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Regional movement patterns of a small-bodied shark revealed by stable-isotope analysis

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This study used stable-isotope analysis to define the nearshore regional residency and movements of the small-bodied Australian sharpnose shark *Rhizoprionodon taylori*. Plasma and muscle δ^{13}C and δ^{15}N of *R. taylori* were collected from across five embayments and compared with values of seagrass and plankton from each bay. Linear distances between adjacent bays ranged from 30 to 150 km. There was a positive geographic correlation between *R. taylori* tissue and environmental δ^{13}C values. Populations with the highest tissue δ^{15}N were collected from bays that had the highest environmental δ^{15}N values. These results suggest that *R. taylori* did not forage more than 100 km away from their capture location within 6 months to 1 year. The successful application of isotope analysis to define *R. taylori* movement demonstrates that this technique may be used in addition to traditional methods to study the movement of sharks, even within similar habitats across regionally small spatial scales (<100 km).

Key words: habitat connectivity; migration; residency; *Rhizoprionodon taylori*; seagrass.

INTRODUCTION

Mobile sharks link distant environments by moving between them and using local resources (Weng *et al.*, 2007, 2008; Chin *et al.*, 2013). As a result, some species connect otherwise separated food webs and ecosystem processes (Lundberg & Moberg, 2003; McCauley *et al.*, 2012). Fast-growing, small-bodied sharks may be a particularly vital ecological and energetic link between food webs because they are both predators and prey items. Therefore, data on the movements of small-bodied sharks can increase understanding of marine ecosystem function and connectivity. Understanding shark movement patterns may also help predict how species respond to environmental changes. For example, species that can use multiple, distinct and potentially distant habitats will probably be less vulnerable to environmental change than species that

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are highly specialized and exhibit high site fidelity (Thomas *et al.*, 2004; Araújo *et al.*, 2006; Williams *et al.*, 2008; Curtis *et al.*, 2013).

The regional movement patterns (<500 km) of most small-bodied sharks are poorly understood. The current lack of information is due, in part, to the limitations inherent in methods previously used to study movement. For example, mark–recapture studies have been used to investigate the large-scale movements of several small-bodied sharks, such as the spottail shark *Carcharhinus sorrah* (Müller &Henle 1839), the Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson 1836) and the milk shark *Rhizoprionodon acutus* (Rüppell 1837), but failed to supply large movement data sets due to low numbers of tag returns (Kohler *et al.*, 1998; Stevens *et al.*, 2000). To have a better understanding of the regional movements of small-bodied sharks, methods that can evaluate large-scale movements and provide larger continuous data sets over shorter timeframes need to be utilized.

Stable-isotope analysis (SIA) is a commonly employed technique in ecology that can be used to define the regional movements of animals (Hobson, 2008). This approach is based on the fact that an animal's diet is reflected in the chemical composition of its tissues and the composition of δ^{13}C and δ^{15}N in an ecosystem varies beginning at the base of the food web. This variation is the result of different local biogeochemical processes (Boutton, 1991). In animal tissue, δ^{13}C values increase in small amounts from prey to predator and are thus conserved up the food chain (Post, 2002). In contrast, δ^{15}N tissue values increase from prey to predator at a significantly greater rate than δ^{13}C (Deniro & Epstein, 1981; Peterson & Fry, 1987). Therefore, consumers assimilate the δ^{13}C and δ^{15}N value of their prey with minimal and predictable rates of change (Graham *et al.*, 2010). As a result, the isotopic values of resident populations should be similar to or a reflection of the isotopic value of local prey and primary producers (Graham *et al.*, 2010). Resident populations from isotopically distinct habitats or regions should have similarly distinct δ^{13}C and δ^{15}N values. The δ^{13}C and δ^{15}N values of migratory populations should be similar between locations that have been linked *via* foraging (Hobson, 2008). Therefore, δ^{13}C and δ^{15}N values provide a type of intrinsic geographic tag (Rubenstein & Hobson, 2004). Metabolically active tissues, such as liver or plasma, respond to changes in diet more quickly than tissues with a lower metabolic rate, such as muscle (Hobson & Clark, 1992; Buchheister & Latour, 2010). As a result, δ^{13}C and δ^{15}N from different tissues can reveal if an animal's feeding location has changed over time (Newsome *et al.*, 2009).

There are notable benefits from using isotope analysis to assess the long-range movements of animals. Isotope samples can be processed relatively quickly and each animal sampled will return data, as opposed to tagged and released animals that have to be recaptured or detected. Isotope analysis can also provide comparatively long and short-term assessments of animal movement (Dalerum & Angerbjörn, 2005), depending on the tissue sampled. Therefore, in the appropriate situation, SIA may be an effective technique to study the regional movements of small-bodied sharks. Despite these benefits, however, isotope-based shark movement studies are limited and have primarily examined coarse-scale movements between offshore and nearshore areas (Kerr *et al.*, 2006; Abrantes & Barnett, 2011; Carlisle *et al.*, 2012).

The Australian sharpnose shark *Rhizoprionodon taylori* (Ogilby 1915) is a small-bodied, fast-growing, highly productive species found off the coast of northern Australia and the southern coast of Papua New Guinea (Last & Stevens, 2009). Size at birth is *c.* 220–260 mm total length (L_T), males and females mature at *c.* 550 mm L_T

and males grow to 690 mm L_T and females 810 mm L_T (Simpfendorfer, 1992, 1993). Although occasionally captured on the outer continental shelf, *R. taylori* is most commonly found in turbid nearshore waters (Stevens & McLoughlin, 1991; Simpfendorfer & Milward, 1993). Acoustic tracking of *R. taylori* in a shallow nearshore embayment (27 km wide) in north Queensland found that individuals were mostly transient. The annual presence of *R. taylori* ranged from 1 to 112 days (mean ± S.E. = 16·9 ± 4·9) with most individuals spending <7 days in the area. Several *R. taylori* were detected moving into an adjacent bay *c.* 30 km south of the primary study site (Munroe *et al.*, 2014*a*). Based on these findings, it was proposed that the home range of individual *R. taylori* encompassed multiple bays. Due to the constraints of the acoustic array, however, it was not possible to determine how far *R. taylori* moved from the original study site following release.

The aim of this study was to evaluate the nearshore regional residency patterns of *R. taylori* using SIA. To determine the physical and temporal extent of *R. taylori* residency, plasma and muscle $\delta^{13}C$ and $\delta^{15}N$ of captured *R. taylori* were compared with $\delta^{13}C$ and $\delta^{15}N$ baselines (established using seagrass, macroalgae and plankton) from a series of embayments. The results of this study will improve understanding of regional residency and movement of small-bodied sharks.

MATERIALS AND METHODS

FIELD METHODS

Rhizoprionodon taylori tissue samples were collected from five bays on the north-east coast of Queensland, Australia, between July 2012 and April 2013. The five bays (from south to north) were Repulse Bay (RE), Upstart Bay (UP), Bowling Green Bay (BG), Cleveland Bay (CB) and Rockingham Bay (RO) (Fig. 1). Linear distances between adjacent bays ranged from 30 to 150 km. Each bay was sampled twice, once in the austral summer (November to March) and once in the austral winter (June to August).

Individuals were captured using a combination of bottom-set 400–800 m longlines and 200–400 m long, 11·45 cm mesh gillnets. Longlines were constructed 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. 50–70 size 14/0 Mustad tuna circle hooks were used per longline and baited with threadfin bream *Nemipterus* spp., squid *Loligo* spp., blue threadfin *Eleutheronema tetradactylum* (Shaw 1804) and mullet *Mugil cephalus* L.1758. Longlines and gillnets were set for 45–60 min. Individuals captured were measured to the nearest mm stretch total length (L_{ST}), sexed and tagged with a uniquely numbered rototag in the first dorsal fin. Muscle and plasma tissues were collected for SIA and individuals were released. One cm^3 of muscle was sampled from behind the first dorsal fin. Blood samples were collected using a heparinized needle and syringe from the caudal vein anterior to the tail. Two ml of blood was collected from each individual. A portable centrifuge was used to spin and separate blood samples into plasma and red blood cell (RBC) components (www.benchmarkscientific.com). Plasma and RBC layers were pipetted into separate 1·5 ml Eppendorf safe lock microcentrifuge tubes (www.eppendorf.com). There is evidence to suggest that juvenile stable-isotope profiles may incorporate maternal feeding patterns (Olin *et al.*, 2011). To help ensure maternal isotope values did not affect the isotope values of captured specimens, *R. taylori* were only sampled if the umbilical scar was healed (Kinney *et al.*, 2011). All *R. taylori* samples collected in CB were kept on ice in the field and frozen (−20° C) upon return to the laboratory. Due to their remote locations, samples collected from the remaining four bays were kept on ice in the field and stored in a Taylor–Wharton CX100 Dry Shipper (−80° C) (www.taylorwharton.com) until return to the laboratory where samples were frozen (−20° C).

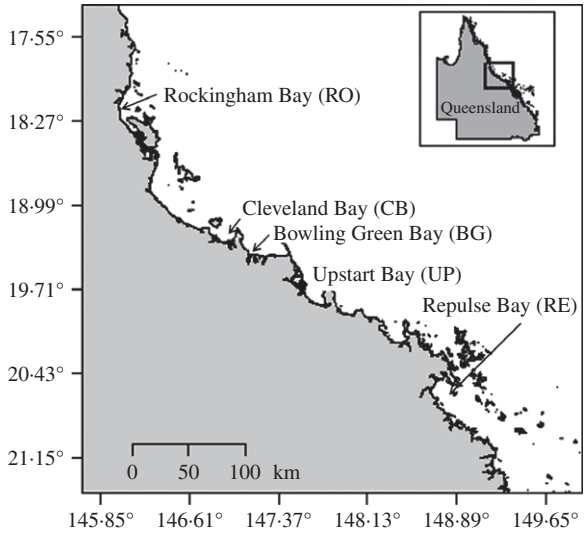

FIG. 1. Stable-isotope sampling region for *Rhizoprionodon taylori* indicating the five sample bays. Inset indicates location along the north Queensland coast, Australia.

Data suggest that *R. taylori* is a demersal predator, although it could not be conclusively determined if they forage from benthic and pelagic food chains within nearshore areas (Simpfendorfer, 1998). Therefore, baseline benthic and pelagic $\delta^{13}C$ and $\delta^{15}N$ food web sources were collected from each bay to establish local values. Seagrass and macroalgae were used to establish benthic food web $\delta^{13}C$ and $\delta^{15}N$ sources and were sampled opportunistically from fishing locations in each bay. Plankton was used to establish pelagic $\delta^{13}C$ and $\delta^{15}N$ food web sources and were collected using horizontal surface tows with a 0·85 m long, 300 mm diameter plankton net (53 μ mesh) (www.entosupplies.com.au). Plankton samples were collected from a central location in each bay *c*. 5 km from shore. Plankton samples included zooplankton and some invertebrates. Samples of all plant and plankton material were kept on ice while in the field and frozen upon return to the laboratory as described for *R. taylori* tissues.

SAMPLE PREPARATION AND ISOTOPE ANALYSIS

Rhizoprionodon taylori tissue samples were freeze dried and ground into a powder with a mortar and pestle. Seagrass and macroalgae were thawed, rinsed in distilled H_20 and cleaned of visible residue and epiphytes. Zooplankton and phytoplankton were not separated to ensure that there was sufficient plankton sample volume for analysis. After cleaning, seagrass and macroalgae were oven dried at 60° C for 48 h and ground into a powder. Plankton samples were filtered through GF/F Whatman glass microfibre filters (0·7 µm pore size) (www.gelifesciences.com) using a vacuum pump (300 mm Hg). Plankton samples were rinsed with distilled H_20 during filtration to remove any salt from the samples. After filtration, large detritus were removed from the filters. Filters were oven dried at 60° C for 24 h and stored in Petri dishes prior to analysis.

Lipids in animal tissues are reportedly depleted in $\delta^{13}C$ in comparison with proteins and carbohydrates. The inclusion of lipids may result in unreliable isotope data where differences in the lipid content between organisms and tissues may produce more negative $\delta^{13}C$ (Post *et al.*, 2007). To correct for this, fish tissues and plankton samples underwent lipid extraction using a modified Bligh & Dyer (1959) method. A volume of 1·9 ml of 2:1 chloroform–methanol was combined with the powdered samples, agitated for 10 s and put in a water bath (30° C) for 24 h. Lipid extracted samples were removed from the bath, centrifuged for 3 min and decanted. A volume of 1·9 ml of 2:1 chloroform–methanol was added a second time followed by another

round of agitation and centrifugation before the final decant. The tissue pellet that was produced was left in a fume hood to dry for 48 h. Urea was not separately extracted from fish tissues as previous work has shown that the lipid extraction process also removes soluble urea (Hussey *et al.*, 2012*a*). Masses of 400–600 μg of dried muscle, 700–900 μg of dried plasma, 3000–4000 μg of dried plant material and 4000–5000 μg of dried plankton were analysed for δ^{13}C using a continuous flow isotope-ratio mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan; www.thermoscientific.com) equipped with an elemental analyser (Costech; www.costechanalytical.com).

Stable-isotope ratios were expressed in δ notation as deviations from standards in parts per thousand (‰) using the following calculation: $\delta X = 1000\ [(R_{\text{sample}}R_{\text{standard}}{}^{-1}) - 1]$, where X is ^{13}C or ^{15}N, R_{sample} is the ratio (^{13}C:^{12}C or ^{15}N:^{14}N) in the sample and R_{standard} is the ratio in the standard. The standard reference for carbon was Pee Dee Belemnite carbonate and nitrogen was atmospheric N_2. Laboratory and National Institute of Standards and Technology (NIST) standards were analysed for every 12 samples to determine analytical precision. The analytical precision (S.D.) for NIST standard 1577c (bovine *Bos taurus* liver, $n = 42$) and an internal laboratory standard [tilapia *Oreochromis niloticus* (L. 1758) muscle, $n = 42$] for δ^{13}C was 0·07 and 0·11‰, and for δ^{15}N was 0·16 and 0·14‰.

STATISTICAL ANALYSIS

Bayesian inferences were used for all data analysis in this study because there was concern that more traditional methods of spatial analysis may not be able to detect some of the subtle geographic differences in δ^{13}C and δ^{15}N values. Bayesian analysis is better able to incorporate uncertainty (due to variability in isotope ratios) and the small and variable sample size in some locations (Bernardo & Smith, 1994; Berger, 2006). Therefore, a Bayesian analysis of variance (ANOVA) (Gelman & Hill, 2007) was used to access differences between bays in benthic and pelagic δ^{13}C and δ^{15}N values. The Bayesian ANOVA used vague, non-informative priors and was calculated according to the following:

The likelihood

$$y_{ij} \sim \text{Normal}\left(\mu + \alpha_i,\ \sigma^2\right) \tag{1}$$

The priors

$$\mu \sim \text{Normal}\left(0, 10^{-6}\right) \tag{2a}$$

$$\alpha_i \sim \text{Normal}\left(0, 10^{-6}\right), \tag{2b}$$

where μ was the overall mean and α_i was the effect due to the ith sample bay. Differences between locations were considered significant if the 95% credibility intervals of posterior draws did not overlap.

Linear Bayesian correlation analysis (Gelman & Hill, 2007; McCarthy, 2007) was used to determine if there was a correlation between benthic and pelagic δ^{13}C or δ^{15}N values based on geographic location. The results were used to establish if there was a consistent geographic pattern in benthic and pelagic δ^{13}C or δ^{15}N that could be compared with *R. taylori* δ^{13}C and δ^{15}N values to assess regional movement. Correlation analysis was calculated according to the following:

The likelihood

$$C_i \sim \text{ Multivariate normal}\left(\left[\mu_1, \mu_2\right], \sum\right), \tag{3}$$

where $C_i = (C_{i,1},\ C_{i,2})$.

The priors

$$\mu_1, \mu_2 \sim \text{Normal}\left(0, 10^3\right) \tag{4a}$$

$$\sigma_1, \sigma_2 \sim \text{Normal}\left(0, 10^3\right) \tag{4b}$$

$$\rho \sim \text{Uniform}\left(-1, 1\right) \tag{4c}$$

$$\sum = \begin{pmatrix} \sigma_1^2 & \rho\sigma_1\sigma_2 \\ \rho\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix}, \tag{5}$$

where $C_{i,1}$ and $C_{i,2}$ were the δ^{13}C or δ^{15}N values of group one and two respectively, μ_1 and μ_2 were the means of group one and group two, Σ was the covariance matrix and ρ defined the correlation parameter. ρ ranged from -1 to 1, indicating the strength and direction of the correlation. Correlations were considered significant if the 95% credibility intervals of the posterior draws did not overlap with 0.

There were no estimates for the isotopic incorporation rates of *R. taylori*. Therefore, tissue turnover rates were approximated based on the data available for other elasmobranchs. Logan & Lutcavage (2010) found that complete isotopic δ^{13}C turnover for captive juvenile sandbar sharks *Carcharhinus plumbeus* (Nardo 1827) was >300 days in whole blood and >500 days in muscle. Kim *et al.* (2012) found that complete isotopic δ^{13}C turnover for captive leopard sharks *Triakis semifasciata* Girard 1855 was somewhat longer with *c*. 300 days in plasma and >700 days in muscle. Malpica-Cruz *et al.* (2012), however, found that the isotopic turnover rates of small, faster-growing captive *T. semifasciata* were faster than turnover rates of the larger, more slowly growing individuals. Moreover, Olin *et al.* (2011) found that *R. terraenovae*, a close relative of *R. taylori*, had high isotopic turnover rates due to the species' high growth rate. Previous studies of other taxa have also demonstrated that small body size, fast growth rate and high metabolic rate increase δ^{13}C and δ^{15}N turnover (Trueman *et al.*, 2005; Tarboush *et al.*, 2006; Carleton & Del Rio, 2010; Weidel *et al.*, 2011). Due to their relatively small size and fast growth rate, *R. taylori* probably have faster δ^{13}C and δ^{15}N turnover rates than slow-growing, larger-bodied sharks (Olin *et al.*, 2011). Therefore, based on the estimates of previous work, *R. taylori* plasma isotopic δ^{13}C and δ^{15}N turnover was estimated to take *c*. 6 months (*c*. 180 days) and muscle was estimated to take *c*. 1 year (*c*. 365 days) (Olin *et al.*, 2011; Malpica-Cruz *et al.*, 2012).

A two-factor Bayesian ANOVA (Gelman & Hill, 2007) was used to test for differences in δ^{13}C and δ^{15}N between bays and sexes in muscle and plasma. The two-way Bayesian ANOVA was calculated according to the formulations:

The likelihood

$$y_{ijk} \sim \text{Normal}\left(\mu + \alpha_i + \beta_j + \gamma_{ij}, \sigma^2\right) \tag{6}$$

The priors

$$\mu \sim \text{Normal}\left(0, 10^{-6}\right) \tag{7a}$$

$$\alpha_i \sim \text{Normal}\left(0, 10^{-6}\right) \tag{7b}$$

$$\beta_j \sim \text{Normal}\left(0, 10^{-6}\right) \tag{7c}$$

$$\gamma_{ij} \sim \text{Normal}\left(0, 10^{-6}\right), \tag{7d}$$

where β_j was the effect due to sex and γ_{ij} was the effect due to the interaction between the *i*th bay and sex.

A three-way ANCOVA was considered to examine the effect of L_{ST}, sex and sample bay on *R. taylori* tissue δ^{13}C and δ^{15}N; however, preliminary analysis showed that the effect of L_{ST} was highly variable between bays. Therefore, a series of linear Bayesian regressions were used to

determine if there was a relationship between muscle and plasma δ^{13}C and δ^{15}N and L_{ST} for each bay. Regression analysis used vague, non-informative priors and was calculated according to the following:

The likelihood

$$y_{ij} \sim \text{Normal}\left(\mu + S_i, \sigma^2\right) \tag{8}$$

The priors

$$\mu \sim \text{Normal}\left(0, 10^{-6}\right) \tag{9a}$$

$$S_i \sim \text{Normal}\left(0, 10^{-6}\right) \tag{9b}$$

where S_i was the effect due to L_{ST}. Relationships between size and δ^{13}C and δ^{15}N were considered significant if the 95% credibility intervals of the posterior draws did not overlap with 0.

Linear Bayesian correlation analysis was used to determine if there was a correlation between benthic and pelagic, and *R. taylori* tissue δ^{13}C and δ^{15}N values based on location. All posterior draws were built using three Markov chains with 10 000 iterations per chain and a thinning interval of 10. Chain mixing trace plots and autocorrelation values were used to access each applied version of the models. All Bayesian models were fitted using the package R2jags (Su & Yajima, 2014) in R 3.0.2 (R Development Core Team; www.r-project.org) and JAGS version 3.4.0 (Plummer, 2003).

RESULTS

STUDY SITE Δ^{13}C AND Δ^{15}N

A total of 47 pelagic (plankton) and 55 benthic (seagrass and macroalgae) samples were collected from the five bays (Table I). Benthic δ^{13}C values were higher than pelagic values in all bays [Table I and Fig. 2(a)]. Sample bay accounted for 45·3 and 45·4% of the estimated variance components (% S.D.) in benthic and pelagic δ^{13}C values, respectively. Benthic δ^{13}C values from UP, BG and CB were significantly higher than the benthic δ^{13}C values from RO (Fig. 2). Benthic δ^{13}C values in BG and CB were also significantly higher than the δ^{13}C values from RE. Although the absolute δ^{13}C values were different, pelagic samples exhibited similar geographic patterns in relative δ^{13}C compared with benthic samples. Pelagic δ^{13}C values from UP and CB were significantly higher than the δ^{13}C values from RO. Pelagic δ^{13}C values from UP were also significantly higher than the δ^{13}C values from RE. Linear Bayesian correlation analysis indicated that there was no significant geographic correlation between benthic and pelagic δ^{13}C (median, 95% credibility intervals = 0·50, −0·406 to 0·999).

Benthic δ^{15}N values were lower than pelagic δ^{15}N values in all bays, most likely because pelagic samples contained some zooplankton. Sample bay accounted for 46·3 and 49·0% of the estimated variance components (% S.D.) in benthic and pelagic δ^{15}N values. Benthic δ^{15}N in RE was significantly higher than the δ^{15}N values from BG and CB. Pelagic δ^{15} N values in RE were significantly higher than pelagic δ^{15} N from UP, BG and CB. Pelagic RO δ^{15}N was also significantly higher than δ^{15} N values from UP and BG. Linear Bayesian correlation analysis indicated that there was no significant correlation between benthic and pelagic δ^{15}N based on location (median, 95% credibility intervals = 0·39, −0·57 to 0·98).

TABLE I. Sample size (n) and $\delta^{13}C$ and $\delta^{15}N$ range (mean ± S.D.) of benthic and pelagic sources from each location: Repulse Bay (RE), Upstart Bay (UP), Bowling Green Bay (BG), Cleveland Bay (CB) and Rockingham Bay (RO)

Location	Benthic (n)	Pelagic (n)	Benthic $\delta^{13}C$	Benthic $\delta^{15}N$	Pelagic $\delta^{13}C$	Pelagic $\delta^{15}N$
RE	12	5	−19·6 to −12·1 (−16·1 ± 2·3)	2·9 to 6·8 (4·9 ± 1·3)	−20·8 to −19·9 (−20·4 ± 0·3)	6·7 to 7·6 (6·9 ± 0·4)
UP	11	13	−20·5 to −10·3 (−14·4 ± 4·0)	0·6 to 4·5 (2·1 ± 1·7)	−20·5 to −14·6 (−17·7 ± 2·6)	3·7 to 5·0 (4·4 ± 0·5)
BG	7	12	−19·3 to −9·5 (−12·4 ± 4·3)	2·4 to 5·7 (3·7 ± 1·4)	−20·1 to −18·7 (−19·5 ± 0·4)	1·2 to 5·9 (3·7 ± 1·8)
CB	13	8	−17·2 to −8·4 (−12·4 ± 2·2)	1·3 to 3·6 (2·2 ± 0·8)	−19·4 to −18·2(−18·8 ± 0·5)	4·7 to 5·7 (5·1 ± 0·3)
RO	11	9	−23·2 to −15·2 (−19·1 ± 2·8)	1·3 to 4·9 (3·7 ± 1·0)	−23·3 to −18·7 (−21·0 ± 2·0)	5·2 to 6·2 (5·6 ± 0·3)

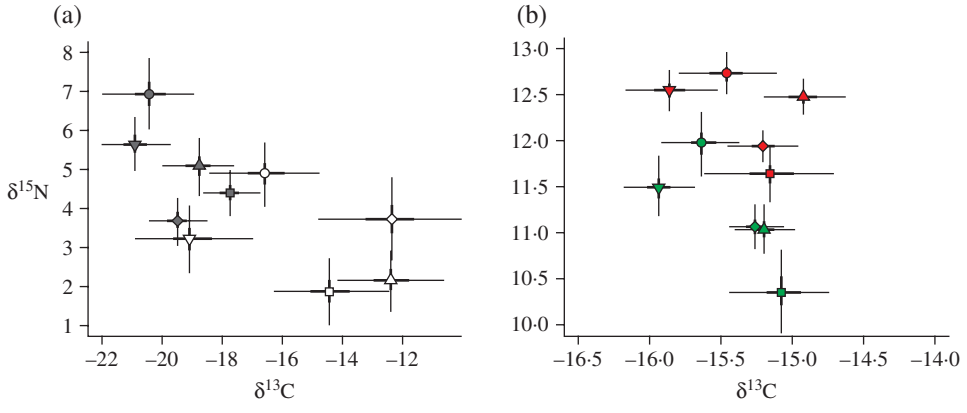

FIG. 2. Median δ^{13}C and δ^{15}N values from Bayesian ANOVA of (a) benthic (▭), pelagic (▭), (b) female *Rhizoprionodon taylori* muscle (▭) and plasma (▭) samples in Repulse Bay (●), Upstart Bay (■), Bowling Green Bay (◆), Cleveland Bay (▲) and Rockingham Bay (▼). ——, 50 and 95% credibility intervals of posterior draws.

Despite the lack of significant correlation in benthic and pelagic isotope values across sample locations, there was evidence of consistent geographic patterns in the δ^{13}C and δ^{15}N in primary producers. Specifically, benthic and pelagic δ^{13}C from UP, BG and CB was higher than δ^{13}C from RO and RE. RE had the highest δ^{15}N values compared with any other bay for both benthic and pelagic sources. RO also had relatively high benthic and pelagic δ^{15}N compared with other bays. Sample location accounted for a large component of the estimated variance, suggesting that location was a strong determinant of benthic and pelagic δ^{13}C and δ^{15}N. Therefore, these results indicated that there was a relatively consistent geographic trend in δ^{13}C and δ^{15}N that could be used to assess *R. taylori* residency and foraging between bays.

SHARK TISSUE Δ^{13}C AND Δ^{15}N

A total of 146 *R. taylori* (30 males and 116 females) were sampled from the five study bays from 2012 to 2013 (Table II). Across all sample bays, *R. taylori* size ranged from 415 to 780 mm L_{ST} (mean ± S.D. = 663 ± 66). Muscle δ^{13}C and δ^{15}N ranged from −18·1 to −12·8 and 10·6 to 13·8, respectively. Plasma δ^{13}C and δ^{15}N ranged from −16·8 to −13·7 and 8·3 to 12·7, respectively. An insufficient number of males were captured in RE and UP to investigate the effect of sex on δ^{13}C and δ^{15}N in these bays (Table II).

L_{ST} had an inconsistent and mostly insignificant influence on *R. taylori* δ^{13}C and δ^{15}N. Linear Bayesian regression analysis showed that only BG muscle δ^{13}C (median, 95% credibility intervals; 0·006, 0·004–0·008), BG plasma δ^{13}C (median, 95% credibility intervals; 0·003, 0·0006–0·006 δ^{13}C), CB muscle δ^{13}C (median, 95% credibility intervals; 0·005, 0·0007–0·009) , CB plasma δ^{13}C (median 95% credibility intervals; 0·003, 0·0008–0·005) and RE muscle δ^{13}C (median 95% credibility intervals; 0·006, 0·001–0·01) had a significantly positive relationship with L_{ST}. Only BG plasma δ^{15}N was significantly correlated with *R. taylori* L_{ST} (median 95% credibility intervals; 0·003, 0·000–0·005). Sex also had an inconsistent effect

TABLE II. *Rhizoprionodon taylori* male (M) and female (F) sample size, and combined stretch total length (L_{ST}) and $\delta^{13}C$ and $\delta^{15}N$ range (mean ± S.D.) from Repulse Bay (RE), Upstart Bay (UP), Bowling Green Bay (BG), Cleveland Bay (CB), and Rockingham Bay (RO)

Bay	M	F	L_{ST} (mm)	Muscle $\delta^{13}C$	Muscle $\delta^{15}N$	Plasma $\delta^{13}C$	Plasma $\delta^{15}N$
RE	1	20	595 to 755 (699 ± 41)	−16·6 to −14·5 (−15·5 ± 0·5)	12·0 to 13·4 (12·7 ± 0·4)	−16·7 to −14·7 (−15·6 ± 0·5)	10·2 to 12·7(11·9 ± 0·8)
UP	0	11	674 to 780 (714 ± 35)	−16·0 to −14·2 (−15·2 ± 0·5)	11·1 to 12·3 (11·6 ± 0·5)	−15·9 to −14·5 (−15·1 ± 0·5)	9·2 to 11·4 (10·4 ± 0·8)
BG	18	37	462 to 753 (641 ± 68)	−16·6 to −12·8 (−15·3 ± 0·7)	10·6 to 13·2 (12·0 ± 0·6)	−16·7 to −13·7 (−15·4 ± 0·6)	9·6 to 12·0 (11·1 ± 0·7)
CB	7	28	415 to 744 (650 ± 80)	−18·1 to −13·3 (15·04 ± 1·0)	10·7 to 13·5 (12·5 ± 0·6)	−16·5 to −14·2 (−15·2 ± 0·5)	8·3 to 12·3 (11·0 ± 0·9)
RO	4	20	625 to 755 (678 ± 38)	−17·0 to −14·5 (−15·8 ± 0·6)	11·6 to 13·8 (12·7 ± 0·5)	−16·8 to −14·5 (−16·0 ± 0·5)	10·0 to 12·5 (11·6 ± 0·6)

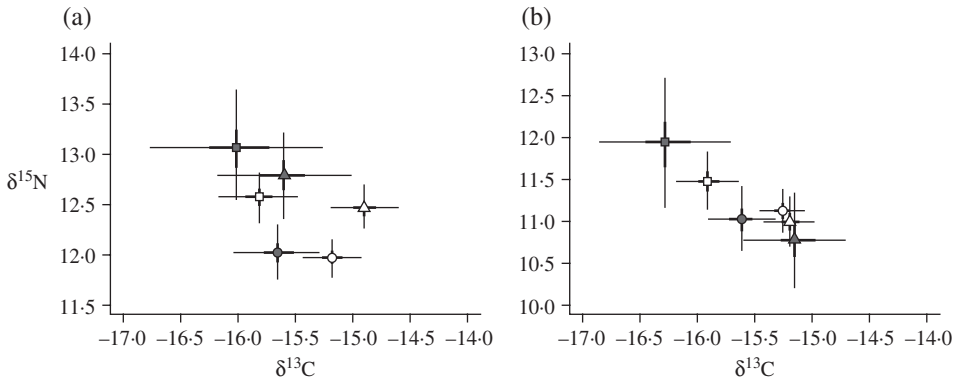

FIG. 3. Median δ13C and δ15N values of Bayesian analysis of variance (ANOVA) of female (▭) and male (▬) *Rhizoprionodon taylori* for (a) muscle and (b) plasma tissue in Bowling Green Bay (●), Cleveland Bay (▲) and Rockingham Bay (■). ⎯, 50 and 95% credibility intervals of posterior draws.

on *R. taylori* δ^{13}C and δ^{15}N. Female muscle and plasma δ^{13}C from BG and muscle from CB was significantly higher than male δ^{13}C (Fig. 3). There was no significant difference, however, in δ^{13}C between sexes in RO or plasma tissue from CB. There was no significant difference in δ^{15}N between sexes for muscle or plasma tissue (Fig. 3). As a result of the inconsistent effect of sex on δ^{13}C and δ^{15}N and the small, uneven sampling of males between locations, males were excluded from between-bay comparisons.

When compared with the primary producers, female *R. taylori* muscle and plasma δ^{13}C values fell within the range of the combined benthic and pelagic δ^{13}C values of their respective capture locations. Sample bay accounted for 33·0 and 38·2% of the estimated variance components (% S.D.) in muscle and plasma δ^{13}C. The results of the Bayesian ANOVA showed that female *R. taylori* muscle δ^{13}C values from UP, BG and CB were significantly higher than muscle δ^{13}C values from RO (Fig. 2). Muscle δ^{13}C from CB was also significantly higher than muscle δ^{13}C from RE. Plasma δ^{13}C in UP, BG and CB was significantly higher than plasma δ^{13}C from RO and RE (Fig. 2). It was not possible to differentiate between the δ^{13}C values of individuals captured in UP, BG and CB. These results show that there was a high degree of similarity in *R. taylori* δ^{13}C between adjacent bays (*i.e.* those within 100 km), while *R. taylori* from more distant bays (>100 km separation) had less similar δ^{13}C values. Overall, differences in *R. taylori* δ^{13}C between locations were more pronounced in plasma than in muscle.

The results of the Bayesian ANOVA showed that sample bay accounted for 45·6 and 45·1% of the estimated variance components (% S.D.) in muscle and plasma δ^{15}N. Female *R. taylori* muscle δ^{15}N from RE and RO was significantly higher than muscle δ^{15}N from BG and UP (Fig. 2). Plasma δ^{15}N from RE was also significantly higher than plasma δ^{15}N in UP, BG and CB. Plasma δ^{15}N from RO was significantly higher than plasma δ^{15}N in UP. Muscle and plasma δ^{15}N values from UP, BG and CB closely overlapped. The differences in *R. taylori* δ^{13}N between sample bays were more pronounced in plasma than in muscle. Similar to the δ^{13}C analysis, δ^{15}N analysis showed that *R. taylori* from more distant bays (>100 km separation) had more distinct δ^{15}N values.

TABLE III. Results of linear Bayesian correlation analysis between the $\delta^{13}C$ and $\delta^{15}N$ of *Rhizoprionodon taylori* and the benthic and pelagic producers across sample bays. ρ defined the correlation parameter. Correlations were considered significant if the 95% credibility intervals (C.I.) of the posterior draws did not overlap with 0

Isotope	Comparison	Median ρ value	95% C.I. ρ value
$\delta^{13}C$	Benthic muscle	0·815	0·063 to 0·996
$\delta^{13}C$	Pelagic muscle	0·626	−0·262 to 0·992
$\delta^{13}C$	Benthic plasma	0·723	−0·081 to 0·099
$\delta^{13}C$	Pelagic plasma	0·825	0·123 to 0·998
$\delta^{15}N$	Benthic muscle	0·383	−0·503 to 0·960
$\delta^{15}N$	Pelagic muscle	0·661	−0·239 to 0·994
$\delta^{15}N$	Benthic plasma	0·700	−0·1452 to 0·996
$\delta^{15}N$	Pelagic plasma	0·603	−0·278 to 0·996

Linear Bayesian correlation analysis indicated significant positive geographic correlation between muscle and benthic $\delta^{13}C$ values and plasma pelagic $\delta^{13}C$ values (Table III). None of the $\delta^{15}N$ tissue–primary producer geographic correlations were significant. Although not all correlations between tissues and study site $\delta^{13}C$ and $\delta^{15}N$ were significant, the geographic patterns in female *R. taylori* $\delta^{13}C$ and $\delta^{15}N$ were similar to the geographic patterns in benthic and pelagic $\delta^{13}C$ and $\delta^{15}N$. Shark, benthic and pelagic $\delta^{13}C$ values from UP, BG and CB were often significantly higher than the $\delta^{13}C$ values in RE and RO. Similarly, *R. taylori*, benthic and pelagic samples from RE and RO had the highest $\delta^{15}N$ values compared with UP, BG and CB. These results suggest that individuals in RE and RO did not forage extensively in the centralized bays within the study area.

DISCUSSION

The results of this study suggest that female *R. taylori* do not forage between areas that are >100 km apart on the Queensland coast over short periods of time (*c.* 6 months). Less pronounced geographic differences in *R. taylori* muscle $\delta^{13}C$ and $\delta^{15}N$ compared with plasma could indicate that individuals forage between more distant bays (>100 km) over 6 months to 1 year. *Rhizoprionodon taylori* muscle $\delta^{13}C$ and $\delta^{15}N$ also reflected the geographic trends in benthic and pelagic $\delta^{13}C$ and $\delta^{15}N$ values. Therefore, while some *R. taylori* probably foraged between distant bays, some may have spent extended periods of time (*c.* 1 year) near their respective capture locations. Therefore, these results suggest that *R. taylori* may not make large regional movements (>100 km) over a period of time spanning from *c.* 6 months to 1 year.

The regional movement patterns demonstrated by *R. taylori* in this study contrasts with the movement patterns of *R. terraenovae*, which has a similar life history (Loefer & Sedberry, 2003) and nearshore residency patterns (Carlson *et al.*, 2008). In contrast to *R. taylori*, *R. terraenovae* is known to move broadly (Kohler *et al.*, 1998; Carlson *et al.*, 2008; Suárez-Moo *et al.*, 2013). Tag and recapture data of *R. terraenovae* from the Gulf of Mexico showed that one individual travelled 169 km in 35 days, and another individual travelled 322 km in 228 days (Carlson *et al.*, 2008). Given the biological and

behavioural similarities between *R. taylori* and *R. terraenovae*, it was anticipated that *R. taylori* would exhibit similar large-scale regional movement patterns. Instead, female *R. taylori* appeared to be similar to the closely related *R. acutus*, another small-bodied, fast-growing species that has a similar geographic range to *R. taylori* (Last & Stevens, 2009). Although data on the movement and site fidelity of *R. acutus* are limited, stock structure analysis indicates that this species exhibits moderate site fidelity with some long-distance movements (Ovenden *et al.*, 2011; Schroeder, 2011).

Although muscle and plasma δ^{13}C and δ^{15}N values suggest limitations in the regional foraging and dispersal of *R. taylori*, the results do not necessarily indicate long-term residency within individual bays. Female *R. taylori* sampled from adjacent bays (UP, BG and CB) had indistinguishable plasma and muscle δ^{13}C values. The δ^{15}N values of *R. taylori* UP, BG and CB were all relatively low and closely overlapped, particularly in plasma. There are several possible explanations for the similarity in values between these locations. The first is that similarity in isotopic baselines between UP, BG and CB resulted in similar isotope values for sharks feeding in those areas. A second explanation is that *R. taylori* captured in UP, BG and CB regularly moved between and fed within these bays, thus accumulating similar isotope profiles. The observed similarity could be the result of a combination of these two explanations. Acoustic tracking indicated that *R. taylori* move between bays *c.* 30 km apart (Munroe *et al.*, 2014*a*); therefore, it is likely that the similar isotope values in *R. taylori* sampled in UP, BG and CB were, at least in part, the result of regular movement between these neighbouring bays.

Given that *R. taylori* probably moved between bays within 100 km in the central part of the study region, it is unlikely that individuals captured in RE and RO only used their respective capture bays over 6 months. If the movement patterns of *R. taylori* in RE and RO are consistent with those in UP, CB and BG, it is probable that *R. taylori* captured in RE and RO moved to other nearby bays within 6 months to 1 year. Therefore, it is likely that the baseline δ^{13}C and δ^{15}N values used to establish dietary sources for *R. taylori* in RE and RO did not account for all possible δ^{13}C and δ^{15}N that *R. taylori* in RO and RE could have been exposed to. The similar geographic pattern in δ^{13}C and δ^{15}N values, in combination with relatively fast tissue turnover in *R. taylori*, however, supports the general conclusion that *R. taylori* in RE and RO were not travelling as far as CB, BG or UP within 6 months to 1 year.

Previous nearshore acoustic tracking indicated that most *R. taylori* were not resident to individual bays and therefore probably moved into other nearshore areas within 1 year (Munroe *et al.*, 2014*a*). Isotope analysis in this study, however, suggests that *R. taylori* were primarily residential to regions on a scale of 10–100 km, over a period of 6 months to 1 year. Collectively, these studies indicate that *R. taylori* may serve as an important ecological link between bays <100 km apart, but may not be a significant link between more distant bays (>100 km) over the medium term (6–12 months). It has been suggested that small-bodied, fast-growing, productive sharks use multiple nearshore areas because it increases individual access to resources (Heupel *et al.*, 2007; Carlson *et al.*, 2008; Knip *et al.*, 2010; Munroe *et al.*, 2014*a*). The limited regional range demonstrated by *R. taylori* isotope profiles, however, suggests that sufficient resources to support survival, growth and annual reproduction were probably located within <150 km of capture locations. Regional dispersal may have also been limited by the high energetic cost associated with long-range movement (Roff, 1988; Nøttestad *et al.*, 1999; Alerstam *et al.*, 2003). Therefore, female *R. taylori* movement patterns

may represent an energetic balance between maximizing the benefits of using multiple bays and minimizing the reciprocal costs of long-distance movement.

The ability to move into different bays to exploit adequate resources may be a successful survival strategy. By moving between different locations, *R. taylori* are buffered against unproductive conditions in one bay by potentially more productive conditions in another bay (Yates *et al.*, 2012). Thus, the use of multiple locations and habitats may help to stabilize the *R. taylori* population (Secor *et al.*, 2009; Yates *et al.*, 2012). The limited regional range of individuals, however, could leave *R. taylori* vulnerable to large-scale (>100 km) regional changes in environmental conditions.

It should be noted that SIA in sharks is not temporally refined enough to detect sporadic or short-term long-range dispersal (Logan & Lutcavage, 2010; Kim *et al.*, 2012). Individuals may have travelled to more distant bays but if *R. taylori* did not forage in those bays, isotope analysis would not be able to detect the presence of *R. taylori* in those areas. Moreover, although *R. taylori* in CB had higher δ^{13}C values compared with other populations, several individuals had low δ^{13}C values relative to locally available δ^{13}C sources and the majority of the population. This could suggest long-range movement into areas with lower δ^{13}C source values, such as RE and RO. Therefore, this work cannot rule out the possibility that *R. taylori* made occasional long-range movements. There was insufficient data to assess male movement patterns and it is possible that male *R. taylori* exhibit different movement patterns.

The variability in environmental δ^{13}C and δ^{15}N values may have been the result of variable amounts of freshwater input into each bay. Freshwater runoff into nearshore areas, primarily from rivers, reduces the δ^{13}C value in the environment (Boutton, 1991; Hobson, 1999). Fresh water has lower δ^{13}C because it contains ^{13}C-depleted CO_2 derived from the decomposition of terrestrial organic matter (Boutton, 1991; Hobson, 1999). RO and RE typically have high to moderate amounts of freshwater input, respectively, compared with UP which has relatively limited freshwater input. This may explain why RE and RO baseline samples had lower δ^{13}C than UP. BG, however, has relatively high freshwater input but high δ^{13}C. Therefore, other factors are contributing to δ^{13}C values, such as proximity to human development. Higher δ^{15}N in RE and RO may be the result of large expanses of sugarcane farms in the area (Thorburn *et al.*, 2011). Nitrogen runoff from fertilizer used on these farms may have drained into RE and RO and the surrounding areas, resulting in higher local δ^{15}N.

It is possible that because zooplankton and phytoplankton were not separated prior to analysis, comparisons of pelagic δ^{15}N values between bays may be biased as a result of different amounts of zooplankton being collected from each sample location. If certain bays had a higher volume of zooplankton, the baseline pelagic δ^{15}N values reported for those bays would be artificially high in comparison to other locations (Montoya, 2007). Moreover, any amount of zooplankton in the sample would make it difficult to compare baseline δ^{15}N values in seagrass. The similar geographic pattern in δ^{15}N, however, demonstrated by benthic and pelagic samples suggest that the presence of zooplankton in the samples did not obviously bias the results and overall pattern. As δ^{13}C trophic discrimination factors are relatively small, it is unlikely that different amounts of zooplankton between locations would affect the interpretation of the δ^{13}C results.

Dietary variability may also have influenced the variation in tissue δ^{13}C and δ^{15}N between locations. For example, the fact that the benthic primary producers from CB, BG and UP have higher δ^{13}C than the *R. taylori* in those areas (which are probably multiple trophic levels higher) suggests that *R. taylori* in these areas may feed more

regularly from pelagic sources than *R. taylori* captured in RO and RE. Differences in diet between bays have the potential to skew direct interpretations of *R. taylori* movement. Given the strong and consistent geographic patterns in *R. taylori*, pelagic and benthic δ^{13}C and δ^{15}N, however, it is unlikely that differences in *R. taylori* diet between locations would fully account for the isotopic tissue variation between locations.

Until recently, isotope analysis on elasmobranchs has primarily been used to study diet (MacNeill *et al.*, 2005; McMeans *et al.*, 2010; Kinney *et al.*, 2011). Studies that have used isotopes to investigate elasmobranch movement have been conducted at either relatively small scales such as islands (Papastamatiou *et al.*, 2010) and individual bays and inlets (Dale *et al.*, 2011; Reum & Essington, 2013), or at coarse scales across isoscapes that span thousands of km (Carlisle *et al.*, 2012). Abrantes & Barnett (2011) assessed the movement patterns of the broadnose sevengill shark *Notorynchus cepedianus* (Péron 1807) at a similar geographic scale to this study; however, that study focused on nearshore and offshore population segregation. The successful application of isotope analysis to define the regional movement patterns of *R. taylori* between multiple bays demonstrates that this technique may be an affordable and valid alternative to more traditional methods used to study regional movement. Isotope analysis, however, may not be able to define similarly precise regional movements for all species and in all circumstances.

As previously established, slow-growing, large-bodied sharks have relatively slow isotope incorporation rates (Logan & Lutcavage, 2010). As a result, sharks that move quickly through different habitats may not have enough time to assimilate local isotope values. Effective isotope movement analysis requires some previous knowledge of the movement and diet of the study species (*i.e.* catch data and acoustic tracking) to guide sampling procedures (Hussey *et al.*, 2012*b*). In this case, catch and acoustic tracking data were available and helped guide several aspects of this study's methodology, such as study site selection. Regional movement studies require well-defined isotopic baselines that allow for reasonable differentiation between habitats (Hobson, 1999; Rubenstein & Hobson, 2004; Hussey *et al.*, 2012*b*). Ecological differences that researchers are interested in assessing may not always be reflected in the isotopic baselines of the region. In such cases, researchers could consider examining sulphur isotope ratios in addition to carbon and nitrogen (West *et al.*, 2006). Differences in δ^{34}S between environments and producers may be present even when δ^{13}C and δ^{15}N are the same (Connolly *et al.*, 2004; McCauley *et al.*, 2014). Overall, ecological circumstances should be carefully considered before using SIA to study the movement and home range of elasmobranchs.

These results have provided new information on the residency and movement of a small-bodied nearshore shark. The limited evidence for long-distance (>100 km) movements exhibited by *R. taylori* over shorter periods of time suggest that this species may be an important link between adjacent bays and habitats, and potentially more distant bays over longer periods of time. The residency strategies exhibited by *R. taylori* will have a significant effect on how this species responds to environmental fluctuations. Ultimately, *R. taylori* may be more adaptive to environmental change if changes are localized to a single bay and habitat (Yates *et al.*, 2012; Munroe *et al.*, 2014*b*), but may be vulnerable to changes over large spatial scales (>100 km).

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