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

Samantha E.M. Munroe [a,b], Michelle R. Heupel [b,c], Aaron T. Fisk[d], and Colin A. Simpfendorfer [b]

[a] AIMS@JCU, Australian Institute of Marine Science and College of Marine and Environmental Sciences, James Cook University, Townsville, Qld 4811, Australia (SEM Munroe, samantha.munroe@my.jcu.edu.au, (Phone) +61 7 47814158)

[b] Centre for Sustainable Tropical Fisheries and Aquaculture, and College of Marine and Environmental Sciences, James Cook University, Townsville, Qld 4811, Australia (CA Simpfendorfer, colin.simpfendorfer@jcu.edu.au)

[c] Australian Institute of Marine Science Townsville, Qld 4810, Australia (MR Heupel, michelle.heupel@jcu.edu.au)

[d] Great Lakes Institute for Environmental Research, Department of Earth and Environmental Sciences, University of Windsor, Windsor, ON N9B 3P4, Canada (AT Fisk, afisk@uwindsor.ca)

*Corresponding author S.E.M Munroe

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 to $\delta^{13}C$ and $\delta^{15}N$ baselines from multiple embayments to determine the isotopic niche, trophic position, and benthic and pelagic contribution 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.

Key words: Australian sharpnose shark, Bayesian analysis, diet, niche, selection, stable isotope analysis, trophic position

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 & 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 maximise 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 specialised predators may experience severely reduced foraging efficiency when preferred prey populations have decreased (Terraube et al. 2011; Munroe et al. 2014a). As a result, diet specialists may experience a decrease in growth, reproduction, and population size (Suarez & 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. 2012a). The two most commonly used isotopes are $\delta^{13}C$ 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 & Fry 1987; Boutton 1991). Therefore tissue $\delta^{13}C$ can be used to determine the dietary carbon source of a consumer (DeNiro & Epstein 1978; Peterson & Fry 1987). In contrast, $\delta^{15}N$ increases from prey to predator (Deniro & Epstein 1981; Peterson & 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 specialisation 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 & 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, non-lethal alternative (Hammerschalg 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; Simpfendorfer 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. 2014b). 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 one 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; Herbet et al. 1999), 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 to $\delta^{13}C$ and $\delta^{15}N$ baselines from multiple embayments to determine the isotopic niche, trophic position, and the benthic and pelagic contribution to *R. taylori* diet in each area and over time. This study will improve understanding of how predators respond to variability in environmental conditions.

111 # Methods:

112 ## Field Methods

113 Isotope samples were collected from five embayments on the northeast coast of Queensland,
114 Australia between July 2012 and April 2013. The five bays (from south to north) were Repulse
115 Bay (RE), Upstart Bay (UP), Bowling Green Bay (BG), Cleveland Bay (CB), and Rockingham
116 Bay (RO) (Fig. 1). Linear distances between adjacent bays ranged from 30 to 150 km. Each
117 bay was sampled once in austral summer (November-March) and once in austral winter (June -
118 August). A combination of bottom-set (0.5-5.5 m depth) 400-800 m long-lines and 200-400 m
119 long, 11.45 cm mesh gillnets were used to capture *R. taylori*. Long-lines were constructed of 6-
120 mm nylon mainline that was anchored at both ends. Gangions were composed of 1 m of 4-mm
121 nylon cord and 1 m of 1.5-mm wire leader. There were approximately 50-70 size 14/0 Mustad
122 tuna circle hooks per long-line and they were baited with butterfly bream (*Nemipterus sp.*),
123 squid (*Loligo sp.*), blue threadfin (*Eleutheronema tetradactylum*) and mullet (*Mugil cephalus*).
124 Long-lines and gillnets were set for 45 to 60 minutes. Individuals were sexed, tagged with a
125 uniquely numbered rototag in the first dorsal fin, and measured to the nearest millimeter stretch
126 total length (STL). Muscle and plasma were collected and individuals were released. One cm^3
127 of muscle was sampled from behind the first dorsal fin. Two ml of blood was collected using a
128 heparinised needle and syringe from the caudal vein anterior to the tail. A portable centrifuge
129 was used to spin and separate blood samples into plasma and red blood cell components. Red
130 blood cells and plasma components were pipetted into separate 1.5 ml Eppendorf safe lock
131 microcentrifuge tubes.

132

133 There is evidence to suggest that juvenile stable isotopes values may incorporate maternal
134 feeding patterns (Olin et al. 2011).However, previous work has shown that *R. 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 be visible, previous work indicates this process may take approximately one year (Duncan and Holland 2006; Olin et al. 2011).

.

Shark samples collected in Cleveland Bay were kept on ice in the field and frozen (-20^{o}C) upon return to the laboratory. Due to their remote locations samples collected from the other four bays were kept on ice in the field, stored in a Taylor-Wharton CX100 Dry Shipper (-80 ^{o}C) until return to the laboratory where samples were frozen (-20^{o}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 micron 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^{o}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_20, and cleaned of visible

159 residue and epiphytes. Seagrass and macroalgea were oven dried at 60 ^{o}C for 48 hours and
160 ground into a powder. Plankton samples were filtered through GF/F Whatman glass micro-
161 fibre filters (0.7 µm pore size) using a vacuum pump (300 mm Hg). Plankton samples were
162 rinsed with dH_20 during filtration to remove any salt from the samples. Large detritus were
163 removed from the filters. Filters were oven dried at 60 ^{o}C for 24 hours and stored in petri
164 dishes prior to analysis.

165

166 Lipids in animal tissues are depleted in $\delta^{13}C$ in comparison to proteins and carbohydrates. The
167 inclusion of lipids may result in unreliable data where differences in the lipid content between
168 organisms and tissues produce more negative $\delta^{13}C$ (Post et al. 2007). Therefore, shark tissues
169 and plankton samples underwent lipid extraction using a modified Bligh & Dyer (1959)
170 method. Powdered samples were combined with 1.9 ml of 2:1 chloroform-methanol, agitated
171 for 10 seconds and put in a water bath (30° C) for 24 hours. Lipid extracted samples were
172 removed from the bath, centrifuged for three minutes, and decanted. The 1.9 ml of 2:1
173 chloroform-methanol treatment was repeated followed by another round of agitating and
174 centrifuging before the final decant. The tissue pellet that was produced was left in a fume
175 hood to dry for 48 hours. A separate urea extraction process was not carried out as previous
176 work has shown that the lipid extraction process also removes soluble urea (Hussey et al.
177 2012b). For $\delta^{13}C$ and $\delta^{15}N$ determination, 400-600 µg of dried shark muscle, 700-900 µg of
178 dried plasma, 3000-4000 µg of dried plant material, and 4000-5000 µg of dried plankton were
179 analysed using a continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT
180 Delta^{plus}, Thermo Finnigan, San Jose, CA, USA) equipped with an elemental analyser
181 (Costech, Valenica, CA, USA).

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

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

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 $\delta^{15}N$ 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 between these areas over the course of at least one year (Munroe et al. 2014b; 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 one year (Munroe et al. in review).

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

The Likelihood

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

The Priors

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

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

Where σ was the sample variance, μ was the mean response, and α was the effect due to sample area. Differences between locations were significant if the 95% credibility intervals of posterior draws did not overlap. A Bayesian ANOVA (Gelman 2007) was also used to test for differences between 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) $$TP_{individual} = TP_{baseline} + \frac{\delta 15\mathrm{N}_{indvidual} - \delta 15\mathrm{N}_{baseline}}{3.2}$$

Where $TP_{baseline}$ and $\delta 15N_{baseline}$ were the known TP and median $\delta^{15}N$ value 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 between 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 non-informative priors and was calculated according to the formulations:

Likelihood

(5) $$y_i \sim Normal(\mu + S_i, \sigma^2)$$

Priors

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

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

Where *S* was the effect due to *R. taylori* size. Relationships were considered significant when the probability of trends being < or > 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

et al. 2010) in R version 3.0.2 (R Development Core Team, 2013) as described by Jackson et al. (2011). This method uses Bayesian inference techniques to produce (1) 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 breath area (Layman et al. 2007), and (2) Bayesian standard ellipses (SEA_b) which 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 was calculated using a two source Bayesian mixing model with the *SIAR* package in R version 3.0.2 (R Development Core Team, 2013) 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: www.r-project.org) and JAGS, version 3.4.0 (Plummer 2003). Posterior draws were built using three Markov chains with 10000 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 Cleveland Bay Unit had a considerably larger combined benthic and pelagic $\delta^{13}C$ range than RO and RE (Table 1). Cleveland Bay Unit 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. 2a). 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. Repulse Bay 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. Repulse Bay had higher $\delta^{15}N$ than RO and CBU, however, RE $\delta^{15}N$ was only significantly higher than CBU. Rockingham Bay $\delta^{15}N$ 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). *Rhizoprionodon taylori* $\delta^{13}C$ and $\delta^{15}N$ followed similar geographical patterns to environmental isotope baselines (Fig. 2b). 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.

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. 3a). However, credibility intervals from posterior draws indicated that the population in CBU only had a significantly larger isotopic niche compared to RE (Fig. 3c). 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; Fig. 3b,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 due to 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; 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. 2014b).

337 As a result, it was expected that benthic or seagrass-based prey would represent a large
338 component of *R. taylori* diet. Results have confirmed benthic sources are a significant and in
339 some areas a majority contributor to *R. taylori* diet, however, it is also clear that *R. taylori*
340 consume prey from pelagic sources. The wide range of trophic positions of *R. taylori* in each
341 area also suggests this species consumes a variety of prey. These findings are consistent with
342 *R. taylori* stomach content analysis that indicated individuals fed on a variety of prey types,
343 including teleosts, crustaceans and cephalopods (Simpfendorfer 1998). Stomach content
344 analysis also concluded that approximately half of *R. taylori* diet in Cleveland Bay was
345 composed of dermersal prey, while the other half included pelagic prey types (Simpfendorfer
346 1998). Demersal and pelagic prey types do not necessarily stem from benthic and pelagic
347 carbon sources respectively, but the presence of both prey types in *R. taylori* stomachs
348 supports the conclusions of this study. An even division of prey types in *R. taylori* diet in
349 Cleveland Bay is also consistent with mixing model results within the CBU, supporting the
350 accuracy of these results. Therefore, although the analysis present in this chapter is not a direct
351 measure population specialisation (Munroe et al. 2014a), the results presented here indicate *R.*
352 *taylori* has a broad dietary niche and is likely best defined as a mesopredator with a low degree
353 of dietary specialisation, at least at a population level (Matich et al. 2010).

354

355 Results indicated that *R. taylori* $\delta^{15}N$ did not change with size. This contrasts with other
356 elasmobranchs, such as the sandbar shark *Carcharhinus plumbeus* (Shiffman et al. 2014) and
357 the blacktip reef shark *Carcharhinus melanopterus* (Speed et al. 2011), where $\delta^{15}N$ has been
358 shown to significantly increase with size. Changes in $\delta^{15}N$ with body size are often attributed
359 to increases in gape and hunting experience. As sharks grow, they are able to capture larger
360 prey at higher trophic levels. The results in this study suggest that there is limited change in
361 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* (White 2004). Previous isotope analysis of elasmobranchs and teleosts in Cleveland Bay 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 Cleveland Bay 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.

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

386 variation in diet has been documented in a number of shark species, including the bonnethead
387 shark, *Sphyrna tiburo* (Bethea et al. 2007), *R. terraenovae* (Drymon et al. 2012), the
388 narrownose smooth-hound, *Mustelus schmitti,* (Belleggia et al. 2012), the lemon shark,
389 *Negaprion brevirostris* (Cortés & Gruber 1990), *C. plumbeus* (McElroy et al. 2006), and the
390 starrspotted-dogfish, *Mustelus manazo* (Yamaguchi & Taniuchi 2000). A common inference
391 among these studies is that geographic variation in diet is the result of geographic variation in
392 prey availability and the opportunistic feeding strategies of the predators. As generalists, *R.*
393 *taylori* consume a wide range of species and will most likely consume prey that is highly
394 abundant or most beneficial in each area (Mittelbach et al. 1992; Salini et al. 1992;
395 Simpfendorfer et al. 2001; Reeve et al. 2009). As a result, the diet of female *R. taylori* will
396 likely fluctuate based on changes in local prey availability. Therefore, it is probable that
397 benthic prey in RE and RO were more abundant or easily accessible. It is also possible benthic
398 prey are a better source of energy in RE and RO than in the CBU and *R. taylori* may actually
399 be adopting selective strategies. Not all prey found in *R. taylori* stomachs in CB were
400 consumed in equal proportions to local abundance (Simpfendorfer 1998). Therefore either
401 situation could explain why female *R. taylori* consumed a larger proportion of benthic prey in
402 RE and RO.

403

404 The geographic variation in isotope niche breadth may be due to differences in source
405 contributions to diet between locations. The less specialised diet of *R. taylori* in the CBU could
406 result in a larger isotopic niche. However, the CBU also had the largest range in baseline $\delta^{13}C$
407 and $\delta^{15}N$ values. If *R. taylori* were opportunistic and/or generalist predators, presumably the
408 isotopic niche of *R. taylori* would increase as the range in baseline $\delta^{13}C$ and $\delta^{15}N$ values also
409 increased. Therefore, while variation in niche breadth size between locations may be the result

410 of differences in selection and sources contributions, it may also be due to the relative range of
411 $\delta^{13}C$ and $\delta^{15}N$ values of local sources.

412

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

429

430 Comparisons between muscle and plasma suggested limited temporal variation in *R. taylori*
431 diet. The trophic position of *R. taylori* decreased in all three sample areas from muscle to
432 plasma, suggesting a region-wide change in prey availability over time. Previous work has
433 shown that decreases in $\delta^{15}N$ in elasmobranchs is often associated with decreased amounts of

434 teleost consumption (Domi et al. 2005; MacNeil et al. 2005). Teleosts generally have higher
435 $\delta^{15}N$ values and trophic levels. Therefore, it is possible a recent decrease in teleosts at high
436 trophic levels in all areas would have forced female *R. taylori* to consume more prey at lower
437 trophic levels than in previous years. It is also possible that lower order prey became highly
438 abundant and thus formed a larger component of the diet.

439

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

453

454 Results of this study indicate that *R. taylori* are dietary generalists' capable of opportunistic
455 and possibly selective strategies. Therefore, the effect of *R. taylori* on nearshore food webs
456 may change based on local environmental conditions and prey availability. Given individuals
457 likely remain within a 100 km range of their capture location for at least a year (Munroe et al.

458 in review), spatial and temporal variation in *R. taylori* diet may not only indicate differences in
459 local prey biodiversity, but also that this species probably has unique effects on distinct local
460 ecosystems. For that reason, this study emphasises the importance of examining dietary
461 patterns of species over multiple areas and time scales. The results from this work also suggest
462 that female *R. taylori* are likely adaptive to changes in prey availability. Consequently, *R.*
463 *taylori* may be less vulnerable to declines in prey availability of a particular species
464 (McKinney 1997; Colles et al. 2009; Terraube et al. 2011; Curtis et al. 2013). *Rhizoprionodon*
465 *taylori* may compensate for declines in specific prey species by expanding or shifting their
466 dietary niche and consuming other prey that remain available. As habitat (Munroe et al. 2014b)
467 and dietary generalists, *R. taylori* is probably resilient to environmental change, particularly at
468 a local level.

469

470 Acknowledgements

471 The authors of this paper would like to thank the staff and students at the JCU Centre for
472 Sustainable Tropical Fisheries and Aquaculture, including P Yates, S Moore, M Green, L
473 Meyer, D Waltrick, J Smart and many other volunteers for their support of this project; staff
474 and students at the Great Lakes Institute for Environmental Research including A Hussey, N
475 Hussey, B Charron and S Kessel for assistance with sample analysis; and J Elliman at the JCU
476 School of Veterinary and Biomedical Sciences for assistance in preparing tissues. Financial
477 support came from the Australian Government's National Environmental Research Program
478 awarded to MRH and CAS and an International Postgraduate Research Scholarship and
479 AIMS@JCU scholarship supported SEMM. Additional support was provided by James Cook
480 University, the School of Earth and Environmental Science, the Great Barrier Reef Marine
481 Park Authority under the Science for Management Award scheme, and the Joyce Vickery

482 Scientific Research Fund administered by the Linnean Society of New South Wales. All
483 research was conducted in accordance with JCU animal ethics permit A1566 and Great Barrier
484 Reef (G11/346181.1) and DEEDI (144482) permits for animal collection.

485

References

Banks, J., Lea, M-A. Wall, S., McMahon C.R., and Hindell, M.A. 2014. Combining bio-logging and fatty acid signature analysis indicates spatio-temporal variation in the diet of the southern elephant seal, *Mirounga leonina.* J. Exp. Mar. Biol. Ecol. **450**:79-90

Belleggia, M., Figueroa, D., Sánchez, F., and Bremec, C. 2012. The feeding ecology of *Mustelus schmitti* in the southwestern Atlantic: geographic variations and dietary shifts. Environ. Biol. Fishes **95**:99-114.

Ben-David, M., Flynn, R.W., and Schell, D.M. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. Oecologia **111**:280-291.

Bethea, D., Hale, L., Carlson, J., Cortés, E., Manire, C., and Gelsleichter, J. 2007. Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, *Sphyrna tiburo*, from the eastern Gulf of Mexico. Mar. Biol. **152**:1009-1020.

Bethea, D.M., Carlson, J.K., Buckel, J.A., and Satterwhite, M. 2006. Ontogenetic and site-related trends in the diet of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* from the northeast Gulf of Mexico. Bull. Mar. Sci. **78**:287-307.

Bligh, E.G., and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. Can. J. Physiol. Pharmacol. **37**:911-917.

Bornatowski, H., Heithaus, M.R., Abilhoa, V., and Corrêa, M.F.M. 2012. Feeding of the Brazilian sharpnose shark *Rhizoprionodon lalandii* (Müller & Henle, 1839) from southern Brazil. J. Appl. Ichthyol. **28**:623-627.

Boutton, T. 1991. Stable carbon isotope ratios of natural materials: II. Atmospheric, terrestrial, marine, and freshwater environments. Acadmeic Press, Inc, San Diego.

510 Colles, A., Liow, L.H., and Prinzing, A. 2009. Are specialists at risk under environmental
511 change? Neoecological, paleoecological and phylogenetic approaches. Ecol. Lett.
512 **12**:849-863.
513 Cortés, E., and Gruber, S.H. 1990. Diet, feeding habits and estimates of daily ration of young
514 lemon Sharks, *Negaprion brevirostris* (Poey). Copeia **1990**:204-218.
515 Curtis, T.H., Parkyn, D.C., and Burgess, G.H. 2013. Use of human-altered habitats by bull
516 sharks in a Florida nursery area. Mar Coast Fish **5**:28-38.
517 DeNiro M.J., Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in
518 animals. Geochimica et Cosmochimica Acta **42**:495-506
519 Deniro, M.J., and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes
520 in animals. Geochim. Cosmochim. Acta. **45**:341-351.
521 Domi, N., Bouquegneau, J.M., and Das, K. 2005. Feeding ecology of five commercial shark
522 species of the Cletic Sea through stable isotope and trace metal analysis. Mar.
523 Environ. Res. **60**: 551-569.
524 Duncan, K.M., and Holland K.N. 2006. Habitat use, growth rates, and dispersal patterns of
525 juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in a nursery habitat. Mar.
526 Ecol. Prog. Ser. **312**:211-221.
527 Drymon, J.M., Powers, S., and Carmichael, R. 2012. Trophic plasticity in the Atlantic
528 sharpnose shark (*Rhizoprionodon terraenovae*) from the north central Gulf of Mexico.
529 Environ. Biol. Fishes. **95**:21-35.
530 Eide, N.E., Eid, P.M., Prestrud, P., Swenson, J.E. 2005. Dietary responses of arctic foxes
531 *Alopex lagopus* to changing prey availability across an Arctic landscape. Wildlife.
532 Biol. **11**:109-121.
533 Gelman, A., and Hill, J. 2007. Data analysis using regression and multilevel/hierarchical
534 models. Cambridge University Press, Cambridge, UK.

535 Gelsleichter, J., Musick, J.A., and Nichols, S. 1999. Food habits of the smooth dogfish,
536 *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark,
537 *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the
538 northwest Atlantic Ocean. Environ. Biol. Fishes. **54**:205-217.
539 Graham, N.J. 2007. Ecological versatility and the decline of coral feeding fishes following
540 climate driven coral mortality. Mar. Biol. **153**:119-127.
541 Graham, N.A.J., Wilson, S.K., Pratchett, M.S., Polunin, N.V.C., and Spalding, M.D. 2009.
542 Coral mortality versus structural collapse as drivers of corallivorous butterflyfish
543 decline. Biodiver. Conser. **18**:3325-3336.
544 Hammerschlag, N., and Sulikowski, J. 2011. Killing for conservation: the need for
545 alternatives to lethal sampling of apex predatory sharks. *Endangered Species*
546 *Research* **14**: 135–140.
547 Heithaus M.R., 2005. Habitat use and group size of pied cormorants (*Phalacrocorax varius*)
548 in a seagrass ecosystem: possible effects of food abundance and predation risk. Mar.
549 Bio. 147:27-35.
550 Heithaus, M.R., Frid, A., Wirsing, A.J., and Worm, B. 2008. Predicting ecological
551 consequences of marine top predator declines. Trends. Ecol. Evol. **23**:202-210.
552 Heithaus, M.R., Wirsing, A.J., and Dill, L.M. 2012. The ecological importance of intact top-
553 predator populations: a synthesis of 15 years of research in a seagrass ecosystem.
554 Mar. Freshw. Res. **63**:1039-1050.
555
556 Herbert, C.E., Shutt, J.L., Hobson, K.A., and Weseloh, D.V.C. 2011. Spatial and temporal
557 differences in the diet of Great Lakes gerring gulls (*Larus argentatus*): evidence from
558 stable isotope analysis. Can. J. Fish. Aquat. Sci. **56**:323-338.
559

560 Hussey, N.E., Dudley, S.F.J., McCarthy, I.D., Cliff, G., and Fisk, A.T. 2011. Stable isotope
561 profiles of large marine predators: viable indicators of trophic position, diet, and
562 movement in sharks? Can. J. Fish. Aquat. Sci. **68**:2029-2045.
563 Hussey, N.E., MacNeil, M.A., Olin, J.A., McMeans, B.C., Kinney, M.J., Chapman, D.D., and
564 Fisk, A.T. 2012a. Stable isotopes and elasmobranchs: tissue types, methods,
565 applications and assumptions. J. Fish. Biol. **80**:1449-1484.
566 Hussey, N.E., Olin, J.A., Kinney, M.J., McMeans, B.C., and Fisk, A.T. 2012b. Lipid
567 extraction effects on stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of elasmobranch muscle
568 tissue. J. Exp Mar. Biol. Ecol. **434-435**:7-15.
569 Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. 2011. Comparing isotopic niche
570 widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in
571 R. J. Anim. Ecol. **80**:595-602.
572 Kim, S.L., del Rio, C.M., Casper, D., and Koch, P.L. 2012. Isotopic incorporation rates for
573 shark tissues from a long-term captive feeding study. J. Exp. Biol. **215**:2495-2500.
574 Kinney, M., Hussey, N., Fisk, A., Tobin, A., and Simpfendorfer, C. 2011. Communal or
575 competitive? Stable isotope analysis provides evidence of resource partitioning within
576 a communal shark nursery. Mar. Ecol. Prog. Ser. **439**:263-276.
577 Klages, J., Broad, A., Kelaher, B.P., and Davis, A.R. 2014. The influence of gummy sharks,
578 *Mustelus antarcticus*, on observed fish assemblage structure. Environ. Biol. Fishes.
579 **97**:215-222.
580 Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud,
581 Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., and
582 Bearhop, S. 2012. Applying stable isotopes to examine food-web structure: an
583 overview of analytical tools. Biol. Rev. **87**:545-562.

584 Last, P.R., and Stevens, J.D. 2009. Sharks and rays of Australia. 2nd Edn. CSIRO Publishing
585 Collingwood, Victoria, Australia.
586 Layman. C.A., Arrington, D.A., Montaña, C.G., and Post, D.M. 2007. Can stable isotope
587 ratios provide for community-wide measures of trophic strucutre? Ecol. **88**:42-48.
588 Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a
589 review and prospectus. Can. J. Zool. **68**:619-640.
590 Logan, J., and Lutcavage, M. 2010. Stable isotope dynamics in elasmobranch fishes.
591 Hydrobiologia. **644**:231-244.
592 Lundberg, J., and Moberg, F. 2003. Mobile link organisms and ecosystem functioning:
593 implications for ecosystem resilience and management. Ecosystems **6**: 0087-0098. doi
594 10.1007/s10021-002-0150-4.
595 MacNeil, M.A., Skomal, G.B., and Fisk, A.T. 2005. Stable isotopes from multiple tissues
596 reveal diet switching in sharks. Mar. Ecol. Prog. Ser. **302**:199-206.
597 Matich P., Heithaus, M,R., and Layman, C.A. 2010. Size-based variation in intertissue
598 comparisons of stable carbon and nitrogen isotopic signatures of bull sharks
599 (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*). Can. J. Fish. Aquat. Sci.
600 **67**:877-885.
601 McElroy, W.D., Wetherbee, B., Mostello, C., Lowe, C., Crow, G., and Wass, R. 2006. Food
602 habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus*
603 *plumbeus*, in Hawaii. Environ. Biol. Fishes. **76**:81-92.
604 McKinney, M.L. 1997. Extinction vulnerability and selectivity: combining ecological and
605 paleontological views. Annu. Rev. Ecol. Syst. **28**:495-516.
606 Mittelbach, G., Osenberg, C., and Wainwright, P. 1992. Variation in resource abundance
607 affects diet and feeding morphology in the pumpkinseed sunfish (*Lepomis gibbosus*).
608 Oecologia **90**:8-13.

609 Munroe. S.E.M., Simpfendorfer, C.A., and Heupel, M.R. 2014a. Defining shark ecological
610 specialisation: concepts, context, and examples. Rev. Fish Biol. Fish. **24**:317-331.
611 Munroe, S., Simpfendorfer, C., and Heupel, M. 2014b Habitat and space use of an abundant
612 nearshore shark, *Rhizoprionodon taylori*. Mar. Freshw. Res.
613 http://dx.doi.org/10.1071/MF13272
614 Munroe, S., Heupel, M., Fisk, A., Logan, M., and Simpfendorfer, C. (*in review*) Regional
615 movement patterns of a small-bodied shark revealed by stable isotope analysis. Mar.
616 Biol.
617 Olin, J.A., Hussey, N.E., Fritts, M., Heupel, M.R., Simpfendorfer, C.A., Poulakis, G.R., and
618 Fisk, A.T. 2011. Maternal meddling in neonatal sharks: implications for interpreting
619 stable isotopes in young animals. Rapid Commun Mass Spectrom. **25**:1008-1016.
620 Oro, D., Genovart, X., Ruiz, X., Jimenez, J., and Garcia-Gans, J. 1996. Differences in diet,
621 population size, and reproductive performance between two colonies of Audouin's
622 Gull *Larus audouinii* affed by a trawling moratorium. J. Avian Biol. **27**: 245-251.
623 Parnell, A., and Jackson, A. 2011. SIAR: stable isotope analysis in R. R package version
624 4.1.3.
625 Parnell, A.C., Inger, R., Bearhop, S., and Jackson, A.L. 2010. Source partitioning using stable
626 isotopes: coping with too much variation. PLoS ONE **5**:e9672.
627 Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol.
628 System. **18**:293-320.
629 Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using
630 Gibbs Sampling. *In* Proceedings of the 3rd International Workshop on Distributed
631 Statistical Computing, Vienna, Austria. 20-22 March 2003.

632 Post, D., Layman, C.A., Arrington, D., Takimoto, G., Quattrochi, J., and Montana, C. 2007.
633 Getting to the fat of the matter: models, methods and assumptions for dealing with
634 lipids in stable isotope analyses. Oecologia **152**:179-189.
635 Post, D.M. 2002. Using stable istopes to estimate trophic position: models, methods, and
636 assumptions. Ecol. **83**:703-718
637 de Queiroz, A., Henke, C., Smith, H.M., and Guyer, C. 2001. Geographic variation and
638 ontogenetic change in the diet of the Mexican Pacific lowlands garter snake,
639 *Thamnophis validus*. Copeia **2001**:1034-1042.
640 Reeve, A., Handy, R.D., and Gruber, S.H. 2009. Prey selection and functional response of
641 juvenile lemon sharks *Negaprion brevirostris*. J. Fish. Biol. **75**:276-281.
642 Richmond, C.E., Breitburg, D.L., and Rose, K.A. 2005. The role of environmental generalist
643 species in ecosystem function. Ecol. Modell. **188**:279-295.
644 Salini, J., Blaber, S., and Brewer, D. 1992. Diets of sharks from estuaries and adjacent waters
645 of the North-eastern Gulf of Carpentaria, Australia. Mar. Freshw. Res. **43**:87-96.
646 Shiffman, D.S., Frazier, B.S., Kucklick, J.R., Abel, D., Brandes, J., and Sancho, G. 2014.
647 Feeding ecology of the sandbar shark in south carolina estuaries revealed through
648 $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis. Mar. Coast. Fish. Dynam. Manag. Ecosys. Sci.
649 **6**:156-169.
650 Shiffman, D.S., Gallagher, A.J., Boyle, M.D., Hammerschlag-Peyer, C.M., and
651 Hammerschlag, N. 2012. Stable isotope analysis as a tool for elasmobranch
652 conservation research: a primer for non-specialists. Mar. Freshw. Res. **63**:635-643.
653 Simpfendorfer, C.A. 1992. Reproductive strategy of the Australian Sharpnose Shark,
654 *Rhizoprionodon taylori* (Elasmobranchii: Carcharhinidae), from Cleveland Bay,
655 Northern Queensland. Mar. Freshw. Res. **43**: 67-75.

Simpfendorfer, C.A. 1993. Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. Enviro. Biol, Fish. **36**: 233-241.

Simpfendorfer, C.A. 1998. Diet of the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Queensland. Mar. Freshw. Res. **49**:757-761.

Simpfendorfer, C.A., and Milward, N.E. 1993. Utilization of a tropical bay as a nursery area by sharks of the families carcharhinidae and sphyrnidae. Environ. Biol. Fishes. **37**: 337-345.

Simpfendorfer, C., Goodreid, A., and McAuley, R. 2001. Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo Cuvier*, from western australian waters. Environ. Biol. Fishes. **61**:37-46.

Speed, C.W., Meeken, M.G., Field, I.C., McMahon, C.R., Abrantes, K., and Bradshaw C.J.A. 2011. Trophic ecology of reef sharks determined using stable isotope analysis and telemetry. Coral Reefs **31**:357-367.

Stevens, J., and McLoughlin, K. 1991. Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. Mar. Freshw. Res. **42**:151-199.

Suarez, A.V., and Case, T.J. 2002. Bottom-up effects on persistence of a specialist predator : Ant invasions and horned lizards. Ecol. Appl. **12**:291-298.

Terraube, J., Arroyo, B., Madders, M., and Mougeot, F. 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. Oikos **120**:234-244.

Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., and Slade, N.A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for δ13C analysis of diet. Oecologia **57**:32-37.

Tilley, A., Lopez-Angarita, J., Turner, J.R. 2013.Diet reconstrcution and resoruce partitioning of a Caribbena marine mesopredator using stable isotope bayesian modelling. Plos One :e79560 DOI: 10.1371/journal.pone.0079560

Yamaguchi, A., and Taniuchi, T. 2000. Food variations and ontogenetic dietary shift of the starspotted-dogfish *Mustelus manazo* at five locations in Japan and Taiwan. Fish. Sci. **66**:1039-1048.

688 Tables

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

690 sample area, Repulse Bay (RE), Cleveland Bay Unit (CBU), and Rockingham Bay (RO).

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

691

692

693 **Table 2**. Total catch, $\delta^{13}C$ and $\delta^{15}N$ range, trophic position (TP) range and mean with standard error (SE), convex hull area, and median .
694 Bayesian Standard Ellipses (SEA_b) area ($‰^2$) of female *Rhizoprionodon taylori* based on $\delta^{15}N$ (diet tissue discrimination factor = 3.2) for each
695 tissue in each sample area, Repulse Bay (RE), Cleveland Bay Unit (CBU), and Rockingham Bay (RO).

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 - -14.5	11.94-13.39	3.2-4.1	3.7 ± 0.04	1.35	0.864
		Plasma	-16.7 - -14.7	10.19-12.66	2.7-3.9	3.5 ± 0.05	2.84	1.34
CBU	76	Muscle	-18.1 - -13.3	10.57-13.35	3.6-4.9	4.3 ± 0.02	9.16	1.67
		Plasma	-16.5- - 13.7	8.33-12.34	2.9-4.6	3.9 ± 0.03	6.84	1.51
RO	20	Muscle	-17.0 - -14.5	11.64-13.76	3.6-4.8	4.2 ± 0.05	3.26	1.19
		Plasma	-16.8- -14.5	9.92-12.52	3.1-4.4	3.8 ± 0.05	2.58	1.16

696

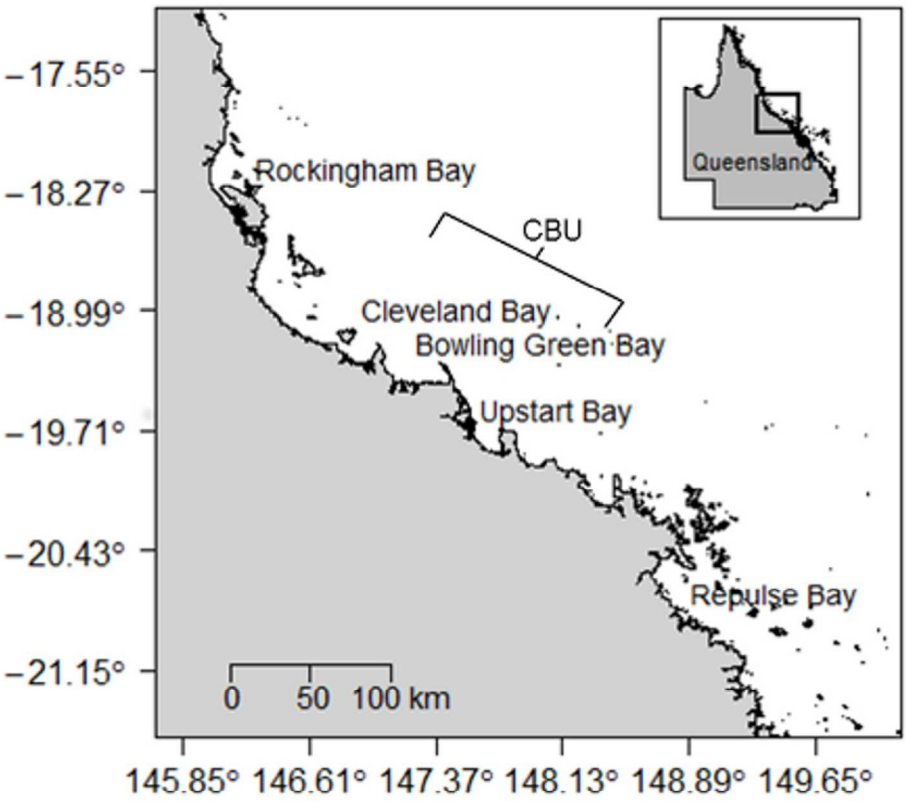
Figure captions

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.

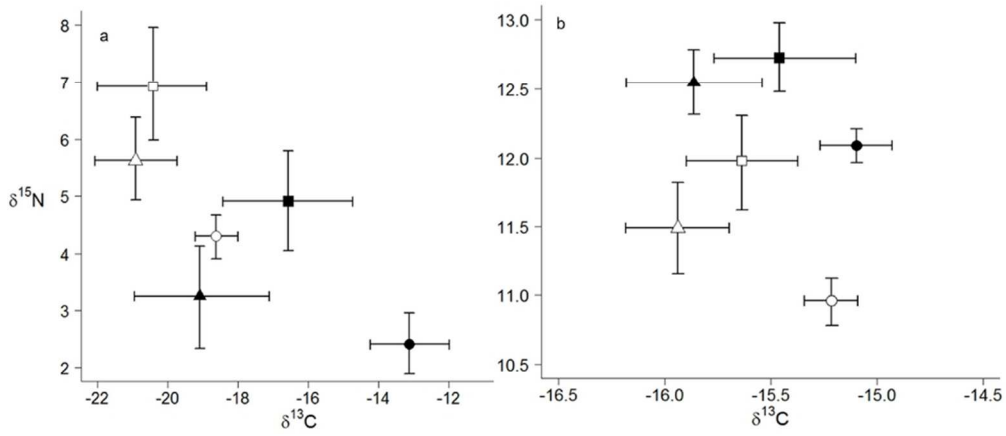
Fig. 2. (a) Median $\delta^{13}C$ and $\delta^{15}N$ results of Bayesian ANOVA of benthic (black) and pelagic baselines (white) in Repulse Bay (■), the Cleveland Bay Unit (●) and Rockingham Bay (▲); (b) median $\delta^{13}C$ and $\delta^{15}N$ results of Bayesian ANOVA of *Rhizoprionodon taylori* for muscle (black) and plasma (white) in Repulse Bay (■), the Cleveland Bay Unit (●) and Rockingham Bay (▲). Black lines show 95% credibility intervals of posterior draws.

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

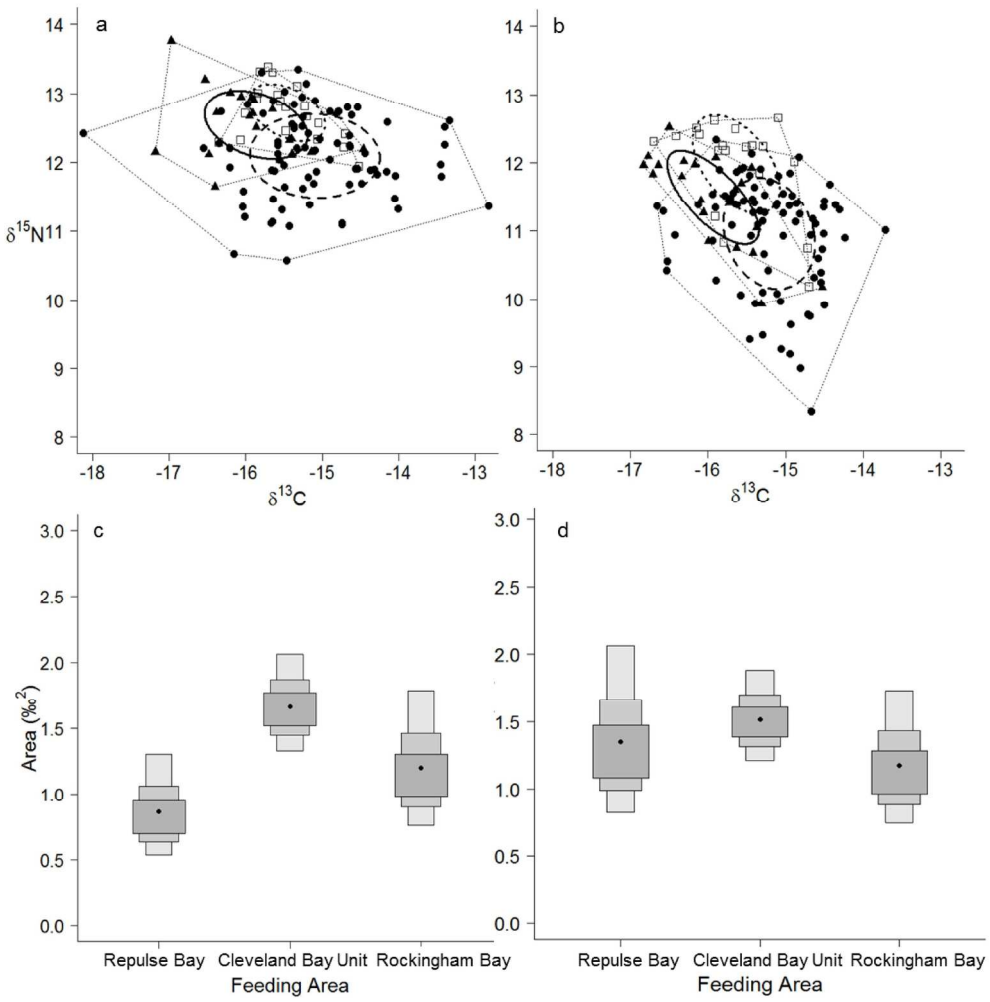
Fig. 4. Proportional contributions of benthic and pelagic food web sources to *Rhizoprionodon taylori* diet using a two-source Bayesian mixing model for plasma and muscle tissue in A) Repulse Bay, B) Cleveland Bay Unit, and C) Rockingham Bay. Shaded boxes are 50, 75, 95 (from dark to light grey) credibility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



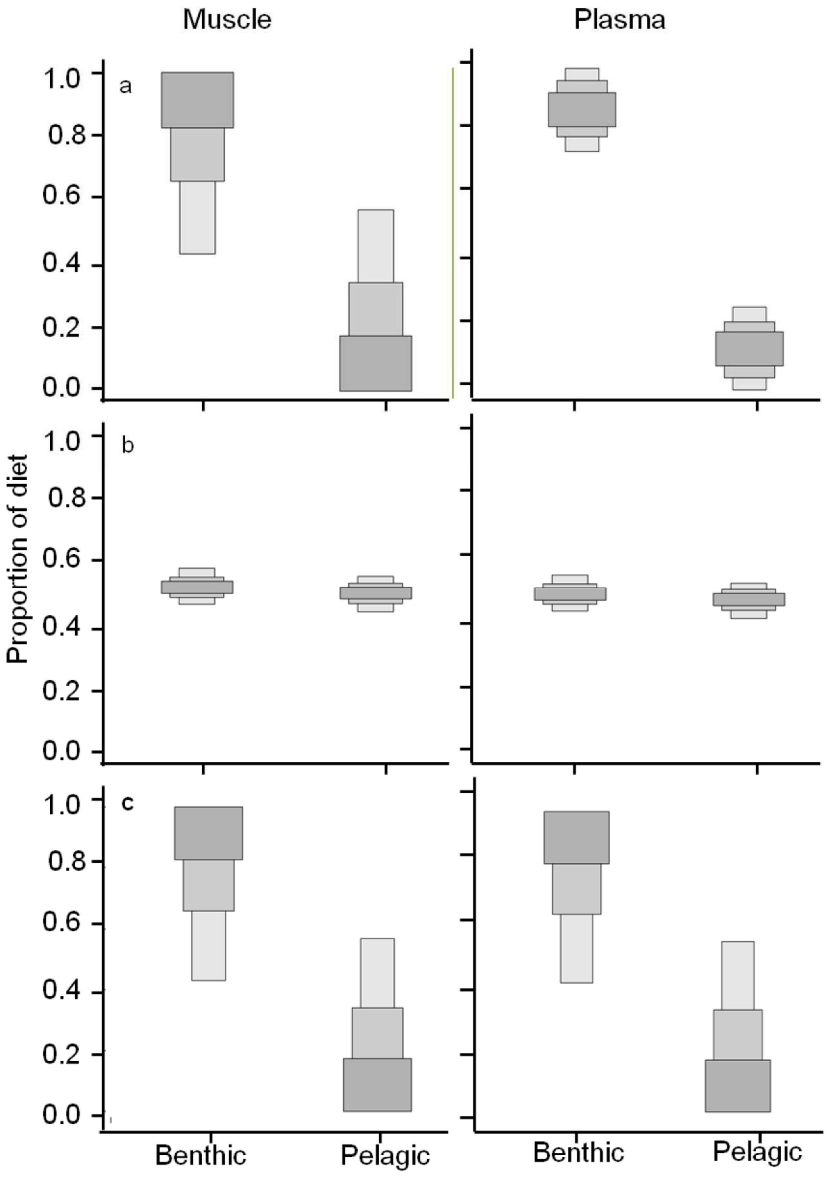
169x170mm (300 x 300 DPI)



81x39mm (300 x 300 DPI)



168x167mm (300 x 300 DPI)



211x302mm (300 x 300 DPI)