



# Interspecific interactions, movement patterns and habitat use in a diverse coastal shark assemblage

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## Abstract

Sharks are a highly diverse predatory taxon and are regularly found in large, potentially competitive, assemblages. However, the mechanisms that enable long-term coexistence and factors that drive complementary movement are poorly understood. As interspecific interactions can have a large influence on survival and trophic linkages, research on shark assemblages could substantially increase our understanding of marine community dynamics. In this study, we used passive acoustic telemetry to compare the activity space size, spatial overlap and habitat use patterns of six co-occurring shark species from the same family in a tropical nearshore embayment. Our results indicated that all sizes of *Rhizoprionodon taylori* (a small-bodied, highly productive species) used significantly larger amounts of space (e.g., mean 95% KUD = 85.9 km<sup>2</sup>) than juveniles of large-bodied, less productive species (e.g., *Carcharhinus amboinensis*; 62.3 km<sup>2</sup>) that use nearshore areas as nursery areas. Most large, less productive species appeared risk averse by using less space, while the smaller more productive species took greater risk by roaming broadly. These movement strategies are likely a means of avoiding predation or gaining access to new or additional resources. Spatial overlap patterns varied substantially between species with overlap in core use areas ranging from 1.2 to 27.6%, but were consistent over time. Most species exhibited low spatial overlap, suggesting spatial partitioning to reduce interspecific competition. While a few species exhibited a high degree of spatial overlap (up to 60% of activity space extent), dietary diversity may reduce competition to support co-occurrence. These data suggest that complex interactions occur in communal nurseries in nearshore waters where species are in direct competition for resources at vulnerable life stages.

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## Introduction

Coastal habitats are both dynamic and highly productive (Allen et al. 2006; Tobin et al. 2014). These habitats are used by a wide array of marine and estuarine species and serve a variety of ecosystem functions (Barbier et al. 2011). For example, coastal habitats serve as nursery areas for a number of species and critical habitat for many others (Beck et al. 2001; Munsch et al. 2016; Heupel et al. 2018a). The reliance of a large number of species on these habitats creates communities that must not only coexist, but survive and thrive in these shared habitats. Although the coexistence of coastal species is widely known, our understanding of niche partitioning and resource use in facilitating coexistence is limited.

Resource partitioning may be a critical component of survival. Limited resources or high levels of competition can have direct impact on the survival of individuals and populations and may require species to employ differing behaviours to reduce niche overlap (White and Potter 2004;

Matley et al. 2016a,b; Matich et al. 2017; Heupel et al. 2018b). For example, recent studies have revealed sympatric species adopt differing diets or movement patterns to reduce competition (Lédée et al. 2016; Matley et al. 2016a, b). Interestingly, different strategies were applied among the species observed. For example, two coral trout species that co-occur on offshore reefs (*Plectropomus leopardus*, *P. laevis*) showed overlapping space use but different diets (Matley et al. 2016a). In contrast, two coral trout species that co-occur on inshore reefs (*P. leopardus*, *P. maculatus*) feed on the same prey items, but segregate spatially in the water column (Matley et al. 2016b). Although employing different strategies, the behaviours of these species work to reduce competition, facilitate coexistence and presumably improve survival. Similar patterns of spatial separation have also been observed in skate (Humphries et al. 2016) and reef shark (Heupel et al. 2018b) populations with species with similar diets segregating by depth.

Animal movement and behaviour patterns are also driven by aspects of their environment (e.g., Schlaff et al. 2014). Species are constrained by physiological limits governed by salinity, temperature or habitat type (e.g., seagrass beds, coral reef). Therefore, the use of habitats and interactions among species are further complicated by the biological limitations and requirements of a given species. As in the examples above for coral trout and reef sharks, species that depend on specific habitat types may need to employ behaviour patterns to reduce competition or interactions, since dispersal to new or different habitats is not feasible or optimal. The intersection of environmental and behavioural factors is a key component of the composition and functioning of coastal ecosystems.

Elasmobranchs (sharks and rays) are one of the planet's most morphologically diverse and mobile predatory taxon (Carrier et al. 2012; Ebert et al. 2013). In the past, research on elasmobranch movement and behaviour has been primarily focused on the influence of factors such as foraging and changes in environmental conditions (Heupel and Hueter 2002; Abascal et al. 2011; Nakamura et al. 2011; Schlaff et al. 2014). However, juvenile elasmobranchs commonly co-occur in coastal habitats for long periods (Castro 1993; Simpfendorfer and Milward 1993; Dale et al. 2011; Bethea et al. 2015; Yates et al. 2015). Since interspecific competition is observed more often than not in most communities (Connell 1983; Schoener 1986), it can be assumed that co-occurring elasmobranchs potentially experience high levels of interspecific interaction and competition. However, the long-term coexistence of sharks in coastal habitats indicates that species have developed strategies to limit competition for resources (White and Potter 2004; Papastamatiou et al. 2006; Speed et al. 2011; Heithaus et al. 2013).

Coastal shark communities typically include individuals exhibiting one of two life history patterns (Knip et al. 2010):

juveniles of large-bodied, slow-growing, late maturing species that use nearshore environments as nursery areas (e.g., Springer 1967; Heupel et al. 2007; Froeschke et al. 2010), and small-bodied, highly productive, fast-growing sharks, which use nearshore habitats throughout their lives (e.g., Carlson et al. 2008; Munroe et al. 2014). Thus, coastal habitats are used for distinct purposes by different shark species with contrasting life histories. These differences have been hypothesized to have a substantial effect on how sharks use space (Knip et al. 2010), but directed comparative movement studies are limited (Heupel et al. 2018b).

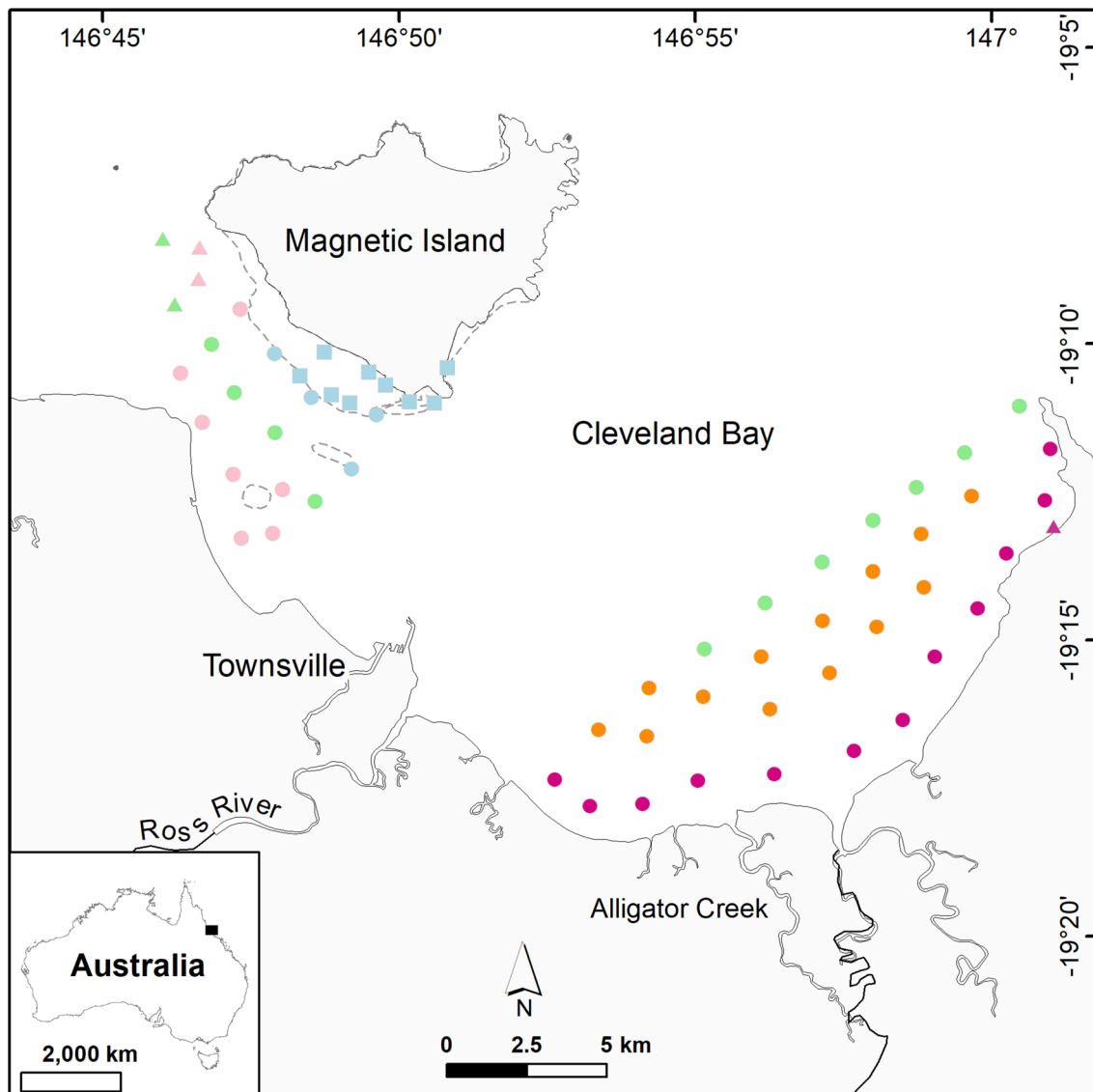
Methods for investigating and comparing how coastal species use space have traditionally used measures of activity space, such as kernel utilisation distributions or minimum convex polygons (Heupel et al. 2004). These types of metrics can be compared between and within species to examine spatial and temporal separation (Munroe et al. 2016), but do not provide information on how individuals move within their activity spaces. Recently, use of network analysis to examine animal movement and space use, especially those tracked using acoustic monitoring, has proved to be a useful analytical tool to resolve additional information about spatial ecology (Jacoby et al. 2012; Lédée et al. 2015; Mourier et al. 2018). Network analysis examines the movement (edges) of animals between locations (acoustic receiver stations, nodes) and provides a series of metrics to understand habitat use and partitioning, and movement pathways.

The aim of this study was to examine the space use, movement, and habitat use of sharks in a coastal bay to determine whether niche separation was present and identifiable based on behaviour patterns. Passive acoustic telemetry and network analysis were used to determine the spatial overlap, relative positioning, and space use of six coastal shark populations over time. Our hypothesis was that coexisting species use different areas, exhibit limited spatial overlap and/or use different movement pathways, and that spatial partitioning provides a mechanism to limit competition for resources. Differences in space use and movement strategies were examined relative to modern coastal shark habitat use theories (Heupel et al. 2007, Knip et al. 2010).

## Methods

### Study site

Cleveland Bay is a shallow embayment on the northeast coast of Queensland, Australia. The bay is 27 km wide and covers an area of approximately 225 km<sup>2</sup> (Fig. 1). Most of the bay is less than 10 m deep, and has a maximum tidal range of 4.2 m. The bay contains a diverse range of habitat types and substrates. The western side of the bay contains rocky substrate composed of coral rubble and sand



**Fig. 1** The acoustic telemetry array in Cleveland Bay, Queensland, Australia. Points indicate locations of acoustic receivers deployed in 2008 (circles), 2009 (squares), and 2011 (triangles). Reef habi-

tat is marked with dashed lines. Colours represent habitat type: green = deep habitat, violet = mudflat, blue = reef flats, pink = sand and orange = seagrass beds

with patches of coral reef on the southern coast of Magnetic Island. The eastern side of the bay is predominantly intertidal mudflat, and in deeper waters the bottom is composed of soft mud and seagrass. Mangroves line the southeastern shore. This area is a well-known communal elasmobranch nursery that is home to approximately 25 shark species (Simpfendorfer and Milward 1993).

An array of up to 61 VR2 and VR2W acoustic receivers (Vemco Ltd., Canada) was installed in Cleveland Bay to monitor shark species movements. Receivers were deployed over a period of several years; 47 receivers were deployed in 2008, an additional 9 in 2009, and 5 more in 2011. Receivers were installed in primary habitats within the bay, specifically

intertidal mudflats, areas with > 5 m depth, sandy inshore substrate, reefs, and seagrass. Data were downloaded from receivers approximately every 3 months.

### Study species

Long-term acoustic tracking data were collected for six shark species that consistently co-occur in Cleveland Bay. Data collection occurred over a period of 7 years and not all species were tracked simultaneously (Table 1). Previous analysis of individual species included in this study showed that species tracked over multiple years exhibited similar presence and movement patterns between years (e.g., Knip

**Table 1** Life history and telemetry data for monitored shark populations in Cleveland Bay

Species	LBIRTH	LMAT/AMAT	TL	Pups per litter	<i>n</i> (adults:juveniles)	Monitoring period
<i>Carcharhinus amboinensis</i>	60–65	210–215/13	280	6–13	23 (0:23)	Dec 2008–Aug 2010
<i>Carcharhinus fitzroyensis</i>	50	80–90/6	100–130	1–7	8 (6:2)	Sep 2012–May 2014
<i>Carcharhinus tilstoni</i>	60	120/5	160–180	1–6	10 (0:10)	Sep 2012–May 2014
<i>Carcharhinus melanopterus</i>	50	105–133/4.2–8.5	140	3–4	17 (12:5)	Oct 2009–Dec 2011
<i>Carcharhinus sorrah</i>	50	90–95/2.5	160	1–8	16 (16:0)	Mar 2009–Nov 2010
<i>Rhizoprionodon taylori</i>	22–26	55/1	69–81	1–10	8 (8:0)	Sep 2011–Apr 2013

Length measurements are given in centimetre

*LBIRTH* approximate length at birth, *LMAT* length at maturity, *AMAT* age at maturity, *TL* total length, pups per litter, *n* number of individuals monitored in Cleveland Bay, and the monitoring period for each species

et al. 2011, 2012). This inter-annual consistency indicated data from different species collected in different years were comparable and suitable for community-level overlap and space use analysis.

Australian sharpnose (*Rhizoprionodon taylori*) and spot-tail (*Carcharhinus sorrah*) sharks are fast-growing, highly productive species that spend their entire lives in shallow coastal habitats (Davenport and Stevens 1988; Simpfendorfer 1992, 1993). The creek whaler *Carcharhinus fitzroyensis* is a medium-bodied coastal shark that is also relatively productive and inhabits shallow coastal areas its entire life (Last and Stevens 2009). However, unlike *C. sorrah* and *R. taylori*, *C. fitzroyensis* primarily uses turbid, muddy, and seagrass habitat (Munroe et al. 2015). Pigeye (*Carcharhinus amboinensis*) and Australian blacktip (*C. tilstoni*) sharks are relatively slow-growing, large-bodied, late maturing species that primarily use nearshore areas as nursery habitat (Knip et al. 2011; Tillett et al. 2011; Harry et al. 2012). Finally, the blacktip reef shark *C. melanopterus*, is a specialized species that primarily uses reef habitats (Chin et al. 2013a, b). In addition to tracking data, diet and life history information is available for most of these species, much of which was gathered from Cleveland Bay (e.g., Simpfendorfer 1993; Simpfendorfer and Milward 1993; Simpfendorfer 1998; Harry et al. 2011; Kinney et al. 2011; Harry et al. 2012, 2013).

## Field methods

Sharks were captured using bottom-set 400 m longlines, 11.45 cm mesh gillnets, and/or baited rod and reel. Longlines were made of 6 mm nylon mainline that was anchored at both ends. Gangions were composed of 1 m of 4 mm nylon cord and 1 m of 1.5 mm wire leader. Capture procedures and bait were the same for all the species. Specific capture procedures have been described in previous publications (Knip et al. 2011, 2012; Munroe et al. 2014, 2015). *Rhizoprionodon taylori* were fitted with V13 (13 mm × 36 mm), while all other species were fitted with V16 (16 mm × 65 mm)

acoustic transmitters (Vemco Ltd., Canada). Transmitters were implanted into the body cavity to ensure long-term retention. An incision was made on the body midline anterior to the cloaca and then the transmitter was inserted into the body cavity. The incision was closed with absorbable sutures. Individuals were measured to the nearest millimetre for their stretch total length (STL), sexed, tagged with an individually numbered Rototag in the first dorsal fin and released. To reduce the overlap of acoustic signals, each transmitter emitted a unique code at 69 kHz on a random repeat interval of 45–75 s. Range testing indicated V13 and V16 transmitters had a maximum detection range of 525 m and 900 m, respectively, based on 5% probability of detection (Kessel et al. 2013). Range testing was conducted in each habitat type and results showed that the maximum detection range was consistent throughout the bay.

## Space use and overlap analysis

Space use comparisons between resident and transitory sharks were considered invalid, because the movement and space use patterns of transitory individuals may not be indicative of local habitat selection and space use strategies. Therefore, space use analysis was restricted to resident individuals that were present for more than 2 consecutive months following release with acoustic transmitters. Individuals were considered present in the bay in a given month if they were detected for 3 or more days in the array. Sharks were considered present on a given day if they were detected at least twice on that day. If a shark was not detected for > 30 days, it was presumed that the shark had left the bay. Based on these criteria, 75 of 157 tagged sharks were excluded from analyses. Majority of the excluded individuals were detected in the bay for less than 6 weeks after release and did not return to Cleveland Bay during the monitoring period. Resident individuals were present in Cleveland Bay for 4–18 months. The only exception was a single *R. taylori*, which was present in Cleveland Bay for 3 months.

Individual positions were estimated for resident individuals using a mean position algorithm to determine centre of activity (COA) locations. COA locations were weighted mean positions for each 30-min interval a shark was detected in the array (Simpfendorfer et al. 2002). COAs were used to calculate individual activity space as 50% (core use) and 95% (extent) kernel utilisation distributions (KUDs) using the *adehabitatHR* package (Calenge 2006) in the R statistical environment (R Core Development Team 2017) version 3.0. To prevent overestimation of KUD size, calculations used an impassable boundary that approximated the Cleveland Bay coastline. This boundary did not extend around the Magnetic Island, as the coastline of this area was too complex to include in the calculations. All KUD calculations used a smoothing parameter of 0.008. Since the total amount of time each individual spent in the bay was variable and individuals were monitored across different years, individual KUDs were calculated for the total amount of time each individual spent in the bay (hereafter referred to as total KUD). To enable more direct comparisons in activity space size between individuals, KUDs were also calculated for each calendar month an individual was present (hereafter referred to as monthly KUD). Total 50% and 95% KUDs were overlaid to establish core and extent activity spaces for each species (Speed et al. 2011). A one-way ANCOVA was used to determine if total 50% and 95% KUD sizes were affected by species or STL ( $p < 0.05$ ). Given the imbalanced nature of the data, all ANCOVAs were run with type III sum of squares. A linear mixed effects model was used to test the effect of species and STL on monthly 50% and 95% KUD size. Individual tag ID was included as a random factor to account for the repeated measures in these data. Monthly and total residency values (number of days detected/monitoring period) were variable between species. For example, *R. taylori* had lower residency values than *C. amboinensis* (Knip et al. 2011; Munroe et al. 2014). These residency trends have been identified previously and may be linked to differences in life history traits between species (Heupel et al. 2007; Knip et al. 2010; Munroe et al. 2014). Since previous work has shown that residency values were consistent within species (e.g., Knip et al. 2010, 2012; Munroe et al. 2014, 2015), we did not include residency as a factor in analyses, because it is correlated with species. Models were computed using the *nlme* package in R (Pinheiro et al. 2012). Models were compared using Akaike's information criterion with a small sample size bias correction (AICc). Likelihood ratio tests were used to compare final models to respective null models. Data were assessed for normality prior to analysis and  $\log_{10}$  transformed if necessary. Total and monthly KUD overlaps were calculated using the *adehabitatHR* package in R (Calenge 2006). Overlap was calculated between all the individuals of all the species and was measured as a percent (%). An ANOVA was used to determine if total 50% and

95% KUD overlap varied between species pairs. A linear mixed effects model was used to determine if monthly 50% and 95% KUD overlap was influenced by species pair and month. As overlap data were measured as a proportion, it was arcsine transformed prior to analysis.

## Network analysis

Network analysis was used to assess species habitat use and partitioning, and movement pathways between different habitats types within Cleveland Bay. Networks were analysed using *sna* (Butts 2013), *igraph* (Csardi and Nepusz 2006) and *met* (Opsahl 2009) packages in R. Detection data for each individual were used to create non-square matrices that counted the frequency of use of habitat type for each individual; frequency was measured by dividing the total detections in each habitat by the number of receivers deployed in that same habitat. The non-square matrices were used to create two-mode habitat networks that represented the habitat use of a species for the entire study period. In this case, because non-square matrices were based on two sets of entities (i.e., habitat and individual), also referred to as nodes, the network created was bipartite, with one node representing habitats and another individuals. Species habitat networks were visualised and canonical correspondence analysis (CCA) was used to examine habitat partitioning within Cleveland Bay.

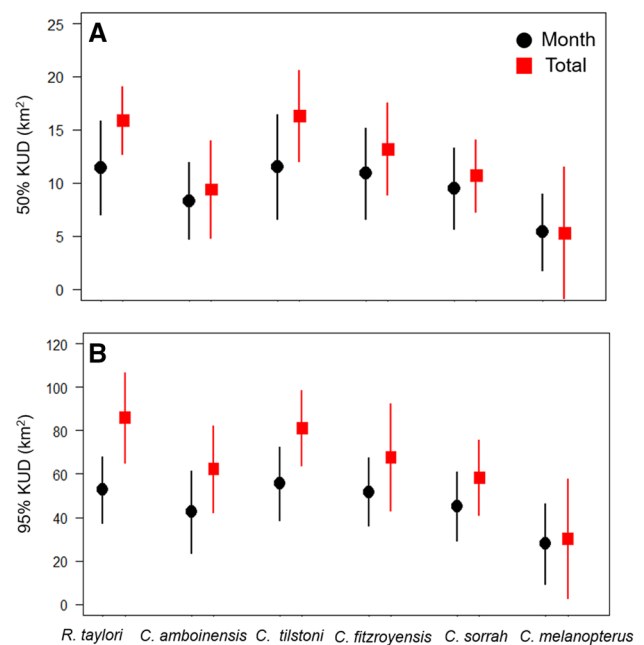
To examine the movement of individuals between habitat types, acoustic receivers deployed within Cleveland Bay were grouped according to the habitat type (Fig. 1). Receivers deployed in deeper habitat of the bay were separated into two groups: eastern deep (e\_deep) and western deep (w\_deep) for movement pathway analyses. Detection data for each individual were used to create square matrices that counted presence at, and relative movements between, habitat types. A 5 min interval was used to filter individuals' detections at the same habitat to filter out possible false detections. Relative movement was defined as the number of times an individual moved between two habitats divided by the total number of movements made by the individual (i.e., total number of edges in the network (Jacoby et al. 2012)). Directed and weighted habitat movement networks representing individual habitat use in the study area were created from the square matrices. Each network was tested for non-random patterns using link re-arrangement (i.e., permutation) via a bootstrap approach ( $n = 10,000$ ; Croft et al. 2011). Observed movements were randomly shuffled between habitat types and new networks were generated using the same degree distribution as the original network. Transitivity was calculated for each random network to compare to values from the observed network using coefficient of variation and likelihood ratio tests ( $\chi^2$ ,  $p < 0.05$ ). Pathway number and frequency were calculated for each individual

habitat movement network. Pathway number refers to the number of routes between two habitats used by an individual and pathway frequency (or relative movement) measures the number of times an individual moved between two habitats divided by the overall number of movements in the network.

Linear mixed effect models using an information theoretic approach were used to investigate the influence of species, STL and their interaction with pathway count and frequency. Linear models were implemented using the *lme* function from the *nlme* package (Pinheiro et al. 2012). Stretched total length was centred to simplify interpretation (Schielzeth 2010). Individual tag ID was included as a random factor to account for the repeated-measures nature of the data (Bolker et al. 2009). Data normality was tested prior to statistical analysis and data were transformed to normal when required. Collinearity between factors was assessed using the variance inflation factors function from the *car* package (Fox and Weisberg 2011). Goodness of fit was evaluated using diagnostics plots (i.e., residuals plot and auto-correlation function plot; Burnham and Anderson 2002; Zuur et al. 2010). Models were fitted with different weights and correlation functions to account for heteroscedasticity and temporal auto-correlation when required; models with the lowest AICc values were selected for analyses. Likelihood ratio tests were used to compare final models to respective null models. Analysis of deviance and post hoc multiple comparisons (Tukey's HSD,  $\alpha=0.05$ ) were used to test the effects of species, STL and their interaction with the pathway count and frequency metrics.

## Results

Eighty-two sharks were tracked in Cleveland Bay between 2008 and 2014. The number of individuals tracked per calendar month was high and consistent for all species except *R. taylori* (Supplementary Table 1). The number of resident *R. taylori* varied from 1 to 5 individuals. Activity space size varied substantially among species (Fig. 2). Species had a significant effect on total 50% (ANCOVA,  $F_{(5,81)}=6.19, p<0.05$ ) and 95% (ANCOVA,  $F_{(5,81)}=4.05, p<0.05$ ) KUD size. *Carcharhinus amboinensis* and *C. melanopterus* had the smallest total KUDs, with *C. melanopterus* using approximately half the space of other species. *Rhizoprionodon taylori* and *C. tilstoni* had the largest total KUDs (Fig. 2). Stretch total length (STL) also had a significant effect on total 50% (ANCOVA,  $F_{(1,31)}=13.55, p<0.05$ ) and 95% (ANCOVA,  $F_{(1,31)}=7.94, p<0.05$ ) KUD size (Supplementary Figure 1). A significant negative trend between shark STL and total KUD size suggested as individuals increased in size, space use decreased. In contrast to total KUD results, the model that best explained monthly 50% and 95% KUD size only included species as a factor



**Fig. 2** Mean and standard deviation for total (red squares) and monthly (black circles) **a** 50% and **b** 95% kernel utilisation distributions (KUD) size for each species in Cleveland Bay

(Table 2; Fig. 2). Monthly KUDs revealed the same pattern where *C. amboinensis* and *C. melanopterus* had the smallest and *R. taylori* and *C. tilstoni* had the largest KUDs compared to other species. However, there was no relationship between shark STL and monthly KUD size.

Distribution patterns also differed substantially between species. Overlaying total 50% and 95% KUDs indicated that some species used large portions of the bay while others repeatedly used small, consistent areas (Fig. 3). Collectively, *R. taylori* and *C. sorrah* used more of the bay than other species and used core areas on both sides of the bay. The unique individual distributions of *R. taylori* and *C. sorrah* suggest high intraspecific variability in movement and habitat use. *Carcharhinus amboinensis*, *C. fitzroyensis*, and *C. tilstoni* consistently used the southeastern part of the bay with core areas centralised in shallow regions near river mouths. *Carcharhinus melanopterus* were almost exclusively detected on the western side of Cleveland Bay over reef habitat and adjacent reef-associated rocky/sandy substrate.

Analysis of total 95% KUD overlap showed that all species had some degree of spatial overlap with other species (Fig. 4), however, there was a significant difference in the degree of spatial overlap between species (ANOVA,  $F_{(14, 32261)}=504.48, p<0.05$ ). *Carcharhinus amboinensis*, *C. fitzroyensis*, and *C. tilstoni* exhibited the highest degree of overlap. This was the result of high residency of these species in the southeastern section of the bay. *Rhizoprionodon taylori* exhibited consistent spatial overlap with

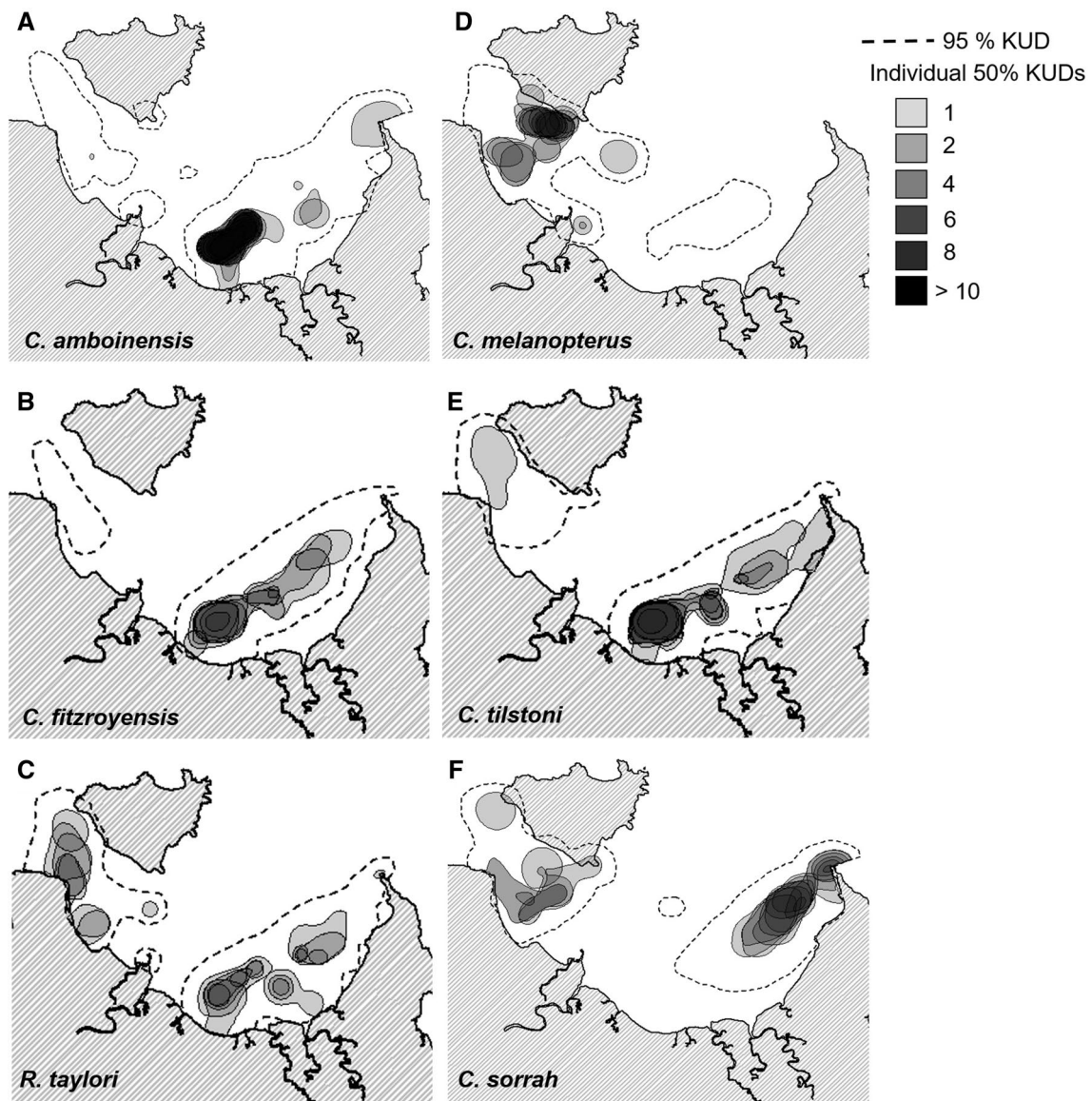
**Table 2** Effect of stretch total length (size) and species on monthly 50% and 95% kernel utilisation distribution (KUD) size (km<sup>2</sup>)

Model	df	50% KUD AICc	95% KUD AICc	50% KUD ΔAICc	95% KUD ΔAICc
KUD ~ 1	3	- 757.1	- 949.7	29.70	24.70
KUD ~ size	4	- 758.7	- 949.9	28.19	24.52
KUD ~ species	<b>8</b>	<b>- 786.8*</b>	<b>- 974.4*</b>	0.00	0.00
KUD ~ size + species	9	- 783.3*	- 971.4*	3.56	3.09

df degrees of freedom, AICc Akaike’s information criterion correction, ΔAICc values are given for each model

AICc values are marked with an asterisk if models were significantly different from the null model using a likelihood ratio test

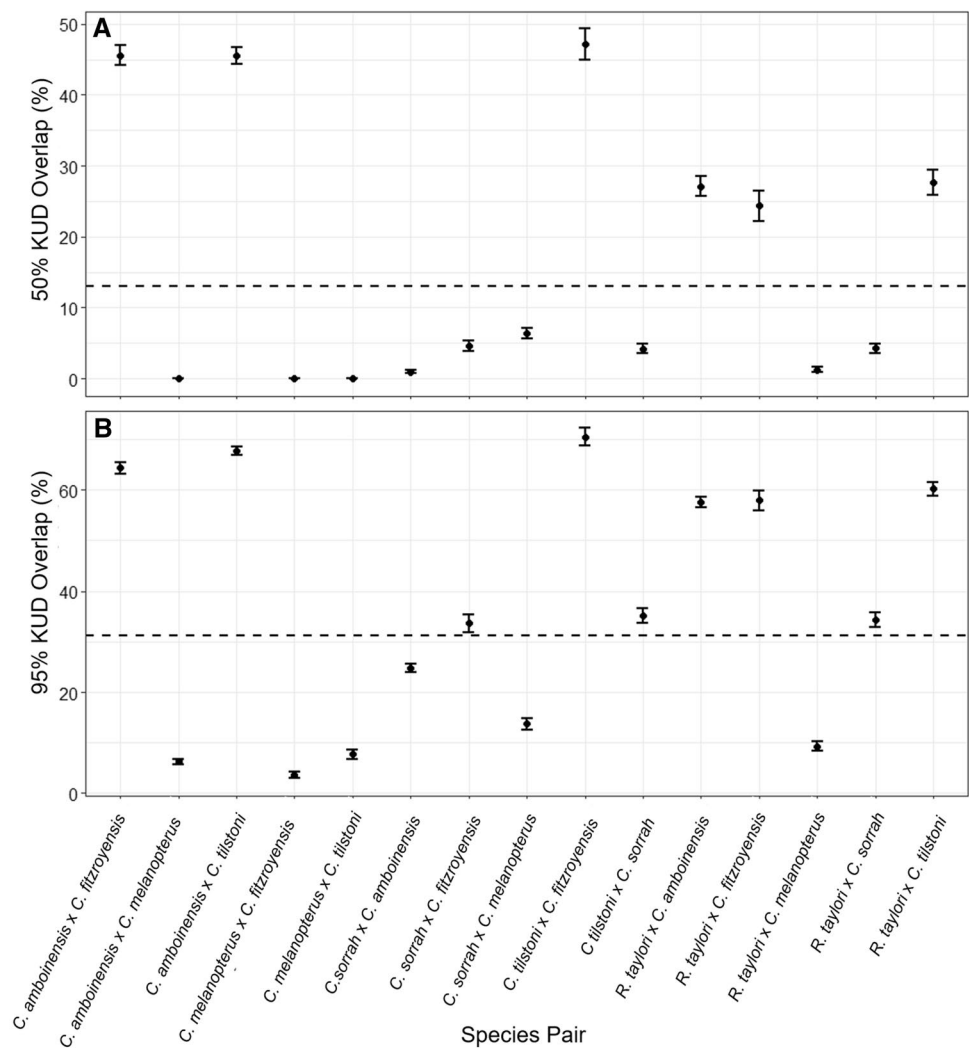
The best fit models are given in bold



**Fig. 3** Total kernel utilisation distributions (KUDs) for **a** *C. amboinensis*, **b** *C. fitzroyensis*, **c** *R. taylora*, **d** *C. melanopterus*, **e** *C. tilstoni* and **f** *C. sorrah*. The 95% KUD contour (dashed line) are the 95%

KUDs (extent of space use) for all individuals combined. The 50% KUDs (core use areas; grey fill) are shown for each individual. Increasingly dark fill indicates more individuals in that area

**Fig. 4** Total 50% (a) and 95% (b) kernel utilisation distribution overlap (%) between species pairs in Cleveland Bay. Points are mean overlap values, lines are standard error. Dotted lines are the mean overlap between all individuals in the study



*C. amboinensis*, *C. fitzroyensis*, and *C. tilstoni*, with mean overlap ranging from 57.5 to 60.1%. Overlap between *C. melanopterus* and all other species was low (< 15%) and driven by limited use of reef and reef-associated habitats by other species. *Carcharhinus sorrah* overlap with all other species (except *C. melanopterus*) was consistent with mean overlap values between 24.7 and 35.1%.

Total 50% KUD overlaps were lower than 95% KUD overlap values and showed greater spatial partitioning between species (Fig. 4). There was a significant difference in 50% KUD overlap between species pairs (ANOVA,  $F_{(14, 32261)} = 583.26$ ,  $p < 0.05$ ). Overlap of 50% KUDs was highest between *C. amboinensis*, *C. fitzroyensis*, and *C. tilstoni*. *Rhizoprionodon taylori* overlap was variable between species pairs, ranging from 1.2 to 27.6%. In contrast, *C. melanopterus* and *C. sorrah* exhibited little or no 50% KUD overlap with other species.

Monthly 50% and 95% KUD overlap values varied significantly between species pairs and months, and there was a

significant interaction between these factors (Table 3). Overlap patterns for monthly 50% and 95% KUDs were consistent with total KUD overlap (Supplementary Tables 2, 3). However, close evaluation of monthly overlap values indicated most species pairs exhibited < 20% variation in overlap between months. In general, species pairs that exhibited low or high total overlap exhibited similar overlap values regardless of time of year. The notable exception to this was *R. taylori*, which exhibited more variable overlap patterns over time. KUD overlap between *R. taylori* and other species varied as much as 50% between consecutive months. This was likely due to the high individual variability in movement patterns and the inconsistent and low number of *R. taylori* monitored each month. Therefore, temporal changes in KUD overlap between *R. taylori* and other species should be interpreted with caution and *R. taylori* were likely driving the observed importance of month in the model output.

Species habitat networks and full CCA (on all six shark species) showed complex habitat partitioning within



**Table 3** Effect of month and species pair on monthly 50% and 95% kernel utilisation distribution overlap (KUDov)

Model	df	50% KUDov AICc	95% KUDov AICc	50% KUDov $\Delta$ AICc	95% KUDov $\Delta$ AICc
KUD~1	3	15,217.1	15,217.13	17,750.05	34,426.83
KUD~month	14	14,717.0*	3986.8*	17,249.96	23,196.49
KUD~species pair	17	1464.9*	-2483.9*	3997.78	16,725.78
KUD~month+species pair	28	822.9*	-3169.8*	3355.80	16,039.92
KUD~month $\times$ species pair	182	<b>-2532.9*</b>	<b>-19,209.7*</b>	<b>0.00</b>	<b>0.00</b>

df degrees of freedom, AICc Akaike's information criterion correction and  $\Delta$ AICc

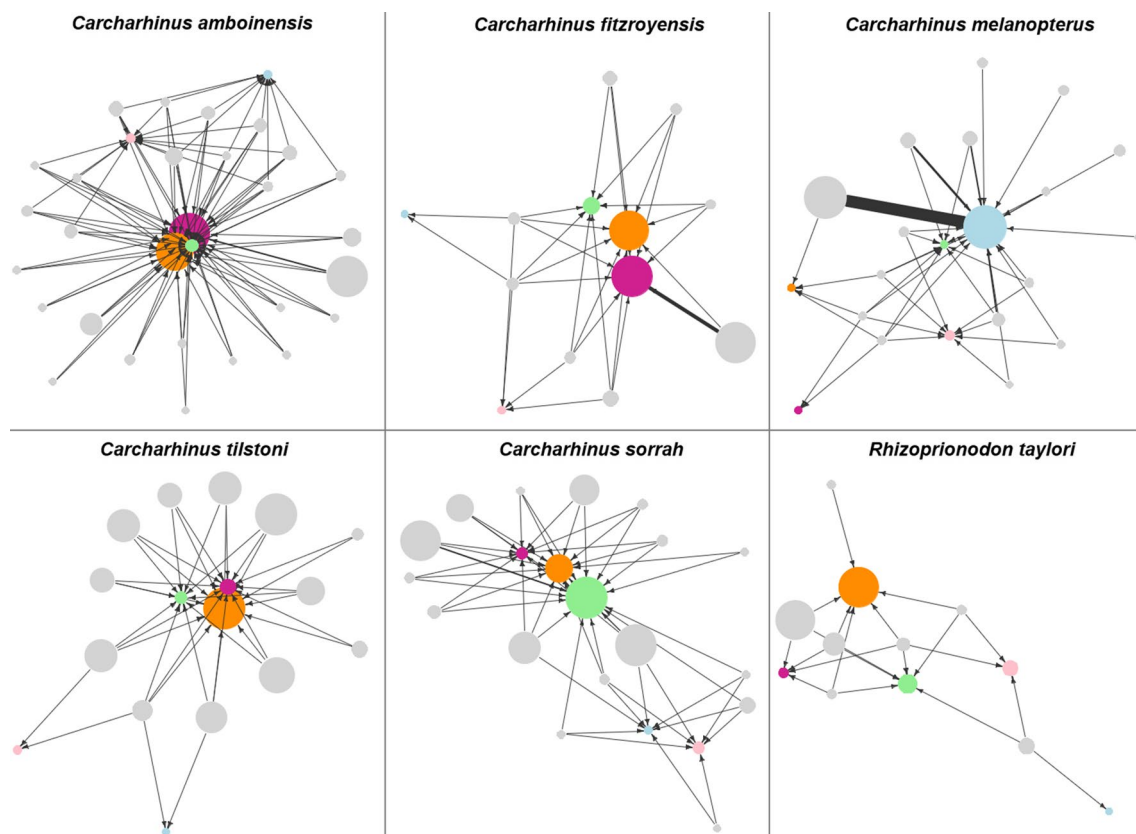
The best fit models are given in bold

AICc values are marked with an asterisk if models were significantly different from the null model using a likelihood ratio test

Cleveland Bay (Fig. 5, 6a and Supplementary Table 4) with *C. melanopterus* using reef and reef-associated habitats more than other species. The other five species followed a depth distribution within the bay with *C. amboinensis* and *C. fitzroyensis* using mudflats followed by *C. tilstoni* and *R. taylori* using seagrass beds and finally *C. sorrah* using deeper habitats (Fig. 6a, b). To confirm this depth distribution pattern, a partial CCA was performed on only five shark species, not including *C. melanopterus*. *Carcharhinus*

*amboinensis*, *C. fitzroyensis*, *C. sorrah*, *C. tilstoni* and *R. taylori* distribution within Cleveland Bay was confirmed by the partial CCA (Fig. 6b). Furthermore, *C. amboinensis*, *C. fitzroyensis* and *C. tilstoni* had a more defined habitat use (smaller ellipses) compared with *C. sorrah* and *R. taylori* in which individuals used various habitats/sides of the bay (western vs. eastern) (Fig. 6b).

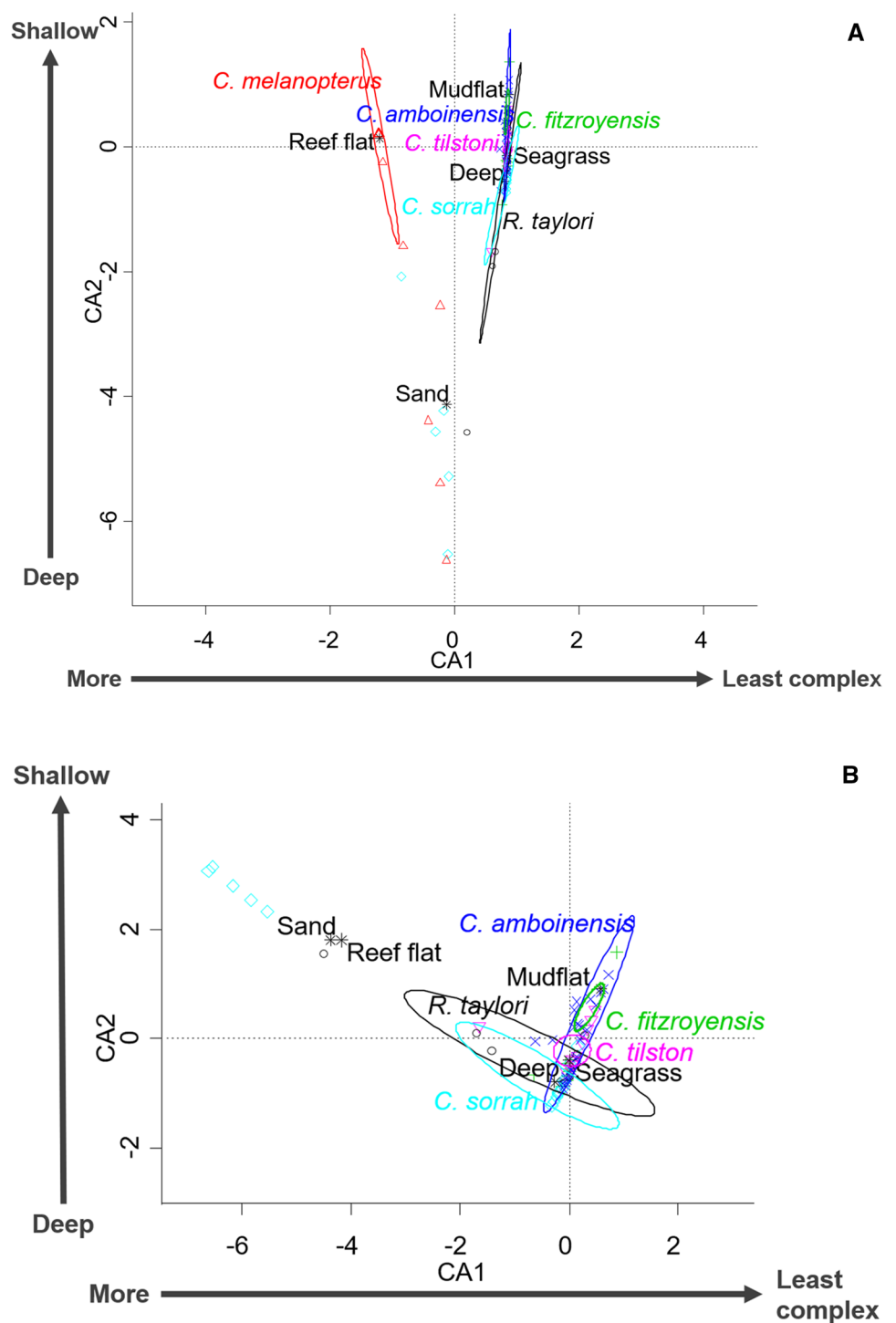
Testing networks (Fig. 7) for random characteristics revealed 4% of *C. amboinensis*, 0% of *C. fitzroyensis*, *C.*



**Fig. 5** Species habitat networks for *Carcharhinus amboinensis*, *C. fitzroyensis*, *C. melanopterus*, *C. tilstoni*, *C. sorrah* and *Rhizoprionodon taylori* within Cleveland Bay, Australia. Node colours represent the different individuals in grey and the different habitat types in

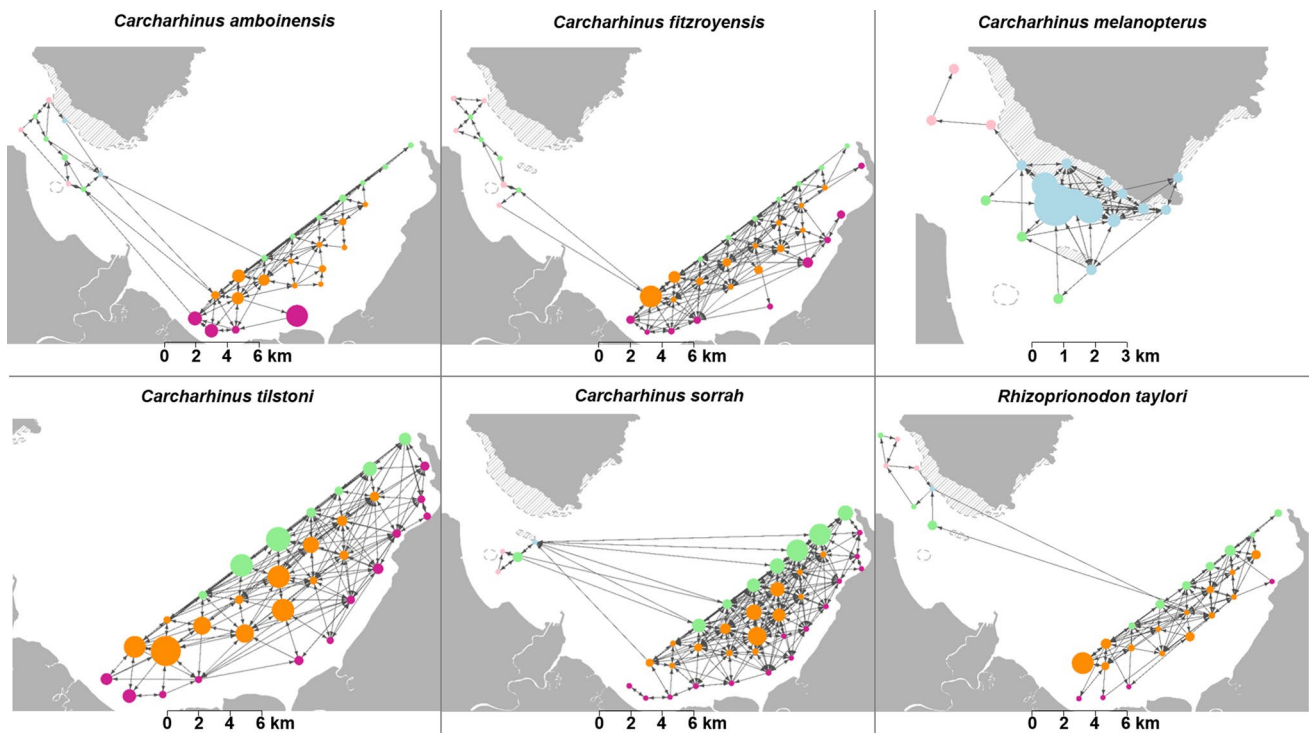
green for deeper habitat within the bay, violet for mudflat, blue for reef flats, pink for sand, orange for seagrass beds. Node size represents the detection count for the individual while in the bay and the frequency of habitat use by the individuals

**Fig. 6** **a** Full canonical correspondence analysis (CCA) showing the position of the six-shark species according to their habitat use. **b** Partial CCA showing the position of five-shark species (not including *C. melanopterus*) according to their habitat use: from more to least complex habitats within the bay on the x-axis and from deeper to shallower habitats within the bay on the y-axis



*melanopterus* and *C. sorrah*, 18% of *C. tilstoni* and 29% of *R. taylori* showed evidence of random movement ( $\chi^2$ ,  $p < 0.05$ ), and these networks were excluded from subsequent analyses. Pathway numbers varied between species (Table 4) with *C. melanopterus* having a significantly lower pathway count than *C. amboinensis* (~90%) and *C. sorrah* (~80%—Table 5a, Supplementary Figure 2). This difference may indicate that *C. melanopterus* moved more selectively

between habitat types than *C. amboinensis* and *C. sorrah*. Pathway frequency (Table 5a, b and Supplementary Figure 3) did not vary significantly between species, although *C. melanopterus* pathway frequency was on average  $\geq 63\%$  higher than any other species. However, the lower pathway frequency median and wider range of *C. melanopterus* suggest that they heavily used a small number of pathways. This result is likely based on the limited amount of reef habitats



**Fig. 7** Example of individual habitat movement network for *Carcharhinus amboinensis*, *C. fitzroyensis*, *C. melanopterus*, *C. tilstoni*, *C. sorrah* and *Rhizoprionodon taylori* within Cleveland Bay, Australia. Node colours represent the different habitat types in green for

deeper habitat within the bay, violet for mudflat, blue for reef flats, pink for sand, orange for seagrass beds. Node size represents the detection count at the habitat used by the individuals

**Table 4** Average pathway count and frequency for six shark species habitat movement networks in Cleveland Bay, Queensland, Australia

	Pathway count			Pathway frequency		
	Mean	Median	Range	Mean	Median	Range
<i>Carcharhinus amboinensis</i>	14.92	13.00	7–31	0.08	0.08	0.03–0.14
<i>Carcharhinus fitzroyensis</i>	13.63	12.50	4–27	0.10	0.08	0.04–0.25
<i>Carcharhinus melanopterus</i>	7.75	6.50	1–27	0.27	0.15	0.04–1.00
<i>Carcharhinus sorrah</i>	13.94	13.50	6–22	0.08	0.08	0.05–0.17
<i>Carcharhinus tilstoni</i>	12.58	9.50	8–29	0.09	0.11	0.03–0.13
<i>Rhizoprionodon taylori</i>	11.57	10.00	8–16	0.09	0.10	0.06–0.13

**Table 5** Species effects on pathway count and frequency

(a) Pathway count			
Factor	$\chi^2$	df	p value
Species	25.84	5	< 0.001*
Fork length	1.21	1	0.27
Species × fork length	9.74	5	0.08
(b) Pathway frequency			
Factor	$\chi^2$	df	p value
Species	7.23	5	0.20
Fork length	0.03	1	0.87
Species × fork length	4.72	5	0.45

Asterisks indicate significant effect ( $p < 0.05$ ) in linear mixed effect

available and subsequently the low number of receivers in this habitat type. The other five species had similar pathway counts and frequencies within their networks, indicating each moved similarly within their habitat. There was no significant effect of STL or species and STL interaction on tested metrics (Supplementary Table 5).

Mean pathway frequency was 0.21 with a median at 0.05 which suggests that a small number of pathways was heavily used compared to others. At the pathway level, frequencies differed between types with pathways within the same habitat type more frequently ( $> 0.05$ ) used (ranging from 0.75 to 1.64) than pathways between different habitat types (ranging from 0.004 to 0.50; Supplementary Figure 3). Furthermore, within habitat pathways were more frequently ( $> 0.05$ ) used by most species. For example, pathways between seagrass beds were frequently used by *C. amboinensis*, *C. fitzroyensis*, *C. tilstoni*, *C. sorrah* and *R. taylori*, while pathways between mudflats were highly used by *C. amboinensis*, *C. fitzroyensis*, *C. tilstoni* and *R. taylori*. This suggests that species moved frequently within their main habitat types (Fig. 5). Pathway frequencies also differed with the region of the bay or with pathway frequency within the same region (east or west) ~92% higher than pathways crossing from one side to the other (Supplementary Figure 3). This may suggest that species mostly used one region within the bay and supports the consistent, relatively small 50% KUD estimates derived.

## Discussion

Coastal habitats are widely recognised as productive areas that support an array of ecosystem services and species. Use of coastal habitats by elasmobranch species has been documented for decades (Springer 1967; Castro 1993), but little attention has been paid to how coexisting species interact. Research by Yates et al. (2015) and others (e.g., Simpfendorfer and Milward 1993; Bethea et al. 2004, 2015) has revealed overlapping distributions of a number of shark species in coastal systems, but few have considered whether coastal habitats are simply productive enough to support these shark species assemblages, or whether species partition habitats, space or prey to reduce or avoid competition. Competition for resources can be detrimental to species, resulting in decreased growth and survivorship (McMahon and Tash 1988; Webster 2004; Benkwitt 2013). Therefore, species will often go to great lengths to reduce competition, including using less favourable habitats, reducing the number of resources they utilise, or moving to new areas (Fausch and White 1981; Taylor et al. 2013). Here, we have demonstrated that six coexisting elasmobranch species from the same family use different habitat types, movement strategies, and amounts of space within a productive coastal bay,

which may be indicative of niche separation to reduce competition for resources.

Differences in space use observed in the monitored species are likely due to two primary factors. First, the range of habitat types present within Cleveland Bay, from coral reef to mudflat and deeper water habitats, could explain species distinct distributions, possibly due to their unique and strong habitat preferences. For example, *C. melanopterus* used the smallest amount of space of any tracked species, had relatively consistent KUD locations, and had highly specialized habitat networks that almost exclusively included reef and reef-associated habitat receivers. This pattern is likely the result of the high dependence of this species on reef and associated habitats and the small and localised amount of these habitats available within Cleveland Bay. Our findings are consistent with the previous analysis by Chin et al. (2013a) who concluded that Cleveland Bay provides a critical habitat for juvenile and adult female *C. melanopterus*. In contrast, *R. taylori*, which had the largest KUDs and most diverse habitat use network, has been shown to be more flexible in its habitat use (Munroe et al. 2014). This flexibility might allow *R. taylori* to move more broadly than species with higher habitat dependence or more specific preferences. The movement patterns, space use, and habitat preferences shown by the six species thus provide for some degree of spatial separation that should reduce the competition for prey. This is supported in part by observations of overlap in diet among species (Simpfendorfer and Milward 1993; Kinney et al. 2011) which would suggest spatial separation is required to reduce competition for resources.

The second factor likely driving species-level variation in space use was that the species tracked had differing life history strategies and were monitored at different stages of maturity. Several species in this study are slow growing and large bodied with low productivity, while others are small to medium bodied, fast growing and highly productive. For example, *C. amboinensis* and *C. tilstoni* only use Cleveland Bay as juveniles with individuals recruiting offshore as they mature. *Carcharhinus melanopterus* has a somewhat similar strategy with juveniles and adult females using the bay, with large males rarely being present (Chin et al. 2013a). Tracking of *C. amboinensis* and *C. melanopterus* has revealed ontogenetic changes in space use by year classes of juvenile individuals with increasing size and age (Knip et al. 2011; Chin et al. 2016). The remaining species (*C. fitzroyensis*, *C. sorrah*, *R. taylori*) use nearshore coastal embayments throughout their life, and adults and juveniles often have overlapping home ranges (Knip et al. 2012; Munroe et al. 2014, 2015). Juveniles of slow-growing, large-bodied species typically use restricted home ranges which increase as they grow (e.g., Duncan and Holland 2006; Conrath and Musick 2010). This space use strategy is believed to decrease the risk of predation and help ensure survival until

reproductive maturity (Heupel et al. 2007). This is likely why juvenile *C. amboinensis* used relatively small amounts of space and a consistent area of the bay. In contrast, small-bodied *C. sorrah* and *R. taylori* may be less risk averse, because their growth rate means they reach maturity more rapidly than species with lower productivity and the greater proportion of individuals reaching maturity can offset the predation risk that results from moving broadly to obtain resources (Knip et al. 2010; Munroe et al. 2014). Thus, differences in age classes tracked and species life history may help explain the contrasting distribution and habitat use patterns of elasmobranchs in Cleveland Bay.

Individual size also appeared to affect activity space size at the community level. Species with the largest activity spaces included the smallest individuals tracked (*R. taylori*) and juveniles of one of the large-bodied species (*C. tilstoni*), while species with the smallest KUDs included larger individuals of *C. melanopterus* and *C. amboinensis*. Collectively, these results indicated that as size increased, home range size decreased. This result appears counterintuitive, because previous work with sharks, as well as a wide range of other species, has shown that activity space size generally increases with body size (Knip et al. 2011; Tamburello et al. 2015). However, the negative trend observed in the present study may be explained by the fact that most species tracked were small-bodied adults or juveniles of large-bodied species. As previously discussed, the life history of the large-bodied species dictates that they will move offshore as they increase in size. This strategy limited our ability to collect movement data for larger *C. amboinensis* and *C. tilstoni*. Adult female *C. melanopterus* were the largest individuals in the data set. Their highly restricted home range, even at large sizes, was therefore the likely driver for this result.

Examination of spatial overlap indicated differences in overlap between species, but also between spatial scales. Overlap ranged from 9 to 70% for 95% KUDs which suggests some species may share large amounts of space. However, the temporal resolution of this analysis is insufficient to determine whether individuals were in the same areas at the same time. In contrast, 50% KUD overlap was greatly reduced (0–47%), indicating that core areas where individuals spent the majority of their time had limited overlap. This result suggests the species in this study used distinct core areas and adopted different space use and movement patterns. Network analyses and the CCA analysis support this finding through the presence of high numbers of pathways within the same habitat, and clear differences in the habitats used by the species. This indicates consistently high use of key habitat types. It is possible that these species partition core areas within selected habitats as a means of niche separation. These results are consistent with previous studies of spatial and dietary overlap of aquatic predator communities. Matich et al. (2017) found that co-occurring bull

sharks, alligators, and dolphins within the resource-limited Shark River estuary (Florida, USA) partitioned both habitat and dietary resources, suggesting these predators used a combination of strategies to reduce competition. Similarly, White and Potter (2004) found evidence of habitat partitioning in a diverse coastal shark community where shark species composition changed markedly between different habitat types. The diverse habitat structure of Cleveland Bay may ultimately play an important role in supporting local elasmobranch habitat partitioning and coexistence. Highly complex ecosystems can facilitate and sustain coexistence by providing species with a variety of distinct and non-overlapping habitats and resources (Almany 2004a, b). Given the similarity in size of most species and commonalities in diet (Simpfendorfer and Milward 1993), it is likely they are in direct competition for prey resources. Thus, the combination of habitat selection and amount of space used might provide a mechanism to reduce interactions and increase survival.

The highest amount of overlap occurred in the southeast corner of the bay where *C. amboinensis*, *C. fitzroyensis* and *C. tilstoni* co-occur. These three species showed 45–47% overlap in their 50% KUD areas, the highest of all species combinations. Species habitat networks based on CCA revealed smaller ellipses for these species and consistent movement within their habitat type (mudflat and seagrass). Consistent use of this area combined with high overlap suggests this region is critical to these three species. It is unclear what benefit is derived from this location. It is possible that this area, which is located near primary river outflows, is highly productive and provides adequate prey resources for these species to coexist. Analysis of the stable isotopes of sharks in Cleveland Bay has shown evidence of some partitioning of prey resources (Kinney et al. 2011), but only amongst some groups of species. They demonstrated that *C. amboinensis* and *C. fitzroyensis* consume different prey and feed at different trophic levels, while *C. fitzroyensis* and *C. tilstoni* have similar diets (Kinney et al. 2011). This suggests that both spatial and dietary partitioning are occurring in Cleveland Bay, and this likely reduced the competition for resources. Dietary partitioning has previously been observed in elasmobranch assemblages (White et al. 2004; Heithaus et al. 2013; O’Shea et al. 2013) and is considered an important way by which elasmobranchs may limit competition in shared areas (Marshall et al. 2008; Sommerville et al. 2011; Yick et al. 2011). The shallow nature of this habitat may also provide protection from predation. Since *C. amboinensis* and *C. tilstoni* are both long-lived species with low productivity, survival of juveniles is critical for population persistence (Kinney and Simpfendorfer 2009). Therefore, predator avoidance may be a key strategy for these species at these early life stages. The shared use of small but protected shallow nurseries may in fact be

a calculated ecological trade-off between the benefits of increased predator avoidance and the negative effects of increased competition for limited resources (Heithaus 2007; Matich and Heithaus 2015). It may be that a combination of these factors is ultimately what drives or enables the use of this area despite the large amount of distributional overlap and potential for competition.

While there are potential detriments to communal habitat use by sharks (e.g., competition for resources), this strategy would not occur if there were no benefits to the species. One potential benefit is increased protection from predation, because adults of large-bodied species are often spatially segregated from their young. This ontogenetic segregation may reduce predation of all species that coexist with young of these species (Simpfendorfer and Milward 1993). This allows individuals of all species to be less vigilant against predation and devote more energy to other important tasks, such as foraging (Beauchamp 2003; Sridhar et al. 2009). In addition, if social behaviours are present, co-occurring individuals may work together to capture prey (Ebert 1991) or learn from one another. For example, Guttridge et al. (2013) have shown that juvenile lemon sharks can learn behaviours from trained conspecifics. Therefore, shared space use and periodic overlap may be beneficial for populations.

Long-term tracking of six shark species revealed distinct differences in their space use that may increase their survival by reducing competition and exposure to predators. Subtle differences in the amount of space used and location of those spaces within coastal bays may provide adequate separation to allow a suite of similar species to coexist. Habitat selection appears to play a key role in the distribution of these species and their ultimate use of the bay. This indicates the importance for maintaining intact ecosystems with a variety of habitat types (Almany 2004a, b). Because it is unclear which ecosystem services are most crucial to these species (prey abundance, preferred environmental conditions, predator avoidance), we must maintain the health of coastal bays and estuaries that serve as critical habitat for multiple life stages of elasmobranch and other resident populations.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All research was conducted in accordance with James Cook University (JCU) animal ethics permit A1566 and Great Barrier Reef (G11/346181.1) and QDAF (144482) permits for animal collection.

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