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ARTICLE

Geographic and temporal variation in the trophic ecology of a small-bodied shark: evidence of resilience to environmental change

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Abstract: Shark dietary patterns can determine how they will respond to changes in prey availability and biodiversity. Geographic variation in diet can also indicate if species have unique structuring roles or feeding strategies in different environments. Unfortunately, little is known about the diet of most shark species and how diet varies over time and space. This study used stable isotope analysis to assess the diet of the Australian sharpnose shark (*Rhizoprionodon taylori*). Plasma and muscle $\delta^{13}C$ and $\delta^{15}N$ of *R. taylori* were compared with $\delta^{13}C$ and $\delta^{15}N$ baselines from multiple embayments to determine the isotopic niche, trophic position, and benthic and pelagic contributions to diet over time and space. Overall, *R. taylori* had a wide trophic position range and consumed prey from benthic and pelagic sources. However, there was geographic and temporal variation in trophic position and benthic and pelagic contributions. These findings indicate *R. taylori* is a dietary generalist, but different populations may have unique effects on distinct ecosystems. Geographic variation in diet also suggests *R. taylori* may be adaptive to changes in prey availability.

Résumé : Les habitudes alimentaires des requins peuvent déterminer leur réaction aux variations de la disponibilité de proies et de la biodiversité. Des variations géographiques du régime alimentaire peuvent également indiquer si des espèces jouent des rôles structurants précis ou ont des stratégies d'alimentation particulières dans différents milieux. Les connaissances sur les régimes alimentaires de la plupart des requins et leurs variations dans le temps et l'espace sont malheureusement très limitées. L'analyse des isotopes stables a été utilisée pour évaluer le régime alimentaire du requin aiguille réchine (*Rhizoprionodon taylori*). Le $\delta^{13}C$ et le $\delta^{15}N$ de plasma et de muscles de *R. taylori* ont été comparés aux $\delta^{13}C$ et $\delta^{15}N$ de référence pour plusieurs baies afin de déterminer la niche isotopique, la position trophique et les contributions benthiques et pélagiques aux régimes alimentaires dans le temps et l'espace. Globalement, les *R. taylori* présentaient une grande fourchette de positions trophiques et consommaient des proies de sources benthiques et pélagiques. Des variations géographiques et temporelles ont toutefois été notées en ce qui concerne la position trophique et les contributions benthiques et pélagiques. Ces résultats indiquent que *R. taylori* est un généraliste sur le plan alimentaire, mais que différentes populations pourraient avoir leurs effets propres sur différents écosystèmes. Les variations géographiques du régime alimentaire donnent également à penser que *R. taylori* pourrait s'adapter aux variations de la disponibilité de proies. [Traduit par la Rédaction]

Introduction

Lethal effects of sharks on prey populations via direct predation are essential to maintaining food web structure and population size (Heithaus et al. 2008). Indirect effects on prey populations, such as altering prey behaviour through risk avoidance, are also important to ecosystem function (Lima and Dill 1990; Heithaus 2005; Heithaus et al. 2012; Klages et al. 2014). Variation in diet over time and space can indicate if species play different roles in different environments or over time. Variation in shark diet can also signify changes in local environmental conditions. Predators may alter their diet and hunting strategies to maximize energy intake in response to changing environmental circumstances (Ben-David et al. 1997; Eide et al. 2005). Therefore, defining the diet and trophic role of sharks over time and space is critical to understanding ecosystem function and species interaction.

Understanding shark dietary patterns can also help to determine how species will respond to changes in prey availability and biodiversity. For example, highly specialized predators may experience severely reduced foraging efficiency when preferred prey populations have decreased (Terraube et al. 2011; Munroe et al. 2014*a*). As a result, diet specialists may experience a decrease in growth, reproduction, and population size (Suarez and Case 2002; Graham 2007; Graham et al. 2009). In contrast, generalist predators are more likely to maintain stable levels of prey capture success when specific prey populations decline (Terraube et al. 2011). Therefore, generalists will probably be less vulnerable to population decline as a result of fluctuations in prey availability.

Stable isotope analysis is an increasingly common method to evaluate the temporal and spatial variation in elasmobranch diets (Hussey et al. 2012*a*). The two most commonly used isotopes are

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$\delta^{13}C$ and $\delta^{15}N$, as they provide complementary information of species dietary patterns (Shiffman et al. 2012). The $\delta^{13}C$ in animal tissues remains relatively constant between prey and predators but varies between different primary producers and environments as a result of different local biogeochemical processes (Tieszen et al. 1983; Peterson and Fry 1987; Boutton 1991). Therefore, tissue $\delta^{13}C$ can be used to determine the dietary carbon source of a consumer (DeNiro and Epstein 1978; Peterson and Fry 1987). In contrast, $\delta^{15}N$ increases from prey to predator (DeNiro and Epstein 1981; Peterson and Fry 1987). As a result, $\delta^{15}N$ in animal tissues can be used to estimate the trophic position of an individual (Post 2002). The $\delta^{13}C$ and $\delta^{15}N$ of individuals can also be used to estimate the isotopic niche of a population (Layman et al. 2012). Collectively, this information can be used to assess the dietary specialization of a population in a given area and (or) a species as whole, depending on the geographic range of the study. Different tissues with different metabolic rates will integrate isotopes from prey over different periods of time, ranging from months to years (Logan and Lutcavage 2010; Kim et al. 2012). Therefore, $\delta^{13}C$ and $\delta^{15}N$ from different tissues can be used to evaluate changes in diet over time. Although isotope analysis provides less detailed data on prey composition than stomach content analysis, isotope analysis is a more cost-effective and, under most circumstances, nonlethal alternative (Hammerschlag and Sulikowski 2011; Hussey et al. 2011).

The Australian sharpnose shark (*Rhizoprionodon taylori*) is a small-bodied, fast-growing, highly abundant species found in the nearshore waters of northern Australia and the southern coast of Papua New Guinea (Stevens and McLoughlin 1991; Simpfendorfer and Milward 1993; Last and Stevens 2009). Size at birth is approximately 220–260 mm total length (TL); males and females mature at approximately 550 mm TL, and males grow to 690 mm TL and females 810 mm TL (Simpfendorfer 1992, 1993). This species is a habitat generalist; however, *R. taylori* has demonstrated a strong preference for seagrass habitat, potentially because seagrass is typically highly productive and abundant in small teleost prey (Munroe et al. 2014*b*). Therefore, benthic food web sources may be a primary contributor to *R. taylori* diet. Previous stomach content analysis of *R. taylori* indicated this species fed on a wide variety of prey types, including teleosts, crustaceans, and cephalopods (Simpfendorfer 1998). Unfortunately, a large proportion of empty stomachs hindered analysis, and the source of prey was not able to be determined (i.e., benthic or pelagic food webs; Simpfendorfer 1998). Recent work has shown *R. taylori* move between bays <100 km apart, but more distant populations are likely separated for greater than 1 year (Munroe et al. in review). It is possible that *R. taylori* in different locations may have distinct diets resulting in unique effects on local environments. Geographically distinct populations of marine mammals (e.g., *Mirounga leonina*; Banks et al. 2014), birds (e.g., *Larus audouinii* and *Larus argentatus*; Oro et al. 1996; Hebert et al. 2011), and reptiles (e.g., *Thamnophis validus*; de Queiroz et al. 2001) have been shown to have distinct diets, likely due to spatial differences in food availability.

The aim of this study was to define the diet of *R. taylori* across multiple environments and time scales using stable isotope analysis. Plasma and muscle $\delta^{13}C$ and $\delta^{15}N$ of *R. taylori* were compared with $\delta^{13}C$ and $\delta^{15}N$ baselines from multiple embayments to determine the isotopic niche, trophic position, and the benthic and pelagic contributions to *R. taylori* diet in each area and over time. This study will improve understanding how predators respond to variability in environmental conditions.

Methods

Field methods

Isotope samples were collected from five embayments on the northeast 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 once in austral summer (November–March) and once in austral winter (June–August). A combination of bottom-set (0.5–5.5 m depth) 400–800 m longlines and 200–400 m long, 11.45 cm mesh gillnets were used to capture *R. taylori*. 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. There were approximately 50–70 size 14/0 Mustad tuna circle hooks per longline, and they were baited with butterfly bream (*Nemipterus* sp.), squid (*Loligo* sp.), blue threadfin (*Eleutheronema tetradactylum*), and mullet (*Mugil cephalus*). Longlines and gillnets were set for 45 to 60 min. Individuals were sexed, tagged with a uniquely numbered rototag in the first dorsal fin, and measured to the nearest millimetre stretch total length (STL). Muscle and plasma were collected and individuals were released. Muscle (1 cm^3) was sampled from behind the first dorsal fin. Blood (2 mL) was collected using a heparinized needle and syringe from the caudal vein anterior to the tail. A portable centrifuge was used to spin and separate blood samples into plasma and red blood cell components. Red blood cells and plasma components were pipetted into separate 1.5 mL Eppendorf safe lock microcentrifuge tubes.

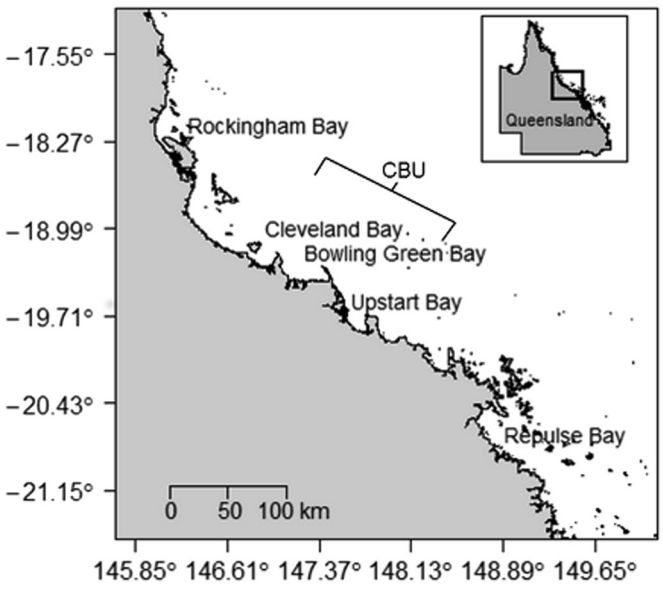


Fig. 1. Map of stable isotope sampling region indicating the five sampling locations and three designated feeding areas (Rockingham Bay, Cleveland Bay Unit (CBU), and Repulse Bay) for *Rhizoprionodon taylori*. Inset indicates location along the north Queensland coast.

There is evidence to suggest that juvenile stable isotopes values may incorporate maternal feeding patterns (Olin et al. 2011). However, previous work has shown that *Rhizoprionodon terraenovae*, a close relative of *R. taylori*, likely replaces the maternal isotope signature with its own dietary isotope signature by the time its umbilical scar has healed but is still visible (4 to 6 weeks; 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 no longer visible (Kinney et al. 2011). Although there is limited information available on how long it takes for umbilical scars to heal and are no longer visible, previous work indicates this process may take approximately 1 year (Duncan and Holland 2006; Olin et al. 2011).

Shark samples collected in CB were kept on ice in the field and frozen (–20 °C) upon return to the laboratory. Owing to their remote locations, samples collected from the other four bays were

kept on ice in the field and stored in a Taylor-Wharton CX100 Dry Shipper (–80 °C) until return to the laboratory where samples were frozen (–20 °C). Baseline benthic and pelagic $\delta^{13}C$ and $\delta^{15}N$ food web sources were collected from each embayment 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. Plankton was used to establish pelagic $\delta^{13}C$ and $\delta^{15}N$ food web sources and were sampled with horizontal surface tows with a 0.85 m long, 300 mm diameter plankton net (53 μm mesh). Plankton samples were collected approximately 5 km from shore from a central location in each bay. Plankton samples included phytoplankton, zooplankton, and small amounts of invertebrates. All plant and plankton material were kept on ice in the field and frozen upon return to the laboratory (–20 °C).

Sample preparation and isotope analysis

Shark tissue samples were freeze-dried, and a mortar and pestle was used to grind samples into a powder. Seagrass and macroalgae were thawed, rinsed in dH_2O, and cleaned of visible residue and epiphytes. 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) using a vacuum pump (300 mm Hg). Plankton samples were rinsed with dH_2O during filtration to remove any salt from the samples. 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 depleted in $\delta^{13}C$ in comparison with proteins and carbohydrates. The inclusion of lipids may result in unreliable data where differences in the lipid content between organisms and tissues produce more negative $\delta^{13}C$ (Post et al. 2007). Therefore, shark tissues and plankton samples underwent lipid extraction using a modified Bligh and Dyer (1959) method. Powdered samples were combined with 1.9 mL of 2:1 chloroform–methanol, 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. The 1.9 mL of 2:1 chloroform–methanol treatment was repeated followed by another round of agitating and centrifuging before the final decant. The tissue pellet that was produced was left in a fume hood to dry for 48 h. A separate urea extraction process was not carried out, as previous work has shown that the lipid extraction process also removes soluble urea (Hussey et al. 2012*b*). For $\delta^{13}C$ and $\delta^{15}N$ determination, 400–600 μg of dried shark muscle, 700–900 μg of dried plasma, 3000–4000 μg of dried plant material, and 4000–5000 μg of dried plankton were analysed using a continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, California, USA) equipped with an elemental analyser (Costech, Valenica, California, USA).

Stable isotope ratios were expressed in δ notation as deviations from standards in parts per thousand (‰) using the following calculation:

$$(1) \qquad \delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

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 every 12 samples to determine analytical precision. The analytical precision (standard deviation) for NIST standard 1577c (bovine liver, $n = 42$) and an internal laboratory standard (tilapia muscle, $n = 42$) for $\delta^{13}C$ was 0.07‰ and 0.11‰ and for $\delta^{15}N$ was 0.16‰ and 0.14‰, respectively.

Statistical analysis

Previous work using passive acoustic telemetry and stable isotopes analysis revealed female *R. taylori* captured in UP, BG, and CB likely move among these areas over the course of at least 1 year (Munroe et al. 2014*b*; Munroe et al., in review). Thus UP, BG, and CB presumably represent a single potential feeding area for *R. taylori* captured in any one of these bays. Previous analysis also indicated that female *R. taylori* captured in UP, BG, and CB were not likely to move to RE or RO within the time span of plasma and muscle tissue turnover. Therefore, to accurately represent the likely extent of dietary sources available to *R. taylori*, isotopic values of environmental baselines and *R. taylori* were grouped into three areas, RO, RE, and the Cleveland Bay Unit (CBU) that included UP, BG, and CB. These groupings were referred to as sampling or sample areas. Large-scale movement patterns could only be established for female *R. taylori*; therefore, males were excluded from analyses. *Rhizoprionodon taylori* plasma $\delta^{13}C$ and $\delta^{15}N$ turnover was estimated to take approximately 6 months, while muscle was estimated to take 1 year (Munroe et al., in review).

A Bayesian ANOVA (Gelman and Hill 2007) was used to access differences among sample areas in benthic and pelagic $\delta^{13}C$ and $\delta^{15}N$ baselines. The Bayesian ANOVA used noninformative priors and was calculated according to the following formulations:

The likelihood:

$$(2) \qquad y_{ij} \sim \text{Normal}(\mu + \alpha_i, \sigma^2)$$

The priors:

$$(3a) \qquad \mu \sim \text{Normal}(0, 10^{-6})$$

$$(3b) \qquad \alpha_i \sim \text{Normal}(0, 10^{-6})$$

where σ was the sample variance, μ was the mean response, and α was the effect due to sample area. Differences among locations were significant if the 95% credibility intervals of posterior draws did not overlap. A Bayesian ANOVA (Gelman and Hill 2007) was also used to test for differences among sample areas in $\delta^{13}C$ and $\delta^{15}N$ in muscle and plasma.

Individual trophic positions (TP) were calculated for each tissue in each sample area according to Post (2002) using a constant $\delta^{15}N$ diet tissue discrimination factor of 3.2:

$$(4) \qquad TP_{individual} = TP_{baseline} + \frac{\delta^{15}N_{individual} - \delta^{15}N_{baseline}}{3.2}$$

where $TP_{baseline}$ and $\delta^{15}N_{baseline}$ were the known TP and median $\delta^{15}N$ value, respectively, of environmental baselines (based on the results of Bayesian analysis). Seagrass $\delta^{15}N$ (TP 1) and plankton (TP 1.5) were calculated separately, and the range was combined. Plankton was given a TP of 1.5 because it was combination of phytoplankton and zooplankton.

Preliminary analysis showed the effect of size on $\delta^{13}C$ and $\delta^{15}N$ was highly variable among areas. For that reason, linear Bayesian regressions were used to determine if there was a relationship between muscle and plasma $\delta^{13}C$ and $\delta^{15}N$ and size for each sample area. Regression analysis used noninformative priors and was calculated according to the following formulations:

Likelihood:

$$(5) \qquad y_i \sim \text{Normal}(\mu + S_i, \sigma^2)$$

Priors:

$$(6a) \quad \mu \sim \text{Normal}(0, 10^{-6})$$

$$(6b) \quad S_i \sim \text{Normal}(0, 10^{-6})$$

where S was the effect due to *R. taylori* size. Relationships were considered significant when the probability of trends being less than or greater than 0 was ≥95%.

Rhizoprionodon taylori $\delta^{13}C$ and $\delta^{15}N$ values were used to calculate the isotopic niche for each tissue in each sample area. The isotopic niche was calculated using the package SIAR (Parnell and Jackson 2011) in R version 3.0.2 (R Development Core Team; http://www.r-project.org) as described by Jackson et al. (2011). This method uses Bayesian inference techniques to produce (*i*) the smallest convex hulls that contain all individual $\delta^{13}C$ and $\delta^{15}N$ values within a group (i.e., sample area) to represent total niche breadth area (Layman et al. 2007) and (*ii*) Bayesian standard ellipses (SEA_b) that incorporate the 40% densest data points within a dataset and thus better represents the "average" isotopic niche breadth of the population (Jackson et al. 2011). This method was chosen because a Bayesian framework for isotopic niche calculations better accounts for sources of uncertainly and variability inherent in stable isotope analysis and allows for more robust comparisons between groups, particularly for small and (or) variable sample sizes (Parnell et al. 2010).

Relative contributions of benthic and pelagic sources to *R. taylori* diet for each tissue in each sample area were calculated using a two-source Bayesian mixing model with the SIAR package in R version 3.0.2 (R Development Core Team; http://www.r-project.org) as described by Jackson et al. (2011). All other Bayesian models were fitted using the package R2jags (Su and Yajima 2014) in R version 3.0.2 (R Development Core Team; http://www.r-project.org) and JAGS version 3.4.0 (Plummer 2003). 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 assess each applied version of the models.

Results

Study site $\delta^{13}C$ and $\delta^{15}N$

Forty-seven pelagic and 55 benthic samples were collected from across the three sampling areas. The CBU had a considerably larger combined benthic and pelagic $\delta^{13}C$ range than RO and RE (Table 1). CBU also had a slightly larger range of $\delta^{15}N$ values. RO and RE had relatively similar baseline $\delta^{13}C$ and $\delta^{15}N$ ranges, although the RO $\delta^{13}C$ range was slightly larger than the RE $\delta^{13}C$ range.

Benthic samples had greater $\delta^{13}C$ values than pelagic samples in all areas (Fig. 2*a*). In contrast, pelagic samples were higher in $\delta^{15}N$ than benthic samples in all areas. In benthic baselines, CBU had significantly higher $\delta^{13}C$ than RO and RE. RE had significantly higher $\delta^{15}N$ than RO and CBU. Similar to benthic $\delta^{13}C$, CBU pelagic baselines had higher $\delta^{13}C$ than RO and RE; however, CBU $\delta^{13}C$ was only significantly higher than RO. RE had higher $\delta^{15}N$ than RO and CBU; however, RE $\delta^{15}N$ was only significantly higher than CBU. RO $\delta^{15}N$ values were also significantly higher than CBU $\delta^{15}N$ values.

Shark $\delta^{13}C$ and $\delta^{15}N$

From 2012 to 2013, 116 female *R. taylori* were sampled from across the three sample areas (Table 1); sizes ranged from 543 to 780 mm (mean ± SE = 681 ± 5.0 mm). *Rhizoprionodon taylori* $\delta^{13}C$ and $\delta^{15}N$ followed similar geographical patterns to environmental isotope baselines (Fig. 2*b*). Plasma and muscle $\delta^{13}C$ from female *R. taylori* captured in CBU was higher than the $\delta^{13}C$ values in RO and RE. Plasma and muscle $\delta^{15}N$ from *R. taylori* in RE and RO was higher than $\delta^{15}N$ in CBU.

The trophic position of *R. taylori* spanned more than one trophic level (~3.2‰) across all populations and indicated each population was composed of secondary and (or) tertiary consumers (Table 2). However, trophic position varied between locations and tissues. *Rhizoprionodon taylori* in RE had a lower range of TPs than *R. taylori* in RO and CBU. Muscle TPs were higher than plasma TPs in all three locations. The magnitude of decrease in TP from muscle to plasma was similar in each location.

Table 1. The $\delta^{13}C$ and $\delta^{15}N$ range of combined pelagic and benthic baselines from each sample area.

Location	$\delta^{13}C$ range	$\delta^{15}N$ range
RE	−23.28 to −15.15 (−19.9±2.5)	1.33 to 6.22 (5.5±1.4)
CBU	−20.54 to −8.44 (−15.9±3.9)	0.62 to 6.78 (3.4±1.7)
RO	−21.46 to −12.05 (−17.7±2.9)	2.94 to 7.26 (4.6±1.3)

Note: RE, Repulse Bay; CBU, Cleveland Bay Unit; and RO, Rockingham Bay.

Size influenced *R. taylori* $\delta^{13}C$; however, the effect was inconsistent. Muscle and plasma $\delta^{13}C$ from CBU and muscle $\delta^{13}C$ in RE had a significantly positive relationship with size (>95%), but there was no relationship between $\delta^{13}C$ and size in any other bay. There was no significant relationship between size and $\delta^{15}N$ in any location or tissue (<95%).

Isotopic niche breadth calculations for *R. taylori* varied between locations and tissues. Analysis of muscle $\delta^{13}C$ and $\delta^{15}N$ indicated the CBU population had a larger isotopic niche than RE and RO (Table 2; Fig. 3*a*). However, credibility intervals from posterior draws indicated that the population in CBU only had a significantly larger isotopic niche compared with RE (Fig. 3*c*). Analysis of plasma $\delta^{13}C$ and $\delta^{15}N$ revealed all three populations had similar niche breadth sizes, although CBU was still the largest (Table 2; Figs. 3*b*, 3*d*). Isotopic niche size remained relatively constant in CBU and RO between muscle and plasma, although there was a shift in isotopic niche space to lower $\delta^{15}N$ levels in plasma. In contrast, the niche breadth of *R. taylori* in RE substantially increased from muscle to plasma (Table 2). This large increase in RE niche breadth was primarily the result of an increase in the range of $\delta^{15}N$ of *R. taylori* captured in that area. However, *R. taylori* in RE also underwent a shift in niche space because of a decrease in absolute $\delta^{15}N$ values.

Pelagic and benthic contributions to *R. taylori* diet varied between locations (Fig. 4). In CBU, the mixing model showed that for both muscle and plasma, the diet was split equally between benthic and pelagic sources. In contrast, the diets of *R. taylori* in RE and RO were primarily composed of benthic sources. However, wide ranging credibility intervals from posterior draws of RE muscle and RO muscle and plasma mixing models suggest *R. taylori* in these areas likely still consume prey from pelagic food webs. The constrained credibility intervals of the RE plasma mixing model strongly indicated benthic prey were the primary dietary source in this area.

Discussion

Small-bodied, highly productive, moderately mobile predators such as *R. taylori* (Munroe et al., in review; Munroe et al. 2014*b*; Simpfendorfer 1993) represent an important link in marine food webs. Abundant, small-bodied sharks can connect habitats and environments through movement and serve as both a predator and prey item (Lundberg and Moberg 2003). Geographic and (or) temporal changes in the diet of species like *R. taylori* can provide valuable information on species ecological role in different marine communities, species vulnerability to environmental change, and indicate variation in environmental conditions throughout an area. Therefore, data on the diet of small-bodied species are critical to a better understanding of marine ecosystems.

Previous research has shown *R. taylori* select for nearshore seagrass habitat, potentially because this habitat is highly productive and abundant in suitable prey (Munroe et al. 2014*b*). As a result, it was expected that benthic or seagrass-based prey would represent a large component of *R. taylori* diet. Results have confirmed benthic sources are an important and in some areas a majority contributor to

Fig. 2. (*a*) Median $\delta^{13}C$ and $\delta^{15}N$ results of Bayesian ANOVA of benthic (solid symbols) and pelagic baselines (open symbols) in Repulse Bay (squares), the Cleveland Bay Unit (circles), and Rockingham Bay (triangles). (*b*) Median $\delta^{13}C$ and $\delta^{15}N$ results of Bayesian ANOVA of *Rhizoprionodon taylori* for muscle (solid symbols) and plasma (open symbols) in Repulse Bay (squares), the Cleveland Bay Unit (circles), and Rockingham Bay (triangles). Black lines show 95% credibility intervals of posterior draws.

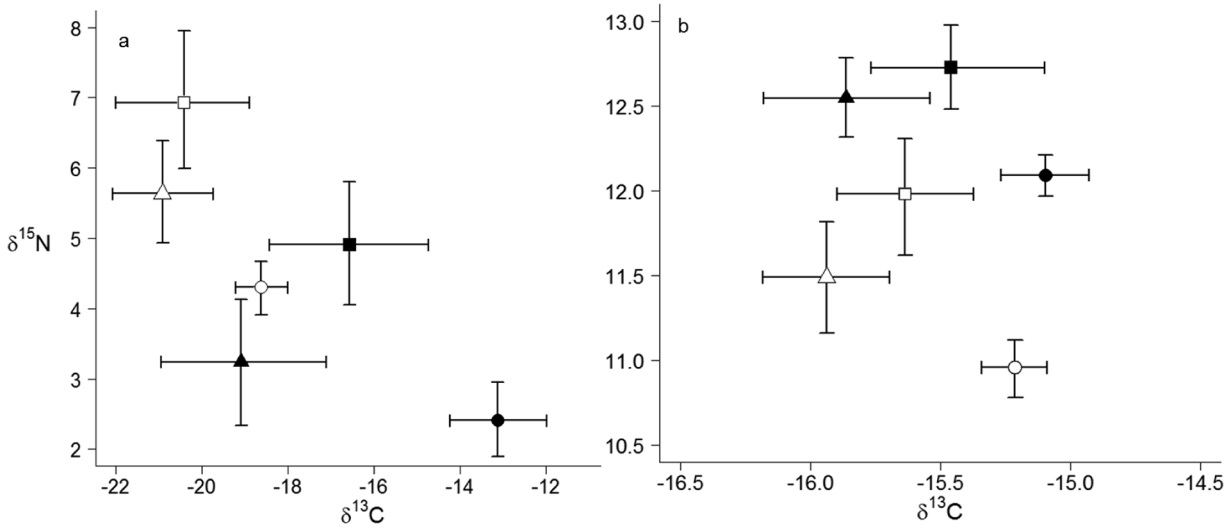


Table 2. Total catch (number of sharks), $\delta^{13}C$ and $\delta^{15}N$ range, trophic position (TP) range and mean with standard error (SE), convex hull area, and median.

Sample area	Total catch	Tissue	$\delta^{13}C$ range	$\delta^{15}N$ range	TP range	Mean TP ±SE	Convex hull area	Median SEA_b
RE	20	Muscle	−16.6 to −14.5	11.94 to 13.39	3.2 to 4.1	3.7±0.04	1.35	0.864
		Plasma	−16.7 to −14.7	10.19 to 12.66	2.7 to 3.9	3.5±0.05	2.84	1.34
CBU	76	Muscle	−18.1 to −13.3	10.57 to 13.35	3.6 to 4.9	4.3±0.02	9.16	1.67
		Plasma	−16.5 to −13.7	8.33 to 12.34	2.9 to 4.6	3.9±0.03	6.84	1.51
RO	20	Muscle	−17.0 to −14.5	11.64 to 13.76	3.6 to 4.8	4.2±0.05	3.26	1.19
		Plasma	−16.8 to −14.5	9.92 to 12.52	3.1 to 4.4	3.8±0.05	2.58	1.16

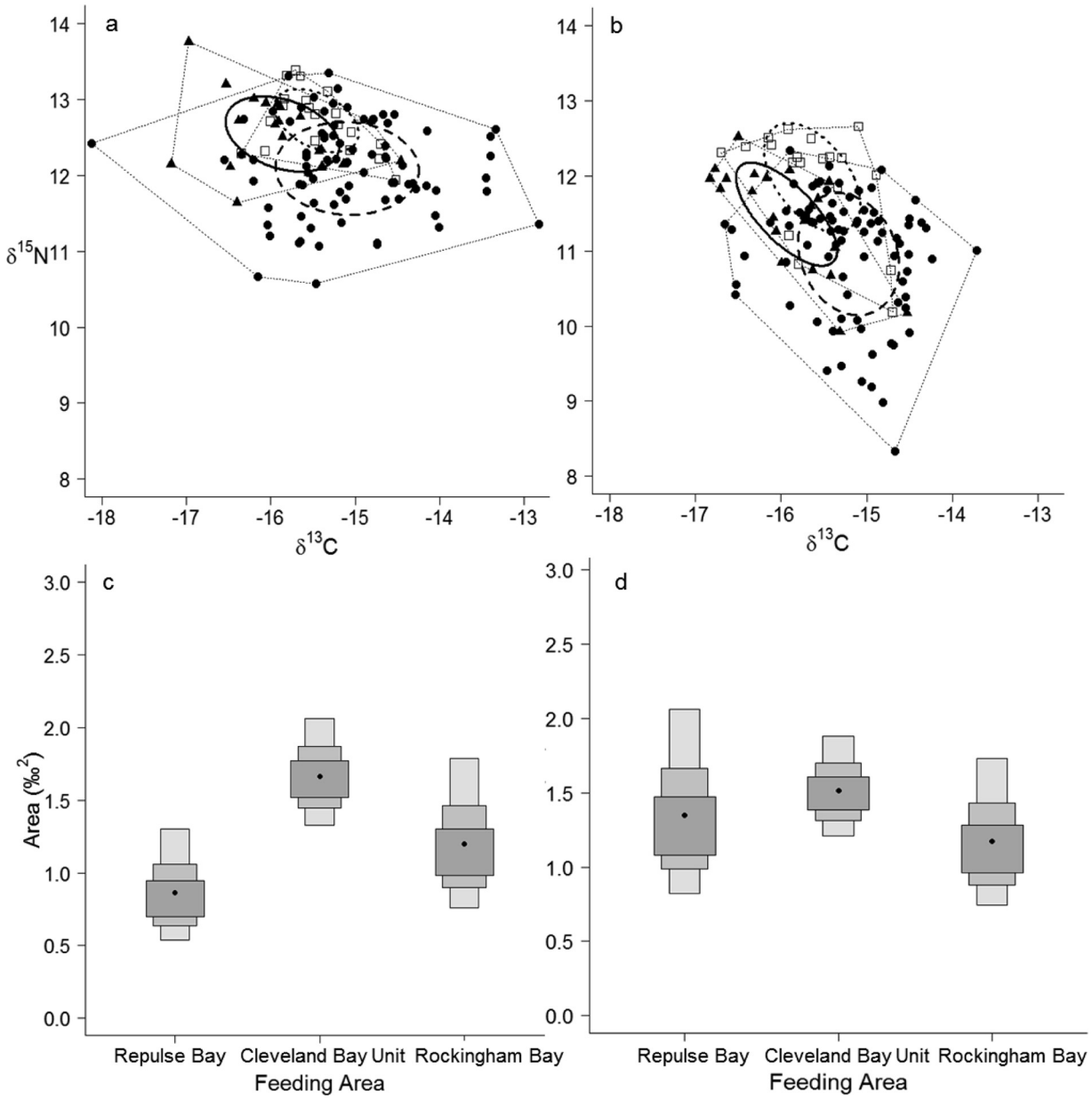
Note: Bayesian standard ellipses (SEA_b) area (‰^{2}) of female *Rhizoprionodon taylori* is based on $\delta^{15}N$ (diet tissue discrimination factor = 3.2) for each tissue in each sample area. RE, Repulse Bay; CBU, Cleveland Bay Unit; and RO, Rockingham Bay.

R. taylori diet; however, it is also clear that *R. taylori* consume prey from pelagic sources. The wide range of trophic positions of *R. taylori* in each area also suggests this species consumes a variety of prey. These findings are consistent with *R. taylori* stomach content analysis that indicated individuals fed on a variety of prey types, including teleosts, crustaceans, and cephalopods (Simpfendorfer 1998). Stomach content analysis also concluded that approximately half of *R. taylori* diet in CB was composed of dermersal prey, while the other half included pelagic prey types (Simpfendorfer 1998). Demersal and pelagic prey types do not necessarily stem from benthic and pelagic carbon sources, respectively, but the presence of both prey types in *R. taylori* stomachs supports the conclusions of this study. An even division of prey types in *R. taylori* diet in CB is also consistent with mixing model results within the CBU, supporting the accuracy of these results. Therefore, although this analysis is not a direct measure of population specialization (Munroe et al. 2014*a*), the results presented here indicate *R. taylori* has a broad dietary niche and is likely best defined as a mesopredator with a low degree of dietary specialization, at least at a population level (Matich et al. 2010).

Results indicated that *R. taylori* $\delta^{15}N$ did not change with size. This contrasts with other elasmobranchs, such as the sandbar shark (*Carcharhinus plumbeus*) (Shiffman et al. 2014) and the blacktip reef shark (*Carcharhinus melanopterus*) (Speed et al. 2011), where $\delta^{15}N$ has been shown to significantly increase with size. Changes in $\delta^{15}N$ with body size are often attributed to increases in gape and hunting experience. As sharks grow, they are able to capture larger prey at higher trophic levels. The results in this study suggest that there is limited change in diet with growth, indicating that regardless of size, individual *R. taylori* feed at similar trophic levels. However, previous studies that found changes in $\delta^{15}N$ with size investigated change between more distinct age classes. The comparatively limited change in total length exhibited by *R. taylori* once they reach maturity (Simpfendorfer 1992) may explain why $\delta^{15}N$ and body size were not correlated.

The broad dietary niche and trophic position exhibited by *R. taylori* collectively across all sampling regions is similar to other species within this genera, such as the Atlantic sharpnose shark (*Rhizoprionodon terrenovea*) (Gelsleichter et al. 1999; Bethea et al. 2006), the Brazilian sharpnose shark (*Rhizoprionodon lalandii*) (Bornatowski et al. 2012), and the milk shark (*Rhizoprionodon acutus*) (Ba et al. 2013). Previous isotope analysis of elasmobranchs and teleosts in CB also found that *R. taylori* had similar carbon ranges as similarly sized generalist predators, specifically the hardnose shark (*Carcharhinus macloti*), the milk shark (*R. acutus*), and the barramundi (*Lates calcarifer*) (Kinney et al. 2011). These results suggest that *R. taylori* in CB likely consumed similar carbon sources as other local generalist mesopredators. The niche breadth of *R. taylori* is also comparable to other small-bodied mesopredators in distant locations. The isotopic niche breadth of the generalist mesopredator the southern stingray (*Dasyatis americana*) was similar to the niche breadth of *R. taylori* in the CBU (Tilley et al. 2013). As generalists, these small-bodied species are likely important maintainers of ecosystem function and biodiversity (Richmond et al. 2005). *Rhizoprionodon taylori* likely influences the population size and structure of numerous nearshore species in both benthic and pelagic food webs.

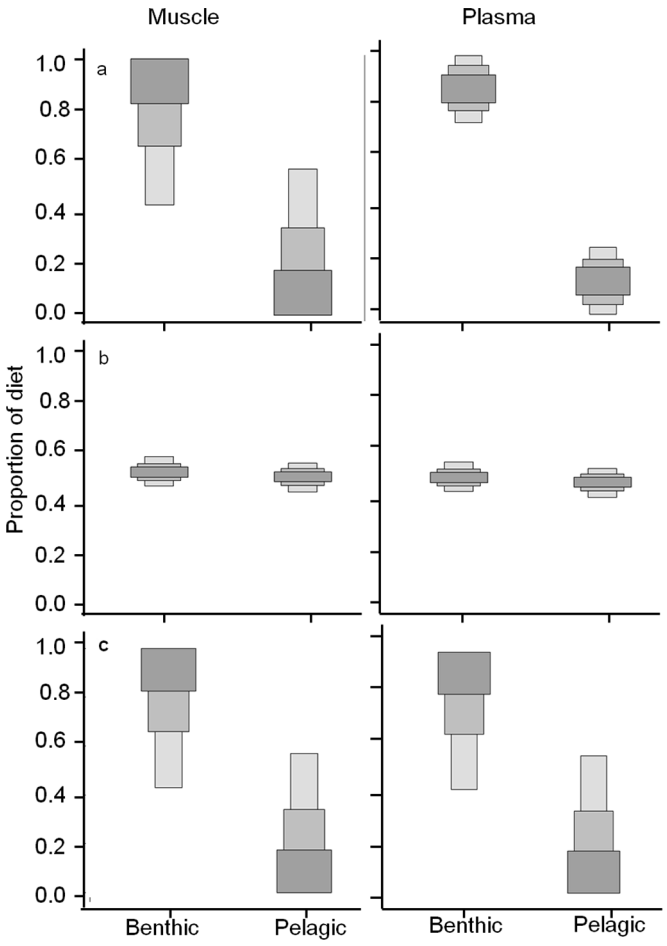
Fig. 3. Isotopic niche breadth of *Rhizoprionodon taylori*. Convex hulls of total niche width of muscle (*a*) and plasma (*b*) are dotted lines. Bayesian standard ellipses (SEA_b) showing isotope niches are shown for Repulse Bay (squares, dotted line), Cleveland Bay Unit (circles, dashed line), and Rockingham Bay (triangles, solid line). SEA_b area calculations are also given as 50, 75, and 95 credibility intervals (dark to light grey, respectively) of posterior draws for muscle (*c*) and plasma (*d*); black dots indicate median values.



The structural influence of *R. taylori*, however, probably differs based on location, as there was considerable geographic variation in source contribution to diet and niche breadth. Geographic variation in diet has been documented in a number of shark species, including the bonnethead shark (*Sphyrna tiburo*) (Bethea et al. 2007), *R. terraenovae* (Drymon et al. 2012), the narrownose smoothhound (*Mustelus schmitti*) (Belleggia et al. 2012), the lemon shark (*Negaprion brevirostris*) (Cortés and Gruber 1990), *C. plumbeus* (McElroy et al. 2006), and the starspotted dogfish (*Mustelus manazo*) (Yamaguchi and Taniuchi 2000). A common inference among these studies is that geographic variation in diet is the result of geographic variation in prey availability and the opportunistic feeding strategies of the predators. As generalists, *R. taylori* consume a wide range of species and will most likely consume prey that is highly abundant or most beneficial in each area (Mittelbach et al. 1992; Salini et al. 1992; Simpfendorfer et al. 2001; Reeve et al. 2009). As a result, the diet of female *R. taylori* will likely fluctuate based on changes in local prey availability. Therefore, it is probable that benthic prey in RE and RO were more abundant or easily accessible. It is also possible benthic prey are a better source of energy in RE and RO than in the CBU, and *R. taylori* may actually be adopting selective strategies. Not all prey found in *R. taylori* stomachs in CB were consumed in equal proportions to local abundance (Simpfendorfer 1998). Therefore, either situation could explain why female *R. taylori* consumed a larger proportion of benthic prey in RE and RO.

The geographic variation in isotope niche breadth may be due to differences in source contributions to diet between locations. The less specialized diet of *R. taylori* in the CBU could result in a larger isotopic niche. However, the CBU also had the largest range in baseline $\delta^{13}C$ and $\delta^{15}N$ values. If *R. taylori* were opportunistic and (or) generalist predators, presumably the isotopic niche of *R. taylori* would increase as the range in baseline $\delta^{13}C$ and

Fig. 4. Proportional contributions of benthic and pelagic food web sources to *Rhizoprionodon taylori* diet using a two-source Bayesian mixing model for plasma and muscle tissue in (*a*) Repulse Bay, (*b*) Cleveland Bay Unit, and (*c*) Rockingham Bay. Shaded boxes are 50, 75, and 95 (from dark to light grey, respectively) credibility intervals of posterior draws of SEA_b.



$\delta^{15}N$ values also increased. Therefore, while variation in niche breadth size between locations may be the result of differences in selection and sources contributions, it may also be due to the relative range of $\delta^{13}C$ and $\delta^{15}N$ values of local sources.

There was also geographic variation in female *R. taylori* $\delta^{15}N$ and to a lesser extent trophic position. Much of this variability is likely due to variability in $\delta^{15}N$ at the base of the food chain, as shark tissues exhibited similar geographic trends in $\delta^{15}N$ as environmental baselines. The higher $\delta^{15}N$ in RE and RO may have been because these bays are adjacent to large expanses of sugarcane farms and thus exposed to high levels of nitrogen runoff (Munroe et al., in review). However, trophic position calculations, which accounted for variation in $\delta^{15}N$ baselines, found *R. taylori* in RE were consuming prey at lower trophic positions than in other areas. This could indicate there was a lower abundance of higher trophic level prey in RE compared with RO and CBU. It is also possible that lower trophic level prey were abundant or beneficial in RE and thus form a larger component of local diet. The fact that *R. taylori* in RO and RE consumed similarly large proportions of benthic food web sources but had a different range of trophic positions suggests that specific prey composition of *R. taylori* diet may vary among areas. Overall, the differences in diet among locations suggest prey availability likely varies among locations and that *R. taylori* may have different effects on prey structure in each area. For example, female *R. taylori* in RE and RO may have a lesser influence on pelagic food web sources than those in the CBU.

Comparisons between muscle and plasma suggested limited temporal variation in *R. taylori* diet. The trophic position of *R. taylori* decreased in all three sample areas from muscle to plasma, suggesting a region-wide change in prey availability over time. Previous work has shown that decreases in $\delta^{15}N$ in elasmobranchs is often associated with decreased amounts of teleost consumption (Domi et al. 2005; MacNeil et al. 2005). Teleosts generally have higher $\delta^{15}N$ values and trophic levels. Therefore, it is possible a recent decrease in teleosts at high trophic levels in all areas would have forced female *R. taylori* to consume more prey at lower trophic levels than in previous years. It is also possible that lower order prey became highly abundant and thus formed a larger component of the diet.

Despite changes in trophic level, the relative contributions of benthic and pelagic sources to *R. taylori* diet were consistent over time in all areas. Niche breadth size in RO and CBU was also consistent, while niche breadth in RE increased from muscle to plasma. Collectively, these results suggest that *R. taylori* in all three sample areas recently consumed prey at lower trophic levels, but maintained a large niche breadth that incorporated both food webs over approximately 1 year. The unique increase in niche breadth in RE could be energetic compensation for the decline in higher trophic prey or some other preferred prey. It is also possible that previously unavailable prey types became available relatively recently in the RE area, resulting in niche expansion. Although the direct cause(s) of changes in *R. taylori* diet are difficult to determine without more detail on local prey availability, the occurrence of temporal and spatial variability in diet indicates *R. taylori* are probably highly adaptive consumers. Female *R. taylori* are likely capable of adjusting their hunting strategies to local conditions and fluctuations in prey availability.

Results of this study indicate that *R. taylori* are dietary generalists capable of opportunistic and possibly selective strategies. Therefore, the effect of *R. taylori* on nearshore food webs may change based on local environmental conditions and prey availability. Given individuals likely remain within a 100 km range of their capture location for at least a year (Munroe et al., in review), spatial and temporal variation in *R. taylori* diet may not only indicate differences in local prey biodiversity, but also that this species probably has unique effects on distinct local ecosystems. For that reason, this study emphasises the importance of examining dietary patterns of species over multiple areas and time scales. The results from this work also suggest that female *R. taylori* are likely adaptive to changes in prey availability. Consequently, *R. taylori* may be less vulnerable to declines in prey availability of a particular species (McKinney 1997; Colles et al. 2009; Terraube et al. 2011; Curtis et al. 2013). *Rhizoprionodon taylori* may compensate for declines in specific prey species by expanding or shifting their dietary niche and consuming other prey that remain available. As habitat (Munroe et al. 2014*b*) and dietary generalists, *R. taylori* is probably resilient to environmental change, particularly at a local level.

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