Gap analysis of acoustic tracking data reveals spatial and temporal segregation in sympatric reef sharks

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Abstract

Background There are now a wide array of field and laboratory techniques available for gaining insight into the movement and behaviour of sharks. Although acoustic telemetry may lack the fine-scale resolution of satellite telemetry, the low cost and longer battery life make it a powerful tool for investigating elasmobranch behaviour. Here, in the absence of satellite tracking data, we develop a novel approach to analysing acoustic telemetry data, using detection gaps to infer movement patterns to and from monitored reef habitats, to investigate spatial and temporal segregation between two sympatric shark species in a large remote MPA.

Methods A total of 102 grey reef and 76 silvertip sharks were fitted with long-term acoustic transmitters and tracked inside a large acoustic array of reef-based receivers in the British Indian Ocean Territory MPA, between 2014 and 2018. From the resulting dataset (768,081 movements), movements between receivers and recursive loops to the same receiver were identified. Using the durations of inter-receiver movements (i.e. detection gaps), individual behaviours were classified into 'restricted' or 'wider ranging' movements. Drivers of these movements were identified using network analysis, generalised linear mixed models and multi-model inference starting from an a priori set of explanatory variables.

Results In general, silvertip sharks were more likely to undertake 'wider ranging' movements than grey reef sharks. 'Wider ranging' movements were more common at night compared to during the day, and during the wet season compared to the dry season. In addition, the difference in 'wider ranging' movements between the two species increased at night. These results suggest spatial segregation and temporal segregation of movements between grey reef and silvertip sharks in the region.

Conclusions We present a novel analysis of detection gaps from acoustic telemetry data to infer differential movement patterns and describe how species organise in space and time. Furthermore, this approach shows that acoustic telemetry gap analysis can be used for comparative studies, or combined, with other research techniques to better understand the functional role of sharks in reef ecosystems, moving towards more informed strategies for the conservation and management of the marine environment.

Background

Due to the continued decline of global elasmobranch populations (1, 2), investigating the movement ecology, spatial distribution and behaviour of these species is of continued importance for their conservation and management. There are now a wide array of field and laboratory techniques available for gaining insight into the movement and behaviour of sharks (3). Geolocations from satellite telemetry, such as pop-up satellite archival tags (PSATs), can be used to reconstruct estimated tracks of tagged animals that rarely come to the surface, but they are limited by battery life and the low spatial and temporal resolution of estimated positions (4). Acoustic telemetry is regularly used for analysing the long-term movement patterns of coastally affiliated elasmobranch species, with a longer battery life enabling data collection over greater time scales, but it too, is limited by both the detection range of the receivers and the low positional accuracy in nonoverlapping arrays (5). Thus, combining methodological approaches, where possible, can minimise these limitations, helping to reveal the mechanisms behind important ecological processes that might aid how elasmobranchs are conserved in the future (6).

The British Indian Ocean territory (BIOT) is a large, remote archipelago declared a 'notake' Marine Protected Area (MPA) in 2010, the reefs of which are home to multiple elasmobranch species (7, 8). Reef-associated elasmobranchs inhabit or frequent coral reefs for foraging and mating opportunities, nursery and pupping areas, and protection from larger predators (9–11). Multiple elasmobranch species may coexist in reef ecosystems through differential use of space and time, allowing sympatric species utilise resources and habitat but avoid interspecific competition (12, 13). Subordinate species may avoid areas of regular use or high population density of more dominant species, or may alter diel or seasonal rhythms to reduce temporal activity overlap (13, 14). As limited resources and high levels of competition can significantly impact an individual's fitness, spatial and temporal segregation can be a critical component of survival (13, 15–17). Investigations into spatio-temporal segregation are, therefore, emerging as an important focus area in elasmobranch ecological research (5–7).

Acoustic telemetry can be a powerful tool for investigating elasmobranch behaviour. It has been used to measure or infer multiple aspects of elasmobranch ecology (18), such as social structuring (19–21) and individual social preferences (22), but is also regularly employed to investigate the spatio-temporal distribution and movement dynamics of elasmobranchs (5, 15, 23, 24). The temporal dynamics of elasmobranch species movement are important for understanding how predators can affect prey both directly, through ingestion, and indirectly, through predation risk (25). This can lead to top down effects through mortality and antipredator behaviour, resulting in changes to prey communities and species abundance (26–29). Temporal changes in the movements of elasmobranchs may also have bottom up effects by impacting nutrient cycle timings in marine ecosystems, such as coral reefs (23). Consequently, the distribution and timing of

acoustic detection data can be extremely informative at daily, monthly, seasonal, and annual scales. However, there is also an important temporal component within the absences between detections that is often overlooked. Thus, it is important to identify not only the frequency and periodicity of movements to areas of interest (e.g. feeding and breeding areas, resting refugia etc.), but also the time taken for movements between these and other areas (30), specifically, the periods when they are not being detected.

Network analyses of movements derived from acoustic telemetry are becoming more commonplace for exploring spatial and temporal movement patterns within acoustic detection data (18, 21, 31). To date, gap analysis has been used for studying the ecology of marine vertebrates, particularly using time periods between location fixes from satellite telemetry to determine directed or restricted movements for optimal foraging theory in pinnipeds (32). However, currently, network analyses using acoustic telemetry often ignore the gaps between detections. These gaps can be informative for inferring the length of time (which might be a proxy for tortuosity) taken between movements considered as the edge duration within a movement network (31), and therefore coarse scale behaviour and its associated timings. For example, they can be used to inform the likelihood of elasmobranchs moving out of protected marine areas, into unprotected waters, where they may be vulnerable to exploitation from commercial fisheries (6). These gaps can also be used to estimate the timings of ontogenetic habitat shifts, when individuals begin leaving nursery areas for longer periods (33) and more accurately determining the timings and thresholds to define residency events for spatial distribution and movement analyses (34). As sharks play important direct and indirect roles in marine ecosystems (35, 36), detection gaps also have potential to provide information into ecological function in elasmobranchs species, particularly in areas or systems where finescale movement data from satellite telemetry is unavailable. The analysis of detection gaps within acoustic telemetry data can thus directly complement static analyses of presence data, in addition to other telemetric and physiological data, to greatly aid the overall understanding of the role of multi-species predator assemblages within coral reef ecosystems (15).

In this paper we use data gathered across a large array of acoustic receivers monitoring reef-associated shark species throughout the BIOT MPA. In the absence of receivers in pelagic areas and sufficient satellite telemetry data to make population level inferences, we aim to analyse the detection gaps from the acoustic time-series to characterise 'restricted' or 'wider ranging' movement patterns in grey reef and silvertip sharks investigating the spatial and temporal segregation between these two species in coral reef ecosystems.

Methods

Acoustic tracking

Data collection was undertaken in the BIOT MPA between February 2013 and April 2019. Throughout the archipelago there have been situated up to 93 permanent and temporary acoustic receivers (VR2W, VR4-UWM, VR4G and VR2AR receivers, Vemco Inc, Nova Scotia, Canada), as configured in Fig. 1. The BIOT MPA is characterised by numerous small islanded atolls with submerged banks and reefs, with waters of 1 km depth or more separating each atoll or reef system (37). As such, acoustic receivers in the BIOT MPA are mainly based on areas accessible to divers, such as coral reef systems, with few receivers covering the deep pelagic waters of the region. This array was initially started in 2013, expanded throughout subsequent years [for more information see [Carlisle et al. (6)]], covering a perimeter of 700 km and an area of 25,500 km² within the MPA, for the detection of acoustically tagged marine fauna, with 82 of the 93 receivers in waters of depths 45 m or less. All receivers were situated far enough apart to avoid overlap in their detection range, with mean distance to closest receiver 2.15 km, with a range of 0.55–4.57 km. The frequency distribution of inter-receiver distances can be found in Additional file 1: Figure S1. Although range testing has not been undertaken for this array due to financial and logistical constraints of vessel time in the BIOT MPA, other studies conducted around coral atolls in the Indian Ocean using the same or similar equipment have found detection ranges between 300 and 500 m (12, 38–40). Maps of the different reef systems with acoustic coverage with an estimated 500 m detection range, can be found in Additional file 1: Figure S2-4.

We tagged 102 grey reef and 76 silvertip sharks with acoustic transmitters across nine different locations following the methodology described by Carlisle et al. (6). Of tagged grey reef sharks, 76 were female and 26 were male. Of the tagged silvertip sharks, 45 were female and 31 were male. As in previous studies (41, 42), silvertip sharks (mean total length, TL = 123.56 cm ± 19.14) were on average larger than grey reef sharks (mean TL = 119.15 cm ± 18.07). Detailed information on metadata for each tagged individual can be found in Additional file; Table S1. Tags acoustically transmit a unique ID code with a nominal delay of 60–180 secs for the duration of their battery life (~10 years), providing a long-term time series of detection data. Receivers were downloaded and serviced annually at the same time each year (March-May), with data last downloaded April 2019.

Only complete years were included in the analysis, with the final data set covering shark detections from 2014–2018. Prior to analysis, data from the seamounts were removed. Seamounts in the BIOT MPA differ ecologically from the rest of the archipelago and recent

analyses suggest that they are potentially important drivers of silvertip shark movement (unpublished data). While we acknowledge the ecological importance of seamounts, we only had acoustic equipment on two of these features in the south of the MPA. We felt that in order to robustly investigate segregation of reef sharks in coral reef habitat, seamount data should be excluded.

Movement classification

Using a movement network approach a 'transition' was deemed to have occurred when an individual left one receiver and arrived at another in a new location (24). Alternatively, an animal might leave a receiver, move out of detection range and then return to the same location, a 'self-loop' in network parlance, but here called a 'recursion'. Classification of 'restricted' and 'wider ranging' activity was, therefore, inferred based on the duration of these two different types of movement (hereafter transitions and recursions) before being used as a binary response variable in subsequent models (Fig. 2).

Classification of 'restricted' and 'wider ranging' movements, was conducted using an optimal classification method, where similar data values are placed in the same class by minimising an objective measure of classification error (43). For recursions, detection gaps of less than six minutes (minimum of two detections) were removed from the data as an initial filter to ensure a recursion had taken place, rather than an animal had stayed in the same location but a detection had been missed. Time differences for recursive movements per species were log transformed to normalise the data, and the `classInt` package in R (44) used to calculate thresholds between 'restricted' and 'wider ranging' movements. The Fisher algorithm was used, which determines thresholds by minimising the sum of absolute intra-class mean variance, as well as maximising inter-class mean variance (43, 45). This resulted in a threshold of 91 minutes for grey reef sharks and 64 minutes for silvertip sharks for 'restricted' activity, beyond which it was assumed that the shark had conducted more 'wider ranging' movements.

Transitions were subject to a separate filtering process. Unlike recursions, no initial filter was required for transitions as the detection of an individual on one followed by another receiver is immediately indicative of a movement from one location to another. Temporal gaps in the detection data for any given pair of receivers were informed by both the distance and species-specific minimum sustainable swim speeds (0.69 m/s for grey reef sharks and 0.73 m/s for silvertip sharks) (46). For example, the predicted transition duration of a direct movement of a shark between two receivers, without deviation, would be the ratio between distance and speed. As such, by first calculating expected time for a transition using swim speeds and distance between receivers, the relative deviation from this expected time (RDET) between any pair of receivers was determined by dividing the expected transition time by the observed transition time. RDET values of > 1 were movements faster than expected, and values of < 1 slower/more tortuous than expected.

For transitions, log transformed RDET were constructed for both species, and, as with recursions, an optimal classification method for determining thresholds was used. Movement values of greater than the threshold value of 0.164 for grey reef sharks and 0.128 for silvertip sharks were determined as 'restricted', with values less than the thresholds determined as 'wider ranging'. Animals rarely travel in straight lines and often vary in their tortuosity depending on factors such as resource use, habitat quality, competition and predation (47–49). These thresholds of 0.164 and 0.128 are, therefore, very conservative to allow for a tortuous movement to occur and still be classified as 'restricted' in each species. Finally, recursions and transitions were combined so that every movement was categorised as a binary response (restricted = 0, wider ranging = 1) (Fig. 2).

Data analysis

To explore the influence of explanatory variables on 'wider ranging' movements, an information theoretic approach was taken, which accounts for model selection uncertainty (50, 51), using a generalised linear mixed model (GLMM). In recent years, information theoretic approaches have become a staple for modelling ecological systems, particularly those where explanatory models describing the system may have similar complexity and fit the data equally well, such as understanding the spatial distribution (52–54), behaviour (55, 56), and anthropogenic impact on survival of wildlife populations (57, 58). To limit exploratory analyses, and prevent model overfitting, an a priori selection of variables and interactions based on previous research and theory was conducted (51, 59, 60). Explanatory variables included in the model were 'species', 'sex', 'size', 'season' (wet/dry) and 'diel period' (day/night) (15, 42, 61–63). As size had a non-normal distribution it was log transformed. The BIOT MPA is located near the equator and has a roughly 12-hour day/night cycle. As such, day was designated from 0700 to 1900 and night from 1900 to 0700 following sunrise and sunset times obtained from <https://www.timeanddate.com>. The MPA experiences distinct Indian Ocean wet and dry seasons with wet season running from October to March, and dry season from April to September (64). Seasonal variability is often greater than monthly variability in tropical ocean systems (65, 66), and, therefore we deemed season a more biologically relevant driver of shark movement. All analyses were conducted in R version 3.6.0 (67).

All variables used in the model were assessed for multicollinearity. Multicollinearity, which occurs when predictors in a multiple regression are highly correlated (68), was assessed by producing a variance inflation factor (VIF) using the 'check_collinearity' function in the 'performance' package in R (69). VIF measures the degree of multicollinearity in a regression model by providing an index of how much the variance of the model variables increases due to collinearity (70). No evidence of collinearity was found, with all variables having a $VIF \leq 1.05$, less than the critical threshold of 5.0 (see Additional file 1: Table S2) (68, 71). As such, all a priori selected explanatory variables were included in the global model.

A global model was subsequently created using a GLMM (family binomial) in the glmmTMB package (72). To explore putative spatial and temporal segregation between grey reef and silvertip sharks, 'species' was included as interaction term with all explanatory variables and individual ID as random factor. As the likelihood of a movement between locations decays as a function of distance (D. Jacoby unpublished data), receiver location was also included as an independent random factor. Residuals of the global model were checked for heteroscedasticity, autocorrelation and errors were checked for binomial distribution using the functions 'resid', 'fitted', and 'acf' from the 'stats' package in R (67) and found free from autocorrelation and heteroscedasticity of residuals (Additional file 1: Figure S5).

To generate the model set from the global model, the dredge function from the MuMIn package was used (73). These models were ranked by Akaike information criterion (AIC) values. If no single parsimonious model resulted from the model set, a group of confidence models, most likely to represent the system, were selected. Only models with $\Delta AIC < 2$ were chosen for the confidence model set (50, 74). A model averaging approach was then undertaken on the confidence set of models (60) using the model averaging function in the MuMIn package (73). This function calculates model weights based on the confidence set of models (60). Model averaged estimates and confidence intervals (97.5%) for each explanatory variable and interactions were calculated (51). The relative importance of each predictor variable (relative to other variables in the confidence set of models) was calculated by summing Akaike weights for all confidence set models containing them (50).

Model averaged estimate values indicate the probability of observing a 'wider ranging' movement as the value for continuous predictor variables increase. Categorical predictor variables were compared to the categorical variable level used as the model baseline. Positive estimates indicate an increased probability of 'wider ranging' and a decreased probability of 'restricted' movements; negative estimates, a decreased probability of 'wider ranging' and increased probability of 'restricted' movements. It is important to note that using this method it is possible that some levels of categorical predictors may display a high relative importance value but show no significant result in the model averaged estimates, as these are dependent on the baseline chosen (75). Therefore, both the relative importance and model averaged estimate results should be considered in combination (55, 60). To assess variance in the fixed effects and the entire model, marginal R^2 and conditional R^2 values were calculated using r.squaredGLMM in the MuMIn package (73, 76).

Model cross-validation

To assess the predictive capabilities of our final model, analysis was conducted on 80% of the data. Cross-validation of the model averaged estimate values from the confidence set of models was conducted on the remaining 20% of data as confirmatory analysis to quantify how well the selected model performed (51). The predict function in the glmmTMB package was used to validate the expected outputs of the multi-model inference on the observed values from the reserved 20% of the data. Area under the receiver operating characteristic curve (AUC) values designate the probability that positive and negative instances are correctly classified (77). As such, AUC was calculated using the pROC package (78), as a thresholdindependent method to check the robustness of the model. An AUC value of greater than 0.7 indicates better than random performance and that the model is a good representation of the system being evaluated (77, 79, 80).

Results

There were 768,081 movements (transitional and recursive) identified from 102 grey reef sharks and 76 silvertip sharks between 2014–2018.

Model selection

Following the dredge of the global model, no single parsimonious model was found. The weight of the best model was 0.17 (Additional file 1: Table S3). If the weight of the 'best' model is less than 0.9, model averaging is recommended over model comparison (60). Six models had $\Delta AIC < 2$ and formed the confidence model set for model averaging (Table 1). As part of model averaging, model weights are recalculated (60). The results from model averaging are presented in Table 2. Five variables and three interactions had a relative

importance greater than 0 and were deemed as important explanatory variables of 'wider ranging' movements (Table 2). Three variables and one interaction had a significant effect on 'wider ranging' movements (Table 2).

Table 1
Confidence set of models resulting from model selection.

Model	diel stage	size	season	sex	species	diel stage:species	size:species	season:species	sex:species
54	+	NA	+	NA	+	+	NA	NA	NA
182	+	NA	+	NA	+	+	NA	+	NA
62	+	NA	+	+	+	+	NA	NA	NA
318	+	NA	+	+	+	+	NA	NA	+
190	+	NA	+	+	+	+	NA	+	NA
56	+	-0.13	+	NA	+	+	NA	NA	NA
Model	df	logLik	AICc	ΔAIC	ω				
54	7	-179034.1632	358082.3267	0.00	0.28				
182	8	-179033.5974	358083.1951	0.87	0.18				
62	8	-179033.6551	358083.3104	0.98	0.17				
318	9	-179032.8144	358083.6291	1.30	0.15				
190	9	-179033.0848	358084.17	1.84	0.11				
56	8	-179034.0975	358084.1952	1.87	0.11				
Presence of a variable or interaction in a model indicated by the + symbol. Degrees of freedom (df), Akaike information criterion (AIC), ΔAIC and Akaike weights (ω) presented for each model.									

Table 2
Model averaging results following model selection for wider ranging movements.

	Estimate	Std. Error	CI	z value	p value	RI
Intercept	-2.02	0.636	-3.448 -0.956	3.465	0.001	NA
diel period						
night	0.133	0.011	0.110.155	11.593	0.000	1.000
season						
wet season	0.169	0.011	0.1470.19	15.304	0.000	1.000
species						
silvertip shark	0.805	0.148	0.5151.094	5.445	0.000	1.000
diel period:species						
night:silvertip shark	0.076	0.018	0.0390.112	4.092	0.000	1.000
season:species						
wet season:silvertip shark	-0.021	0.02	-0.0590.018	1.065	0.287	0.292
sex						
male	0.203	0.182	-0.1550.56	1.111	0.266	0.429
sex:species						
male:silvertip shark	-0.37	0.285	-0.9270.188	1.298	0.194	0.146
size	-0.133	0.367	-0.8520.586	0.362	0.717	0.110
Estimates with standard error, 97.5% confidence intervals (CI) and associated p values are presented. Significant results are highlighted in bold. Relative importance (RI) of each model calculated by summing Akaike weights (Table 1) for all set of confidence models containing them. A value of one indicates a variable is very important and occurred in all confident set of models, a value of 0 indicating a variable is unimportant and did not occur in any confidence set of models.						

Model averaging

Species, diel period and season were significant predictors of 'wider ranging' movements. Silvertip sharks were overall more likely to undertake 'wider ranging' movements compared to grey reef sharks ($p < 0.001$, Table 2) indicating spatial segregation between the species. However, as both species still undertook regular 'wider ranging' and 'restricted' movements, this segregation is not discrete. Wider ranging' movements were more likely to occur at night than during the day ($p < 0.001$, Table 2) (Fig. 3a), and during the wet season than the dry season ($p < 0.001$, Table 2) (Fig. 3b). Interaction effects revealed temporal segregation of movements between the species with the difference in 'wider ranging' movements between silvertip sharks and grey reef sharks greater at night than during the day ($p < 0.001$, Table 2) (Fig. 3a). The variance and standard deviation of the random factors were 0.67 and 0.82 for individual ID, and 0.77 and 0.88 for receiver location respectively. Marginal R^2 (R^2_m) was 0.03 and conditional R^2 (R^2_c) 0.36. Model validation results calculated an AUC value of 0.741, indicating a good performance of the model.

Discussion

Understanding the spatial and temporal distribution and movement patterns of reef sharks in the BIOT MPA is important for effective conservation management and MPA enforcement efforts. Current analyses of acoustic telemetry data often neglect the timings and periodicity of detection gaps. In the absence of more accurate movement data for large numbers of animals, which can be prohibitively expensive for satellite telemetry, we have developed a new approach, which utilises gaps in detections from acoustic telemetry to infer presence or absence from regions of interest, such as coral reef systems, at a coarse scale. Prior research on patterns of movements between coral reef-associated elasmobranch species have been limited but primarily focus on differences in space use (15, 81, 82). To date, temporal aspects of segregation are rarely considered (83, 84). As seen here, the use of time dependent factors, such as detection gaps, has the potential, albeit at coarse scales, to identify both spatial and temporal differences in movement in sympatric shark species enhancing our understanding of the organisation and reorganisation of reef predator assemblages.

Grey reef and silvertip sharks in the BIOT MPA had significant differences in inferred 'wider ranging' activity. Overall, silvertip sharks were more likely to undertake 'wider ranging' movements than grey reef sharks. These results suggest spatial segregation between these species, with grey reef sharks, probabilistically, more likely to inhabit reef-based areas while silvertip sharks were more mobile and conducted more widespread movements (Fig. 3). Our results indicate that although there is spatial segregation between the species, there is overlap between the two in the areas they reside. This supports evidence from isotope data which suggests resource partitioning between these two species in the BIOT MPA, with both species utilising both reef and pelagic areas for foraging, but with grey reef sharks obtaining 78% of their biomass from reef resources, but silvertip sharks only 60% (85). In addition, our results are consistent with work from the Great Barrier Reef suggesting grey reef sharks are true reef sharks, and silvertip sharks less reliant on reef-based resources in this region (86). Further, these results extend previous research describing variable patterns of movement and activity in both grey reef sharks and silvertip sharks globally (87–89). Locally, previous research in the BIOT MPA found that silvertip sharks had higher mobility, larger activity spaces, and lower reef residency compared to grey reef sharks, which had small activity spaces and rarely moved more than five to ten kilometres from their tagging location (6). This study has shown that not only can gaps in detections be used to help interpret and support other types of data, but, even at coarse scales, can potentially be used to provide insight into the differences in spatio-temporal movements that underpin reef predator sympatry.

Although 'wider ranging' movements of reef sharks in the BIOT MPA increased at night, this is perhaps biased by silvertip shark propensity to range more during the night, with grey reef sharks showing very little diel change in 'wider ranging' movements (Fig. 3a). Differing patterns from the literature suggest that diel movement patterns may be population dependent, possibly driven by interspecific interactions and/or local environmental conditions (38, 87, 88). For example, grey reef shark populations in Palau utilise shallower reef platforms for foraging during the night, with deeper, pelagic, waters exploited during the day (88). The same species around Palmyra Atoll in the Central Pacific Ocean, however, are detected on the forereef frequently during the day with far fewer detections at night (87), suggesting they move away from the reefs during these periods. To date only a few studies have been conducted on movement behaviour of silvertip sharks, but work by Espinoza et al. (89) on the Great Barrier Reef found that silvertip sharks undertook deeper dives and were detected less during the day, possibly due to foraging. An alternative explanation for the reduction in detections at night, could be the avoidance of transient apex predators, such as tiger sharks (*Galeocerdo cuvier*), which are known to feed on reef-associated mesopredators, like silvertip sharks (35, 36, 90). Further research should be conducted in order to investigate regional and population patterns of movement both within and between different reef shark species.

The diel variance in 'wide-ranging' movements found in the study also indicates temporal segregation of movements between the two species, with the difference in spatial segregation of grey reef and silvertip sharks increasing at night (Fig. 3a). The reasons behind the increase in spatial segregation at night are not immediately clear. At several other reef locations grey reef sharks are central place foragers (86, 87, 91), while silvertip sharks are more dispersive, and less site attached (86, 89). As foraging occurs at night, it may be that silvertip sharks move offreef to forage, therefore increasing 'wider ranging' movements at night, while grey reef sharks forage on-reef, which would support the differential patterns of resource use found between these species (85). Or, alternatively, it may be that silvertip sharks occupy a greater spatial range at night during foraging, as has been seen in other reef shark species, such as whitetip reef sharks, *Triaenodon obesus* (92) and blacktip reef sharks, *Carcharhinus melanopterus* (87), but grey reef shark spatial range rarely changes. However, currently little is known about the foraging ecology of these two species in this region, and further studies will be needed to investigate the apparent diel differences in 'wider ranging' movements between these two species in the region.

There was also seasonal variation in the 'wider ranging' movements of both species (Fig. 3b). Knowledge of seasonal patterns of elasmobranch movement in the region is important to aid enforcement efforts to prevent illegal or unregulated fishing in the BIOT MPA (93). Like diel period, seasonal patterns of movement are common in multiple elasmobranch species. Such seasonality may be driven by mating in adults, ontogenetic expansion of home range, or foraging opportunities (63, 94, 95). Additionally, environmental conditions across the BIOT MPA are subject to considerable changes associated with the Indian Ocean monsoon current. In many species however, seasonal changes in movement may not be clear, with movements either unpredictable or subject to individual behavioural variability (95). Indeed, our model results suggest that inter-individual variability also plays an important role in explaining the probability of 'wider ranging' movements. Interindividual variability in movement behaviour is seen across shark species (96–98), and may be driven by differences in age class, sex, morphology, health and even personalities (99, 100) but currently is not fully understood (101). Model results also indicated an increase in 'wider ranging' movements during the wet season. However, the reasons for this increase are unclear. As the wet season (October – March) coincides with the peak historic pelagic fishing season in the BIOT MPA (102), this increase in movement may possibly be linked to a seasonal food resource, as previously hypothesised by Curnick et al. (85). Although food may be a primary driver of temporal changes in movement, it may also be driven by factors such as thermoregulation or predator avoidance, or by environmental variables such as sea surface temperature, salinity or current (89, 103). Despite recent developments to our understanding of how environmental

variables effect elasmobranch movement (103, 104), they are still relatively poorly understood and investigations should be undertaken to further explore their impact on both spatial and temporal aspects of elasmobranch movement in this region.

Because acoustic telemetry only measures presence, array design and detection ranges can significantly impact results obtained using this technology (6). An inability to detect an animal could be due to the animal leaving the study area, or because it moved out of detection range (5), and consequently might result in some mis-designated movements in this study. Detection ranges for the region vary between 300 and 500 m (12, 38–40), and distances between receivers ranged, between 0.55–4.57 km with mean distance to closest receiver 2.15 km, with minimal overlap between receivers (Additional file 1; Figure S1-4). We acknowledge that this could lead to significant 'blind spots', where a shark could be swimming and not detected rather than engaging in 'wide-ranging' movements. We consider the impact of these, however, to be minimal for the following reasons; classification thresholds of movement were very conservative, giving considerable leeway for an animal to move around a reef area, detections to be missed, and still the movement be classed as 'restricted'; furthermore, neither of these species are able to rest motionless on the bottom, as they are required to ram ventilate (105), increasing the chances of them being detected on the same or additional receivers even when frequenting 'blind spots' within the array.

In addition, animals using the lagoons of these atolls would also not necessarily be detected on the array, and movements across the lagoons could also be mis-designated. However, lagoon use in these species tends to be minimal (41, 106, 107) and the isotope signatures obtained from these two species indicate they are not using lagoons for foraging (85). As such, in addition to our findings complementing the work of Curnick et al. (85), we believe these potential issues should not have impacted our results significantly. However, we stress that this is an inference method being used in lieu of more accurate measurements for large numbers of free-ranging individuals and may not be suitable for regions with large gaps in receiver detection ranges, particularly when the study species may exhibit bouts of sedentary behaviour.

Although the consistent nature of our results with those obtained from stable isotope work (85) help to validate our methodological approach, further validation of our classifications could be carried out using more accurate positional data. Although there were several silvertip sharks double tagged with both acoustic and PSAT tags, unfortunately the positional data from these satellite tags was not of a high enough resolution to fully confirm our claims. At low latitudes, the error associated with light-level geolocation estimates from PSAT tags can be very high (4). For example the geolocation error from a silvertip shark tagged with a PSAT in the BIOT MPA was estimated at 0.25° or 27.83 km at the equator (6). In addition, geolocation algorithms used to reconstruct positions from PSAT data only produce a single position per day, which limits their ability to investigate diel differences in location. Although not feasible in this study, the accuracy of this technique should be validated in future studies with more accurate positional data, such as those derived from Fastloc GPS tags (e.g. Smart Positioning and Temperature transmitting tags).

There are no single 'silver bullet' research techniques for investigating elasmobranch ecology at an appropriate and meaningful spatial and temporal scale; each methodology has its limitations. However, by combining data from multiple approaches the limitations of any individual methodology can be overcome, and a more holistic understanding of elasmobranch ecology can be attained. Here we show that, in the absence of finer scale movement data beyond the boundaries of our acoustic detection ranges, gaps in detections can be used to support and extend conclusions about how variable behavioural strategies can influence interspecific species organisation on coral reef systems.

Conclusion

In the absence of accurate satellite tracking data, we have developed a novel methodological approach for analysing acoustic telemetry data, using absences in detections to classify 'restricted' and 'wider ranging' activity in two sympatric shark species. Our results highlight coarse diel and seasonal differences in the movements of grey reef and silvertip sharks in the BIOT MPA, potentially providing evidence of spatial and temporal segregation in these species. As apex or mesopredators, shark species play an important role in the ecological function of reef, pelagic and coastal ecosystems (23, 27). Knowledge of how sympatric shark species interact with each other is therefore important to further determine their ecological function in coral reef ecosystems, which is currently poorly understood. Analysis of movement to investigate segregation in elasmobranchs has, to date, primarily focused on how spatial aspects of movement vary (15, 81). However, temporal aspects of movement are also important for investigating interspecific interactions. Despite potential limitations for the technique for some regions and species, this methodology has the potential for investigating movement ecology of marine species in the absence of more accurate, expensive, technologies, or where receivers only cover a singular habitat. To our knowledge, this is the first analysis of acoustic telemetry data to focus on temporal gap analysis to informing movement ecology and to infer both spatial and temporal segregation between two species. This is critical information for the management and conservation of threatened ecosystems

such as coral reef systems (81), as well as aiding enforcement efforts of MPAs to mitigate against illegal fishing activity that still threatens many protected reserves today.

Abbreviations

AIC

Akaike Information Criterion

AUC

Area Under the receiver operating characteristic Curve

BIOT

British Indian Ocean Territory

EEZ

Exclusive Economic Zone

GLMM

Generalised Linear Mixed Model

MPA

Marine Protected Area

PSAT

Pop-up Satellite Archival Tag

RDET

Relative Deviation from Expected Time

Declarations

Ethics approval and consent to participate

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

Consent for publication

Not applicable

Availability of data and material

The datasets and code for the analyses conducted during the current study are available from the corresponding author on reasonable request.

Competing interests

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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Author Contributions

MJW and DMPJ designed and implemented the research. MJW analysed the data. MJW, DMPJ, EJT and TPD wrote the manuscript. FF, ABC, TKC, RJS, DMPJ, DMT, BB and DJC collected data and contributed to revisions of the manuscript.

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Author information

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Figures

Figure 1

Acoustic array in the BIOT MPA with the locations of 93 acoustic receivers shown in red, adapted from Carlisle et al. (6). Insert shows the location of the BIOT MPA in the Indian Ocean, with the Exclusive Economic Zone (EEZ) and MPA boundary indicated by the dotted line. Gray lines show the contours of major submerged geographic features. Shallow reefs are < 20 m in depth, with deep reefs between 20 and 100 m in depth.

Figure 2

Schematic describing designation of 'restricted' and 'wider ranging' movements. Black and grey arrows indicate a movement either to and from the same point (recursion), or between two points (transition). Time between detections for recursions, and relative deviation from expected time (RDET) for transitions, are represented by length, curvature and colour of the arrow. As time and RDET increase, length and curvature increase, and colour gets lighter indicating less directed movement. Red dashed line indicates our cut-off detection gap (91 minutes for grey reef sharks and 64 minutes) for silvertip sharks for recursions and RDET (0.128 for grey reef sharks and 0.164 for silvertip sharks) for transitions.

Figure 3

a) Frequency density plots of grey reef shark (grey) and silvertip shark (blue) diel variance in percentage ‘restricted’ and ‘wider ranging’ movements, with the sun indicating day-time movements and moon indicating night-time movements. Mean percentage movements for each species are indicated by dashed lines. b) For a more detailed visualisation of seasonality, bar plots of monthly movement anomalies (%) from the annual mean of ‘wider ranging’ movements in grey reef (left) and silvertip (right) sharks. Wet (blue) and dry (orange) seasons are highlighted.

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