Habitat and space use of an abundant nearshore shark, *Rhizoprionodon taylori*

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Abstract. Shark resource-use strategies affect how they will respond to changes within their environment and, as such, may be important to consider in conservation and management. Movement data on sharks that use nearshore areas is particularly valuable because these habitats are highly dynamic. The present study used passive acoustic telemetry to examine the space-use, habitat-selection and habitat-specialisation patterns of the Australian sharpnose shark, *Rhizoprionodon taylori*, in a nearshore area. Habitat selectivity and specialisation were assessed across five benthic habitat types, including outer bay, seagrass, reef, sandy inshore and intertidal mudflats. The majority of *R. taylori* sharks were present for short periods of time, ranging from 1 to 112 days (mean ± s.e. = 16.9 ± 4.9). Activity-space analysis indicated that *R. taylori* roamed widely, but monthly activity-space size was consistent among individuals and through time. Both the population and individuals displayed wide habitat niches, indicating that the species may be resilient to environmental change. However, *R. taylori* consistently selected for seagrass over other habitats, potentially for feeding. Therefore, declines in seagrass availability may reduce *R. taylori* presence in nearshore areas and may be relevant to spatial management of this species.

Additional keywords: kernel-utilisation distributions, residency, small-bodied sharks.

Introduction

Quantifying shark habitat and space use is essential to understanding relationships of a species with the environment and other species (Heupel and Simpfendorfer 2008; Clarke *et al.* 2011; Knip *et al.* 2011*a*). Knowledge of habitat and space use can also reveal a great deal about shark ecology and life history. For example, shark activity-space size and location have been shown to vary between sexes (Sims *et al.* 2001) and sizes (Goldman and Anderson 1999; Knip *et al.* 2011*a*). Movement data can also indicate how sharks respond to environmental fluctuations. Previous work has demonstrated that factors such as salinity (Ubeda *et al.* 2009), temperature (DiGirolamo *et al.* 2012), bottom type (Morrissey and Gruber 1993*a*) and prey availability (Sims *et al.* 2006) can influence shark presence, space use and habitat selection. Movement data have also been used to assess the efficiency of marine protected areas to manage and conserve shark populations (Garla *et al.* 2006; Knip *et al.* 2012*a*).

Information on habitat and space use can also be used to determine vulnerability to environmental change and degradation. Species that use a limited array of habitat types may be more vulnerable to environmental change than species that have wider habitat niches (Futuyma and Moreno 1988; Carlton *et al.* 1991; Wilson and Yoshimura 1994). Selective or highly specialised species may not be able to use different habitats if their preferred habitat declines in health or abundance (Colles *et al.* 2009; Clavel *et al.* 2011; Curtis *et al.* 2013), whereas species with broader habitat niches can more easily use different habitats or locations (Marvier *et al.* 2004). Therefore, species that can use diverse habitats are more likely to maintain high levels of fitness in the face of environmental change (Marvier *et al.* 2004; Richmond *et al.* 2005).

Because of their high productivity, nearshore areas contain key habitats for many sharks and often function as important foraging and nursery grounds (Beck *et al.* 2001; Heupel *et al.* 2007; Knip *et al.* 2010; Gutteridge *et al.* 2011). Unfortunately, nearshore habitats also have some of the highest levels of exposure to sources of anthropogenic influence (Harley *et al.* 2006; Halpern *et al.* 2008; Bulleri and Chapman 2010; Chin *et al.* 2010). As a result, sharks that use nearshore areas may be susceptible to population decline (Chin *et al.* 2010). Vulnerability to decline or localised depletion may increase if the population demonstrates strong site attachment to specific locations or habitats within nearshore areas. Therefore, data on the habitat

and space use of nearshore sharks are critical to species conservation and management.

The Australian sharpnose shark, *Rhizoprionodon taylori*, is an abundant coastal shark endemic to northern Australia and the southern coast of Papua New Guinea (Last and Stevens 2009). This species is commonly found in nearshore waters and is a small-bodied, fast-growing, highly productive species (Stevens and McLoughlin 1991; Simpfendorfer 1992, 1993; Simpfendorfer and Milward 1993). Although *R. taylori* has been the focus of several life-history and reproductive studies, there are no published data on *R. taylori* habitat use or movement. However, because *R. taylori* is highly abundant and closely associated with nearshore areas, this species may influence nearshore ecosystem dynamics and may be affected by changes within nearshore areas.

The purpose of the present study was to define the movement patterns of *R. taylori* in a nearshore environment and examine the species vulnerability to change. Passive acoustic monitoring was used to quantify *R. taylori* residency, space use, habitat use, and define whether increased wet-season river discharge affects movement. Results from the study will increase our understanding of how small-bodied sharks use nearshore areas and how *R. taylori* responds to its environment.

Materials and methods

Study site

The study was conducted in Cleveland Bay, Queensland, a shallow embayment on the north-eastern coast of Australia (Fig. 1). Cleveland Bay covers an area of ~225 km², is 27 km wide, and the majority of the bay has a depth of less than 10 m and a maximum tidal range of 4.2 m. The dominant habitat is soft mud substrate and to a lesser extent sandy substrate. The bay also contains patches of seagrasses (*Cymodocea serrulata*, *Halophila* spp., *Halodule uninervis*) and coastal reefs. The southern shore of the bay is lined with mangroves. The main river outlets are on the south-eastern side of the bay and are adjacent to intertidal mudflats and seagrass habitat. Sixty-three VR2W acoustic receivers (Vemco, Halifax, Canada) were deployed inside Cleveland Bay to monitor shark movements. Receivers were deployed in primary habitat types within the bay, specifically intertidal mudflats, outer-bay mud substrate (>5-m depth), sandy inshore substrate, reefs, and seagrass. Data were downloaded from receivers every 3 months. An additional nine receivers were deployed by the Australian Institute of Marine Science (AIMS) in Bowling Green Bay adjacent to the south-east of Cleveland Bay. The majority of these receivers were deployed between depths of 9.2 and 11.0 m with mud substrate. Therefore, they were classified as outer-bay mud substrate receivers. Data from these receivers were not included in habitat, space use or residency analysis.

Field methods

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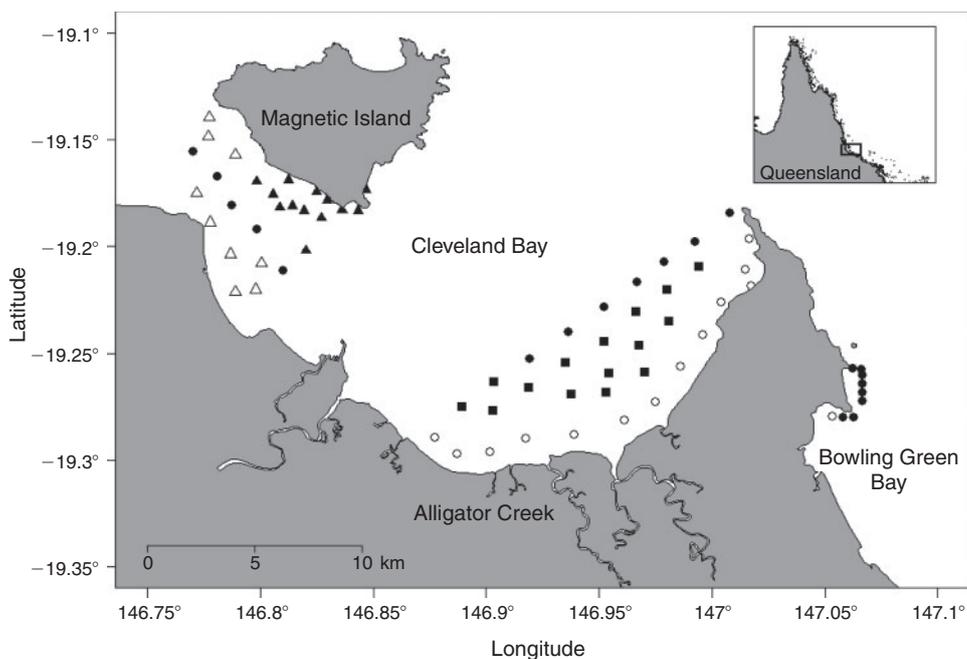

Fig. 1.   Cleveland Bay, Queensland, locations of receivers in intertidal mudflat (○), seagrass (■), outer-bay mud substrate (●), inshore sand (△) and reef habitat (▲).

Rhizoprionodon taylori individuals were fitted with V13 acoustic transmitters (Vemco). Transmitters were implanted into the body cavity to ensure long-term retention. An incision was made and the transmitter inserted into the body cavity. The incision was closed with absorbable sutures. Individuals were measured to the nearest millimetre stretch total length (STL), sexed, tagged with an individually numbered rototag in the first dorsal fin, and released. Range-testing analysis found that transmitters had a maximum detection range of 525 m on the basis of 0.05 probability of detection (Kessel *et al.* 2013) and emitted a unique code as a pulse series at 69 kHz. Unique transmitter codes allowed for the identification of individuals.

Statistical methods

Residency

Presence was assessed each day. Individuals were considered present if it was detected two or more times in the array in a given day. Residency was determined using a residency index that calculated the number of days an individual was present in the array as a proportion of the total days monitored (e.g. Abecasis and Erzini 2008; Werry *et al.* 2014). The index ranged from 1 to 0, indicating high to low residency, respectively. A two-factor ANCOVA was used to test for differences in residency between years and sexes, with STL as a covariate.

Individuals were sorted into two groups on the basis of the number of days they were detected in the array. Individuals that spent more than 2 weeks in the array were considered resident, individuals that spent less than 2 weeks were determined to be transitory. Because of the potential bias of including individuals with low presence, transitory animals were not included in space use analysis and some habitat-use analysis.

Space use

Individual positions were estimated using the mean position algorithm described by Simpfendorfer *et al.* (2002) to determine individual centre-of-activity (COA) locations. The COA produced a weighted mean position for each 30-min interval the animal was detected within the acoustic array. COA locations were used to calculate individual monthly activity space as 50% and 95% kernel-utilisation distributions (KUDs) for resident individuals using the *adehabitatHR* package in R version 3.0 (Calenge 2006). An impassable boundary was added to the KUD calculations to represent the Cleveland Bay coastline and prevent overestimation of KUD size. A smoothing parameter of 0.008 was used in all KUD calculations. A linear mixed-effects model was used to determine whether there were differences in 50% and 95% KUD size between months, with individual as a random factor, using the *nlme* package in R (Pinheiro *et al.* 2013). Linear regression was used to determine whether there was a relationship between 50% and 95% KUD size and animal size (STL). Activity-space overlap between consecutive months was calculated for each *R. taylori* as a percentage, by using the *adehabitatHR* package in R (Calenge 2006).

Habitat selection

Cleveland Bay was divided into regions on the basis of the distribution of five distinct habitat types. Receivers were assigned a habitat type on the basis of their location in the bay. Habitat availability was determined by calculating the proportion of receivers in each habitat. Proportional habitat use by individuals was determined by comparing the amount of time spent in a habitat to the total amount of time spent in the array.

The proportion of time spent in each habitat by individuals was compared with habitat availability by using Strauss's (1979) linear selectivity index (L_i), to determine whether *R. taylori* individuals were selecting for or avoiding habitats, as follows:

$$L_i = r_i - p_i, \tag{1}$$

where r_i is the proportion of Habitat i used and p_i is the proportion of Habitat i available in the study site. $L_i < 0$ indicated negative selection or avoidance. $L_i > 0$ indicated positive selection. $L_i = 0$ indicated the habitat was neither positively nor negatively selected for and was used opportunistically (Strauss 1979). Habitat-selection analysis was performed for both resident and transitory individuals. The mean of resident individual L_i values was calculated for each year and each 2-week time period within each year to assess population habitat selection over time. A chi-squared goodness-of-fit test was used to compare the proportion of time spent in each habitat by the population to habitat availability to determine whether mean annual selection was significant.

Spearman's rank correlation coefficient was used to compare habitat selection values of resident individuals and river discharge rates ($m^3 s^{-1}$). Northern Queensland is subject to high rainfall and river discharge during the Austral summer (November to March). Increased river discharge increases freshwater input into the bay, which decreases salinity in waters adjacent to rivers, especially in the south-eastern portion of Cleveland Bay (Walker 1981). River-discharge rates from Alligator Creek, a large creek that drains into south-eastern Cleveland Bay, were used to evaluate changes in freshwater input to the bay. River-discharge data were provided by the Queensland Government Department of Natural Resources and Mines.

Habitat niche breadth

Niche breadth of resident individuals was measured using Hutchinson's niche definition that included only which habitats a species used and in what proportions (Hutchinson 1957; Devictor *et al.* 2010). On the basis of this definition, a modified Freeman–Tukey statistic was used to calculate population niche breadth (Smith 1982), as follows:

$$FT = \sum_{i=1}^{R} (p_i q_i)^{\frac{1}{2}}, \tag{2}$$

where q_i is the proportion of Habitat i available in the study site, p_i is the proportion of Habitat i used, and R is the total number of habitats available. The output ranged from 1, which indicated a large niche, to 0, which indicated a narrow niche and a highly specialised species.

A variation of Eqn 2 was used to calculate individual niche overlap (Arlettaz 1999), as follows:

$$FT = \sum_{i=1}^{R} (p_{ik} p_{jk})^{\frac{1}{2}}, \tag{3}$$

where p_{ik} and p_{jk} were the proportions of Habitat R used by Individuals i and j, respectively. The output similarly ranged from 1 to 0. A value of 1 indicated a complete overlap in habitat niche breadth between a given pair of individuals and 0 indicated no overlap in habitat niche breadth between a given pair of individuals. Where applicable, all data were checked for normality by using normality and homogeneity of variance diagnostics in R, version 3.0 (R Development Core Team: www.r-project.org) and data were $\log_{10}$ transformed if necessary.

Results

Forty *R. taylori* individuals with acoustic transmitters were released in Cleveland Bay between September 2011 and November 2012. The majority of individuals ($n = 34$) were captured and released on the eastern side of Cleveland Bay. Twenty *R. taylori* individuals (7 male, 13 female) were released in Year 1 of the study (September 2011 to September 2012). Twenty *R. taylori* individuals (7 males, 13 female) were released in Year 2 (September 2012 to April 2013). Four *R. taylori* individuals released in Year 1 and one released in Year 2 died or were not detected following release, and were excluded from analysis. Animal size ranged from 489 to 771 mm in STL (mean $\pm$ s.e. $= 657 \pm 21.0$) in Year 1 and from 485 to 763 mm in STL (mean $\pm$ s.e. $= 659 \pm 15.2$) in Year 2. Size ranges indicated that the majority of *R. taylori* individuals were either mature or nearing sexual maturity (Simpfendorfer 1993). There were no significant differences in sizes between years (ANOVA,

$F_{1,31} = 0.0193$, $P > 0.05$); however, females were significantly larger than males (ANOVA, $F_{1,31} = 27.45$, $P < 0.05$).

Residency

Rhizoprionodon taylori was present in Cleveland Bay for 1–106 days (mean $\pm$ s.e. $= 11.4 \pm 7.4$) in Year 1 and for 1–112 days (mean $\pm$ s.e. $= 20.6 \pm 6.6$) in Year 2. Two *R. taylori* individuals released in Year 1 (2 female) and seven released Year 2 (2 male, 5 female) were present for more than 2 weeks. The remaining 26 individuals spent less than 2 weeks in the array. Residency index was low in both years and ranged from 0.00 to 0.40 (mean $\pm$ s.e. $= 0.053 \pm 0.03$) in Year 1 and from 0.00 to 0.56 (mean $\pm$ s.e. $= 0.11 \pm 0.04$) in Year 2 (Fig. 2). Residency data were not normal and were $\log_{10}$ transformed. Animal size had no effect on *R. taylori* residency (ANCOVA, $F_{1,27} = 0.727$, $P > 0.05$). There was a significant difference in residency between years (ANCOVA, $F_{1,27} = 4.48$, $P < 0.05$), but not between sexes (ANCOVA, $F_{1,27} = 0.284$, $P > 0.05$). There was no seasonal pattern in *R. taylori* movement out of Cleveland Bay. After last detection in Cleveland Bay, seven *R. taylori* individuals (3 male, 4 female) were detected on receivers inside Bowling Green Bay for a maximum of seven consecutive days after (M. R. Heupel, unpubl. data).

Space use

Because of the low number of resident individuals, it was not possible to perform population analysis of the activity-space habitat-use patterns of *R. taylori* in Year 1. Therefore, all
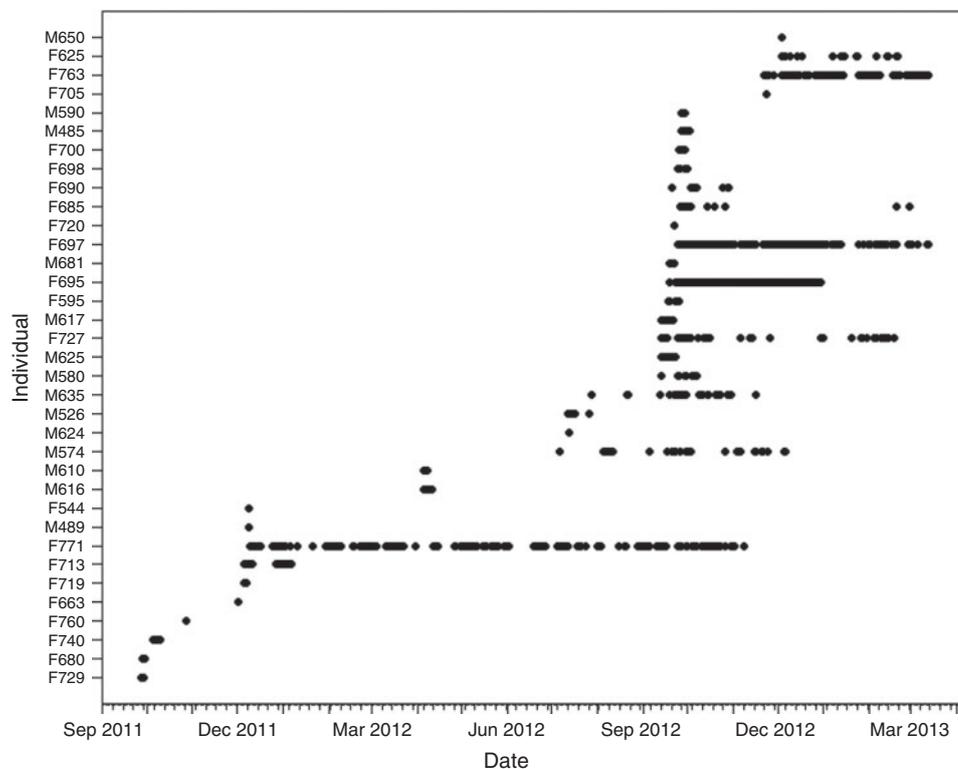

Fig. 2. Daily presence of *Rhizoprionodon taylori* released with acoustic transmitters in Cleveland Bay in 2011–2013. Individuals are identified by sex and stretch total length (mm).

activity-space analysis was based on data from sharks monitored in Year 2. Individual monthly activity space of resident individuals ranged between 4.3 and 21.4 km^2 (mean ± s.e. = 11.3 km^2 ± 0.90) for 50% KUDs and between 21.5 and 80.4 km^2 (mean ± s.e. = 51.0 km^2 ± 3.9) for 95% KUDs. There was no significant difference in KUD size between months for 50% (linear mixed-effects model, $F_{6,18} = 0.883$, $P > 0.05$) or 95% (linear mixed-effects model, $F_{6,18} = 1.043$, $P > 0.05$) KUDs. There was also no relationship between animal size and activity-space size for either 50% (linear regression, $r^2 = 0.006$, $F_{1,23} = 0.136$, $P > 0.05$) or 95% (linear regression, $r^2 = 0.041$, $F_{1,23} = 0.971$, $P > 0.05$) KUDs.

The majority of *R. taylori* movements were on the eastern side of the bay, specifically in seagrass habitat. However, 57% of individuals were detected on both sides of the bay. Individual monthly KUD overlap was highly variable and ranged between 0.0 and 88.6% (mean ± s.e. = 34.1 ± 6.2, $n = 17$) for 50% KUDs and between 34.2% and 92.7% (mean ± s.e. = 61.0 ± 3.8, $n = 17$) for 95% KUDs. The most distinct shift in *R. taylori* KUD location occurred between months of low (December 2012) and high river discharge (January and February 2013). Monthly KUD locations of some individuals (all female) shifted from the south-eastern to the north-western side of Cleveland Bay between December 2012 and February 2013 (Fig. 3a, b), resulting in low space-use overlap for those individuals during that time. However, one individual remained on the eastern side of Cleveland Bay in January and February 2013 (Fig. 3c). Individual monthly KUD overlap was recalculated with months of low and high river discharge excluded to remove their effect on the results. However, secondary results were similar to the original calculations. Individual monthly KUD overlap again ranged between 0.0 and 88.6% (mean ± s.e. = 30.5 ± 6.7, $n = 14$) for 50% KUDs and between 34.2% 92.7% (mean ± s.e. = 60.85 ± 4.5, $n = 14$) for 95% KUDs. There was also no

consistent pattern in the degree of activity-space overlap of each individual. Highly variable KUD overlap values indicated that individual *R. taylori* did not use the same core areas between months, regardless of freshwater input. Most activity-space relocations during periods of low river discharge were on eastern side of the bay. However, one individual made regular trips between the eastern and western side of the bay when river discharge was low.

Habitat selection and niche breadth

The majority of transient *R. taylori* individuals selected for seagrass habitat (Table 1). Of the 26 transient individuals, 11 exclusively selected for seagrass, whereas seven selected for seagrass and at least one other habitat (intertidal mudflat and/or outer-bay mud substrate). Eight transient *R. taylori* individuals avoided seagrass. Reef was avoided by all transient individuals, except for one adult female.

The two resident females monitored in Year 1 had contrasting selection patterns. One female selected for sandy inshore habitat, outer-bay mud substrate and seagrass (Fig. 4a), whereas the other selected only for mudflat habitat (Fig. 4b). Resident individuals in Year 2 were detected in all five primary habitat types at least once during the monitoring period, but on average spent the majority of time in seagrass habitat (Table 2). Mean individual Strauss selection values of resident individuals in Year 2 indicated that, on an annual basis, outer-bay mud substrate was used
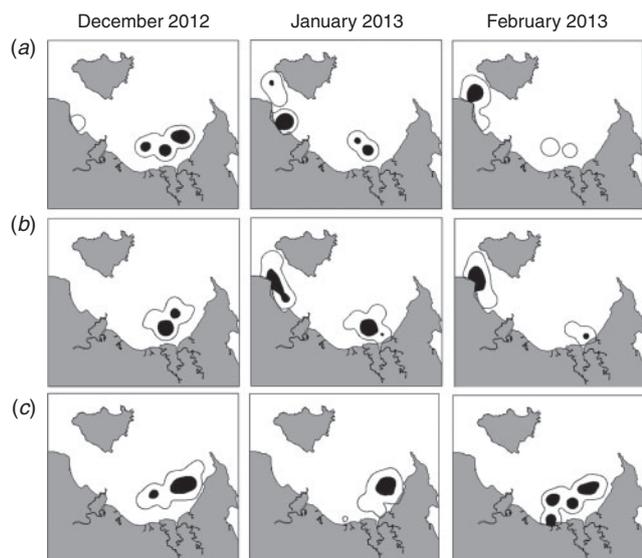
Table 1. Values of Strauss selectivity index of low-residency animals (<2 weeks detected), for each primary habitat in the bay, indicating sex as male (M) or female (F) and size as stretch total length (in mm) for each individual

Sex	Size	Days detected	Seagrass	Outer-bay mud substrate	Reef	Sandy inshore	Intertidal mudflat
M	580	8	0.16	−0.01	−0.14	−0.04	0.03
M	620	10	0.54	−0.21	−0.21	−0.14	0.02
M	617	9	0.67	−0.21	−0.21	−0.14	−0.11
F	595	5	0.64	−0.21	−0.21	−0.14	−0.08
M	681	4	0.75	−0.21	−0.21	−0.14	−0.19
F	700	4	0.40	0.15	−0.21	−0.14	−0.21
M	485	6	0.72	−0.21	−0.21	−0.14	−0.16
F	705	1	0.76	−0.21	−0.21	−0.14	−0.21
M	650	1	0.16	0.39	−0.21	−0.14	−0.21
F	698	5	0.69	−0.13	−0.21	−0.14	−0.21
F	720	1	0.36	−0.21	−0.21	−0.14	0.19
M	590	3	0.76	−0.21	−0.21	−0.14	−0.21
F	685	13	0.62	−0.06	−0.21	−0.14	−0.21
F	690	8	−0.11	0.30	−0.20	0.18	−0.17
F	663	1	0.76	−0.21	−0.21	−0.14	−0.21
F	760	1	−0.24	0.13	−0.21	−0.14	0.46
F	719	2	−0.24	0.79	−0.21	−0.14	−0.21
M	616	7	−0.06	−0.21	−0.21	−0.14	0.61
M	610	4	0.73	−0.21	−0.21	−0.14	−0.17
M	489	1	−0.24	−0.21	−0.21	−0.14	0.79
M	624	1	−0.24	0.79	−0.21	−0.14	−0.21
F	544	1	−0.24	−0.21	−0.21	−0.14	0.79
F	740	6	0.16	0.39	−0.21	−0.14	−0.21
F	680	3	0.35	0.21	−0.21	−0.14	−0.21
F	729	3	−0.24	−0.21	0.45	0.20	−0.21

Fig. 3. *Rhizoprionodon taylori* monthly activity spaces of (a–c) three individuals in December 2012, January 2013 and February 2013. Each panel shows the 95% (black line) and 50% (black fill) kernel utilisation distributions.

(a)

(b)

Legend:
- ■ Outer bay mud subustrate
- ■ Seagrass
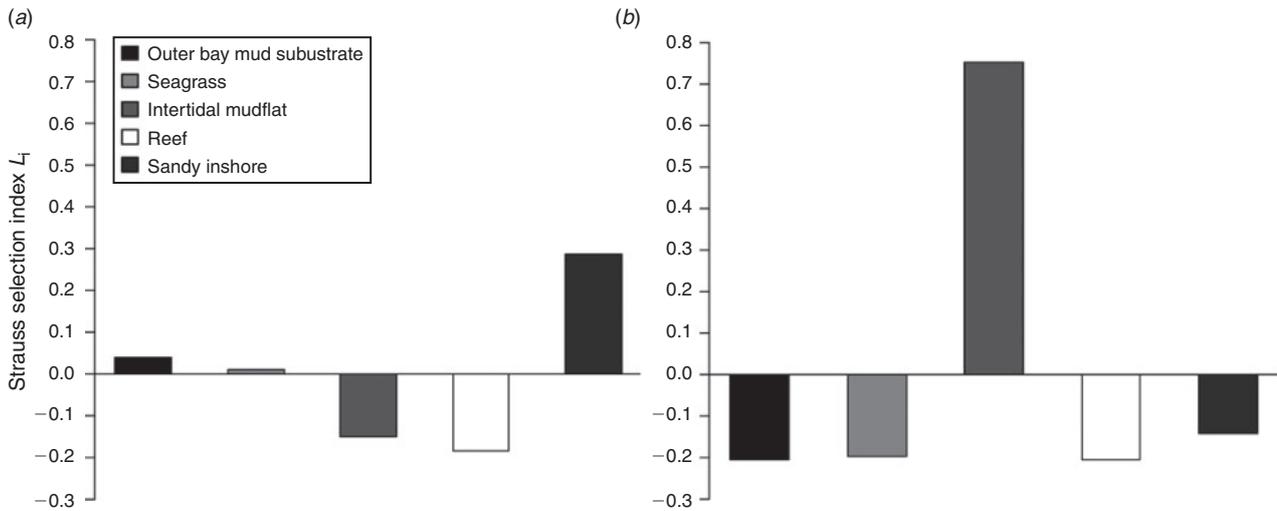- ■ Intertidal mudflat
- □ Reef
- ■ Sandy inshore

Fig. 4. Strauss linear selection-index values of resident (>2 weeks) *Rhizoprionodon taylori* individual released in Cleveland Bay: (a) female 574 mm in stretch total length (STL) and (b) female 713 mm in STL.

Table 2.   Mean time spent in each habitat in Cleveland Bay, measured as a percentage with ± s.e. of high residency (>2 weeks detected) *Rhizoprionodon taylori* (n = 7)

Habitat type	Mean time spent (%)
Seagrass	48.4 ± 9.6
Outer-bay mud substrate	21.2 ± 3.1
Reef	0.1 ± 0.07
Sandy inshore	24.3 ± 8.9
Intertidal mudflat	5.7 ± 2.2

Fig. 5. Values of mean Strauss linear selection index for resident (>2 weeks) *Rhizoprionodon taylori* in Cleveland Bay (n = 7) between September 2012 and April 2013. Vertical bars indicate s.e.

opportunistically, reef and mudflat habitats were avoided, and seagrass and sandy inshore habitats were positively selected (Fig. 5). A chi-square goodness-of-fit test showed that selection was significant ($\chi^2_4 = 63.888$, $P < 0.05$). Mean fortnightly selection values revealed that during Year 2, reefs and intertidal mudflats were consistently avoided, whereas seagrass was consistently favoured, except in January 2013 when river discharge increased. Selection for sandy inshore substrate and outer-bay mud substrate was more variable (Fig. 6).

Selection of outer-bay mud substrate of resident individuals fluctuated between low negative and positive values, with individuals generally spending little time in the area (less than one consecutive day). Selection for sandy inshore habitat was also irregular and varied between negative and positive values over time and among individuals. The majority of resident individuals in Year 2 did not enter sandy inshore habitat before December 2012, except for one female that made regular excursions into sand habitat for variable periods of time (7–14 consecutive days). However, between December and February 2013, the majority of resident individuals abruptly selected sandy inshore habitat while avoiding seagrass and this coincided with increased river discharge. Spearman's rank correlation revealed a strong negative correlation between sandy inshore and seagrass selection of resident individuals ($r_s = -0.694$, $N = 14$, $P < 0.05$). Spearman's rank correlation also revealed
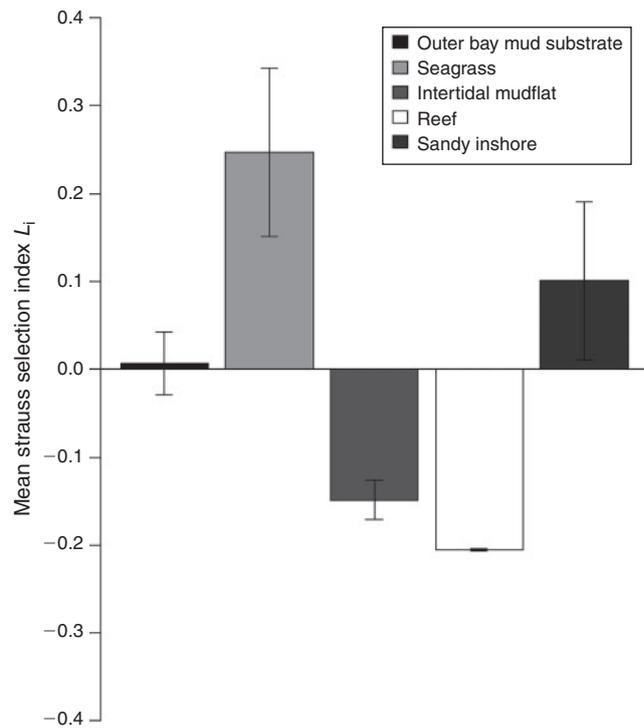
a positive relationship between increased river discharge and selection for sandy inshore habitat ($r_s = 0.305$, $N = 14$, $P < 0.05$). There was a negative relationship between selection for seagrass and increased river discharge (Spearman's rank correlation, $r_s = -0.308$, $N = 14$, $P < 0.05$).

Annual mean individual niche breadth for resident *R. taylori* in Year 2 was moderately large and ranged from 0.73 to 0.90 (mean ± s.e. = 0.79 ± 0.02, $n = 7$). These values indicated that
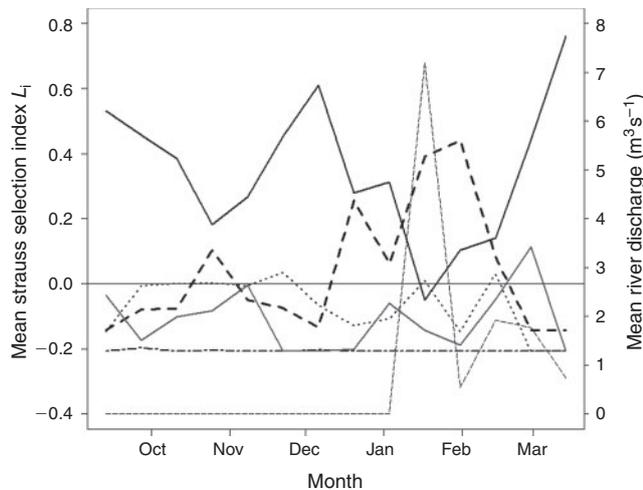
Fig. 6. Values of mean fortnightly individual Strauss linear selection index for resident individuals of *Rhizoprionodon taylori* from Year 2 for seagrass (black solid line), sand (thick black dashed line), outer-bay mud substrate (grey solid line), intertidal mudflat (black dotted line) and reef (black dot-dashed line). Mean fortnightly river discharge was measured in $m^3 s^{-1}$ (thin black dashed line).

individuals had wide habitat niches and, therefore, had low degrees of habitat specialisation. Mean individual overlap was also relatively large and ranged from 0.62 to 0.95 (mean $\pm$ s.e. $= 0.83 \pm 0.03$, $n = 7$).

Discussion

The movement patterns and low degree of habitat specialisation exhibited by *R. taylori* contrasts with those of some other small-bodied sharks that have demonstrated high residency and site fidelity to nearshore areas, including juvenile lemon sharks, *Negaprion brevirostris* (Morrissey and Gruber 1993*b*), juvenile blacktip sharks, *Carcharhinus limbatus* (Heupel *et al.* 2004), adult spottail sharks, *C. sorrah* (Knip *et al.* 2012*b*) and juvenile pigeye sharks, *C. amboinensis* (Knip *et al.* 2011*a*). It has been suggested that small-bodied sharks, in particular juveniles, are highly resident in shallow nearshore habitats to avoid large predators (Heupel *et al.* 2007; Knip *et al.* 2010). However, the residency patterns of *R. taylori* were consistent with those of the closely related Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, which has a life history similar to that of *R. taylori*. Monitored *R. terraenovae* in a north-western Florida bay were present only between 1 and 37 days and were absent for extended periods of time (Carlson *et al.* 2008). Both *R. taylori* and *R. terraenovae* are small-bodied species, but are fast growing and highly productive. Therefore, selection for long-term residency may not provide the same advantages as it does for juveniles of large-bodied, slow-growing species (Carlson *et al.* 2008; Knip *et al.* 2010). Moreover, given that there are large-bodied juvenile sharks within Cleveland Bay, *R. taylori* predation risk may be similarly high inside and outside of nearshore habitats. Therefore, nearshore areas may not provide *R. taylori* with a significantly greater level of protection from predators than do offshore habitats. As a result, there may be limited benefit for *R. taylori* to stay in one bay for long periods.

Low residency values suggest that *R. taylori* moves in and out of nearshore areas and may use several bays. Detections of *R. taylori* in Bowling Green Bay support the conclusion that individuals regularly move between different nearshore areas, potentially along the shoreline. Tag–recapture data in north Queensland also indicate that *R. taylori* moves between neighbouring bays (C. A. Simpfendorfer, unpubl. data). The use of multiple bays may increase an individual's access to prey resources, potentially increasing their foraging success (Knip *et al.* 2010).

The habitat- and space-use patterns of *R. taylori* within Cleveland Bay may have also been adopted to increase foraging success. Activity-space overlap results suggest that most resident *R. taylori* individuals exhibited roaming movement patterns, typically within seagrass habitat. However, a few resident individuals ranged throughout the monitoring area. Similar patterns in space use were observed among bonnethead sharks, *Sphyrna tiburo*, in a Florida estuary (Heupel *et al.* 2006). Like *R. taylori*, individual *S. tiburo* used consistent amounts of space but activity-space locations were highly variable. Heupel *et al.* (2006) suggested that the roaming movement patterns exhibited by *S. tiburo* may have been a prey-search strategy. By moving to new areas within the bay, *R. taylori* may increase its prey-encounter rates, particularly if resources have been depleted in a previously occupied area. Seagrass habitat is productive and usually abundant in small fish and demersal prey (Connolly 1994; Jackson *et al.* 2001). Previous research has shown *R. taylori* primarily feeds on small teleosts as well as crustaceans and squid (Simpfendorfer 1998). Therefore, the large abundance of preferred prey in seagrass habitat may explain why both resident and transient individuals primarily used this habitat. Other shark species have also selected for seagrass habitat because it functioned as a productive foraging ground (Heithaus *et al.* 2002, 2006; Heupel *et al.* 2006). Overall, the use of multiple bays in combination with roaming movements and the use of seagrass habitat may combine to provide a more effective foraging strategy than does long-term residency in a single site.

Although seagrass habitat was consistently positively selected by both resident and transitory individuals, the overall low presence and degree of habitat specialisation of the population, as well as the expansive roaming movement patterns of individuals, suggest *R. taylori* are probably not dependant on a single habitat. The *R. taylori* population also exhibited low levels of individual specialisation, indicating that, overall, individuals used similar proportions of the same habitats. Large individual niches and low levels of individual specialisation imply that the *R. taylori* population in Cleveland Bay is composed of individual habitat generalists. However, as previously indicated, *R. taylori* did not use all habitats opportunistically. Avoidance of reef and mudflat by the majority of resident and transitory individuals suggests that these habitats did not fulfil biological requirements or are suboptimal in some way, such as having insufficient prey abundance. Individuals may have also avoided mudflat habitat because larger sharks (e.g. *C. amboinensis*) that may prey on *R. taylori* utilise this habitat (Knip *et al.* 2011*a*). Thus, avoidance of these regions may reduce predation risk or competition with other species using this habitat. Low sample size and residency made it difficult to determine why *R. taylori* used outer-bay mud substrate. Opportunistic use of outer bay

mud substrate by highly resident individuals may be the result of short-term foraging excursions or a response to short-term environmental fluctuations. Detections in outer-bay mud substrate may have also resulted from *R. taylori* passing through while moving between sides of the bay and because some outer-bay receivers fringe seagrass habitats. Selectivity indices cannot measure the importance of a habitat, only its relative use; therefore, outer-bay mud substrate may serve an important but undefined short-lived purpose.

As discussed earlier, seagrass may provide beneficial foraging habitat, which could explain the consistent positive selection of this habitat. There is also some evidence to suggest that changes in seagrass availability and abundance may affect the habitat use and presence of *R. taylori*. Significantly lower residency in Year 1 occurred at the same time as a substantial decline in seagrass within Cleveland Bay, beginning in 2010. Heavy rainfall in 2010–2011, in combination with Category 5 Cyclone Yasi, destroyed much of the seagrass in Cleveland Bay (Marshall *et al.* 2011; Devlin *et al.* 2012; Mckenzie *et al.* 2012; Seagrass Watch 2013). Low seagrass abundance may have precipitated a decline in *R. taylori* prey and thus shark presence. In 2012–2013, seagrass cover increased to levels similar to those before the 2010–2011 wet season (Seagrass Watch 2013). Greater seagrass cover, and potentially higher prey-resource levels, may explain the increased presence of *R. taylori* in Year 2 of the study. Low seagrass availability during Year 1 may also explain the contrasting selection patterns of resident *R. taylori* in Year 1 and Year 2. The two resident females monitored in Year 1 may not have selected for seagrass because the habitat was either in poor condition or had decreased prey abundance.

Selection for sandy inshore habitat by resident *R. taylori* in Year 2 may have been influenced by freshwater input. Some *R. taylori* transitioned from seagrass to sandy inshore habitat during a large increase in river discharge into Cleveland Bay. Individuals may have moved to the western side of the bay and used sandy inshore habitats as a secondary foraging ground in an effort to avoid increased freshwater input into eastern seagrass habitat. Movement in response to changes in freshwater has been observed in other shark species, including *C. amboinensis* (Knip *et al.* 2011b), bull sharks, *Carcharhinus leucas* (Heupel and Simpfendorfer 2008), and *S. tiburo* (Ubeda *et al.* 2009). However, not all *R. taylori* individuals moved to the western side of the bay when freshwater input increased. For that reason, low tolerance to reduced salinity may not fully explain this movement. It is also possible that increased freshwater discharge altered the distribution of prey species and some *R. taylori* individuals may have followed, whereas others remained to feed on less mobile or euryhaline prey. It is also possible that selection for sandy inshore habitat was related to reproduction. Female *R. taylori* gives birth between December and January each year (Simpfendorfer 1992), but it is not known where parturition occurs. It may be that some *R. taylori* individuals moved into sandy inshore areas to give birth before leaving the bay or returning to seagrass habitat. Few transitory individuals selected for sandy inshore habitat, supporting the suggestion that the use of sandy inshore habitat may be less common or irregular among the *R. taylori* population. Although several possible explanations exist, more data are needed to

better understand movements such as the spatial shift from the eastern to western part of the bay.

The results of the present study indicated that *R. taylori* is a species that has a low degree of habitat specialisation and large activity spaces that are likely to span multiple bays. As a result, *R. taylori* is probably resilient to localised environmental change and can avoid potentially detrimental environmental changes by moving to different areas or habitats. However, the presence and accessibility of seagrass may affect residency and habitat-use patterns. Increased coastal development and the effects of climate change have been highlighted as major ongoing and future contributors to seagrass decline (Duarte 2002). Severe regional declines in seagrass abundance as a result of large storms, sea-level rise, urban runoff and development may decrease presence and fitness of local *R. taylori* (Orth *et al.* 2006; Hughes *et al.* 2009; Waycott *et al.* 2009). Decreased seagrass availability is a potential concern for this species, but further study of the habitat use by *R. taylori* in other nearshore areas is needed to assess this possibility. Understanding the dynamics of how small-bodied sharks use nearshore areas and how environmental change may affect their movement and habitat use will help define the resilience of coastal shark communities.

Acknowledgements

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