

Research

Spatial separation without territoriality in shark communities



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Spatial separation within predator communities can arise via territoriality but also from competitive interactions among and within species. However, linking competitive interactions to predator distribution patterns is difficult and theoretical models predict different habitat selection patterns dependent on habitat quality and how competition manifests itself. While models generally consider competitors to be either equal in ability, or for one phenotype to have a fixed advantage over the other, few studies consider that an animal may only have a competitive advantage in specific habitats. We used > 10 years of telemetry data, habitat surveys and behavioral experiments, to show spatial partitioning between and within two species of reef shark (grey reef *Carcharhinus amblyrhinchos* and blacktip reef sharks *C. melanopterus*) at an un-fished Pacific atoll. Within a species, sharks remained within small ‘sub-habitats’ with very few movements of individuals between sub-habitats, which previous models have suggested could be caused by intra-specific competition. Blacktip reef sharks were more broadly distributed across habitat types but a greater proportion used lagoon and backreef habitats, while grey reef sharks preferred forereef habitats. Grey reef sharks at a nearby atoll where blacktip reef sharks are absent, were distributed more broadly between habitat types than when both species were present. A series of individual-based models predict that habitat separation would only arise if there are competitive interactions between species that are habitat-specific, with grey reefs having a competitive advantage on the forereefs and blacktips in the lagoons and backreef. We provide compelling evidence that competition helps drive distribution patterns and spatial separation of a marine predator community, and highlight that competitive advantages may not be constant but rather dependent on habitats.

Keywords: competition, movement, telemetry

Synthesis

Animals will often segregate spatially either among or within species, often due to territoriality or competition. We show through telemetry and surveys, that two shark species at a remote atoll display some degree of spatial separation between and within the species. Competition models commonly assume these patterns arise from one species being the superior competitor, but our combination of behavioral experiments and computer simulations provides another explanation. Predators may have a competitive advantage in certain habitats only, and these habitat-specific advantages lead to rapid spatial separation without the need for territoriality, even if the competitive advantages are weak. We suggest habitat-specific competitive advantages or dominance should be considered in competition studies.



Introduction

Animals often partition space both among and within species. Spatial separation is commonly assumed to be a function of territoriality, but may also arise via memory-based foraging strategies or competitive interactions (Wakefield et al. 2013, Potts and Lewis 2014, Riotte-Lambert et al. 2015). Partitioning of space among individuals or populations is a mechanism for alleviating potential competition between or within species (Wilson 2010, Wakefield et al. 2013). However, while the importance of intra and inter-specific competition in community dynamics are recognised, linking their role to the shaping of predator distribution patterns is notoriously difficult (Connell 1961, Gurevitch et al. 1992, Wilson et al. 2014). It is also very rare for studies to simultaneously consider intra and inter-specific competitive interactions within studies of predators (Ratcliffe et al. 2014).

Central place refuging (CPR) occurs when multiple individuals share a common central place from which they make predictable movements. It is common to see spatial separation between CPR colonies, which is due to density-dependent competitive interactions among and within these colonies (Wakefield et al. 2013, Jones et al. 2015). CPR predators will select habitats within which they establish their 'refuge' and competitive interactions with other species may influence which habitats are selected based on habitat quality and individual competitive ability. Identifying competition as the driver of habitat selection is difficult as partitioning is not by itself proof of competitive interactions, and for large animals, traditional experimental manipulations (e.g. removal of a competitor) are not feasible (Connell 1961, Munday et al. 2001). A rich theoretical framework predicting distribution patterns of animals between habitats exists, based around the ideal free distribution (IFD). According to the IFD, if all individuals are equivalent in their competitive ability, have perfect knowledge of habitats, and are free to move unhindered, then individuals will distribute themselves between habitats proportionally to habitat quality (Fretwell and Lucas 1970). However, this is rarely realistic as individuals will differ in their competitive abilities through differences in dominance hierarchies, prey handling or search times (Holmgren 1995). IFD models that consider unequal competitors and a two habitat system predict two distribution patterns 1) a (semi)truncated distribution where the dominant individuals are only found in the high quality habitat, while subordinates are found in both high and low quality habitats or only low-quality habitats, or 2) a mixed distribution where dominants and subordinates are both found across both habitat types (Holmgren 1995, Tregenza et al. 1996, Smallegange and van der Meer 2009). The only study to apply these model predictions to habitat use by an apex predator, found that there was a mixed distribution with both adult and sub-adult polar bears found in both high and low quality habitats (Pilfold et al. 2014). While IFD provides a useful framework, the model assumptions are likely to be violated and in many cases an animal's phenotypic competitive advantage will not be constant in space or time, but vary by habitat (Humphries et al. 2001). For example, there are differences in the relative competitive abilities among

patches for cichlid fish (Tregenza and Thompson 1998). Habitat-specific competitive advantages make general predictions difficult, and custom made individual-based models (IBM) are necessary to more accurately link data with theory (Humphries et al. 2001).

Coral reef sharks are a group of predators that often show strong patterns of residency and some species behave as CPRs (Klimley and Nelson 1984, McKibben and Nelson 1986). Multiple individuals will use small core areas during the day but disperse over a larger area at night, before returning to or remaining within the central place at dawn (Klimley and Nelson 1984, McKibben and Nelson 1986). Reef sharks show no evidence of territoriality, but patterns of space use among and within coexisting species can vary and include high spatial overlap or strong spatial separation (Speed et al. 2011, Lea et al. 2016). There is evidence that competitive effects may be prevalent within reef shark communities, potentially leading to food-limited growth and habitat separation or even competitive exclusion (Stevens 1984, Papastamatiou et al. 2006, Lea et al. 2016). No study has yet attempted a mechanistic understanding of the role of competitive interactions in driving space use patterns both within and among co-occurring species of shark.

We use a combination of telemetry, fishing, and visual surveys to quantify space use, movements, and relative abundance of two species of reef shark (grey reef sharks *Carcharhinus amblyrhinchos*, blacktip reef sharks *C. melanopterus*) at Palmyra Atoll, a remote unfished location in the central Pacific Ocean, with shark populations likely at carrying capacity (Bradley et al. 2017). Grey and blacktip reef sharks are very similar morphologically, although grey reef sharks reach a larger size, and coloration patterns are different. The diet of both species primarily consists of small reef fishes, molluscs and crustaceans (Papastamatiou et al. 2006, Frisch et al. 2016). Both species at Palmyra and other locations behave as CPR, occupying core areas during the day and moving over a larger area at night (McKibben and Nelson 1986, Papastamatiou et al. 2009a, Speed et al. 2011, Heupel and Simpfendorfer 2015). We predict that within habitats, strong levels of intraspecific competition will lead sharks of a single species to use localized sub-habitats with little movement of individuals between sub-habitats. Generally, dominance hierarchies in sharks appear size-based, with smaller individuals 'giving-way' to larger ones during interactions (Myrberg and Gruber 1974). We hypothesize that the larger grey reef sharks will be dominant and primarily use higher quality habitats, whereas the smaller blacktip reef shark will be found in both low and high quality habitats (i.e. a semi-truncated distribution, Holmgren 1995). We then compare the distribution of grey reef sharks at Palmyra with those at Kingman Reef, a neighboring atoll (60 km northwest of Palmyra) with similar habitat types, but where blacktip reef sharks are naturally absent, providing some indication of habitat use in the absence of a competitor (Friedlander et al. 2010). Finally, to understand the drivers of spatial separation between the species, we build a series of individual-based models where we predict shark distribution patterns based on a variety of competitive interaction rules.

Methods

Study locations

Palmyra Atoll (5°54'N; 162°05'W) and Kingman Reef (6°24'N, 162°24'W) are 60 km apart, located at the northern extent of the Line Island chain, Central Pacific, and have been US National Wildlife Refuges since 2001 (Fig.1). Their remote location and protected status has kept anthropogenic activities to a minimum and both locations contain large numbers of mesopredators, including reef sharks (DeMartini et al. 2008, Friedlander et al. 2010, Bradley et al. 2017). The atolls consist of three clearly distinguishable habitat types: a) lagoons (L) that are up to 50 m deep adjacent to shallow sandflats, b) backreefs (BR) of 2–3 m depth, clear water and high coral rugosity, and c) forereefs (FR) with high coral cover, low rugosity and a steep slope leading to pelagic ecosystems. Palmyra has several islets with forested

habitats, while Kingman only has a single rubble beach that is above the waterline. Details on habitat types can be found in DeMartini et al. 2008 and Friedlander et al. 2010.

Movements and habitat use

We acoustically tagged blacktip reef sharks from 2004–2014 and grey reef sharks from 2010–2012 at Palmyra Atoll. Sharks were caught on hook and line and surgically implanted with a Vemco V16 or V9 acoustic transmitter (69 kHz). The incision was closed with a single suture and the shark was released. Shark movements were tracked by a network of over 70 underwater listening stations (VR2Ws) that were strategically positioned within all habitat types around the atoll and downloaded annually (for details see Papastamatiou et al. 2015, Weng et al. 2015). The complete set of receivers were only in place from 2010, so we analyzed data from blacktip reef sharks tagged prior to 2010 separately.

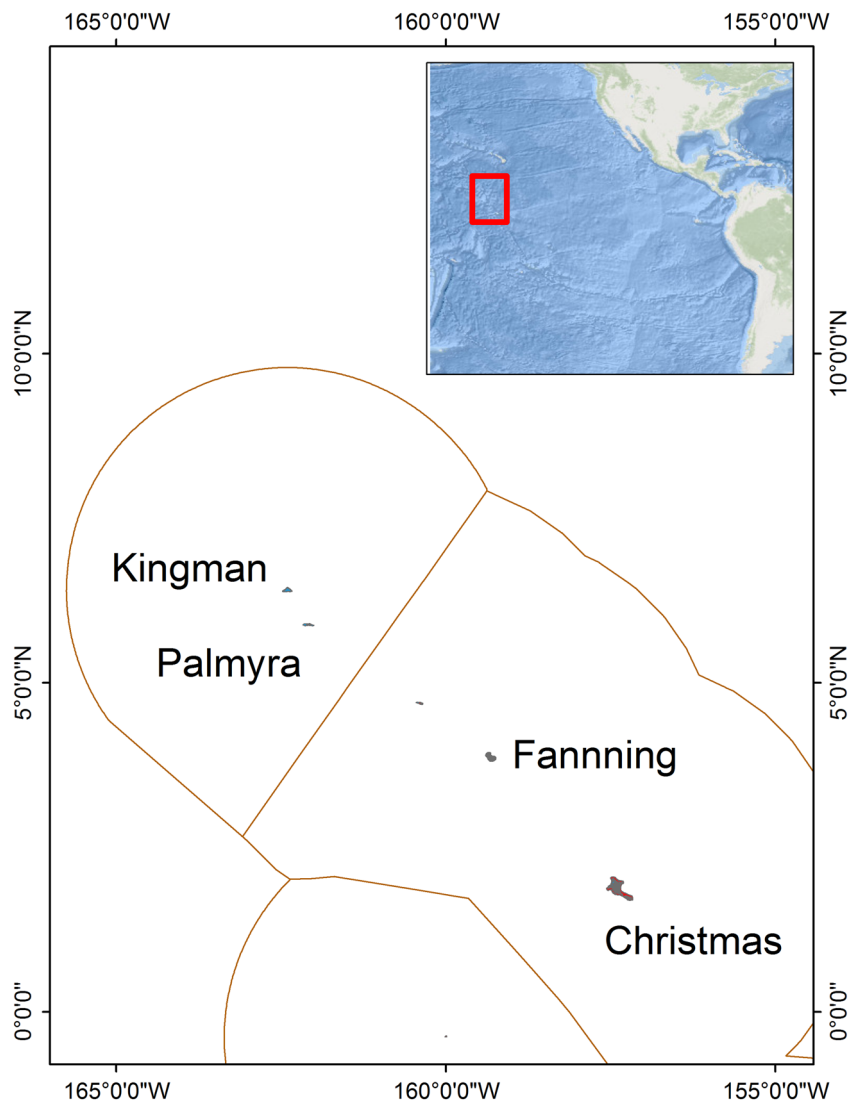


Figure 1. Map of Palmyra atoll and Kingman Reef within the Line Islands, central Pacific.

Species were tagged in the habitats where they were seen or where we could catch them, which primarily led to blacktip reef sharks being tagged in L and BR habitats and grey reef sharks within the FR.

We used telemetry to answer two questions: 1) what is the order of habitat preference and movement rates between habitats for blacktip and grey reef sharks, and 2) what is the degree of intra-specific movement rates of individuals between 'sub-habitats' within habitat types? To determine species level habitat preferences and movement among habitats, we performed spatial empirically derived Markov chain (EDMC) analyses (Stehfest et al. 2015). EDMC analysis is a form of spatial network analysis that uses a discrete time, stationary Markov chain approach to model the temporal dimension of movements including residency and transition duration (Stehfest et al. 2015). EDMC analysis requires several model assumptions (reported in Stehfest et al. 2015), which were met by the general movement of grey and blacktip reef sharks and the telemetry data used in the analysis.

To prepare data for EDMC analysis, movement data were aggregated to hourly intervals for each tagged shark in order to reduce computation time. Data were further aggregated spatially by assigning receivers into unique groups. Two types of groupings were considered: 1) grouping by habitats (FR, BR, L) for inter-specific comparisons, and 2) grouping by adjacent receiver 'sub-habitats' for intra-specific comparisons, where adjacent receivers were those with potentially overlapping ranges (~300–500 m apart) or those that commonly detected the same individual within the same hour. Sub-habitat groupings were also based on geographic locations around the atoll (e.g. western or eastern tip, northern reef, south reef etc.). These data were ultimately organized into one-hour time steps with spatial states defined by habitat grouping (FR, BR, L) or receiver sub-habitat grouping ($n=8$ for grey reefs, $n=4$ for blacktips). Each hourly time period with an associated detection at a given spatial state was assigned a 1 and those without an associated detection were assigned to an absent state 0. Movement count matrices were constructed in which each movement occurred at 1 h time steps and movement counts contained movements from each spatial state to itself (residency periods) and movements from each state to another state or into the absent state (transition periods outside of the receiver detection range, Stehfest et al. 2015). Data from both sexes were combined.

To identify preferred areas and the differences in space-use between species, we constructed movement network matrices that contained the counts of movements between states (FR, BR, L or sub-habitat groups). We then constructed stochastic transition probability matrices by dividing the number of transitions made from one state to another or itself by the total number of transitions from that state (Stehfest et al. 2015). Dominant eigenvector centralities of the transpose of the transition matrices were calculated as a representation of the probability of a shark being in a given state, regardless of starting state (Stehfest et al. 2015). The eigenvector centrality is a measure of the weighted proportion of the number

of paths in the network leading to or originating from a given node (in our case each spatial state was a node) and were calculated using the power method described by Stehfest et al. (2015). For blacktips tagged prior to 2010, we compared transition probabilities between the east and west L and BR only. EDMC analyses were performed in R (<www.r-project.org>) using code provided by Stehfest et al. (2015).

To quantify and compare vertical habitat use between the species, nine of the acoustically tagged blacktips and 13 of the grey reef sharks, were fit with V16PT sensors, which also recorded swimming depth. Finally, in order to observe competitive interactions, we fit two grey reef sharks and one blacktip reef with DVL400 video cameras that recorded at 640×480 pixels at 30 frames s^{-1} . The video cameras were programmed to turn on the day after the animal was released, to avoid the period of stress associated with tagging. Cameras turned on at 07:00–08:00 and recorded continuously until the battery ran out (5 h for the blacktip, 11 h each for the grey reef sharks). Cameras were embedded in syntactic foam floats attached to the dorsal fin via tie wraps, and a time-release mechanism caused the package to detach 3–5 days after deployment. Tags floated to the surface where an embedded VHF transmitter was used to locate and retrieve them.

Habitat distribution and dominance hierarchies

To compare the distribution and relative abundance of sharks between habitats at Palmyra and Kingman, we used diver surveys (Kingman), fishing, and baited remote underwater video (BRUV) surveys (Palmyra). Diver spatial point count (SPC) surveys were conducted by NOAA's Coral Reef Ecosystem Program at Kingman Reef between 2007–2015 (NOAA CREP 2015). For each survey, a pair of divers recorded the number, size and species of all fishes observed within a visually estimated cylinder with a 15 m diameter over a 5 min interval (NOAA CREP 2015). Surveys were conducted in L ($n=27$), BR ($n=41$), and FR ($n=86$) habitats in April 2008, 2010, 2015 and May 2012. Fishing was performed with handlines and consisted of spatially-explicit, non-extractive catch per unit effort (CPUE) data from 59 days of fishing conducted during four unique sampling periods in 2013–2014 across all habitats.

A BRUV unit consisted of a GoPro camera mounted to a frame, with a mesh bait cage in view of the camera. Bait type and amount were kept constant ($0.5 \text{ kg survey}^{-1}$) and all BRUVs were deployed for 90 min, with the first 60 min of footage analyzed for each 'survey'. BRUV surveys were conducted at 38 unique locations in June 2014, and August–September 2015, in lagoon ($n=6$), backreef ($n=8$), and forereef ($n=33$) habitats (total = 47 surveys). BRUVs were deployed during daylight hours (08:00–17:00 h), with forereef BRUVs set between 10–30 m depth, and repeat surveys of the same site were conducted > 24 h apart. Maximum number of sharks seen in a single frame (MaxN) was determined for each species within each habitat as a metric

of relative abundance to avoid double-counting individuals. Poisson generalized linear models (GLMs) were used to assess differences in shark abundance from SPC, CPUE and BRUV data across habitats (FR, BR, L). Pairwise differences between habitats were examined using general linear hypotheses and multiple comparisons for parametric models, implemented with the *multcomp* (Hothorn et al. 2008) package in R. Overall model goodness of fit was assessed using a χ^2 -test of the residual deviance ($p > 0.05$ indicates adequate model fit).

Our predictions based on the IFD with unequal competition assume that grey reef sharks are dominant over blacktips (Holmgren 1995). To test this, we used BRUV video footage collected during 2014 at Palmyra, to quantify potential dominance in interactions between blacktips and grey reef sharks. Video footage was analyzed for periods when an individual shark of one species approached the bait, but turned away if another individual of the other species approached it (1 for the dominant individual, 0 for the individual who gave way). We analyzed the full 27 h of video collected in 2014 and used a χ^2 -test to determine if the ratio of dominant interactions between the two species differed significantly from unity. Some individuals of both species would always approach the bait in almost all BRUV deployments.

Individual-based model

We developed a range of two-dimensional individual-based models to examine the impact of different interspecific competitive interactions on the extent of habitat separation in isolation from abiotic factors such as specific topography and oceanography. Generally, FR and BR habitats have higher densities of reef fishes, and therefore potential prey, than L habitats. However, defining 'habitat quality' is difficult as it may also include factors connected with how safe the habitat is to prey (i.e. the extent of shelter or refuges), and fish abundance on sandflats (where it is too shallow to survey) can be high (DeMartini et al. 2008, Friedlander et al. 2010, D. McCauley unpubl.). As a result, we did not attempt to create models detailing all interspecific interactions or aspects of habitat quality (Grimm and Railsback 2005). Instead, we used a simplified modelling environment to create increasingly complex competitive interactions between the two 'species' across the three habitat types. These models were used to examine the relative importance of different competitive interactions in potentially creating habitat separation, rather than revealing how habitat separation could emerge de novo from model rules. Models were further used to predict how manipulating the strength of these competitive interactions might affect habitat occupancy.

All models were constructed in the individual-based multi-agent modeling environment Netlogo 5.3 (Wilensky 1999). Simulated sharks moved and foraged within an environment consisting of a fixed number of prey patches (100) randomly distributed across three equally sized habitat blocks. The number of prey patches and initial number

of sharks was arbitrarily fixed to provide a balance between simplicity and tractability in model runs. Model space comprised an unbounded torus so that movement was freely possible within and between all habitats. Prey patches (e.g. reef fishes) are likely semi-predictable in space as a result of diel and tidally influenced movements (Meyer et al. 2010), so prey patches moved following a random walk with step length drawn from a normal distribution (mean = 0, SD = 2). In addition, to incorporate less predictable movements by prey species, at each time step there was a 5% chance of prey patches relocating to another random position in model space. Undiscovered prey patches were detectable by simulated sharks at short distances (0.3 unit radius). Once feeding commenced, prey patches became visible to other sharks at a four-fold greater distance, mimicking passive public information transfer including visual and chemical cues in the water, and enabling individuals from both species to identify and aggregate around prey patches. Discovered prey patches also had an increased probability of dispersing, mimicking predator avoidance and escape behavior. Dispersal movements could be either localized or larger jumps as described above, and their likelihood increased through a doubling of the acceptability threshold for movement from a random draw made at each time-step. Simulated shark lifespans were constrained by an energy term, with individuals dying if this term reached zero. All individuals began a simulation with the same quantity of energy (800 energy units), and subsequently lost one energy unit per time step while searching for prey patches. Successfully locating a prey patch resulted in a 150 unit energy gain for the shark. If individuals gained sufficient energy (individual energy score > 1000 units) then their probability of reproducing a single offspring was randomly drawn from a log-normal distribution (reflecting the low reproductive rates of these species). The energy values were set following initial trial runs to impose a degree of constraint on simulated individuals. Starting and gain values could not be overly high as this would reduce any 'need' for individuals to be reliant on successfully discovering food patches and render simulations ineffective for our purposes. Similarly, values needed to be sufficiently large to ensure model outcomes were not based on sharks needing to rapidly discover a prey patch to 'survive', and thus limited by the stochasticity of starting positions relative to prey patches. However, variation from these fixed values (± 10 or 20%) did not qualitatively affect model results.

All simulations began with 100 individual sharks in a 50:50 interspecific ratio. Individuals moved at a constant speed of 0.6 m s⁻¹ for grey reef sharks and 0.5 m s⁻¹ for blacktip reef sharks, based on data from swim speed sensors deployed on both species at Palmyra (Watanabe et al. 2015). Running simulations with both species moving at 0.5 m s⁻¹ (i.e. all individuals having an equal swimming speed) did not qualitatively affect model outputs or conclusions. All sharks initially used a naive random search pattern. However, on discovering a prey patch, simulated individuals remained there until the prey moved, at which point the

predator commenced a more restricted search pattern based on a tighter turn angle for 300 time-steps. This behavior mimicked a successful CPR predator's ability to learn about productive areas, where individuals will often remain in, or return to, an area where they had previously achieved a higher success rate (Wakefield et al 2015). Directed movements and area restricted searching also approximate observed reef shark movements, which include directed movements towards known prey patches, and more random movements among patches within the home range (Papastamatiou et al. 2009a).

The null model was made more complex by including different combinations of competitive interactions (Table 1). These considered such effects as competitive exclusion of one species at food patches by the other ('Dominance'); and competitive advantages that could be a result of one or many factors e.g. handling speed, searching efficiency ('Foraging advantage'). A 'Foraging advantage' consisted of a greater energy gain in a habitat to simulate greater foraging success (i.e. an individual may have greater familiarity with a specific environment or be better camouflaged within a particular location, etc.). Simulations were run using a range of symmetric and asymmetric advantages based on species and habitat (Table 1). Different multiples of the 'Foraging advantage' were also explored, to investigate how the strength of an advantage could affect model outcomes. 'Foraging advantage' scenarios include those where one species has a competitive advantage in all habitats, and those where each species has an advantage in specific habitats only ('Habitat specific foraging advantage' HSFA, Table 1). HSFA consisted of grey reef sharks having an advantage in the FR while blacktips had the advantage in L and BR habitats. One hundred simulations were run for each model type, and where relevant, for each value of the advantage multiplier, which remained consistent within an individual model run, and ranged from 2 to 4 (and was 1 for all habitats and species for models with no advantage). Each simulation was then run for 5000 time steps, with the number of individuals from each species in each habitat recorded. A burn-in of 1000 time-steps at the start of each simulation allowed individuals to explore their environment so that they were not completely naive, and some degree of prey patch knowledge was established. All model details in Supplementary material Appendix 1.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.qq06v> (Papastamatiou et al. 2017).

Results

Movements and habitat use

We acoustically tagged 56 blacktip reef sharks (30 F: 26 M, 95 ± 25 cm total length (TL), mean detection duration 280 ± 319 days; range 8–1400 days) and 40 grey reef sharks (26 F: 13 M: 1 unknown, 142 ± 18 cm TL, duration: 1012 ± 429 days, range 5–1545 days) at Palmyra Atoll (shark details Supplementary material Appendix 2). Blacktip reef sharks tagged in the lagoons (pre-2010) were fitted with older model transmitters, which likely had significantly shorter battery lives. Transmitter type most likely explains the lower detection durations for blacktip reef sharks, especially as those individuals tagged with the same transmitters as grey reefs (i.e. those tagged after 2010) had similar detection durations as grey reef sharks. The eigenvalue centrality ranks indicated that grey reef sharks preferred FR habitats, followed by BR and then L habitats (Fig. 2A). Grey reef sharks in the FR had a 56% chance of staying in the FR, a 2% chance of moving to the BR and < 0.1% probability of moving to the lagoon (Fig. 2A). One individual grey reef shark was resident within the L. Blacktip reef shark habitat selection followed BR > L > FR (Fig. 2B). Blacktips in the BR had a 70% chance of remaining in the BR and a 1% probability of moving to the FR. Blacktips in the lagoons showed a 49% chance of remaining there and < 0.1% probability of moving to the BR (Fig. 2B). Note however, that FR receivers were not in place pre-2010 when most lagoon blacktips were tagged. Hence, we could have missed movements between L and FR, although this is likely minimal based on satellite-tracked individuals (Papastamatiou et al. 2010). At the intra-specific level, grey reef sharks showed strong residency within sub-habitats with only a 0–8% probability of movement by sharks between sub-habitats (Fig. 3A). Similarly, blacktip reef sharks tagged in the BR post-2010 showed no movement to the L (Fig. 3B). There was a 0–1% probability of blacktips transiting between the eastern and western lagoons (Fig. 3B).

Table 1. Details on the series of IBM models run to investigate the importance of different competitive interactions between foraging reef shark species. BT blacktip reef shark, GR grey reef shark, FR forereef, BR backreef, L lagoon.

Competitive interaction	Rules
Null	sharks forage with no competitive interactions
Dominance (D)	GR dominant everywhere – no difference in competitive advantage
Foraging advantage (FA) – one species has advantage in all habitats	only one species has a foraging advantage in all habitats. BT in FR, L, BR
Habitat specific foraging advantage (HSFA)	habitat specific advantage – GR in FR, BT in L, BR
D plus HSFA for GR only	GR dominant and get FR advantage
D plus HSFA for BT only	GR dominant but BT get BR/L advantage
D plus FA for BT	GR dominant but BT gets FR/BR/L advantage
D plus HSFA	GR dominant everywhere with advantage in FR, BT with advantage in BR/L

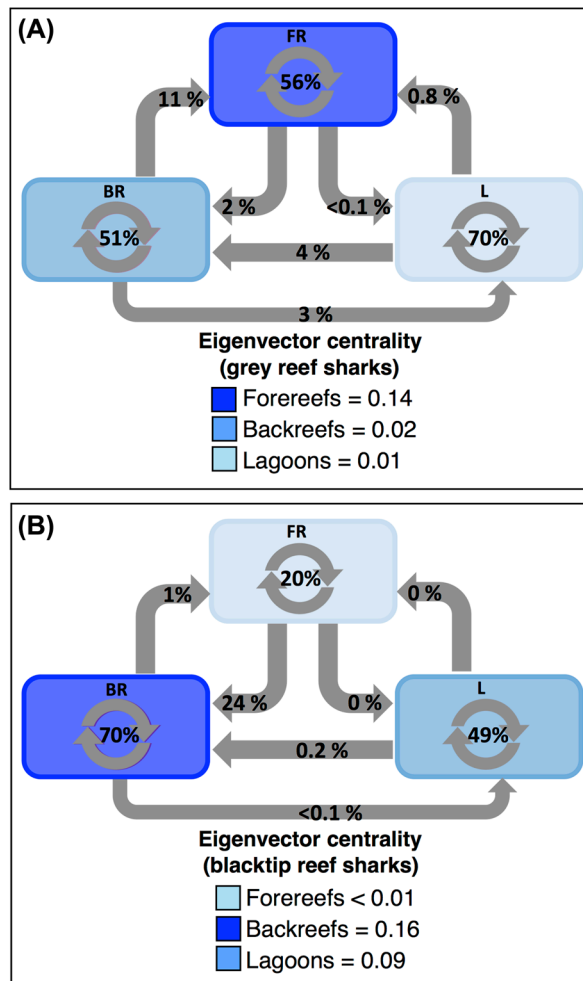


Figure 2. Habitat preferences and movement transition probabilities for reef sharks at Palmyra atoll, determined using acoustic telemetry. Habitat preference has been color coded and ranked by the relative eigenvector centrality value, for grey reef (A) and blacktip reef sharks (B). Arrows show transition probabilities of individuals moving from one habitat type to another, or remaining within a habitat (circular arrows).

Grey reef sharks swam at modal depths of 20 m (range 0–130 m), while blacktip reef sharks had a much shallower depth distribution with a modal swimming depth of 3 m (range 0–87 m, Supplementary material Appendix 3). Shark-borne camera footage from two grey reef sharks (22 h) showed both animals occupying FR or pelagic habitats. No blacktips were seen during any footage. One blacktip reef shark fitted with a camera (5 h) exclusively occupied the BR habitats; no grey reef sharks were observed in the recorded footage at any point (Papastamatiou et al. 2015).

Habitat distribution and dominance hierarchies

Fishing and BRUV surveys at Palmyra supported telemetry results for grey reef sharks. Grey reef sharks were primarily caught in FR habitat (catch per unit effort (CPUE), 7.21 ± 0.42 sharks h^{-1} [mean \pm SE]), and rarely caught in the BR (0.05 ± 0.03 sharks h^{-1}) and L (0.05 ± 0.02 sharks h^{-1}), but CPUE was significantly different in the FR and BR ($p < 0.001$), FR and L ($p < 0.001$), but not significantly different in the BR and L habitats ($p = 0.99$, Fig. 4A).

Similarly, for BRUV surveys MaxN was highest in the FR for grey reefs (1.15 ± 0.20 sharks), lower in the BR (0.38 ± 0.18 sharks), and none were observed in the L; however these differences were not statistically significant (Fig. 4B). Fishing surveys for blacktip reef sharks revealed the highest CPUE for the BR (3.47 ± 0.84 sharks h^{-1}), slightly lower CPUE for the L compared to the BR (1.50 ± 0.17 sharks h^{-1} , $p < 0.001$), and very low values in the FR compared to the BR (0.18 ± 0.06 sharks h^{-1} , $p < 0.001$, Fig. 4A). CPUE for blacktips were significantly different across all habitats, including the FR and L ($p < 0.001$). At some FR sites, blacktip reef sharks were seen during fishing surveys but were rarely caught because they were out competed by grey reef sharks for the bait (Papastamatiou unpubl.). BRUVs verified that blacktip reef sharks use shallow FR habitats (2.39 ± 0.24 sharks), less than BR (3.75 ± 0.59 sharks) and L (4.66 ± 0.33 sharks) habitats; shark relative abundance differences were significantly different between FR and L ($p = 0.05$), marginally significant between FR and BR ($p = 0.09$), and not significant between BR and L ($p = 0.77$, Fig. 4B).

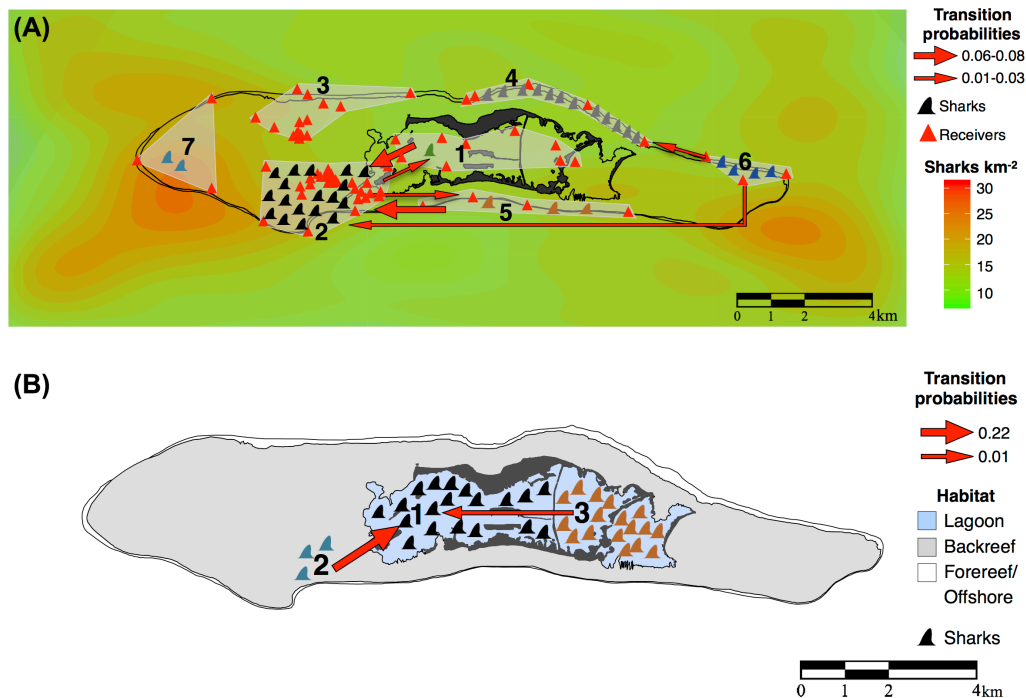


Figure 3. Movement transition probabilities of reef sharks among sub-habitats. Arrow size is relative to probability and was calculated from Markov modelling of acoustic telemetry data. Number of fins per sub-habitat represent number of tagged individuals within each sub-habitat. Data are for (A) grey reef sharks (2010–2015), and (B) blacktip reef sharks (2004–2010). Grey reef shark data is displayed relative to spatially explicit shark density contours determined from a mark–recapture study (Bradley et al. 2017). Red triangles in (A) are acoustic listening stations. The numbers in (A) represent the sub-habitat group.

Taken together, grey reef sharks are primarily found in FR, only occasionally in BR and rarely in L, while blacktip reef sharks are found in all habitat types but more so in L and BR. Diver surveys at Palmyra also reported no grey reef sharks in the L habitats (D. McCauley unpubl.). Diver surveys at Kingman Reef showed the greatest abundance of grey reef sharks on the FR (2.55 ± 0.29 sharks, $p < 0.001$ for FR-BR and FR-L, Fig. 5), but sharks were also observed in the BR and L, with no significant difference in relative abundance between those habitats (BR: 1.07 ± 0.32 , L: 0.67 ± 0.21 , $p = 0.20$, Fig. 4C). No blacktips were seen on dive surveys at Kingman. χ^2 goodness of fit tests of the residual deviance for all models reported $p > 0.05$, indicating adequate model fit.

While actual aggressive interactions were never observed between blacktip and grey reef sharks within the BRUV frame (e.g. biting), there were 16 cases where one individual approaching the bait would give way to another approaching individual. In 75% of observed instances, blacktips gave way to grey reefs and the ratio of dominant interactions between the species was different from unity ($\chi^2 = 4$, $p = 0.04$). Interspecific interactions were only seen on the FR (21 videos on BR, 33 on FR). These are likely an underestimate of dominance as often blacktips would not approach the bait if a grey reef shark was feeding (hence no interaction was seen).

Individual-based model

The IBM suggested that dominance alone created little habitat separation compared to a null model (Fig. 5A).

This was also true when a constant competitive foraging advantage was given to one species over the other in all habitats (Fig. 5B). Indeed, if one species had a complete advantage, it simply resulted in a more even distribution of that species across habitats. However, separation could readily emerge at even low levels of advantage when the competitive advantage was habitat specific ('habitat specific foraging advantage (HSFA)', Fig. 5C). Combining this HSFA with Dominance produced greater habitat separation than HSFA alone, but only when the degree of competitive advantage was small. At higher competitive ratios there was no difference in the degree of separation between HSFA and HSFA + dominance (Fig. 5D). In model simulations with HSFA, the greatest proportion of grey reef sharks were found on the FR, with much lower (and equal) proportions found in the L and BR. For blacktip reef sharks, approximately equal proportions of the population were found in L and BR habitats, while much lower proportions were found on the FR (Fig. 5C–D).

Discussion

The shark community at Palmyra Atoll conforms to a semi-truncated distribution at the habitat scale, with further reduction in niche hyper-volume overlap between the species occurring via segregation of vertical habitat and diet (i.e. the distribution is more truncated). Our combination of movement and abundance data, with predictions from

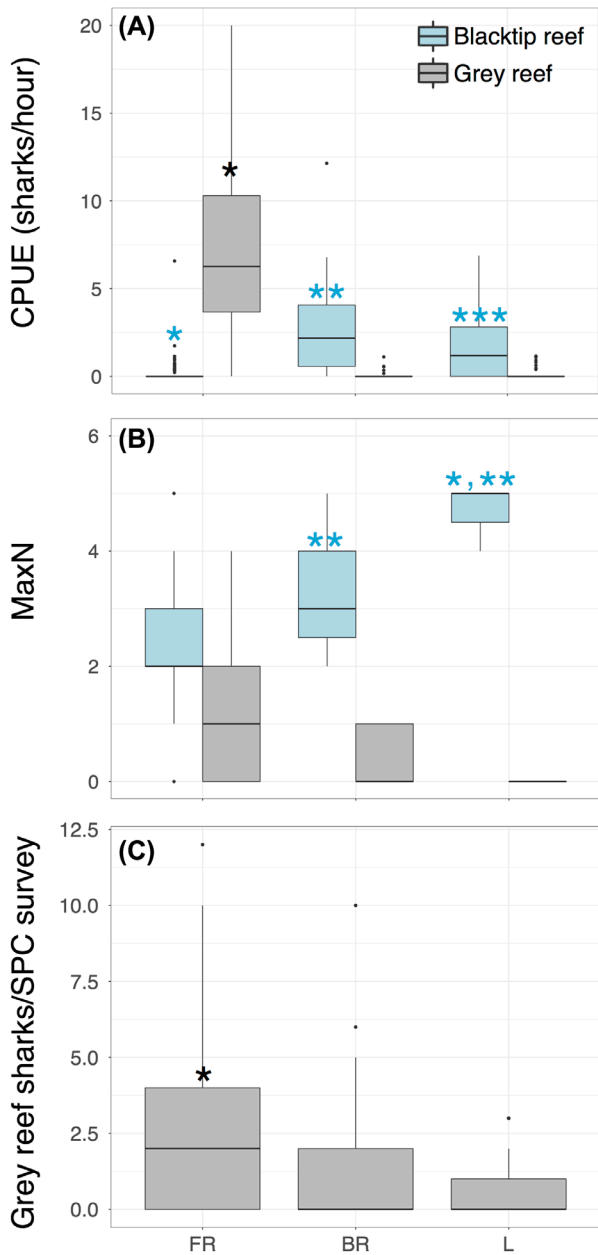


Figure 4. Reef shark distribution and relative abundance between habitats at Palmyra Atoll and Kingman Reef. (A) Catch per unit effort determined from fishing surveys at Palmyra, (B) max number of individuals recorded during BRUV surveys at Palmyra, (C) grey reef shark relative abundance at Kingman Reef determined from diver stationary point counts (data from NOAA CREP 2014). No blacktips were seen during surveys at Kingman. Columns with the same number of * are statistically the same.

individual-based models, provides strong support that inter- and inter-specific competition helps shape the distribution of reef sharks across and within habitats. Furthermore, our results suggest that competitive advantages between species are likely to be habitat specific and not caused by one species having a constant advantage over the other.

The role of intra-specific competition in generating spatial separation between colonial predators is convincingly documented (Wakefield et al. 2013), but here we demonstrate that this extends to non-colonial CPR reef sharks and potentially other species as well. As we predicted, individuals within a species separated into sub-habitat groups within habitat types. Models for colonial CPR animals suggest spatial separation between colonies arise via a combination of density-dependent competition between colonies and public information transfer between colony members (Wakefield et al. 2013). Such publicly available information does not necessarily require complex processes or decision-making; for example, it could simply involve naïve individuals following knowledgeable ones to locate food patches (Wakefield et al. 2013). There is increasing evidence that sharks can form social associations and may be able to learn from other individuals, including for grey reef sharks at Palmyra (Mourier et al. 2012, Guttridge et al. 2013, Jacoby et al. 2016).

There could be other reasons for the lack of movement among sub-habitats by individuals, such as size and sexual segregation (e.g. female sharks avoid males). Sex ratios of adult blacktip reef sharks are female dominated on the BR but equal in the L habitats (Papastamatiou et al. 2009b). Juvenile blacktip reef sharks are only seen in the L habitats and over the very shallow sandflats (Papastamatiou et al. 2009 a, b). However, size and sex would not explain the lack of movement of adults between lagoons, or lack of movements of female blacktips to the forereef. It would also not explain the lack of movement among sub-habitat groups by grey reef sharks on the forereefs, which are female biased (Bradley et al. 2017).

Sharks at Palmyra showed clear patterns of habitat separation, which match the predictions of the IFD with unequal competitors that differ in dominance (a semi-truncated distribution, Holmgren 1995). However, at Kingman, where blacktips are absent, grey reefs show some occupancy of lagoon habitats. There of course are other differences between Palmyra and Kingman, including atoll size, and lack of terrestrial habitats at Kingman (Friedlander et al. 2010). However, seeing, as grey reef sharks are dominant, why would they expand their habitats use at Kingman if they do not use similar habitats in Palmyra? Furthermore, the vertical habitat segregation between species within the forereefs leads to an overall more truncated distribution. An alternative explanation arises from our individual-based models which show that theoretically, and in a simplified ecological context, habitat-specific foraging advantages (HSFA) are more important than dominance interactions alone in producing separation between the species. Our model predicts no spatial separation even under an extreme dominance situation (without an additional HSFA) in which the inferior competitor never gains food from a superior competitor and always loses out even when in initial possession of prey. The habitat separation would also not arise simply from species differences in swim speed, or if one species had a constant com-

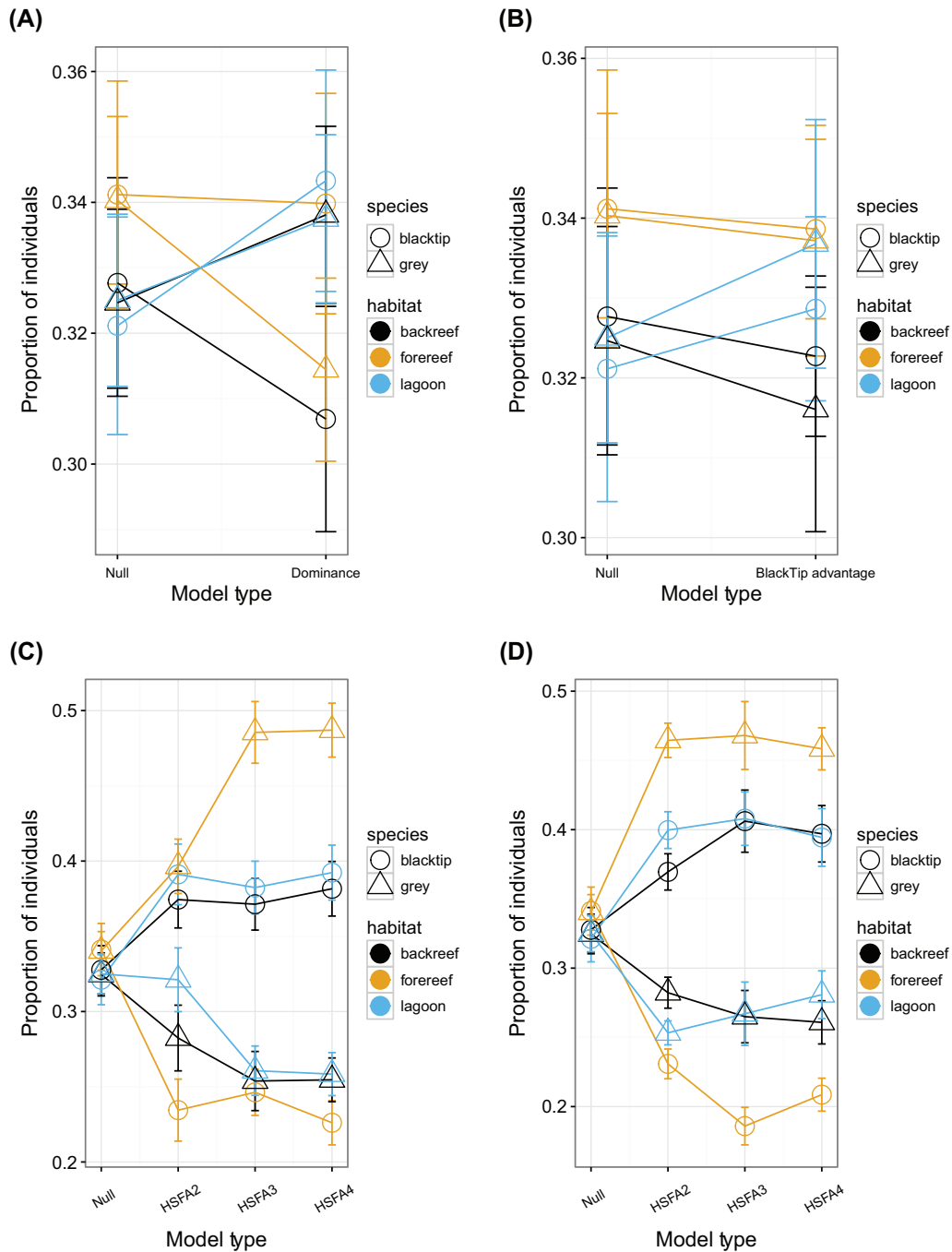


Figure 5. Individual-based model simulations predicting habitat distribution of blacktip and grey reef sharks based on different competitive rules. In all panels, values represent mean proportion by species within each habitat type with standard errors, calculated over all 100 iterations at each advantage ratio (where the latter is present in a model). In the null model, rules are identical across species, and individuals of each species occupy all habitats in approximately equal proportions. (A) grey reef sharks dominant in all habitats, (B) blacktip reef sharks have a foraging advantage (FA) in all habitats, (C) habitat specific foraging advantage (HSFA), with grey reefs having a foraging advantage in the forereef habitat and blacktips having the advantage in lagoons and backreefs, (D) HSFA and dominance of grey reef sharks. For HSFA, different ratios of the extent of the competitive advantage are given (i.e. HSFA2-HSFA4 represent increasing relative competitive advantages for each species in their habitats).

petitive advantage. Furthermore, our model predicts that spatial separation would not require any interference or an IFD, but could simply involve exploitation (e.g. competitors

consume the same prey but do not interfere with each other) as long as there is an HSFA. How competitive advantages manifest themselves is unclear, but could

include familiarity with prey types in terms of searching and handling. Another potential advantage for blacktips in lagoon/sand-flat habitats, is that their coloration makes them less conspicuous than grey reef sharks on sandflats and ledges, which are microhabitats used extensively by blacktips (Papastamatiou et al. 2009a, Papastamatiou unpubl., Supplementary material Appendix 4). We hypothesize that blacktips have a cryptic advantage in lagoon/sand-flat habitats due to their coloration patterns.

Coexistence between carnivores may involve complex mechanisms, including dietary and spatio-temporal partitioning (Vanak et al. 2013, Karanth et al. 2016). Within terrestrial ecosystems, competing predators may partition their time of activity, or share space but exhibit fine scale avoidance behaviors, resulting in complex spatio-temporal segregation (Vanak et al. 2013, Droge et al. 2016, Karanth et al. 2016). In some cases, there may be spatial separation between species, but this normally involves intra-guild predation or extreme interference (where dominant competitors kill subordinates), and predator avoidance may play a more important role than alleviating competition in driving spatial separation (Droge et al. 2016, Karanth et al. 2016). For example, wild dogs avoid areas where lions and hyenas are found (both of which are known to kill wild dogs) but share space with cheetahs, which they also compete with (Droge et al. 2016). Overall, spatial separation between competing terrestrial predators does not appear to be common unless there is also intra-guild predation or strong interference (Neale and Sacks 2001, Droge et al. 2016, Mueller et al. 2016, Gutiérrez-González and López-González 2017). Our simple model predicts that one competitor being dominant, or having a competitive advantage in all habitats will not lead to spatial separation, which could explain why spatial separation is rare (without territoriality or intra-guild predation).

In marine ecosystems, clear patterns of spatial separation between competing predators are common, including for teleosts, seabirds and marine mammals (Wilson 2010, Ratcliffe et al. 2014, Jones et al. 2015, Matley et al. 2016). In cases where spatial overlap occurs, niche-hyper-volume partitioning may arise via individuals foraging at different depths or consuming different prey (e.g. penguins, Wilson 2010, Ratcliffe et al. 2014). Similarly, in the one habitat where grey and blacktip reef sharks overlap (the forereef), sharks differ in their vertical habitat use (grey reef sharks use deeper habitats), time of maximum activity (Papastamatiou et al. 2015, unpubl.), and diet (McCauley et al. 2012). There is also likely to be greater use of pelagic habitats by grey reef sharks (McCauley et al. 2012), a habitat where we could not track individuals. Within teleost fishes, both horizontal and vertical separation between sympatric species can occur (Matley et al. 2016). One of the few studies that also assessed behavioral interactions, found that there was high spatial overlap between two species of snapper, where one species appeared to have a constant foraging advantage over the other (Davis et al. 2015). Again, the role or presence of HSFAs in these studies was not determined.

Our combination of methods provides a first step in elucidating the mechanisms behind spatial separation within shark communities. Without the ability to experimentally remove a competing species and observe how distribution patterns change, we can only assess mechanisms by comparing observations with predictions from simulations and with locations where one competitor is absent. There are of course caveats, primarily that we do not know how shark foraging success actually varies by habitat type or species prey preferences. While we assumed no difference in habitat quality in our IBM, this is unlikely the case and habitat quality will vary based on prey distribution and habitat characteristics (e.g. refuge for prey). Clearly, grey reef sharks are more abundant on the FR habitats, regardless of the presence/absence of blacktip reef sharks. Input of habitat quality may change IBM predictions to improve comparisons with empirical data. We were also not able to tag many blacktips on the FR due to their absence or because they were outcompeted for bait by grey reefs. BRUV surveys clearly confirm their presence on the shallow FR but it is unclear whether these are FR resident individuals, or if they represent very brief excursions to the FR by some of the large number of BR resident individuals.

Understanding the influence of competitive effects on predator distributions is challenging, but we provide compelling evidence that habitat-specific competitive advantages are helping to drive spatial separation within and between shark species. Being able to predict how the presence of one species may influence the distribution of the other also has important conservation implications. Reef sharks at atolls are often vulnerable to overexploitation from fishing pressure, which may impact sympatric species differentially (Graham et al. 2010). We would predict that removal of one shark species would cause some expansion of the other into different habitats, and potentially lead to an expansion of dietary niche width despite the current dietary partitioning (McCauley et al. 2012). Therefore, we caution against assuming that dietary partitioning between sympatric predators implies a lack of functional redundancy at the ecosystem level, as removal of one species may cause the other to expand into its vacant niche space. Finally, we can now include non-colonial CPRs within the marine environment to the growing list of animals that separate spatially without requiring territoriality.

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References

- Bradley, D. et al. 2017. Resetting predator baselines in coral reef ecosystems. – *Sci. Rep.* 7: 43131.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. – *Ecology* 42: 710–723.
- NOAA CREP 2015. Coral Reef Ecosystem Program; Pacific Islands Fisheries Science Center 2014. National Coral Reef Monitoring Program: stratified random surveys (StRS) of reef fish, including benthic estimate data of the US Pacific Reefs since 2007. – NOAA National Centers for Environmental Information. Unpublished dataset. <<https://inport.nmfs.noaa.gov/inport/item/24447>>.
- Davis, W. T. et al. 2015. Spatial and dietary overlap creates potential for competition between red snapper (*Lutjanus campechanus*) and Vermilion snapper (*Rhomboplites aurorubens*). – *PLoS One* 10: e0144051.
- DeMartini, E. E. et al. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. – *Mar. Ecol. Prog. Ser.* 365: 199–215.
- Droge, E. et al. 2016. Spatial and temporal avoidance of risk within a large carnivore guild. – *Ecol. Evol.* 7: 189–199.
- Fretwell, S. D. and Lucas, H. L. Jr. 1970. On territorial behavior and other factors influencing habitat distribution. – *Acta Biotheor.* 14: 16–36.
- Friedlander, A. M. et al. 2010. Spatial patterns of the structure of reef fish assemblages at a pristine atoll in the central Pacific. – *Mar. Ecol. Prog. Ser.* 410: 219–231.
- Frisch, A. J. et al. 2016. Reassessing the trophic role of reef sharks as apex predators on coral reefs. – *Coral Reefs* 35: 459–472.
- Graham, N. A. J. et al. 2010. Reef shark decline in remote atolls highlight the need for multi-faceted conservation action. – *Aquat. Conserv. Mar. Freshwater Ecol.* 20: 543–548.
- Grimm, V. and Railsback, S. F. 2005. Individual-based modeling and ecology. – Princeton Univ. Press.
- Gurevitch, J. et al. 1992. A meta-analysis of competition in field experiments. – *Am. Nat.* 140: 539–572.
- Gutiérrez-González, C. E. and López-González, C. A. 2017. Jaguar interactions with pumas and prey at the northern edge of jaguars' range. – *PeerJ*. 2886.
- Guttridge, T. L. et al. 2013. Social learning in juvenile lemon sharks, *Negaprion brevirostris*. – *Anim. Cogn.* 16: 55–64.
- Heupel, M. R. and Simpfendorfer, C. A. 2015. Long-term movement patterns of a coral reef predator. – *Coral Reefs* 34: 679–691.
- Holmgren, N. 1995. The ideal free distribution of unequal competitors: predictions from a behavior-based functional response. – *J. Anim. Ecol.* 64: 197–212.
- Hothorn, T. et al. 2008. Simultaneous inference in general parametric models. – *Biomet. J.* 50: 346–363.
- Humphries, S. et al. 2001. Unequal competitor ideal free distributions: predictions for differential effects of interference between habitats. – *J. Anim. Ecol.* 70: 1062–1069.
- Jacoby, D. M. et al. 2016. Inferring animal social networks and leadership: applications for passive monitoring arrays. – *J. R. Soc. Interface* 13: 20160676.
- Jones, E. L. et al. 2015. Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. – *Mar. Ecol. Prog. Ser.* 534: 235–249.
- Karanth, K. U. et al. 2016. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. – *Proc. R. Soc. B.* 284: 20161860.
- Klimley, A. P. and Nelson, D. R. 1984. Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. – *Behav. Ecol. Sociol.* 15: 45–54.
- Lea, J. S. E. et al. 2016. Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. – *Proc. R. Soc. B* 283: 20160717.
- Matley, J. K. et al. 2016. Contrasting patterns of vertical and horizontal space use of two exploited and sympatric coral reef fish. – *Mar. Biol.* 163: 253–265.
- McCauley, D. J. et al. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. – *Ecol. Appl.* 22: 1711–1717.
- McKibben, J. N. and Nelson, D. R. 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. – *Bull. Mar. Sci.* 38: 89–110.
- Meyer, C. G. et al. 2010. Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. – *Mar. Biol.* 157: 1499–1511.
- Mourier, J. et al. 2012. Evidence of social communities in a spatially structured network of a free-ranging shark species. – *Anim. Behav.* 83: 389–401.
- Mueller, A. K. et al. 2016. Intraguild predation leads to cascading effects on habitat choice, behavior and reproductive performance. – *J. Anim. Ecol.* 85: 774–784.
- Munday, P. L. et al. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. – *Ecology* 82: 2177–2189.
- Myrberg A. A. and Gruber, S. H. 1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. – *Copeia* 2: 358–374.
- Neale, J. C. C. and Sacks, B. N. 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. – *Oikos* 94: 236–249.
- Papastamatiou, Y. P. et al. 2006. Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. – *Mar. Ecol. Prog. Ser.* 320: 239–251.
- Papastamatiou, Y. P. et al. 2009a. Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. – *Ecology* 90: 996–1008.
- Papastamatiou, Y. P. et al. 2009b. Distribution, size frequency and sex ratios of blacktip reef sharks, *Carcharhinus melanopterus* at Palmyra Atoll: a predator-dominated ecosystem. – *J. Fish Biol.* 75: 647–654.
- Papastamatiou, Y. P. et al. 2010. Long-term movement patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll. – *J. Exp. Mar. Biol. Ecol.* 386: 94–102.
- Papastamatiou, Y. P. et al. 2015. Drivers of daily routines in an ectothermic marine predator: hunt warm rest warmer? – *PLoS One* 10: e0127807.
- Papastamatiou, Y. P. et al. 2017. Data from: Spatial separation without territoriality in shark communities. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.qqo6v>>.
- Pilfold, N. W. et al. 2014. Influence of intraspecific competition on the distribution of a wide-ranging, non-territorial carnivore. – *Global Ecol. Biogeogr.* 23: 425–435.

- Potts, J. R. and Lewis, M. A. 2014. How do animal territories form and change? Lessons from 20 years of mechanistic modelling. – Proc. R. Soc. B 281: 20140231.
- Ratcliffe, N. et al. 2014. Love thy neighbor or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. – J. Biogeogr. 41: 1183–1192.
- Riotte-Lambert, L. et al. 2015. How memory-based movement leads to non-territorial spatial segregation. – Am. Nat. 185: E103–E116.
- Smallegange, I. M. and van der Meer, J. 2009. The distribution of unequal predators across food patches is not necessarily (semi) truncated. – Behav. Ecol. 20: 525–534.
- Speed, C. W. et al. 2011. Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. – Mar. Ecol. Prog. Ser. 429: 261–275.
- Stehfest, K. M. et al. 2015. Markov models and network analysis reveal sex-specific differences in the space-use of a coastal apex predator. – Oikos 124: 307–318.
- Stevens, J. D. 1984. Life history and ecology of sharks at Aldabra Atoll, Indian Ocean. – Proc R. Soc. B 222: 79–106.
- Tregenza, T. and Thompson, D. J. 1998. Unequal competitor ideal free distribution in fish? – Evol. Ecol. 12: 655–666.
- Tregenza, T. et al. 1996. Interference and the ideal free distribution: models and tests. – Behav. Ecol. 7: 379–386.
- Vanak, A. T. et al. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. – Ecology 94: 2619–2631.
- Wakefield, E. D. et al. 2013. Space partitioning without territoriality in gannets. – Science 341: 68–70.
- Wakefield, E. D. et al. 2015. Long-term individual foraging site fidelity—why some gannets don't change their spots. – Ecology 96: 3058–3074.
- Watanabe, Y. Y. et al. 2015. Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. – Proc. Natl Acad. Sci. USA 112: 6104–6109.
- Weng, K. C. et al. 2015. Umbrella species in marine systems: using the endangered wrasse to conserve coral reefs. – Endang. Spec. Res. 27: 251–263.
- Wilensky, U. 1999. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL. <<http://ccl.northwestern.edu/netlogo/>>.
- Wilson, R. P. 2010. Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. – Funct. Ecol. 24: 646–657.
- Wilson, R. P. et al. 2014. Options for modulating intra-specific competition in colonial pinnipeds: the case of harbor seals (*Phoca vitulina*) in the Wadden Sea. – PeerJ. 3: e957.

Supplementary material (available online as Appendix oik-04289 at <www.oikosjournal.org/appendix/oik-04289>). Appendix 1–4.