Wet-season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis,* in tropical nearshore waters

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Abstract.   Tropical nearshore environments are highly dynamic systems owing to extreme freshwater flow and flooding episodes that occur in wet-season months. We hypothesised that juvenile sharks in tropical nearshore waters respond to seasonal freshwater inflow by moving away from areas of strong flow. An array of fifty-eight acoustic receivers deployed in Cleveland Bay, north Queensland, Australia, passively tracked thirty-two juvenile pigeye sharks, *Carcharhinus amboinensis*, throughout two wet seasons from 2008 to 2010. Influences associated with wet seasons appeared to play a role in habitat use by juvenile *C. amboinensis* in this region. Home ranges and distribution of individuals showed distinct changes, with individuals moving north away from sources of freshwater inflow during high flows. The location of individuals within the bay was strongly influenced by freshwater inflow in both years. Although juvenile *C. amboinensis* moved in response to freshwater inflow, home-range sizes remained stable, and the amount of space individuals used did not change in relation to freshwater inflow. By defining the response of juvenile sharks to highly variable freshwater flow events, this research provides useful information for understanding species behaviour in a dynamic and changing climate, and contributes towards effective management of tropical river systems.

Additional keywords: environmental effects, passive acoustic monitoring.

Introduction

Freshwater flow and flooding has a major impact on nearshore regions (e.g. bays, lagoons and estuaries) and can cause large fluctuations in the physical characteristics of an environment (Finlayson and McMahon 1988; Fraser 1997). Tropical regions are susceptible to increased amounts of freshwater impinging on these systems as a result of extreme rainfall events occurring in wet-season months (Balek 1983). Rainfall in the tropics is generally around $2000 \, \text{mm year}^{-1}$, with some regions experiencing up to $10\,000 \, \text{mm year}^{-1}$ (Latrubesse *et al.* 2005). Such a significant input of freshwater causes high variability in the flows of tropical river systems, especially rivers in northern Australia, which are affected by annual monsoonal events (Balek 1983; Finlayson and McMahon 1988). Understanding the effects of extreme annual flow and flooding episodes on nearshore inhabitants is important, as freshwater flow influences species differently (Ter Morshuizen *et al.* 1996; Flannery *et al.* 2002), and may even cause mortality in some species (Whitfield and Paterson 1995).

Mobile fish species can modify their behaviour or physiology to cope with fluctuating environmental conditions, or may leave

a region when conditions extend beyond their physiological limitations. For example, some teleost species move from deep to shallow water in response to low dissolved-oxygen concentrations (Pihl *et al.* 1991). Similar results have been found with sharks; for example, leopard sharks (*Triakis semifasciata*) leave nearshore regions during anoxic periods (Carlisle and Starr 2009) and bonnethead sharks (*Sphyrna tiburo*) leave estuaries when salinity declines (Ubeda *et al.* 2009). Few studies have, however, investigated the specific response of individual animals (e.g. movement and distribution) to seasonal variation (e.g. freshwater inflow) in tropical nearshore regions. Studies have found a general decrease in the abundance and diversity of fish species in tropical nearshore regions during wet-season events (Cyrus and Blaber 1992; Fraser 1997). One study specifically examined the movement and distribution of juvenile bull sharks (*Carcharhinus leucas*) in the estuarine portion of a Florida river and determined that individuals moved downriver with decreasing salinity and increasing freshwater flow rate (Heupel and Simpfendorfer 2008).

The pigeye shark, *Carcharhinus amboinensis*, inhabits tropical nearshore regions in the Indo–West Pacific, and in Australia
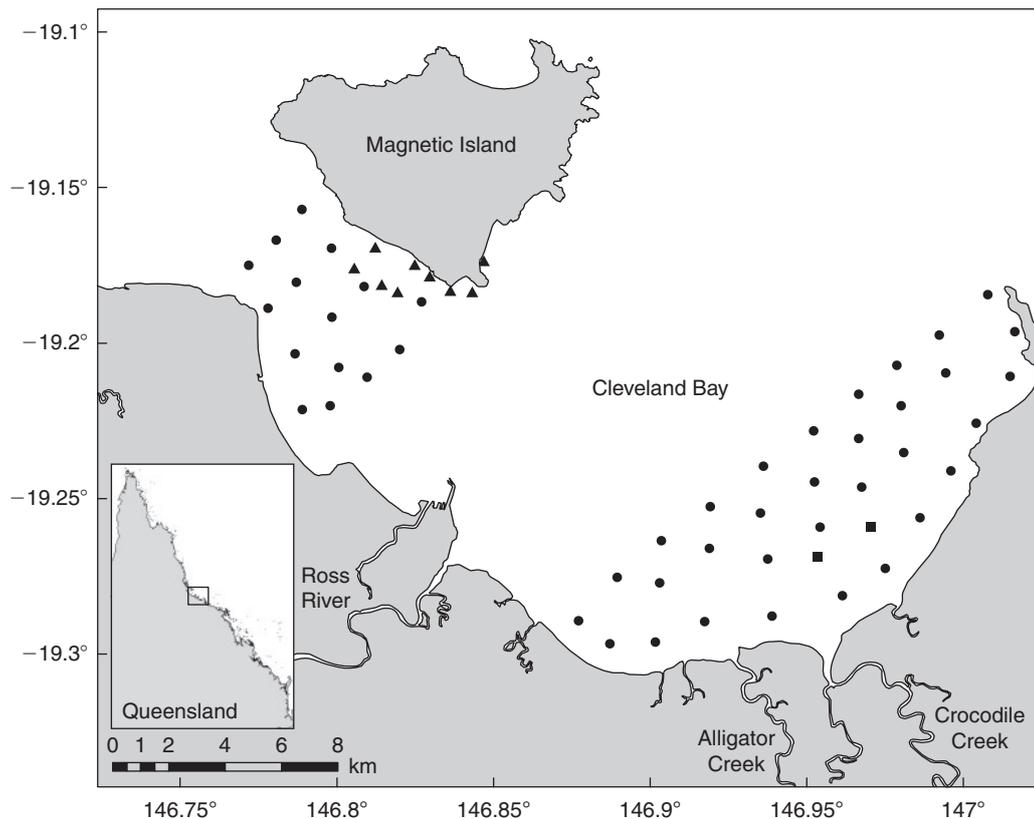
Fig. 1. Cleveland Bay. Locations of acoustic receivers deployed in November 2008 (●); locations of acoustic receivers deployed in August 2009 (▲); locations of acoustic receivers deployed in March 2010 (■). Inset shows location of Cleveland Bay relative to the Queensland coast.

it ranges throughout northern waters from Brisbane (Queensland) to Carnarvon (Western Australia) (Compagno 1984; Last and Stevens 2009). Size at birth is 60–65 cm, maximum size is ~280 cm and diet mainly consists of teleost fish, crustaceans, cephalopods and molluscs (Compagno 1984; Last and Stevens 2009). Unlike its close relative, the widely-distributed *C. leucas*, little is known about the movement of *C. amboinensis* and how it uses nearshore habitats. In northern Australia, *C. amboinensis* was reported to have relatively localised movements (Stevens *et al*. 2000; Last and Stevens 2009). In addition, *C. amboinensis* is thought to occasionally enter brackish water, and in South Africa individuals were reported using warm turbid waters close to large estuaries and river mouths (Cliff and Dudley 1991; Last and Stevens 2009). Tropical nearshore regions provide habitat for early life-stages of many populations of sharks (Heupel *et al*. 2007). Similar to other large-bodied shark species, juvenile *C. amboinensis* may use nearshore regions as nursery areas. Thus, understanding how this predator uses nearshore regions and what factors affect its movement and distribution is crucial to defining its early life-history and ecology within nearshore systems.

The purpose of this study was to determine how freshwater flows during the wet season affect movement and distribution of juvenile *C. amboinensis* in a tropical nearshore environment. Individual sharks were tracked over two consecutive years (two wet seasons) using passive acoustic monitoring. Home-range size, home-range location and distribution of individuals were examined in relation to freshwater inflow across seasons. With altered climate scenarios an increasing concern for tropical nearshore regions, a better understanding of species responses to environmental and seasonal variability is needed. The data from this study were used to test the hypothesis that juvenile *C. amboinensis* respond to increased freshwater inflow by shifting their distribution away from sources of strong flows.

Materials and methods

Study site

Cleveland Bay is a shallow and dynamic coastal habitat on the north-east coast of 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 ~225 km^2 and supports 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 river systems that run into the bay, and increased freshwater flow during the wet season causes strong currents and large decreases in salinity in the south-east portion of the bay.

The wet season in northern Queensland is variable. Average annual rainfall in Townsville is around 1200 mm but has been higher over the past two years; Townsville received ~1830 mm of rainfall from December 2008 to April 2009, and 1460 mm of
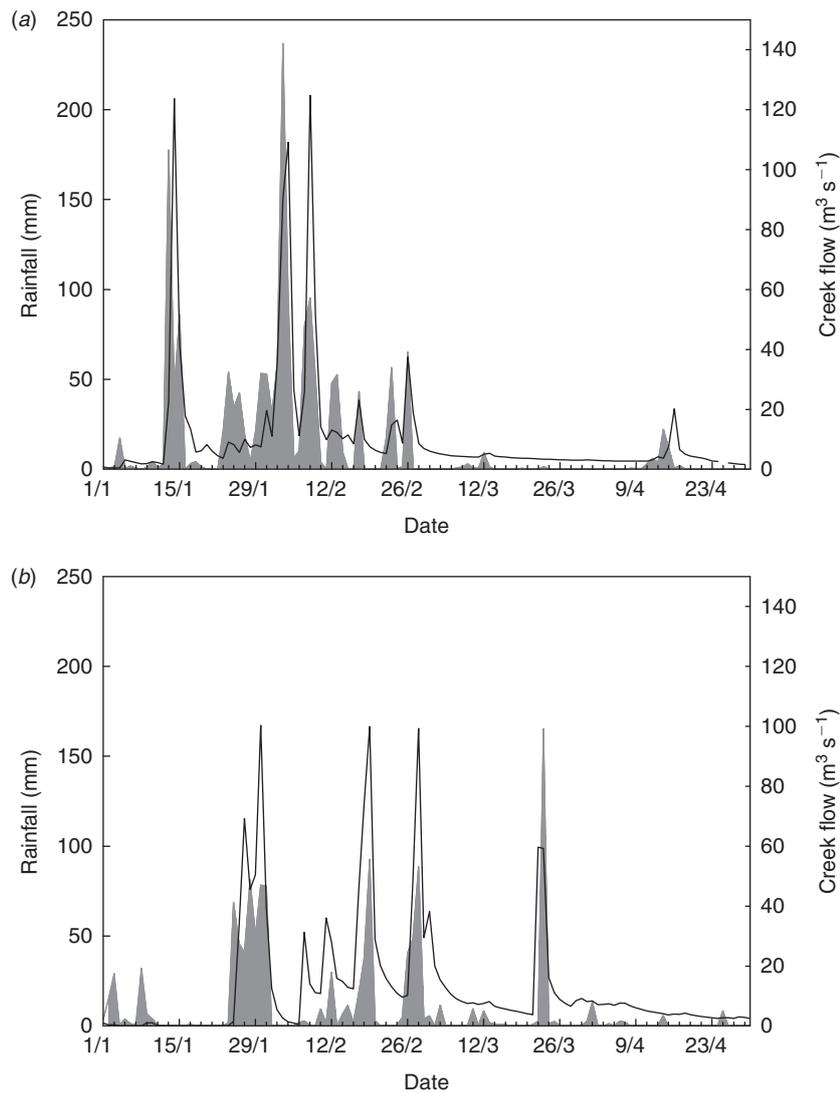
Fig. 2. Mean daily rainfall for Townsville (grey fill) and Alligator Creek flow (solid line) from January to April for (*a*) 2009 and (*b*) 2010.

rainfall from December 2009 to April 2010 (Fig. 2). In 2009, 88% of total wet-season rainfall occurred in February and March, whereas in 2010, only 64% of wet-season rainfall occurred in these two months (Fig. 2). Freshwater inflow from creeks adjacent to Cleveland Bay is directly influenced by rainfall, with the largest flow rates occurring immediately after rainfall events (Fig. 2). Owing to the variability in rainfall between the two years of this study, the amount and pattern of freshwater inflow also varied. A major consequence of increased freshwater inflow during the wet season is decreased salinity in Cleveland Bay, and the lowest salinity levels have been recorded at times of highest freshwater inflow (Walker 1981).

Field methods

Monitoring of target species within the study site was conducted using passive acoustic monitoring. Forty-seven VR2 or VR2W acoustic receivers (Vemco Ltd, Canada) were deployed in Cleveland Bay in November 2008 (Fig. 1). To cover additional area and habitats, nine receivers were added to the array in August 2009, and two were added in March 2010 (Fig. 1). The detection range of V16 acoustic transmitters within the study site was ∼900 m. The array 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 6–8 weeks.

Sharks were captured with baited hooks on short long-lines. Long-lines were 500-m bottom-set mainlines (8-mm nylon rope) 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 tetradactylum*) or fresh trevally

(*Caranx* sp.). All captured sharks were identified, measured to the nearest mm, sexed and tagged with a rototag in the first dorsal fin and a single-barb dart tag in the dorsal musculature for identification before release. Juvenile *C. amboinensis* were also fitted with a V16 acoustic transmitter (Vemco Ltd, Canada), which was surgically implanted into the body cavity to ensure long-term retention. A small incision (3–4 cm) was made in the abdomen and the transmitter inserted. The wound was closed by suturing both the muscle and skin layers to ensure adequate wound closure and healing. 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 interval of 45–75 s with a battery life of ~18 months.

Data analysis

Data collected from acoustic receivers included date, time and identity of individuals detected. Only data from acoustic receivers on the eastern side of the array were included in this analysis for two reasons: first, detections of *C. amboinensis* on the western array of receivers were rare, and second, the western array did not cover areas of high freshwater inflow. Locations for sharks in the bay 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 represent an individual's mean position for the set time-step. For small sharks, the error of COA estimates in relation to real-time locations has been calculated to be ~225 m (Simpfendorfer *et al.* 2002).

Home ranges of individual *C. amboinensis* were calculated based on COA estimates using 95 and 50% kernel utilisation distributions (95 and 50% KUD) with the adehabitat package in R (Calenge 2006). Home ranges were calculated at weekly and monthly intervals to examine changes in distribution and habitat use over time. Home ranges were plotted in ArcView 3.3 (Esri Products, Redlands, CA, USA) to show spatial and temporal distribution patterns of individual sharks.

To examine the effects of a tropical wet season on the movement of juvenile *C. amboinensis* and to remain consistent between years, data were analysed from December to April for two years (2008–2009 and 2009–2010). Freshwater inflows from creeks into Cleveland Bay are of similar magnitude, and data from Alligator Creek were used as flow data available at this site were continuous. The latitudes of COA locations of juvenile *C. amboinensis* were used to represent the distribution of animals in the bay relative to the mouths of the main sources of freshwater inflow, which were all on the southern boundary of the bay. Mean weekly latitude locations and home-range sizes of *C. amboinensis* were compared and correlated against creek flow.

The normality of the data (both latitude locations and home ranges) was checked by examination of quantile–quantile plots, and in all cases the data satisfied the assumptions for parametric testing. Tests of regression analysis demonstrated that there was no significant difference between fitting linear, polynomial, or segmented models to the data. The strength of each model was the same, and a linear model was used for further statistical testing of the data. Analysis of covariance (ANCOVA) was used to test for differences in latitude location and home-range size of *C. amboinensis* between age cohorts and years. Analysis of

variance (ANOVA) was used to test for significance of creek flow on latitude location and home-range size of *C. amboinensis*. ANOVA was also used to test for differences in latitude location of *C. amboinensis* across dry season weeks. All data analyses were conducted in R (R Development Core Team 2009).

Results

Thirty-two juvenile *C. amboinensis* were released with acoustic transmitters in Cleveland Bay from 2008 to 2010 (Table 1). Young-of-the-year individuals were released in February 2009 ($n = 15$; 5 female, 10 male) and February–March 2010 ($n = 13$; 5 female, 8 male). One-year-old individuals were released in December 2008 ($n = 2$; 2 male) and December 2009 ($n = 2$; 2 male). Two young-of-the-year individuals released in 2009 were present in the bay the following year and were therefore included in the one-year-old cohort for the second year of the study. No effort was made to have an equal ratio of males and females and transmitters were fitted to animals regardless of sex. The size range of young-of-the-year individuals was 63–82 cm stretch total length (STL) and the size range of one-year-old individuals was 92.5–100 cm STL. All *C. amboinensis* individuals were sexually immature, and young-of-the-year individuals were identified by an umbilical scar (either open or closed).

Distribution and freshwater inflow

Distributional shifts of juvenile *C. amboinensis* during wet-season months occurred at times of greatest freshwater inflow from Alligator Creek (Fig. 3). During periods of high freshwater inflow, juvenile *C. amboinensis* responded by moving north away from the creek mouths (Fig. 3). As freshwater inflow decreased following the wet season, juvenile *C. amboinensis* responded by returning to the southern portion of the bay adjacent to the creek mouths (Fig. 3). Regression analysis showed that creek flow strongly influenced latitude location of sharks in the bay ($r^2 = 0.441$, $P < 0.001$) (Fig. 4). Although the residuals appeared non-uniform with regression analysis, the assumption of linearity was met ($F_{3,58} = 14.530$, $P < 0.001$). There was no significant difference in mean weekly latitude location between cohorts in a year (2008–2009: $F_{1,28} = 0.040$, $P = 0.843$; 2009–2010: $F_{1,26} = 0.135$, $P = 0.717$) and freshwater inflow did not affect mean weekly latitude location of cohorts differently (2008–2009: $F_{1,28} = 3.569$, $P = 0.069$; 2009–2010: $F_{1,26} = 0.689$, $P = 0.414$), indicating that freshwater inflow affected young-of-the-year and one-year-old individuals in the same manner. Although the relationship between freshwater inflow and latitude location was stronger in 2008–2009, freshwater inflow was a significant factor influencing the location of juvenile *C. amboinensis* in Cleveland Bay in both years (2008–2009: $F_{1,19} = 26.190$, $P < 0.001$; 2009–2010: $F_{1,18} = 9.194$, $P = 0.007$). There was no significant difference in the effect of freshwater inflow on latitude location of juvenile *C. amboinensis* between years ($F_{1,37} = 1.178$, $P = 0.285$).

Home range

Home ranges of juvenile *C. amboinensis* typically encompassed areas in the southern portion of Cleveland Bay adjacent to the

Table 1.   Tagging data for juvenile *C. amboinensis* passively monitored in Cleveland Bay during two consecutive wet seasons (December 2008–April 2009 and December 2009–April 2010)
juv, juvenile; yoy, young of year. Date last detected is the last detection during period analysed

ID	Date tagged	Days monitored	Date last detected	Age class	Length (mm)	Sex
579	11 Dec 2008	92	25 Apr 2009	Juv	990	M
563	18 Dec 2008	101	30 Apr 2009	Juv	925	M
487	18 Feb 2009	51	28 Apr 2009	Yoy	740	M
490	18 Feb 2009	40	26 Apr 2009	Yoy	790	F
495	18 Feb 2009	7	02 Mar 2009	Yoy	785	M
562	18 Feb 2009	69	30 Apr 2009	Yoy	720	M
573	18 Feb 2009	55	20 Apr 2009	Yoy	770	M
574	18 Feb 2009	22	25 Mar 2009	Yoy	820	M
575	18 Feb 2009	8	26 Feb 2009	Yoy	770	F
577[A]	18 Feb 2009	50, 70	22 Apr 2010	Yoy	770	F
3460[A]	18 Feb 2009	37, 24	25 Mar 2010	Yoy	760	F
3461	19 Feb 2009	4	28 Feb 2009	Yoy	810	M
3462	19 Feb 2009	37	28 Mar 2009	Yoy	780	M
3463	19 Feb 2009	41	22 Apr 2009	Yoy	742	M
3464	19 Feb 2009	4	24 Feb 2009	Yoy	690	F
3466	19 Feb 2009	6	27 Feb 2009	Yoy	800	M
3467	19 Feb 2009	6	25 Feb 2009	Yoy	690	M
63606	03 Dec 2009	55	31 Jan 2010	Juv	1000	M
63607	03 Dec 2009	57	21 Apr 2010	Juv	990	M
63610	16 Feb 2010	53	20 Apr 2010	Yoy	705	M
63612	16 Feb 2010	31	20 Apr 2010	Yoy	775	F
63614	17 Feb 2010	43	22 Apr 2010	Yoy	770	F
63621	17 Feb 2010	12	10 Mar 2010	Yoy	770	M
63622	17 Feb 2010	37	19 Apr 2010	Yoy	735	M
63615	23 Feb 2010	10	08 Mar 2010	Yoy	790	F
63618	23 Feb 2010	39	18 Apr 2010	Yoy	770	M
63619	23 Feb 2010	36	22 Apr 2010	Yoy	760	F
63620	23 Feb 2010	2	24 Feb 2010	Yoy	790	M
63611	03 Mar 2010	46	22 Apr 2010	Yoy	740	M
63613	03 Mar 2010	49	22 Apr 2010	Yoy	775	M
63617	03 Mar 2010	3	09 Mar 2010	Yoy	740	F
63623	03 Mar 2010	30	22 Apr 2010	Yoy	765	M

[A]Individuals monitored in both years.

creek mouths (Fig. 5). During February (the peak of the wet season), however, core home ranges (50% KUDs) shifted away from the creek mouths, and total home ranges (95% KUDs) included more area in the northern portion of the bay (Fig. 5). After the wet season (April), home-range analysis indicated that juvenile *C. amboinensis* remained in the southern portion of the bay (Fig. 5). Small portions of 95% KUDs overlapped with land in some individual cases (Fig. 5), suggesting some slight over-estimations of the amount of space used. Home-range location did not change outside wet-season weeks. Juvenile *C. amboinensis* remained in the southern portion of the bay and there was no significant difference in latitude location between dry season weeks ($F_{9,9} = 1.057$, $P = 0.468$).

Although juvenile *C. amboinensis* shifted location in response to freshwater inflow, total weekly home-range size remained stable (mean: 29.05 km^2). Regression analysis revealed no relationship between mean weekly home-range size and creek flow ($r^2 = 0.009$, $P = 0.249$) (Fig. 6). There was no significant difference in mean weekly home-range size between cohorts in a year (2008–2009: $F_{1,28} = 0.126$, $P = 0.726$; 2009–2010: $F_{1,26} = 1.149$, $P = 0.294$), young-of-the-year and one-year-old individuals used the same amount of space, and freshwater inflow did not affect home-range size of cohorts differently (2008–2009: $F_{1,28} = 2.108$, $P = 0.158$; 2009–2010: $F_{1,26} = 1.383$, $P = 0.250$). Freshwater inflow did not significantly influence home-range size of juvenile *C. amboinensis* in Cleveland Bay, with mean total weekly home-range size in the wet season (31.56 km^2) similar to that in the dry season (26.15 km^2) (2008–2009: $F_{1,19} = 0.391$, $P = 0.539$; 2009–2010: $F_{1,18} = 3.434$, $P = 0.080$), thus indicating that these animals used the same amount of space regardless of freshwater inflow.

Discussion

Effects of freshwater inflow

The results of this study demonstrate that juvenile *C. amboinensis* responded to wet-season freshwater flows by changing the way they used Cleveland Bay. Although the same amount of space was used, their location within this nearshore habitat showed a distinct seasonal change. This response to freshwater inflow is similar to that reported for other shark species, such as *S. tiburo* in central Florida (Ubeda *et al*. 2009). The response of
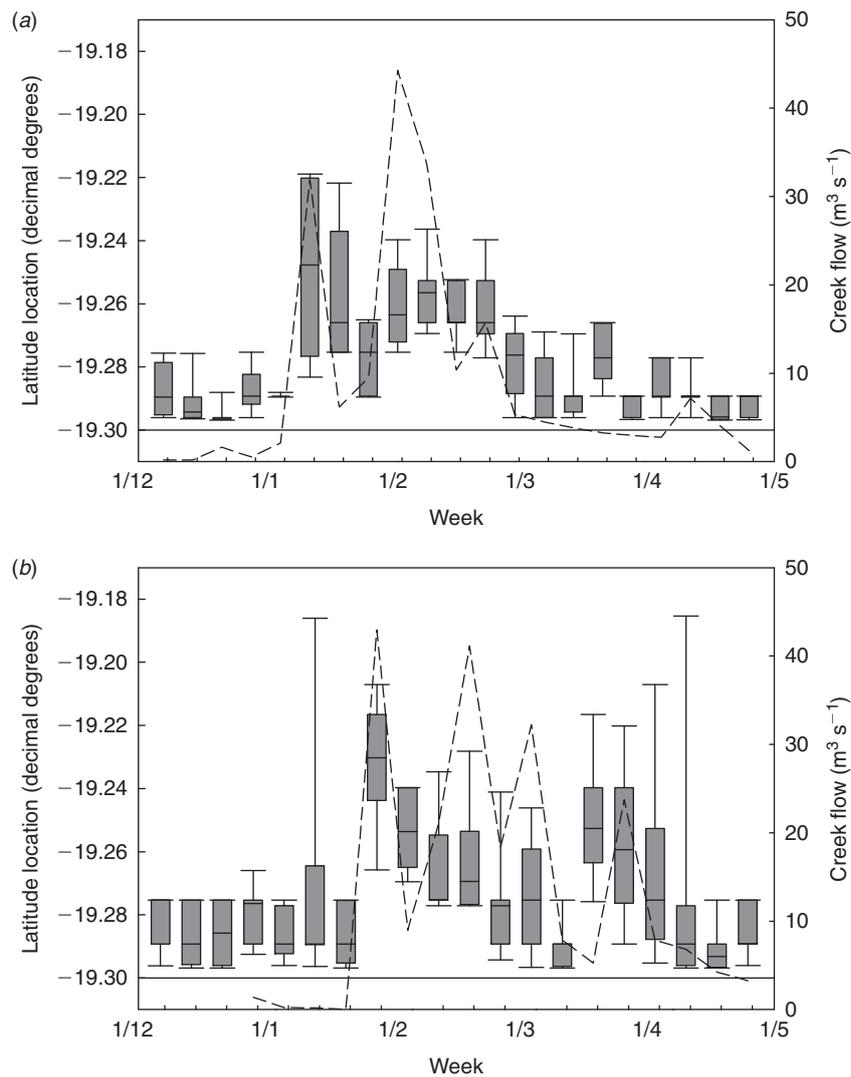
Fig. 3. Boxplot of latitude locations of juvenile *C. amboinensis* by week for (*a*) 2008–2009 and (*b*) 2009–2010. Solid line is latitude location of the mouth of Alligator Creek. Dashed line is mean weekly flow of Alligator Creek.

sharks to these changing conditions suggests a lack of tolerance for lower salinity levels, a preference for alternative conditions, or some other ecological factor.

Increased freshwater inflow may cause decreased salinity levels in nearshore environments and in Cleveland Bay a strong inverse relationship has been reported between freshwater inflow and salinity (Walker 1981). During this study, salinity levels in Cleveland Bay generally remained between 30 and 35, but in the wet season salinity dropped as low as 8 (surface) and 15.5 (bottom) near the creek mouths (D. Knip, unpubl. data). Thus, it is possible that the distribution of juvenile *C. amboinensis* was in part influenced by the low salinity levels that occurred during wet-season months. However, the closely related *C. leucas* is a euryhaline species, with juveniles showing an affinity for low salinities ranging from 7 to 17 within estuarine environments (Simpfendorfer *et al*. 2005; Heupel and Simpfendorfer 2008). Being close relatives, it could be presumed that *C. amboinensis*

has similar physiological capabilities and behavioural characteristics to *C. leucas*. Although previous studies have reported *C. amboinensis* using brackish water and turbid areas adjacent to creek and river mouths (Cliff and Dudley 1991), this species has not been found to penetrate freshwater. Also unlike *C. leucas*, juvenile *C. amboinensis* appeared to avoid creeks and rivers during times of high freshwater inflow. For example, juvenile *C. leucas* moved down river in a Florida estuary with increasing freshwater flow, but individuals continued using estuarine habitat even at times of high flow ($>113 \, \mathrm{m^3 \, s^{-1}}$) (Heupel and Simpfendorfer 2008). At similar flow rates, juvenile *C. amboinensis* moved away from creek mouths and used deeper marine areas. Further, in February 2009 when juvenile *C. amboinensis* were spatially displaced within Cleveland Bay, young-of-the-year *C. leucas* were captured in fishing nets in both Alligator and Crocodile Creeks (A. Tobin, unpubl. data). Therefore, the results of this study suggest that *C. amboinensis* is less tolerant

of high freshwater inflow than *C. leucas*, and provide evidence that low salinity levels (e.g. 7–17) may be beyond the physiological limits of *C. amboinensis*.

Variation in rainfall during this study resulted in different freshwater inflow patterns between years. The total amount of freshwater inflow was similar in both years, with maximum flow occurring in February, but in 2010, high freshwater inflow continued throughout March. The movement response from juvenile *C. amboinensis* may not only depend on the total amount of freshwater inflow, but the rate of inflow as well. A large volume of freshwater inflow concentrated in a shorter time period (i.e. 2009) resulted in a stronger movement response from juvenile *C. amboinensis*. In 2009, there were only two large peaks of freshwater inflow in a short period of time and the response of juvenile *C. amboinensis* was strong, with individuals moving away from the southern portion of the bay until high freshwater inflow ceased. Because there were, however, multiple peaks of freshwater inflow spread out over a longer
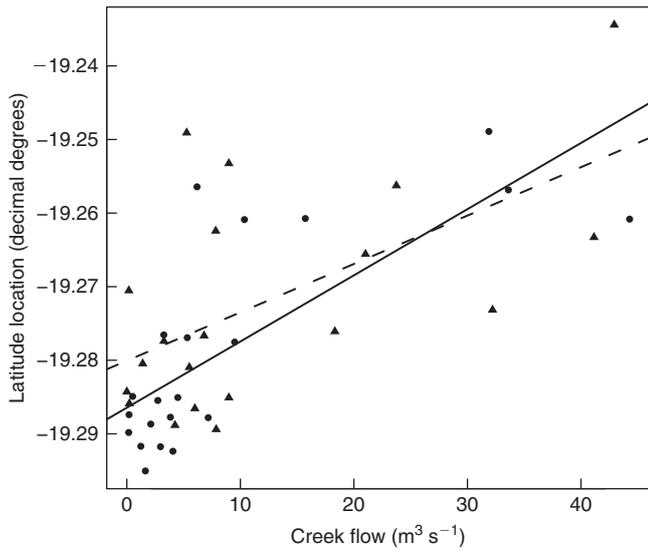
Fig. 4. Regression lines of mean latitude locations of all juvenile *C. amboinensis* pooled by week and mean weekly flow of Alligator Creek for 2008–2009 (● and solid line) and 2009–2010 (▲ and dashed line).
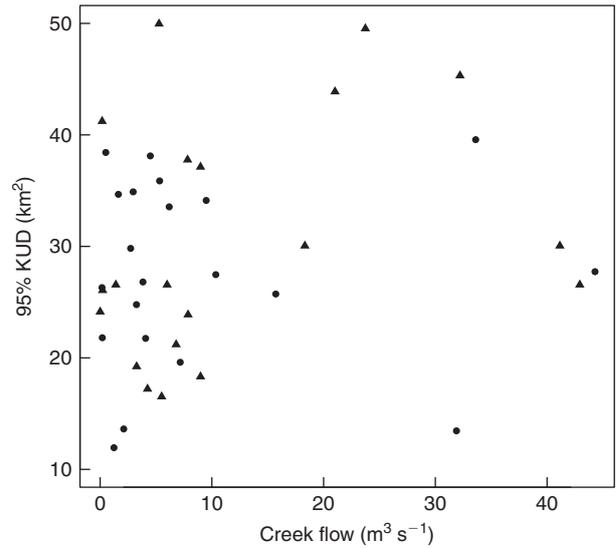
Fig. 6. Regression of mean home ranges (95% kernel utilisation distribution) of all juvenile *C. amboinensis* pooled by week and mean weekly flow of Alligator Creek for 2008–2009 (●) and 2009–2010 (▲).
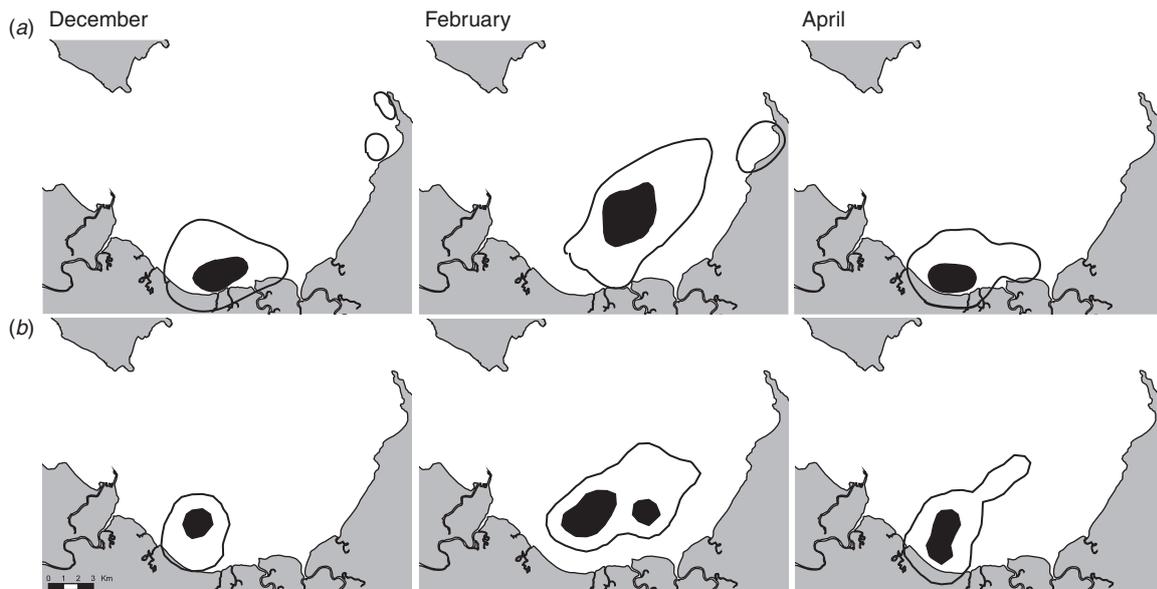
Fig. 5. Monthly home ranges of two juvenile *C. amboinensis* for (*a*) 2008–2009 and (*b*) 2009–2010. Home ranges are shown for the months of December (before wet season), February (during wet season) and April (after wet season). Each panel shows 50% (black fill) and 95% (black line) kernel utilisation distributions.

period of time in 2010, the relationship between flow and distribution of juvenile *C. amboinensis* was weaker. Individuals still moved away from creek mouths during times of highest freshwater inflow, but distribution was more spread out over time and some individuals continued using northern portions of the bay into the month of April. In both years, however, individuals displayed a strong association with creek mouth habitat, consistently returning to and remaining in southern portions of the bay after times of high freshwater inflow.

Moving in response to strong currents and flows has been reported in other shark species. For example, juvenile sandbar sharks (*Carcharhinus plumbeus*) inhabiting estuaries in the north-west Atlantic moved with tidal flow and showed greatest straight-line movement when currents were strongest (Medved and Marshall 1983; Wetherbee and Rechisky 1999). In a south-west Florida estuary, juvenile blacktip sharks (*Carcharhinus limbatus*) also moved with tidal flow (Steiner and Michel 2007), and was considered a possible strategy to minimise energetic costs associated with swimming in strong currents. It is possible that juvenile *C. amboinensis* moved away from creek mouths during times of high freshwater inflow to avoid strong currents and preserve energy. Unlike *C. amboinensis* and these other examples, juvenile *C. leucas* were not found to swim with tidal flow and movements of young individuals were random and not influenced by strong currents (Steiner and Michel 2007). These examples suggest that the behaviour of juvenile *C. amboinensis* is more similar to other young carcharhinid sharks than to the closely related *C. leucas*.

The greatest northward movement of juvenile *C. amboinensis* away from creek mouth habitat in both years occurred during the first peak of freshwater inflow. In tropical environments, the wet season occurs during summer, which is when water temperature is highest. Increased water temperature results in increased biological productivity (i.e. algal blooms), which in turn decreases dissolved oxygen concentrations and may even cause anoxic conditions in creeks, rivers and estuaries (NOAA 1998; Perna and Burrows 2005). It is likely that the first flooding event of a wet season pushes low quality water with low dissolved oxygen concentrations into nearshore regions. Thus, the first freshwater flow probably had the largest impact on the physical environment of Cleveland Bay, explaining why juvenile *C. amboinensis* had the greatest movement response with the first peak of freshwater inflow. Dissolved oxygen has been found to influence the movement and distribution of other shark species. For example, juvenile *C. leucas* using an estuarine habitat were caught in higher abundances in areas of high dissolved oxygen (Heithaus *et al*. 2009) and low dissolved oxygen caused the exodus of *T. semifasciata* from shallow nearshore environments (Carlisle and Starr 2009). It is possible that lower dissolved oxygen concentrations during times of increased freshwater inflow may in part influence the movement of juvenile *C. amboinensis* away from shallow nearshore waters adjacent to creek habitats.

Displacement and space use

High freshwater flow rates can be a disturbance for some inhabitants of rivers, creeks and estuaries. Mobile fish species may respond by leaving areas at times of high flow, and it is common for the community structure of these nearshore environments to vary seasonally (Rayner *et al*. 2008). Fish generally leave an area of high flow to seek refuge from high flow rates or to target prey items that have also left the high flow environment (Winemiller and Jepsen 1998). Thus, it is possible that the increased freshwater inflow that occurred during this study moved fish species from adjacent creeks into Cleveland Bay. Juvenile *C. amboinensis* may have moved away from the creeks at times of high freshwater inflow to follow target prey species that also left the creek habitat at that time. Changes in the movement of predators in relation to prey distribution as a result of wet-season events have been documented with other tropical species, such as the water python (*Liasus fuscus*) (Madsen and Shine 1996). Thus, predator species may change their behaviour in relation to prey distribution, and sharks have been reported to show an association with habitats where prey is most abundant (Heithaus *et al*. 2002).

Although juvenile *C. amboinensis* moved in response to increased freshwater inflow and used areas outside of creek mouth habitat during the wet season, the amount of space individuals used remained consistent. Some predatory fish species have been documented to move greater distances and use more space at times of high freshwater flow (de Morais and Raffray 1999; Scruton *et al*. 2005). Increased movement and home-range expansion during the wet season was attributed to greater amounts of water available, and to individuals needing to move greater distances to locate adequate prey. The fact that habitat is similar throughout the eastern side of Cleveland Bay, and space use of juvenile *C. amboinensis* did not differ between wet and dry seasons, suggests that this region provides adequate food resources for this species in both seasons, even when individuals are using areas outside of creek mouth habitat.

Conclusions

This study is the first to document fine-scale movements of *C. amboinensis* and determine environmental variables that influence its distribution. It appears that juvenile *C. amboinensis* individuals associate with shallow creek mouth habitats in tropical nearshore regions, but are highly influenced by freshwater inflow and move away from creeks in response to increased flow rates during the wet season. Whether the main driver of this movement response is freshwater inflow itself or a result of freshwater inflow (e.g. changes in salinity, dissolved oxygen or prey distribution) is yet to be determined. Unexpectedly, the behaviour of *C. amboinensis* was unlike that of its close relative *C. leucas*, with juvenile *C. amboinensis* appearing to display a low tolerance for high-flow and low-salinity environments. This suggests that the physiological capabilities of *C. amboinensis* are different to that of *C. leucas*. Further studies analysing movement and habitat use of *C. amboinensis* in relation to different environmental factors (e.g. salinity and dissolved oxygen) are needed to determine the specific requirements and physiological limitations of this species. Additional future work should also include biological studies, such as defining how foraging behaviour or diet may shift with seasonal changes.

Tropical nearshore regions are highly dynamic environments with fluctuating conditions, and are predicted to experience

further changes and become more variable owing to factors associated with climate change. In northern Australia, nearshore regions are most vulnerable to changes in rainfall patterns and freshwater inflow, which will alter the habitats, productivity and physical characteristics of these environments (Chin *et al.* 2010). The results of this study indicate that *C. amboinensis* responds strongly to changes in freshwater inflow, so is likely to be highly exposed to the effects of altered rainfall and changing salinity levels. Specifically, intensified rainfall and periods of flooding in tropical nearshore regions may result in this species having more sporadic and extreme movements (Chin *et al.* 2010). Uncertainty in future projections of rainfall in tropical nearshore regions presents a concern for species vulnerable to the effects of a changing climate. However, by defining the response of juvenile *C. amboinensis* to highly variable freshwater flow events, this research provides a better understanding of species behaviour and responses within a dynamic and changing environment. With an increased risk of changing conditions in nearshore regions, knowledge of species behaviours and capabilities is needed to implement effective management initiatives. Thus, the results of this study provide information that will be useful for both river regulation and control in tropical regions and predicting responses in species behaviour as a result of changing climate scenarios.

Acknowledgements

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