Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region

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ABSTRACT: Tropical nearshore regions provide habitat for a diverse assemblage of shark species, and although a range of age classes may use these environments, ontogenetic shifts in movement and habitat use remain relatively unclear. The hypothesis of this study was that home range size and range of depths used by juvenile sharks in a tropical nearshore region will increase with age. An array of 58 acoustic receivers deployed in Cleveland Bay, north Queensland, Australia, passively tracked 43 juvenile pigeye sharks *Carcharhinus amboinensis* of 3 age classes from 2008 to 2010. Individuals were present in the study site for long periods, ranging from 4 to 587 d (median = 134). Juvenile *C. amboinensis* associated strongly with shallow turbid habitats, and core home ranges of all monitored individuals consistently remained in areas adjacent to creek and river mouths. Significant differences in minimum convex polygon measures of home range revealed that older juveniles used larger areas and undertook excursions from core ranges more frequently than younger juveniles. Movements of all *C. amboinensis* were related to the tidal cycle, but changes in water depth associated with the tide had the strongest influence on the youngest juveniles. Young-of-the-year individuals constrained their movements to shallower depths than older (2-yr-old) individuals (medians = 205 and 283 cm, respectively), presumably as a refuging strategy and to decrease intraspecific competition. By defining transitions in habitat use behaviour among juvenile sharks, this study provides a better understanding of the implications associated with coastal shark species of multiple age classes using a shared environment.

KEY WORDS: Tide · Depth · Home range · Refuging · Intraspecific competition · Age class · Passive acoustic monitoring · Pigeye shark

INTRODUCTION

Nearshore regions are highly dynamic environments consisting of a network of habitats and areas that include rivers, estuaries, lagoons and bays. These regions are typically shallow and characteristically have large variations in physical parameters (e.g. salinity, temperature, depth, dissolved oxygen, flow and turbidity) over a range of temporal scales, due to changes in tide, rainfall, freshwater inflow, season and weather (Walker 1981, Rodriguez et al. 1994). Although less extreme than large-scale changes associated with seasonal or weather events, fluctuations occurring on short temporal scales (i.e. hours) still have a considerable impact on nearshore communities. For example, diel changes and recurring changes in water depth due to the tidal cycle can influence the movement and habitat use of inhabitants over the course of a day; species move to select for certain habitats (Bellquist et al. 2008), avoid predators (Wetherbee et al. 2007) and exploit foraging opportunities (Ackerman et al. 2000).

Despite potentially taxing conditions, the high biodiversity and productivity of nearshore regions suggests that these areas contain important habitat for a wide range of species (Beck et al. 2001). In particular for sharks, nearshore regions provide habitat for many different functions, including foraging and use of nursery areas (Castro 1993, Bethea et al. 2004, Heupel et al. 2007). Previous research has found that multiple shark species may inhabit the same nearshore region, with different species presumably using the same or similar resources (Castro 1993, Simpfendorfer & Milward 1993). Further studies have examined how different shark species share space within these environments and have found that habitats are partitioned on both spatial and temporal scales (White & Potter 2004, Pikitch et al. 2005, DeAngelis et al. 2008). Although these interspecific differences in habitat use among sharks have been investigated, equivalent intraspecific differences have been given less consideration. For example, both small and large juvenile individuals commonly use nearshore regions, but only a limited number of studies have examined differences in movement and habitat use between age classes of the same species (e.g. bull shark *Carcharhinus leucas*; Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). If individuals of different age classes use the same areas and resources there may be resulting implications, such as increased competition. With nearshore regions being used by a range of age classes of multiple shark species, individuals not only have to compete with other species but also amongst themselves, which likely has the greatest impact on the youngest least experienced individuals.

The pigeye shark *Carcharhinus amboinensis* inhabits tropical nearshore regions in the Indo-West Pacific, and ranges in Australia throughout northern waters from Brisbane (Queensland) to Carnarvon (Western Australia) (Compagno 1984, Last & Stevens 2009). *Carcharhinus amboinensis* is a slow growing, large-bodied shark: size at birth is 60 to 65 cm and individuals attain a maximum size of ~280 cm (Last & Stevens 2009). Unlike its close relative, the widely-distributed *C. leucas*, little is known about the movements of *C. amboinensis* and how it uses nearshore habitats. Throughout its range, *C. amboinensis* has been reported to inhabit warm turbid waters close to estuaries and river mouths and occasionally enter brackish habitats (Cliff & Dudley 1991, Last & Stevens 2009). However, in northern Australia, juvenile individuals were found to be highly influenced by freshwater inflow and actively avoided low salinity and high flow environments (Knip et al. in press). Similar to other large-bodied coastal species, *C. amboinensis* may use nearshore areas as nursery habitat during early life-stages (Heupel et al. 2007, Knip et al. 2010). As a common inhabitant of some tropical nearshore regions, understanding the habitat use of *C. amboinensis* is crucial to defining its early life-history and ecological role within these systems.

The purpose of this study was to examine how juvenile *Carcharhinus amboinensis* use nearshore habitats by defining factors that influence movement and determining how movement and habitat use varies among age classes. Previous research has found that home ranges of young sharks increase in size over time (Heupel et al. 2004) and that segregation may occur between different age classes of juveniles (Simpfendorfer et al. 2005). Thus, passive acoustic monitoring was used to test the following hypotheses in this study: (1) younger juveniles use shallower depths and have movements more influenced by physical factors than older juveniles and (2) home range size and the range of depths used increase with age class.

MATERIALS AND METHODS

Study area. Cleveland Bay (19.20° S, 146.92° E) is a tropical, coastal habitat located on the northeast coast of Queensland, Australia adjacent to Townsville (Fig. 1). Most of the bay is <10 m deep and maximum tidal range reaches 4.2 m. The bay covers an area of ~225 km^2 and comprises a diverse range of habitats. The main substrate is soft mud, but there are also small patches of coastal reefs, areas of seagrass (*Cymodocea serrulata*, *Halodule uninervis* and *Halophila* spp.) and the southern shore is lined with mangroves. Ross River, Crocodile Creek and Alligator Creek are the main freshwater river systems that run into Cleveland Bay, and these enter the bay from the south.

Field methods. Passive acoustic monitoring of target species within the study site was conducted using 47 VR2 or VR2W acoustic receivers (Vemco) deployed in Cleveland Bay in November 2008 (Fig. 1). Twelve of these receivers (hereafter referred to as 'shallow water receivers') were placed in the intertidal zone along the eastern side of Cleveland Bay. They were in shallower water than the rest of the receivers in the array (hereafter referred to as 'deep water receivers') and became exposed at low tides (at tidal stages ~80 cm or less). To cover additional area and habitats, 9 receivers were added to the array in August 2009 and 2 in March 2010 (Fig. 1). As part of a separate study, 1 receiver was deployed in Ross River in January 2010 (Fig. 1). Detection range of V16 acoustic transmitters within the study site was ~900 m (M. R. Heupel unpubl. data). The array of receivers included all representative habitats within the bay: reef, seagrass, sand, mud and river mouths. Coverage allowed target species to be monitored

throughout all available habitat types. Downloading of data from receivers occurred every 6 to 8 wk.

Sharks were captured on long-lines (500 m bottom-set mainline—8 mm nylon rope) that were anchored at both ends and soaked for 1 h. Gangions consisted of 1 m of 5 mm nylon cord and 1 m of wire leader. Size 14/0 Mustad tuna circle hooks were used and baited with frozen butterfly bream *Nemipterus* sp., mullet *Mugil cephalus*, blue threadfin *Eleutheronema tetra-dactylum* or fresh trevally *Caranx* sp. All captured sharks were identified, measured to the nearest milli-metre, sexed and tagged with a rototag in the first dor-sal fin and a single-barb dart tag in the dorsal muscu-lature for identification prior to release. Sharks were given 2 tags to minimise probability of tag loss. Juve-nile *Carcharhinus amboinensis* were also fitted with a V16 acoustic transmitter (Vemco), which was surgi-cally implanted into the body cavity to ensure long-term retention (see Heupel et al. 2006 for methods). Each transmitter had a unique code and emitted a pulse series at 69 kHz to identify each individual shark tagged. Transmitters pulsed on a random repeat inter-val of 45 to 75 s with a battery life of ~18 mo.

Data analysis. Data collected from acoustic receivers were used to analyse presence, home range and move-ment patterns of juvenile *Carcharhinus amboinensis* in Cleveland Bay. Locations of monitored *C. amboinensis* in the study site were estimated every 30 min using a mean position algorithm that provided an individual's centre of activity (COA) (Simpfendorfer et al. 2002). COA locations represented an individual's mean posi-tion for the set time-step. For small sharks, the error of

Fig. 1. Cleveland Bay. Locations of acoustic receivers deployed in November 2008 (shallow [○] and deeper [●] water), August 2009 (▲) and March 2010 (♦); the Ross River receiver was deployed as part of a different project in January 2010 (■). Inset: location of Cleveland Bay relative to the Queensland coast

COA estimates in relation to real-time locations is ca. 225 m (Simpfendorfer et al. 2002).

Presence. Presence was examined daily, with indi-viduals considered present if 2 or more detections were heard on any receiver in the study site on a given day. Presence plots were created to provide a daily timeline to indicate when individuals were present within the study site. Total number of days monitored and number of continuous days present were calculated for each in-dividual to analyse patterns in presence. Data were checked for normality with Quantile-Quantile plots and either $\log(x)$ or $\log(x + 1)$ transformed if required. Two-factor analysis of variance (ANOVA) was used to test for differences in total days present and continuous days monitored between years and age classes.

Home range. Home ranges of individual *Carcharhi-nus amboinensis* were calculated based on COA esti-mates using 50 and 95% kernel utilisation distributions (KUD) and minimum convex polygons (MCP) with the adehabitat package in R (Calenge 2006). Home ranges were calculated at monthly intervals to examine changes in distribution and habitat use over time. Home ranges were plotted in ArcGIS 9.3 to show spa-tial and temporal distribution patterns of individual sharks. Home range data were examined for normality with Quantile-Quantile plots and $\log(x + 1)$ trans-formed, if required. Three-factor ANOVA was used to test for differences in all measures of home range between age classes, months and years.

Movement. Detection data from acoustic receivers were examined to define patterns in movement of juvenile *Carcharhinus amboinensis* based on time of day and tidal stage. Due to limited detections for indi-viduals with short presence times, data were only analysed for individuals that were consistently present in the study site for >2 wk (n = 28). For time of day analysis, the number of detections was calculated per hour for each individual and summed across hours. Chi-square goodness-of-fit tests were used to test for differences in detections with time of day. For tidal stage analysis, hourly tidal stages for the Townsville region were obtained from tide tables provided by Maritime Safety Queensland (Queensland Transport, Australia). Hourly tidal stages were summed into 20 cm bins and the hourly shark detections were placed into the corresponding tide bins and summed for the entire duration each individual was monitored. Chi-square goodness-of-fit tests were used to compare the frequency of detections in each 20 cm tidal bin to the frequency of tidal stages in that bin.

To determine whether individuals moved between shallow and deeper water areas with the tidal cycle, detection frequencies for the 12 shallow water receivers were examined separately to the deep water receivers. The proportion of detections for each 20 cm
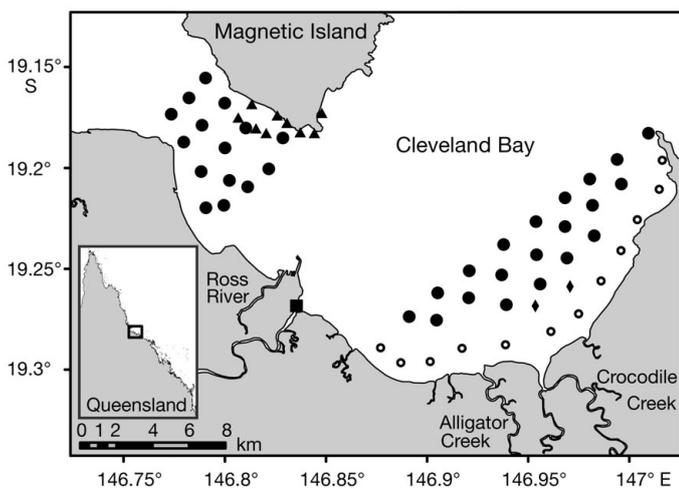
tidal stage interval was plotted against the actual tidal stage distribution for each individual shark for each group of receivers (shallow and deep). Detection data were examined for normality with Quantile-Quantile plots and met the assumptions for parametric testing; *t*-tests were used to test for differences in detections based on tidal stage between years and receiver groups for each age class.

Spectral analysis was conducted to identify regular signals in the detection data. Detections were summed by hour for each age class at both receiver locations (shallow and deep), providing 6 time series datasets. A fast Fourier transform with a Hamming window was applied to each time series and a spectral density function plotted. Cycles in the data were detected by peaks in spectral density and were equal to the inverse of the frequency. For example, since detections were based on an hourly time period, a daily signal would have a frequency of 0.042 (24^{-1}) and a tidal signal would have a frequency of 0.087 (11.5^{-1}). Spectral analysis was conducted in Statistica (StatSoft 2007).

Habitat use by depth. Depths used were analysed for all monitored individuals in the study site to further examine how water depth influences habitat use of juvenile *Carcharhinus amboinensis*. Depth was estimated throughout the study site by calculating a mean depth at each receiver station by hour. Depth and tidal stage were recorded simultaneously at each receiver station and the difference between them was added to the tidal stage for every hour, providing an estimation of depth at each receiver by hour. Mean hourly depth used by each individual was calculated by averaging the depths associated with the receivers that an individual was detected at in that hour. Depth data were examined for normality with Quantile-Quantile plots, met the assumptions for parametric testing, and *t*-tests were conducted to test for differences in depths used between years.

The depths individuals used were compared to the depths available within the study site to determine if juvenile *Carcharhinus amboinensis* displayed electivity or avoidance for specific water depths using Chesson's α (Chesson 1978):

$$\alpha = (r_i/p_i)/\Sigma(r_i/p_i) \tag{1}$$

where r_i is the proportion of time an individual spent at depth i in the study site, and p_i is the proportion of depth i available in the study site. Both the available depths in the study site and the depths used by each shark were tallied into 50 cm intervals. Values of α range from 0 to 1, with values >1/(number of intervals) indicating electivity and values <1/(number of intervals) indicating avoidance. Depths were analysed separately for each age class. Tallies of available depths and used depths for each interval were converted to

proportions and values of electivity calculated. Electivity values were standardised by subtracting 1/(number of intervals) and the resulting deviations plotted. Unless stated otherwise, data analyses for this study were conducted in the R environment (R Development Core Team 2009).

RESULTS

From 2008 to 2010, 43 juvenile *Carcharhinus amboinensis* were released with acoustic transmitters in Cleveland Bay. Young-of-the-year (YOY) individuals were released in January to February 2009 (n = 18; 6 female, 12 male) and December 2009 to May 2010 (n = 16; 6 female, 10 male). One-year-old (1YO) individuals were released in December 2008 (n = 2; 2 male) and December 2009 (n = 3; 1 female, 2 male). Two-year-old (2YO) individuals were only released in the second year of the study from October to December 2009 (n = 4; 4 female). No effort was made to equalize the number of males and females, and transmitters were fitted to animals regardless of sex. Size range was 63–82 cm stretch total length (STL) for YOY individuals, 92.5–100 cm STL for 1YO individuals and 120–129 cm STL for 2YO individuals. All *C. amboinensis* were sexually immature, and YOY individuals were identified by an umbilical scar (either open or closed).

Six *Carcharhinus amboinensis* individuals were either not detected or had limited detections, so they were not included in the analysis. Remaining individuals were present in Cleveland Bay during all seasons throughout the year. In 2009, 3 YOYs were removed from the study by recreational (n = 2) or commercial (n = 1) fishers. Two of these individuals were recaptured within Cleveland Bay and the other at ~10 km north of the study site, with time at liberty ranging from 128 to 375 d.

Presence

Monitored individuals were present in the study site from 4 to 587 d (mean = 158, median = 134) (Fig. 2, Table 1). Although there was variation among individuals, there was no significant difference in total days monitored based on year (ANOVA: $F_{1,32} = 0.20$, p = 0.654), age class ($F_{2,32} = 3.07$, p = 0.060) or the interaction of year and age class ($F_{1,32} = 2.08$, p = 0.159). Continuous days present for individuals in the study site ranged from 1 to 73 d (mean = 4.4, median = 2) (Table 1). There was no significant difference in continuous days present between years ($F_{1,625} = 3.11$, p = 0.078), but a significant difference between age classes was evident ($F_{2,625} = 7.48$, p = 0.006). Mean continuous
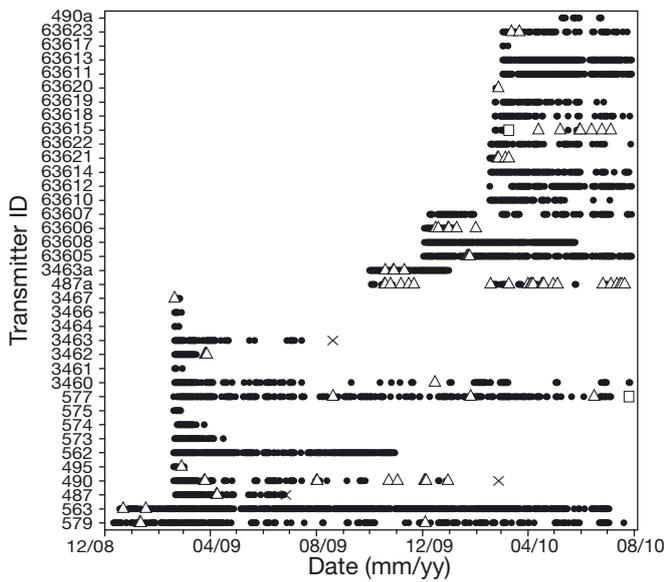
Fig. 2. *Carcharhinus amboinensis.* Presence of juvenile *C. amboinensis* by day in the study site of Cleveland Bay. Symbols: days detected on the eastern array (●), western array (△), Ross River receiver (□) and days when individuals were removed by fishers (✕)

days present was considerably greater for 2YOs (mean = 7.5 d) when compared to the 2 younger age classes (mean range = 3.5 to 4.8 d), indicating presence patterns varied with age. There was no significant difference in continuous days present based on the interaction term of year and age class ($F_{1,625}$ = 0.85, p = 0.355), indicating that age classes behaved similarly across years.

Home range

Most movements of juvenile *Carcharhinus amboinensis* were confined to the eastern side of Cleveland Bay. Half of the monitored individuals made movements to the western side of the bay (Fig. 2), which included 38% of the YOYs, 75% of the 1YOs and 75% of

the 2YOs. These proportions indicate that older juveniles moved farther than younger juveniles, but the frequency and length of these movements varied between individuals. Two individuals (one YOY and one 1YO) were detected in Ross River, each on a single day (Fig. 2). Although the Ross River receiver was deployed for a shorter period of time (January to August 2010), lack of detections on this receiver suggests that *C. amboinensis* did not spend much time in the river.

For all juvenile *Carcharhinus amboinensis* monitored, 50% monthly KUDs ranged from 2.58 to 25.01 km^2 (mean = 7.66 km^2, median = 6.48 km^2) and 95% monthly KUDs ranged from 3.96 to 101.05 km^2 (mean = 37.86 km^2, median = 35.86 km^2) (Fig. 3). There was no significant difference based on year or age class for 50% (year: $F_{1,156}$ = 1.95, p = 0.164; age class: $F_{2,156}$ = 1.00, p = 0.372) or 95% (year: $F_{1,156}$ = 0.16, p = 0.684; age class: $F_{2,156}$ = 2.67, p = 0.072) monthly KUDs. Month was a significant factor for both 50 and 95% KUDs (50%: $F_{19,156}$ = 6.82, p < 0.001; 95%: $F_{19,156}$ = 5.88, p < 0.001) and there was some fluctuation between home ranges across months, with largest home ranges generally occurring during summer wet season months (January to March) (Fig. 3). There was no significant difference between monthly MCPs based on year ($F_{1,156}$ = 0.25, p = 0.614), but a highly significant difference between age classes was present ($F_{2,156}$ = 10.58, p < 0.001). Monthly MCPs ranged from 0.01–180.53 km^2 for YOYs (mean = 35.78 km^2, median = 14.17 km^2), 0.03–201.88 km^2 for 1YOs (mean = 24.79 km^2, median = 15.68 km^2) and 3.09–212.52 km^2 for 2YOs (mean = 57.29 km^2, median = 39.24 km^2). Thus, mean monthly MCPs increased with age class, indicating that older juveniles used more space than younger juveniles (Fig. 4). MCPs include all detection locations while 95% KUD calculations are probability distributions based on 95% of locations and may exclude rare movements, such as excursions into additional areas (Fig. 4). Therefore, significant differences in MCPs between age classes suggest that larger individuals ranged more widely within Cleveland Bay than smaller individuals.

Table 1. *Carcharhinus amboinensis.* Presence of *C. amboinensis* in Cleveland Bay, including sample size (n), minimum, maximum and mean (SE) number of days individuals were monitored and number of days they were continuously present by year and age class. Year is year of release

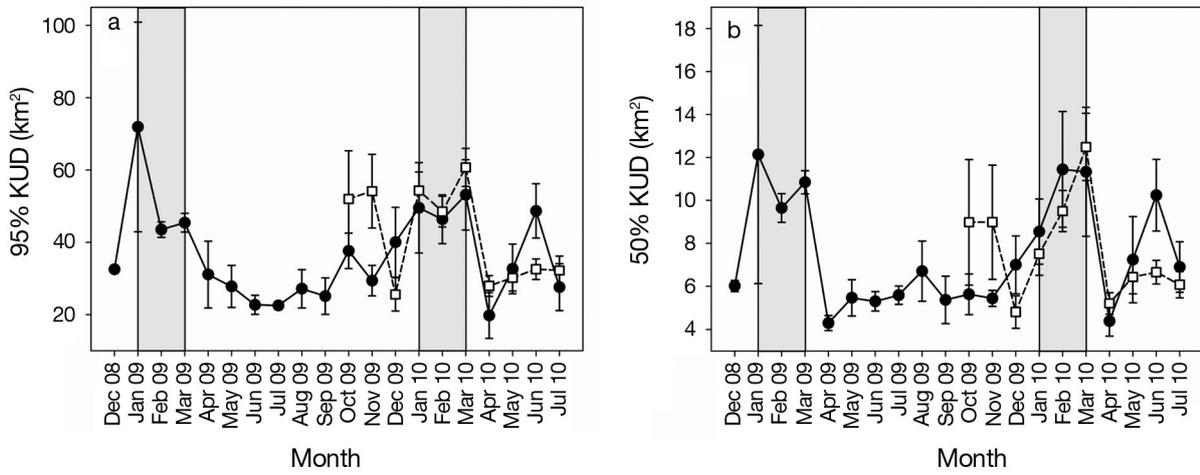| Year	Age class	n	Total days monitored			Continuous days present		
			Min.	Max.	Mean	Min.	Max.	Mean
2008–2009	0	15	6	524	136 (47)	1	40	3.5 (0.3)
	1	2	563	587	575 (12)	1	28	4.5 (0.4)
2009–2010	0	14	4	164	112 (17)	1	73	4.8 (0.7)
	1	2	60	233	147 (87)	1	22	4.2 (1.0)
	2	4	92	292	200 (43)	1	51	7.5 (1.4)

Fig. 3. *Carcharhinus amboinensis.* Mean ± SE monthly home ranges for juvenile *C amboinensis* released in 2008–2009 (● and solid line) and 2009–2010 (□ and dashed line) calculated with (a) 95% and (b) 50% kernel utilisation distributions (KUDs). Shading: months that typically receive the most rainfall during the monsoonal wet season in the Townsville region
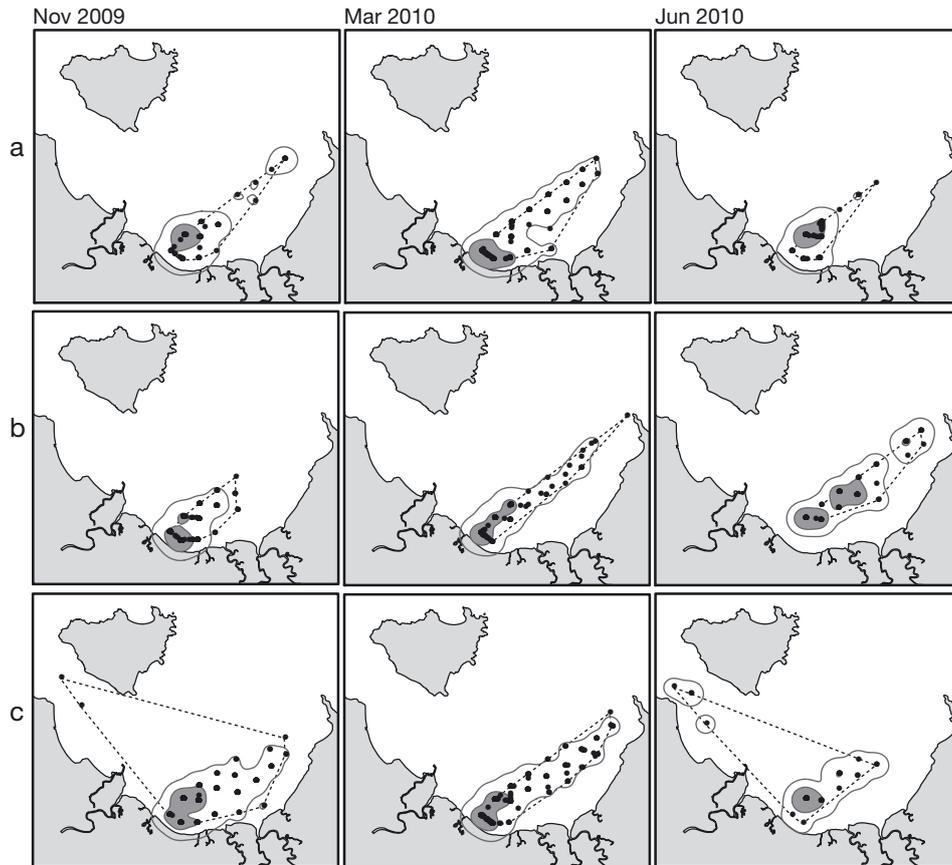

Fig. 4. *Carcharhinus amboinensis.* Monthly home ranges of 9 juvenile *C. amboinensis* individuals, including (a) Young-of-the-year (YOYs), (b) 1 yr olds (1YOs) and (c) 2 yr olds (2YOs) for November 2009, March 2010 and June 2010. Panels are 95% kernel utilisation distributions (KUDs) (grey solid line), 50% KUDs (grey fill) and minimum convex polygons (MCPs) (black dashed line). Black dots: centre of activity (COA) locations used to calculate home ranges

Table 2. *Carcharhinus amboinensis.* χ^2 values based on number of detections for each shark vs. time of day and tidal stage (by year and age class). p-values were significant (p <0.001) in all cases

Transmitter ID	Time of day χ^2	Most detections	Tidal stage χ^2
2008–2009: YOYs			
487	1271.7	No pattern	2364.2
490	339.2	No pattern	618.2
562	2175.6	Night	1775.2
573	609.3	No pattern	656.7
574	520.2	No pattern	831.6
577	1532.2	Night	1260.7
3460	261.1	No pattern	798.1
3462	305.4	No pattern	343.9
3463	311.4	No pattern	978.5
2008–2009: 1YOs			
579	446.1	No pattern	434.5
563	1786.5	No pattern	1082.1
2009–2010: YOYs			
63610	308.6	No pattern	704.2
63612	1041.9	Night	948.7
63614	461.1	No pattern	1207.2
63621	401.1	Day	450.0
63622	795.6	No pattern	1816.8
63615	468.6	No pattern	707.9
63618	357.9	No pattern	549.8
63619	363.8	No pattern	925.4
63611	3587.4	Night	5086.8
63613	4388.4	Night	5257.2
63623	1610.2	Night	1736.6
2009–2010: 1YOs			
63606	266.5	No pattern	381.2
63607	3755.1	Day	1562.6
2009–2010: 2YOs			
487a	276.1	No pattern	1048.2
3463a	668.3	No pattern	195.7
63605	611.6	Day	1222.1
63608	2952.3	No pattern	1265.8

Movement

Examination of detection data by time of day (h) revealed significant differences for all juvenile *Carcharhinus amboinensis* (Table 2). Although detections were not evenly distributed across hours, there was no consistent pattern in behaviour. Six individuals were detected more often during the day, 3 were detected more often during the night and the remaining 19 showed no daily patterns in detections. Overall, there was a large degree of individual variability in detection patterns when analysed with time of day, and different behaviours resulted in some individuals being detected more often either during the day or night.

Similarly, analysis of detection data showed significant differences for all juvenile *Carcharhinus amboi-*

nensis in relation to tidal stage, indicating that individuals were detected more frequently during certain stages of the tide (Table 2). Analysing shallow and deep water receivers separately revealed that movements of juvenile *C. amboinensis* were influenced by the tidal cycle (Fig. 5). Individuals moved into shallow intertidal habitat with the rising tide and were detected more frequently at shallow water receivers than deep water receivers during high tides. There was no significant difference in detections based on tidal stage between years (*t*-tests YOYs: $t_{12.031} = -0.032$, p = 0.975; 1YOs: $t_{1.002} = 0.360$, p = 0.780) so data were pooled across years. Although all juvenile individuals moved with the tidal cycle, movement varied with age class. For shallow water receivers, detections occurred during tidal stages ranging from 71–409 cm for YOYs (median = 248 cm), 79–409 cm for 1YOs (median = 230 cm) and 73–406 cm for 2YOs (median = 211 cm) (Fig. 6). For deep water receivers, detections occurred during tidal stages ranging from 22–397 cm for YOYs (median = 187 cm), 29–410 cm for 1YOs (median = 188 cm) and 29–397 for 2YOs (median = 181 cm) (Fig. 6). Comparing detections based on tidal stage between shallow and deep receivers revealed significant differences among all age classes (YOYs: $t_{31.25} = 10.58$, p < 0.001; 1YOs: $t_{4.64} = 5.72$, p = 0.002; 2YOs: $t_{5.47} = 3.81$, p = 0.011).

Spectral analysis revealed up to 4 peaks in the time series detection data of juvenile *Carcharhinus amboinensis* (Fig. 7). An initial peak at 0.00 was indicative of autocorrelation in the data. A peak at 0.042 reflected a daily pattern (24 h), a peak at 0.087 reflected a tidal pattern (11.5 h) and a peak at 0.125 corresponded to an 8 h signal, which could be due to a tide lag in the movement response of *C. amboinensis*. The strength of these signals varied between receiver location (shallow and deep) based on age class. Relative to the initial peak in the data, YOYs and 1YOs had strong signals on the shallow receivers and either weak or no signals on the deep receivers. 2YOs had weaker signals on the shallow receivers when compared to the deep receivers, though the signals on the deep receivers were less defined with more variability (Fig. 7). This result demonstrates that daily changes in the environment (i.e. changes in water depth due to the tidal cycle) had the strongest influence on the movements of the youngest juveniles in shallow nearshore habitat. However, movements associated with daily and tidal patterns appeared to be an important behaviour for all age classes of juvenile *C. amboinensis*, and older juveniles had similar movement patterns in deeper habitats, indicating a shift in habitat use with increasing age and/or size.
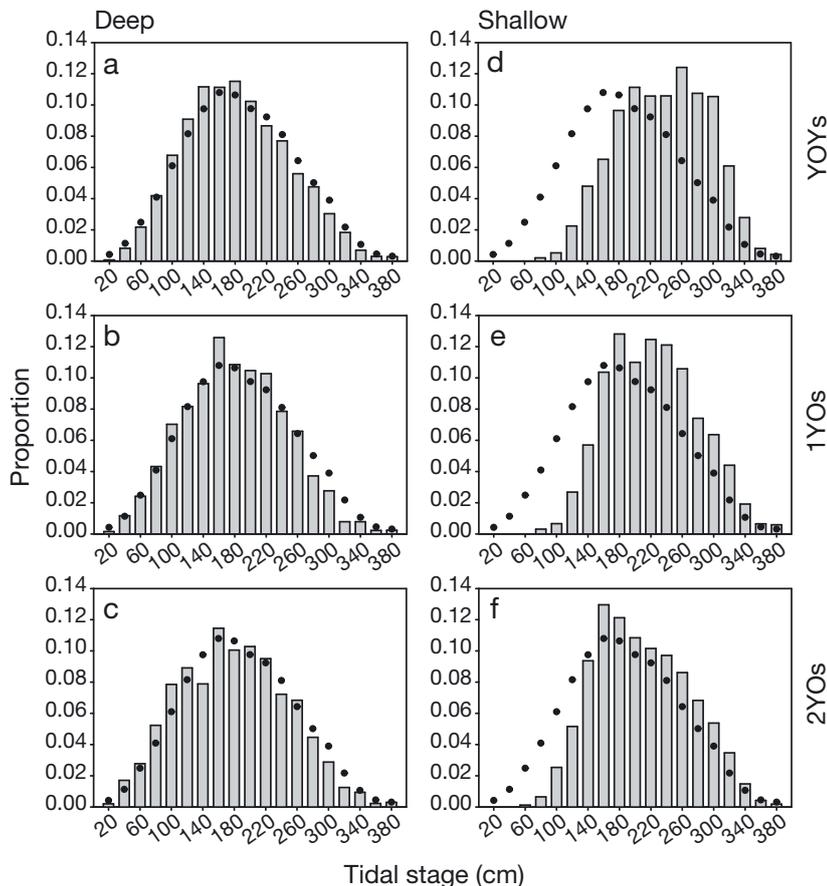
Deep

Shallow

Tidal stage (cm)

Fig. 5. *Carcharhinus amboinensis.* Proportion of detections during each 20 cm tidal stage (grey bars) and tidal stage distribution (●) on deep (a–c) and shallow (d–f) receivers for 3 age classes of juvenile *C. amboinensis*: YOYs (a,d), 1YOs (b,e), 2YOs (c,f). See Fig. 4 for definitions

Habitat use by depth

There was no difference in depths used between years (YOYs: $t_{17.981} = -0.377$, p = 0.710; 1YOs: $t_{1.008} = -0.003$, p = 0.998) so data were pooled across years for depth analyses. Approximately 40% of the depth available in the study site was >400 cm, but all age classes of juvenile *Carcharhinus amboinensis* spent at least 80% of their time in depths <400 cm (Fig. 8a). In addition, the amount of time individuals spent in <200 cm of water, which consisted of only 24% of the depth available in the study site, was 41% for YOYs, 35% for 1YOs and 29% for 2YOs (Fig. 8a). Thus, juvenile *C. amboinensis* used depths disproportionately to what was available in the study site and there was variation among age classes, with YOYs using shallower depths (median = 205 cm) than 1YOs (median = 279 cm) and 2YOs (median = 283 cm).

Electivity analysis revealed that juvenile *Carcharhinus amboinensis* had affinities for different depths based on age class (Fig.8b). Affinity of YOYs peaked

around 200 cm and then decreased until 400 cm where avoidance for depths >400 cm was evident. Affinity of 1YOs increased to a peak at 100 cm and declined until 250 cm before peaking again at ~300 cm. 2YOs showed greatest affinity for deeper depths of 300 to 400 cm. Both 1YOs and 2YOs displayed increasing avoidance of depths >550 cm. Thus, depth of use varied among age classes of juvenile *C. amboinensis*, with the youngest individuals having affinity for shallower depths than older individuals. In addition, 1YOs showed high affinity for both shallow (100 cm) and deeper (300 to 400 cm) depths, which may be an indication of these individuals expanding their movements into deeper habitats as they grow larger.

DISCUSSION

Presence

Juvenile *Carcharhinus amboinensis* were present in Cleveland Bay during all seasons throughout the year, with some individuals monitored for >500 d. Long-term presence was common across years and age classes, although there were some individuals that left the study site after shorter periods of time. Similar long-term presence patterns have been documented in other coastal elasmobranch species, including *C. leucas* (Heupel et al. 2010b), the scalloped
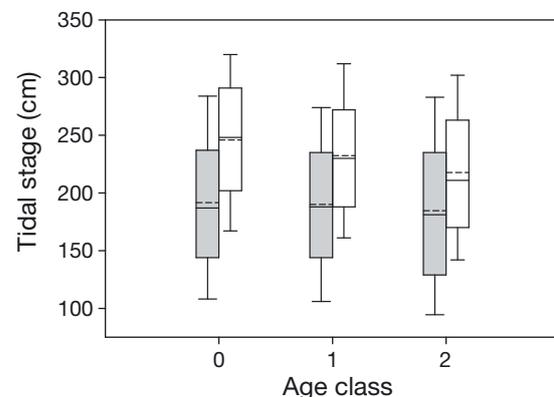

Fig. 6. *Carcharhinus amboinensis*. Boxplots with 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boxes), mean (dashed line) and median (solid line) of detections based on tidal stage for deep (grey) and shallow (white) receivers for 3 age classes of juvenile *C. amboinensis*

hammerhead shark *Sphyrna lewini* (Duncan & Holland 2006) and the cownose ray *Rhinoptera bonasus* (Collins et al. 2008). Patterns in presence varied among age classes of *C. amboinensis*, with older juveniles continuously present for longer periods than younger juveniles. Older juveniles had more extensive movements than younger juveniles and likely used more areas within a day as a result, which would increase

their chance of being detected within the receiver array over consecutive days.

Presence patterns showed that juvenile *Carcharhinus amboinensis* generally used the eastern side of Cleveland Bay, with individuals occasionally moving across the bay to the western side. Although all individuals monitored during this study were released on the eastern side of the bay, catch data verified that *C.*
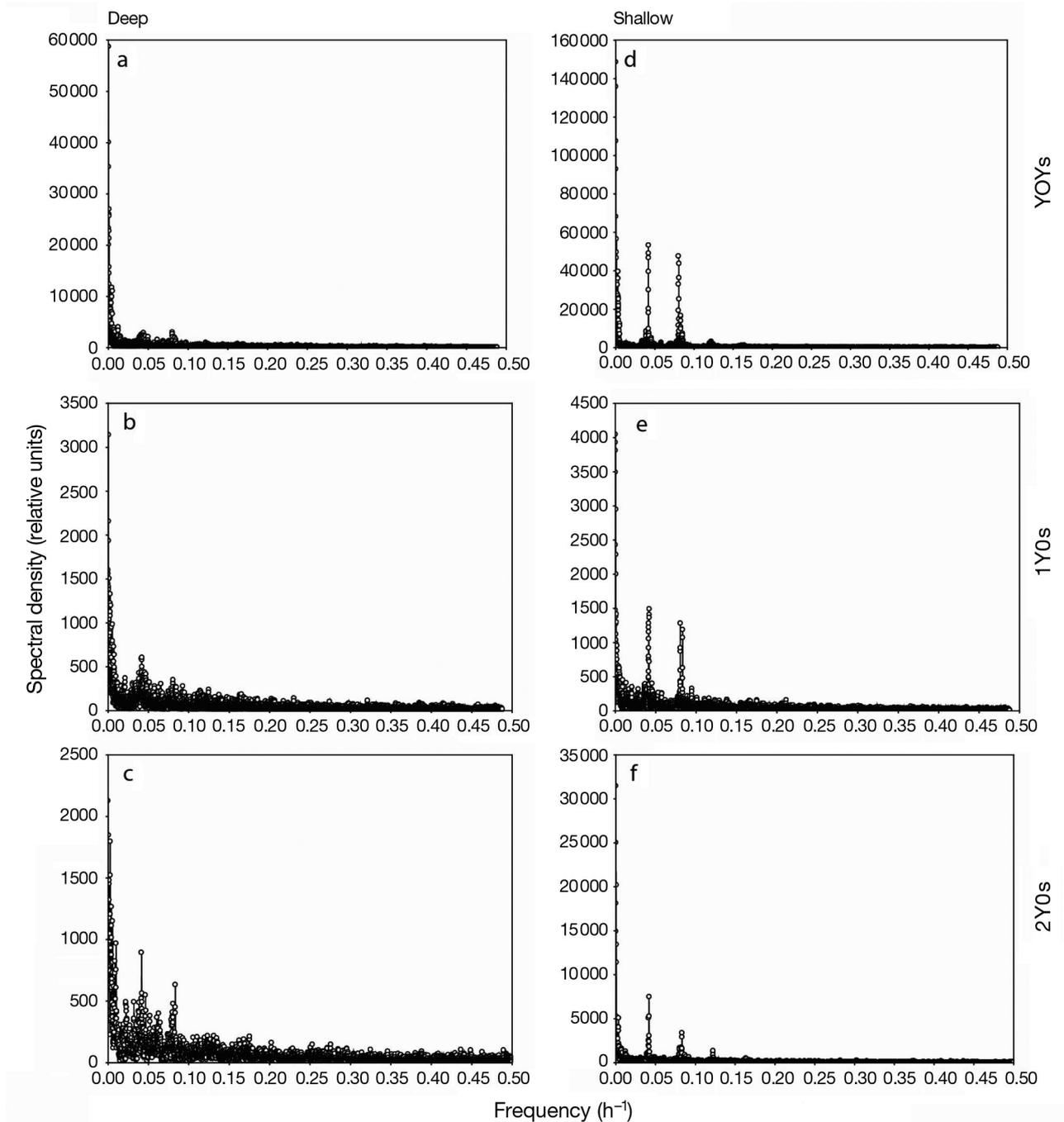

Fig. 7. *Carcharhinus amboinensis*. Spectral density of hourly detections on deep (a–c) and shallow (d–f) receivers for 3 age classes of juvenile *C. amboinensis*: YOYs (a,d), 1YOs (b,e), 2YOs (c,f). See Fig. 4 for definitions
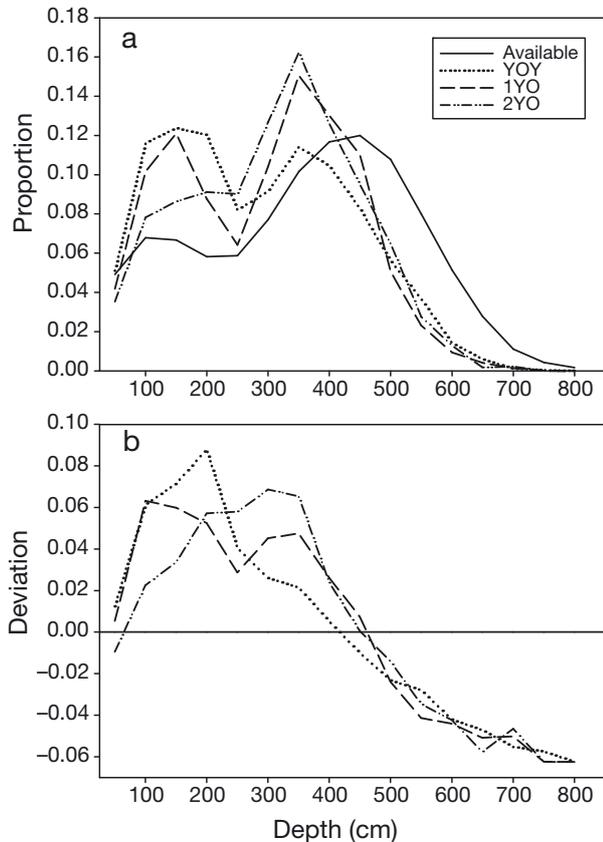
Fig. 8. *Carcharhinus amboinensis*. (a) Proportion of depths available in Cleveland Bay (solid line) and that used by YOY, 1YO and 2YO *C. amboinensis*. (b) Electivity analysis of depth for YOY, 1YO and 2YO *C. amboinensis*, with values >0 (solid line) indicating affinity. See Fig. 4 for definitions

Home range

Limited movements of juvenile *Carcharhinus amboinensis* were also supported by home range analyses. Individuals maintained relatively small core home ranges, but used additional areas to encompass larger total ranges overall. Using areas outside of core ranges could be attributed to exploratory movements, with individuals searching for other suitable habitats or additional resources. Total home ranges of juvenile *C. amboinensis* sometimes included areas in both the northern and western portion of Cleveland Bay, but core home ranges consistently remained in the southern portion of the bay adjacent to the creek mouths, where individuals displayed a strong association with shallow, turbid habitats. This finding is similar to that of Cliff & Dudley (1991), who reported *C. amboinensis* in South African waters using turbid areas in close proximity to estuaries and rivers. However, limited detections of juvenile *C. amboinensis* on the Ross River receiver suggest that individuals rarely moved up or used the creeks and rivers. *Carcharhinus amboinensis* has been reported using brackish water, but unlike its close relative *C. leucas*, has not yet been found to penetrate freshwater systems (Last & Stevens 2009). Rather, juvenile *C. amboinensis* have been reported to move away from rivers at times of high freshwater inflow (Knip et al. in press), so it is likely that this species does not have a tolerance for low salinities or high flows, which are characteristic of river environments. Other studies have suggested that competitive exclusion or habitat partitioning might occur between *C. amboinensis* and *C. leucas* (Bass et al. 1973, Compagno 1984). Competitive exclusion may be occurring to some degree in Cleveland Bay, as juvenile *C. leucas* are commonly caught in adjacent rivers and creeks, and juvenile *C. amboinensis* are not (A. J. Tobin unpubl. data). Thus, it is possibly a combination of habitat preference, physical limitation and resource partitioning that dictates the home range and habitat use of juvenile *C. amboinensis* in Cleveland Bay.

Although there were no differences in home range size between age classes of juvenile *Carcharhinus amboinensis* based on KUDs, significant differences were apparent between age classes using MCP measures. There were a lower number of older juveniles monitored, but these individuals had larger MCPs than younger individuals, which may indicate an ontogenetic shift in the movement and home range behaviour of juvenile *C. amboinensis*. Home range size has been found to increase with increasing body size in other elasmobranch species, including *Rhinoptera bonasus* in a Florida estuary (Collins et al. 2007) and the lemon shark *Negaprion brevirostris* in the Bahamas (Morrissey & Gruber 1993). Increasing MCP size with age

amboinensis were rarely found elsewhere in Cleveland Bay (D. M. Knip unpubl. data). Individuals that undertook movements across the bay did so in all months and there was no evident pattern or cue that triggered these movements. Moving 10 km across the bay appeared to be an occasional event for most individuals, indicating that juvenile *C. amboinensis* had relatively localised movements. In addition, the 3 sharks removed from the study were all caught in close proximity to Cleveland Bay, with the individual recaptured ~10 km north of the study site at liberty for 375 d. Similar localised movements have been reported for *C. amboinensis* along the northern coast of Australia (Stevens et al. 2000). The eastern side of Cleveland Bay has areas of strong tidal flow and high turbidity, due to the 3 main river systems that enter the bay along the southeast shore. The shallow turbid habitat within this relatively localised area along the eastern side of Cleveland Bay may offer sufficient and/or preferred resources for juvenile *C. amboinensis*, which could result in their limited movement from this specific area.

class suggests that older *C. amboinensis* juveniles roamed farther and had more extensive movements than younger juveniles. Imansyah et al. (2008) found a similar result with komodo dragons *Varanus komodoensis* in Indonesia, where the youngest hatchlings used smaller spaces than older juveniles. Likewise, Simpfendorfer et al. (2010) found that home range size increased with age class among juvenile smalltooth sawfish *Pristis pectinata* in Florida waters, but also that home range sizes remained consistent among individuals within the same age class. These authors hypothesised that the differences in space use were due to age classes being affected by different selective pressures. A similar situation may be occurring among age classes of juvenile *C. amboinensis*. Young juveniles may have been more influenced by factors like predation risk and as such, consistently used smaller areas and did not move as far. Older juveniles may need to have been more driven by resource acquisition and so increased their use of space to include additional habitats. To meet resource needs as a larger individual, older juveniles may roam farther to obtain larger-sized and a higher diversity of prey items. However, while they are young, juvenile *C. amboinensis* may restrict their movements and use smaller spaces as a refuging strategy to increase survival. Movements and home ranges likely increase as juveniles grow larger and become more successful competitors and less vulnerable to different risks (e.g. predation).

Home range patterns of juvenile *Carcharhinus amboinensis* remained consistent across years but varied significantly between months. In general, both 50 and 95% KUDs increased and became more variable in the months of January to March. These months coincide with the monsoonal wet season in the Townsville region, during which an increased, though highly variable, amount of rainfall occurs (Bureau of Meteorology, Australia). Juvenile *C. amboinensis* were found to shift their home ranges to more northern parts of Cleveland Bay during the wet season, but home range size remained stable across weeks, indicating that individuals used the same amount of space each week even though they used different areas (Knip et al. in press). Thus, larger monthly home ranges indicate times when individuals shifted their activity due to freshwater flow, resulting in larger overall home ranges during wet season months. However, an increase in monthly home ranges could also indicate times when individuals made excursions from their core home ranges, such as movements across the bay or north towards Cape Cleveland. Thus, variation in home range across months could be due to differences in excursion frequency, particularly by older juveniles who tended to move more sporadically and roam farther than younger juveniles.

Movement and depth

Although diel movement patterns have been reported in other coastal shark species, this pattern was not evident in juvenile *Carcharhinus amboinensis*. Some individuals were detected more often during the day or at night, but for most individuals, there was no pattern in detection frequency with hour of the day. This result is similar to that found with the bonnethead shark *Sphyrna tiburo* in a Florida estuary and the grey reef shark *C. amblyrhynchos* within the Great Barrier Reef, where most individuals displayed no consistent pattern in movement with time of day (Heupel et al. 2006, 2010a). Although there was no pattern found with detections and time of day for juvenile *C. amboinensis*, a large daily signal was evident in the spectral analysis for all age classes. A daily signal in the detection data could be a result of several factors, including the strong tidal pattern in the data as well as the 9 individuals that had a higher detection frequency either during the day or night. In addition, daily physical (e.g. wind) and biological (e.g. crepuscular noise) patterns in the environment may have affected equipment performance, resulting in an hourly variation of detection frequency. Lack of a consistent pattern between detections and time of day for juvenile *C. amboinensis* suggests that factors other than diel changes have a more important role in their movements.

Changes in water depth associated with the tidal cycle strongly influenced the movements of juvenile *Carcharhinus amboinensis*. Individuals of all age classes moved into the intertidal zone with the rising tide and back out to deeper areas with the falling tide. Cleveland Bay has a relatively high maximum tidal range (4.2 m), which allowed individuals to use the tide to their advantage and move onto the shallow mud flats that usually dry out at low tide. However, it is unclear what factors were driving these tidal movement patterns. Juvenile *C. amboinensis* may be moving into the intertidal zone at high tides to increase foraging opportunities by accessing additional habitats and prey items. Similar tidal movements have been documented for the leopard shark *Triakis semifasciata* in 2 California bays. Both Ackerman et al. (2000) and Carlisle & Starr (2010) found that *T. semifasciata* moved with the tide to maximise foraging area by using regions that could only be reached at high tide. Tidal fluctuations have also been found to influence the movements of several fish species, which in turn may affect the movements of predators foraging on those species (Sogard et al. 1989). Thus, juvenile *C. amboinensis* may be moving with the tide to follow and forage on moving prey items. Examination of tidal signals in the detection data indicated that movements of the youngest juveniles were the most influenced by

the tide in shallow areas. Similarly, the smallest *Negaprion brevirostris* juveniles at an atoll in Brazil were also the most influenced by the tide and this restricted their movements to the shallowest tide pools (Wetherbee et al. 2007). The authors believed these young individuals moved with the tide so they could remain in depths shallow enough to avoid predators using the same region. Large sharks are encountered often throughout Cleveland Bay (D. M. Knip unpubl. data) and presumably present a predatory threat to small *C. amboinensis*. Thus, moving with the tide to remain in shallower depths may also be a refuging strategy for juvenile *C. amboinensis*. Small individuals are likely the most vulnerable, which may be why tidal movement patterns were the strongest among the youngest juveniles in shallow habitats.

Perhaps not as important as predator avoidance (Steele 1998), differences in movement and habitat use among age classes of juvenile *Carcharhinus amboinensis* may also act as a mechanism to reduce intraspecific competition. Remaining in shallower habitats would allow young juveniles to avoid older individuals using deeper waters, who would likely out-compete them for similar resources. Age class segregation has been reported with *C. leucas* in Florida waters, where the youngest juveniles remained up river while older juveniles used areas farther downstream towards the coast (Simpfendorfer et al. 2005). These authors suggested that younger juveniles used different habitat to that of older juveniles to decrease predation risk, but also to reduce competition associated with larger individuals. Being smaller in size, young juveniles are presumably weaker competitors as well as less skilled at acquiring prey when compared to older juveniles. Spina (2000) found that age segregation occurred in rainbow trout *Oncorhynchus mykiss*, with older individuals using deeper habitats. Although this ontogenetic shift in habitat use may have been due to size specific habitat requirements, it also reduced intraspecific competition (Spina 2000). Similarly, age segregation in *C. amboinensis* may be driven by size specific habitat requirements, with individuals shifting their habitat use behaviours as they grow. This may reduce intraspecific competition between individuals of different sizes and ultimately increase population success.

Ontogenetic shifts in depth among age classes of juvenile *Carcharhinus amboinensis* showed that individuals used the shallowest depths while they were young, and expanded their use of habitats to include deeper depths when they become older. Similarly, studies that examined habitat use of *Pristis pectinata* in Florida waters and freshwater sawfish *P. microdon* in a Western Australia river reported differences in depths used among juvenile age classes, with the youngest individuals using shallower depths (Whitty et al. 2009,

Simpfendorfer et al. 2010). These authors suggested that using shallow water was a predator avoidance mechanism for smaller juveniles. Small *C. amboinensis* may similarly be using shallow depths as a refuging strategy, but it is also likely that these young individuals were constrained to a narrower depth range due to their restricted movements. Since older juveniles typically had more extensive movements and expanded their use of space, they probably also used deeper depths as a result.

Changes in habitat use among age classes of juvenile *Carcharhinus amboinensis* were also strongly supported by spectral analyses. The shift in tidal signal strength from shallow to deep water receivers with the 2YO age class suggests a transition occurred in the movement and habitat use behaviour of juvenile *C. amboinensis*. A tidal signal on the deep receivers indicates that older juveniles were using additional areas in deeper water but continued undertaking movements similar to those of their younger counterparts. In addition, a weaker tidal signal for older juveniles on the shallow receivers suggests that moving with the tide to remain in shallow depths was not as important for them as it was for younger juveniles. Similar ontogenetic shifts in habitat use have generally not been well documented in coastal elasmobranch species, but have been reported in some teleost fishes. For example, specific habitat preference of juvenile sparids *Diplodus* sp. in the Mediterranean Sea was found to decrease as individuals grew (Macpherson 1998), and habitat use of Roanoke logperch *Percina rex* in a river in the eastern United States was reported to change based on age class (Rosenberger & Angermeier 2003). Similarly, *C. amboinensis* showed the greatest preference for a specific habitat during the earliest life-stages, where young juveniles restricted their movements to depths typically <2 m and only occasionally moved out of core home ranges adjacent to creek mouth habitat. When juvenile *C. amboinensis* reached around 2 yr of age, they showed less preference to that specific habitat region and began using different behaviours and habitats, such as making more frequent excursions from core ranges and using more space. This transitioning behaviour may be an ontogenetic strategy for this species, in which older juveniles prepare for eventually leaving shallow nearshore regions to use deeper habitats further offshore.

CONCLUSIONS

Long-term presence of *Carcharhinus amboinensis* in Cleveland Bay suggests that this nearshore region provides important habitat for a range of juvenile age classes. By monitoring individuals over a period of

years, this study confirmed that *C. amboinensis* associate strongly with shallow, turbid habitats adjacent to creek and river mouths. Individuals only occasionally used areas outside of this habitat and also rarely moved up the creeks or rivers, indicating that the movements and home range of *C. amboinensis* are constrained to a relatively narrow habitat range within this tropical nearshore region, especially for the youngest juveniles. This result demonstrates that the habitat use of *C. amboinensis* differs to that of its close relative *C. leucas*, a species that uses river habitat almost exclusively as juveniles.

The results of this study help define intraspecific differences in habitat use between age classes of a coastal shark species, a topic that has remained relatively unstudied to date. The tidal cycle strongly influenced the movements of *Carcharhinus amboinensis*, particularly for the youngest juveniles, and moving to remain in shallow water may have been a refuging strategy for these individuals. An ontogenetic shift in depth, home range and excursion frequency suggests that older juveniles were influenced by other factors. Being larger in size, older *C. amboinensis* juveniles may have changed their movement and habitat use behaviour to meet different needs, such as acquiring additional or different resources. Although juvenile *C. amboinensis* expanded their movements and used deeper habitats when they reached 2 yr of age, they still continued to have movement patterns associated with the tide. Thus, moving with the tide may be a learned behaviour in this species and possibly a strategy crucial for survival during the first years of life.

This study captured a transition phase in the movement and habitat use patterns of juvenile sharks, where older individuals were shifting between behavioural strategies they used while young and those they would need to be successful as sub-adults. By providing information on ontogenetic shifts in the movement and habitat use of a coastal shark species, this study establishes a better understanding of the implications associated with multiple age classes using the same areas and sharing space. The youngest juveniles are likely among the most vulnerable, and these individuals will need to use a suitable strategy if they are to be successful survivors that grow into better competitors.

LITERATURE CITED

Ackerman JT, Kondratieff MC, Matern SA, Cech JJ Jr (2000) Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environ Biol Fishes 58:33–43

Bass AJ, D'Aubrey JD, Kistnasamy N (1973) Sharks of the east coast of southern Africa. 1. The genus *Carcharhinus* (Carcharhinidae). Investigational Report 33, Oceanographic Research Institute, Durban

Beck MW, Heck KL, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51:633–641

Bellquist LF, Lowe CG, Caselle JE (2008) Fine-scale movement patterns, site fidelity, and habitat selection of ocean whitefish (*Caulolatilus princeps*). Fish Res 91:325–335

Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol Prog Ser 268:245–264

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Carlisle AB, Starr RM (2010) Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. Environ Biol Fishes 89:31–45

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fishes 38: 37–48

Chesson J (1978) Measuring preference in selective predation. Ecology 59:211–215

Cliff G, Dudley SFJ (1991) Sharks caught in the protective gill nets off Natal, South Africa. 5. The java shark *Carcharhinus amboinensis* (Muller & Henle). S Afr J Mar Sci 11: 443–453

Collins AB, Heupel MR, Motta PJ (2007) Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. J Fish Biol 71: 1159–1178

Collins AB, Heupel MR, Simpfendorfer CA (2008) Spatial distribution and long-term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. Estuaries Coasts 31:1174–1183

Compagno LJV (1984) FAO species catalogue, Vol 4. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO Fish Synop 125:251–655

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. Mar Ecol Prog Ser 358:257–271

Duncan KM, Holland KN (2006) Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. Mar Ecol Prog Ser 312:211–221

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat Biol 1:277–289

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive acoustic monitoring techniques. Environ Biol Fishes 71:135–142

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. Environ Biol Fishes 76:47–67

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

Heupel MR, Simpfendorfer CA, Fitzpatrick R (2010a) Large-scale movement and reef fidelity of grey reef sharks. PLoS ONE 5:e9650

Heupel MR, Yeiser BG, Collins AB, Ortega L, Simpfendorfer CA (2010b) Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. Mar Freshw Res 61:1–10

Imansyah MJ, Jessop TS, Ciofi C, Akbar Z (2008) Ontogenetic differences in the spatial ecology of immature Komodo dragons. J Zool (Lond) 274:107–115

Knip DM, Heupel MR, Simpfendorfer CA (2010) Sharks in nearshore environments: models, importance, and consequences. Mar Ecol Prog Ser 402:1–11

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (in press) Wet season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. Mar Freshw Res

Last PR, Stevens JD (2009) Sharks and rays of Australia, 2nd edn. CSIRO Division of Fisheries, Cronulla

Macpherson E (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. J Exp Mar Biol Ecol 220:127–150

Morrissey JF, Gruber SH (1993) Home range of juvenile lemon sharks, *Negaprion brevirostris.* Copeia 1993:425–434

Pikitch EK, Chapman DD, Babcock EA, Shivji MS (2005) Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). Mar Ecol Prog Ser 302:187–197

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rodriguez RW, Webb RMT, Bush DM (1994) Another look at the impact of hurricane Hugo on the shelf and coastal resources of Puerto Rico, USA. J Coast Res 10:278–296

Rosenberger A, Angermeier PL (2003) Ontogenetic shifts in habitat use by the endangered Roanoke logperch (*Percina rex*). Freshw Biol 48:1563–1577

Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ Biol Fishes 37: 337–345

Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can J Fish Aquat Sci 59:23–32

Simpfendorfer CA, Freitas GF, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida Estuary. Estuaries 28:78–85

Simpfendorfer CA, Wiley TR, Yeiser BG (2010) Improving conservation planning for an endangered sawfish using data from acoustic telemetry. Biol Conserv 143: 1460–1469

Sogard SM, Powell GVN, Holmquist JG (1989) Utilization by fishes of shallow, seagrass-covered banks in Florida Bay: 2. Diel and tidal patterns. Environ Biol Fishes 24: 81–92

Spina AP (2000) Habitat partitioning in a patchy environment: considering the role of intraspecific competition. Environ Biol Fishes 57:393–400

Steele MA (1998) The relative importance of predation and competition in two reef fishes. Oecologia 115:222–232

Stevens JD, West GJ, McLoughlin KJ (2000) Movements, recapture patterns, and factors affecting the return rate of Carcharhinid and other sharks tagged off Northern Australia. Mar Freshw Res 51:127–141

Walker T (1981) Seasonal salinity variations in Cleveland Bay, northern Queensland. Aust J Mar Freshwater Res 32: 143–149

Wetherbee BM, Gruber SH, Rosa RS (2007) Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. Mar Ecol Prog Ser 343:283–293

White WT, Potter IC (2004) Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Mar Biol 145:1023–1032

Whitty JM, Morgan DL, Peverell SC, Thorburn DC, Beatty SJ (2009) Ontogenetic depth partitioning by juvenile freshwater sawfish (*Pristis microdon*: Pristidae) in a riverine environment. Mar Freshw Res 60:306–316