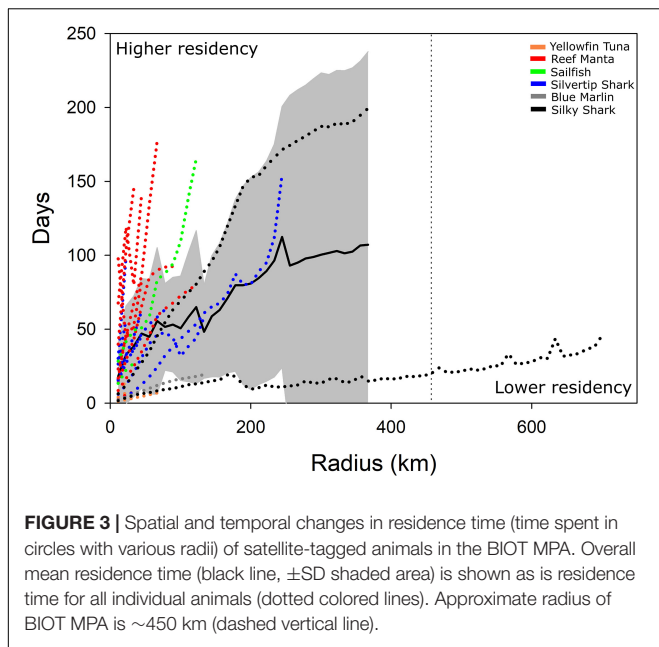


FIGURE 3 | Spatial and temporal changes in residence time (time spent in circles with various radii) of satellite-tagged animals in the BIOT MPA. Overall mean residence time (black line, \pm SD shaded area) is shown as is residence time for all individual animals (dotted colored lines). Approximate radius of BIOT MPA is \sim 450 km (dashed vertical line).

Acoustic Tagging

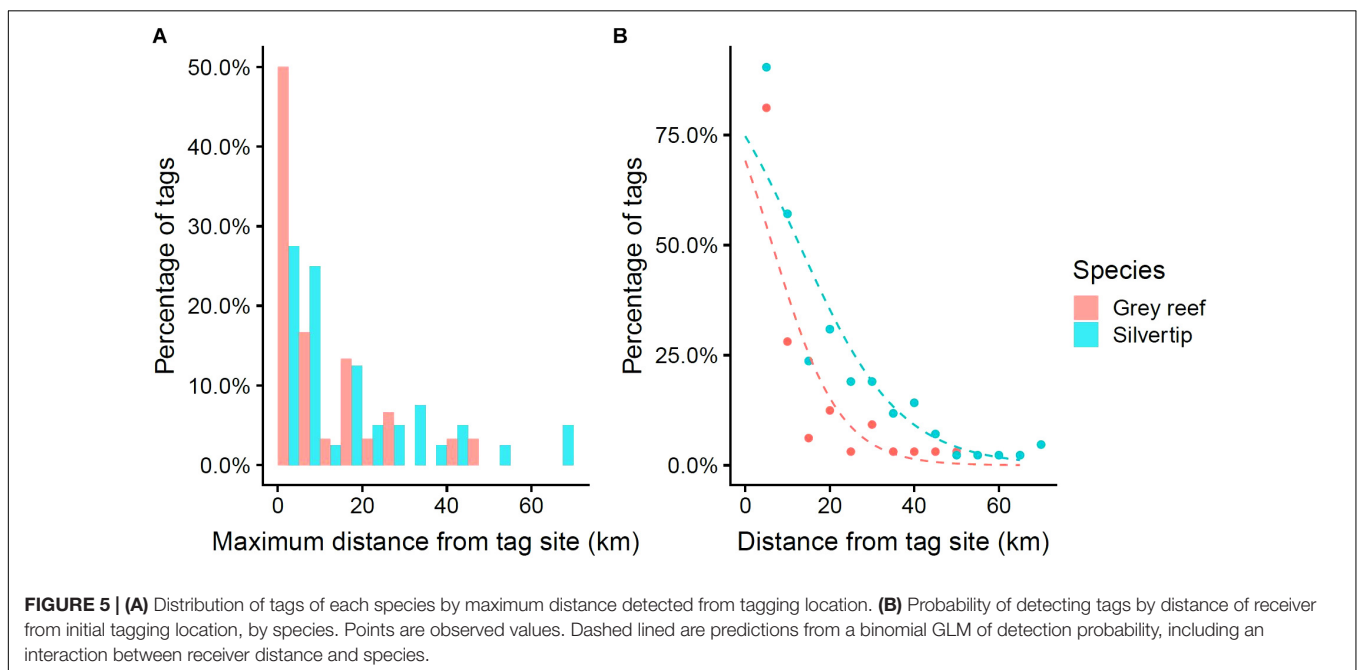
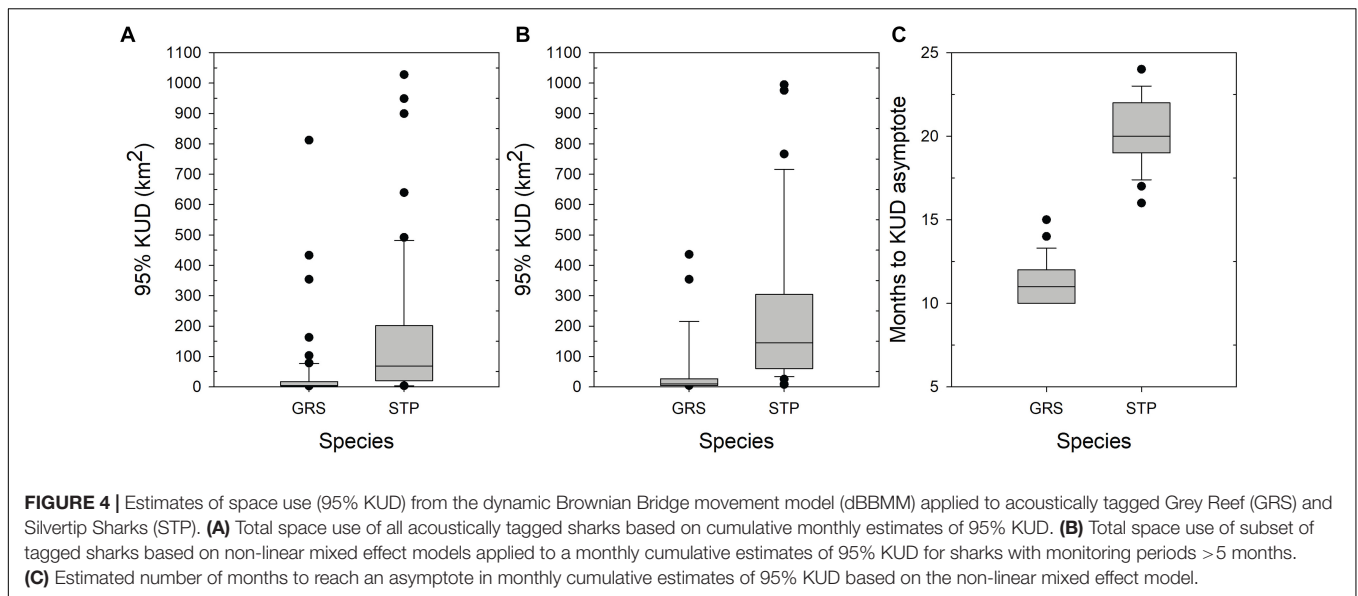
A total of 121 Grey Reef and Silvertip Sharks were acoustically tagged and monitored from February 2013 to March 2016 (Table 2). Our tagging of Grey Reef Sharks was biased toward females but had an even mix of mature and immature animals (Last and Stevens, 2009), whereas Silvertips had a relatively equal representation between the sexes but were primarily immature animals (Last and Stevens, 2009). Cumulative 95% KUDs were estimated for 61 Grey Reef Sharks (mean TL 112.7 cm \pm 17.4 SD) and 60 Silvertip Sharks (mean TL 121.9 cm \pm 22.4 SD). Animals tagged in 2013 were monitored for up to a maximum of 40 months (Grey Reef: maximum 1,197 days, Silvertip: 1,122 days), while animals tagged later in the study had shorter monitoring periods.

Dynamic Brownian Bridge Movement Model estimates of space use based on cumulative monthly 95% KUD estimates for the full data sets of Grey Reef and Silvertip Sharks were roughly half the size of those of the subsets of animals used in the non-linear mixed effects model, reflecting shorter tracks with more restricted movements across the array (Table 2 and Figure 4). Based on the cumulative dBBMM, Grey Reef Sharks used in the model ($n = 26$) had a median space use of 8.3 km² (3.7–38.1 IQR, mean 50.4 km² \pm 107.2 SD), whereas for all Grey Reef Sharks ($n = 61$) it was 4.5 km² (2.8–17.3 IQR, mean 41.4 km² \pm 124.4 SD). On average the tagged Grey Reef Sharks reached this level of space use after approximately 11 months (median, 10.0–12.0 IQR) (Figure 4). Silvertip Sharks used in the model ($n = 33$) had a median cumulative 95% KUD of 134.4 km² (74.4–333.2 IQR, mean 278.6 km² \pm 331.7 SD), while for all tagged Silvertips ($n = 60$) it was 68.8 km² (20.3–201.4 IQR, mean 170.1 km² \pm 274.6 SD), which was reached after approximately 20 months (19.0–22.0 IQR) (Figure 4). For the subset of sharks used in the non-linear mixed effects model, the estimated space use from the model was consistent with

TABLE 2 | Metadata and median and interquartile range (IQR) 95% KUD estimates for acoustically tagged Grey Reef (GRS) and Silvertip (STP) Sharks based on the dynamic Brownian Bridge movement model (dBBMM).

Species	n	Sex (F/M/U)	TL (cm)			Monitoring time (days)			# Detections			BB 95% KUD (km ²)			Mod. 95% KUD (km ²)			Months to asymptote		
			Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
GRS (Model)	26	16/7/4	111.5	104.8–125.0	408.0	348.8–746.0	7828.5	4127.5–12124.0	8.3	3.7–38.1	10.0	4.3–26.9	11.0	10.0–12.0	na	na	na	na	na	na
GRS (All)	61	41/17/3	110.0	103.5–124.5	255.0	92.5–426.0	1042.0	190.0–6822.0	4.5	3.7–17.3	na	na	na	na	na	na	na	na	na	na
STP (Model)	33	14/16/3	119.0	108.5–131.5	492.0	315.5–710.5	1587.0	718.0–5386.5	134.4	74.4–333.2	144.7	60.4–304.5	20.0	19.0–22.0	na	na	na	na	na	na
STP (All)	60	29/25/6	117.0	107.2–130.2	347.5	220.2–626.0	726.0	419.8–2129.5	68.8	20.3–201.4	na	na	na	na	na	na	na	na	na	na

95% KUD shows space use estimates based on the dBBMM, whereas Mod. 95% KUD shows estimated space use based on a non-linear mixed effect models applied to the cumulative monthly dBBMM KUD estimates for individual sharks. Note that a subset of data were used in the model (tracks > 5 months). The non-linear mixed effect model also estimated time it takes to reach an asymptote in cumulative monthly dBBMM estimates (Months to asymptote). For animals used in the mixed effect model, we present the modeled KUD estimates as well as the dBBMM estimate for the entire dataset for those individual sharks.

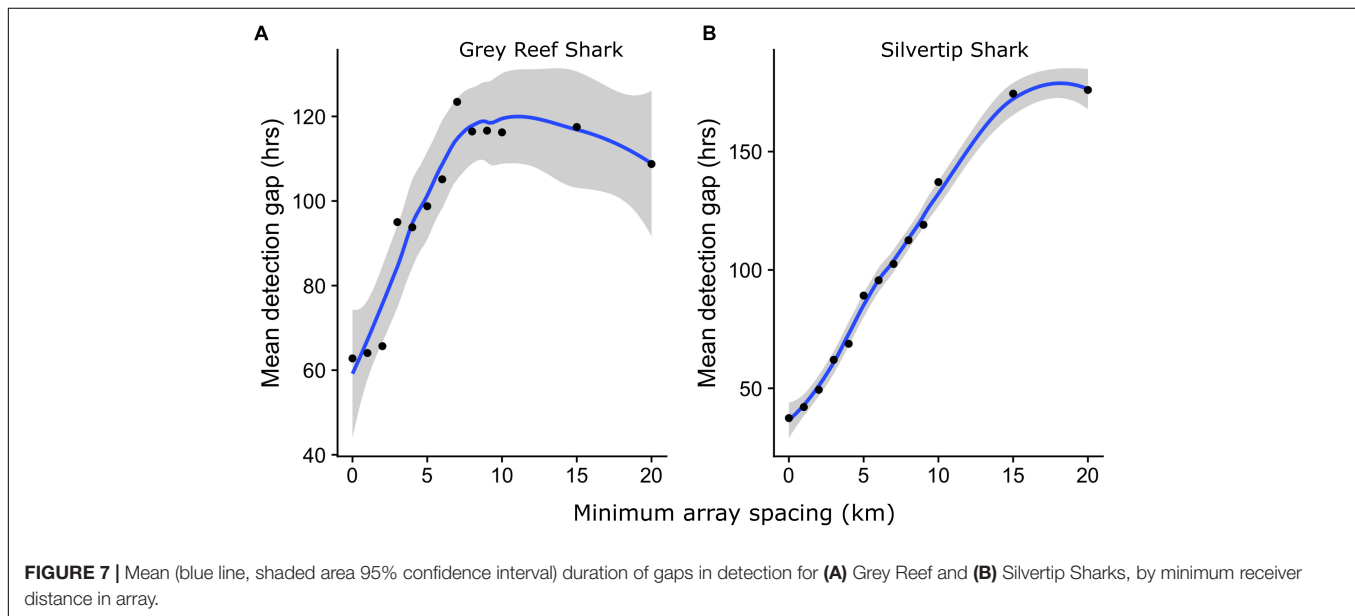
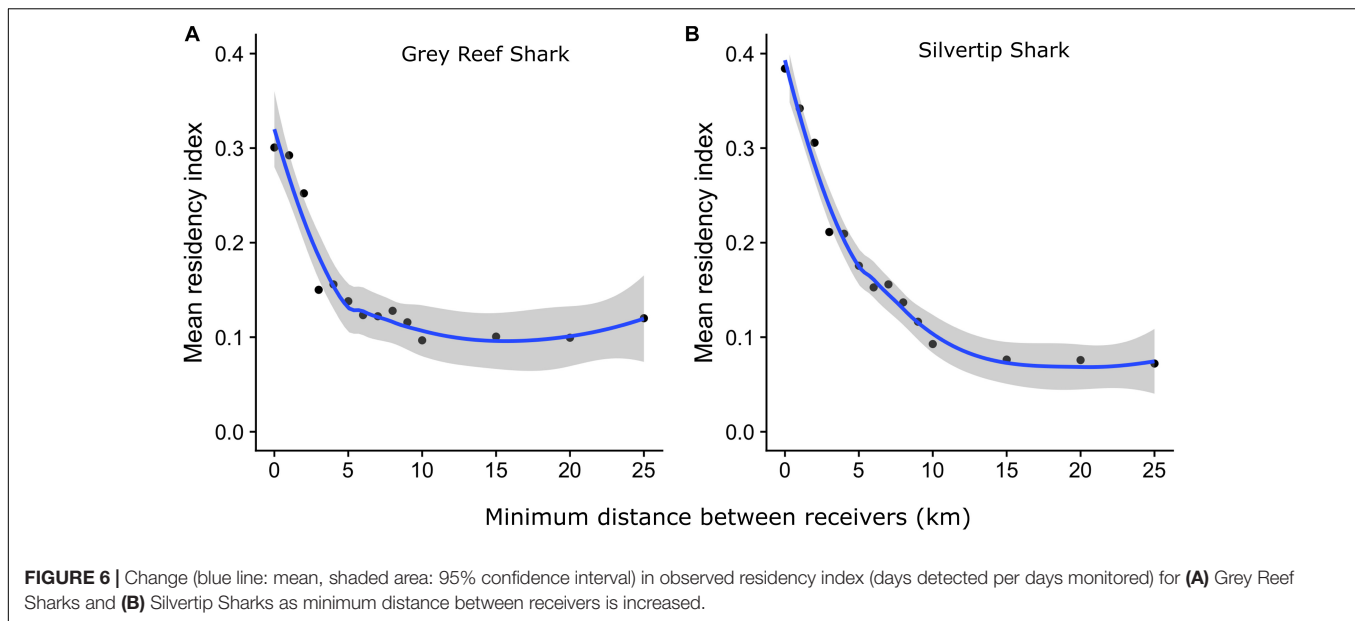


estimates from the cumulative dBBM for all tagged sharks (Table 2). Both species exhibited a high degree of intraspecific variability in space use.

Based on the duration of the gaps in detection and average swimming speed of both species, 52% of the acoustically tagged Grey Reef Sharks and 78% of the Silvertip Sharks could have left the BIOT MPA during gaps in detection (Supplementary Table S4). Of the sharks that potentially left the MPA, on average they had 2–3 gaps of sufficient duration (>7–8 days) to allow them to have potentially crossed the MPA boundary and returned. This does not indicate that sharks actually left the BIOT MPA, just that they theoretically could have under the least conservative scenario (swimming straight to the MPA boundary).

Array Spacing Simulations

Grey reef and Silvertip Sharks both showed a steep decline in detection probability with distance from their tagging site, with the effect more pronounced for Grey Reef Sharks. The maximum distance recorded in a Grey Reef Shark was 45 km, but over half of the animals were never detected more than 5 km from their tagging site. Silvertips on the other hand roamed further afield, with 70% traveling more than 5 km from their tagging site, visiting an average of 6.5 sites each versus 3.3 for Grey Reefs ($t = 3.316, p < 0.001$), and moving up to 70 km from their original location (Figure 5). The odds of detecting a Grey Reef Shark 5 km from its tagging site was three times that of detecting it at 10 km. The probability of Silvertip Shark detection declined more

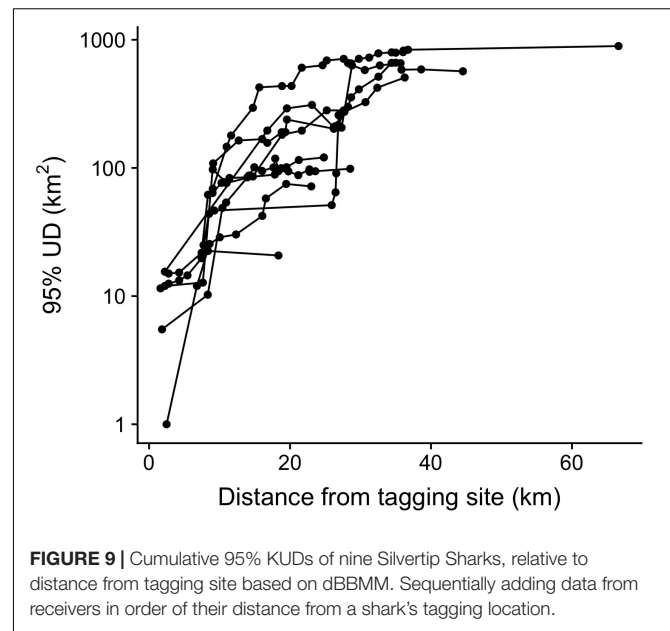
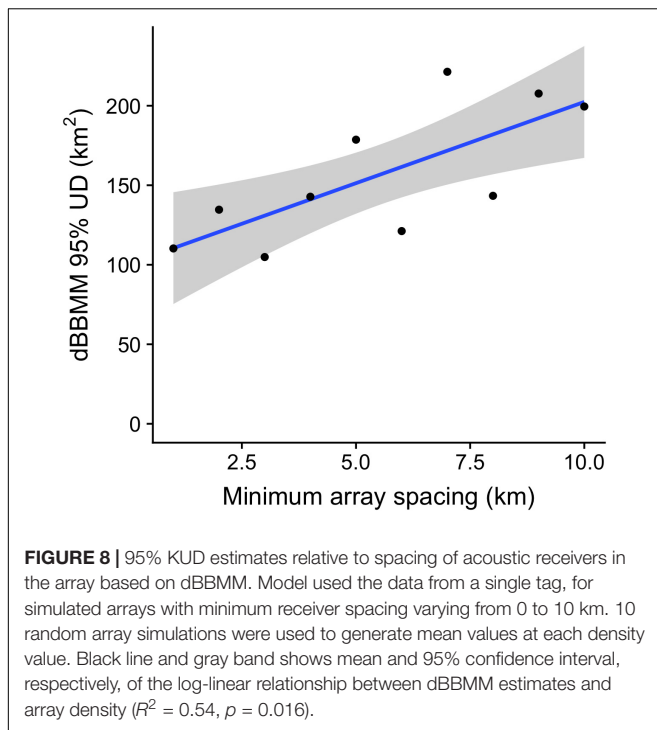


slowly with distance, with detection at 5 km only 1.5 times that at 10 km (**Figure 5**). A binomial generalized linear model (GLM) found a significant interaction between species and tagging-site-to-receiver distance, with the probability of detection remaining consistently higher for Silvertips with increasing distance (**Supplementary Table S3**). The probability of detecting individuals of both species declined with distance away from the tagging site, but detection probability declined more gradually for Silvertips (**Figure 5** and **Supplementary Table S3**).

When we modeled the effect of decreasing array density by subsampling the receiver array based on minimum distance thresholds, the residency index of both species declined with increasing separation of the receivers (**Figure 6**). Consistent with the species-specific relationships between detection probability and tagging-site-to-receiver distance reported above, Grey Reef

Sharks showed a greater sensitivity to array spacing than Silvertips, although observed residency and tag detection declined to similar levels for both once receiver spacing exceeded 10–15 km and this plateau was reached earlier in Grey Reef Sharks than Silvertips.

The mean duration of gaps in detection increased with increasing receiver separation for both species (**Figure 7**). The mean duration of gaps in detection increased sharply for Grey Reef Sharks as the spacing between receivers increased, plateauing at around 120 h in arrays with 10 km receiver spacing. The mean detection gap for Silvertips increased more slowly and plateaued once receiver spacing exceeded 15 km. Since acoustic telemetry provides presence-only data, such gaps represent blind spots in our monitoring of animals. Dynamic Brownian Bridge Movement Models attempt to fill in these gaps



by assuming that animals follow a conditional random walk (a random walk between known starting and ending positions) between subsequent detections. However, the randomness of a movement increases with detection gap length, all other things being equal, as the animal has more time to wander and so certainty over where it might go decreases. We tested the effect of reduced receiver coverage on the activity space estimates generated by a dBBMM, by generating KUD estimates for detections within different sub-arrays for a single shark with high baseline residency and broad use of the receiver network. 95% KUD estimates increased with receiver separation (Figure 8), consistent with the increase in detection gap length (Figure 7) and reduction in number of total detections (Supplementary Figure S3).

Finally, we looked at the role of receiver coverage, relative to tagging location, in influencing KUD estimates derived by dBBMM. KUD estimates for a subset of Silvertip Sharks increased as receivers were added to the area around their tagging site, up to a distance of approximately 30 km whereupon data from additional receivers made little difference to KUD estimates (Figure 9). This is consistent with the overall pattern of Silvertip Sharks which showed that the majority of animals were only ever detected within 30 km of their tagging site (Figure 4A).

DISCUSSION

Electronic tagging of pelagic and reef species in the BIOT MPA suggests that the MPA is large enough to provide significant spatial protection to marine species with diverse spatial ecologies, and that even some highly mobile pelagic species may spend extended periods within its borders. This result was

consistent across all approaches, and did not change even when incorporating the error associated with different tag technologies. Hence, with effective enforcement, MPAs on the scale of the BIOT MPA potentially offer considerable protection to a range of pelagic and reef species. However, intraspecific variability in movement dynamics suggests that, in particular for pelagic species, only a portion of a given population may be sufficiently resident within an MPA to benefit from protection, with the most mobile individuals, or life history stages, remaining vulnerable to fishing outside of the MPA boundaries, regardless of the size of the MPA. However, our ability to fully characterize the full space use of animals in the BIOT MPA is hindered by limitations that are typical of electronic tagging studies, including low sample size, limited deployment duration, acoustic receiver coverage, and a limited ability to tag both sexes across ontogenetic stages and seasons.

While sample size and deployment duration were limited for all pelagic animals in this remote archipelago, tagging data provided evidence that even some highly mobile pelagic species may derive some protection from the BIOT MPA. A Silky Shark was the only animal observed outside the boundaries of the BIOT MPA, even accounting for significant error in estimated positions, and the areas used by all other tagged pelagic animals, based on all metrics, were much smaller than the size the BIOT MPA. Some pelagic species spent extended periods of time within the BIOT MPA as well. For example, Sailfish spent the duration of their tag deployments within the BIOT MPA (up to 180 days), consistent with other studies showing that they are more abundant around islands, reefs, and other neritic habitats, relative to other pelagic species (Nakamura, 1985). This suggests a higher degree of residency around neritic habitats, and that this species should be more amenable to protection by large MPAs that enclose such features.

Satellite tagging demonstrated that MPAs on the scale of the BIOT MPA are large enough to provide protection to mobile reef

species (Silvertips and Reef Mantas). All tagged Silvertips and Reef Mantas spent the duration of their satellite tag deployments within the boundary of the BIOT MPA, had high residency estimates for areas much smaller than the MPA, and had activity spaces smaller than pelagic species and much smaller than the area of the BIOT MPA. While a pelagic Silky Shark was observed leaving the MPA, a Reef Manta was the only satellite-tagged reef-associated species to exhibit a potential pelagic excursion away from the archipelago. It is unclear whether or not this apparent movement was a result of SSM error, however, the estimated location error (~ 60 km) during the offshore movement was less than the minimum distance to land at its furthest point (~ 100 km), suggesting the offshore movement was real. However, the manta returned to the tagging location (Egmont Atoll) prior to the tag popping up, suggesting that if it did move offshore then it had some degree of fidelity to that site.

Intraspecific Variability in Space Use

Our results demonstrate that intraspecific variability in spatial ecology can impact the ability of MPAs to protect both pelagic and reef species. While there are populations or sub-populations of teleosts and elasmobranchs that show high fidelity to oceanic archipelagos, particularly isolated ones such as the BIOT MPA (Cowen et al., 2000; Planes et al., 2009), even reef-associated species such as reef sharks often display some degree of large scale dispersal or movements (Whitney et al., 2012; Chin et al., 2013; White et al., 2017). These large scale movements outside the MPAs boundary can expose them to fishing, which often is focused around MPA boundaries to take advantage of 'spillover' effects (Kellner et al., 2007; Boerder et al., 2017). Both satellite and acoustic tags demonstrated that intraspecific variability in space use will affect the ability of large MPAs, like the BIOT MPA, to protect all individuals of a species. For example, the two Silky Sharks tagged in this study displayed completely different patterns of residency within the MPA, despite being a similar size (~ 2 m): one spent the entire 270-day deployment within the BIOT MPA, while the other one was the only tagged animal to be observed leaving the MPA (Figures 2, 3). Even amongst reef-associated species, individual activity spaces could vary by orders of magnitude. The high degree of intraspecific variability in activity space for Silvertip Sharks based on acoustic and satellite tag data suggests vulnerability to fishing outside MPAs, especially for MPAs of smaller scale, may vary significantly within a population. Reef Mantas, due to their smaller activity spaces and lower intra-specific variability (Table 1), may be more amenable to protection at smaller spatial scales compared to Silvertip Sharks.

Importance of Study Duration

For reef-associated species, or pelagic species that exhibit some degree of association with atolls, reefs, or other bathymetric features, acoustic tags and arrays can provide insight into their space use. One major benefit of acoustic tags is that tag batteries can last > 10 years, meaning that data from monitored animals can provide insight into changes in activity space across years and ontogenetic stages. This approach would offer a more complete understanding of the activity space of these

species, as well as provide the opportunity to estimate their full activity space, or home range. Using cumulative dBBMM KUDs we were able to show that estimates of activity space are sensitive to study duration, and that the time required for space use estimates to reach an asymptote is species dependent, and variable across individuals. Grey Reef Sharks required at least 11 months of acoustic monitoring before KUD estimates approached an asymptote. For Silvertips this period was 20 months, reflecting their higher mobility and lower residency to individual reefs. However, the sample size, skewed sex ratio for Grey Reef Sharks, skewed size distribution in Silvertip Sharks, and current study duration limited our ability to evaluate longer term changes related to ontogeny and sex. Continued monitoring should start to reveal ontogenetic changes in activity space, and begin to outline the actual full home range of individual animals, loosely defined as "the area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943). These results show the necessity of maintaining acoustic monitoring infrastructure over extended periods if reliable estimate of species' activity spaces are to be achieved.

Effect of Array Design

To provide insight into how receiver spacing influences the ability of our acoustic receiver array to characterize the space use of species with different spatial ecologies, we modeled the hypothetical impact of different array designs by varying the minimum distance between receiver elements in subsets of the real array, treating our actual array and full dataset as the baseline. Movement and residency metrics calculated on the resulting detection data subsets from arrays of different receiver densities were compared with baseline results, by species, and showed clear inter-specific differences in the impact of array design choices, which were related to differences in species spatial ecology. Consistent with the activity space analysis discussed above, Grey Reef Sharks generally showed higher site fidelity and dispersed shorter distances from their tagging sites, with over half the individuals never detected more than 5 km from their original location. While these limited movements are consistent with prior studies of Grey Reef Sharks (Bond et al., 2012; Vianna et al., 2013; Espinoza et al., 2015), our study was biased toward females, which have been reported to exhibit a higher degree of site fidelity than males (Espinoza et al., 2015), suggesting that we may be underestimating space use for the Grey Reef Shark population in the BIOT MPA. Silvertips were further ranging, with 70% traveling more than 5 km from their tagging site and sharks being detected up to 70 km from their original tagging location.

Residency indices were sensitive to reductions in array density (increased spacing between receivers). Residency indices declined to 30% of baseline values once spacing exceeded 5 km for Grey Reef Sharks and 10 km for Silvertips, suggesting that residency estimates for both species are biased downward in sparse receiver arrays. The shape of the curves suggests that our baseline metrics, and acoustic receiver array, may also underestimate true residency since both increase sharply as receiver spacing is reduced and reached a maximum of between 0.3 and 0.4 for both species.

The length of gaps between detections also increases with the distance between receivers, an intuitive finding that has the potential to bias space estimates obtained using Brownian Bridge based methods that seek to overcome the “presence only” nature of acoustic telemetry data. This is potentially important, for during extended gaps with no detection, we are unable to evaluate whether an animal could have left the MPA boundaries or was simply outside the detection range of the receivers. However, our results suggest that overall our tagged animals had relatively few gaps long enough (>7–8 days) for them to leave the MPA under the least conservative scenarios (straight line movement to MPA boundaries and back). Importantly, satellite tag data indicated that no Silvertips left the MPA, so extended gaps in the acoustic detection record for this species (and Grey Reef Sharks as well) likely do not indicate that sharks left the MPA. Thus, the MPA can potentially provide significant conservation value for mobile reef and pelagic fishes. However, the efficacy of any MPA is also largely dependent on effective enforcement (Edgar et al., 2014). In the case of the BIOT MPA, IUU (Ferretti et al., 2018; Tickler et al., 2019) and drifting fish aggregation devices (dFADs) (Davies et al., 2017) still pose significant management concerns within the MPA boundary.

Using dBBMM to estimate space use for a single Silvertip Shark, which exhibited a high degree of residency to the array but which moved widely within the array, we found that 95% KUD estimates increased as array spacing was reduced, with estimates showing a high degree of variability between different receiver sub-arrays. Furthermore, using data from a subset of Silvertips, we demonstrate that increasing the size of the array in terms of distance from tagging location increases 95% KUD dBBMM estimates. However, we found that extending the array to distances beyond ~30 km from tagging location did not have a large effect on 95% KUD estimates for Silvertip Sharks. dBBMMs using acoustic telemetry data appear highly sensitive to the size, location and number of elements in the array generating the detection data, and extended and irregular gaps in detections. Hence, any inferences about space use will likely be heavily biased by the interaction between the tagging location and home range of an individual sharks and the size and density of the array. This calls into question the reliability of these techniques for estimating home range from aquatic acoustic data sets that are inherently irregular in periodicity, as opposed to the terrestrial tracking data for which they were developed (Horne et al., 2007). However, our results do indicate that relative differences between species, within a given array, can be detected. This is useful information for management, even if the absolute values of the home range estimates are likely a consequence, in part, of how the model data were collected.

Consistent with previous studies (Bond et al., 2012; Vianna et al., 2013; Espinoza et al., 2015), the movements of individual Grey Reef Sharks are much more restricted than Silvertips, hence a denser, smaller array (maximum receiver spacing 1–5 km) will provide better estimates of space use for Grey Reef Sharks than for Silvertips, which require a larger array (maximum spacing 1–10 km) to capture their wider ranging movements. Hence, in areas with similar habitat types as this study (series of coral reef atolls and submerged shoals in relatively close proximity),

having smaller, more dense receiver arrays will provide more robust estimates of space use than would ones that are less dense but geographically more expansive. Furthermore, tagging should occur near the center of the receiver array in order to optimize the efficiency of the receiver array. We suggest that tagging locations be identified prior to deployment of the array if working in larger scale atolls or reef systems or if that is not possible to attempt to tag within the center of the array. Based on our data, an array that extends further than 20 km or 30 km from the tagging location will provide little added value for Silvertips and Grey Reef Sharks, respectively, though how applicable this result is to these species in other parts of their distribution remains to be tested.

Overall, our array modeling exercise demonstrates how array design can affect common estimates of space use derived from acoustic receiver data and how this sensitivity will be driven by the underlying spatial ecology of the study species. In most acoustic tagging studies, data are analyzed and interpreted without directly assessing how the array design may be influencing the results. Our results suggest that sensitivity analyses, similar to what we have done, should be conducted to understand how array design may be influencing the results and interpretations. These types of analyses can provide valuable insight into what the data are and are not able to reliably tell you, and can provide useful insight into the spatial ecology of the species as well.

Other Methodological Considerations

Electronic tagging remains one of the best ways to understand the spatial ecology of mobile marine fishes, however, there are important limitations to this approach. Due to logistical challenges, expense of tags, and battery and tag retention limitations, it can be challenging to use electronic tags to fully characterize the space use of mobile marine taxa. Tags are generally applied to animals that can be caught and tagged, which often leads to particular size classes and ontogenetic stages being studied (Hazen et al., 2012). In order to fully characterize the home range of a species and understand the ability of MPAs to provide protection to a given population, the space use of animals of all life history stages needs to be characterized and understood. Ontogenetic shifts in habitat are ubiquitous in the natural world, including in teleosts and chondrichthyan fishes (Grubbs, 2010). As a result, the habitats used and space required by juveniles will be very different than that of adults, affecting their vulnerability to different stressors (e.g., fishing pressure). Tagging can also be limited to times or seasons when animals are available for study, or by whether field work can occur, leading to seasonal bias in tagging, which will affect our understanding of species movement dynamics and vulnerability to different sources of mortality.

Even if the full activity space of a species has been characterized, this information may not capture the full ecological requirements of a species within an MPA. Stable isotope analysis suggests that Grey Reef Sharks at Palmyra Atoll in the Pacific may receive a substantial trophic subsidy from offshore pelagic ecosystems outside of the MPA, whether through movements of the sharks or their prey (McCauley et al., 2012b; White et al., 2017). Seabirds return to colonies on islands and atolls and fertilize local ecosystems with resources from distant

pelagic habitats (McCauley et al., 2012a). Other isolated oceanic habitats, such as seamounts, also may require trophic subsidies to support populations of large, upper trophic level predators (Koslow, 1997). Hence, factors from outside the boundary of an MPA can still affect the ecosystem function and ecology of species within an MPA through cross-system trophic linkages and subsidies (Curnick et al., 2019). Hence, these potential linkages need to be characterized and understood to understand how an MPA, and the species it supports, fits into the broader regional and oceanic context.

Logistical and financial challenges associated with electronic tagging in a remote location, tag attachment, and the difficulty of finding and tagging species on short expeditions make it difficult to fully characterize seasonal, interannual, or longer term (decadal or ontogenetic) changes in animal behaviors. Hence to fully characterize the space use of these animals, and to understand how effective MPAs of various sizes will be at protecting them across their full life history, there must be significant investment in long term studies that are able to capture the full temporal and spatial dynamics of monitored populations. This is important as fully characterizing the spatial ecology of marine species, and understanding its variability, is a prerequisite for designing effective MPAs able to protect animal populations occurring within their boundaries. Yet MPAs are often designed and implemented without having access to or considering this type of information. However, by fully characterizing the spatial ecology of marine species, and understanding its variability, it should be possible to design MPAs that confer protection on a meaningful proportion of the population, thus achieving the desired conservation outcomes. This suggests that, if properly enforced, the expansion of very large oceanic MPAs that has occurred over the last decade should provide effective protection to local populations of mobile reef-associated species as well as several pelagic species that exhibit the necessary degree of site fidelity. However, our results demonstrate that to develop effective science-based conservation and management strategies that account for the spatial ecology of a mobile marine species requires sustained investment in research that uses technologies and study designs that are able to fully account for the intraspecific diversity in movement patterns across sexes and ontogeny.

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DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

All procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) under permit APLAC-10765.

AUTHOR CONTRIBUTIONS

AC, DT, JD, FF, DC, TC, RS, MC, and BB contributed to the design and implementation of the research. AC, DT, JD, and FF collected, processed, and analyzed the data and wrote the manuscript. DC, TC, RS, MC, and BB collected data and helped to writing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00256/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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