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Final Report

Drivers of juvenile shark biodiversity and abundance in inshore ecosystems of the Great Barrier Reef

Colin A. Simpfendorfer, Andrew J. Tobin, Michelle R. Heupel, Peter Yates and Samantha Munroe

Australian Government
Department of the Environment

Reef & Rainforest RESEARCH CENTRE

Drivers of juvenile shark biodiversity and abundance in inshore ecosystems of the Great Barrier Reef

Final Summary

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Introduction

Sharks play an important role in marine ecosystems but are facing increasing pressure from fishing and other anthropogenic factors (Dulvy et al. 2014). Along the Queensland coast inshore waters play an important role as nursery areas for sharks (Simpfendorfer & Milward 1993). However, the same inshore waters are also most prone to fisheries exploitation (Harry et al. 2011) and effects of freshwater discharge from coastal streams and rivers (Knip et al. 2011). This project examined the importance of different types of inshore habitat (protected bay vs open coastline) and marine park zoning (open and closed to gillnet fishing), and how environmental factors such as freshwater discharge from rivers effect how these nursery areas function. The project has two broad objectives:

A. Investigate the spatial and temporal changes in the biodiversity and abundance of sharks in inshore nursery areas along the central GBR coast.
B. Determine the effect of environmental drivers on inshore shark biodiversity along the central GBR coast.

The first of these objectives was achieved by undertaking seasonal surveys in a number of bays along the central Great Barrier Reef (GBR) coast. The second objective was achieved in two ways. Firstly, by collecting environmental data during the nursery area surveys and relating these data to the presence and abundance of shark caught; and secondly, by conducting acoustic monitoring studies in shark nursery areas that enabled environmental data to be related to the movements of sharks. Two species of common inshore shark were examined in detail as part of this work – the creek whaler (*Carcharhinus fitzroyensis*) and Australian sharpnose shark (*Rhizoprionodon talyori*).

Methodology

Shark nursery area surveys

Study areas

Sampling was conducted within coastal bays along approximately 400 km of the tropical north coast of Queensland (146.0–148.8ºE, 18.1–20.6ºS; Figure 1). Initially, nine bays were sampled from November 2011–March 2012. Thereafter, a subset of five bays, ranging in size from approximately 200–500 km2 (Table 1), was selected for ongoing seasonal sampling: Rockingham, Bowling Green, Upstart, Edgecumbe and Repulse Bays. This selection included a variety of habitat types and environmental characteristics, and thus permitted investigation of spatial diversity in the distribution patterns of sharks as well as the factors that influenced this diversity.

The coastal environments sampled were spatially and temporally variable. For example, rainfall was seasonal with 60–80% typically occurring during the summer wet season (November–April), which in turn influenced significant seasonal fluctuations in the physical and trophic dynamics of these systems. The supply of freshwater from rivers typically varied among the bays depending on catchment size and the spatial distribution of rainfall. Average river runoff volumes, presented as a general guide in Table 1, should be viewed with consideration of inter-annual fluctuation and transport of river plumes beyond their bay of origin. Typically, the earth's Coriolis force and south-easterly trade winds combine to deflect river plumes towards the north. For example, large flood plumes from the Burdekin River can extend for hundreds of kilometres along the coast and influence physio-chemical conditions in Bowling Green, Cleveland, Halifax and Rockingham Bays.

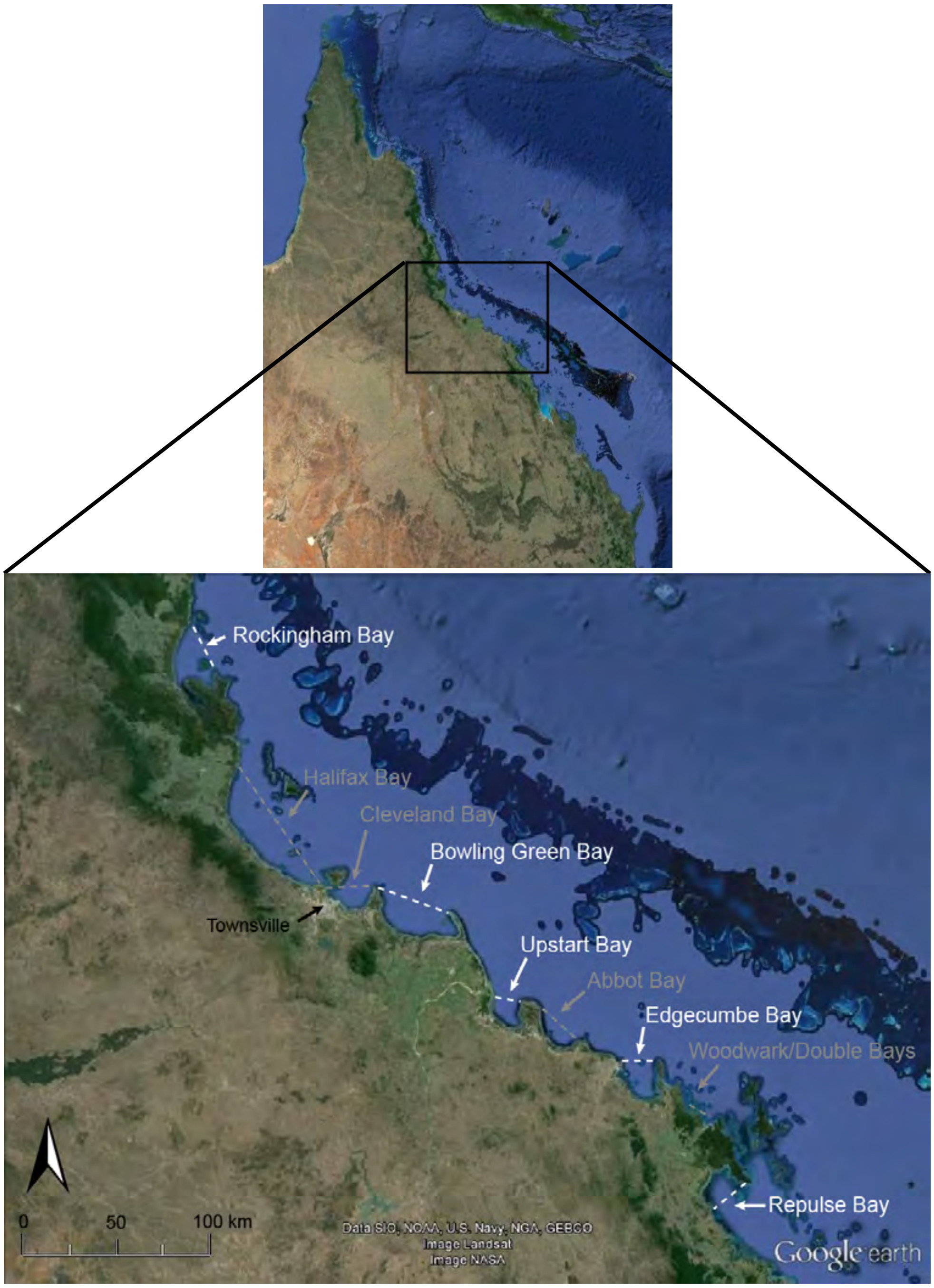

Figure 1: Study region. Google EarthTM aerial image of the nine study bays and their location along northern Queensland, Australia.

Table 1: Details of bays surveyed for juvenile sharks along the central Great Barrier Reef coast.

Bay	Size (km^2)	GBRMPA zones (largest areas in bold)	Freshwater input (adjusted runoff volume, km^3)[2]
Rockingham*	481.7	**General use, conservation park**, habitat protection, marine national park	High. Tully River (3.29), Murray River (1.06)
Halifax	1180	**General use, marine national park,** conservation park, habitat protection	High. Herbert River (4.01), Black River (0.38)
Cleveland	247.4	**Non marine park (port zone), conservation park**, general use, habitat protection	Moderate. Ross River (0.49)
Bowling Green*	518.9	**General use, marine national park**, conservation park, habitat protection	Moderate. Haughton River (0.74)
Upstart*	219.8	**General use, marine national park**, conservation park, habitat protection	Limited. Burdekin River (10.29; usually transported north[2])
Abbot	126.4	**General use**, conservation park, habitat protection, marine national park	Limited, Don River 17km to the ESE (0.75)
Edgecumbe*	365.5	**Habitat protection,** general use zone, conservation park	Limited
Woodwark/Double	31.3	**General use**, conservation park, habitat protection, marine national park	Negligible
Repulse*	277.9	**Marine national park**, general use, habitat protection	Moderate. Proserpine River (1.08), O'Connell River (1.54)

The bays were shallow (predominantly < 15 m) and sheltered from ocean swells by the Great Barrier Reef. Consequently, they were dominated by silty substrates and mudflat or mangrove-lined foreshores. Seagrass abundance was higher during the dry season, and in areas with low or medium relative wave exposure and a small tidal range.

All sampling sites were within the Great Barrier Reef Marine Park which includes a variety of management zones defining the activities which can occur in specific locations. North Queensland's East Coast Inshore Finfish Fishery (ECIFF) accounts for the majority of commercial shark landings. Carcharhiniform sharks contribute a large component of the ECIFF as well as a small component of local recreational fisheries.

Surveys were designed to facilitate comparison of shark catch between multiple bays throughout the year. Between November 2011 and March 2014, eight rounds of fishery-independent surveys were undertaken to collect data on shark fauna across the region. In each round, the bays were sampled in an order largely guided by weather conditions. Within each bay, sampling occurred randomly within 16 0.9-km-wide strips. Two groups of eight strips were placed within each bay to spread the sampling across different habitat types and management zones where possible (i.e. open and closed to commercial gill-net fishing). During each round, each bay was sampled over four days allowing for two days of sampling in each group of strips. The bays vary in size and so the relative proportion of the area and coastline sampled varied between bays.

Sampling methods

Two methods were used to sample across a broad range of shark sizes. A minimum of five longline shots or four gill-net shots were deployed per day between dawn and dusk. A random-number generator was used to select transect strips to be sampled on each day. During a total of 183 days of sampling, 504 longline shots and 386 gill-net shots were deployed totaling 413.3 and 349.0 h, respectively. Sampling in five focal bays spanned 162 days.

Bottom-set gill-nets comprised 18-ply, 11.4-cm-stretched monofilament mesh with a depth of 33 meshes (c. 3.2 m fishing depth). A single gill-net was deployed for c. 1 h (81% between 45 and 75 min) and checked every 15 min to minimise capture mortalities, and facilitate tagging and release. In accordance with the Great Barrier Reef Marine Park Authority's Dugong Protection Areas, a maximum net length of 200 m was used in 'Dugong Sanctuary A' zones (Cleveland Bay, Upstart Bay and southern portions of Rockingham and Halifax Bays) and within 2 m water depth in 'Dugong Sanctuary B' zones (Bowling Green Bay, Edgecumbe Bay and northeastern Repulse Bay). Gill-nets up to 400 m in length were used elsewhere.

Bottom-set longlines comprised 800 m of 6-mm nylon mainline, with an anchor and float at both ends. Gangions were attached to the mainline c. 8–10 m apart, and comprised 1 m of 4-mm nylon cord, 1 m of 1.5-mm wire leader, and a baited size 14/0 Mustad tuna circle hook. A variety of fresh and frozen baits were used, which consistently comprised a combination of squid *Loligo* sp. and various teleost fish (butterfly bream *Nemipterus* sp., blue threadfin *Eleutheronema tetradactylum* and mullet *Mugil cephalus*). Up to two longlines were deployed simultaneously for c. 40 min sets (72% between 40 and 60 min). Longline and gill-net shot durations were the length of time in which the entire gear was deployed (i.e. excluding the time taken to deploy and retrieve the gear). Longline and gill-net sampling was conducted in water depths of 0.5–5 m. Longlines were usually deployed parallel to the shore whereas gill-nets were deployed perpendicular to the shore or significant depth contours where possible. Each round comprised a minimum of eight gill-net samples bay–1 round–1 and 10 longline samples bay–1 round–1.

Captured sharks were identified to species level, tagged on the first dorsal fin (Dalton Rototag or Superflex tag), measured, sexed, assessed for clasper calcification, examined for umbilical scar condition, and released at their capture site. Small sharks (≤ 1000 mm) were placed ventral side down on a measuring board and measured to the nearest mm with the upper lobe of the caudal fin depressed in line with the body axis. Larger sharks were secured beside the boat and measured to the nearest cm with a measuring tape. Additional measurements of fork length and pre-caudal length were recorded.

Life-history stage was determined using length-at-age data and observation of umbilical scars and clasper calcification. Young-of-the-year (YOY) sharks were either ≤ length at one year or had un-healed umbilical scars. Juvenile sharks were between the length at one year and length at 50% maturity. Mature sharks were ≥ length at 50% maturity or were males with calcified claspers. Some sharks escaped prior to the collection of these data and thus their life-history stage was unknown.

Two morphologically similar species, Australian blacktip *Carcharhinus tilstoni* and common blacktip *Carcharhinus limbatus*, were indistinguishable in the field and therefore grouped together as unidentified blacktip sharks *C. tilstoni*/ *C. limbatus*. *Carcharhinus limbatus* matures at a larger size than *C. tilstoni* and therefore the proportions of each life-history stage for unidentified blacktip sharks were considered approximations. The length-at-age estimates for *C. tilstoni* were used to determine life-history stage to ensure that no mature sharks were misclassified as immature.

For each fishing deployment, water depth was recorded to the nearest 0.1 m using the vessel's depth sounder (Garmin EchoTM 500C) and taken as the mean of measurements from both ends of the deployment. Sea-surface water temperature (ºC), salinity (ppt), and

DO (mg/L) were recorded using a YSI Model 85 multiprobe (YSI Incorporated). Secchi depth was recorded to the nearest 0.1 m as a proxy for turbidity. The secchi disk was visible on the sea floor during 7% of fishing shots, however these occurrences were spread across the full range of depths sampled. Therefore, the secchi disk being visible on the bottom was not a reliable indicator of low turbidity and so these occurrences were treated as missing values (e.g. in shallow water the secchi disk may be visible on the bottom even in relatively turbid conditions). Geographic coordinates were recorded at both ends of fishing deployments. Mangrove proximity was calculated using ArcMap 10.2.1 (ESRI) as the shortest straight-line distance (km) to any mangrove polygon within the same bay.

Data analysis

A wide range of analytical approaches were used to analyse the survey data. Detailed methods can be found in the Final Report for Project 6.2 or the published scientific papers:

- Yates PM, Heupel MR, Tobin AJ, Moore SK, Simpfendorfer CA. Diversity in immature shark communities along a tropical coastline. In press at Marine and Freshwater Research.
- Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA. Spatio-temporal occurrence patterns of young sharks in tropical coastal waters. Submitted to Marine Biology.
- Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA. Ecological drivers of shark distributions along a tropical coastline. Submitted to PLOS ONE.
- Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA. Benefits of Marine Protected Areas for tropical coastal sharks. To be submitted to Biological Conservation

Acoustic monitoring

Study site

Acoustic monitoring was conducted in Cleveland Bay, Queensland, a shallow embayment on the northeast coast of Australia (Figure 2). Cleveland Bay covers an area of approximately 225 km2, is 27 km wide, and the majority of the bay has a depth of less than 10 m and a maximum tidal range of 4.2 m. The dominant habitat is soft mud substrate and to a lesser extent sandy substrate. The bay also contains patches of seagrasses (*Cymodocea serrulata, Halophila* spp., *Halodule uninervis*) and coastal reefs. The southern shore of the bay is lined with mangroves. The main river outlets are on the southeastern side of the bay and are adjacent to intertidal mudflats and seagrass habitat. Sixty-three VR2W acoustic receivers (Vemco Ltd., Canada) were deployed inside Cleveland Bay to monitor shark movements. Receivers were deployed in primary habitat types within the bay, specifically intertidal mudflats, outer bay mud substrate (> 5 m depth), sandy inshore substrate, reefs, and seagrass. Data were downloaded from receivers every three months. An additional nine receivers were deployed by the Australian Institute of Marine Science (AIMS) in Bowling Green Bay adjacent to the southeast of Cleveland Bay. The majority of these receivers were deployed between depths of 9.2 to 11.0 m with mud substrate. Therefore they were classified as outer bay mud substrate receivers. Data from these receivers were not included in habitat, space use, or residency analysis.

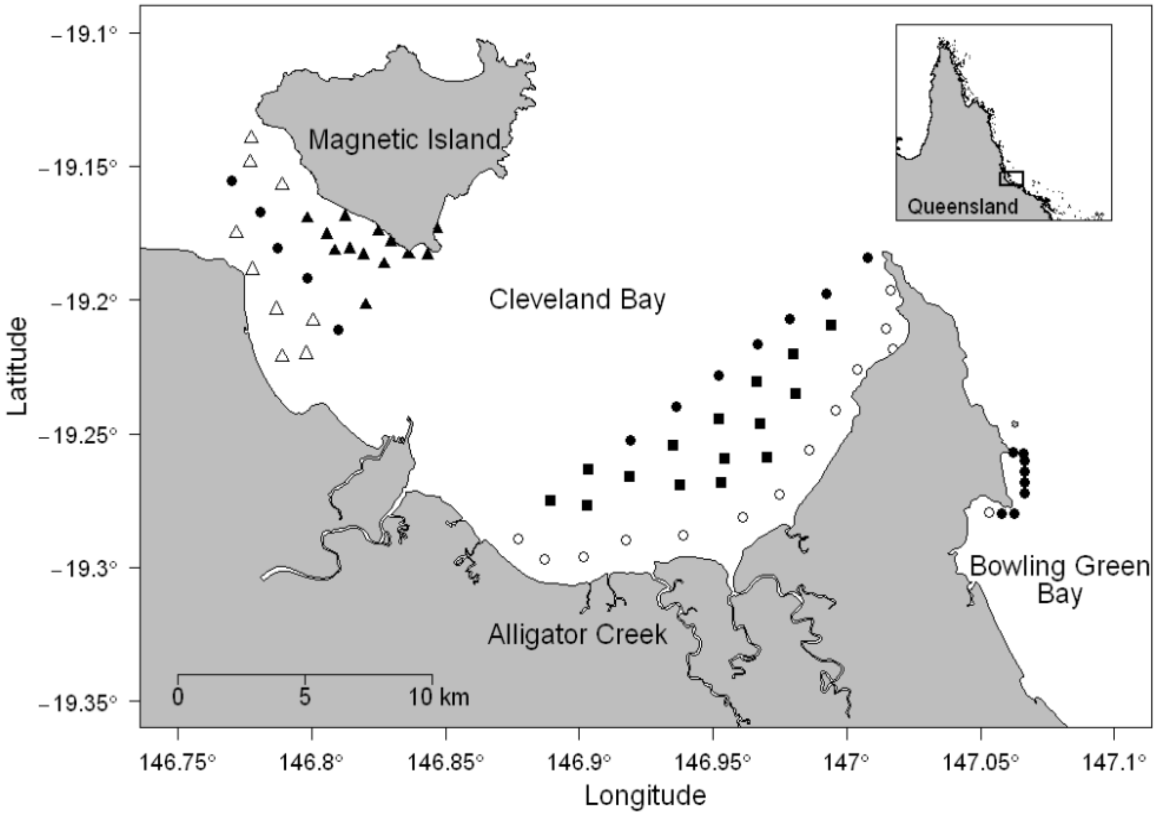

Figure 2: Locations of acoustic receivers in intertidal mudflat ( ), seagrass ( ), outer bay mud substrate (Δ), inshore sand ( ), and reef habitat ( ) in Cleveland Bay, Queensland, Australia.

Rhizoprionodon taylori and *Carcharhinus fitzroyensis* were captured using bottom-set 400-m long-lines, 200-m long 11.45-cm mesh gillnets, and baited rod and reel. Long-lines were made of 6-mm nylon mainline that was anchored at both ends. Gangions were composed of 1m of 4-mm nylon cord and 1 m of 1.5-mm wire leader. Approximately 50-70 size 14/0 Mustad tuna circle hooks were used per long-line and baited with butterfly bream (*Nemipterus* sp.), squid (*Loligo* sp.), blue threadfin (*Eleutheronema tetradactylum*) or mullet (*Mugil cephalus*). Long-lines were set for 45 to 60 minutes, gillnets were set for 15 to 20 minutes.

Rhizoprionodon taylori were fitted with V13 acoustic transmitters and *C. fitzroyensis* fitted with V16 transmitters. Transmitters were implanted into the body cavity to ensure long-term retention. An incision was made and the transmitter inserted into the body cavity. The incision was closed with absorbable sutures. Individuals were measured to the nearest millimeter stretch total length (STL), sexed, tagged with an individually numbered rototag in the first dorsal fin, and released. Range testing analysis found transmitters had a maximum detection range of 525 m based on 0.05 probability of detection and emitted a unique code as a pulse series at 69 kHz. Unique transmitter codes allowed for the identification of individuals.

Data analysis

A wide range of analytical approaches were used to analyse the acoustic telemetry data. Detailed methods can be found in the Final Report for Project 6.2 or the published scientific papers:

- Munroe SEM, Simpfendorfer CA, Heupel MR. Habitat and space use of an abundant nearshore shark, *Rhizoprionodon taylori*. Marine and Freshwater Research 65:959-968.
- Munroe SEM, Simpfendorfer CA, Molony J, Heupel MR. Nearshore movement ecology of a medium-bodied shark the creek whaler *Carcharhinus fitzroyensis*. Submitted to Animal Biotelemetry.

Results and Discussion

Shark nursery area surveys

A total of 1806 sharks were captured from six families, comprising 84% of the total elasmobranch catch by number (Table 2). Of the 22 shark species encountered, 19 species of carcharhiniform sharks made up 99.2% of the total shark catch. *Rhizoprionodon taylori* (52%) and *C. tilstoni/ C. limbatus* (12%) were numerically dominant. *Carcharhinus sorrah* (7%), *Carcharhinus amboinensis* (5%), *Sphyrna lewini* (5%), *Rhizoprionodon acutus* (5%) and *Carcharhinus coatesi* (5%) were moderately abundant. Species selectivity varied between longlines and gill-nets with some species captured predominantly by one gear type. For example, longlines contributed 96% and 70% of the total catch of *C. sorrah* and *R. acutus*, respectively. Conversely, gill-nets captured 77% of *S. lewini.*

Length-frequency distributions for the eight most abundant shark species indicated interspecific variation in body sizes and the proportion of immature sharks (Figure 3). Overall, small sharks (i.e. < 1 m stretch total length) comprised 88% of all measured sharks. Further, mature and immature sharks shared similar cumulative length profiles (Figure 4), indicating broadly similar body sizes across the sampled community. Although there was overlap in stretch total lengths between longline and gill-net caught individuals, the length-frequency distributions were significantly different (KS-test, $D = 0.31$, $P < 0.00$). Longlines sampled a broader range of sizes (325–3700 mm, mean ± SD = 848 ± 335 mm, n = 896) compared to gill-nets (395–2550 mm, mean ± SD = 708 ± 197 mm, n = 86).

Of the 1806 sharks, 1196 were mature and 567 were immature, including 336 YOY individuals, and 43 did not have maturity stage recorded. Excluding the abundant *R. taylori*, 308 sharks were mature and 519 were immature including 296 YOY. Eighteen of 22 shark species occurred as YOY or juveniles, however there was interspecific variation in the life-history stages present. Samples of *C. tilstoni/ C. limbatus, S. lewini, C. amboinensis, C. leucas, Sphyrna mokarran* and *Carcharhinus brevipinna* were biased towards immature individuals. In contrast, *R. taylori* and *C. coatesi* were predominantly mature.

Table 2: Life-history stage composition of 22 shark species captured during fishery-independent sampling along the tropical coast of Queensland. Data are pooled across study bays and sampling rounds (years 2012 and 2013 only). The number of sharks in each category is followed by its proportion of the species' total maturity-assigned catch in parentheses. YOY = young-of-the-year. In the presence of > 1 life-history stage the most prevalent stage is indicated in bold. Details of bays surveyed for juvenile sharks along the central Great Barrier Reef coast.

			Life-history stage				
Family	Species	Common name	YOY	Juvenile	Mature	Unknown	Total
Carcharhinidae	*Carcharhinus amboinensis*	Pigeye shark	**47 (0.49)**	**47 (0.49)**	1 (0.02)	4	99
	Carcharhinus brevipinna	Spinner shark	**3 (0.60)**	2 (0.40)		1	6
	Carcharhinus cautus	Nervous shark		5 (0.28)	**13 (0.72)**		18
	Carcharhinus coatesi	Whitecheek shark	4 (0.05)	2 (0.02)	**81 (0.93)**		87
	Carcharhinus fitzroyensis	Creek whaler	4 (0.15)	10 (0.38)	**12 (0.46)**	1	27
	Carcharhinus leucas	Bull shark	5 (0.45)	**6 (0.55)**			11
	Carcharhinus macloti	Hardnose shark			3 (1.00)		3
	Carcharhinus melanopterus	Blacktip reef shark			1 (1.00)		1
	Carcharhinus sorrah	Spot-tail shark	26 (0.20)	33 (0.25)	**73 (0.55)**	1	133
	Carcharhinus tilstoni/ C. limbatus	Unidentified blacktip	**110 (0.51)**	71 (0.33)	35 (0.16)	7	223
	Galeocerdo cuvier	Tiger shark	1 (0.11)	**5 (0.56)**	3 (0.33)	8	17
	Rhizoprionodon acutus	Milk shark	17 (0.19)	19 (0.21)	**54 (0.60)**		90
	Rhizoprionodon taylori	Australian sharpnose	40 (0.04)	8 (0.01)	**888 (0.95)**	10	946
		Unidentified whaler shark				9	9
Hemigaleidae	*Hemigaleus australiensis*	Australian weasel shark		1 (0.17)	**5 (0.83)**		6
	Hemipristis elongata	Fossil shark			2 (1.00)		2
Sphyrnidae	*Eusphyra blochii*	Winghead shark		1 (1.00)			1
	Sphyrna lewini	Scalloped hammerhead	**76 (0.83)**	2 (0.02)	14 (0.15)	1	93
	Sphyrna mokarran	Great hammerhead	4 (0.21)	**12 (0.63)**	3 (0.16)	1	20
Ginglymostomatidae	*Nebrius ferrugineus*	Tawny nurse shark			1 (1.00)		1
Hemiscylliidae	*Chiloscyllium punctatum*	Grey carpetshark		1 (0.25)	**3 (0.75)**		4
Stegostomatidae	*Stegostoma fasciatum*	Zebra shark		**6 (0.67)**	3 (0.33)		9
Total			336 (0.19)	231 (0.13)	**1196 (0.68)**	43	1806

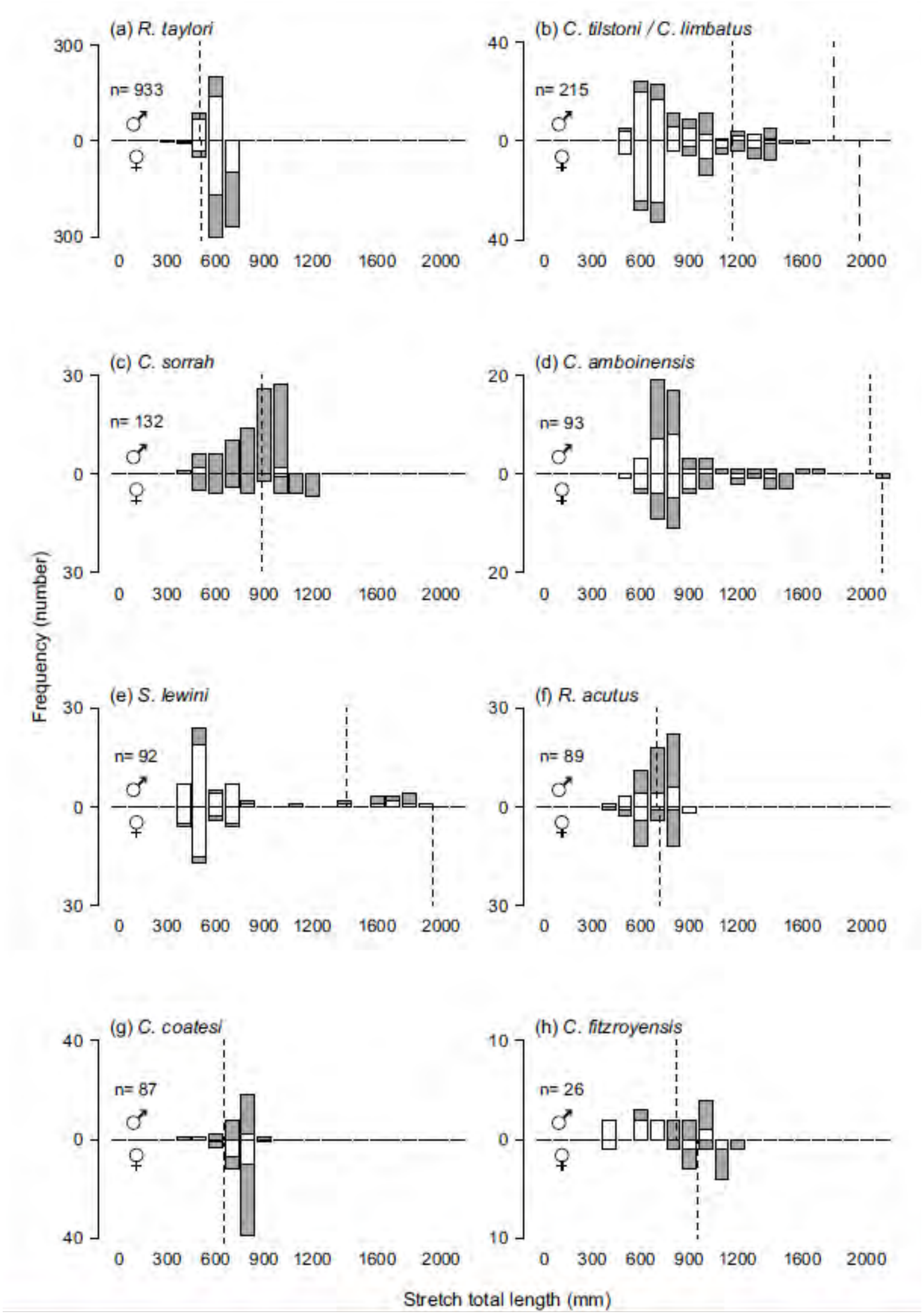

Figure 3: Length-frequency distributions of the most abundant sharks. n, the number of length measurements recorded for each species. Bar shading denotes the sampling method (white, gill-net; grey, longline).

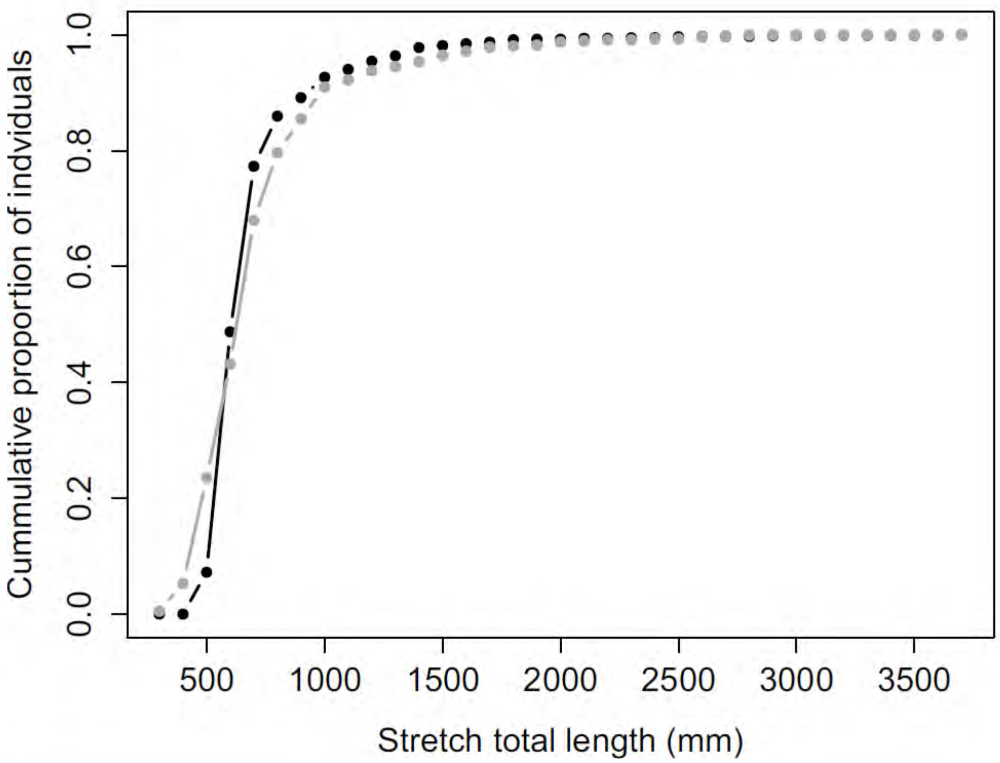

Figure 4: Comparison of cumulative length profiles between immature (grey) and mature (black) sharks. Data are pooled into 100 mm bins.

Immature shark community structure

Mean numbers of common species indicated spatial variation in immature shark community structure (Figure 5). For example, *S. lewini* contributed 14% of the total catch of immature sharks, of which 71% were caught in Rockingham Bay. In contrast, *S. lewini* were not recorded in Edgecumbe Bay and were relatively scarce elsewhere. Further, although *C. amboinensis* were also relatively scarce in Edgecumbe Bay, *C. brevipinna* were only recorded there. The MDS ordination showed some separation in immature shark community structure between bays (Figure 6). For example, samples from Edgecumbe Bay formed a cluster that was largely non-overlapping with samples from Repulse or Rockingham Bays. However, some overlap of samples between bays, such as Rockingham and Upstart Bays, was indicative of broad similarities in shark fauna across the region. Two-way crossed ANOSIM identified significant variation in immature shark communities across the five bays while accounting for any variation between rounds (Global R = 0.23, P = 0.017) or years (Global R = 0.29, P = 0.001). Conversely, when the effects of bay were removed no significant variation in immature shark communities were detected between rounds (Global R = 0.06, P = 0.347) or years (Global R = 0.18, P = 0.067). Taken together, the MDS ordination and modest ANOSIM Global R values indicate that differences between bays were not extreme. However, there were significant differences between bays in species composition and the occurrence of individual species, and thus the null hypothesis of no 'bay' effect was rejected.

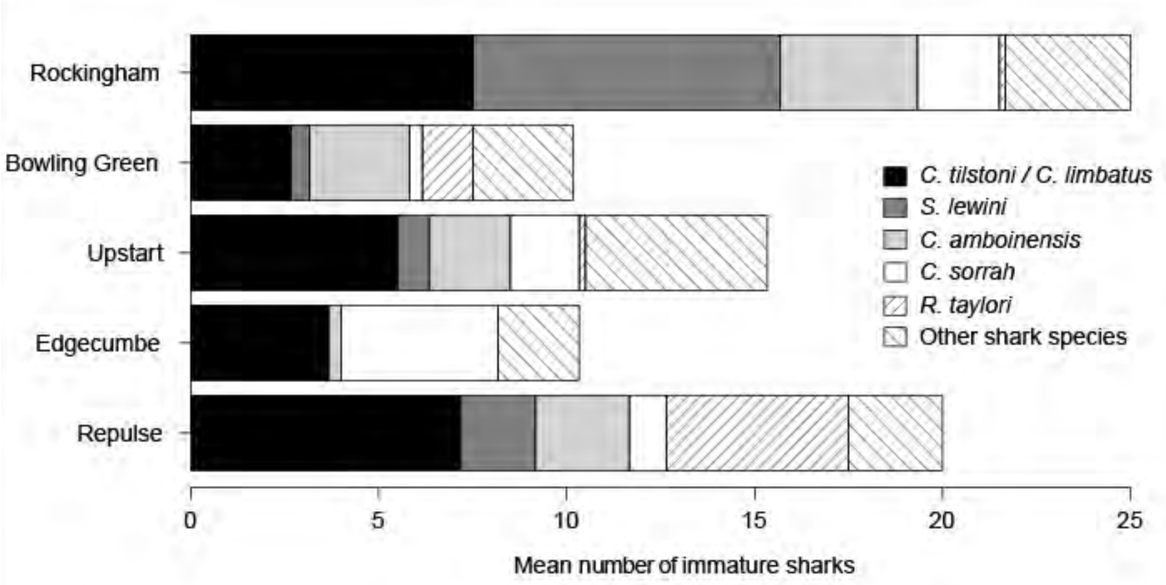

Figure 5: Immature shark catch compositions. Mean relative abundance and species composition of immature sharks in five bays. Count data are averaged across sampling rounds.

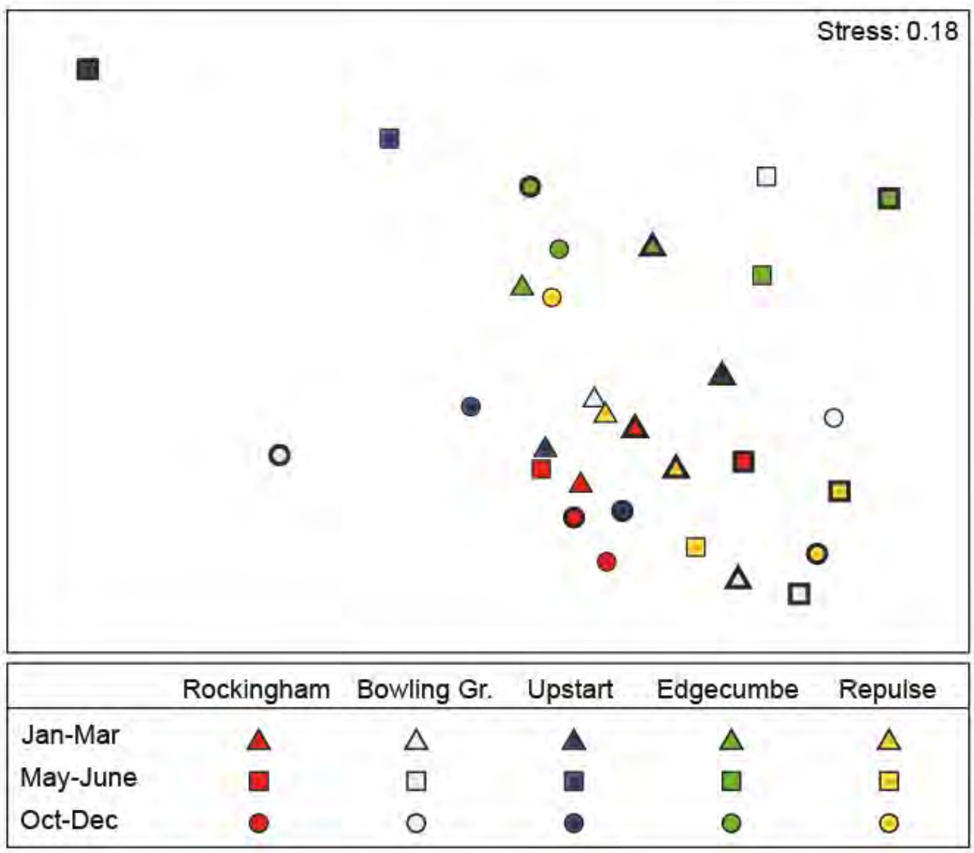

Figure 6: Ordination of immature shark communities. Non-metric multidimensional scaling ordination of the Bray-Curtis similarity matrix derived from the catch of immature sharks from 15 species groupings (*Carcharhinus tilstoni* and *Carcharhinus limbatus* were grouped together). Each symbol appears twice with narrow outlines for 2012 samples and thick outlines for 2013 samples. Stress value is shown in the top-right corner.

In general, the more abundant species were primarily responsible for typifying the catch within individual bays. *Carcharhinus tilstoni/ C. limbatus* accounted for 39%, 25%, 49% and 38% of the average similarities within Bowling Green, Upstart, Edgecumbe and Repulse Bays, respectively, where it was the most typifying species group. *Carcharhinus amboinensis* was the second-highest contributor to average similarities within Bowling Green (19%) and Repulse (19%) Bays. Carcharhinus sorrah was the second-highest contributor to average similarities within Edgecumbe (31%) and Upstart (24%) Bays. *Sphyrna lewini* followed by *C. tilstoni/ C. limbatus* were the highest contributors to average similarities within Rockingham Bay, contributing 37% and 30%, respectively.

Pairwise comparisons (one-way ANOSIM) showed that the overall variation in immature shark communities was primarily driven by differences between Edgecumbe and Rockingham ($R = 0.64$, $P = 0.002$) Bays, and Edgecumbe and Repulse ($R = 0.46$, $P = 0.009$) Bays. Relatively small R values < 0.30 indicated that variations in immature shark communities between other bay pairings contributed relatively little overall.

Environmental drivers of juvenile shark abundance

Blacktip sharks

A total of 86 and 161 blacktip sharks were captured using longlines and gill-nets, respectively. Of these, 60 and 141 immature individuals were included in longline and gill-net analyses, respectively. For longlines, a weakly significant effect of mangrove proximity was detected (Table 3, 4), however the explained deviance of 4% indicated that the influence of this variable was negligible. Turbidity and depth were highly influential in gill-net samples (Table 3, 4). In addition, the influence of mangrove proximity in gill-net samples corroborates the otherwise equivocal longline results. Overall, blacktip shark abundance decreased with decreasing turbidity (i.e. increasing secchi depth) and distance from mangroves, and increased with depth. These three variables were present in all best-performing models and together explained 18% of deviance in blacktip shark abundance in gill-nets.

Table 3: Comparisons of best-performing models of immature shark abundance. Each row contains the intercept and coefficients that comprised a single model, along with the number of parameters (df), log-likelihood and Akaike metrics.

Intercept	Turbidity	Salinity	Mangrove	Depth	Temp.	Salinity* turbidity	depth* turbidity	*df*	log-likelihood	AIC	ΔAIC	*w*
Blacktip shark *Carcharhinus tilstoni/ C. limbatus* on longlines												
-0.60	-	-	-0.47	-	-	-	-	3	-168.5	343.0	0.00	0.266
-0.34	-0.19	-	-0.46	-	-	-	-	4	-168.2	344.4	1.34	0.136
0.03	-	-	-0.47	-	-0.02	-	-	4	-168.4	344.8	1.74	0.111
-0.71	-	-	-0.49	0.04	-	-	-	4	-168.5	345.0	1.92	0.102
Blacktip shark *Carcharhinus tilstoni/ C. limbatus* in gill-nets												
-0.59	-1.28	-	-0.31	0.30	-	-	-	5	-237.7	485.5	0.00	0.203
-2.48	-1.35	0.06	-0.32	0.32	-	-	-	6	-237.1	486.3	0.80	0.136
-1.92	-1.21	-	-0.29	0.27	0.05	-	-	6	-237.2	486.3	0.85	0.133
-5.56	2.83	0.15	-0.33	0.32	-	-0.12	-	7	-236.5	487.0	1.50	0.096
-3.59	-1.28	0.05	-0.30	0.29	0.05	-	-	7	-236.6	487.3	1.80	0.083
-0.53	-1.34	-	-0.31	0.28	-	-	0.02	6	-237.7	487.5	1.99	0.075
Pigeye shark *Carcharhinus amboinensis* on longlines												
-15.07	14.36	0.43	-0.31	0.36	-	-0.45	-	7	-157.1	328.1	0.00	0.182
-14.46	13.89	0.40	-	0.29	-	-0.44	-	6	-158.1	328.2	0.07	0.176
-13.22	14.19	0.39	-	-	-	-0.44	-	5	-159.2	328.4	0.25	0.160
-13.46	14.59	0.41	-0.22	-	-	-0.46	-	6	-158.7	329.3	1.17	0.101
-13.73	13.87	0.42	-0.33	0.38	-0.04	-0.44	-	8	-156.9	329.8	1.64	0.080
-13.52	13.54	0.39	-	0.31	-0.02	-0.43	-	7	-158.0	330.0	1.89	0.071
Pigeye shark *Carcharhinus amboinensis* in gill-nets												
-27.88	30.01	0.53	-0.79	3.04	-	-0.77	-1.71	8	-80.7	177.4	0.00	0.432
-27.21	30.52	0.49	-	3.03	-	-0.78	-1.86	7	-82.7	179.3	1.90	0.167
-27.29	29.92	0.52	-0.80	3.05	-0.01	-0.77	-1.71	9	-80.7	179.4	1.98	0.160
Scalloped hammerhead shark *Sphyrna lewini* in gill-nets												
-7.64	8.20	0.08	-	-	0.15	-0.29	-	6	-131.8	275.6	0.00	0.287

-8.04	8.43	0.09	-	0.15	0.14	-0.30	-	7	-131.7	277.3	1.66	0.125
-0.99	-1.37	-0.14	-	-	0.17	-	-	5	-133.7	277.3	1.70	0.123
-7.65	8.24	0.09	-0.06	-	0.15	-0.29	-	7	-131.8	277.6	1.92	0.110

All models contained fishing effort as an offset. AIC = Akaike Information Criterion, ΔAIC = increase in AIC relative to the lowest-AIC model, *w* = Akaike weight.

Table 4: Effects of highly influential variables (identified using Relative Variable Importance values, RVI). Standardised model-averaged coefficients (with shrinkage) ± standard error are followed by the associated P-value in brackets (i.e. Pr(>|Z|))Details of bays surveyed for juvenile sharks along the central Great Barrier Reef coast.

	C. tilstoni/ C. limbatus		*C. amboinensis*		*S. lewini*
	Longline	Gill-net	Longline	Gill-net	Gill-net
Turbidity		-0.48 ± 1.28 (0.71)**	17.42 ± 3.97 (< 0.001)	36.81 ± 11.52 (0.001)	5.53 ± 5.30 (0.30)
Salinity			1.87 ± 0.67 (0.006)	2.35 ± 1.27 (0.07)	0.14 ± 0.47 (0.77)
Mangrove	-0.93 ± 0.41 (0.02)	-0.27 ± 0.13 (0.04)*			
Depth		0.26 ± 0.15 (0.08)*		5.12 ± 1.32 (< 0.001)	
Salinity*Turbidity			-19.14 ± 4.20 (<0.001)	-33.29 ± 11.44 (0.004)	-7.11 ± 5.61 (0.21)
Temperature					0.55 ± 0.28 (0.05)
Depth*Turbidity				-8.87 ± 3.16 (0.005)	

Coefficients are on the linear (log) scale and so their effect is additive. Variables are listed according to mean RVI across species/sampling method combinations. Asterisks denote variables that were not significant in model averaging but were significant ($P < 0.05$*; $P < 0.0001$**) in a single model containing high-RVI variables. Although the coefficients for turbidity for pigeye sharks and scalloped hammerhead sharks were positive, strong interaction with salinity or depth produced an overall negative relationship with decreasing turbidity.

Pigeye sharks

A total of 68 and 44 pigeye sharks were captured using longlines and gill-nets, respectively. Of these, 63 and 41 immature individuals were included in longline and gill-net analyses, respectively. For both sampling methods, turbidity and its interaction with salinity were the most influential drivers of shark abundance (Table 3, 4). Abundance generally decreased with decreasing turbidity, however the opposite occurred at low salinities using both sampling methods (c. 30–31 ppt). For gill-nets, interaction between turbidity and depth suggested that relatively low-turbidity and shallow environments provided suitable habitat for young pigeye sharks. All high-order parameters were significant in model averaging (Table 4), and together explained 13% and 45% of deviance in pigeye abundance in longline and gill-net samples respectively. A negative relationship between pigeye shark abundance and distance from mangroves was also included in two of the three best-performing gill-net models (Table 3), however the RVI was relatively low (0.78), the model-averaged coefficient was non-significant ($Z = 1.34$, $P = 0.18$), and the coefficient in a single high-RVI model was weakly significant ($Z = -2.17$, $P = 0.03$). Therefore results on the influence of mangrove proximity on pigeye sharks were inconclusive.

Scalloped hammerhead sharks

A total of 81 scalloped hammerhead sharks were captured in gill-nets and 73 immature individuals were included in the analysis. Scalloped hammerhead abundance decreased with decreasing turbidity, however this trend deteriorated at low salinities around 31 ppt. In addition, scalloped hammerhead shark abundance increased with temperature. Turbidity, salinity and temperature were present in all best-performing models (Table 3, 4) and, together with interaction between turbidity and salinity, explained 29% of deviance in scalloped hammerhead shark abundance in gill-nets.

Benefits of marine protected areas to inshore sharks

Total shark abundance in longline samples was significantly higher in closed zones compared to open zones; and in Bowling Green Bay compared to Rockingham (Table 5, Tukey multiple comparisons test, $P < 0.0001$). Significant interaction between bay and zone was detected for total shark abundance in gill-net samples. Although no pair-wise factor-levels combinations were significantly different using gill-net data (Tukey multiple comparisons, $P \geq 0.05$), estimated shark abundances in open and closed zones of Bowling Green Bay were outside of each other's 95% confidence interval, suggesting higher shark abundance in closed areas of Bowling Green Bay compared to open areas.

Significant interaction between bay and zone characterised the abundance of Australian sharpnose sharks using both gears (Table 5), indicating spatial variation at a finer spatial scale than that of entire bays. However, this variation did not coincide consistently with zoning, indicating that zoning was an unlikely driver of spatial variation in Australian sharpnose abundance. Abundance in longline samples was highest in Bowling Green Bay, and there were variable and insignificant pairwise variations between zones within individual bays using longlines and gill-nets (Tukey multiple comparisons, $P \geq 0.05$; Table 5).

For blacktip, pigeye, scalloped hammerhead and spot-tail sharks; open and closed zones did not coincide with measurable heterogeneity in shark abundance (Table 5). However, there were variations in the abundances of these species among bays using ≥ 1 sampling method. Rockingham Bay had high relative abundances of blacktip and scalloped hammerhead sharks, Bowling Green Bay had low relative abundances of blacktip and spot-tail sharks, and Upstart Bay had a low relative abundance of pigeye sharks.

Table 5: Relationship between shark abundance and spatial covariates

Species	Sampling method	No. of sharks (% samples with ≥ 1 shark)	Factor	*df*	χ^2	*P*
All species	Longline	627 (72)	Zone	1	4.72	0.03*
			Bay	2	28.82	<0.0001*
			Zone*Bay	2	2.15	0.34
	Gill-net	576 (59)	Zone*Bay	2	9.70	0.008*
Aust. sharpnose	Longline	293 (39)	Zone*Bay	2	8.03	0.02*
	Gill-net	292 (33)	Zone*Bay	2	11.60	0.003*
Blacktip	Longline	57 (16)	Zone	1	1.29	0.26
			Bay	2	3.72	0.16
			Zone*Bay	2	5.10	0.08
	Gill-net	104 (23)	Zone	1	3.65	0.06
			Bay	2	8.12	0.02*
			Zone*Bay	2	3.64	0.16
Pigeye	Longline	45 (10)	Zone	1	0.04	0.84
			Bay	2	32.06	<0.0001*
			Zone*Bay	2	1.35	0.51
	Gill-net	30 (6)	Zone	1	0.46	0.50
			Bay	2	0.54	0.76
			Zone*Bay	2	0.83	0.66
Scalloped h.	Gill-net	69 (13)	Zone	1	2.12	0.15
			Bay	2	18.04	0.0001*
			Zone*Bay	2	3.95	0.14
Spot-tail	Longline	68 (17)	Zone	1	0.02	0.90
			Bay	2	8.30	0.02*
			Zone*Bay	2	4.15	0.13

Length-frequency distribution

Stretch total length was measured for 1163 of the 1203 sharks captured during fishery-independent surveys within Rockingham, Bowling Green and Upstart Bays. Across the three bays, median STL of Australian sharpnose (longline samples), blacktip (longline and gill-net samples), and pigeye (longline samples) sharks were significantly larger inside closed areas (Table 6). For blacktip and pigeye sharks, these differences were predominantly due to an absence or relative scarcity of larger size classes in open zones compared to closed zones. In addition, significant variation in median STL between bays was detected for Australian sharpnose sharks in gill-net samples (Table 6), whereby the presence of a relatively larger proportion of medium sized sharks c. 550-650 mm in Bowling Green likely influenced a significantly smaller median size there (660 mm) compared to Upstart Bay (690 mm; Kruskal-Wallis multiple comparison test, $P < 0.05$). For Australian sharpnose sharks, the small and inconsistent effect of zone between sampling gears indicated that spatial variation in STL was not necessarily attributable to zoning. No significant spatial variations in STL were detected for scalloped hammerhead or spot-tail sharks (Table 6).

Table 6: Comparison of length-frequency distributions between bays and zones

	Bay KW			Zone KW			Zone KS	
	df	χ^2	*P*	*df*	χ^2	*P*	*D*	*P*
Aust. Sharpnose LL	2	5.84	0.05	1	32.67	<0.0001*	0.39	<0.0001*
Aust. Sharpnose GN	2	15.58	0.0004*	-	-	-	0.15	0.09
Blacktip LL	1	0.96	0.33	1	8.53	0.003*	0.53	0.001*
Blacktip GN	2	0.29	0.87	-	-	-	0.60	<0.0001*
Pigeye LL	1	0.01	0.92	1	20.47	<0.0001*	0.73	<0.0001*
Sc. hammerhead GN	x	x	x	1	2.75	0.10	0.32	0.13
Spot-tail LL	1	3.44	0.06	1	3.68	0.05	0.32	0.07

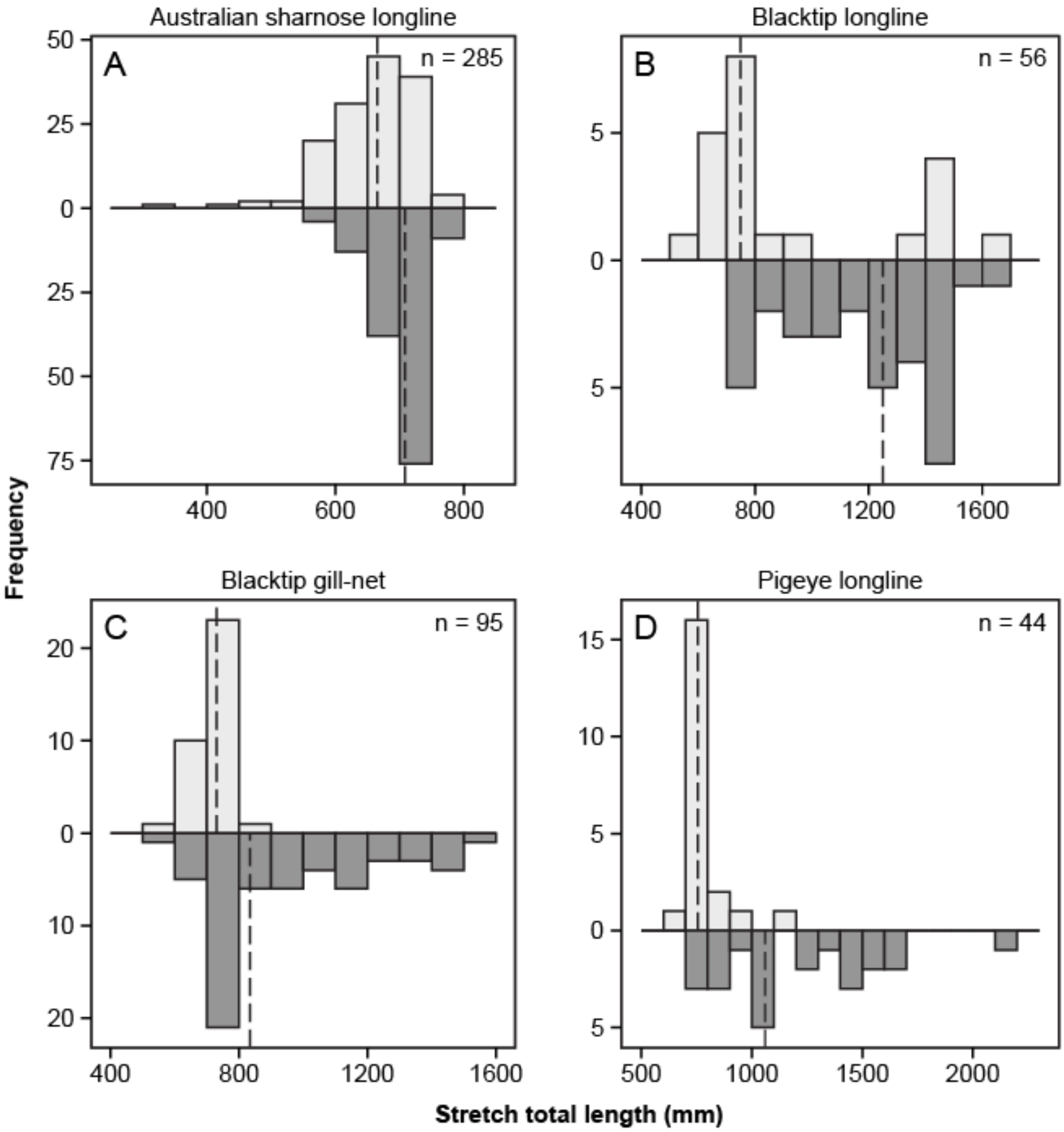

Figure 7: Significantly different length-frequency distributions between open (light grey) and closed (dark grey) zones (Kruskal-Wallis rank sum test and Kolmogorov-Smirnov test, $P < 0.05$). Broken lines indicate sample median. Data are pooled across bays. Note that the axes vary among panels.

Species composition

A total of 1197 sharks were identified to species level in Rockingham, Bowling Green and Upstart Bays. The MDS ordination did not reveal obvious differentiation in shark community structure between zones. However, there was a significant effect of zone (ANOSIM; $R = 0.20$, $P = 0.001$) and bay (ANOSIM; $R = 0.29$, $P = 0.001$) on species composition. The small magnitude of the R statistic indicated that these differences were not extreme. Eight species cumulatively contributed up to 70% of the average Bray-Curtis dissimilarity between open and closed zones. The average relative abundances of seven of these eight species were higher in closed zones compared to open zones. This high relative abundance of multiple species in closed zones aligned with the results for all species pooled abundance data.

Acoustic monitoring

Australian sharpnose sharks (Rhizoprionodon talyori)

Forty *Australian sharpnose sharks* with acoustic transmitters were released in Cleveland Bay between September 2011 and November 2012. The majority of individuals ($n = 34$) were captured and released on the eastern side of Cleveland Bay. Twenty (7 male, 13 female) were released in year one of this study (September 2011 to September 2012). Twenty (7 males, 13 female) were released in year two (September 2012-April 2013). Four individuals released in year one and one released in year two died or were not detected following release and were excluded from analysis. Animal size ranged from 489 to 771 mm STL (mean ± SE = 657± 21.0) in year one and 485 to 763 mm (mean ± SE = 659 ±15.2) STL in year two. Size ranges indicated that the majority were either mature or nearing sexual maturity (Simpfendorfer 1993). There were no significant differences in sizes between years (ANOVA, $F(1,31) = 0.0193$, $P > 0.05$), however, females were significantly larger than males (ANOVA, $F(1,31) = 27.45$, $P < 0.05$).

Residency

Australian sharpnose sharks were present in Cleveland Bay for 1-106 days (mean ± SE =11.4 ± 7.4) in year one and 1-112 days (mean ± SE = 20.6 ± 6.6) in year two. Two individuals released in year one (2 female) and seven released year two (2 male, 5 female) were present for more than two weeks. The remaining 26 individuals spent less than two weeks in the array. Residency index was low in both years and ranged from 0.00-0.40 (mean ± SE = 0.053 ± 0.03) in year one and 0.00-0.56 (mean ± SE = 0.11 ± 0.04) in year two (Figure 8). Residency data was not normal and was log10 transformed. Animal size had no effect on residency (ANCOVA, $F(1,27) = 0.727$, $P > 0.05$). There was a significant difference in residency between years (ANCOVA, $F(1,27) = 4.48$, $P < 0.05$), but not between sexes (ANCOVA, $F(1,27) = 0.284$, $P > 0.05$). There was no seasonal pattern in movement out of Cleveland Bay. After last detection in Cleveland Bay, seven (3 male, 4 female) were detected on receivers inside Bowling Green Bay for a maximum of seven consecutive days after.

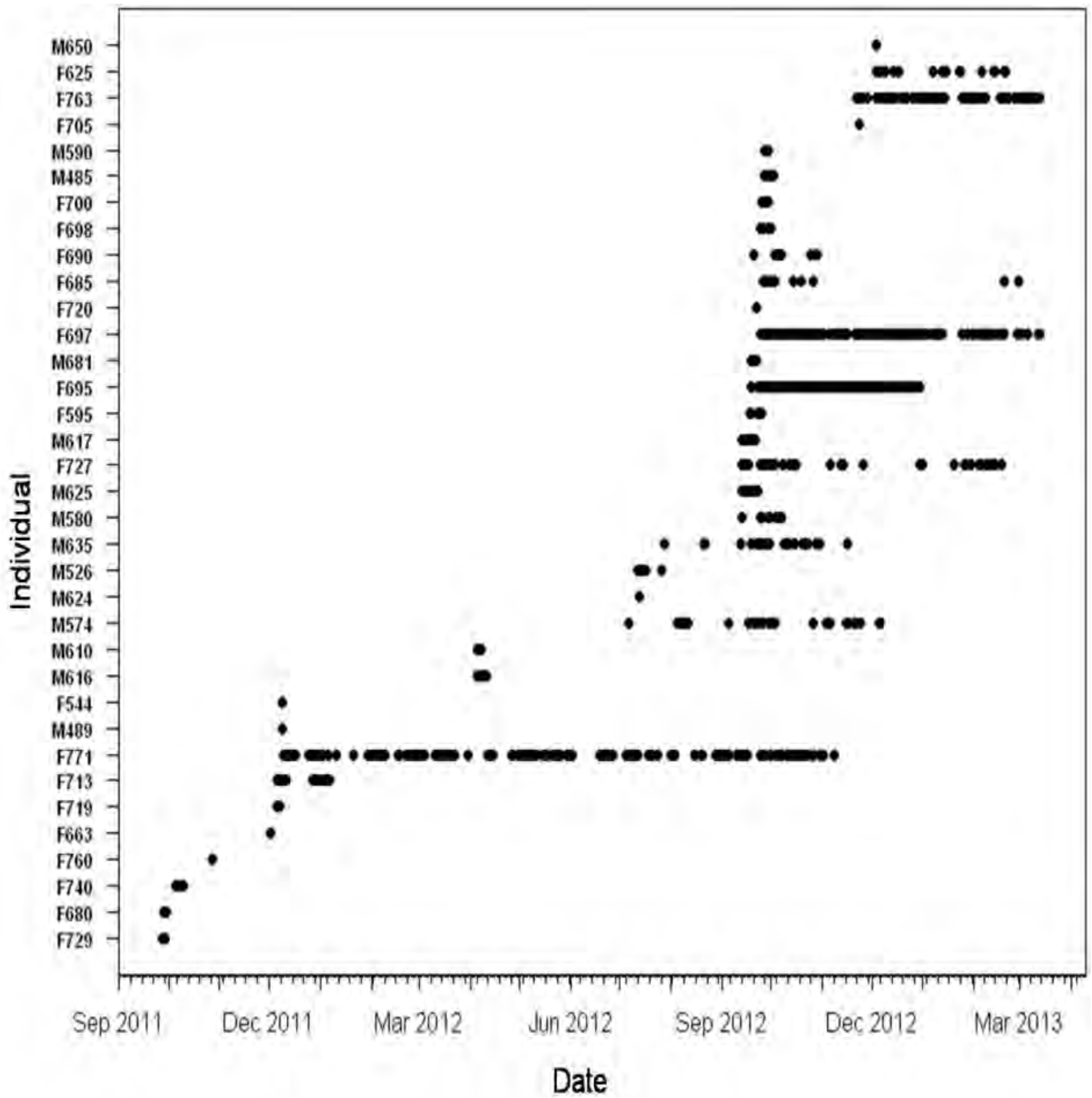

Figure 8: Daily presence of *Rhizoprionodon taylori* released with acoustic transmitters in Cleveland Bay in 2011- 2013. Individuals are identified by sex and stretch total length (mm).

Space use

Due to the low number of resident individuals, it was not possible to perform population analysis of the activity space habitat use patterns in year one. Therefore, all activity space analysis was based on data from sharks monitored in year two. Individual monthly activity space of resident individuals ranged between 4.3 and 21.4 km2 (mean ± SE =11.3 km2 ± 0.90) for 50% KUDs and 21.5 and 80.4 km2 (mean ± SE = 51.0 km2 ± 3.9) for 95% KUDs. There was no significant difference in KUD size between months for 50% (Linear mixed effects model, $F(6,18)=0.883$, $P > 0.05$) or 95% (Linear mixed effects model , $F(6,18) = 1.043$, $P > 0.05$) KUDs. There was also no relationship between animal size and activity space size for either 50% (Linear regression, r2=0.006, $F(1,23)=0.136$, $P > 0.05$) or 95% (Linear regression, r2=0.041, $F(1, 23)=0.971$, $P > 0.05$) KUDs.

The majority of movements were on the eastern side of the bay, specifically in seagrass habitat. However, 57% of individuals were detected on both sides of the bay. Individual monthly KUD overlap was highly variable and ranged between 0.0-88.6.% (mean ± SE = 34.1 ± 6.2, n = 17) for 50% KUDs and 34.2-92.7% (mean ± SE = 61.0 ± 3.8, n = 17) for 95% KUDs. The most distinct shift in KUD location occurred between months of low (December 2012) and high river discharge (January and February 2013). Monthly KUD locations of some individuals (all female) shifted from the southeastern to the northwestern side of Cleveland Bay between December 2012 and February 2013 (Figure 9), resulting in low space use overlap for those individuals during that time. However, one individual remained on the eastern side of Cleveland Bay in January and February 2013.

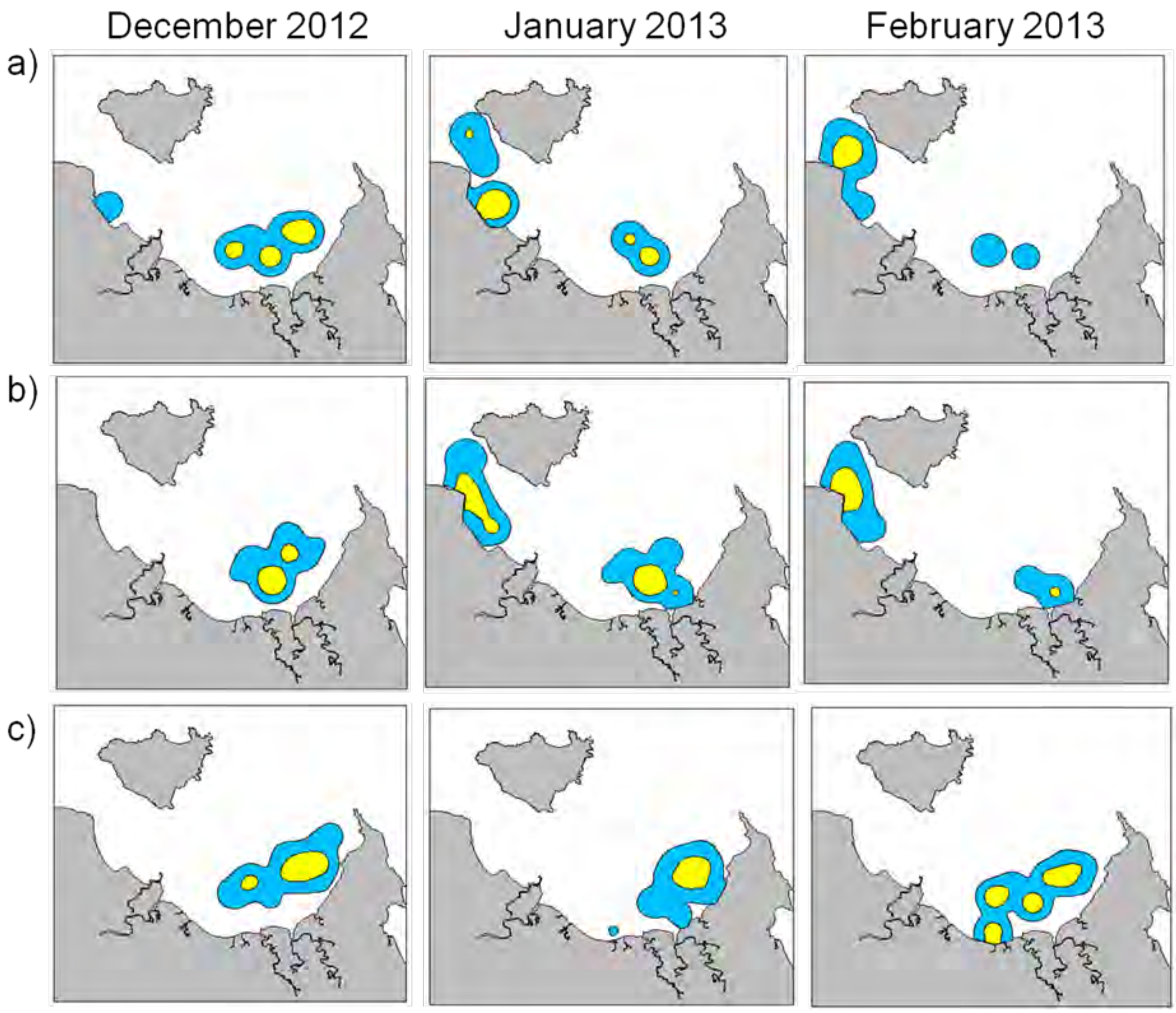

Figure 9: *Rhizoprionodon taylori* monthly activity spaces of three individuals (a, b, c) in December 2012, January 2013 and February 2013. Each panel shows the 95% (blue fill) and 50% (yellow fill) kernel utilisation distributions.

Habitat selection

The majority of transient individuals selected for seagrass habitat. Of the 26 transient individuals, 11 exclusively selected for seagrass while seven selected for seagrass and at least one other habitat (intertidal mudflat and/or outer bay mud substrate). Eight transient individuals avoided seagrass. Reef was avoided by all transient individuals except for one adult female.

The two resident females monitored in year one had contrasting selection patterns. One female selected for sandy inshore habitat, outer bay mud substrate, and seagrass while the other only selected for mudflat habitat. Resident individuals in year two were detected in all five primary habitat types at least once during the monitoring period, but on average spent the majority of time in seagrass habitat. Mean individual Strauss selection values of resident individuals in year two indicated that on an annual basis outer bay mud substrate was used opportunistically, reef and mudflat habitats were avoided, and seagrass and sandy inshore habitat were positively selected (Figure 10). A chi-squared goodness-of-fit test showed that selection was significant (X24=63.888, P < 0.05).

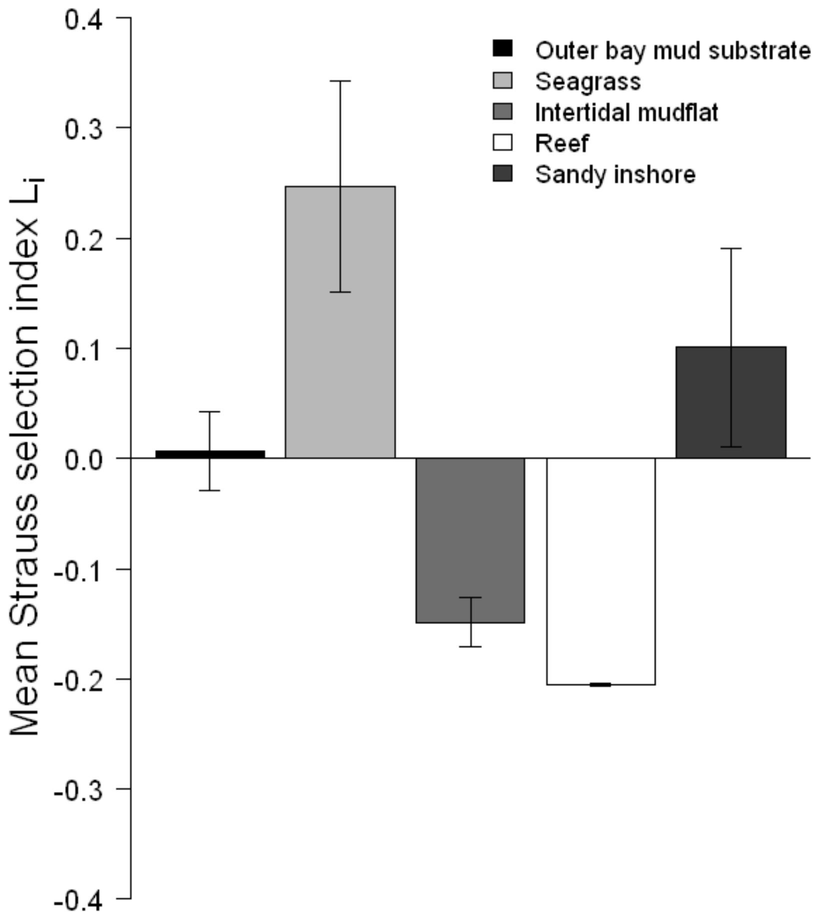

Figure 10: Mean Strauss linear selection index values of resident (> 2 weeks) *Rhizoprionodon taylori* in Cleveland Bay (n = 7) between September 2012 to April 2013. Bars indicate standard error.

Creek whalers (Carcharhinus fitzroyensis)

Sixteen creek whalers (3 male, 13 female) were caught and released with acoustic transmitters on the eastern side of Cleveland Bay between February and September 2012. Size ranged from 679 to 1370 mm STL (mean ± SE = 943 ± 48.9). Five were not detected or died following release and were excluded from analysis, as was one immature female recaptured and collected by a local commercial fisherman 36 km north of the original release location approximately two weeks after release. The remaining 10 (1 male, 9 female) were monitored in Cleveland Bay from September 2012 to May 2014. Size indicated the male was immature, while seven females were mature and two were immature.

Residency

Presence in Cleveland Bay ranged by individual from 1 to 452 days (mean ± SE = 205 ± 53) (Figure 11). Three individuals left the array within two weeks of release and did not return within the monitoring period. Residency index in the sample population ranged from 0.002-0.74 (mean ± SE = 0.34 ± 0.09). There was no significant relationship between residency and size (ANCOVA, $F(1,18) = 0.1616$, $P > 0.05$) or sample year (ANCOVA, $F(1,18) = 0.1379$, $P > 0.05$). There was also no clear seasonal pattern in presence except for one mature female that was consistently present from September to December in 2012 and 2013, was briefly present in April 2013 and 2014, and was never detected between May and August during any year of the study.

Four mature females were detected on receivers in Bowling Green Bay. These individuals were some of the most highly resident to Cleveland Bay. Two were only detected in Bowling Green Bay for single days before returning to Cleveland Bay. However, the two other females made brief excursions into Bowling Green Bay throughout the monitoring period.

Space use

With the exception of one individual, all resident individuals exclusively used the eastern side of Cleveland Bay (Figure 12). Individual monthly activity space ranged from 2.6 to 19.8 km2 (mean ± SE =10.6 km2 ± 0.3) for 50% KUDs and 9.1 to 81.9 km2 (mean ± SE = 47.9 km2 ± 1.0) for 95% KUDs. Shark length appeared to have little or no effect on KUD size, and immature and mature individuals utilized similar amounts of space within the bay. KUD size was larger during the day than at night for both 50% and 95% KUDs. The influence of month on KUD size was most prominent in May and August. In May, there was a distinct increase in 50% and 95% KUD size compared to all other months of the year. In contrast, August 50% and 95% KUD size was considerably smaller than all other months. KUD locations also fluctuated on a monthly basis according to this pattern. In August, activity space was centralized adjacent to the south-eastern creek mouths in Cleveland Bay (Figure 12). During the rest of the year, but most notably in May, KUD positions were more widely spread throughout the eastern half of the bay. The monthly pattern in KUD location was observed in immature and mature individuals.

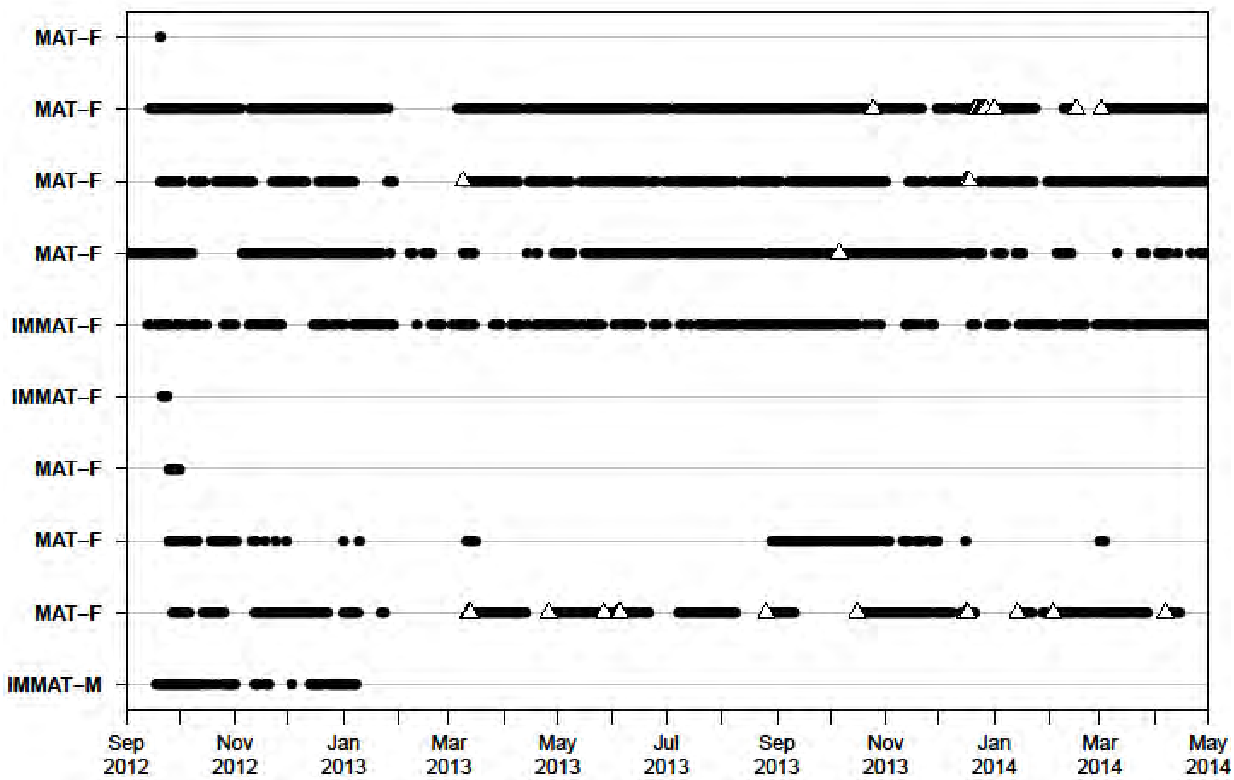

Figure 11: Daily presence of *Carcharhinus fitzroyensis* released with acoustic transmitters in Cleveland Bay in 2012- 2014. Individuals are identified by maturity (mature=MAT, immature=IMMAT) and sex (male=M, female=F). Detections in Cleveland Bay are indicated by black circles. Additional detections in Bowling Green Bay are indicated by white triangles.

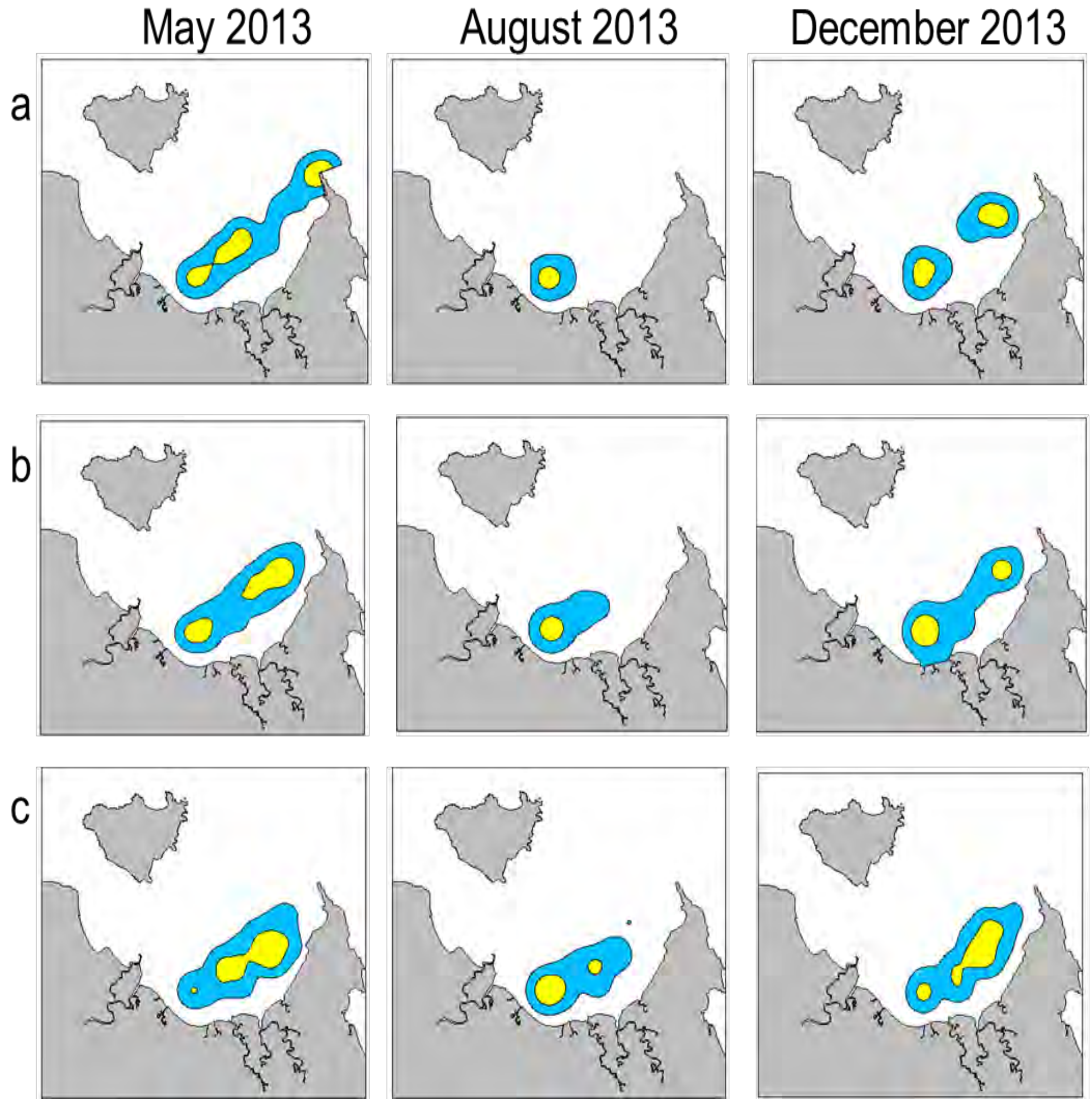

Figure 12: Monthly activity spaces of one immature (a) and two mature (b, c) *Carcharhinus fistzroyensis* in Cleveland Bay in May 2013, August 2013 and December 2013. Each panel shows the 95% (blue fill) and 50% (yellow fill) kernel utilisation distributions.

Habitat Selection

Individuals were detected in all five habitat types; however, the majority of time was spent in seagrass habitats. As there was no significant difference in time spent in each habitat between immature and mature individuals (Chi-squared test, X216=20.00, P > 0.05), all individuals were grouped for habitat selectionspecialisation analysis. Mean individual Strauss selection values for the entire monitoring period indicated creek whalers selected for seagrass habitat, used outer bay mud substrate opportunistically, and avoided reef, mudflat and sand inshore habitats (Figure 13). A Chi-squared goodness of fit test indicated selection was significant (X24=144.758, P < 0.05).

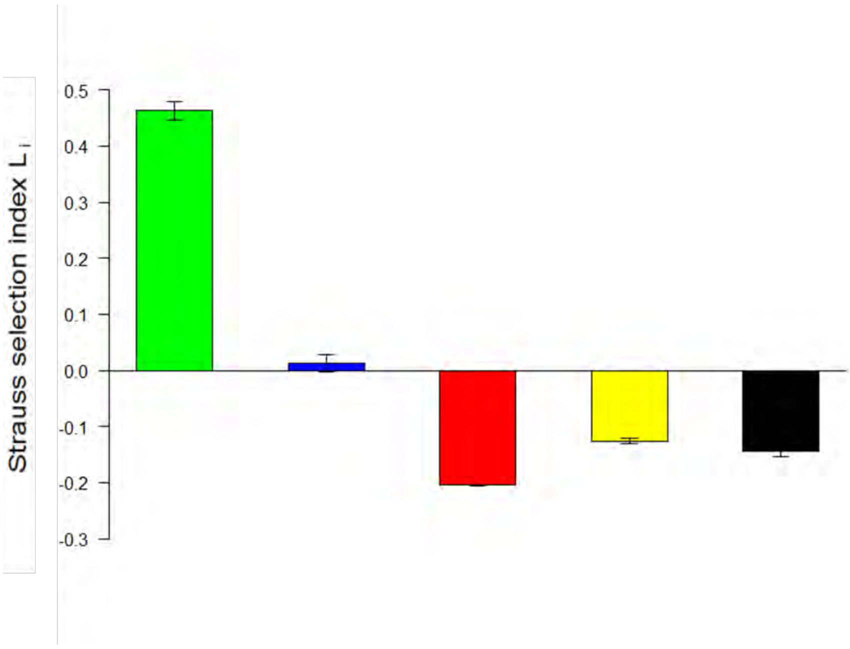

Figure 13: Mean Strauss linear habitat selection index values of potential seagrass (green), outer bay mud substrate (blue), reef (red), sandy inshore (yellow) and mudflat (black) habitats by *Carcharhinus fitzroyensis* in Cleveland Bay between September 2012 to May 2014. Bars indicate standard error.

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