

Telemetry reveals spatial separation of co-occurring reef sharks

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ABSTRACT: The ability to understand the functioning of ecosystems requires an understanding of the role individual or groups of species play within that environment. Defining ecological roles is challenging in complex ecosystems such as coral reefs. While it is well known that multiple reef-associated shark species coexist on a single reef, their patterns of space use and interactions have been difficult to define. Here we used acoustic telemetry data to analyse activity space, depth use and spatial networks to examine the interplay of these species relative to their roles in coral reef ecosystems. Integration of multiple analyses revealed that species with similar sizes and similar diets displayed clear spatial segregation, both between habitats and depth. This distribution is likely to reduce competition for prey among these species. In contrast, species that are dietary generalists or that have unique diets moved more broadly and overlapped with all other species. These results suggest competition for prey may be a driving factor in the distribution and space use of reef-associated sharks, revealing complex, interdependent functional roles within these systems. Results of this analysis demonstrate the advanced information that can be obtained through application of multiple methods and directed, simultaneous study of multiple species.

KEY WORDS: Acoustic tracking · *Carcharhinus* · *Galeocerdo* · *Triaenodon* · *Hemigaleus* · Network analysis · Kernel utilisation distribution · IMOS Animal Tracking Facility

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INTRODUCTION

The ecological roles of sharks are of considerable interest for science, conservation and management of coral reef ecosystems. Several recent studies have explored and categorised the roles of reef sharks based on currently available data (e.g. Heupel et al. 2014, Frisch et al. 2016, Roff et al. 2016). The conclusion of each of these studies was that the roles of sharks vary within reef ecosystems. For example, Heupel et al. (2014) suggested that medium-bodied species such as grey reef *Carcharhinus amblyrhynchos*, blacktip reef *C. melanopterus* and whitetip reef *Triaenodon obesus* sharks function as mesopredators within coral-reef ecosystems, while larger-bodied species such as bull *C. leucas*, tiger *Galeocerdo cuvier* and

hammerhead *Sphyrna* spp. sharks play the role of top predator. The model proposed by Heupel et al. (2014) was based in part on the size of these species, but also on their diet and influence on behaviour of prey species. Subsequent research by Frisch et al. (2016) reinforced this model by indicating that the trophic level of medium-bodied reef sharks (e.g. *C. amblyrhynchos*, *C. melanopterus*, *T. obesus*) is similar to that of large predatory fishes such as groupers and snappers. These insights into the functional role of reef sharks have led to new questions about species interactions and resource partitioning.

Interactions among reef-associated sharks are intrinsically linked with distribution, movement and behaviour patterns of individuals and species. Numerous studies have been conducted to define the

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movement patterns of medium-bodied reef sharks (e.g. Garla et al. 2006, Papastamatiou et al. 2010, Vianna et al. 2013, Espinoza et al. 2015a,b). As a result, movement patterns of some species have been well described at a reef or region scale. Movements of large species like *G. cuvier* and *C. leucas* in reef regions are also present in the literature (e.g. Meyer et al. 2010, Werry et al. 2014, Espinoza et al. 2016), but their long-range movements and use of multiple habitats have limited the applicability of these data to defining influences on reef communities. Few studies have monitored multiple species of shark within the same reef system, although there are exceptions (e.g. Speed et al. 2011, Espinoza et al. 2015b, Lea et al. 2016). Lack of simultaneous study of multiple species has hampered our understanding of inter-specific dynamics among sharks and how resources are shared among those that are potentially competing for prey. In fact, based on diet and trophic studies (e.g. Frisch et al. 2016), several common sharks possibly directly compete for resources among themselves and with large teleosts that share reef habitats.

Reef-associated species are habitat specialists indicating high reliance on reef ecosystems for survival (e.g. Roff et al. 2016). Reef habitats must therefore provide all of the required resources; but defining how species move to access and share resources in these high diversity habitats is difficult. Movement behaviours directly contribute to the role a species plays within an ecosystem. For example, species that move large distances can serve as mobile links through connectivity and energy transfer among ecosystems (Nyström & Folke 2001, Lundberg & Moberg 2003). Localised or small-scale movement patterns may also play a role in defining resource use and energy transfer within an ecosystem or community. A recent study of spatial and trophic niches of sympatric coral trout species (*Plectropomus* spp.) has revealed that 2 co-occurring species used similar amounts of reef area and had similar diets, but had different depth-use profiles (Matley et al. 2017). The authors suggested segregation by depth was a means of reducing competition between these 2 species within a single reef. These results indicate that movement and habitat use of individuals can play a role in resource partitioning within reef systems.

Given recent exploration of the role of reef sharks and growing evidence

that medium-bodied sharks serve as mesopredators, we examined the movement and habitat-use patterns of multiple shark species tracked simultaneously using passive acoustic monitoring. Movement and behaviour patterns were examined using activity space and network analysis metrics to define species-specific patterns. Individual movements were represented as a network, with acoustic receivers functioning as nodes and movement of an individual between receivers as edges (Jacoby et al. 2012, Lédée et al. 2015). Activity space and network analysis were used to test the hypothesis that all reef shark species would have overlapping space use. Shark movement patterns were tested against known movement styles (e.g. Lévy-flight) to define any patterns or categories of movement that may explain or result in spatial difference among individuals and species. Outputs of movement analyses were used to refine shark ecological roles in reef communities.

MATERIALS AND METHODS

Study site and acoustic monitoring

The study area consisted of 3 offshore reefs; Heron (HR), Sykes (SR) and One Tree (OTR) reefs, located in the southern Great Barrier Reef, Queensland, Australia (Fig. 1). Reefs have similar characteristics (i.e. structure, slope and habitat), but differ in size (Heupel & Simpfendorfer 2014, Matley et al. 2015). Heron Reef is the largest at approximately 35 km², while SR and OTR are approximately 12 and 15 km², respectively. At low tide, the lagoon areas of HR and OTR are largely isolated, while SR lacks a distinct

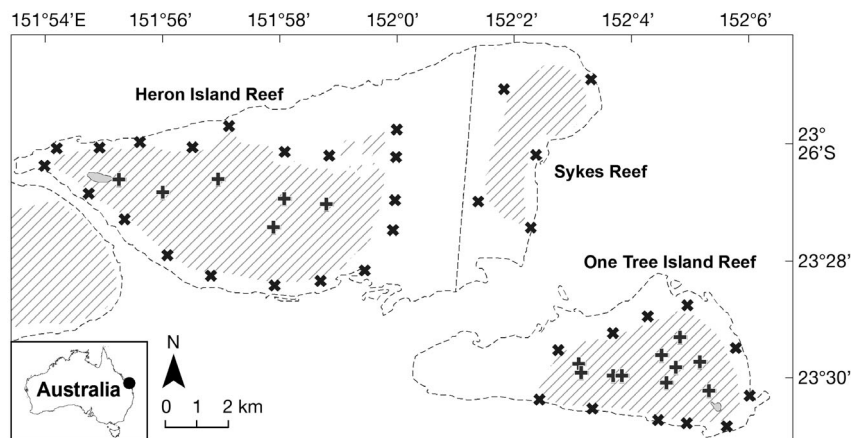


Fig. 1. Map of Heron, Sykes and One Tree Reefs. ✕ represent receiver locations around the reefs and + in lagoon areas; dashed line indicates reef perimeter and grey hatching indicates lagoon areas

lagoon. Depth within the region varies from 0 to 70 m (Beaman 2010). Passive acoustic monitoring was used to track grey reef *Carcharhinus amblyrhynchos*, blacktip reef *C. melanopterus*, whitetip reef *Triaenodon obesus*, tiger, *Galeocerdo cuvier* and Australian weasel *Hemigaleus australiensis* sharks between 2011 and 2015. Fifty-one acoustic receivers (VR2W Vemco)—25 at HR, 5 at SR and 21 at OTR—were deployed as part of the Integrated Marine Observing System Animal Tracking Facility to track shark movements (Fig. 1). For a detailed description of receiver deployment methodology see Currey et al. (2015). Acoustic receivers were deployed on average 1 to 2 km apart and had a detection range of ~270 m based on sentinel tag detections, so there was limited overlap in receiver detection ranges. Receiver data were downloaded twice per year.

Shark tagging

Individuals were captured from March 2011 to March 2013 using rod and reel or long-line; details on fishing techniques are available in Heupel & Simpfendorfer (2014). After capture, individuals were measured to the nearest cm fork length, sexed, tagged on the first dorsal fin with a Rototag for external identification and surgically fitted with an acoustic transmitter (V16P-4H, 16 × 65 mm, Vemco). Small individuals were handled on board the research vessel with all procedures occurring in holding tanks, while large individuals were restrained next to the vessel as per previous studies (e.g. Heupel & Hueter 2001, Heupel & Simpfendorfer 2015). Transmitters emitted a coded acoustic signal at 69 kHz with a pseudo-random ping rate between 50 and 100 s and an estimated battery life of 832 d. Transmitters were equipped with depth sensors with a maximum depth rating of 50 m. Individuals were retained for a maximum of 10 min during tagging.

Data analysis

Data for individual sharks were analysed using the R statistical environment (R Core Team 2014). The days each individual was detected (at least twice) were used to produce presence histories plotted relative to dates of tag release and termination. Residency and roaming indices were calculated from presence histories (e.g. Heupel & Simpfendorfer 2014). Residency index was the number of days an individual was present divided by the total days that

it could have been detected. Days of potential detection were either the life of the tag, or for those tags that were still active at the final download, the number of days from release to 10 March 2015. A roaming index was calculated from the number of receivers at which an individual was detected, divided by the total number of receivers available. This index is similar to node density in network analysis. Residency and roaming indices were plotted against each other to visualise species-specific patterns. Individuals with very low residency values (<0.05) were excluded from further analysis because the period of residency would not have been sufficient to obtain a representative roaming score. Residency and roaming indices were arcsine transformed and compared between species using MANOVA with species as the factor. Post-hoc 1-way ANOVAs were performed for each of the indices and Tukey HSD tests run to identify species that differed significantly.

Activity space

Centre-of-activity (COA) (Simpfendorfer et al. 2002) locations were estimated every 2 h and used in activity space estimation. Latitude and longitude COAs were converted to Universal Transverse Mercator projection to standardise units to metres. Two-dimensional horizontal kernel utilisation distributions (KUD) were calculated for each individual for each calendar month it was detected at more than 10 unique locations. Core (50 %) and extent (95 %) KUD values were calculated using the 'adehabitatHR' package in R (Calenge 2006) to represent the monthly activity space of individuals. Activity space values were natural logtransformed before analysis to normalise the data. Differences in 50 and 95 % KUD activity space between species were examined using a generalised linear mixed effects model with individual as a random factor. The model included species, calendar month, the interaction between species and month and fork length. Predictor variables were tested for collinearity using a Spearman's rank correlation matrix to ensure none had values > 0.75 . The model was run in the R package 'nlme' (Pinheiro et al. 2012).

Depth use

Depth data from all individual detections for the 5 species was combined to provide a single data set. Receivers at which detections occurred were identified as either 'reef' or 'lagoon'. Depth data were

square root transformed before analysis to normalise the data. Depth use was compared among species using the same generalised linear mixed effects model as for activity space. Two separate models were considered. The first included all data, and the second contained only data from reef receivers (i.e. no lagoon data). The second model was used because of the constrained depth of the lagoon (maximum depth ~5 m) and so allowed direct comparison of species when a wide range of depths was available.

Network analysis

Detection data for each individual were analysed with the 'igraph' package (Csárdi & Nepusz 2006) in R. Detection data were used to create square matrices that counted presence at, and relative movements between, acoustic receivers (i.e. nodes) within the study area. A 5 min interval was used to filter detections at the same receiver. Relative movement (i.e. edge weight) was defined as the number of times an individual moved between 2 specific receivers divided by the total number of movements made by the individual within its activity space (i.e. total number of edges in the network, Jacoby et al. 2012). Square matrices were used to create directed and weighted networks which represented individual space use in the study area. Each network was tested for non-random patterns by link re-arrangement (i.e. permutation) using a bootstrap approach ($n = 10\,000$, Croft et al. 2011). Observed movements were randomly shuffled between receivers and new networks were generated using the same degree distribution as the original network. Metrics (average path length [APL], clustering coefficient and diameter, see description below) were calculated for each randomisation to compare with those from the observed network using a coefficient of variation and likelihood ratio tests (χ^2 , $p < 0.05$).

Descriptive analysis

Movement networks were assessed by calculating the number of receivers, paths, relative movements, average path length, degree, clustering coefficient and diameter for each network. A path was a route (or edge) between 2 acoustic receivers in the network. Degree measured receiver connections to assess how different sections of reef were connected (Minor & Urban 2008), whereas clustering coefficient measured local density to determine how closely connected/clustered sections of the reef were (Watts

2004). Average path length measured separation within the network to examine extent of mobility within the network (Rayfield et al. 2011), while diameter indicated network size (Urban & Keitt 2001). Differences in receivers, path and movement numbers, average path length, degree, clustering coefficient and diameter between species were examined using ANOVA. Post-hoc multiple comparisons (Tukey's HSD, $\alpha = 0.05$) were used to determine differences between species where significant differences were detected.

Network modelling

Movement networks were simplified (i.e. edge weight, direction and matrix diagonal were removed) and compared with 3 theoretical networks—circular, small-world and scale-free—with recognized properties. Movement networks were constructed to determine if observed movement was directed (non-random), showed preferential use of areas, or resembled any recognised ecological patterns. Five properties were evaluated for each individual network. First, degree and clustering coefficient were calculated for each receiver within the network. Then, APL, diameter, ratio between diameter and receiver number, and node degree distribution (i.e. skewed and power-law) were measured for each network. Skewness referred to the symmetry of the distribution with positive skewness indicating the mean was larger than the median (i.e. right-skewed), and was measured using the skewness function from the 'moments' package (Komsta & Novomestky 2015). Lastly, a Kolmogorov-Smirnov test was run to confirm if node degree distribution fitted a power-law distribution; $p < 0.05$ indicated the node degree distribution did not fit a power-law distribution.

All theoretical networks were created using the same number of receivers, paths and/or density as the simplified movement network. To determine if movement of individuals was circular (i.e. swimming around the reef from one receiver to the next), a circular network was used for comparison. Circular networks included receivers that were only connected to 2 adjacent receivers where edges did not cross each other (Csárdi & Nepusz 2006). Small-world networks were generated following Watts & Strogatz (1998) and characterized as having short pathways between receivers. Lastly, a scale-free network (generated following Barabasi & Albert 1999) was examined to determine if movement was concentrated on a small part of the reef rather than the whole area.

RESULTS

During the course of the study 84 sharks were fitted with acoustic transmitters and tracked for periods of 18–832 d (Table 1). Size varied within and among species, with *C. melanopterus* and *C. amblyrhynchos* similar in size, while *T. obesus* and *H. australiensis* were slightly smaller and *G. cuvier* were larger than all others. No attempt was made to select individuals for tracking based on sex or size.

Residency and roaming indices

Residency and roaming indices were variable among and within species. However, individual species groupings could be identified in the visualisation (Fig. 2) and significant differences in residency and roaming indices between species were present (MANOVA, $F_{4,64} = 5.63$; $p < 0.001$). For residency indices, post-hoc testing showed significant differences in pair-wise comparisons for: *H. australiensis* (low residency) and *C. melanopterus* (high residency), *C. amblyrhynchos* (moderate residency) and *C. melanopterus* (high residency), and *T. obesus* (low residency) and *C. melanopterus* (high residency). A comparison of the roaming index between species showed that the index for *G. cuvier*

Table 1. Details of sharks monitored at Heron, Sykes and One Tree Reefs in the southern Great Barrier Reef region between 2011 and 2015. Ranges are given for fork length (median in parentheses) and days monitored

Species	Sample size	Fork length (mm)	Sex ratio (M:F)	Days monitored
<i>Carcharhinus melanopterus</i>	32	82–132 (117)	13:19	13–827
<i>Carcharhinus amblyrhynchos</i>	31	55–150 (126)	18:14	32–832
<i>Galeocerdo cuvier</i>	10	170–301 (202)	0:10	20–802
<i>Hemigaleus australiensis</i>	6	76–97 (94)	1:5	4–350
<i>Triaenodon obesus</i>	5	65–99 (90)	4:1	73–559

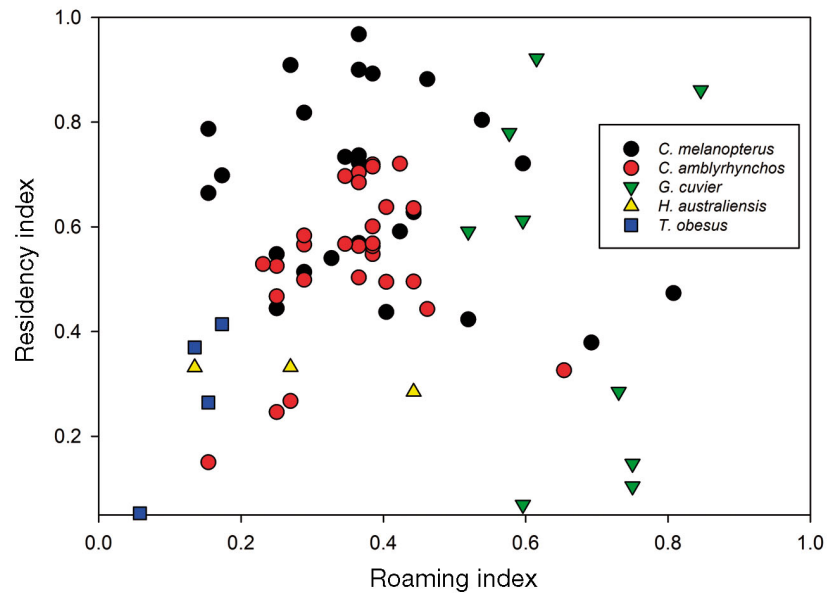


Fig. 2. Residency-roaming indices plot for 5 species of shark at Heron, Sykes and One Tree Reefs. Each symbol represents a value for an individual shark

was significantly higher than for all other species, and for *C. melanopterus* significantly higher than for *T. obesus*.

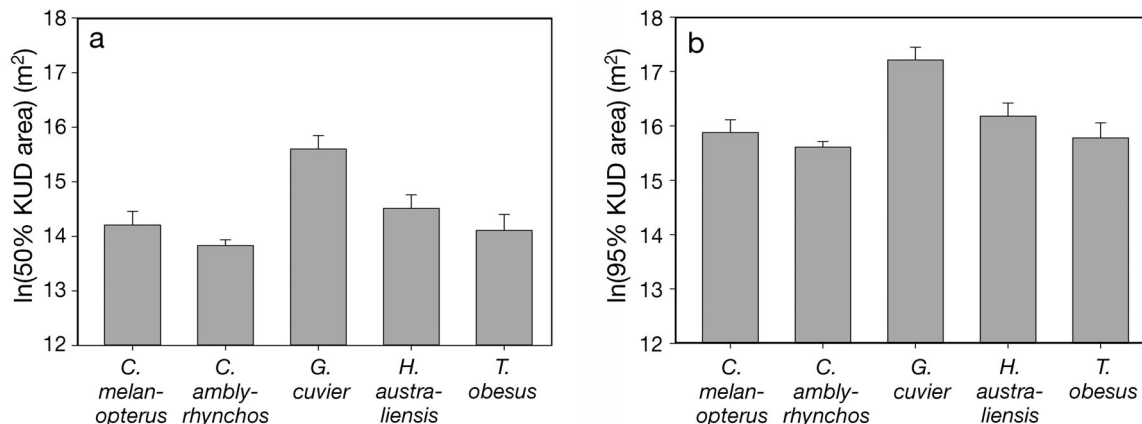


Fig. 3. Mean \pm SD (a) 50 % and (b) 95 % kernel utilisation distributions (KUDs) for 5 species of sharks at Heron, Sykes and One Tree Reefs

Space use

Activity space varied among species (Fig. 3; 50 % KUD $F_{4,62} = 27.53$, $p < 0.001$; 95 % $F_{4,62} = 24.65$, $p < 0.001$), with *G. cuvier* having larger activity spaces than the other species. There was a significant interaction between species and month (50 % KUD $F_{44,1137} = 2.35$, $p < 0.001$; 95 % $F_{44,1137} = 2.44$, $p < 0.001$). *C. melanopterus*, *G. cuvier* and *H. australiensis* exhibited seasonal patterns in activity space, while *C. amblyrhynchos* and *T. obesus* showed no seasonal trends (Fig. 4). *C. melanopterus* activity space increased in the austral winter and spring (July to November), while for *G. cuvier* and *H. australiensis* it decreased during the same period. Fork length of individuals had no significant effect on monthly 50 or 95 % activity space (50 % KUD $F_{1,62} = 0.00$, $p = 0.951$; 95 % $F_{1,62} = 0.02$, $p = 0.887$). Despite similarities in the amount of space used for several species, the location of space use varied (Fig. 5). Although sharks tended to use space near their capture location, there was no other evidence of horizontal segregation or preferential use of reef regions (i.e. all species occurred around the entire reef). Locations of activity space indicated that *C. amblyrhynchos* and *T. obesus* predominantly used reef slope habitats. In contrast, *C.*

melanopterus used mainly lagoon and reef rim regions. *H. australiensis* used a variety of habitats including rim, slope and lagoon areas. *G. cuvier* also used all available habitats, but on a much broader scale than *H. australiensis*.

Depth use

Depth use differed significantly among species for all data ($F_{4,68} = 26.12$, $p < 0.001$) and reef-only data ($F_{4,68} = 14.92$, $p < 0.001$). With all data included *C. melanopterus* and *G. cuvier* had shallow mean depths (~2.9 m) while the other 3 species had similar, but deeper means (6.2–7.8 m) (Fig. 6a). However, when only reef data were used, there was a gradation of mean depth use: *C. melanopterus* < *G. cuvier* = *C. amblyrhynchos* < *H. australiensis* < *T. obesus* (Fig. 6b). There were significant species by month interactions in both models (all data $F_{44,1925210} = 228.02$, $p < 0.001$; reef-only data $F_{44,1925210} = 143.60$, $p < 0.001$), but month to month differences for all species were small and showed no systematic seasonal trends. There was no significant effect of size in either model (all data $F_{1,68} = 2.65$, $p = 0.108$; reef-only data $F_{1,68} = 1.18$, $p = 0.281$).

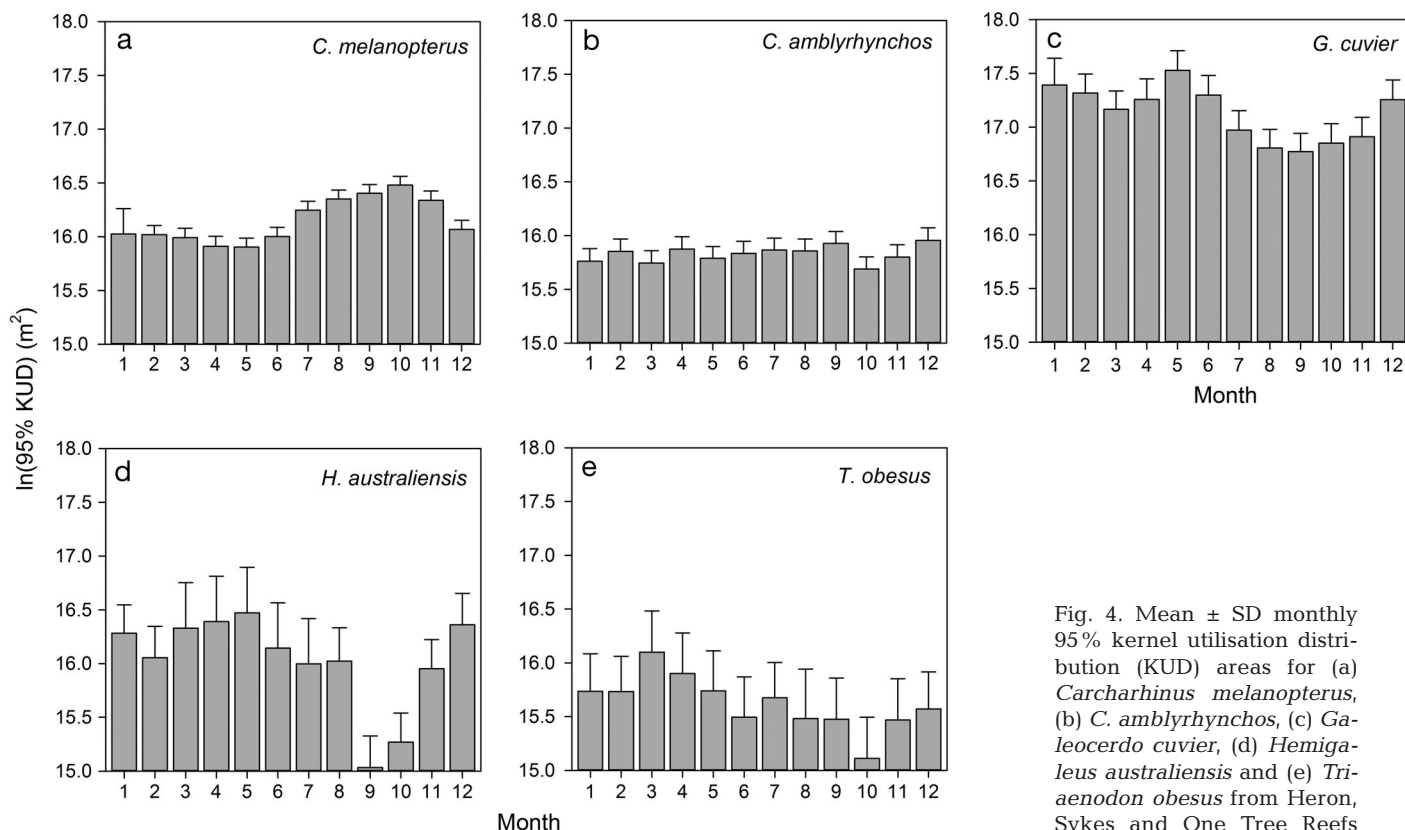
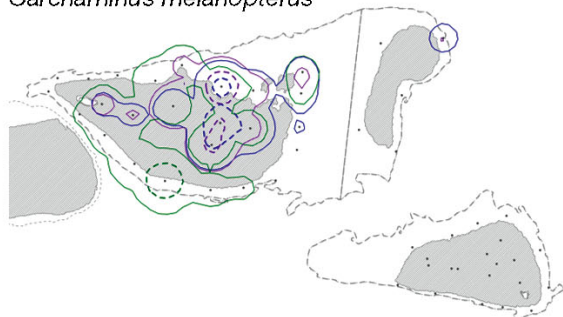
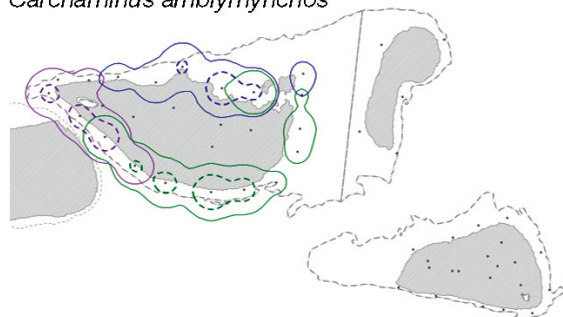
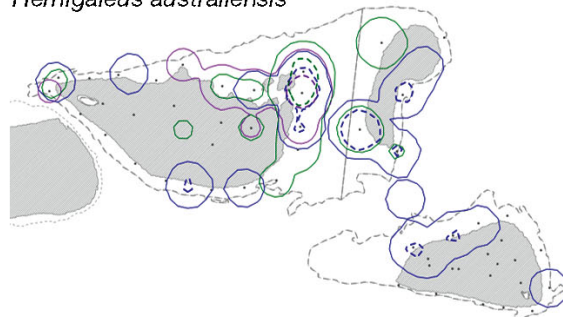
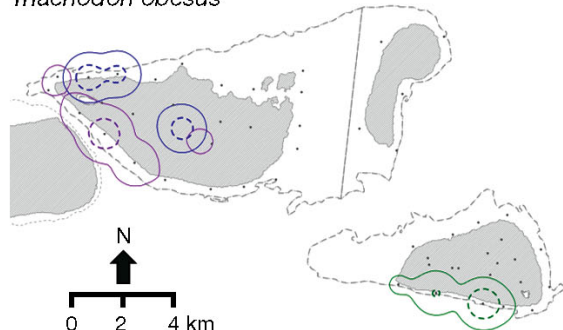


Fig. 4. Mean \pm SD monthly 95 % kernel utilisation distribution (KUD) areas for (a) *Carcharhinus melanopterus*, (b) *C. amblyrhynchos*, (c) *Galeocerdo cuvier*, (d) *Hemigaleus australiensis* and (e) *Triacodon obesus* from Heron, Sykes and One Tree Reefs

Carcharhinus melanopterus*Carcharhinus amblyrhynchos**Galeocerdo cuvier**Hemigaleus australiensis**Triaenodon obesus*

Network analysis

For 100 % of *C. melanopterus*, *G. cuvier*, *H. australiensis* and *T. obesus* networks and 97 % ($n = 30$) of *C. amblyrhynchos* networks, there was no evidence of random movement (χ^2 , $p < 0.05$), therefore these networks were included in the subsequent analysis.

Descriptive analysis

Network metrics significantly differed between species (Table 2, Fig. 7, see the Supplement at www.int-res.com/articles/suppl/m589p179_supp.pdf). *G. cuvier* used significantly more sections of reef (greater number of receivers) with significantly more connected (i.e. higher degree) and diverse routes (greater number of pathways) within their activity space than all other species (Table 3). In contrast, *T. obesus* used significantly fewer sections of reef and more unique routes compared with other species. *C. amblyrhynchos* showed significantly larger space use (diameter) with more movement, longer APLs and lower clustering coefficient than *C. melanopterus*. *H. australiensis* had significantly smaller space use and longer APL than *T. obesus* and significantly more unique routes, less clustering coefficient and less movement than *C. melanopterus*. The overall results suggest that all species moved and used reef space differently.

Network modelling

Comparison of species data to known movement networks revealed that species networks were comparable to the constructed scale-free network, with 100 % of *H. australiensis* and *T. obesus*, 87 % of *C. amblyrhynchos*, 66 % of *C. melanopterus* and 60 % of *G. cuvier* networks having a power-law degree distribution. In addition, 34 % of *C. melanopterus*, 30 % of *G. cuvier* and 13 % of *C. amblyrhynchos* had right-skewed degree distributions. Both of these distributions suggest individuals were using specific sections of a reef more than others. Species also had networks

Fig. 5. Activity spaces of individuals of 5 species of shark at Heron, Sykes and One Tree Reefs. Three individuals are represented for each species (by colour) to display the level of similarity among individuals of the same species and patterns of space use across species. Dashed lines indicate 50 % kernel utilisation distribution (KUD) and solid lines indicate 95 % KUD

Table 2. Statistical comparison of network analysis metrics between 5 reef shark species monitored at Heron, Sykes and One Tree Reefs in the southern Great Barrier Reef region. All values are significant ($\alpha = 0.05$)

	ANOVA	p
Receivers	$F_{4,69} = 26.84$	<0.001
Paths	$F_{4,72} = 27.22$	<0.001
Relative movement	$F_{4,73} = 9.53$	<0.001
Average path length	$F_{4,74} = 15.32$	<0.001
Clustering coefficient	$F_{4,65} = 6.10$	<0.001
Degree	$F_{4,74} = 26.30$	<0.001
Diameter	$F_{4,69} = 5.11$	<0.002

comparable to the constructed small-world network, with 80 % of *H. australiensis*, 75 % of *T. obesus*, 60 % of *G. cuvier* and *C. melanopterus* and 37 % of *C. amblyrhynchus* networks having higher clustering coefficient, smaller average path length than random and small networks relative to the number of receivers used by individuals (Table 3). This result suggests rapid and direct movement between sections of the reef. Finally, 50 % of *T. obesus* and no (0 %) *C. melanopterus*, *C. amblyrhynchus*, *G. cuvier* or *H. australiensis* networks had properties of circular networks. However, by visually checking *T. obesus* networks ($n = 2$), 1 individual could have crossed the reef flat (i.e. not detected elsewhere on the reef slope) and the other was detected on only 3 receivers, therefore neither individual could be classified as moving in a circular direction, indicating that reef sharks do not simply swim around the perimeter of a reef. Consequently, overall, species networks had characteristics of scale-free and small-world, and individual networks rarely fit neatly into one network type, with variation present within and among species (Fig. 8).

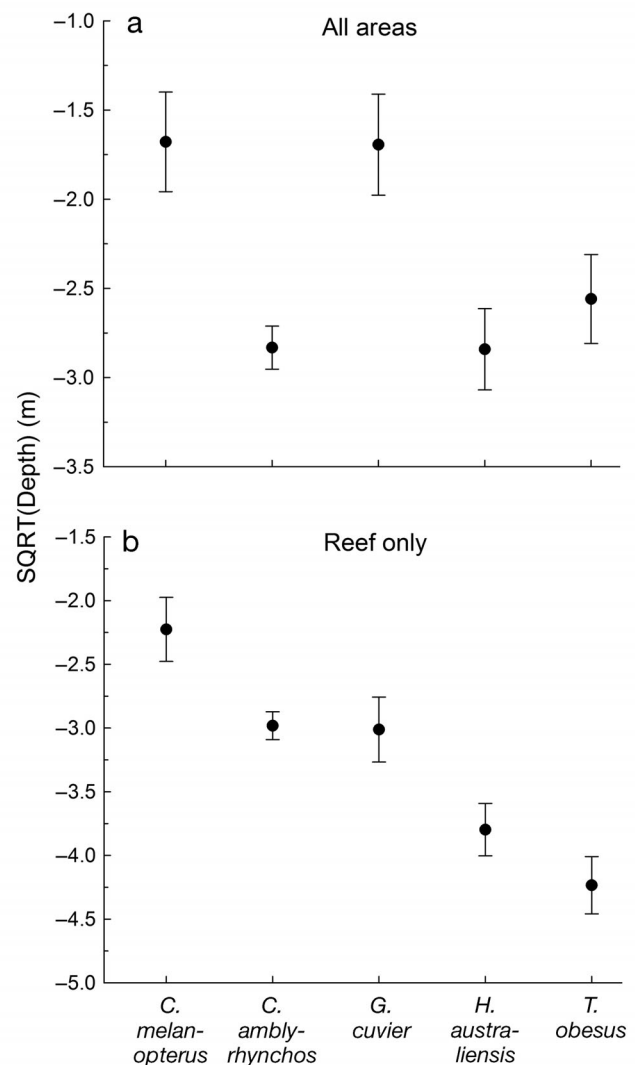
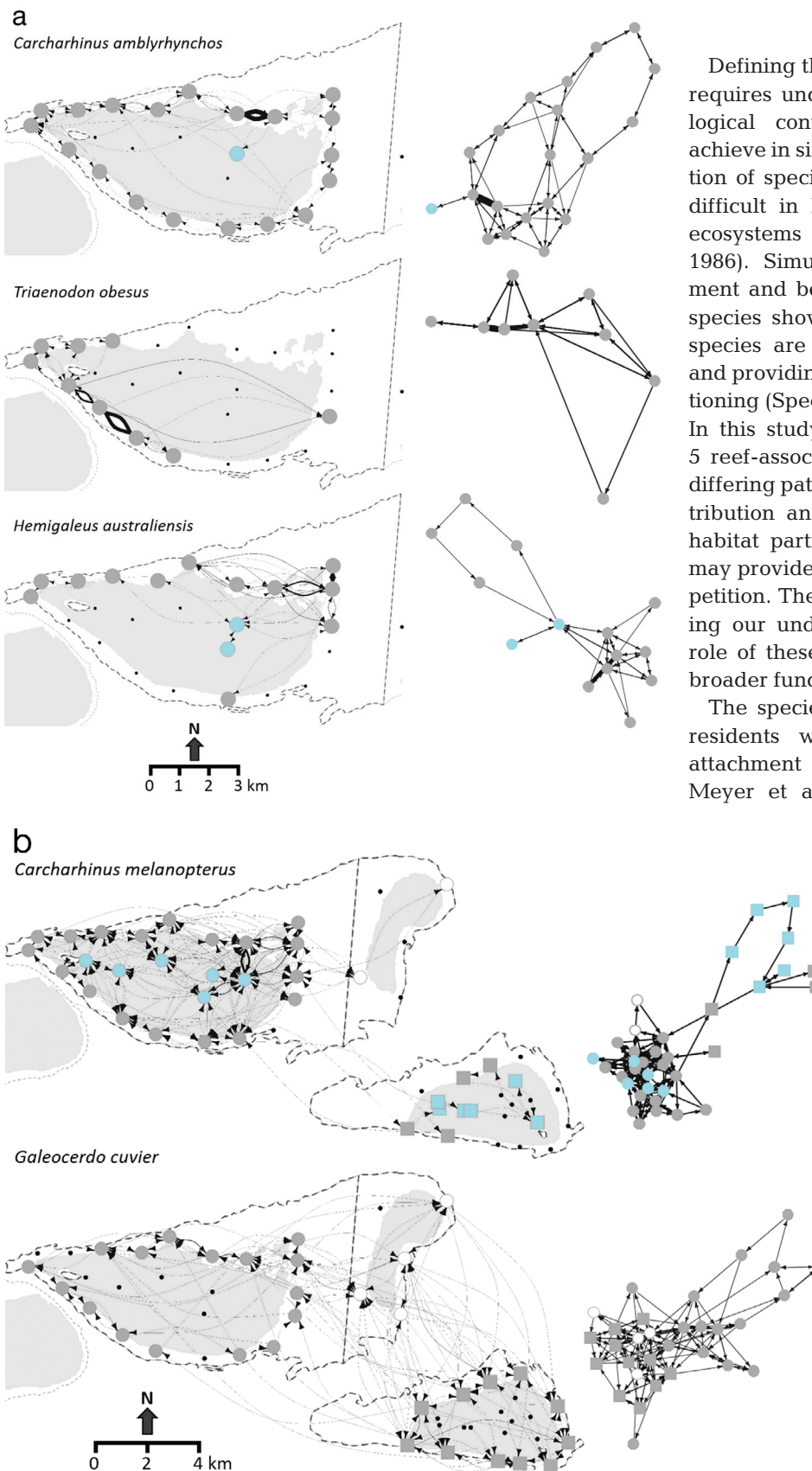


Fig. 6. Square root of mean \pm SD depth use of 5 species of shark (see Table 1) at Heron, Sykes and One Tree Reefs for (a) all data, and (b) reef-only data (i.e. no lagoon data)

Table 3. Network analysis metrics describing movement patterns of 5 reef shark species monitored at Heron, Sykes and One Tree Reefs in the southern Great Barrier Reef region

Species	Receivers (\pm SD)	Paths (\pm SD)	Relative movement (\pm SD)	Average path length (\pm SE)	Clustering coefficient (\pm SE)	Degree (\pm SE)	Diameter (\pm SE)	Skewness (\pm SE)
<i>Carcharhinus melanopterus</i>	19.09 \pm 7.61	93.06 \pm 58.01	1088.13 \pm 893.02	2.35 \pm 0.12	0.54 \pm 0.03	5.92 \pm 0.39	95.75 \pm 7.62	0.9 \pm 0.12
<i>Carcharhinus amblyrhynchus</i>	18.37 \pm 5.37	59.1 \pm 23.71	1905.93 \pm 1180.87	3.22 \pm 0.12	0.5 \pm 0.02	3.93 \pm 0.17	127.7 \pm 8.48	0.62 \pm 0.11
<i>Galeocerdo cuvier</i>	33.1 \pm 8.91	281.2 \pm 164.79	1332.6 \pm 1276.52	2.17 \pm 0.12	0.55 \pm 0.05	10.85 \pm 1.32	96.2 \pm 13.91	0.93 \pm 0.17
<i>Hemigaleus australiensis</i>	15 \pm 6.44	38.8 \pm 28.51	190.2 \pm 190.03	3 \pm 0.38	0.39 \pm 0.06	3.27 \pm 0.46	143.6 \pm 43.52	1.02 \pm 0.35
<i>Triaenodon obesus</i>	7 \pm 2.71	16.25 \pm 11.00	344.75 \pm 263.30	1.83 \pm 0.24	0.32 \pm 0.13	2.35 \pm 0.46	61.25 \pm 28.66	0.05 \pm 0.11



DISCUSSION

Defining the ecosystem role of a species requires understanding the broader ecological context, which is difficult to achieve in single-species research. Definition of species roles becomes even more difficult in highly complex and diverse ecosystems such as coral reefs (Ross 1986). Simultaneous tracking of movement and behaviour patterns of multiple species shows promise for defining how species are interacting within a habitat and providing insights into resource partitioning (Speed et al. 2011, Lea et al. 2016). In this study, the movement patterns of 5 reef-associated shark species revealed differing patterns in movement, depth distribution and space use, which indicate habitat partitioning on a reef scale that may provide a mechanism to reduce competition. These data are valuable in refining our understanding of the ecological role of these co-occurring predators and broader functioning of reef ecosystems.

The species examined are known reef residents with evidence of high site attachment (Papastamatiou et al. 2009, Meyer et al. 2010, Speed et al. 2011,

Fig. 7. Indicative networks of 5 species of shark at (a) Heron Reef for *Carcharhinus amblyrhynchos*, *Triaenodon obesus* and *Hemigaleus australiensis*; and (b) at Heron (grey circles), Sykes (white circles) and One Tree (squares) Reefs for *C. melanopterus* and *Galeocerdo cuvier*. Networks on the left are geographic networks; networks on right are shown in network space. Size of arrows indicates frequency of path use (the thicker the more frequently used the path is). Blue circles and squares represent the lagoon acoustic receivers, grey and white circles and grey squares represent reef edge acoustic receivers. Small black dots represent acoustic receivers within the study area that were not used by the individual

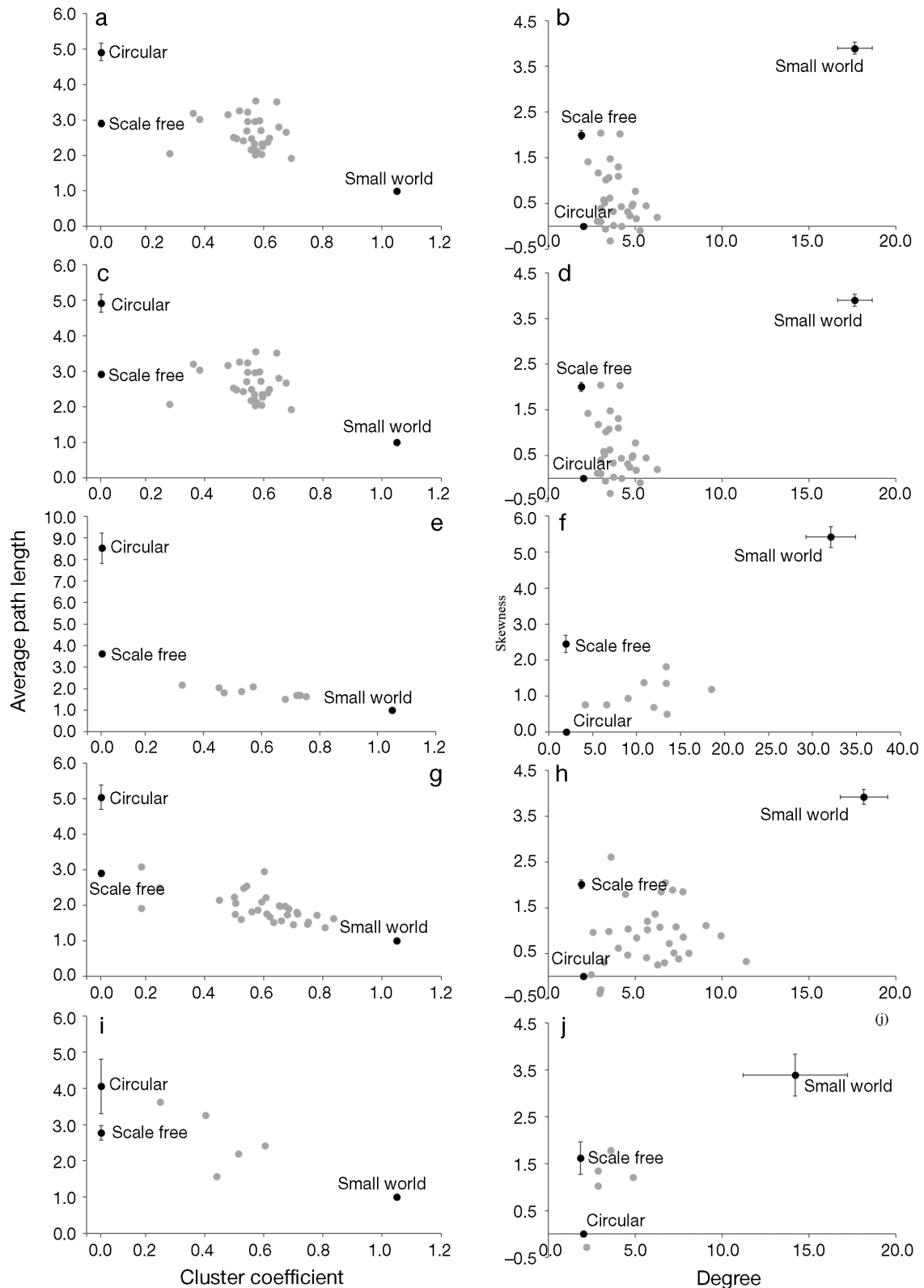


Fig. 8. (a,c,e,g,i) Small-world and (b,d,f,h,j) scale-free properties for individual networks compared with theoretical network values for (a,b) *Carcharhinus melanopterus*, (c,d) *C. amblyrhynchos*, (e,f) *Galeocerdo cuvier*, (g,h) *Hemigaleus australiensis* and (i,j) *Triaenodon obesus*. Black symbols indicate theoretical values of network types, grey dots represent values from individual sharks. Data are mean \pm SE

Espinoza et al. 2015b). Data collected here revealed some variability in residence among species, with *Carcharhinus melanopterus* and *C. amblyrhynchus* showing consistently high residency (Papastamatiou et al. 2009, 2010, Chin et al. 2013), whereas *Triaenodon obesus* and *Hemigaleus australiensis* exhibited lower residency than the other 3 species. It is likely that these results are at least in part influenced by the habitat use of these species. As a cephalopod specialist (Taylor & Bennett 2008), it is assumed *H. australiensis* spend significant amounts of time foraging in and around reef structure where prey may take refuge, thus reducing transmitter detection. In addition, *T. obesus* are known to shelter under ledges or in caves during the day (Randall 1977, Whitney et al. 2012). Therefore, the lower residency index for both these species may be explained by reduced detection efficiency due to the complex reef structure interfering with transmitter signals (Welsh et al. 2012) and thus are not necessarily indicative of movement away from the reef. Roaming indices indicated *C. melanopterus*, *C. amblyrhynchus* and *H. australiensis* were detected on similar numbers of receivers, while *T. obesus* were detected on the fewest number of receivers. Network analysis also revealed *T. obesus* had more consistent and restricted movements compared to *C. melanopterus* and *C. amblyrhynchus*. These patterns may reflect foraging and movement patterns, with *T. obesus* the only species known to remain in specific ledge habitats for extended periods (e.g. Whitney et al. 2012). In contrast, *Galeocerdo cuvier* moved widely with more unique routes and were detected on a larger number of receivers. While this is not surprising given their larger size compared to other species, some *G. cuvier* showed high residency and site attachment. Resident individuals tended to be from smaller size classes, with individuals at or near 3 m less resident, suggesting a change in movement patterns with size. This result is consistent with reports of ontogenetic behaviour changes in this species (Lowe et al. 1996, Simpfendorfer et al. 2001). Thus, residency patterns are species-specific and reflect the different behaviour patterns present in this shark assemblage.

Despite similarities in roaming index and activity space sizes, *C. amblyrhynchus*, *T. obesus* and *C. melanopterus* displayed distinct patterns in depth and habitat use. For example, *C. amblyrhynchus* and *T. obesus* were most common in reef slope habitats, consistent with previous reports for both of these species (Wetherbee et al. 1997, Whitney et al. 2012, Vianna et al. 2013, Rizzari et al. 2014, Lea et al. 2016). Speed et al. (2011) also reported high overlap in

activity space estimates for *C. amblyrhynchus* and *T. obesus*, suggesting spatial overlap and co-occurrence are common. However, examination of depth patterns in the current study revealed *T. obesus* were generally deeper than *C. amblyrhynchus*, indicating vertical separation and differences in habitat use. This result is not surprising given the typically benthic nature of *T. obesus* (Fitzpatrick et al. 2011, Whitney et al. 2012) and the more pelagic behaviour of *C. amblyrhynchus* (Wetherbee et al. 1997, Heupel et al. 2010). Furthermore, movement within activity spaces differed. Network analysis revealed that *T. obesus* had smaller networks and shorter unique routes compared to *C. amblyrhynchus*, suggesting that although both used reef slope areas, *T. obesus* movements were more restricted. In contrast, *C. melanopterus* were most commonly detected in lagoon and reef rim habitats, displaying smaller networks compared to *C. amblyrhynchus*, which had more dispersed, larger networks, indicative of repeated use of large sections of reef slope habitat. Depth-use patterns of *C. melanopterus* also revealed frequent use of shallow habitats, especially the lagoon. Previous findings suggest this is a common behavioural pattern for this species. For example, Papastamatiou et al. (2010) and Lea et al. (2016) both described restricted movements and high occupancy in lagoon habitats by this species.

The distribution and presence of *C. amblyrhynchus*, *C. melanopterus* and *T. obesus* at Heron Reef reflects patterns described by Rizzari et al. (2014) who found species richness increased in slope habitats when compared to back reef and reef flat areas. Although Rizzari et al. (2014) did not find evidence of habitat partitioning, the more detailed data provided by acoustic telemetry revealed differences in movement and distribution patterns. These results indicate that, despite similar sizes of individuals and size of activity space, the 3 species are segregating by habitat and/or depth.

H. australiensis and *G. cuvier* showed surprising similarities in behavioural pattern, despite being the smallest and largest individuals in the sample, respectively. Both species had larger activity space sizes than the other 3 species, and both showed similar habitat use (reef slope and lagoon). *G. cuvier* tended to use lagoon habitats more than *H. australiensis* and it is possible that this habitat functions as a productive feeding area for resident *G. cuvier*. *H. australiensis* showed patchy activity space use and a propensity to move between patches, which resulted in increased activity space estimates. This behaviour was also supported by network analysis, with *H. australiensis* displaying large and patchy networks with

more unique routes and long path lengths, indicating movement between reef sections. This pattern might represent movement between foraging patches where they search for cephalopod prey. Similar patch-based movements have been described for bonnethead Sharks *Sphyrna tiburo*, which feed primarily on blue crabs (Heupel et al. 2006). There was also direct evidence of overlap in space use by *G. cuvier* and *H. australiensis* in the catch data from this research. On several occasions, both species were captured on the same long line and often within 2–3 hooks of one another (M. R. Heupel unpubl. data). This indicated that both species were present in the same locations simultaneously, despite the potential for *G. cuvier* to prey on the much smaller *H. australiensis*. However, depth data indicate that *H. australiensis* tended to remain deeper than *G. cuvier*, which would result in at least some vertical separation between individuals.

The distribution and space use of *G. cuvier* and *H. australiensis* overlapped with those of the other 3 species within the study area. The co-occurrence of *H. australiensis* with *C. melanopterus*, *C. amblyrhynchos* and *T. obesus* may be facilitated based on differences in diet. If competition for prey is a driving factor in the fine-scale differences in habitat use among reef sharks, then segregation among the largely piscivorous species (*C. amblyrhynchos*, *C. melanopterus*, *T. obesus*) is expected, while spatial overlap with the cephalopod specialist *H. australiensis* can occur with little or no competition for resources. *G. cuvier*, with their larger size and gape, are capable of feeding on an array of species, including other sharks (Lowe et al. 1996, Simpfendorfer et al. 2001). As such, *G. cuvier* are also not in direct competition for the prey of the other reef shark species. It should be noted, however, that *G. cuvier* could be seen as a predator of the other species and therefore may be affecting behaviour via predation risk (Heithaus & Dill 2002, 2006). This would appear to be a reason for the other 4 species to avoid or segregate themselves from *G. cuvier*. However, the broad use of habitat and thus variable presence of *G. cuvier* in a given location would reduce interactions with other species, decreasing risk level and the need to alter habitat use over longer periods. These findings indicate complex interactions and relationships among predators and competitors within reef ecosystems, which warrant further study.

Similar to analysis by Lédée et al. (2015) and Espinoza et al. (2015b), differences in shark movement patterns were reflected in both activity space and network analyses. Network modelling supports the differing patterns of habitat use in these species.

This indicated purposeful movement, rather than circular swimming around the reef, and preferential use of sections of reef and movement paths. Species networks showed scale-free movements similar to the Lévy-flight pattern often associated with predators feeding on patchily distributed prey (Sims et al. 2012). This likely represents patrolling behaviour as individuals search the area for potential prey. In addition to clarifying paths used, network modelling indicated preferential use of some sections of reef as shown by the small-world characteristics of networks, which reflect the distribution of activity space. High, repeated use of reef sections revealed how individuals are moving to access required resources and the apparent differences among species. This integration of network analysis and traditional home range approaches provides a more comprehensive view of space use and movement paths within activity space (Jacoby et al. 2012, Mourier & Planes 2013, Espinoza et al. 2015b, Lea et al. 2016).

This study demonstrated the advanced information that can be obtained from simultaneously tracking individuals of multiple species, as well as applying multiple analytical approaches. Single-species research could not have revealed the subtle differences in habitat use among species, and traditional home range or activity space alone would not have provided enough resolution to differentiate spatial separation. Subtle differences in habitat use and variations in diet appear to be mechanisms to allow a number of reef predators to coexist within the confines of individual reefs. Definition of the interactions among species is crucial to understanding complex coral reef food webs and ecosystem function. This research indicates that subtle differences may be key to the resilience of coral reef predator communities. Future studies should explore these differences and investigate the broader predator relationships among large teleosts and medium-bodied sharks in reef ecosystems.

Tracking multiple individuals simultaneously provided a platform for comparative, multi-species study within a dynamic ecosystem. As tracking technology continues to advance and become more widely accessible, this type of research should be pursued. Modern ecology is striving to answer detailed questions about ecosystem roles and ecosystem dynamics, and multi-species telemetry approaches provide the potential to address these questions and provide answers which have so far evaded us. Concurrent, comparative species-level studies have great capacity to identify functional roles and intra-specific relationships. This type of research should be a priority in complex and threatened habitats such as coral reefs.

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