

Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management

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Abstract. Understanding the efficacy of marine protected areas (MPAs) for wide-ranging predators is essential to designing effective management and conservation approaches. The use of acoustic monitoring and network analysis can improve our understanding of the spatial ecology and functional connectivity of reef-associated species, providing a useful approach for reef-based conservation planning. This study compared and contrasted the movement and connectivity of sharks with different degrees of reef association. We examined the residency, dispersal, degree of reef connectivity, and MPA use of grey reef (*Carcharhinus amblyrhynchos*), silvertip (*C. albimarginatus*), and bull (*C. leucas*) sharks monitored in the central Great Barrier Reef (GBR). An array of 56 acoustic receivers was used to monitor shark movements on 17 semi-isolated reefs. *Carcharhinus amblyrhynchos* and *C. albimarginatus* were detected most days at or near their tagging reef. However, while *C. amblyrhynchos* spent 80% of monitoring days in the array, *C. albimarginatus* was only detected 50% of the time. Despite both species moving similar distances (<50 km), a large portion of the population of *C. albimarginatus* (71%) was detected on multiple reefs and moved more frequently between reefs and management zones than *C. amblyrhynchos*. *Carcharhinus leucas* was detected less than 20% of the time within the tagging array, and 42% of the population undertook long-range migrations to other arrays in the GBR. Networks derived for *C. leucas* were larger and more complex than those for *C. amblyrhynchos* and *C. albimarginatus*. Our findings suggest that protecting specific reefs based on prior knowledge (e.g., healthier reefs with high fish biomass) and increasing the level of protection to include nearby, closely spaced reef habitats (<20 km) may perform better for species like *C. albimarginatus* than having either a single or a network of isolated MPAs. This design would also provide protection for larger male *C. amblyrhynchos*, which tend to disperse more and use larger areas than females. For wide-ranging sharks like *C. leucas*, a combination of spatial planning and other alternative measures is critical. Our findings demonstrate that acoustic monitoring can serve as a useful platform for designing more effective MPA networks for reef predators displaying a range of movement patterns.

Key words: acoustic telemetry; acoustic telemetry in fisheries management; *Carcharhinus albimarginatus*; *Carcharhinus amblyrhynchos*; *Carcharhinus leucas*; conservation; coral reefs; Great Barrier Reef; management; marine protected areas; networks; wide-ranging predators.

INTRODUCTION

Movement of animals between habitats is a key process maintaining connectivity, and thus population persistence (Olds et al. 2012). Therefore, understanding how animals move and use specific habitats is central to conservation ecology and has direct application to spatial management planning (Fletcher et al. 2011). Ultimately, knowledge of the extent to which a species uses a particular habitat can provide important information for defining its role in the ecosystem

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(McCauley et al. 2012, Heithaus et al. 2014). Acoustic monitoring has become an increasingly popular tool to quantify the movement of wide-ranging predators, and thus could provide important information for assessing the risk of exposure to fisheries, habitat loss, and climate change (Chin et al. 2010, Espinoza et al. 2014). Given that some species of reef-associated sharks have experienced large population declines in the Caribbean (Ward-Paige et al. 2010) and Indo-Pacific regions (Graham et al. 2010, Nadon et al. 2012), acoustic monitoring data can also help develop spatial management approaches that may ensure shark conservation. However, marine protected areas (MPAs) typically consist of relatively small and isolated reserves (Gaines et al. 2010), and are often designed with little prior knowledge of a species' spatial ecology, which may underestimate the amount of time individuals spend within reserve boundaries (Chapman et al. 2005, Heupel et al. 2010, Pittman et al. 2014).

Despite limited behavioral data, numerous studies have demonstrated that reef shark abundances are generally greater inside than outside MPAs (Heupel et al. 2009, Bond et al. 2012, Ruppert et al. 2013, Espinoza et al. 2014). Although the conservation value and benefits of MPAs for sharks remain poorly understood (Heupel et al. 2010, Davidson 2012), species with strong site attachment and limited movements are expected to obtain greater protection than more mobile ones. For example, a wide range of species, including grey reef (*Carcharhinus amblyrhynchos*; Barnett et al. 2012, Heupel and Simpfendorfer 2014, Espinoza et al. 2015b), Caribbean reef (*C. perezi*; Bond et al. 2012), whitetip reef (*Triaenodon obesus*; Barnett et al. 2012), and blacktip reef (*C. melanopterus*; Papastamatiou et al. 2010) sharks are known to spend most of their time on a single reef or in relatively small areas. Therefore, targeting specific reefs (e.g., reefs with high biomass, coral cover, and size) may provide a large conservation benefit for some species. Conversely, some of these species are also capable of moving long distances across deep water (Chapman et al. 2005, Heupel et al. 2010, Chin et al. 2013). There is also growing evidence that shark dispersal is influenced by the degree of reef isolation. For example, sharks monitored on closely spaced coral reef habitats along continental shelves are known to undertake regular excursions away from their tagging reef (Heupel et al. 2010, Chin et al. 2013, Espinoza et al. 2015b), whereas at remote and isolated habitats (e.g., Palmyra Atoll in the Central Pacific, Osprey Reef in the Coral Sea, Rowley Shoals in the Indian Ocean), movement is more limited (Papastamatiou et al. 2010, Barnett et al. 2012), at least over ecological time scales (Whitney et al. 2012). This suggests that the behavior and spatial ecology of a species may not be representative across reef habitats, and thus the level of protection sharks gain from MPAs may be influenced by the degree of reef isolation.

While some species of sharks exhibit a strong association with coral reefs, others tend to use a wider range of habitats (Papastamatiou et al. 2013, Daly et al. 2014, Werry et al. 2014), potentially acting as energy links in the transfer of nutrients from one system to another (McCauley et al. 2012, Heupel et al. 2015). Coral reefs provide important ecological services to a wide range of predators, including species that are more cryptic in their reef use patterns, such as silvertip (*C. albimarginatus*; Barnett et al. 2012, Espinoza et al. 2015a), tiger (*Galeocerdo cuvier*; Papastamatiou et al. 2013, Werry et al. 2014), scalloped hammerhead (*Sphyrna lewini*; Hearn et al. 2010, Ketchum et al. 2014), and bull (*C. leucas*; Brunnschweiler and Barnett 2013) sharks. Therefore, incorporating information on habitat connectivity can improve the design and functionality of MPAs and help define the functional role of a wide range of predators in marine ecosystems.

Network analysis (NA) is emerging as a powerful ecological tool for assessing animal connectivity across landscapes/seascapes, providing a novel approach for conservation planning (Croft et al. 2011, Fletcher et al. 2011). Although NA has been used widely in landscape ecology, limited studies have examined structural connectivity on coral reefs (Tremblay et al. 2008, Kininmonth et al. 2009), and few have investigated functional connectivity of wide-ranging marine predators (Jacoby et al. 2012, Mourier et al. 2012). Network analysis examines the relationship between nodes, and a network represents all the connections (or links) between the nodes (West 2001). Additional information about the physical or environmental attributes can also be added to node and link properties. Consequently, NA can be adapted to various situations and scales to answer a wide range of ecological and behavioral questions (Stehfest et al. 2013). Applied to coral reef ecosystems, nodes can represent individual reefs, while links represent animals moving between nodes. Therefore, coral reefs represent an ideal system to examine functional connectivity of reef-associated species using NA, as well as the implications of reef-based spatial management.

In the present study, acoustic telemetry data were used to quantify movements and MPA use of reef-associated sharks (*C. amblyrhynchos*, *C. albimarginatus*, and *C. leucas*; see Plate 1) in the central Great Barrier Reef (GBR) Marine Park, Australia. This region is characterized by semi-isolated reef habitats (5–25 km apart) separated by relatively deep (40–70 m), sandy channels across 130 km (Espinoza et al. 2015b). Shark movements and residency were compared and contrasted among species. In addition, NA of individuals was conducted to (1) assess the degree of connectivity within and between coral reef habitats, and (2) examine intra- and interspecific differences in networks. A “reef removal” analysis was performed to determine the relative importance of the tagging reef to the network and examine the effect of reef isolation on shark

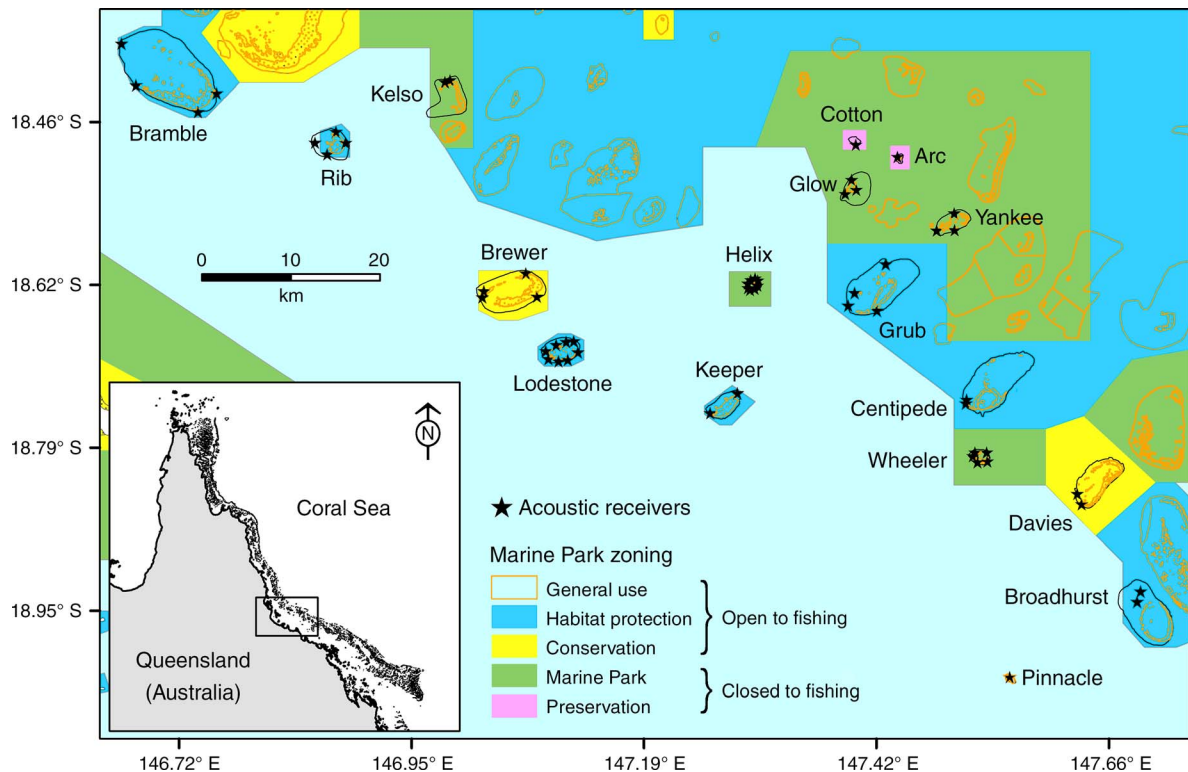


FIG. 1. Map of the study reefs showing the location of acoustic receivers used to monitor shark movements in the central Great Barrier Reef (GBR), Australia. The GBR's Marine Park zoning included (1) general use, with areas open to multiple activities, including fishing; (2) habitat protection, where line fishing and netting are allowed; (3) conservation park, where extractive activities are limited to single line fishing and netting is prohibited; (4) Marine National Park, which is closed to fishing (boating and diving are allowed); and (5) preservation, where entry is only allowed under research permit. Stars indicate locations of acoustic receivers.

movements and habitat connectivity. In more site-attached species and/or individuals, removing the tagging reef is expected to have a larger impact on network persistence than for more mobile species. Similarly, if the degree of reef isolation plays a key role in the spatial ecology of sharks, then removing reefs adjacent to the reef where a shark was released would have an effect on the network of individuals that disperse less, but would be negligible in more mobile individuals. Finally, the application of NA for marine reserve planning was investigated by quantifying the change in proportion of movements between management zones (i.e., reefs open and closed to fishing) for the full network and after each “reef removal” scenario.

METHODS

Study design

From May 2012 to October 2014, an array of 56 VR2W acoustic receivers (Vemco, Bedford, Nova Scotia, Canada) was used to monitor shark movements on a network of 17 semi-isolated coral reefs (Fig. 1). The study site was located in the midshelf region off Townsville (TSV; Queensland, Australia) in the central GBR and covered ~130 km along the GBR and an area of ~7010 km². Less than 2% of this area has been

mapped as coral reef based on spatial data layers from the GBR Marine Park Authority. Reefs are separated by relatively deep channels (40–70 m), and have similar morphologies and a well-developed reef slope (steep on the NE face; Done 1982). Acoustic receivers were deployed along reef slopes at depths between 12 and 20 m, and suspended in the water column ~1 m above the reef substrate by a subsurface buoy. Receiver data were downloaded every 4–6 months. Based on data from permanent sentinel acoustic transmitters deployed at several locations within the TSV array, detection range was estimated to vary between 150 and 350 m (M. Espinoza, *unpublished data*). Acoustic coverage for each reef was calculated as the total reef area available divided by the sum of detection range areas of the receivers deployed at each reef (Appendix A). This was based on the assumption that each receiver had a maximum detection range of 250 m. Although acoustic coverage is likely to vary at each receiver and between each reef for a number of reasons (e.g., habitat complexity, environmental noise, wind generating waves, etc.), this provided an estimate of potential acoustic coverage in the system. Acoustic coverage ranged from 2.1% to 100%, with a mean \pm SD of $27.1\% \pm 31.9\%$.

Besides the TSV array, five additional receiver arrays located in the northern (Lowe Isles [LOI]), central (Cleveland Bay [CB] and Orpheus Island [ORI]) and southern GBR (Lady Elliot Island [LEI] and Capricorn Bunker reefs, including Heron, Sykes, and One Tree Island [HI]) were used to examine broadscale movement and connectivity (Appendix B). The number of receivers varied by site: $n = 15$ (LOI), $n = 33$ (ORI), $n = 56$ (TSV), $n = 74$ (CB), $n = 50$ (HI), and $n = 6$ (LEI), representing a combined network of 234 acoustic receivers within the GBR Marine Park. Receiver arrays were deployed at various times with the earliest (Cleveland Bay) established in 2008, but all were deployed for the entire study period (2012–2014).

Sharks were captured using a variety of fishing methods, including rod and reel, drop-lines, and long-lines (see Espinoza et al. [2015b] for a description of sampling methodology). Tagging efforts for *C. amblyrhynchos* and *C. albimarginatus* were concentrated at Helix, Lodestone, and Wheeler reefs. *Carcharhinus leucas*, however, was more abundant at Lodestone, Brewer, and Rib reefs, and therefore they were tagged opportunistically over multiple trips. All captured individuals were measured to the nearest centimeter (fork length; FL), sexed, tagged with an external identification tag, and surgically implanted with a V16 acoustic transmitter (V16P-4X-R64k, 69 kHz; Vemco). Transmitters were programmed on a pseudo-random repeat rate of 50–100 s and had a battery life of ~824 d. All surgical procedures were conducted following protocols approved by James Cook University Animal Ethics (A1933) and sharks were retained for a maximum of 10 min during measuring and tagging procedures.

Residency and inter-reef movement

A shark was considered present at any given reef if two or more detections within an hour were recorded on the same day. A residency index (RI) was used to examine patterns of shark occurrence at two spatial scales: the main study site (TSV array) and the tagging reef. The RI was defined as the number of days an individual was detected within the study site or tagging reef divided by the number of days monitored (i.e., number of days from the tagging date to the last date of the study period; October 2014). Since the battery life of the transmitters lasted past the end of the study period, the number of days at liberty and days monitored were treated the same for the calculation of residency. The RI ranged from 0 to 1, where values close to 1 indicated high residency to the array or tagging reef.

A center-of-activity (COA) approach was used to calculate mean position (latitude and longitude) from hourly detections weighted by the number of detections at each receiver (Simpfendorfer et al. 2002). Position data were converted to Universal Mercator Projection (m) and minimum linear dispersal and time traveled were calculated. To examine the frequency and duration

(time traveled per distance) of shark dispersal between reefs, we filtered the database for positions that were >5.6 km apart. This allowed including only inter-reef movements rather than the movements within a reef. To quantify the degree of reef connectivity for each species, we constructed a matrix of individual movements from/to each reef. In this matrix, the total number of individuals detected each day for the entire monitoring period was combined at the reef level. We then used a modified circular plot (connectivity plot) to visualize the number of incoming and outgoing movements at the population level. Connectivity plots were implemented using the `circos.trackPlotRegion` function from the `circulize` package (Gu et al. 2014) in R v. 3.0.2 (R Development Core Team 2014).

Network analysis

Shark detection data for each receiver were combined at the reef level, and used to create an inter-reef movement matrix of each individual. The movement matrix counted the presence at and relative movements between reefs. Only detections at the same reef that were ≥ 5 min were included in the network based on previous work (Lédée et al. 2015). Relative movements were defined as the number of times individuals moved between two reefs divided by the total number of movements within its space use (i.e., total number of edges in the network; Jacoby et al. 2012). This matrix was used to create weighted directed networks for each individual that reflected the extent of space use within the array during the entire monitoring period. To determine whether shark movements exhibited non-random patterns, a link rearrangement (i.e., permutation) was performed on each network using a bootstrap approach ($n = 10,000$; Croft et al. 2011). The observed movements were randomly shuffled between reefs and new networks were generated using the same degree distribution as the original network (i.e., the procedure maintains the degree distribution of the network while randomizing the link). Network-level metrics were calculated for each random network to check against metrics from the observed network using a coefficient of variation and likelihood ratio tests (χ^2 , $P < 0.05$).

Centrality metrics were used to assess the relative importance and degree of connectivity of a reef in the network. The relative importance of a reef was determined using three centrality metrics: node strength, closeness, and eigenvector. Node strength measured the connection weight (i.e., total number of incoming/outgoing movements from a reef); reefs with high node strength had more incoming/outgoing movements than reefs with low node strength (Barrat et al. 2004). Closeness measured how central a reef's position was in network space (i.e., smallest number of links connecting reefs; geodesic distance); the lower a reef's geodesic distance, the higher the closeness (Butts 2013). The eigenvector measured how well-linked a reef was within the network; reefs with a high eigenvector had

high node strength and were connected to reefs with similarly high node strength (Bodin et al. 2011). The degree of reef connectivity was calculated using the probability of connectivity (PC) index (Saura and Pascual-Hortal 2007). The PC was defined as the probability that two animals randomly placed within coral reefs fall into reefs that are reachable from each other (interconnected) given a set of n reefs and the connections (p_{ij}) among them (Saura and Pascual-Hortal 2007)

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i \times a_j \times p_{ij}^*}{A_L^2}$$

where n was the number of monitored reefs, $a_i \times a_j$ was a measure of intra-reef connectivity (i.e., number of detections at each reef standardized by the number of receivers used), and A_L (total landscape area) was the sum of all detections in the coral reef system. Observed movement between reefs was considered as a probability of movement between reefs i and j (p_{ij}^* ; Saura and Pascual-Hortal 2007). All analyses were done in R v. 3.0.2 (R Development Core Team 2014), using Conefor Sensinode 2.2 command line (Saura and Torné 2009) and the libraries igraph and sna (Csardi and Nepusz 2006, Butts 2013).

Reef removal analysis was performed to determine the relative importance of the tagging reef and the effect of reef isolation on the network. For each individual, the tagging reef and the two closest reefs from the tagging reef were subsequently removed and new networks constructed. Only networks with >2 reefs were used in this analysis. After each scenario, new network metrics (diameter, density, and component) were calculated to determine removal effects (i.e., decrease in network centrality) using igraph in R (Csardi and Nepusz 2006, R Development Core Team 2014). Diameter measured the longest path between any pair of reefs in the network, and was an indicator of the size of the network (Urban and Keitt 2001). To account for long-range dispersal to other receiver arrays, a “distance” weight was added to each inter-reef movement in the calculation of network diameter. Movements to arrays that were far apart were assigned higher weights and ranged from 1 for TSV to 2 for CB/ORI, 3 for LOI, and 4 for HI/LEI. Network density measured route selection (ranging from 0 to 1); when all reefs were connected to all others, the network had a density of 1 (Bodin et al. 2011). Components identified clusters of reefs connected to each other, but separated from the rest of the network (i.e., where movements between two components cannot be made) and represented the level of network fragmentation (Minor and Urban 2008). The relative importance of each reef in the network (dI) was calculated as: $dI = ((M - M')/M) \times 100$, where M was the network metric before removing any reef (i.e., full network) and M' was the metric value after each removal scenario (see Pascual-Hortal and Saura 2006). High dI reefs were

considered more important in the network and removing them resulted in higher isolation. To determine the importance of a link or corridor, individual movements between pairs of reefs were summed ($A \rightarrow B + B \rightarrow A$) to obtain the weight for each link. Then, the impact of link loss on reef connectivity was examined using the PC index after each link removal in Conefor Sensinode (Saura and Torné 2009) in R (R Development Core Team 2014).

A one-way ANOVA was used to examine differences in network metrics (e.g., number of nodes or reefs, number of edges, density, and diameter) among species. Post-hoc multiple comparisons (Tukey's HSD, $\alpha = 0.05$) were used to determine which species were significantly different from each other. At the species level, general linear models (GLMs) were used to examine the influence of different factors (e.g., sex, FL, number of days detected, number of days monitored) on network metrics. Each individual tagged represented a unique observation of the network. Significant differences of factors and interactions (sex and FL) were evaluated with maximum likelihood ratio tests (χ^2 , $P < 0.05$). Models were tested for multicollinearity using the variance inflation factor (VIF) in the AED package (Zuur et al. 2009) and by examining pairwise correlation plots between predictors. General linear models were implemented using the glm function in R (R Development Core Team 2014).

MPA utilization

Acoustic arrays monitored reefs that were closed and open to fishing. To investigate the extent to which closed reefs protected shark species, we used two metrics: (1) the proportion of days individuals were detected on reefs closed to fishing; and (2) the number of movements to protected reefs for each individual (i.e., daily movement within closed reefs and/or movements from open to closed reefs). Individuals were considered present on a closed reef if two or more detections were recorded on the same day. If an individual was detected at two or more reefs on a single day, the reef with the highest frequency of detections (standardized by the number of receivers) was selected. GLMs with binomial distribution were used to examine the effects of sex and FL on shark protection. Here, shark protection was defined as the number of daily movements of each individual within/to closed reefs relative to the total number of movements, and expressed as a proportion. Since the tagging location of a shark can be a confounding factor, separate GLMs were performed for open and closed reefs for each species. Significant differences of factors and interactions (sex and FL) were evaluated with maximum likelihood ratio tests (χ^2 , $P < 0.05$). General linear models were implemented using the glm function in R (R Development Core Team 2014). The applicability of network analysis for marine reserve planning was also investigated by quantifying the change in shark

TABLE 1. Tagging information of reef-associated sharks monitored in the central Great Barrier Reef, Australia.

Species, by tagging reef	Zoning	N	Female ratio	Size range (cm)	DM	RI
<i>C. amblyrhynchos</i>						
Lodestone	open	13	0.54	72.2–140	430–825	0.83 ± 0.06
Helix	closed	8	0.37	59–139	597–825	0.59 ± 0.12
Wheeler	closed	7	0.71	97–142	535–537	0.82 ± 0.10
Glow	closed	5	0.80	69.9–112	606–825	0.71 ± 0.14
Rib	open	2	0.00	107–118	603–604	0.79 ± 0.14
Brewer	open	1	0.00	121	725	0.86
<i>C. albimarginatus</i>						
Wheeler	closed	9	0.56	80–163	538–539	0.52 ± 0.10
Keeper	open	6	0.33	100–176	235–825	0.52 ± 0.10
Glow	closed	3	0.67	72–138	333–810	0.45 ± 0.22
Helix	closed	3	0.67	102–162	240–600	0.50 ± 0.26
Brewer	open	1	1.00	120	619	0.24
Lodestone	open	1	1.00	145	237	0.78
Rib	open	1	0.00	182	735	0.43
<i>C. leucas</i>						
Lodestone	open	12	0.75	176–235	238–734	0.23 ± 0.06
Brewer	open	6	0.67	172–235	726–728	0.09 ± 0.04
Rib	open	4	1.00	150–200	606–737	0.11 ± 0.03
Helix	closed	3	1.00	207–237	242–538	0.21 ± 0.15
Keeper	open	2	1.00	220–269	384–611	0.07 ± 0.06
Bramble	open	2	0.50	164–210	387	0.17 ± 0.12
Broadhurst	open	1	1.00	200	380	0.25
Centipede	open	1	0.00	185	442	0.26
Davies	open	1	1.00	165	380	0.04
Wheeler	closed	1	0.00	205	540	0.69

Notes: Zoning refers to reefs open and closed to fishing; *N* to number of sharks tagged; size range refers to range in fork length (cm). Other information includes number of days monitored (DM) and residency index (RI; proportion of days an individual was detected relative to monitoring days [mean ± SE]). Species shown are grey reef shark (*Carcharhinus amblyrhynchos*), silvertip shark (*C. albimarginatus*), and bull shark (*C. leucas*).

protection of the full network relative to each reef removal scenario.

RESULTS

Residency and inter-reef movements

Movement data from 36 *C. amblyrhynchos*, 24 *C. albimarginatus*, and 33 *C. leucas* acoustically tagged in the TSV array were examined (Table 1). For *C. amblyrhynchos* and *C. albimarginatus*, a similar proportion of males and females across the whole size range were tagged; however, 74% of *C. leucas* monitored were female, and all *C. leucas* were classified as adults. Most *C. amblyrhynchos* (78%) were tagged at Lodestone, Helix, and Wheeler reefs, whereas 63% of *C. albimarginatus* were tagged at Wheeler and Keeper reefs, and 67% of *C. leucas* were tagged at Lodestone, John Brewer, and Rib reefs (Table 1). Residency to the TSV array ranged from 0.02 to 1.0 (mean ± SD: 0.76 ± 0.27) in *C. amblyrhynchos*, 0.01–0.97 (0.53 ± 0.28) in *C. albimarginatus*, and 0.001–0.69 (0.19 ± 0.19) in *C. leucas* (Fig. 2a). There were no differences in residency between the TSV array and the tagging reef for *C. amblyrhynchos* ($t = 0.289$, $df = 70$, $P = 0.773$) and *C. albimarginatus* ($t = 0.624$, $df = 44$, $P = 0.536$), indicating that these two species remained most of the time at or near the reef where they were captured (Fig. 2a). Residency of *C.*

leucas was considerably lower than the other species, and individuals were detected less at their tagging reef than in the entire array ($t = 3.211$, $df = 66$, $P = 0.002$; Fig. 2a). Moreover, seven *C. leucas* were never detected at their tagging reef; however, four individuals spent >50% of the monitoring days (330–734 d) within the TSV array.

Movements between reefs were observed in all three species, but the number of reefs visited, dispersal, and mean time traveled varied considerably among species (Fig. 3). Overall 42% of *C. amblyrhynchos*, 71% of *C. albimarginatus*, and 100% of *C. leucas* were detected on two or more reefs. *Carcharhinus amblyrhynchos* (Fig. 3a) and *C. albimarginatus* (Fig. 3c) were detected at fewer reefs than *C. leucas* (Fig. 3e). Interestingly, although not significantly, *C. amblyrhynchos* that were detected on multiple reefs showed higher residency to their tagging reef (0.81 ± 0.27) than individuals that were detected on a single reef (0.69 ± 0.29; $t = 1.218$, $df = 31$, $P = 0.232$). Similarly, in *C. albimarginatus*, residency did not differ between individuals detected on a single reef (0.55 ± 0.27) and individuals that moved to several reefs (0.44 ± 0.29; $t = 0.889$, $df = 13$, $P = 0.390$). Despite some *C. amblyrhynchos* and *C. albimarginatus* undertaking regular excursions, most individuals returned and/or remained close to their tagging reef for long periods.

Both *C. amblyrhynchus* (Fig. 3b) and *C. albimarginatus* (Fig. 3d) moved similar distances between monitored reefs in the TSV array (~50 km), but *C. albimarginatus* showed higher frequency of dispersal than *C. amblyrhynchus*, particularly in the range of 5–10 km. *Carcharhinus leucas* were detected on up to 13 different reefs from the TSV array and showed high dispersal frequency (Fig. 3f). In addition, a large portion of the population of *C. leucas* (42%) was detected at other arrays from the GBR. Some of these arrays were relatively closed to TSV (e.g., CB and ORI; <80 km), whereas others, including HI and LEI, were separated by over 650 km (Appendix A: Fig. A1). The mean time traveled between reefs was lower in *C. amblyrhynchus* than *C. albimarginatus* and *C. leucas* (Fig. 3), which suggests that inter-reef movements of *C. amblyrhynchus* were more directed. For example, it took *C. amblyrhynchus* $\sim 11.2 \pm 1.4$ h to move distances <10 km, whereas for *C. albimarginatus* (16.8 ± 1.7 h) and *C. leucas* (20.7 ± 5.8 h), it took double that time to travel similar distances.

Network analysis

From all the networks constructed, there was no evidence that shark movements were random (χ^2 , $P < 0.001$). Therefore, all networks were included in subsequent analysis. From the network metrics examined, component was the only metric that did not vary among species ($F_{2,91} = 0.802$, $P = 0.451$; Appendix C). The number of nodes, number of edges, and network diameter were significantly higher in *C. leucas* compared to *C. amblyrhynchus* and *C. albimarginatus* (Tukey's HSD tests, $P < 0.001$). *Carcharhinus amblyrhynchus* and *C. albimarginatus* networks had similar diameter and nodes, but differed in density and number of edges, which were significantly higher in *C. albimarginatus* (Appendix C). At the species level, sex and FL had a significant effect on all network metrics of *C. amblyrhynchus* (Table 2a). Networks from larger *C. amblyrhynchus* had a greater number of nodes and edges; the density and diameter also increased with increasing size. In addition, for all of the metrics examined, male *C. amblyrhynchus* had significantly larger values than females (Appendix D). The number of days monitored and the number of days detected in the array did not influence network metrics of *C. amblyrhynchus*. A significant interaction between sex and FL was observed in the number of nodes, edges, and network diameter of *C. albimarginatus*; none of the predictors had an effect on network density (Table 2b). Networks from large-sized male *C. albimarginatus* had more nodes, edges, and were larger than those of smaller individuals and/or females (Appendix E). A positive relationship was found between the number of days detected in the TSV array and the number of nodes and edges in the network of *C. leucas* (Appendix E). Larger-size *C. leucas* also had networks with more edges. None of the predictors had a

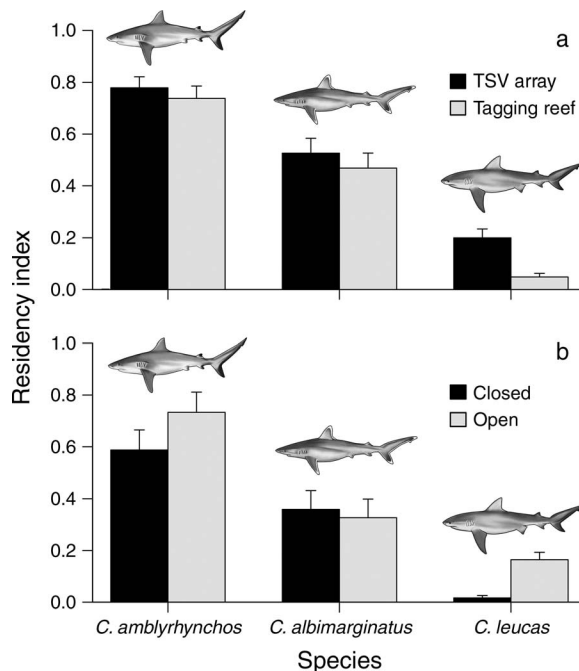


FIG. 2. (a) Residency index (mean and SE) of reef-associated sharks (*Carcharhinus amblyrhynchus*, *C. albimarginatus*, and *C. leucas*) to the Townsville (TSV; Queensland, Australia) array and tagging reef; and (b) residency index of sharks in open and closed fishing reefs. Residency index is the proportion of days an individual was detected relative to monitoring days (mean).

significant effect on network density and diameter (Table 2c).

The relative importance of the tagging reef and the effect of reef isolation on networks were investigated by performing a reef removal analysis. Networks for *C. leucas* were typically more complex than for the other species, as most individuals used a larger number of reefs and exhibited a higher frequency of inter-reef movements (Figs. 3, 4). This was more evident after removing reefs from the system, which resulted in smaller and less variable changes in metrics from the full network (either positive or negative) in *C. leucas* compared to *C. amblyrhynchus* and *C. albimarginatus* (Fig. 5). However, network metrics were affected in different ways after each removal scenario. While removing reefs from the network negatively impacted the number of edges and diameter, component had a positive change and density had relatively little change (Fig. 5). Therefore, removing reefs from the network reduced the size and also the number of inter-reef movements in all species, but also increased the number of components or clusters of isolated reefs. In *C. albimarginatus*, removal of the tagging reef produced the largest changes in all network metrics (Fig. 5). Interestingly, the other scenarios showed relatively small changes from the full network.

The tagging reef was the most central reef in the network for all *C. amblyrhynchus* and most *C. albimar-*

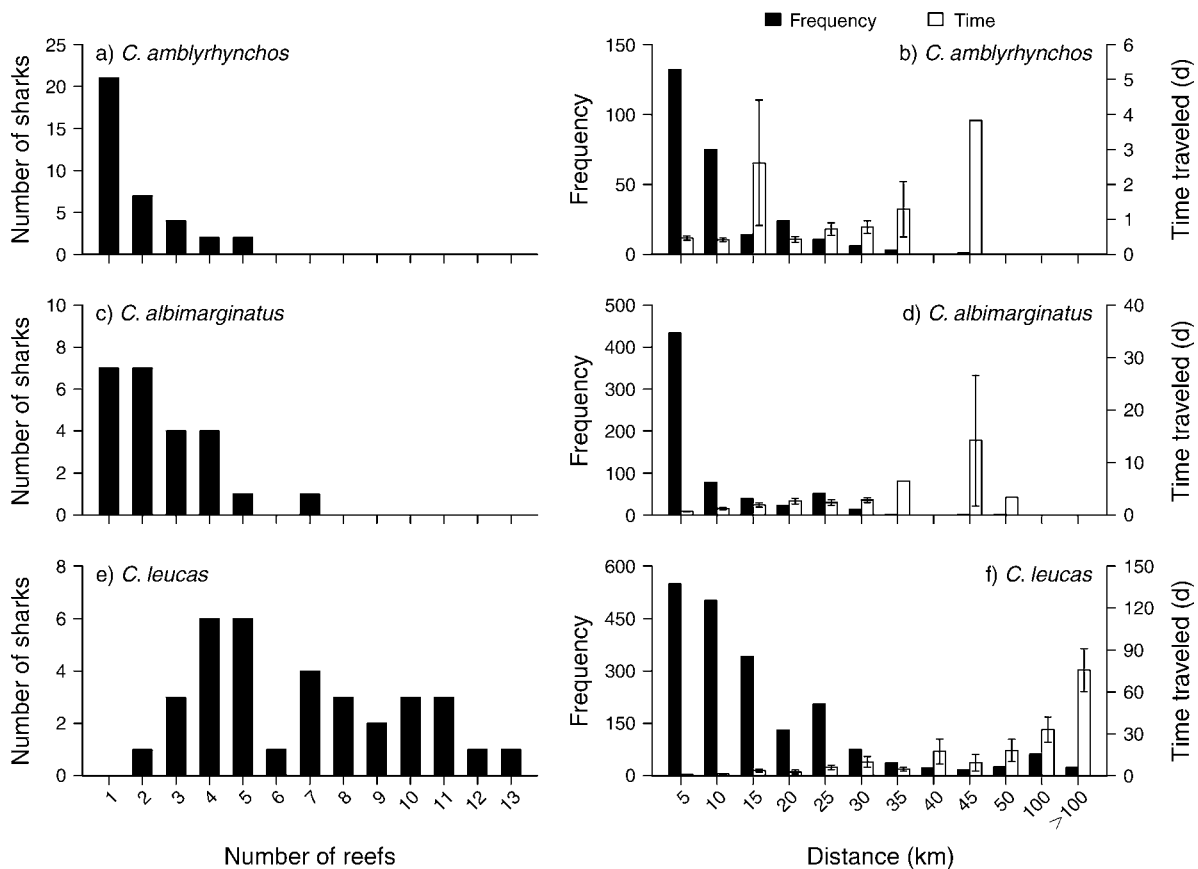


FIG. 3. (a, c, e) Number of sharks detected at different coral reef habitats (number of reefs). (b, d, f) Frequency of shark dispersal and time traveled per distance (mean \pm SE). Note differences in y-axis scales.

ginatus (except for three individuals; Appendix F). Wheeler, Lodestone, and Helix reefs had the greatest node strength and dPC (sum of intra- and inter-patch connectivity) in the networks of *C. amblyrhynchos*, and thus were identified as important reefs for their connectivity (Appendix F). In addition, the links (corridors) between Helix–Lodestone, Brewer–Lodestone, and Yankee–Glow showed the greatest dPC values (Appendix G). In *C. albimarginatus*, Wheeler and Rib reefs had the largest node strength (Appendix F), and the links between Centipede–Wheeler, Kelso–Keeper, and Brewer–Rib were also important for maintaining connectivity (Appendix G). In only 39% of *C. leucas* was the tagging reef the most central in the network (Appendix F). A large number of reefs contributed to connectivity within the TSV array, and Lodestone, Brewer, Rib, and Wheeler reefs had the largest node strength. Links between Centipede–Wheeler, Lodestone–Brewer, and Helix–Grub were identified as important corridors for connectivity within the TSV array; in other arrays, Heron–One Tree Island had a large dPC (Appendix G). At the population level, *C. amblyrhynchos*, *C. albimarginatus*, and *C. leucas* showed relatively low, intermediate, and high degrees of reef

connectivity, respectively (Fig. 6). Most movements for *C. amblyrhynchos* and *C. albimarginatus* were within their tagging reef with some occasional excursions to other reefs. However, *C. albimarginatus* showed a higher frequency of inter-reef movement than *C. amblyrhynchos*. *Carcharhinus leucas*, on the other hand, exhibited a more complex pattern of inter-reef connectivity within the TSV array, with some individuals undertaking long-range excursions (>300 km) to other arrays.

MPA utilization

Carcharhinus amblyrhynchos spent a similar proportion of days at open and closed reefs (Fig. 2b); however, a marginal interaction between sex and management zone was detected ($F_{1,60} = 4.337$, $P = 0.044$). For example, males were detected less at closed reefs (RI of 0.43 ± 0.40) than females (RI of 0.75 ± 0.30). Shark protection (i.e., proportion of movements within/to closed reefs) did not differ between males and females tagged at closed reefs, but larger *C. amblyrhynchos* received less protection than smaller individuals (Table 3). At open reefs, shark protection was influenced by both sex and FL; male *C. amblyrhynchos* had greater protection than females and larger sharks gained more

TABLE 2. General linear model results of factors that influence network metrics of reef-associated sharks.

Effect	a) <i>Carcharhinus amblyrhynchos</i>			b) <i>Carcharhinus albimarginatus</i>			c) <i>Carcharhinus leucas</i>		
	Dev.	Res. Dev.	<i>P</i>	Dev.	Res. Dev.	<i>P</i>	Dev.	Res. Dev.	<i>P</i>
Nodes									
Null		0.865			0.716			1.029	
Sex	0.212	0.652	<0.001	0.001	0.715	0.865	0.066	0.963	0.112
FL	0.196	0.456	<0.001	0.088	0.628	0.049	0.085	0.878	0.072
DM	0.000	0.456	0.978	0.048	0.580	0.145	0.003	0.875	0.749
DD	0.003	0.452	0.614	0.027	0.552	0.271	0.136	0.740	0.023
Sex × FL	0.047	0.406	0.063	0.146	0.406	0.011	0.007	0.733	0.612
Edges									
Null		3.827			3.374			3.586	
Sex	0.944	2.883	<0.001	0.004	3.369	0.844	0.121	3.466	0.205
FL	0.870	2.013	<0.001	0.429	2.941	0.047	0.319	3.147	0.039
DM	0.000	2.013	0.949	0.311	2.629	0.090	0.000	3.147	0.967
DD	0.037	1.976	0.429	0.188	2.442	0.188	1.014	2.133	<0.001
Sex × FL	0.185	1.790	0.078	0.494	1.948	0.033	0.032	2.101	0.513
Density									
Null		0.467			0.337			0.069	
Sex	0.063	0.404	0.014	0.001	0.337	0.833	0.004	0.065	0.199
FL	0.078	0.326	0.006	0.003	0.333	0.663	0.001	0.064	0.535
DM	0.012	0.313	0.278	0.005	0.328	0.581	0.001	0.064	0.583
DD	0.000	0.313	0.944	0.008	0.320	0.511	0.003	0.061	0.255
Sex × FL	0.004	0.309	0.529	0.006	0.314	0.562	0.000	0.061	0.901
Diameter									
Null		1.940			1.091			0.649	
Sex	0.474	1.466	<0.001	0.015	1.077	0.518	0.040	0.609	0.167
FL	0.449	1.017	<0.001	0.107	0.969	0.079	0.012	0.596	0.441
DM	0.006	1.012	0.664	0.059	0.911	0.195	0.011	0.585	0.460
DD	0.004	1.008	0.722	0.022	0.889	0.433	0.000	0.585	0.974
Sex × FL	0.096	0.912	0.075	0.260	0.629	0.006	0.000	0.584	0.880

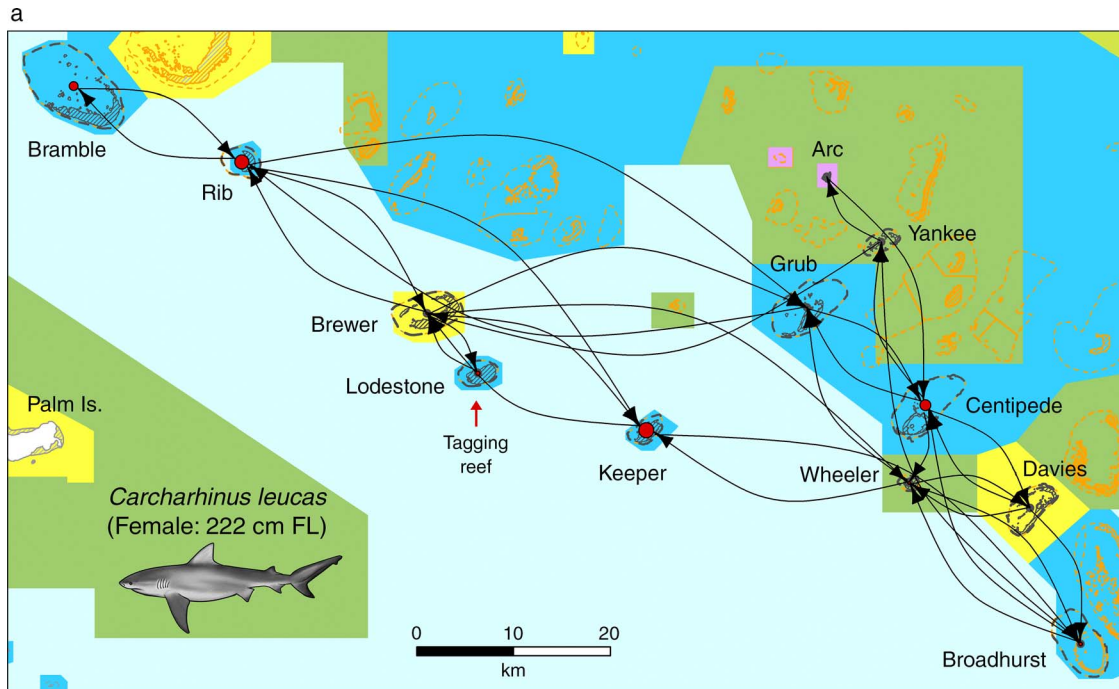
Notes: For all models, $df = 1$. Null refers to the intercept-only model. Nodes are number of nodes, edges are number of edges. DD refers to number of days detected within the tagging array. Sex refers to differences between male and female sharks, FL to the effect of fork length, Dev. refers to deviance and Res. Dev. to residual deviance. Significant differences were evaluated with maximum likelihood ratio tests (χ^2 , $P < 0.05$).

protection than smaller ones (Table 3). *Carcharhinus albimarginatus* was also detected a similar proportion of days at open and closed reefs (Fig. 2b). However, smaller sharks tagged at open reefs received more protection than larger individuals. Moreover, a significant interaction between sex and FL was detected for *C. albimarginatus* tagged at closed reefs: shark protection declined in large males but remained constant for females across the size range (Table 3). In *C. leucas*, individuals spent more days detected at open than closed reefs ($F_{1,58} = 16.476$, $P < 0.001$); sex did not have an effect on the proportion of days detected ($F_{1,58} = 0.654$, $P > 0.05$; Fig. 2). Protection also differed between males and females tagged at open and closed reefs, but size did not have an effect (Table 3). Female *C. leucas* tagged at open reefs had greater protection than males, whereas males tagged at closed reefs had greater protection than females. Removal of the tagging reef had a negative effect on the degree of protection of all species (Fig. 7). *Carcharhinus albimarginatus* experienced the largest decrease in protection (33% from full network), followed by *C. amblyrhynchos* (11%) and *C. leucas* (8%). Conversely, removing any of the closest reefs to the

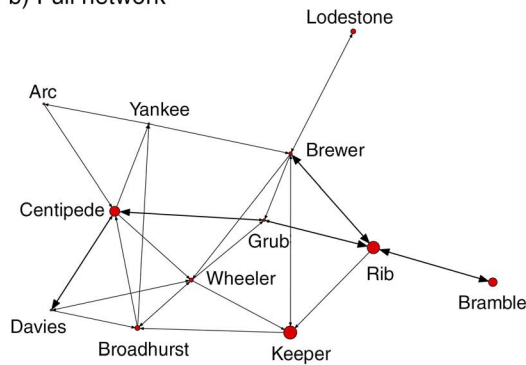
tagging reef produced little change in protection (more movements to closed reefs) in *C. amblyrhynchos* (1%) and *C. leucas* (1%), but increased up to 7% in *C. albimarginatus* (Fig. 7).

DISCUSSION

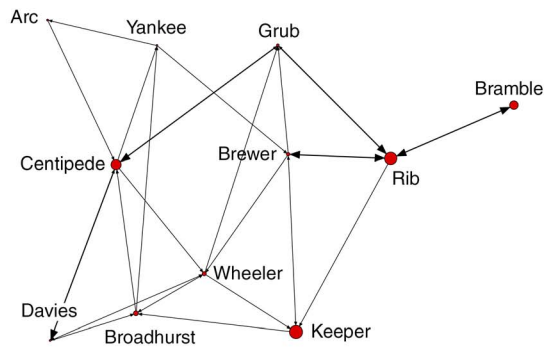
Understanding how species move in heterogeneous environments is essential for (1) identifying critical habitats or corridors that may be important for maintaining population connectivity (Pascual-Hortal and Saura 2006, Fletcher et al. 2011); (2) making meaningful predictions about the future fate of populations (Hein et al. 2004, Olds et al. 2012); and (3) developing management strategies that may ensure long-term conservation (Bond et al. 2012, Knip et al. 2012). These concepts have been the foundation of landscape ecological theory (Urban and Keitt 2001, Rizkalla et al. 2008), but have received less attention in marine environments (Jones et al. 2009, Olds et al. 2012, Lédée et al. 2015), mainly because of the challenges of adequately quantifying movements of wide-ranging marine species. More recently, however, large arrays of acoustic receivers have allowed tracking shark move-



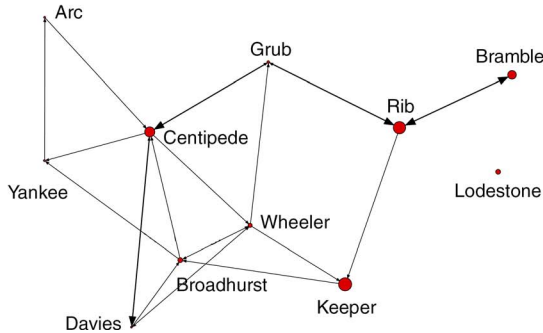
b) Full network



c) Network (- tagging reef)



d) Network (- prox. reef 1)



e) Network (- prox. reef 2)

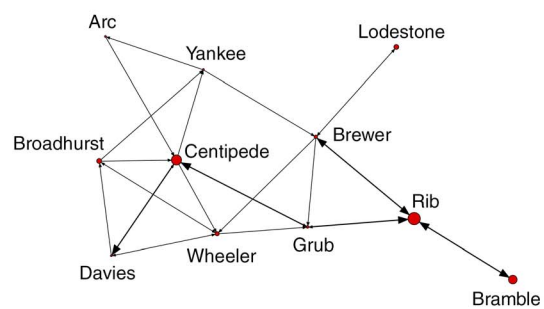


FIG. 4. (a) Network of a female bull shark (*C. leucas*) monitored in the central GBR. Lower panel includes (b) the full network; (c) the network without the tagging reef (Lodestone); (d) the network without the closest reef to the tagging reef (prox. reef 1; Brewer); and (e) the network without the second-closest reef to the tagging reef (prox. reef 2; Keeper). Red circles represent the node strength (number of incoming/outgoing movements from a reef) and arrows indicate the edges or movement paths. Female size is given in fork length (FL).

ments over scales of 10–1000 km (IMOS 2009), thus increasing our understanding of complex ecological processes such as dispersal, partial migration, and connectivity (Papastamatiou et al. 2013, Werry et al. 2014, Heupel et al. 2015). In this study, tracking multiple shark species simultaneously also enabled comparing and contrasting their spatial ecology, as well as quantifying the benefits they may gain from a coral reef MPA network. The use of NA provided a potentially powerful tool for understanding functional connectivity over different spatial scales, further revealing the importance of the tagging reef for more site-attached species and the effect of reef isolation on population connectivity. Our findings showed that acoustic monitoring data can serve as a useful platform for designing more effective MPA networks for a wide range of reef-associated species.

Habitat isolation and individual-specific movement capabilities can influence the distribution and spatial ecology of a species, metapopulation dynamics, and ultimately persistence (Hanski 1998, Hein et al. 2004, Hawkes 2009). This has important implications for the management and conservation of a species, as remote and isolated reefs may by default increase shark protection. Our two-year monitoring study showed that *C. amblyrhynchos* spent 80% of monitoring days in the array, whereas *C. albimarginatus* was only detected 50% of the time. *Carcharhinus amblyrhynchos* also spent most days at or near their tagging reef, a behavior that seems to be representative across a wide range of habitats with different degrees of reef isolation (Barnett et al. 2012, Vianna et al. 2013, Heupel and Simpfendorfer 2014, Espinoza et al. 2015b). *Carcharhinus albimarginatus* were often detected at their tagging reef, but a large portion of the population (71%) moved to other reefs. These results are consistent with previous work on *C. albimarginatus* (Espinoza et al. 2015a). Our data also showed that *C. albimarginatus* moved more frequently between reefs and management zones, and spent more time traveling similar distances between reefs than *C. amblyrhynchos*. Larger sharks typically have higher energy requirements than smaller ones, and consequently the size of their activity space is expected to increase with body size (Papastamatiou et al. 2009, Grubbs 2010, Speed et al. 2010). Therefore, given that *C. albimarginatus* is larger than *C. amblyrhynchos*, we hypothesized that these two species have different energy requirements and foraging strategies in coral reef ecosystems.

Despite the increasing number of studies on reef-associated sharks, there is limited knowledge about how wide-ranging species interact with coral reefs (Papastamatiou et al. 2013, Daly et al. 2014, Ketchum et al. 2014). Our study showed that *C. leucas* spent less than 20% of monitoring days within the TSV array and almost half of the population (42%) either moved to nearby inshore habitats or undertook coastal migrations along the GBR. This type of behavior has been

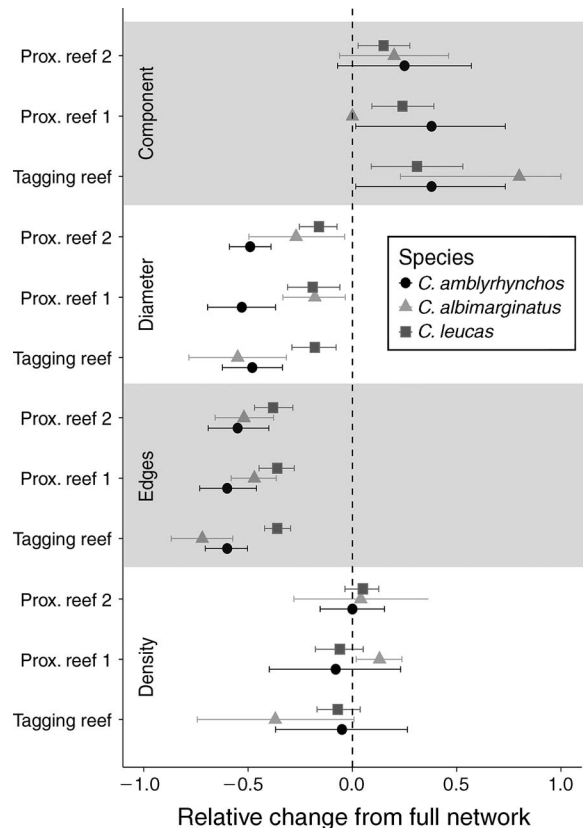


FIG. 5. Relative change in network metrics of reef-associated sharks under different “reef removal” scenarios. The following scenarios were examined: network without the tagging reef (Tagging reef); network without the closest reef to the tagging reef (Prox. reef 1); and network without the second-closest reef to the tagging reef (Prox. reef 2). Network metrics include density (measure of route selection), number of edges, diameter (size of the network), and component (number of clusters of reefs within the network).

previously reported in tiger sharks (*Galeocerdo cuvier*) (Papastamatiou et al. 2013), and more recently in *C. leucas* (Daly et al. 2014, Heupel et al. 2015). In Australia, Heupel et al. (2015) showed that ~3% of the population of *C. leucas* tagged in TSV moved to temperate waters in Moreton Bay and New South Wales (NSW), Australia, while over 25% of individuals tagged in NSW moved to the central and southern GBR. Inshore movements of *C. leucas* to shallow estuarine habitats along the east coast of Australia generally occurred for short periods (<5 days) during the summer, and were only observed in mature females (M. Espinoza, unpublished data). Interestingly, some *C. leucas* spent between 50% and 69% of the days monitored in the TSV array. The TSV region is thought to be an important foraging ground for *C. leucas*, particularly during spawning aggregations (October–November) of Spanish mackerel (*Scomberomorus commerson*) along inner mid-shelf reefs (e.g., Bramble, Rib, Brewer, and Lodestone; M. Espinoza, unpublished data). These findings suggest

that a portion of the population of *C. leucas* undertakes seasonal reproductive migrations to bays and estuaries, whereas other individuals remain near the array to feed opportunistically from coral reefs. Further studies are needed to understand complex movement decisions and migratory dynamics of large marine predators, especially when they only involve a portion of the population.

Networks for *C. leucas* were larger and more complex than those for *C. amblyrhynchos* and *C. albimarginatus*, as fewer individuals from these two species moved beyond their tagging reef and those that moved generally used fewer reefs. This is not unexpected, given that *C. leucas* uses a wider range of habitats and is not restricted to coral reefs (Daly et al. 2014, Heupel et al. 2015). However, this makes direct comparisons with site-attached species challenging, as large spatial scales are likely to underestimate the network of highly mobile species if acoustic coverage is not adequate. This is true for all network metrics except diameter (network size), which is the only metric that could be adjusted to account for long-range movements between arrays. Our study indicated that large male *C. amblyrhynchos* had larger networks than smaller individuals and/or females. Espinoza et al. (2015) showed that male *C. amblyrhynchos* monitored in the TSV array tend to disperse more than females, and suggested that a male-biased dispersal strategy may be advantageous to increase (1) genetic diversity and population connectivity; and (2) foraging opportunities while reducing competition with larger resident females. A similar pattern was observed in *C. albimarginatus*, where large males dispersed more and had larger networks than females. A recent study suggested that male *C. albimarginatus* may increase their activity space as they grow, while female and immature individuals may be resident to the TSV array over longer periods (>1 year; Espinoza et al. 2015a). None of the predictors examined had an effect on the size of the network of *C. leucas*; however, networks from individuals that spent more days in the array had a greater number of nodes and edges. These findings suggest that although *C. leucas* only spent a limited amount of time in the array, both males and females may have similar patterns of reef use and habitat connectivity.

Movement studies using acoustic telemetry are often limited by the density of receivers, acoustic coverage, and behavior of aquatic animals (Heupel et al. 2006, Espinoza et al. 2011). For wide-ranging species, this can mean long periods of absence even if animals are within the study site but outside the detection range of the receivers (Chapman et al. 2005, Heupel et al. 2010). Consequently, it is essential to understand these biases and acknowledge the limitation of acoustic monitoring data in order to adequately describe the behavior and spatial ecology of a species. The results from our movement study may have been compromised by (1) the disproportionate receiver coverage among reefs; (2)

variability in acoustic range and detection efficiency; (3) number of unmonitored reefs (i.e., reefs without acoustic coverage, mainly located in the outer shelf); and (4) behavioral differences among shark species, particularly *C. leucas*, which is known to use a diverse range of habitats and undertake coastal migrations (Daly et al. 2014, Heupel et al. 2015). Low receiver coverage within the array may have influenced the node strength of reefs by underestimating their importance. Node strength is based on incoming/outgoing movements between reefs, so missing movements due to low receiver coverage underestimates the strength of that reef for a particular individual. Similarly, limited acoustic coverage can underestimate the importance of a reef after its removal (i.e., if there are missing movements, network metrics such as density can be negatively impacted). Despite some of these issues, the fact that all three species had similar levels of residency across reefs that differ in acoustic coverage and size suggests that our results are robust and representative of the study area. Moreover, the number of days monitored (“days at liberty”) did not influence any of the network metrics, indicating the NA was consistent despite behavioral differences in residency. Shark populations are not homogeneously distributed across coral reefs, which means that some reefs may be ecologically more important than others (McCauley et al. 2014) and/or habitats within a reef can support a higher diversity and abundance of sharks (Dale et al. 2011, Rizzari et al. 2014). For example, recent studies of *C. amblyrhynchos* and *C. albimarginatus* monitored within the TSV array revealed a preference for specific areas around the reef (e.g., reef slopes and crests) that are generally exposed to stronger current flow (Espinoza et al. 2015a, b). These areas, which presumably offer highly productive grounds to sharks and other reef predators, were generally selected as the main focus of our long-term acoustic monitoring, and thus may have increased the probability of detection on larger reefs.

Management implications

From a management perspective, considering behavioral differences within a multispecies context makes spatial planning challenging. What may be effective for one species or even a particular sex/life stage may not necessarily work for another (Heupel et al. 2010, Knip et al. 2012, Espinoza et al. 2015b). For example, variation in movement of *C. amblyrhynchos* and *C. albimarginatus* can affect the pressures these two species are exposed to and subsequent conservation and management actions. As demonstrated in this study, even in systems with semi-isolated coral reefs, smaller species with strong site attachment are likely to gain more protection from MPAs than larger, wider-ranging predators. This is also likely to vary during ontogeny and with increasing reef isolation. Moreover, sex-based movement patterns would result in male *C. amblyrhynchos* and *C. albimarginatus* receiving less protection from MPAs than

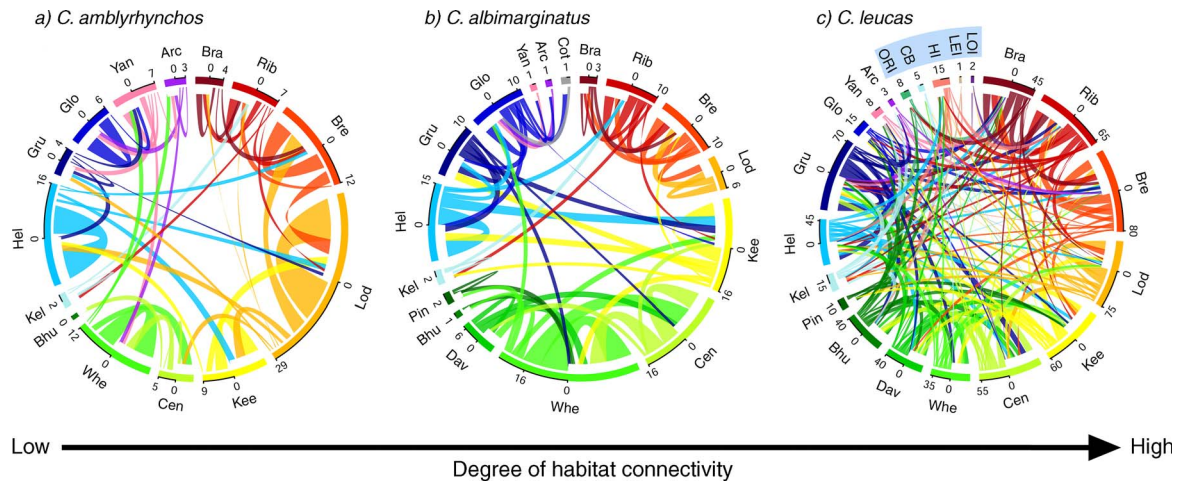


FIG. 6. Reef connectivity plots of sharks monitored in the GBR. Scale indicates the frequency of daily outgoing movements within and between reefs. The degree of habitat connectivity increases from low (a) to high (c). Reefs include Bramble (Bra), Rib, Brewer (Bre), Lodestone (Lod), Keeper (Kee), Centipede (Cen), Wheeler (Whe), Davies (Dav), Broadhurst (Bhu), Pinnacle (Pin), Kelso (Kel), Helix (Hel), Grub (Gru), Glow (Glo), Yankee (Yan), Arc, and Cotton (Cot). Other arrays in Queensland are highlighted (blue box in panel c) and include Orpheus Island (ORI), Cleveland Bay (CB), Heron/One Tree Island (HI), Lady Elliot Island (LE), and Low Isles (LOI).

females who remain resident over longer periods, where the home reef of females is closed to fishing.

Given the wide range of species and diverse life histories of reef-associated sharks, reserve design should consider variability in residency patterns, species-specific habitat requirements, sex-based dispersal, and inter-reef connectivity to maximize conservation benefits. Application of acoustic telemetry revealed that both *C. amblyrhynchos* and *C. albimarginatus* spent similar proportions of time at open and closed reefs. This is an important result, as it shows that both species were mainly present at their tagging reef despite the management category (i.e., open, closed to fishing). Protection of all species decreased after removing the tagging reef, indicating that for most individuals this reef occupied a

central place in the network. In contrast, removing nearby reefs from the network generally increased the level of protection of all species. This was more evident in *C. albimarginatus*, which according to this study moved more frequently to nearby reefs, but also showed high fidelity to their tagging reef. Alternatively, some sharks may gain more protection because of the location of their tagging reef and/or the distribution of management zones in the system (Barnett et al. 2012, Espinoza et al. 2014). Consequently, targeting specific reefs based on prior knowledge (e.g., healthier reefs that naturally have greater abundances of sharks) and increasing the level of protection to include closely spaced habitats (<20 km) may perform better for species like *C. albimarginatus* than having a single reserve or a network

TABLE 3. General linear model results of factors that influenced shark protection (proportion of movements within/to closed reefs relative to movements within/to open reefs).

Terms, by species	Open reefs				Closed reefs			
	df	Dev.	Res. Dev.	P	df	Dev.	Res. Dev.	P
<i>C. amblyrhynchos</i>								
Null			180.74				11.40	
Sex	1	57.27	123.47	<0.001	1	0.02	11.37	0.879
FL	1	5.28	118.19	0.022	1	8.12	3.26	0.004
<i>C. albimarginatus</i>								
Null							608.47	
Sex	1	0.93	327.80	0.335	1	158.05	450.42	<0.001
FL	1	55.19	272.61	<0.001	1	258.96	191.47	<0.001
Sex × FL	1	2.73	269.87	0.098	1	18.63	172.84	<0.001
<i>C. leucas</i>								
Null			190.11				142.99	
Sex	1	9.90	180.21	0.002	1	125.55	17.45	<0.001
FL	1	0.05	180.20	0.945	1	1.44	16.01	0.230

Note: Significant differences were evaluated with maximum likelihood ratio tests (χ^2 , $P < 0.05$).

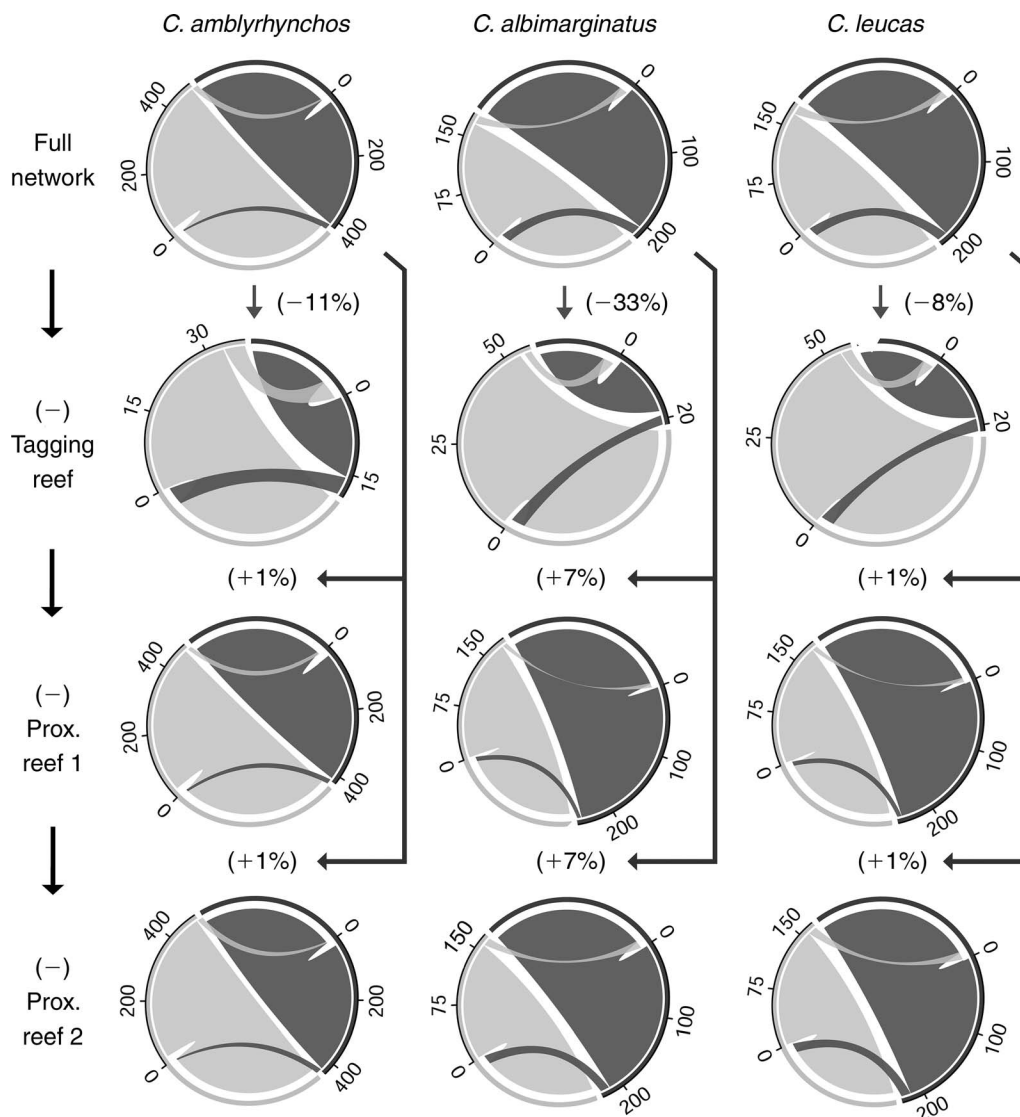


FIG. 7. Relative change in shark protection (number of movements within/to closed reefs relative to the total number of movements) between the full network and each reef removal scenario. Scenarios included (1) network without the tagging reef; (2) network without the closest reef to the tagging reef (prox. reef 1); and (3) network without the second closest reef to the tagging reef (prox. reef 2). Dark gray portion of each circle indicates the number of moves within/from reefs closed to fishing for each species standardized by the number of individuals tagged in closed reefs; light gray portion of each circle indicates the number of moves within/from reefs open to fishing for each species standardized by the number of individuals tagged in open reefs. Arrows indicate negative or positive changes in protection relative to the full network.

of isolated protected reefs. This design would also ensure protection for larger male *C. amblyrhynchos*, which tend to disperse more and use larger areas than females (Espinoza et al. 2015b).

Individuals are known to alter their movements according to the density and spatial distribution of habitats and/or prey patches (Hein et al. 2004, Papastamatiou et al. 2012). In coral reef systems, coral cover is presumed to be an important driver maintaining shark populations (Espinoza et al. 2014). Thus it is possible that some species of sharks may avoid moving to and/or spending time in less productive and degraded reef habitats. This is particularly relevant as recent data

for the GBR have shown large declines (~50%) in coral cover due to increased frequency of disturbances (De'ath et al. 2012). The loss of coral cover can result in large changes in the abundance and composition of fish communities (Wilson et al. 2006, Sandin et al. 2008, Espinoza et al. 2014). Therefore, hypothetically removing reefs from the system can serve as a proxy to evaluate the effects of habitat loss and/or degradation on shark connectivity. For wide-ranging species like *C. leucas*, reef removal did not have a major effect on the network mainly because the tagging reef did not occupy a central position. However, in *C. amblyrhynchos* and *C. albimarginatus*, removing the tagging reef negatively



PLATE 1. Grey reef shark (*Carcharhinus amblyrhynchos*) swimming along the reef edge (top panel). Feeding aggregation of bull sharks (*C. leucas*) (lower panel). Photo credits: C. A. Simpfendorfer.

affected the size and number of edges in the network (e.g., most incoming/outgoing movements originated from the tagging reef). Interestingly, similar networks were observed after removing nearby reefs for *C. albimarginatus*, confirming that this species tends to use larger areas than *C. amblyrhynchos*. Therefore, knowledge of the functional connectivity of a species combined with reef health assessments could become valuable tools for shark conservation planning.

Consideration of movement corridors relative to spatial management is also critical (Fletcher et al. 2011, Lédée et al. 2015). Our study highlighted the

importance of movement corridors used by reef-associated sharks. These included paths between closely spaced reefs such as Lodestone–Brewer, Wheeler–Centipede, and Brewer–Rib that made a large contribution to the connectivity of their populations. This may indicate that some individuals move more regularly between known reefs based on experience (i.e., mental map of available reefs) or proximity. Unfortunately, little is known about spatial memory and navigation strategies of reef-associated sharks (Montgomery and Walker 2001, Meyer et al. 2005). Identifying movement corridors is important to maintaining or restoring

connectivity but also for maximizing conservation efforts. For example, landscape NA has been used to examine the importance of corridors to help prioritize the conservation of carabid beetles (Jordán et al. 2003) and bears (Chetkiewicz et al. 2006), but few studies have used it for shark species (Lédée et al. 2015). Our data suggest that increasing protection of reefs and inter-reef habitats along the inner shelf may provide a greater conservation benefit (e.g., a disproportionate number of individuals moved more regularly along inner shelf reefs than across the outer shelf), particularly for wide-ranging species. However, NA assumed that movement corridors were linear, which is not necessarily a true depiction of how sharks move, and also is likely to vary across species and/or at different spatial scales (Papa-stamatiou et al. 2011). Consequently, conservation planning relying heavily on NA could overestimate the importance of movement corridors.

After the 2004 rezoning of the GBR Marine Park, ~33% of the area was designated as no-take zones (Fernandes et al. 2005). This rezoning aimed to protect a wider range of bioregions within the Marine Park rather than protecting mobile predators (McCook et al. 2010, Heupel et al. 2015). The rezoning plan grouped protected reef patches into clusters (i.e., areas closed to fishing), which according to this study may be a more effective strategy for protecting some shark species than having the same amount of randomly distributed protected areas covering individual reef platforms. For wide-ranging sharks like *C. leucas*, the results of this study showed that spatial protection alone is unlikely to be an effective strategy. The high individual variability in residency and large-scale connectivity along the east coast of Australia creates additional challenges for the management of *C. leucas* across multiple jurisdictions. Other alternative measures (e.g., limited allocation of fishing licenses, total allowable catch, size or bag limits, restricted take or protection of high risk species, gear modifications, by-catch reduction devices, or better reporting mechanisms) are needed to improve the protection and sustainability of populations (Heupel et al. 2015).

Given the variability in movement strategies of reef-associated sharks, effective management and conservation strategies require species-specific data. Here, we used acoustic tracking data to determine the efficacy of a network of MPAs as a conservation tool to protect reef-associated sharks. To maximize shark protection for species with strong site attachment and those that move more regularly to nearby reefs, it is critical to design networks based on reef proximity (e.g., closely spaced reefs), and ideally select healthier sites (Espinoza et al. 2014). It is also important to understand that while MPA networks can be an effective tool for some sharks, any spatial approach aiming to protect highly mobile species should be used in conjunction with alternative management options. Moreover, without proper enforcement, public education, and in some

cases multifaceted and integrated conservation policy, it will be difficult to guarantee the protection of wide-ranging predators that are currently vulnerable or threatened (Graham et al. 2010, Dulvy 2013, Dulvy et al. 2014).

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SUPPLEMENTAL MATERIAL

Ecological Archives

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