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Habitat and Dietary Selectivity of Nearshore Shark Populations

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Abstract

The resource use strategies species exhibit affects their role within communities and how they respond to environmental change. Species that adopt generalist strategies are typically less vulnerable to environmental fluctuations than specialists. However, specialists often have lower energy costs and are more efficient at extracting and processing preferred resources. This dissertation defines shark ecological specialisation in order to evaluate the resource use patterns of nearshore sharks and discusses how shark resource use patterns can affect their vulnerability to environmental change.

Sharks are traditionally classified as generalists that use a variety of habitats and prey. While this is an accurate description of some species, sharks exhibit a range of resource use strategies that includes highly selective or specialised behaviours. However, discussion on how to define the ecological specialisation of sharks has been limited. This dissertation presents a conceptual framework within which to define the specialisation of sharks that can be applied to different environmental scales. Shark species with varying degrees of specialisation are presented within the proposed context.

Passive acoustic telemetry was used to examine the residency, space use, and habitat selection and specialisation patterns of the small-bodied Australian sharpnose shark, *Rhizoprionodon taylori*, and the medium-bodied creek whaler *Carcharhinus fitzroyensis*, in Cleveland Bay, Queensland, Australia. Stable isotope analysis of $\delta^{13}C$ ($^{13}C/^{12}C$) and $\delta^{15}N$ ($^{15}N/^{14}N$) was used to define the regional nearshore residency, movements, trophic level, and benthic and pelagic contributions to the diet of *R. taylori*. $\delta^{13}C$ values vary at the base

of the food chain but are conserved up the food chain. $\delta^{15}N$ values increase in predictable quantities between trophic levels. Therefore**,** $\delta^{13}C$ and $\delta^{15}N$ values can be used to indicate the foraging location and diet of populations. Plasma and muscle $\delta^{13}C$ and $\delta^{15}N$ of *R. taylori* were collected from five embayments, including Cleveland Bay, on the northeast coast of Queensland.

Results of the acoustic tracking showed the majority of *R. taylori* were present in Cleveland Bay for short periods of time, ranging from 1 to 112 days (mean ± SE = 17 ± 5). The majority of individuals were present in Cleveland Bay for less than two weeks. Low residency suggests that *R. taylori* home ranges likely span multiple bays. Individual monthly activity space ranged from 4.3 and 21.4 km^2 (mean ± SE =11.3 km^2 ± 0.90) for 50% kernel utilisation distributions (KUDs) and 21.5 and 80.4 km^2 (mean ± SE = 51.0 km^2 ± 3.9) for 95% KUDs. Space use analysis indicated *R. taylori* roamed widely throughout the bay, but monthly activity space size was consistent among individuals and over time. Sex and size had no influence on *R. taylori* residency or activity space size. Both the population and individuals occupied wide habitat niches which included seagrass, outer bay mud substrate, and sandy inshore habitat. However, both resident and transitory *R. taylori* consistently selected for seagrass over other habitats, potentially for feeding. Mudflat and reef habitats were generally avoided. Habitat selection appeared to be influenced by changes in freshwater input into Cleveland Bay. Selection for seagrass habitat, which is adjacent to large river mouths, decreased during periods of high river flow, suggesting *R. taylori* may have limited tolerance to low salinity.

Stable isotope analysis showed that there was a positive correlation between *R. taylori* tissue and environmental (seagrass and plankton) $\delta^{13}C$ values based on location. Shark populations with the highest tissue $\delta^{15}N$ were collected from areas with the highest baseline $\delta^{15}N$ values. Moreover, populations from bays that were > 100 km apart had distinct isotopic values. These results indicate *R. taylori* were not foraging more than 100 km from their capture location within 6 to 12 months. However, $\delta^{13}C$ values of individuals in nearby bays (30-70 km apart) were indistinguishable, suggesting individuals foraged and moved between bays that were within 100 km of each other during a 6 to 12 month period. Therefore, isotope results were consistent with the low residency exhibited by *R. taylori* in Cleveland Bay. Isotope analysis also revealed *R. taylori* had a wide trophic range and consumed prey from benthic and pelagic sources. In all areas, benthic sources were important to the diet, suggesting benthic habitats (e.g. seagrass) may be important to *R. taylori*. However, there was geographic and temporal variation in *R. taylori* diet. These results indicate *R. taylori* has a broad dietary niche, but different populations may have unique effects on distinct areas. Variation in diet also suggests *R. taylori* may be adaptive to changes in prey availability.

In contrast to *R. taylori*, most *C. fitzroyensis* were highly resident and present in Cleveland Bay for long periods of time, ranging 1 to 452 days (mean ± SE = 205 ± 53). However, a few individuals spent less than two weeks in the bay, suggesting broader movements occur in a portion of the population. Size and sex had no effect on presence. Individual monthly activity space ranged from 2.6 to 19.8 km^2 (mean ± SE =10.6 km^2 ± 0.3) for 50% KUDs and 9.1 to 81.9 km^2 (mean ± SE = 47.9 km^2 ± 1.0) for 95% KUDs. Activity space size varied between months and diel period but was not affected by animal size. Activity spaces in August were significantly smaller and concentrated closer to the shore than in other months. This simultaneous shift in space use by all individuals may have been to due biotic changes in the bay, such as changes in prey availability. Larger day time activity spaces suggest *C. fitzroyensis* may be primarily diurnal feeders. All resident *C. fitzroyensis* spent the majority of time in seagrass and to a lesser extent outer bay mud substrate habitat. Seagrass was consistently selected for throughout the monitoring period while use of outer bay mud substrate was highly irregular. Shallow mudflat, sandy inshore, and reef habitats were rarely used. There was no difference in space or habitat use between immature and mature individuals, indicating different age classes shared space and habitats.

The results of acoustic and isotope analyses indicated that seagrass habitat is the preferred habitat of *R. taylori* and *C. fitzroyensis*. Seagrass is typically highly productive and may be an important foraging habitat for these species. For that reason, seagrass conservation will be an important consideration for the future spatial management of these species. However, *R. taylori* used different habitats and embayments and had a broad diet. Therefore, results indicate *R. taylori* has a low degree of resource specialisation and is probably adaptive to local environmental change. In contrast, the movement patterns exhibited by *C. fitzroyensis* suggest this species has a moderately high degree of habitat specialisation and is highly resident. Although diet information is not available for *C. fitzroyensis*, the movement patterns of *C. fitzroyensis* indicate this species will likely be more vulnerable to local environmental change, specifically a decline in seagrass abundance. By evaluating the resource use patterns of nearshore sharks, this dissertation has provided valuable information on the potential vulnerabilities of poorly understood shark species while also developing a conceptual framework for future resource specialisation investigations.

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Chapter 1

General Introduction

Tropical nearshore areas are highly productive environments that contain a diverse range of habitats including mangroves, rivers, and reefs (Nixon *et al.* 1986; Spalding *et al.* 2007). In addition to diverse habitats, nearshore areas often experience large-scale changes in environmental factors such as salinity, water temperature, oxygen content and nutrient availability (Breitburg 1990; Clarke and Leakey 1996; Meynecke and Lee 2011). This diversity and productivity sustains a high abundance of species over a broad range of taxa (Beck *et al.* 2001). However, as a result of its productivity, diversity, and proximity to human settlements, nearshore environments are also heavily exploited (Suchanek 1994). A high level of historically unmonitored inshore fishing has resulted in the decline of numerous nearshore species (Jackson *et al.* 2001). Human development in coastal areas, such as dredging and construction (e.g. seawalls), often result in habitat destruction or decline (Lotze *et al.* 2006; Bulleri and Chapman 2010). Pollution is also a major contributor to nearshore environmental deterioration (Shahidul Islam and Tanaka 2004). Chemical contaminants such as herbicides and heavy metals have been linked to nearshore habitat damage and disease in a variety of marine taxa (teleosts, marine mammals, etc.) (Kennish 1998; Haynes *et al.* 2000). Therefore, nearshore species may be highly susceptible to population decline as a result of decreasing habitat quality due to human-induced change.

A diverse range of shark species use nearshore areas (Compagno 2001). Body types range from large-bodied requiem sharks, such as the sandbar shark *Carcharhinus plumbeus*

(Compagno 1984), to dorsoventrally flattened species, such as the Pacific angel shark *Squatina californica* (Gaida 1997). A variety of reproductive strategies, from viviparity (e.g. the bonnethead shark; Parsons 1993) to oviparity (e.g. The Port Jackson shark, *Heterodontus portusjacksoni*; McLaughlin and O'Gower 1971), are found among sharks in nearshore areas. Species also exhibit a broad range of behaviours and nearshore resource use strategies. Sharks have been found in a wide variety of nearshore habitats, including rivers (Heupel *et al.* 2010; Pillans *et al.* 2010), mudflats and soft substrate (Espinoza *et al.* 2011), seagrass (Heithaus *et al.* 2006), and rocky substrate or coastal reefs (Carraro and Gladstone 2006). Different species also spend variable periods of time in nearshore areas. For example, leopard sharks *Triakis semifasciata* were found to be highly resident in estuarine environments (Carlisle and Starr 2009), while the sevengill shark *Notorynchus cepedianus* exhibited seasonal patterns of presence in Pacific estuarine embayments (Williams *et al.* 2012). Other species, such as the spottail shark *Carcharhinus sorrah,* have demonstrated high individual variability (i.e. different patterns) in presence in nearshore areas (Knip *et al.* 2012b). Although most shark species have been reported to use a wide range of nearshore habitats and prey (Hanchet 1991; Gelsleichter *et al.* 1999; Carlson *et al.* 2008), some species exhibit strong preferences for specific nearshore habitats, potentially due to high prey availability (Heithaus *et al.* 2002; Carlisle and Starr 2009) or the protection these areas provide from predators (Branstetter 1990; Morrissey and Gruber 1993; Heupel and Hueter 2002). As a result, some species consume a relatively narrow range of spatial and/or dietary resources in coastal areas (Cortes *et al.* 1996; Simpfendorfer *et al.* 2001; Chin *et al.* 2013).

The diversity of resource use patterns observed in nearshore sharks is the result of a variety of factors, including physiology (Pillans *et al*. 2005), morphology (Edmonds *et al.* 2001), and resource needs (Carlisle and Starr 2010). However, the life history of a species can also have a substantial influence on its presence in nearshore habitats and its resource use patterns (Cortés 2000). Juveniles of large-bodied, slow growing, late maturing species, such as the blacktip shark *Carcharhinus limbatus* (Heupel, *et al*. 2010) or the bull shark *Carcharhinus leucas* (Ortega *et al.* 2009; Werry *et al.* 2011), commonly use nearshore environments as nursery areas (Springer 1967; Grubbs 2010). Shallow nearshore areas can provide juvenile sharks with protection from predators and function as highly productive foraging grounds (Branstetter 1990; Heithaus 2007). Therefore, high residency to these areas helps to ensure juveniles reach sexually maturity (Heupel *et al.* 2007). As a result, juveniles typically spend long periods of time, sometimes several years, in a single nearshore embayment (Conrath and Musick 2010; Knip *et al.* 2011). Large-bodied adults have significantly larger home ranges that include offshore habitats (Dicken *et al.* 2008; Carlson *et al.* 2010). Consequently, juvenile and adult populations are often spatially segregated (Grubbs 2010).

The nearshore movement patterns of small-bodied, highly productive, fast growing sharks, such as the milk shark *Rhizoprionodon acutus* (Henderson *et al.* 2006; Schroeder 2011), strongly contrast with those of large-bodied species. Small-bodied sharks are typically found in nearshore areas throughout their lives, where juveniles and adults simultaneously use the same nearshore habitats (Simpfendorfer and Milward 1993; Knip *et al.* 2010). There is also evidence to indicate that, despite their small size, individuals regularly move between different nearshore areas (Kohler *et al.* 1998; Carlson *et al.* 2008), in contrast to the juveniles of large-bodied species. However, compared to large-bodied species, little information is available on how small coastal species use nearshore areas.

The nearshore resource use patterns of medium-bodied species, such as the whiskery shark *Furgaleus macki* (1500 mm total length), or the nervous shark *Carcharhinus cautus* (1200-1400 mm total length), are also poorly understood (Last and Stevens 2009). The life history traits of these species are sometimes an intermediate of those exhibited by large- and small-bodied sharks (Lyle 1987; Simpfendorfer *et al.* 2000). Therefore, medium-bodied sharks may demonstrate unique coastal movement patterns compared to large- and small-bodied species.

Given their variability in use of nearshore regions, sharks play a variety of ecological roles in nearshore ecosystems. Sharks can control prey populations via direct predation (Stevens *et al.* 2000; Heithaus *et al.* 2008), and have also been shown to alter prey behaviour via risk avoidance (Heithaus and Dill 2002; Heithaus *et al.* 2012). However, biological factors such as morphology will influence the effect sharks have on nearshore environments. For example, large-bodied species often occupy high trophic positions within nearshore food chains and prey on larger coastal fauna, whereas small-bodied mesopredators exert top-down control over smaller-bodied nearshore species and may also be prey for larger sharks (Cortés 1999). Mobility will also affect the influence sharks have on nearshore ecosystems. Highly mobile or migratory species may connect separated food webs by moving between them and consuming local resources (Lundberg and Moberg 2003). Less mobile or more resident populations will likely have a more localized on nearshore regions.

The behaviour and resource use patterns exhibited by nearshore sharks will also affect their vulnerability to environmental change. Species that are highly mobile and use a wide range of resources (i.e. habitats or prey) will be less vulnerable to environmental change than species that are highly specialised and use a narrow range of resources (Futuyma and Moreno 1988;

Wilson *et al.* 2008). This is because highly specialised species may not be able to use new or additional resources if preferred resources decline in health or availability (Colles *et al.* 2009; Clavel *et al.* 2010). In contrast, during periods of environmental change or decline, species that use large resource niches should be able to use supplemental resources and thus maintain a relatively high level of fitness (Marvier *et al.* 2004). Therefore, defining resource use patterns of sharks, most notably the degree of specialisation, is critical to understanding their role in nearshore ecosystems and their vulnerability to change.

Given current knowledge gaps and research needs, the primary aims of this dissertation were to: 1) develop a definition of shark resource specialisation, 2) use this definition to evaluate the resource use patterns (i.e. habitat and diet) of poorly understood nearshore shark species, and 3) discuss how the observed resource use patterns affect vulnerability to nearshore environmental change. To accomplish these aims the ecological literature on niche theory, specialisation, and shark resource use was reviewed to create a definition for shark ecological specialisation (Chapter 2). The application and interpretation of this definition was explored using past shark resource use studies. Acoustic telemetry (Chapters 4 and 7) and stable isotope analysis (Chapter 5 and 6) were used to investigate the movement and resource use patterns of a small-bodied and a medium-bodied nearshore shark species. The accumulated data were then used to evaluate and compare these species' vulnerability to nearshore environmental change (Chapter 8). This dissertation provides new and important information on the resource use patterns of poorly understood nearshore shark species and will contribute to marine coastal management as well as the study of other shark species.

Chapter 2

Defining Shark Ecological Specialisation: Concepts, Context, and Examples

2.1 Introduction

Sharks are found in the majority of aquatic environments and as higher trophic level consumers they have direct and indirect influences on community structure and function (Stevens *et al*. 2000; Heithaus *et al*. 2008). To quantify sharks relationship with the environment, a growing body of literature has evaluated shark habitat use, distribution, and diet (e.g. Carlisle and Starr 2009; Cabrera-Chávez-Costa *et al*. 2010; Cartamil *et al*. 2010; Clarke *et al*. 2011). These data are critical to the creation of successful management solutions for declining and endangered populations as well as ecosystems as a whole. Recognition of differing strategies leads to a better understanding of the strengths and vulnerabilities of a species in their environment and aids conservation programs (Dulvy *et al*. 2008; Chin *et al*. 2010; Simpfendorfer *et al*. 2011).

Two broad resource use strategies exist among organisms. There are generalists that have large ecological niches and use a wide range of resources; and specialists that have relatively small ecological niches and use a comparatively narrow range of resources (Futuyma and Moreno 1988; Irschick *et al*. 2005). In the past sharks have been depicted as mobile generalists with wide, sometimes global, ranges that feed opportunistically rather than foraging for specific prey items (Wetherbee *et al*. 1990). While this is an accurate description for some species, research has revealed others specialise on a narrow range of habitat and prey. In reality, species exhibit strategies across the continuum between these two extremes

(Compagno 1990). The use of generalist or specialist strategies has distinct implications for the populations that adopt them, with costs and benefits resulting from each (DeWitt 1998; Richmond *et al*. 2005; Colles *et al*. 2009). Therefore, knowledge of which species uses each strategy is essential to not only understanding ecological interactions but also to the development of appropriate management schemes. For these reasons, as shark research advances, a greater number of studies will aim to define shark resource use as selective, opportunistic, specialised or generalised. The application of ecological theory to analyse variability in resource use is also likely to increase.

Unfortunately, similar to other fields of ecological research, definitions for what is meant by "selection", "specialist" or "generalist" are rarely stated in literature. Lack of definition has led to confusion in shark ecology over the appropriate application of these important concepts. As a consequence of this confusion, specialisation is either poorly articulated in publications or inferred using inappropriate methodologies. Incorrect classifications inhibit discussion and make it difficult to accurately compare one species to another. There are two primary reasons for the absence of definition in shark literature. First, there is inherent difficulty associated with applying ecological theory to an analytical framework (Chase and Leibold 2009). Second, it has only recently become possible to develop accurate theoretical guidelines for defining and measuring shark resource use due to advancements in animal tracking and dietary analysis. As a result, there has been limited scientific discussion on how to define specialisation and classify sharks. However, as the aforementioned terms are used more often (ex. Taylor and Bennett 2008; Wilga *et al*. 2012), it is important to link applied science with the theoretical concepts of resource use. Lack of definition will lead to the continued misuse of concepts, the incorrect classification of species, hinder research progress, and impede successful management efforts.

Definitions of each concept and how best to measure them can vary based on context and the authors analytical intent (Berenbaum 1996; Poisot *et al*. 2012). Therefore, a well-structured definition and conceptual framework for specialisation should be tailored for specific types of research. How specialisation should be defined is dependant not only on broader ecological theory, but also on the organism, the scale of the study (species to individual), and the type of specialisation being evaluated (e.g. behavioural, dietary, habitat) (Irschick *et al*. 2005; Devictor *et al*. 2010). Moreover, selection and specialisation have similar quantitative and qualitative characteristics. Therefore, it is important to define each term in context to prevent interchangeable and inconsistent use. To alleviate the current confusion in shark literature, highlight the importance of contextual definitions in shark ecology, and showcase the diversity of strategies among sharks I will (1) discuss the theoretical differences between the related but distinct ideas of selection and specialisation; (2) propose an ecological definition and conceptual framework for resource specialisation widely applicable to shark species; (3) review a range of ecological adaptations of sharks within the proposed context in two important foci: diet and habitat; and (4) briefly discuss the potential implications of these strategies on species resilience.

2.2 Defining Shark Specialisation: Terminology and the Continuum Concept

Multiple forms of specialisation exist among sharks, including morphological specialisations such as the long upper caudal lobe of the common thresher shark *Alopias vulpinus* (Aalbers *et al*. 2010); behavioural specialisations such as the ectoparasitic feeding strategy of the cookie cutter shark *Isistius brasiliensis* (Papastamatiou *et al*. 2010); and ecological specialisations such as the specialised cephalopod-based diet of the whiskery shark *Furgaleus macki*

(Simpfendorfer *et al*. 2001b). Therefore differentiation between unique forms of specialisation requires definitions designed to suit the goals and scale of the research (Futuyma and Moreno 1988; Irschick *et al*. 2005). I am focused on defining shark ecological specialisation. Therefore, all terminology has been tailored to fit within that context.

Four terms are primarily used to describe shark resource use. Selection is defined as the use of resources out of proportion or in different proportions to their availability. Opportunism, selection's conceptual opposite, is defined as the use of resources in the same proportion as their availability (Johnson 1980; Buskirk and Millspaugh 2006). Selective animals bypass certain resources in favour of others; whereas opportunistic animals use whatever is available. It is typically quantified for one resource at a time. Measurements of several resources are compared to each other to determine relative levels of selection for any given resource (Manly *et al*. 2002). The term specialist describes species, populations, or individuals that have a narrow or restricted niche breadth. Generalists are species, populations, or individuals that have a large niche breadth (Vandermeer 1972; Devictor *et al*. 2010). Niche breadth is a collective measurement of all resources used relative to the resources available within the environment as a whole (Colwell and Futuyma 1971). Although selection and specialisation may seem quite similar (i.e. a highly selective species is likely to have small niche breadth), the terms are not interchangeable. The main difference being one is measured in reference to an animal's niche (specialisation and generalisation) and the other measures the proportion of an animal's resource use (selection and opportunism). Therefore analytical methods that can determine an animal's selectivity may not be equally capable of measuring specialisation.

To build a definition for specialisation that is more specific and better suited to shark resource use, an ecologically appropriate conceptual framework must be developed. Although animals are often defined using the opposing categories of specialist or generalist, in nature, specialisation is more accurately depicted as a continuum, where species are ranked along a specialisation gradient ranging from the largest to smallest possible niche. In this framework, sharks become less specialised with increasing niche breadth. Highly specialised species are those with very small niche breadths. A continuum context for defining shark specialisation is beneficial because while some sharks may be good examples of specialists or generalists, most sharks will not meet the strict requirements of either definition. Such species cannot be easily categorized. For example, a hypothetical species that selects for specific resources in a given environment, while avoiding others, cannot be defined as a generalist without exception because it has a somewhat restricted niche. However, if the same species has a large niche compared to other species in the environment, it is also not a specialist. Such strategies and resulting niche breadth values exist somewhere between a generalist and a specialist. Therefore, when studying shark resource use patterns and defining behaviours, it is more appropriate to measure and refer to a species' degree of specialisation, rather than categorizing a species as one extreme or the other. This concept is also quantitatively appropriate as most traditional measurements of specialisation use a sliding scale or index to measure specialisation (e.g. Levins 1968; Feinsinger *et al*. 1981; Smith 1982). Modern methods also measure specialisation using some form of gradient or relative comparison (e.g. Julliard *et al*. 2006; Fridley *et al*. 2007; Peers *et al*. 2012).

2.3 Defining Shark Specialisation: The Ecological Niche of a Shark

To finalize a definition and contextual framework for shark specialisation, I must also define the ecological niche of shark species. This is necessary to implement a test for specialisation because it is the main component of the definition. However, there are a number of different definitions and contradictory visions of the niche concept. It is also an unpopular term with some ecologists (Chase and Leibold 2009). As a result there can be confusion as to what ecologists mean when they discuss the niche of a species (Leibold 1995; Peterson *et al*. 2011). I will not enter into a broader discussion of niche theory, as I am only interested in finding a functional definition for niche as it pertains to shark resource use. With that in mind, I will briefly review the most prevalent contributions to niche theory to develop an appropriate definition for shark specialisation.

Two major conceptual contributions to niche theory have dominated modern definitions. The first was put forward by Grinnell (1917) and advanced by Hutchinson (1957). According to these works a niche is defined as the range of resources a species uses in an environment or the conditions in which it can survive. In other words, a Grinnellian niche is defined by “what a species needs” or uses (Devictor *et al*. 2010). The second definition was developed by Elton (1927), who defined a species niche as the role of a species in the environment or by “what the species is doing” (Devictor *et al*. 2010). This definition requires measurements of all the ways in which a species might directly and indirectly effect the environment (Leibold 1995; Devictor *et al*. 2010).

Hutchinson (1957) developed a physical schematic for his definition known as an n-dimensional hyper-volume. Hutchinson proposed that a niche could be plotted on a Cartesian coordinate system where the axes of the plot are environmental variables, such as temperature

(x) or depth (y) (Fig. 2.1). The limiting values or range of values a species uses can be plotted on each axis. The overlapping ranges of each variable result in a figure that represents the niche space for the species. Any point in this space represents an environmental state in which the species can survive. Any point outside of it is not considered a part of the species niche. The space can be defined by any number of relevant environmental variables that affect the species (Hutchinson 1957; Chase and Leibold 2009), eventually creating a multi-dimensional hyper volume. A less specialised species niche space would be distributed among all or a large portion of the environment's resources and conditions (Vandermeer 1972; Fig. 2.2a). A highly specialised species niche space would be relatively concentrated over one or a few resources or conditions (Vandermeer 1972; Fig. 2.2b). Modern applications of niche theory often incorporate both Hutchinson's and Elton's contributions, defining the ecological niche as the response that a species has to each point in Hutchinson's classical environmental space (measured as species survival rate, growth rate, or per capita rate of increase) and the effect that the species has on each point (measured as resource consumption, competition, etc.) (Leibold 1995; Shea and Chesson 2002; Chase and Leibold 2009). Information on species competition and predator-prey relationships is important when trying to define the role of a species in the environment or its relationship with other species. However, Hutchinson's definition is more appropriate when measuring resource specialisation of sharks because it only considers the resource requirements of species, which is precisely what resource use studies quantify. Moreover, although not impossible, it can be difficult to measure the response of a species in the wild and relate that response to a particular point and variable in the niche space. The advantage of using a "requirements only" approach is researchers do not need to measure response variables (Peterson *et al*. 2011).

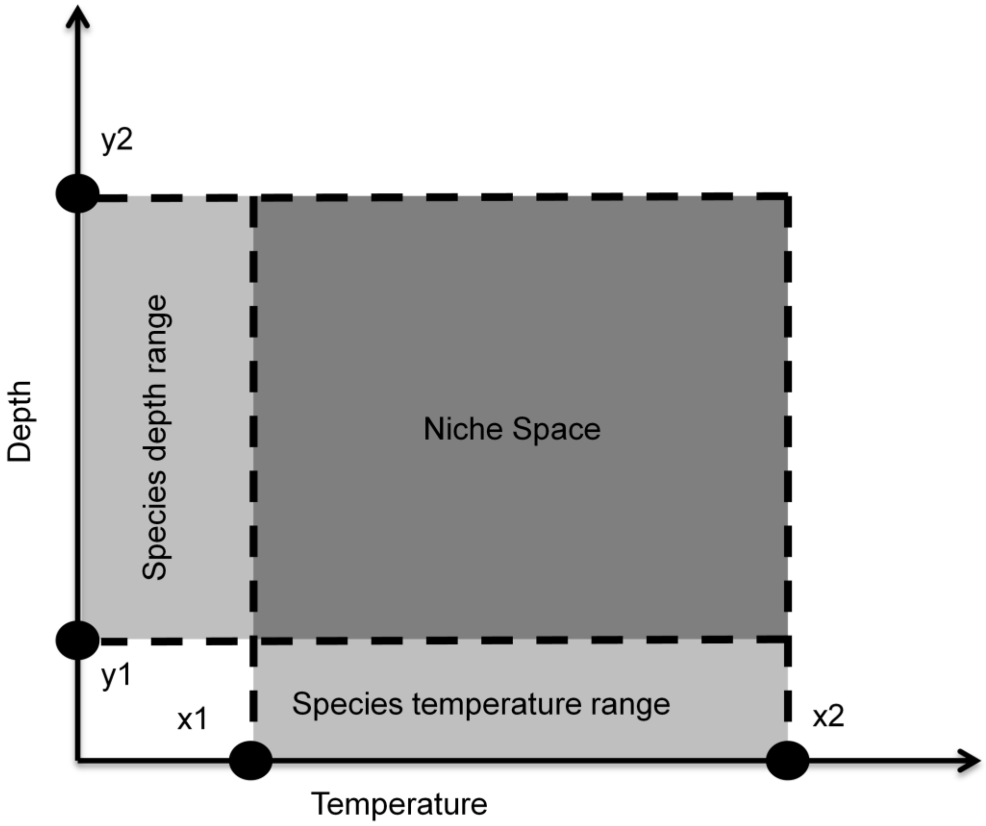

Fig. 2.1. A hypothetical example of Hutchinson's niche space with two commonly examined shark habitat use variables, depth (y) and temperature (x). x1 and x2 denote a species' temperature range, y1 and y2 denote a species' depth range. The dark grey space created by these overlapping ranges is the niche space of an organism, any point within which it can survive.

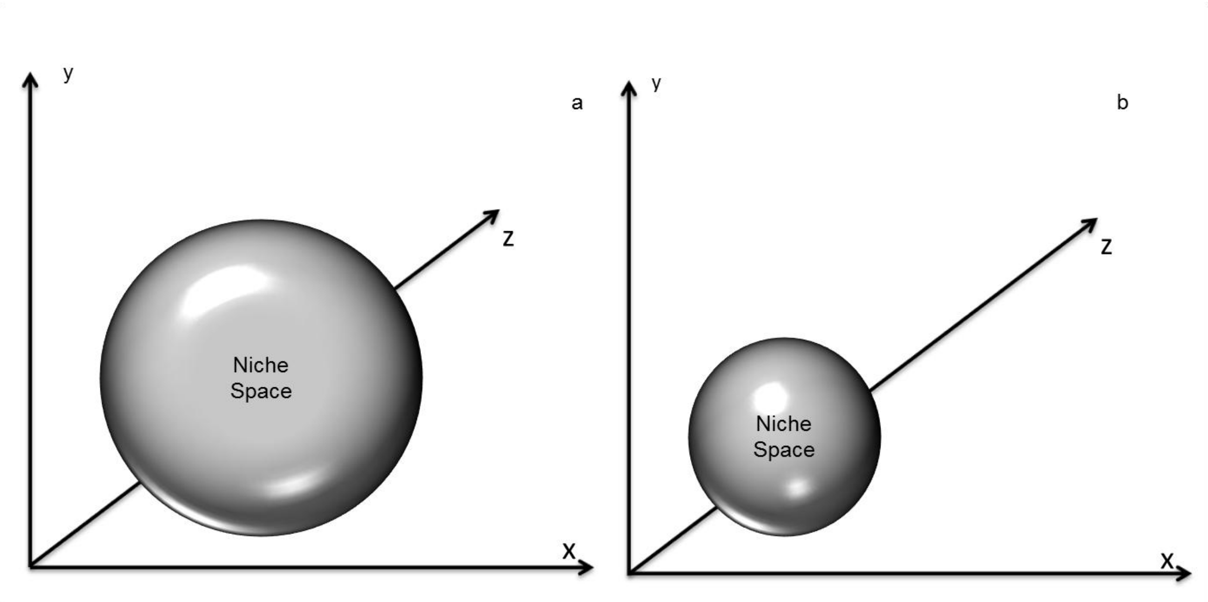

Fig. 2.2. (a) Hypothetical depiction of Hutchinson's (1957) niche hyper-volume of a species with a large niche breadth, indicating a lesser degree of specialisation (b); Hypothetical depiction of Hutchinson's (1957) niche hyper-volume of a species with a narrow niche breadth, indicating a greater degree of specialisation.

There are also numerous methods available to measure specialisation that incorporate Hutchinson's niche model. The best method for analysis will depend on the goals of the experiment. Regardless of the method chosen, at their core tests will compare the range of resources used by a species (the niche space) to the range of resources available in the environment, resulting in the relative niche breadth of the species (e.g. Smith 1982; Basille *et al*. 2008; Poisot *et al*. 2012). The inverse of the relative niche breadth can be used to measure the degree of specialisation.

Using Hutchinson’s definition of niche space and the continuum concept described earlier, it is possible to develop a widely applicable definition for measuring shark specialisation. I propose sharks, rather than being categorically defined, should be ranked along a continuum as more or less specialised relative to an index and other species. Ranks or positions along this continuum should be determined by measuring the resource niche breadth of a species as described by Hutchinson’s hyper-volume. Therefore, a highly specialised species can be defined as one with a relatively narrow niche breadth compared to the range of resources or conditions available within the environment. It is essential that the methods for measuring niche breadth use a scale or index. Methodologies should not rely solely on a binary system of classification or an arbitrarily value within an index above or below which a species is classified as a specialist. This violates the continuum concept that is the core of this definition. Note that the relevant environmental parameters will be based on the scale of the experiment and are best left to the researcher to define. However, definitions of the available environment will affect the interpretation of any measure of specialisation and its comparability to other studies. Therefore environment and scale should be carefully considered when utilizing ecological terminology, choosing appropriate methods, and making assessments.

This definition is well suited to sharks as specialisation is often measured at different temporal and physical scales. The environmental and temporal parameters of any study can be adjusted to suit a ranking system. The use of a continuum concept is also more ecologically realistic as many sharks are not likely to meet the traditional definition of a specialist or generalists. A rank system avoids the use of definitive categorical language when it is not appropriate. Finally, a ranking system which defines species as more or less specialised also makes it easier to compare trends between groups, even those separated over large distances that may be exposed to different resources. A ranking system that compares niche breadth instead of selectivity for a single resource may better account for differences in environmental circumstances.

Unfortunately, limited information on the diet or habitat use of many sharks currently precludes the ability to fully assess species resource specialisation. Therefore, the ranking of some species as more or less specialised will be unavoidably speculative. However, having a clear understanding of what is meant by specialist gives researchers the ability to better classify species, study their role in the environment, and communicate their findings.

2.4 Shark Habitat Specialisation

Species that have a high degree of habitat specialisation inhabit a smaller niche space compared to their less specialised counter parts. As a result habitat restricted species will occupy one end of the specialist continuum and those that use a large number of habitats will occupy the other. More specific rankings of organisms are affected by the scale of the study and the habitat parameters evaluated. Habitat use can be evaluated at large (e.g.Weng *et al*. 2005) or small scales (e.g. Morrissey and Gruber 1993) and specialisation can be measured across numerous variables, including depth (Knip *et al*. 2011), temperature (Campana and Joyce 2004), salinity (Heupel and Simpfendorfer 2008), and bottom type (Espinoza *et al*. 2011). Patterns in habitat use may also change over time (e.g. daily, seasonally) (Carlisle and Starr 2009; Ortega *et al*. 2009). Therefore, when analysing habitat specialisation it is important to clarify the scale of the study in relation to the continuum definition. On a local scale, most sharks are thought to have relatively large habitat ranges; however, there are few measurements of niche breadth or broad studies of habitat use for many shark species. Moreover, scale and methodology differ widely between studies, making it difficult to rank species against one another. Therefore, I will limit this discussion to better studied species and research testing selection or specialisation to highlight the importance of defining scale in resource use studies and the diversity among species.

On a global scale, species with low levels of habitat specialisation include the tiger shark, *Galeocerdo cuvier* and the great white shark *Carcharodon carcharias*. *Galeocerdo cuvier* has been found in temperate and tropical waters with reports of individuals being found as far north as Iceland and the United Kingdom (Compagno 1984; Randall 1992). They are also known to use coastal and offshore habitats (e.g. Randall 1992; Holland *et al*. 1999; Heithaus *et al*. 2007; Meyer *et al*. 2009). *Carcharodon carcharias* also have large, cosmopolitan geographic ranges and use both coastal and oceanic habitats (Compagno 2001; Bruce 2008; Jorgensen *et al*. 2010; Carlisle *et al*. 2012), and are known to undertake wide ranging migrations (Pardini *et al*. 2001; Boustany *et al*. 2002; Bonfil *et al*. 2005; Weng *et al*. 2007).

However, habitat use is more often evaluated at smaller scales (regionally and locally) and low specialisation rankings can be applied to species if the scale of evaluation is clear. For example, species may have low degrees of specialisation over a single environmental parameter. Juvenile lemon sharks *Negaprion brevirostris* acoustically tracked in nursery grounds in Bimini Island, Bahamas, showed no preference for specific water temperatures. Instead, individuals selected for the warmest possible waters during the day and cooler waters in the evening (DiGirolamo *et al*. 2012). As a result, individuals used the range of available temperatures within its home range in a day (DiGirolamo *et al*. 2012). Based on the proposed definition and measured at a local scale, the use of a wide range of temperatures relative to the daily available range indicates this population has a low degree of temperature specialisation. However, DiGirolamo *et al*. (2012) did not directly test species niche breadth or selectivity. Also note that while juveniles have a low degree of specialisation, there was selection for temperatures depending on the time of day. This highlights the importance of separating the concepts of specialisation and selection.

Species that have moderate habitat niches will have neither high nor low degrees of specialisation. Species with varying levels of resource selectivity, that may avoid some habitats while using others, will likely equate to a moderate niche breadth. Such species cannot be easily defined in categorical terms and demonstrate the usefulness of a continuum scheme for specialisation. For example, young bull sharks, *Carcharhinus leucas*, tracked in the Caloosahatchee River Estuary, Florida, showed strong avoidance for areas with salinities less than 7 while showing affinity for salinities between 12 to 20 (Heupel and Simpfendorfer 2008). Heupel and Simpfendorfer (2008) suggested juveniles may have been selecting for salinity ranges that reduced their osmoregulatory costs. The importance of salinity in predicting the distribution of young *C. leucas* was also suggested by Simpfendorfer *et al*.

(2005), however, this study did not use selectivity indices to analyse behaviour. Although niche breadth was not measured, the avoidance of some salinity ranges and the selection of others would likely result in a moderate niche breadth and degree of specialisation for this population. This example also demonstrates the importance of clarifying definitions for selection and specialisation. *Carcharhinus leucas* may be selecting for specific salinities, but they are not highly ecologically specialised along this parameter. Scale and location will also affect how a ranking is determined. For example, although *G. cuvier* utilizes a wide range of habitats globally, on a local scale they appear to select for specific microhabitats. Acoustically tracked *G. cuvier* in Shark Bay, Western Australia, selected for shallow banks covered in seagrass and avoided deeper sand habitats (Heithaus *et al*. 2006). Selectivity was likely the result of increased prey availability within shallow areas (Heithaus *et al*. 2002; Heithaus *et al*. 2006). As a result *G. cuvier* habitat niche breadth in nearshore areas is likely smaller than that expected at a global level.

A lack of studies that measure the habitat niche breadth of sharks makes any speculative rankings presented here potentially controversial. However, some of the best examples of habitat specialisation among sharks are coral reef associated species, a notable exception being the blacktip reef shark, *Carcharhinus melanopterus* (Chin *et al.* 2012). Species with high degrees of specialisation likely include the whitetip reef shark *Triaenodon obesus,* the grey reef shark *Carcharhinus amblyrhynchos,* and the Caribbean reef shark, *Carcharhinus perezi*. *Triaenodon obesus* is most often found within or very near reef habitat and its morphology indicates it is well adapted to forage in reef environments (Randall 1977; Last and Stevens 2009; Whitney *et al*. 2012). *Carcharhinus amblyrhynchos* is almost exclusively found on and near reef habitat (Compagno 1984; McKibben and Nelson 1986; Economakis and Lobel 1998; Heupel and Simpfendorfer 2014), although individuals may make long distance movements between habitat patches (Heupel *et al*. 2010). *Carcharhinus perezi* is also closely associated with reef habitat (Pikitch *et al*. 2005; Garla *et al*. 2006a; Garla *et al*. 2006b; Chapman *et al*. 2007).

Unfortunately, determining where sharks should be placed along the specialist continuum is limited as little is known about the habitat preferences of most species. Data collection is hindered by the difficulties associated with habitat use evaluation, particularly in the marine environment. Traditional techniques used to evaluate animal movements and habitat preferences, such as tag and recapture and fishing surveys, only provide short-term (< 10 yr) data and do not monitor the lifetime of an individual. While these studies can offer valuable insight into animal distribution (Kohler and Turner 2001), population size (Dicken *et al*. 2008), and survival rates (Gruber *et al*. 2001), these techniques only provide snapshots of individual habitat use (Gruber *et al*. 1988; Holland *et al*. 1993; Holts and Bedford 1993). It may also be difficult to measure the availability of various habitat types and variables meaningful to the animals in the environment. Therefore, accumulating data for habitat use assessments can be a slow process and the degree of habitat specialisation of many species will remain uncategorized in the near future. However, based on the previous examples it is clear there is significant variance in the habitat specialisation and selection patterns of sharks. These examples also demonstrate how defining scale and intent has a large influence on the use of ecological terminology and its interpretation. By utilizing a continuum concept of specialisation, parameters can be set according to the needs of the research and result in less arbitrary use of terms. Detailed analysis of shark habitat use incorporating sound definitions as well as new techniques may reveal that more species are highly selective or more specialised than currently known.

2.5 Shark Dietary Specialisation

Optimal foraging theory states that individuals should attempt to forage at maximum efficiency to ensure a large net energy return for their efforts (Townsend and Winfield 1985; Stephens 1986). However, evaluation of foraging theory and dietary specialisation are context dependant. Fluctuating factors such as competition may cause species that naturally adopt opportunistic feeding patterns to become highly selective (e.g. Papastamatiou *et al*. 2006). Diets may differ between species, populations of the same species, and between age classes and sexes within populations (Bethea *et al*. 2006; Edwards *et al*. 2011; Sommerville *et al*. 2011). Reasons for this include differences in body shape and size, ability to locate and capture prey, and ability to process and digest what has been caught (Lowe *et al*. 1996; Heupel and Bennett 1998; Dean *et al*. 2005; Bethea *et al*. 2006; Brischoux *et al*. 2011). Predator avoidance tactics may lead to a different diet than that predicted by optimal foraging theory (Gill 2003) and individuals may forage sub-optimally if doing so reduces their exposure to predation (Heithaus and Dill 2002). Finally, dietary analysis can be skewed by temporal shifts in prey availability where predators switch between prey items as they become more or less available (e.g. Lucifora *et al*. 2006). Therefore, evaluations over short time scales may be misleading in fluctuating environments. The method of evaluation may also affect definitions and interpretations of species dietary patterns. For example, traditional methods such as stomach content analysis provide detailed information on dietary patterns (e.g. Ba *et al*. 2013) , whereas stable isotope analysis, an increasingly popular method for shark diet and movement analysis, can provide long term, integrated data (Hussey *et al*. 2012a). Therefore, when measuring niche breadth or diet selectivity it is necessary to consider environmental and morphological variables and what is available to the predator, both in terms of prey abundance and what it has the ability to capture (Backwell *et al*. 1998). Therefore, similar to habitat analysis, it is important to clarify the temporal and spatial scale and intention of a study when calculating diet specialisation and selection.

At a global scale, species that are traditionally considered to have low degrees of dietary specialisation include the spiny dogfish *Squalus acanthias*, which feeds on a diverse array of prey over its entire range (Jones and Geen 1977; Compagno 1984; Hanchet 1991; Tanasichuk *et al*. 1991; Link and Ford 2006; Brodeur *et al*. 2009). In Argentinean waters, *S. acanthias* feeds on teleosts, squid, ctenophores and molluscs (Alonso *et al*. 2002). In the southeastern Black Sea, *S. acanthias* preys on teleosts, crustaceans, sea anemones and nematodes (Avsar 2001). Larger species with broad diets include *G. cuvier.* In Hawaiian waters, large individuals (>200 cm) were found to have a varied diet that included teleosts, elasmobranchs, crustaceans, birds, mammals, turtles, and cephalopods (Lowe *et al*. 1996). In Australian waters, *G. cuvier* also has a wide dietary niche. Individuals on the western Australian coast feed on teleosts, crustaceans, marine mammals and reptiles, elasmobranchs and cephalopods (Heithaus 2001; Simpfendorfer *et al*. 2001a), while on the north eastern coast *G. cuvier* feed on teleosts, marine reptiles, crustaceans, and to a lesser extent marine mammals and cephalopods (Simpfendorfer 1992a). At a smaller regional scale, stomach content analysis of the small spotted cat shark *Scyliorhinus canicula* from the north eastern Atlantic coast found the species fed on a variety of prey, including crustaceans, teleosts, annelids, and molluscs (Ellis *et al*. 1996). The dietary niche of *S. canicula* was calculated and equated to a low degree of dietary specialisation. In comparison to other species similarly surveyed in the same study, it had one of the largest dietary niches.

Variability in diet selectivity can result in niche breadths that rank species in between the two extremes of the specialisation continuum. For example, Baremore *et al*. (2008) examined the stomach content of Atlantic angel sharks *Squatina dumeril* captured in the northeastern Gulf of Mexico and compared it to the trawl fishery catch composition to calculate *S. dumeril* niche breadth index and dietary selectivity. Stomach content analysis revealed *S. dumeril* fed on a variety of prey, but when compared to prey availability, the diet of *S. dumeril* equated to a moderate niche breadth (Baremore *et al*. 2008). These results indicated *S. dumeril* was neither highly specialised nor generalised. Thus, *S. squatina* demonstrated both opportunistic and selective behaviours by feeding on fish in high abundance (opportunistic) as well as fish and cephalopods found in relatively low abundance (selective). This example also highlights the importance of using the continuum concept to measure specialisation rather than trying to categorically define species as either specialists or generalists. Varied patterns in behaviours and changing conditions may result in niche breadth values that cannot be easily designated as one or the other.

Dietary selectivity can also change as the result of fluctuations in prey abundance and availability over time and space. Changes in dietary patterns can affect niche breadth measurements and alter the predicted placement of a species on a specialisation continuum. For example, although juvenile *N. brevirostris* has a broad dietary niche, and therefore has a low degree of specialisation, a controlled field-pen study found *N. brevirostris* may be a highly selective predator. Caged *N. brevirostris* were fed varying ratios of two prominent prey in their diet, the grey snapper *Lutjanus griseus* and the yellow fin mojarra *Gerres cinereus*. Results showed *G. cinereus* was selected for over *L. griseus* and that selectivity for *G. cinereus* increased as its relative abundance increased, highlighting the effect of changing prey abundance on diet and indicating *G. cinereus* is a preferred prey (Reeve *et al*. 2009).

Both *N. brevirostris* dietary selectivity and preference for mojarra (Gerreidae) were supported by field based stomach content analysis (Newman *et al*. 2010). Populations within the bays of Bimini Island selected for prey based on type and size when environmental conditions were favourable and prey abundance was high (Newman *et al*. 2010). However, populations fed more opportunistically in relatively poor conditions. This result suggests niche breadth and feeding strategies change in response to environmental fluctuations. High levels of selectivity for specific types of prey in favourable conditions may result in a more specialised diet than when conditions are poor.

Competition can also have a powerful influence on dietary selection. Co-occurring shark species surveyed in the coastal waters of Hawaii showed limited dietary overlap, but when the diets of these species were surveyed in areas where they did not co-occur, high dietary overlap was observed (Papastamatiou *et al*. 2006). This suggests that to reduce competition for resources, each species selected for a non-overlapping subset of resources in the environment. However, when competition was removed or reduced, species adopted wider dietary niches. Spatial variation in selection would create variable rankings for the same species and confound a binary attempt to define the species or adjacent populations.

It is important to note that some populations that have large dietary niches may be composed of individual specialists, where each individual uses a subset of resources within the population's broader dietary niche (Bolnick *et al*. 2002). The combination of individual non-overlapping, selective diets results in a wide dietary niche for the population. Surveys of populations that do not test for the presence of individual specialisation may incorrectly classify individuals as having large dietary niches (Bolnick *et al*. 2002; Bolnick *et al*. 2003).

However, it is difficult to determine how common this strategy is among sharks as it has only recently been investigated among a few species. Matich *et al*. 2011 quantified the dietary patterns of *C. leucus* and *G. cuvier*, both of which have traditionally been defined as generalist predators, using several individual specialisation indices. The indices revealed that individual *G. cuvier* had wider ranging diets relative to individaul *C. leucus* which had more specialised dietary profiles. This suggests the broad dietary range of *C. leucas* may be the result of individual specialisation, not each individual feeding on a large number of prey (Matich *et al*. 2011). More detailed analysis will hopefully determine if indivudal specailisation is a widespread or significant strategy within the taxon.

To date there are few studies that have been able to identify species that exhibit high degrees of dietary specialisation and that can be labelled as such without debate. However, there are some examples where species can be classified as highly specialised. On a global scale, deitary specialists include basking sharks *Cetorhinus maximus* and whale sharks *Rhincodon typus*, both of which have a highly specialised feeding mechanism (Hallacher 1977; Colman 1997) evolved to capture prey of a specific size, namely zooplankton (Colman 1997; Sims and Quayle 1998; Stevens 2007). In the case of *R. typus,* prey include fish spawn and plankton (Martin 2007), crab larvae (Meekan *et al*. 2009), copepods (Clarke and Nelson 1997; Motta *et al*. 2010), and krill (Jarman and Wilson 2004). On smaller geographic scales, a potential dietary specialist includes *F. macki*, a species endemic to western Australia (Last and Stevens 2009). Although the diet of *F. macki* was not compared to prey availability, stomach content analysis revealed this species feeds almost exclusively on octopus and other cephalopods. The diet of *F. macki* was significantly less varied than other shark species captured simultaneously in the same habitats (Simpfendorfer *et al*. 2001b). Stomach content analysis of the starry smooth-hound *Mustelus asterias* captured in trawl surveys on the north eastern Atlantic coast showed this species almost exclusively consumed brachyuran crabs. Niche breadth measurements revealed *M. asterias* had a high degree of dietary specialisation in comparison to almost all other elasmobranchs examined in the study (Ellis *et al*. 1996).

The term specialist can also be applied at smaller physical or temporal scales; however context must be clearly articulated. For example, the stomach contents of the school shark *Galeorhinus galeus* surveyed in Anegata Bay, Argentina revealed this species had a broad dietary niche (Lucifora *et al*. 2006). However, Lucifora *et al*. (2006) found that during the astral summer the diet of *G. galeus* became highly specialised when individuals fed almost exclusively on the benthic teleost the Atlantic midshipman *Porichthys porosissimus* (Lucifora *et al*. 2006). This seasonally small niche breadth was likely the result of opportunistic foraging on the seasonally vulnerable *P. porosissimus. Porichthys porosissimus* mates in the spring and summer when males use sound and bioluminescent displays to attract their mates. Lucifora *et al*. (2006) hypothesized these displays make *P. porosissimus* more vulnerable to predators and as a result are more easily targeted in summer than at other times of the year. However, caution should be used when considering a species highly specialised over small scales to ensure there is no confusion over intent.

2.6 Implications of Resource Use Strategies

Ecological theory states that the niche breadth differences between species are the product of an evolutionary trade-off between the ability to use multiple resources and the ability to use each one. Different strategies result in unique costs and benefits for species (Van Tienderen 1991; Kawecki 1994). Ecological specialisation of sharks will also affect their role in an ecosystem, such as the intensity and spread of direct and indirect effects of predation (Heupel *et al*.2014). Therefore, defining the resource use patterns of sharks can help to determine the implications of their depletion or removal. Understanding the trade-offs and vulnerabilities associated with ecological specialisation can create a clearer picture of environmental dynamics and the role of sharks.

The ability to use multiple resources, and therefore have a low degree of specialisation, is advantageous during times of environmental instability (Chapman and Mackay 1984; Heithaus *et al*. 2006; Meyer *et al*. 2010). Species with wide niches can use resources unaffected by environmental fluctuations and/or use multiple resources to compensate for the decline in any one resource (Richmond *et al*. 2005; Julliard *et al*. 2006; Verberk *et al*. 2010). Thus, species with wide resource niches can maintain a high level of fitness in unstable environments and will not be as greatly affected by environmental changes than highly specialised species (Richmond *et al*. 2005; Julliard *et al*. 2006; Chin *et al*. 2010; Verberk *et al*. 2010). However, these plastic adaptations may incorporate anatomical, physiological, or behavioural mechanisms that require high levels of energy (DeWitt *et al*. 1998). If environments are stable, these high energetic costs may outweigh the benefits of being highly adaptive (Van Tienderen 1991; Wilson and Yoshimura 1994; DeWitt *et al*. 1998)

In contrast, high degrees of specialisation are associated with the reduction in or loss of physiological, morphological, or behavioural characteristics, which theoretically reduces energetic costs (Futuyma and Moreno 1988). By adapting to use only one or a few resources, species avoid the high costs of adaptive plasticity (Van Tienderen 1991). Resource detection performance is also greater when an animal is only searching for one item (Futuyma and

Moreno 1988; Bernays and Wcislo 1994; Bernays and Funk 1999). Highly specialised species may also utilize resources and assimilate energy from preferred sources more efficiently than species with broad resource niches (Britt *et al*. 2006). Therefore, if fluctuations in the environment are limited and the preferred environmental state is abundant, specialisation may be a more successful life strategy (Futuyma and Moreno 1988; Richmond *et al*. 2005). However, species with high degrees of specialisation incur costs when their preferred resource is not available. Highly specialised species cannot easily switch between resources and as a result, when environmental conditions are in a state of flux, they may have difficulty adapting to the new environmental equilibrium (Dulvy *et al*. 2004; Munday 2004; Chin *et al*. 2010). Thus, highly specialised shark species are at increased risk to population decline as a result of environmental and anthropogenic changes compared to species with large ecological niches.

2.7 Conclusion

Sharks have been historically described as roaming generalists that feed on whatever resources become available. In reality, various strategies are present among shark species, including selective and opportunistic feeding behaviours as well as highly specialised resource use patterns. As the field of shark ecology expands and advances, it is important to develop clear, inclusive, and theoretically sound definitions and methodologies to study resource use at small and large scales. Doing so will allow for efficient communication of ideas and more comparable research. Shark ecology, compared to other fields of ecological research, is in its early days, and detailed studies of resource selection and niche breadth have only recently become a prominent feature of the shark literature. This provides shark researchers with a unique opportunity. Shark ecologists can avoid some hurdles associated with applied ecological studies by deciding now what the most appropriate theoretical basis is to ground analytical studies.

Although it is difficult to quantify the resource use patterns of many shark species due to limited data, this will change as research progresses, and having a structured paradigm within which to evaluate behaviours will be invaluable to furthering research and communication. Improved knowledge of where shark species fall on the specialisation continuum will result in more accurate predictions of the effects of human induced changes and the development of more effective environmental management. Future research aimed at examining resource use and selectivity of sharks should ensure that tests are based in well supported theoretical schemes and authors clarify their intent by defining terminology and ensuring they are only used when appropriate.

Chapter 3

General Methods

3.1 Acoustic Analysis

3.1.1 Study Site

Acoustic tracking was conducted in Cleveland Bay, Queensland, a shallow embayment on the northeast coast of Australia (Fig. 3.1). Cleveland Bay covers an area of approximately 225 km^2, is 27 km wide, and the majority of the bay has a depth of less than 10 m and a maximum tidal range of 4.2 m. The dominant habitat is soft mud substrate and to a lesser extent sandy substrate. The bay also contains patches of seagrasses (*Cymodocea serrulata, Halophila spp., Halodule uninervis*) and coastal reefs. The southern shore of the bay is lined with mangroves. The main river outlets are on the southeastern side of the bay and are adjacent to intertidal mudflats and seagrass habitat. Sixty-three VR2W acoustic receivers (Vemco Ltd., Canada) were deployed inside Cleveland Bay to monitor shark movements. Receivers were deployed in primary habitat types within the bay, specifically intertidal mudflats, outer bay mud substrate (> 5 m depth), sandy inshore substrate, reefs, and potential seagrass (here after referred to as seagrass). Receiver habitat type was assessed by scuba divers during initial deployment. Benthic habitat assessments in Cleveland Bay by the James Cook University program Seagrass Watch (seagrasswatch.com.au) were also used to determine the habitat designation of each receiver. The distribution of intertidal mudflats, outer bay mud substrate, sandy inshore substrate, and reef was consistent. However, seagrass distribution can change on a seasonal basis. It was not possible to conduct detailed benthic surveys throughout the study, therefore seagrass habitat was designated as potential seagrass habitat to acknowledge potential changes in density of seagrass over time. Data were downloaded from receivers

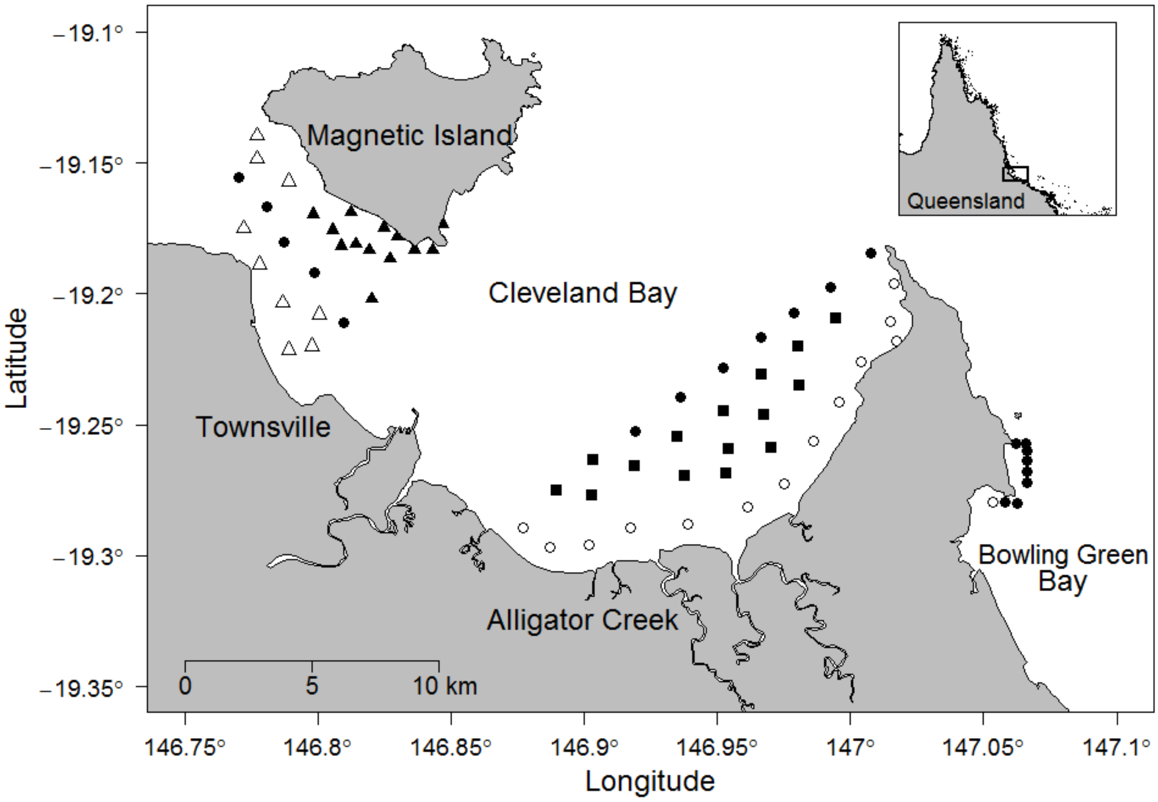

Fig. 3.1. Cleveland Bay, Queensland, Australia, locations of receivers in intertidal mudflat (○), seagrass (■), outer bay mud substrate (●), inshore sand (Δ), and reef habitat (▲).

every three months. An additional nine receivers were deployed by the Australian Institute of Marine Science (AIMS) in Bowling Green Bay adjacent to the southeast of Cleveland Bay. The majority of these receivers were deployed between depths of 9.2 to 11.0 m with mud substrate. Therefore they were classified as outer bay mud substrate receivers. Data from these receivers were not included in habitat, space use, or residency analysis.

3.1.2 Study Species

The study species for this research were the Australian sharpnose shark, *Rhizoprionodon taylori* (family Carcharhinidae; Fig. 3.2) and the creek whaler, *Carcharhinus fitzroyensis* (family Carcharhinidae; Fig. 3.3). *Carcharhinus fitzroyensis* is endemic to northern Australia although *R. taylori* can also be found on the southern coast of Papua New Guinea. The two species have closely overlapping coastal ranges, where *R. tayori* is found from Carnarvon (WA) to Moreton Bay (QLD) and *C. fitzroyensis* is found from Cape Cuvier (WA) to Gladstone (QLD) (Last and Stevens 2009). Both species most commonly inhabit turbid nearshore waters, but *R. taylori* has occasionally been captured on the outer contential shelf (Last and Stevens 2009). Niether species is a major compoenent of northern Australian fisheries. *Rhizoprionodon taylori* is not directly targeted as it is too small to be of any value, however it is occasionally taken in large amounts as by catch in inshore gillnet and trawl fisheries. *Carcharhinus fitzroyensis* is taken in small numbers by the Australian gillnet fishery for meat. Teleosts and crustaceans constitute the majority of the diet of both species (Simpfendorfer 1998; Last and Stevens 2009). Although these species inhabit simalar envorinments and have similarly broad diets, *R. taylori* and *C. fitzroyensis* have distinct life history strategies.

Fig. 3.2. (a) *Rhizoprionodon taylori* from Last and Stevens (2009) and (b) photo of *R. taylori* (photo credit Centre for Sustainable Tropical Fisheries and Aquaculture).

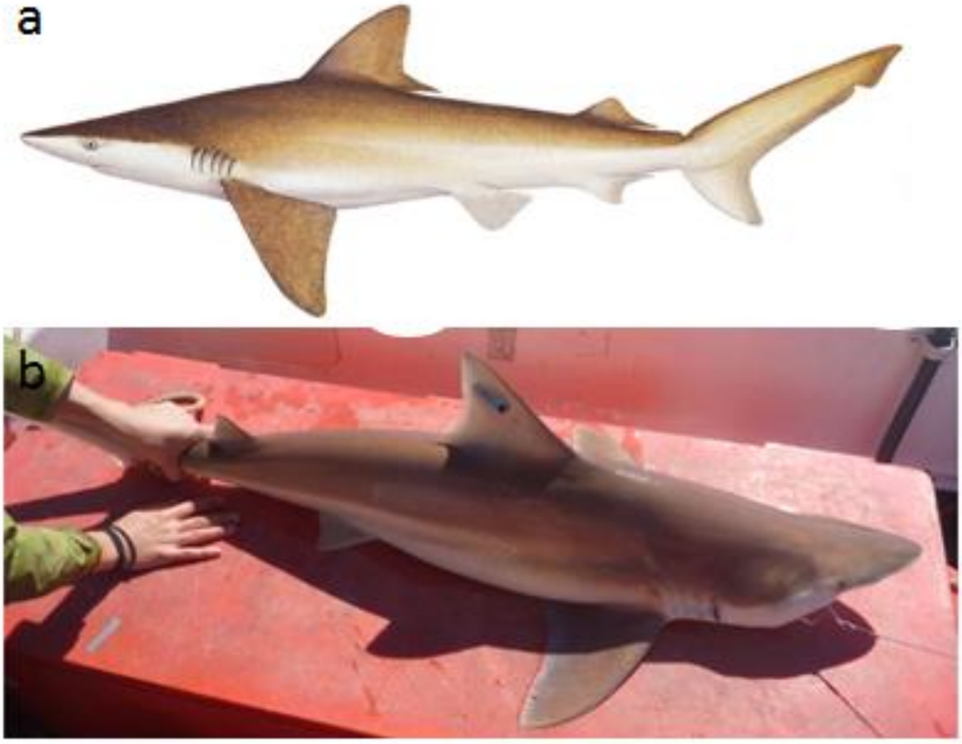

Fig. 3.3. (a) *Carcharhinus fitzroyensis* from Last and Stevens (2009), (b) photo of *C. fitzroyensis* (photo credit Vinay Udyawer).

Rhizoprionodon taylori is an abundant, small-bodied, fast growing, highly productive species (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 to 810 mm TL (Simpfendorfer 1992b; Simpfendorfer 1993). Age at maturity is approximately one year and females can give birth to 1 to 10 pups per litter (mean = 4.5) (Simpfendorfer 1992b; Simpfendorfer 1993). This species has an annual reproductive cycle. Mating occurs in austral summer (December to February) and gestation lasts approximate 11.5 months. *Rhizoprionodon taylori* is the only shark species known to incorporate a period of embryonic diapause in its reproductive cycle. This may allow *R. taylori* to delay giving birth until conditions are favourable (Simpfendorfer 1992b; Waltrick *et al*. 2012).

In contrast, *C. fitzroyensis* is a medium-bodied species that is relatively slow growing and late to mature (Last and Stevens 2009). Size at birth is approximately 500 mm TL; males mature at approximately 800 mm TL and females 900 mm (Garrick 1982; Lyle 1987). Age at maturity is approximately six years. Adults grow to approximately 1350 mm. (Lyle 1987; Last and Stevens 2009). Age and growth estimates suggest females grow 200 mm larger than males (Smart *et al.* 2013). Female *C. fitzroyensis* give birth every year with 1 to 7 pups per litter (mean=3.7) following a gestation period of approximately 7 to 9 months (Lyle 1987).

Little is known about the movement and habitat use of either species. Previous catch data indicates that neonate *C. fitzroyensis* are found in intertidal zones, but appear to move out as they grow (Harry *et al*. 2011). There is no published data on *R. taylori* habitat use or movement. As both these species are closely associated with nearshore environments, *C. fitzroyensis* and *R. taylori* may influence nearshore ecosystem dynamics and may be affected by changes within nearshore areas.

3.1.3 Field Methods

Study species were captured using bottom-set 400-m long-lines, 200-m long 11.45-cm mesh gillnets, and baited rod and reel. Long-lines were made of 6-mm nylon mainline that was anchored at both ends. Gangions were composed of 1 m of 4-mm nylon cord and 1 m of 1.5-mm wire leader. Approximately 50-70 size 14/0 Mustad tuna circle hooks were used per long-line and baited with butterfly bream (*Nemipterus* sp.), squid (*Loligo* sp.), blue threadfin (*Eleutheronema tetradactylum*), or mullet (*Mugil cephalus*). Long-lines were set for 45 to 60 minutes, gillnets were set for 15 to 20 minutes. *Rhizoprionodon taylori* and *C. fitzroyensis* were fitted with V13 and V16 acoustic transmitters (Vemco Ltd., Canada) respectively (Fig. 3.4). Transmitters were implanted into the body cavity (Fig. 3.5a) and the incision was closed with absorbable sutures. Individuals were measured to the nearest millimetre stretch total length (STL), sexed, tagged with an individually numbered Rototag in the first dorsal fin, and released (Fig. 3.5b). Umbilical scar condition, stretch total length (Last and Stevens 2009) and clasper calcification (males) were used to determine individual age and classify individuals as immature or mature. Range testing analysis found V13 and V16 transmitters had a maximum detection range of 525 m and 900 m respectively based on 0.05 probability of detection (Kessel *et al.* 2013) and emitted a unique code as a pulse series at 69 kHz. Unique transmitter codes allowed for the identification of individuals.

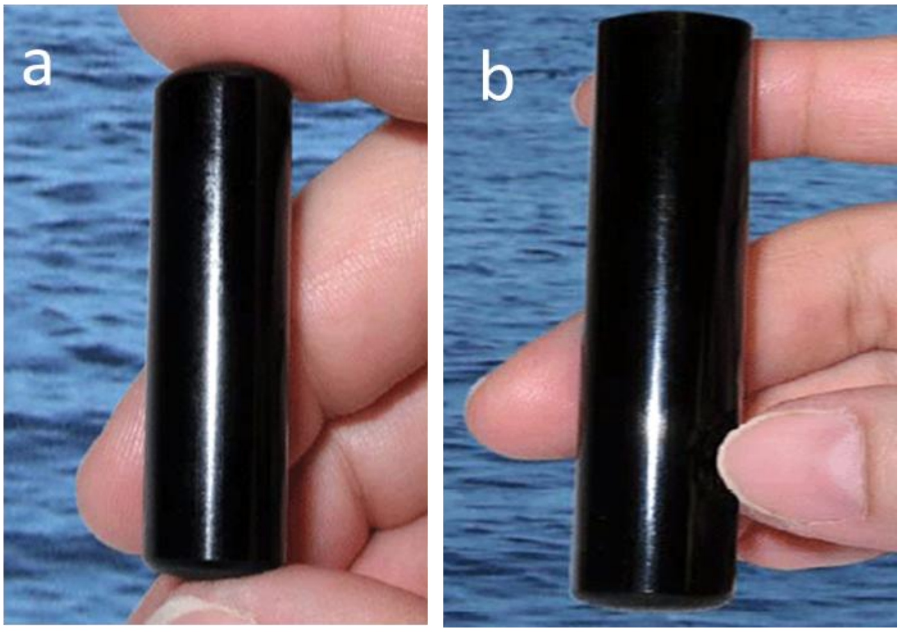

Fig. 3.4. (a) V13 and (b) V16 acoustic transmitters (photo credit Vemco Ltd., Canada).

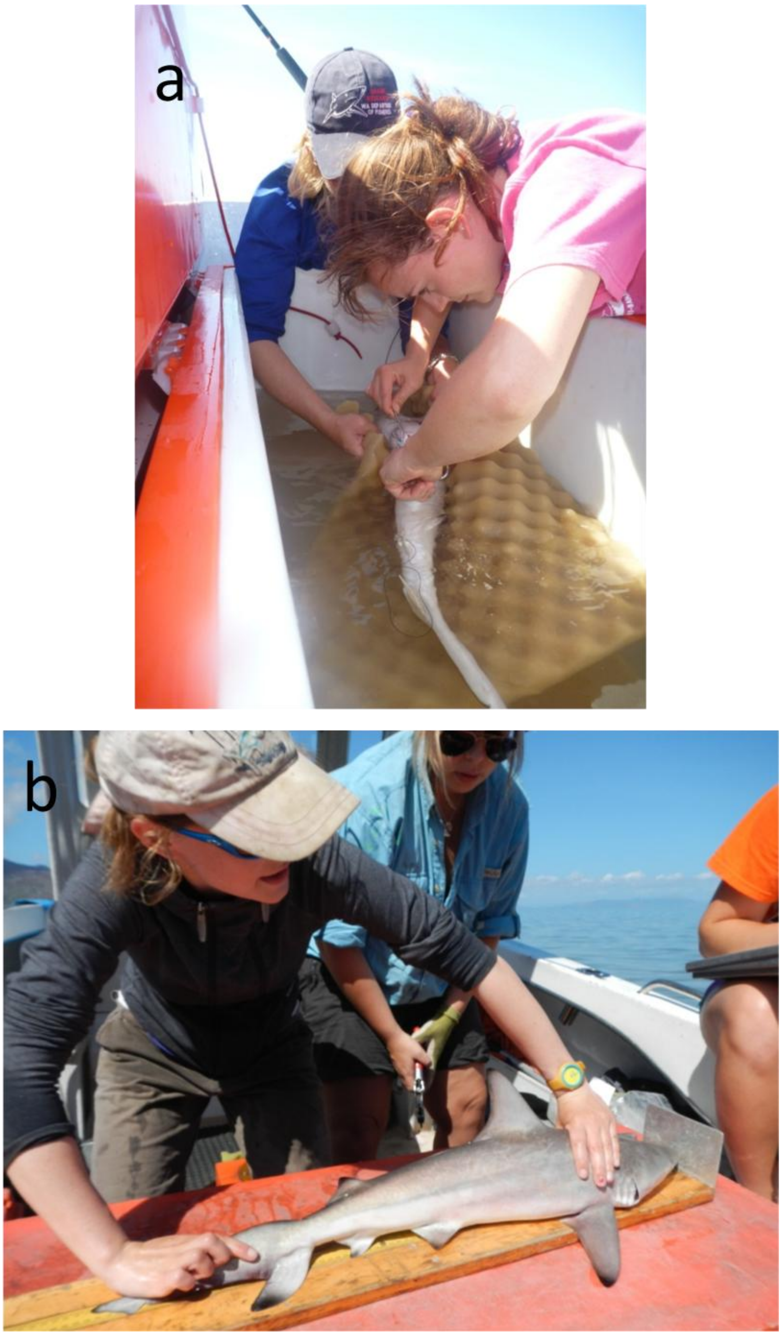

Fig. 3.5. Surgery and processing procedures for sharks, (a) surgical implantation of V13 acoustic transmitter (b) measuring and tagging of a captured shark.

3.2 Stable Isotope Analysis

3.2.1 Study Site

Shark tissue samples were collected from five bays 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. 3.6). Cleveland Bay occupies a central location among the sample bays. Linear distances between adjacent bays ranged from 30 to 150 km.

The primary bottom type in all bays is mud and seagrass beds (GBRMPA 2011). Cleveland Bay and Repulse Bay also contain small patches of reef. Shorelines are primarily composed of sandy beaches, mudflats, and mangroves. Cleveland Bay is adjacent to Townsville, a moderately large north Queensland city. In contrast, the remaining four embayments abut large expanses of farm land that is primarily used to grow sugarcane. Average annual freshwater input is variable between bays. On average, Repulse Bay and Rockingham Bay receive higher volumes of freshwater input annually via rivers than Bowling Green Bay and Cleveland Bay (Furnas 2003). One of the largest rivers in north Queensland, the Burdekin River, drains into the coast at the mouth of Upstart Bay (Furnas 2003). However, the output from Burdekin River generally flows north. As a result, Upstart Bay, which is located south of Burdekin River, receives relatively little freshwater input. Terrestrial areas adjacent to Repulse Bay and Rockingham Bay also receive more rain fall (1600-2400 mm) annually than Cleveland Bay and Bowling Green Bay (1000-1200 mm), with Upstart Bay receiving the least (800-1000 mm) (Australian Government Bureau of Meteorology).

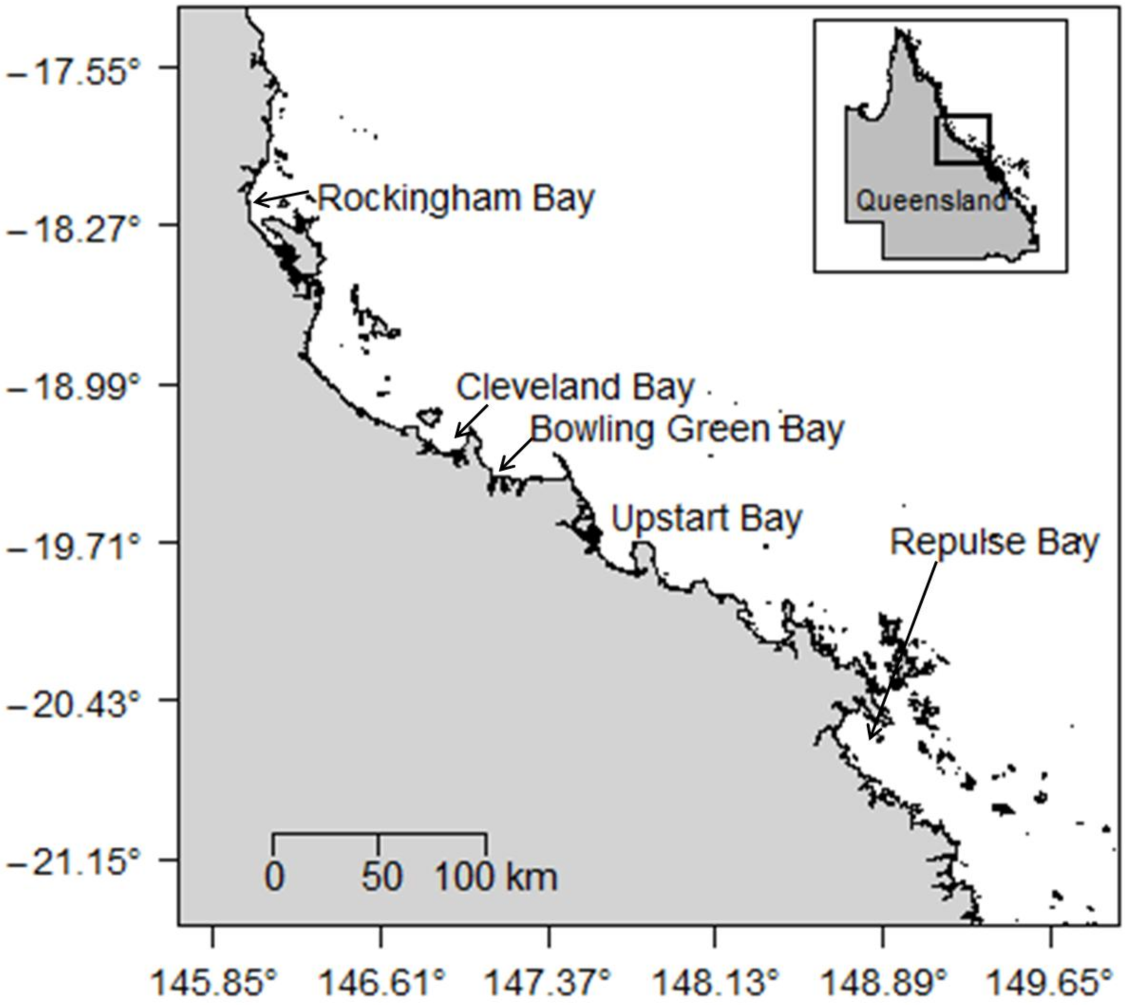

Fig. 3.6. Stable isotope sampling region for *Rhizoprionodon taylori* indicating the five sample bays. Inset indicates location along the north Queensland coast, Australia.

3.2.2 Study Species

Isotope analysis was limited to *R. taylori*. Unfortunately, due to the relative rarity of *C. fitzroyensis* the collection of sufficient samples for isotope analysis for this species was not possible in the available time frame.

3.2.3 Field Methods

Each bay was sampled twice, once in the austral summer (November-March) and once in austral winter (June -August). Individuals were captured using a combination of bottom-set 400-800 m long-lines and 200-400 m long, 11.45 cm mesh gillnets. Long-lines were constructed as described in Section 3.1.3. Approximately 50-70 size 14/0 Mustad tuna circle hooks were used per long-line and baited with butterfly bream (*Nemipterus* sp.), squid (*Loligo* sp.), blue threadfin (*Eleutheronema tetradactylum*) and mullet (*Mugil cephalus*). Long-lines and gillnets were set for 45 to 60 minutes. Captured sharks were measured to the nearest millimetre stretch total length (STL), sexed, and tagged with a uniquely numbered Rototag in the first dorsal fin. Muscle and plasma tissues were collected for stable isotope analysis and individuals were released. One cm^3 of muscle was sampled from behind the first dorsal fin. Blood samples were collected using a heparinised needle and syringe from the caudal vein anterior to the tail. Two ml of blood were collected from each individual (Fig. 3.7a). A portable centrifuge was used on board the vessel to spin and separate blood samples into plasma and RBC (red blood cell) components (Fig. 3.7b). Plasma and RBC layers were pipetted into separate 1.5 ml Eppendorf safe lock microcentrifuge tubes. All 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 remaining four bays

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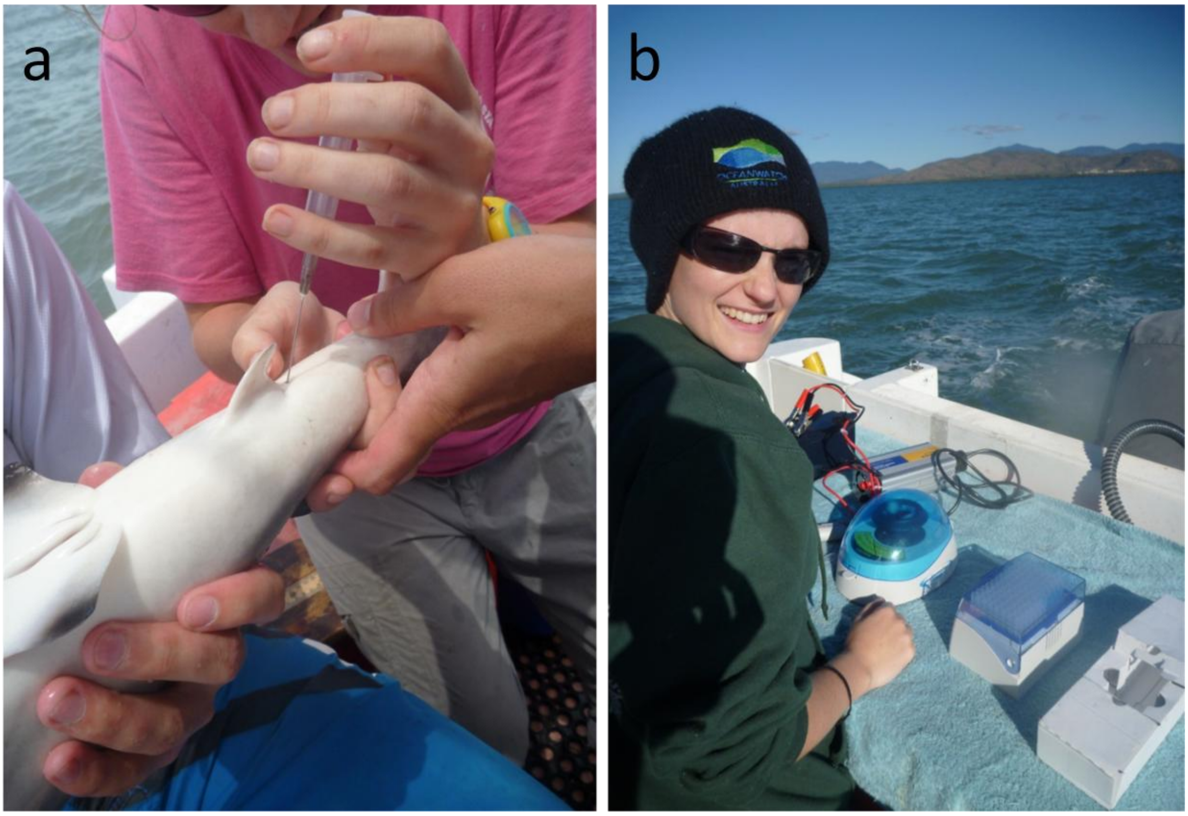

Fig. 3.7. (a) Blood extraction from *Rhizoprionodon taylori* and (b) on board centrifuge equipment.

were kept on ice in the field and stored in a Taylor-Wharton CX100 Dry Shipper (-80^{o}C) until return to the laboratory where samples were frozen (-20^{o}C).

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 *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).

Data suggest *R. taylori* is a demersal predator, although it could not be conclusively determined if they forage from benthic and/or pelagic food chains within nearshore areas (Simpfendorfer, 1998). Therefore, baseline benthic and pelagic $\delta^{13}C$ ($^{13}C/^{12}C$) and $\delta^{15}N$ ($^{15}N/^{14}N$) food web sources were collected from each bay to establish local values. Seagrass and macroalgae were used to establish benthic food web $\delta^{13}C$ and $\delta^{15}N$ sources and were sampled opportunistically from fishing locations in each bay. Plankton was used to establish pelagic $\delta^{13}C$ and $\delta^{15}N$ food web sources and were collected using horizontal surface tows with a 0.85 m long, 300-mm diameter plankton net (53 micron mesh). Plankton samples were collected from a central location in each bay approximately 5 km from shore. Plankton samples included zooplankton and some invertebrates. Samples of all plant and plankton material were kept on ice while in the field and frozen upon return to the laboratory as described for shark tissues

3.2.4 Sample Preparation and Isotope Analysis

Shark tissue samples were freeze dried and ground into a powder with a mortar and pestle. Seagrass and macroalgae were thawed, rinsed in distilled H_20, and cleaned of visible residue and epiphytes. After cleaning, seagrass and macroalgae were oven dried at 60^oC for 48 hours and ground into a powder. Zooplankton and phytoplankton were not separated to ensure there was sufficient plankton sample volume for analysis. Plankton samples were filtered through GF/F Whatman glass micro-fibre filters (0.7 µm pore size) using a vacuum pump (300 mm Hg). Plankton samples were rinsed with dH_20 during filtration to remove any salt from the samples. After filtration, large detritus were removed from the filters. Filters were oven dried at 60^oC for 24 hours and stored in petri dishes prior to analysis.

Lipids in animal tissues are depleted in ^{13}C in comparison to proteins and carbohydrates. The inclusion of lipids may result in unreliable isotope data where differences in the lipid content between organisms and tissues may produce more negative $\delta^{13}C$ (Post *et al*. 2007). To correct for this, shark tissues and plankton samples underwent lipid extraction using a modified Bligh & Dyer (1959) method. 1.9 ml of 2:1 chloroform-methanol was combined with the powdered samples, agitated for 10 seconds and put in a water bath (30°C) for 24 hours. Lipid extracted samples were removed from the bath, centrifuged for three minutes, and decanted. 1.9 ml of 2:1 chloroform-methanol was added a second time 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 hours. A separate urea extraction process was not carried out for shark tissue as previous work has shown that the lipid extraction process also removes soluble urea (Hussey *et al*. 2012b). 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 for $\delta^{13}C$ and $\delta^{15}N$

using a continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA) equipped with an elemental analyser (Costech, Valenica, CA, USA).

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

$$\delta X = [((R_{sample}/R_{standard})-1] \times 1000 \qquad (3.1)$$

Where X is ^{13}C or ^{15}N, R_{sample} is the ratio (^{13}C /^{12}C or $^{15}N/^{14}N$) in the sample, and $R_{standard}$ is the ratio in the standard. The standard reference for carbon was Pee Dee Belemnite carbonate and nitrogen was atmospheric $N_{2.}$ Laboratory and National Institute of Standards and Technology (NIST) standards were analysed 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‰, respectively, and for $\delta^{15}N$ was 0.16‰ and 0.14‰, respectively.

3.3 Permits and Ethics

All research was conducted in accordance with James Cook University animal ethics permit A1566 and Great Barrier Reef (G11/346181.1) and DEEDI (144482) permits for animal collection.

Chapter 4

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

4.1 Introduction

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

Information on habitat and space use can also be used to determine vulnerability to environmental change and degradation. Species that use a limited array of habitat types may be more vulnerable to environmental change than species that have wider habitat niches (Futuyma and Moreno 1988; Carlton *et al.* 1991; Wilson and Yoshimura 1994). Selective or highly specialised species may not be able to use different habitats if their preferred habitat declines in health or abundance (Colles *et al.* 2009;Clavel *et al.* 2010; Curtis *et al.* 2013). Species with broader habitat niches can more easily use different habitats or locations

(Marvier *et al.* 2004). Therefore, species that can use diverse habitats are more likely to maintain high levels of fitness in the face of environmental change (Marvier *et al.* 2004; Richmond *et al.* 2005).

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

In this chapter, I examined the movement patterns of *Rhizoprionodon taylori* in Cleveland Bay and the species' vulnerability to change. Passive acoustic telemetry was used to quantify *R. taylori* residency, space use, habitat use, and define whether increased wet season river discharge affected movement. Results from this chapter will increase our understanding of how small-bodied sharks use nearshore areas and how *R. taylori* responds to the environment.

4.2 Data Analysis

4.2.1 Residency

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

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

4.2.2 Space Use

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

4.2.3 Habitat Selection

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

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

$$L_i = r_i - p_i \tag{4.1}$$

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

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

4.2.4 Habitat Niche Breadth

Niche breadth of resident individuals was measured using Hutchinson’s niche definition which only included which habitats a species used and in what proportions (Hutchinson 1957; Devictor *et al.* 2010). Based on this definition, a modified Freeman-Tukey statistic was used to calculate population niche breadth (Smith 1982):

$$FT = \sum_{i=1}^{R} (p_i q_i)^{1/2} \tag{4.2}$$

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

A variation of equation (4.2) was used to calculate individual niche overlap (Arlettaz 1999):

$$FT = \sum_{i=1}^{R} \left(p_{ik} p_{jk}\right)^{1/2} \tag{4.3}$$

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

4.3 Results

Forty *R. taylori* with acoustic transmitters were released in Cleveland Bay between September 2011 and November 2012. The majority of individuals (*n* = 34) were captured and released on the eastern side of Cleveland Bay. Twenty *R. taylori* (7 male, 13 female) were released in year one of this study (September 2011 to September 2012). Twenty *R. taylori* (7 males, 13 female) were released in year two (September 2012-April 2013). Four *R. taylori* released in year one and one released in year two died or were not detected following release and were excluded from analysis. Animal size ranged from 489 to 771 mm STL (mean ± SE = 657± 21.0) in year one and 485 to 763 mm (mean ± SE = 659 ±15.2) STL in year two. Size ranges indicated that the majority of *R. taylori* were either mature or nearing sexual maturity (Simpfendorfer 1993). There were no significant differences in sizes between years (ANOVA, $F_{(1,31)} = 0.0193$, $P > 0.05$), however, females were significantly larger than males (ANOVA, $F_{(1,31)} = 27.45$, $P < 0.05$).

4.3.1 Residency

Rhizoprionodon taylori were present in Cleveland Bay for 1-106 days (mean ± SE =11.4 ± 7.4) in year one and 1-112 days (mean ± SE = 20.6 ± 6.6) in year two. Two *R. taylori* released in year one (2 female) and seven released year two (2 male, 5 female) were present for more than two weeks. The remaining 26 individuals spent less than two weeks in the array. The residency index was low in both years and ranged from 0.00-0.40 (mean ± SE = 0.053 ± 0.03) in year one and 0.00-0.56 (mean ± SE = 0.11 ± 0.04) in year two (Fig. 4.1). Residency data was not normal and was $\log_{10}$ transformed. Animal size had no effect on *R. taylori* residency (ANCOVA, $F_{(1,27)} = 0.727$, $P > 0.05$). There was a significant difference in residency between years (ANCOVA, $F_{(1,27)} = 4.48$, $P < 0.05$), but not between sexes (ANCOVA, $F_{(1,27)} = 0.284$, $P > 0.05$). There was no seasonal pattern in *R. taylori* movement out of Cleveland Bay. After last detection in Cleveland Bay, seven *R. taylori* (3 male, 4 female) were detected on receivers inside Bowling Green Bay for a maximum of seven consecutive days (Heupel unpubl. data).

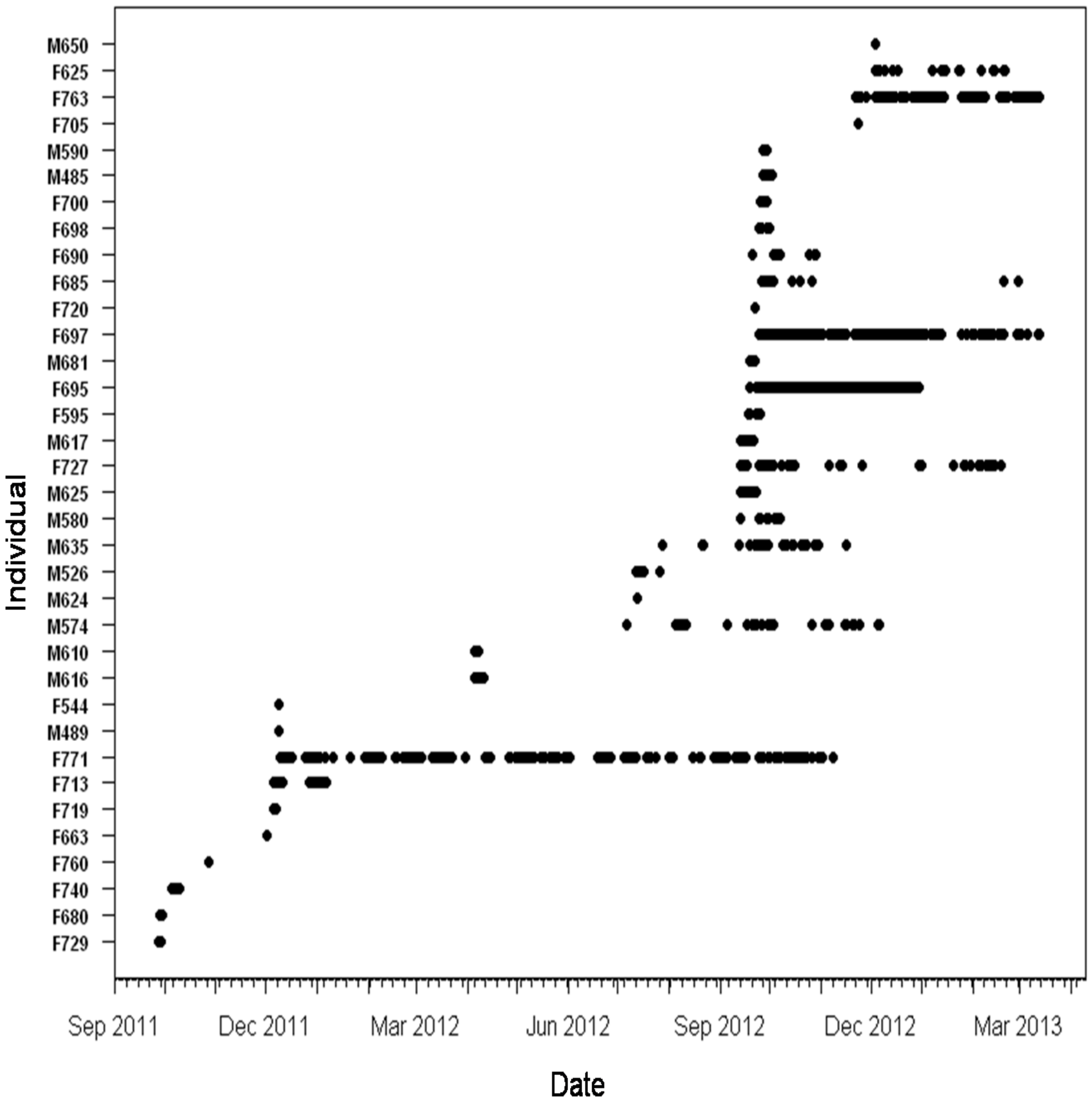

Fig. 4.1. Daily presence of *Rhizoprionodon taylori* released with acoustic transmitters in Cleveland Bay in 2011- 2013. Individuals are identified by sex and stretch total length (mm).

4.3.2 Space Use

Due to the low number of resident individuals, it was not possible to perform population analysis of the activity space patterns of *R. taylori* in year one. Therefore, all activity space analysis was based on data from sharks monitored in year two. Individual monthly activity space of resident individuals ranged between 4.3 and 21.4 km^2 (mean ± SE =11.3 km^2 ± 0.90) for 50% KUDs and 21.5 and 80.4 km^2 (mean ± SE = 51.0 km^2 ± 3.9) for 95% KUDs. There was no significant difference in KUD size between months for 50% (Linear mixed effects model, $F_{(6,18)}$=0.883, P > 0.05) or 95% (Linear mixed effects model, $F_{(6,18)} = 1.043$, $P > 0.05$) KUDs. There was also no relationship between animal size and activity space size for either 50% (Linear regression, r^2=0.006, $F_{(1,23)}$=0.136, $P > 0.05$) or 95% (Linear regression, r^2=0.041, $F_{(1, 23)}$=0.971, $P > 0.05$) KUDs.

The majority of *R. taylori* movements were on the eastern side of the bay, specifically in seagrass habitat. However, 57% of individuals were detected on both sides of the bay. Individual monthly KUD overlap was highly variable and ranged between 0.0-88.6 % (mean ± SE = 34.1 ± 6.2, n = 17) for 50% KUDs and 34.2-92.7% (mean ± SE = 61.0 ± 3.8, n = 17) for 95% KUDs. The most distinct shift in *R. taylori* KUD location occurred between months of low (December 2012) and high river discharge (January and February 2013). Monthly KUD locations of some individuals (all female) shifted from the southeastern to the northwestern side of Cleveland Bay between December 2012 and February 2013 (Fig. 4.2a-b), resulting in low space use overlap for those individuals during that time. However, one individual remained on the eastern side of Cleveland Bay in January and February 2013 (Fig. 4.2c). Individual monthly KUD overlap was recalculated with months of low and high river

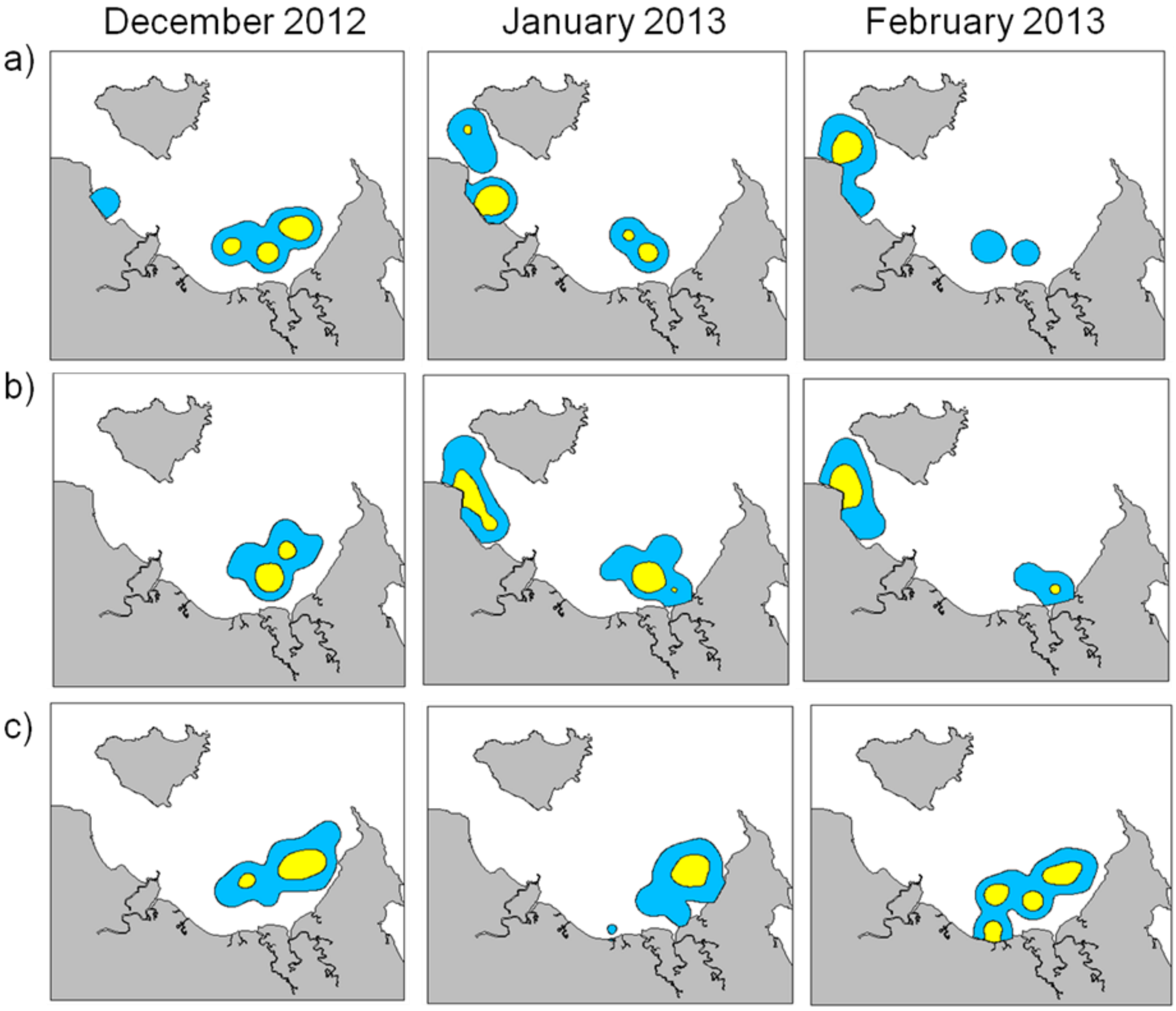

Fig. 4.2. *Rhizoprionodon taylori* monthly activity spaces of three individuals (a, b, c) in December 2012, January 2013 and February 2013. Each panel shows the 95% (blue fill) and 50% (yellow fill) kernel utilisation distributions.

discharge excluded to remove their effect on the results. However, secondary results were similar to the original calculations. Individual monthly KUD overlap again ranged between 0.0-88.57% (mean ± SE = 30.5 ± 6.7, *n* = 14) for 50% KUDs and 34.2-92.7% (mean ± SE = 60.85±4.5, *n* = 14) for 95% KUDs. There was also no consistent pattern in the degree of activity space overlap of each individual. Highly variable KUD overlap values indicate individual *R. taylori* did not use the same core areas between months, regardless of freshwater input. Most activity space relocations during periods of low river discharge were on the eastern side of the bay. However, one individual made regular trips between the eastern and western side of the bay when river discharge was low.

4.3.3 Habitat Selection and Niche Breadth

The majority of transient *R. taylori* selected for seagrass habitat (Table 4.1). Of the 26 transient individuals, 11 exclusively selected for seagrass while seven selected for seagrass and at least one other habitat (intertidal mudflat and/or outer bay mud substrate). Eight transient *R. taylori* avoided seagrass. Reef was avoided by all transient individuals except for one adult female.

The two resident females monitored in year one had contrasting selection patterns. One female selected for sandy inshore habitat, outer bay mud substrate, and seagrass (Fig. 4.3a) while the other only selected for mudflat habitat (Figure 4.3b). Resident individuals in year two were detected in all five primary habitat types at least once during the monitoring period, but on average spent the majority of time in seagrass habitat (Table 4.2). Mean individual

Table 4.1. Strauss selectivity index values of low residency *Rhizoprionodon taylori* (< two weeks detected), for each primary habitat in the bay, indicating sex as M (male) or F (female) and size as stretch total length in mm for each individual.

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

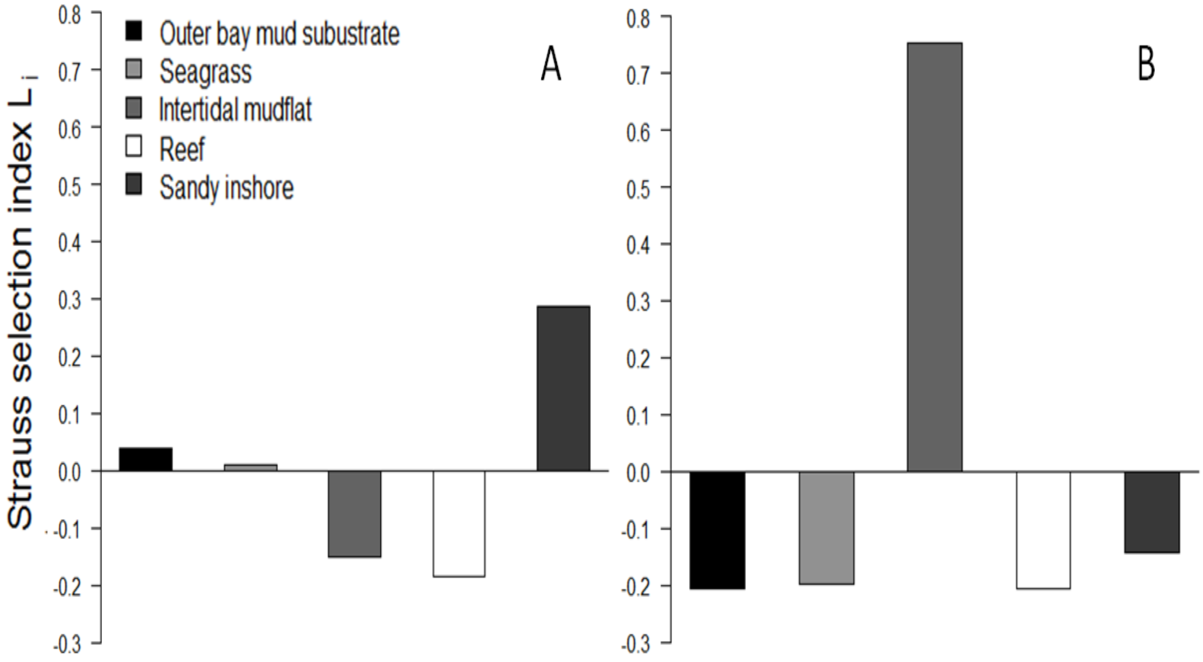

Fig. 4.3. Strauss linear selection index values of resident (> 2 weeks) *Rhizoprionodon taylori* released in Cleveland Bay in year one (September 2011 to September 2012) a) female 574 mm stretch total length (STL) and b) female 713 mm STL.

Table 4.2. Mean and standard deviation of time spent in each habitat by high residency (> 2 weeks) *Rhizoprionodon taylori* (n=7) released in year two (September 2012 to April 2013) in Cleveland Bay, measured as a percent with standard error (SE).

Habitat Type	Mean Time Spent (%)± SE
Seagrass	48.4 ± 9.6
Outer bay mud substrate	21.2 ± 3.1
Reef	0.1 ± 0.07
Sandy inshore	24.3 ± 8.9
Intertidal mudflat	5.7 ± 2.2

Strauss selection values of resident individuals in year two indicated that on an annual basis outer bay mud substrate was used opportunistically, reef and mudflat habitats were avoided, and seagrass and sandy inshore habitat were positively selected (Fig. 4.4). A chi-squared goodness-of-fit test showed that selection was significant (X^2_4=63.888, $P < 0.05$). Mean fortnightly selection values revealed that during year two reefs and intertidal mudflats were consistently avoided while seagrass was consistently favoured, except in January 2013 when river discharge increased. Selection for sandy inshore substrate and outer bay mud substrate was more variable (Fig. 4.5).

Selection of outer bay mud substrate of resident individuals fluctuated between low values of negative and positive selection with individuals generally spending little time in the area (<1 consecutive day). Selection for sandy inshore habitat was also irregular and varied between negative and positive values over time and among individuals. The majority of resident individuals in year two did not enter sandy inshore habitat prior to December 2012, except for one female that made regular excursions into sand habitat for variable periods of time (7-14 consecutive days). However, between December and February 2013, the majority of resident individuals abruptly selected sandy inshore habitat while avoiding seagrass and this coincided with increased river discharge. Spearman's rank correlation revealed a strong negative correlation between sandy inshore and seagrass selection by resident individuals (r_s= -0.694, N = 14, $P < 0.05$). Spearman's rank correlation also revealed a positive relationship between increased river discharge and selection for sandy inshore habitat ($r_s = 0.305$, N =14, $P < 0.05$). There was a negative relationship between selection for seagrass and increased river discharge (Spearman's rank correlation, $r_s = -0.308$, N = 14, $P < 0.05$).

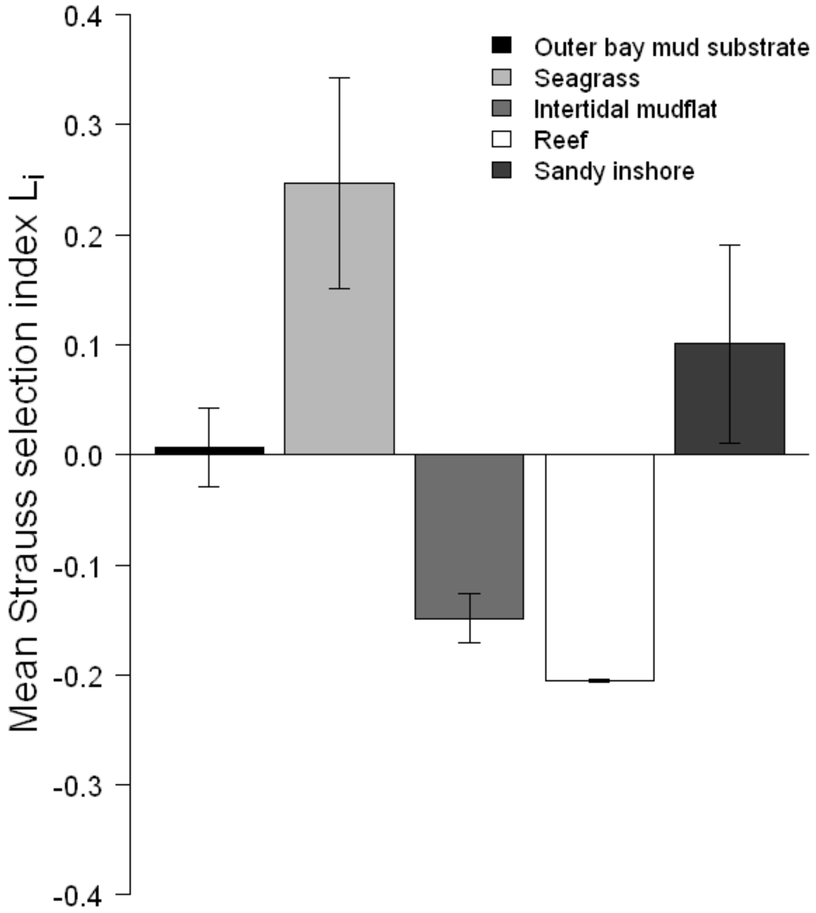

Fig. 4.4. Mean Strauss linear selection index values of resident (> 2 weeks) *Rhizoprionodon taylori* in Cleveland Bay (*n* = 7) between September 2012 to April 2013. Bars indicate standard error.

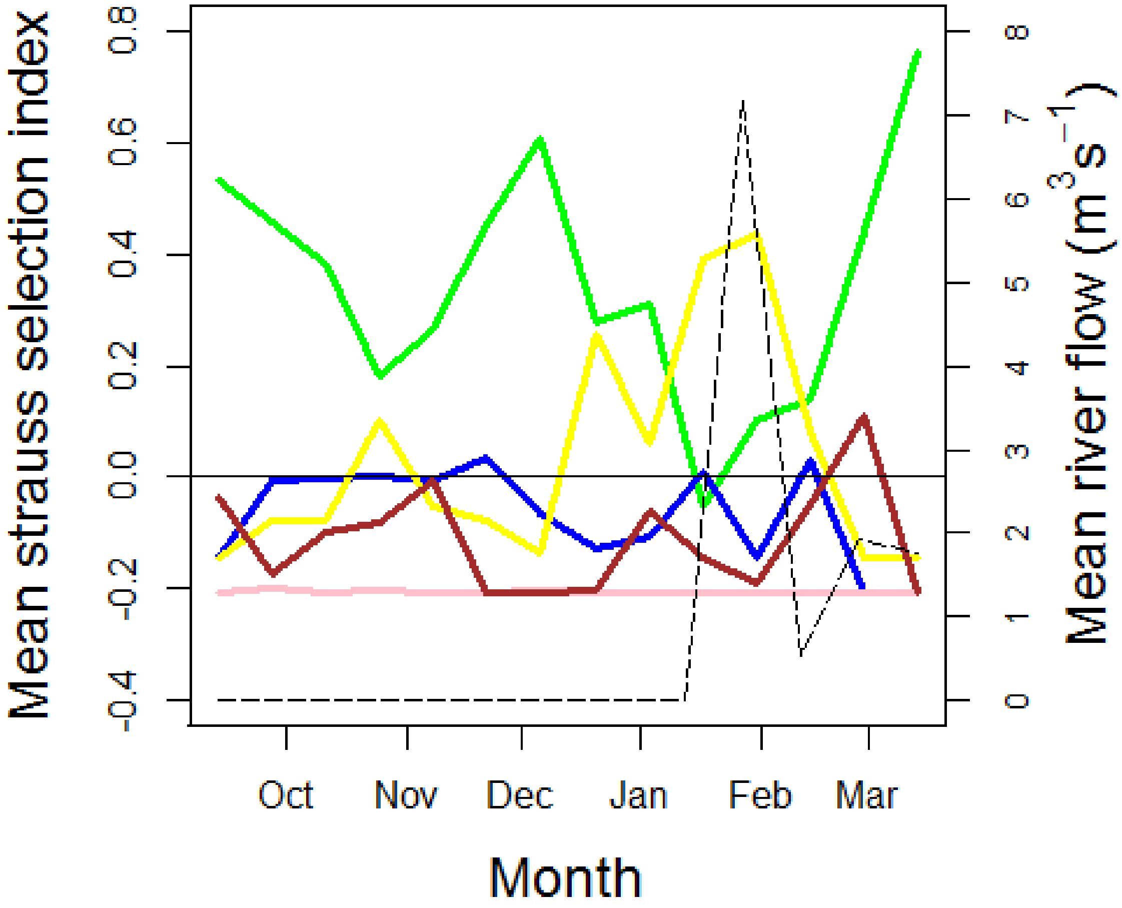

Fig. 4.5. *Rhizoprionodon taylori* mean fortnightly individual Strauss linear selection values for resident individuals from year two (September 2012-April 2013) for seagrass (green line), sand (yellow line), outer bay mud substrate (blue line), intertidal mudflat (brown line), and reef (pink line). Mean fortnightly river discharge was measured in m^3s^{-1} (thin black dashed line).

Annual mean individual niche breadth for resident *R. taylori* in the second year of this study was moderately large and ranged from 0.73 to 0.90 (mean ± SE = 0.79 ± 0.02, *n* = 7). These values indicate that individuals had wide habitat niches and therefore had low degrees of habitat specialisation. Mean individual overlap was also relatively large and ranged from 0.62 to 0.95 (mean ± SE = 0.83 ± 0.03, *n* = 7).

4.4 Discussion

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

taylori with a significantly greater level of protection from predators than offshore habitats. As a result, there may be limited benefit for *R. taylori* to stay in one bay for long periods.

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

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

Although seagrass habitat was consistently positively selected by both resident and transitory individuals, the population's overall low presence and degree of habitat specialisation, as well as the expansive roaming movement patterns of individuals, suggests *R. taylori* are probably not dependant on a single habitat. *Rhizoprionodon taylori* also exhibited low levels of individual specialisation, indicating that overall individuals used similar proportions of the same habitats as each other. Large individual niches and low levels of individual specialisation imply the *R. taylori* population in Cleveland Bay is composed of individual habitat generalists. However, as previously indicated, *R. taylori* did not use all habitats opportunistically. Avoidance of reef and mudflat by the majority of resident and transitory individuals suggests these habitats did not fulfil biological requirements or are suboptimal in some way, such as insufficient prey abundance. Individuals may have also avoided mudflat habitat because larger sharks (e.g. *C. amboinensis*) that may prey on *R. taylori* utilise this habitat (Knip *et al.* 2011a). Thus avoidance of these regions may reduce predation risk or competition with other species using this habitat. Low sample size and residency made it difficult to determine why *R. taylori* used outer bay mud substrate. Opportunistic use of outer bay mud substrate by highly resident individuals may be the result of short-term foraging excursions or a response to short-term environmental fluctuations. Detections in outer bay mud substrate may have also resulted from *R. taylori* passing through while moving between sides of the bay and because some outer bay receivers fringe seagrass habitats. Selectivity indices cannot measure the importance of a habitat, only its relative use, therefore outer bay mud substrate may serve an important but undefined short-lived purpose.

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

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

Overall, results of this chapter indicate *R. taylori* is a species that has a low degree of habitat specialisation and large activity spaces that likely span multiple bays. As a result, *R. taylori* are probably resilient to localised environmental change and can avoid potentially detrimental environmental changes by moving to different areas or habitats. However, the presence and accessibility of seagrass may affect residency and habitat use patterns. Increased coastal development and the effects of climate change have been highlighted as major ongoing and future contributors to seagrass decline (Duarte 2002). Severe regional declines in seagrass abundance as a result of large storms, sea level rise, urban runoff, and development may decrease local *R. taylori* presence and fitness (Orth *et al*. 2006; Hughes *et al.* 2008; Waycott *et al.* 2009). Decreased seagrass availability is a potential concern for this species, but further study of *R. taylori* regional movement and habitat use in other nearshore areas is needed to assess this possibility. Understanding the dynamics of how small-bodied sharks use nearshore areas and how environmental change may affect their movement and habitat use will help define the resilience of coastal shark communities.

Chapter 5

Regional Movement Patterns of a Small-bodied Shark Revealed by Stable Isotope Analysis

5.1 Introduction

Mobile sharks link distant environments by moving between them and exerting predatory pressures on local food webs (Weng *et al.* 2007; Weng *et al.* 2008; Chin *et al.* 2013). As a result, some species connect otherwise separated food webs and ecosystem processes (Lundberg and Moberg 2003). Fast-growing, small-bodied sharks may be a particularly vital ecological and energetic link between food webs because they are both predators and prey items. Therefore, data on the movements of small-bodied sharks can increase understanding of marine ecosystem function and connectivity. Understanding shark movement patterns may also help predict how species will respond to environment change. For example, species that can use multiple, distinct, and potentially distant habitats will be less vulnerable to environmental change than species that are highly specialised and exhibit high site fidelity (Thomas *et al.* 2004; Araújo *et al.* 2006; Williams *et al.* 2008; Curtis *et al.* 2013).

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

Stable isotope analysis (SIA) is a commonly employed technique in ecology that can be used to define the regional movements of animals (Hobson 2008). Isotope analysis evaluates the ratio of heavy to light isotopes of carbon ($^{13}C/^{12}C$; $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$). The $\delta^{13}C$ and $\delta^{15}N$ values in an ecosystem vary beginning at the base of the food web (i.e. primary producers). This variation is the result of different local biogeochemical processes (Boutton 1991). In animal tissue, $\delta^{13}C$ values increase in small amounts from prey to predator and are therefore conserved up the food chain (Post 2002). In contrast, $\delta^{15}N$ tissue values increase from prey to predator at a significantly greater rate than $\delta^{13}C$ (Deniro and Epstein 1981; Peterson and Fry 1987). Therefore, consumers assimilate the $\delta^{13}C$ and $\delta^{15}N$ value of their prey and local environment with minimal and/or predictable rates of change (Graham *et al.* 2010). As a result, the isotopic values of resident shark populations should be similar to or a reflection of the isotopic value of local prey and primary producers (Graham *et al.* 2010). Resident populations from isotopically distinct habitats or regions should have similarly distinct $\delta^{13}C$ and $\delta^{15}N$ values. In contrast, the $\delta^{13}C$ and $\delta^{15}N$ of highly mobile, non-resident populations will be a blend of the different areas or habitats they have foraged in. Thus, the $\delta^{13}C$ and $\delta^{15}N$ values of migratory populations should be similar between locations that have been linked via foraging and movement (Hobson 2008). Therefore, $\delta^{13}C$ and $\delta^{15}N$ values provide a type of intrinsic geographic tag (Rubenstein and Hobson 2004). Metabolically active tissues, such as liver or plasma, respond to changes in diet more quickly than tissues with a lower metabolic rate, such as muscle (Hobson and Clark 1992; Buchheister and Latour 2010). As a result, $\delta^{13}C$ and $\delta^{15}N$

from different tissues can reveal if an animal's feeding location has changed over time (Newsome *et al.* 2009).

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

In Chapter 4, acoustic tracking of *R. taylori* in Cleveland Bay found indivduals were mostly transient and several individuals were detected moving into an adjacent bay approximately 30 km south of the primary study site. Based on these findings, I proposed the home range of individual *R. taylori* encompassed multiple bays. However, due to the contraints of the acoustic array, it was not possbile to determine how far *R. taylori* moved from Cleveland Bay following release. As a highly abundant coastal mesopredator, *R. taylori* may have a significant influence on nearshore ecosystem connectivity, function, and diversity.

The aim of this chapter was to evaluate the nearshore regional residency and movements of *R. taylori* using SIA. To determine the physical and temporal extent of *R. taylori* movements, plasma and muscle $\delta^{13}C$ and $\delta^{15}N$ of captured *R. taylori* were compared to the $\delta^{13}C$ and $\delta^{15}N$ baselines (established using seagrass, macroalgae and plankton) from five embayments on the northeast coast of Queensland (Fig. 3.6), including Cleveland Bay. Cleveland Bay occupied a central location among the sample bays to better understand the movement of *R. taylori* in and out of Cleveland Bay. The results of this chapter will improve understanding of the regional residency and movement of small-bodied coastal sharks.

5.2 Data Analysis

Bayesian inferences were used for all data analysis in this study because there was concern that more traditional methods of spatial analysis may not be able to detect some of the subtle geographic difference in d15N and d13C values. Bayesian analysis is better able to incorporate uncertainty (due to variability in isotope ratios) and the small and variable sample size in some locations (Bernardo and Smith 1994; Berger 2006). A Bayesian ANOVA (Gelman 2007) was used to access differences between bays in benthic (seagrass and macroalgae) and pelagic (plankton) $\delta^{13}C$ and $\delta^{15}N$ values. The Bayesian ANOVA used vague, non-informative priors and was calculated according to the following:

The Likelihood

$$y_{\mathrm{ij}} \sim Normal(\mu + \alpha_{\mathrm{i}}, \sigma^2) \tag{5.1}$$

The Priors

$$\mu \sim Normal(0, 10^{-6}) \tag{5.2a}$$

$$\alpha_{\mathrm{i}} \sim Normal(0, 10^{-6}) \tag{5.2b}$$

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

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

The Likelihood

$$C_i \sim MultivariateNormal([\mu_1, \mu_2], \Sigma) \quad (5.3)$$

Where $C_i = (C_{i,1}, C_{i,2})$

The Priors

$$\mu_1, \mu_2 \sim Normal(0, 10^3) \quad (5.4a)$$

$$\sigma_1, \sigma_2 \sim Normal(0, 10^3) \quad (5.4b)$$

$$\rho \sim Uniform(-1,1) \quad (5.4c)$$

$$\Sigma = \begin{pmatrix} \sigma_1^2 & \rho\sigma_1\sigma_2 \\ \rho\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix} \quad (5.5)$$

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

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

A 2-factor Bayesian ANOVA (Gelman 2007) was used to test for differences in δ^{13}C and δ^{15}N between bays and sexes in muscle and plasma. The 2-way Bayesian ANOVA was calculated according to the formulations:

The Likelihood:

$$y_{\mathrm{ijk}} \sim Normal(\mu + \alpha_{\mathrm{i}} + \beta_{\mathrm{j}} + \gamma_{\mathrm{ij}}, \sigma^2) \tag{5.6}$$

The Priors

$$\mu \sim Normal(0, 10^{-6}) \tag{5.7a}$$

$$\alpha_{\mathrm{i}} \sim Normal(0, 10^{-6}) \tag{5.7b}$$

$$\beta_{\mathrm{j}} \sim Normal(0, 10^{-6}) \tag{5.7c}$$

$$\gamma_{\mathrm{ij}} \sim Normal(0, 10^{-6}) \tag{5.7d}$$

Where β_{j} was the effect due to sex, and γ_{ij} was the effect due to the interaction between the *i*-th bay and sex.

A 3-way ANCOVA was considered to examine the effect of size (STL), sex, and sample bay on shark tissue δ^{13}C and δ^{15}N, however, preliminary analysis showed the effect of size was highly variable between bays. Therefore, a series of linear Bayesian regressions were used to determine if there was a relationship between muscle and plasma δ^{13}C and δ^{15}N and animal size for each bay. Regression analysis used vague, non-informative priors and was calculated according to the following:

The Likelihood

$$y_{ij} \sim Normal(\mu + S_{\mathrm{i}}, \sigma^2) \tag{5.8}$$

The Priors

$$\mu \sim Normal(0, 10^{-6}) \tag{5.9a}$$

$$S_{\mathrm{i}} \sim Normal(0, 10^{-6}) \tag{5.9b}$$

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

Linear Bayesian correlation analysis was used to determine if there was a correlation between benthic and pelagic, and shark tissue δ^{13}C and δ^{15}N values based on location. All 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 access each applied version of the models. All 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).

5.3 Results

5.3.1 Study Site δ^{13}C and δ^{15}N

Forty-seven pelagic (plankton) and 55 benthic (seagrass and macroalgae) samples were collected from the five bays (Table 5.1). Benthic δ^{13}C values were higher than pelagic values in all bays (Table 5.1; Fig. 5.1). Across all sample bays, benthic and pelagic δ^{13}C values ranged from -23.2 to -8.4 and -23.3 to -14.6 respectively. Sample bay accounted for 45.3% and 45.4%

Table 5.1 Sample size (n) and δ^{13}C and δ^{15}N range (mean ± SD) of benthic and pelagic sources from each location, Repulse Bay (RE), Upstart Bay (UP), Bowling Green Bay (BG), Cleveland Bay (CB), and Rockingham Bay (RO).

Location	Benthic (n)	Pelagic (n)	Benthic δ^{13}C	Benthic δ^{15}N	Pelagic δ^{13}C	Pelagic δ^{15}N
RE	12	5	-19.6 - -12.1 (-16.1 ± 2.3)	2.9-6.8 (4.9 ± 1.3)	-20.8 - -19.9 (-20.4 ± 0.3)	6.7-7.6 (6.9 ± 0.4)
UP	11	13	-20.5 - -10.3 (-14.4 ± 4.0)	0.62-4.5 (2.1 ± 1.7)	-20.52 - - 14.63 (-17.7 ± 2.6)	3.7-5.0 (4.4 ± 0.5)
BG	7	12	-19.3- -9.5 (-12.4 ± 4.3)	2.4-5.7 (3.7 ± 1.4)	-20.1- -18.7 (-19.5 ± 0.4)	1.22-5.9 (3.7 ± 1.8)
CB	13	8	-17.2- -8.4 (-12.4 ± 2.2)	1.3-3.6 (2.2 ± 0.8)	-19.4- - 18.2(-18.8 ± 0.5)	4.7-5.7 (5.1 ± 0.3)
RO	11	9	-23.2- -15.2 (-19.1 ± 2.8)	1.3-4.9 (3.7 ± 1.0)	-23.3- -18.7 (-21.0 ± 2.0)	5.2-6.2 (5.6 ± 0.3)

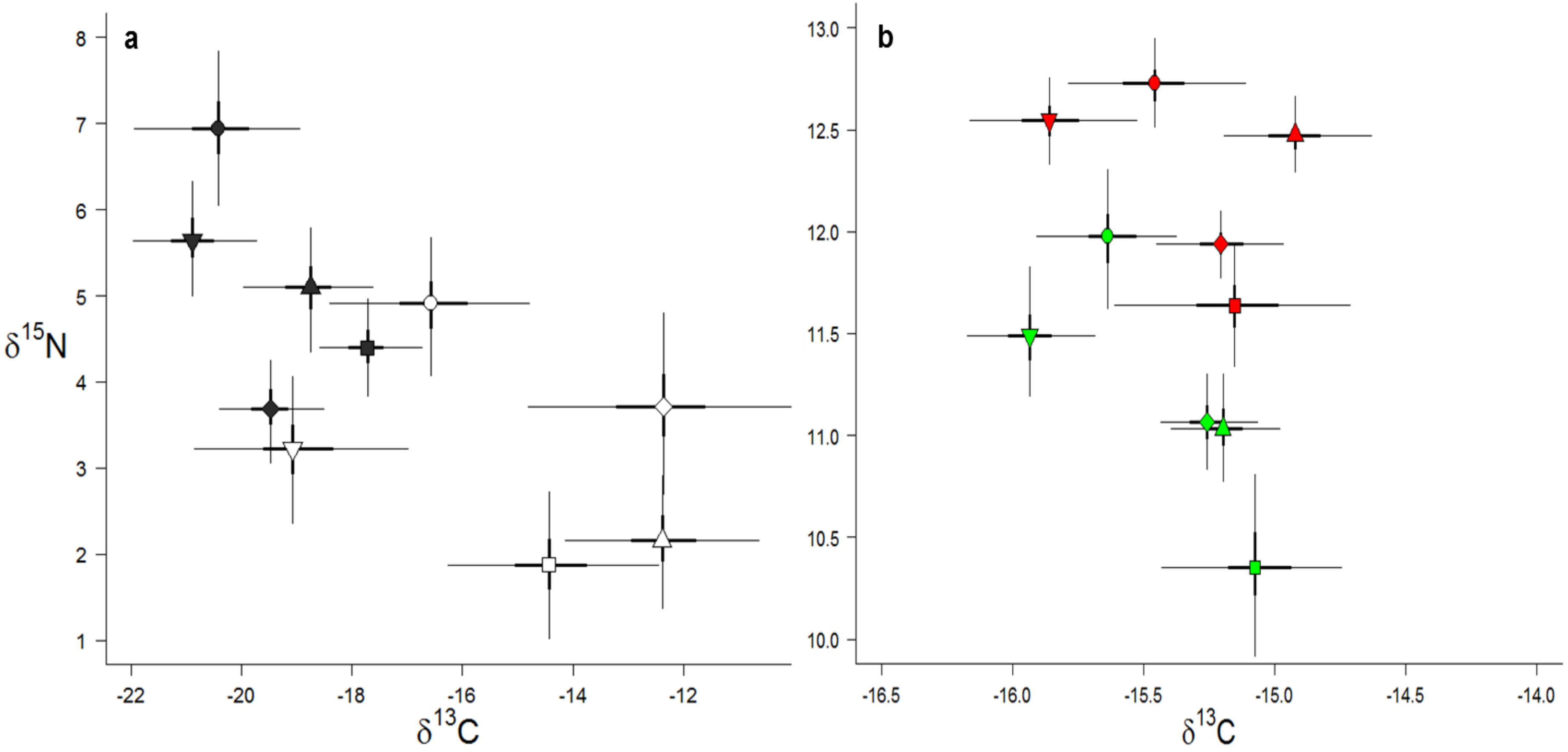

Fig. 5.1. Median δ^{13}C and δ^{15}N values from Bayesian ANOVA of (a) benthic (white), pelagic (dark grey), (b) *Rhizoprionodon taylori* muscle (red), and plasma (green) samples in Repulse Bay (●), Upstart Bay (■), Bowling Green Bay (♦), Cleveland Bay (▲) and Rockingham Bay (▼), black lines show 50% and 95% credibility intervals of posterior draws.

of the estimated variance components (% standard deviation) in benthic and pelagic $\delta^{13}C$ values respectively. Benthic $\delta^{13}C$ values from UP, BG and CB were significantly higher than the benthic $\delta^{13}C$ values from RO (Fig. 5.1). Benthic $\delta^{13}C$ values in BG and CB were also significantly higher than the $\delta^{13}C$ values from RE. Although the absolute $\delta^{13}C$ values were different, pelagic samples exhibited similar geographic patterns in relative $\delta^{13}C$ values compared to benthic samples. Pelagic $\delta^{13}C$ values from UP and CB were significantly higher than the $\delta^{13}C$ values from RO. Pelagic $\delta^{13}C$ values from UP were also significantly higher than the $\delta^{13}C$ values from RE. Linear Bayesian correlation analysis indicated there was no significant correlation between benthic and pelagic $\delta^{13}C$ based on location (median, 95% credibility intervals = 0.50, -0.406-0.999).

Benthic $\delta^{15}N$ values were lower than pelagic $\delta^{15}N$ values in all bays, most likely because pelagic samples contained some zooplankton. Benthic and pelagic $\delta^{15}N$ values ranged from and 0.62 to 6.8 and 1.2 to 7.6 respectively. Sample bay accounted for 46.3% and 49.0% of the estimated variance components (% standard deviation) in benthic and pelagic $\delta^{15}N$ values respectively. Benthic $\delta^{15}N$ in RE was significantly higher than the $\delta^{15}N$ values from BG and CB. Benthic RO $\delta^{15}N$ was also higher than CB and UP $\delta^{15}N$, but the difference was not significant. Pelagic δ^{15} N values in RE were significantly higher than pelagic δ^{15} N from UP, BG and CB. Pelagic RO $\delta^{15}N$ was also significantly higher than δ^{15} N values from UP and BG. Linear Bayesian correlation analysis indicated there was no significant correlation between benthic and pelagic $\delta^{15}N$ based on location (median, 95% credibility intervals = 0.39, -0.57 - 0.98).

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

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

One hundred and forty six *R. taylori* (30 male, 116 female) were sampled from the five study bays from 2012 to 2013 (Table 5.2). Across all sample bays, *R. taylori* size ranged from 415 to 780 mm STL (mean ± SD = 663 ± 66). Muscle $\delta^{13}C$ and $\delta^{15}N$ ranged from -18.1 to -12.8 and 10.6 to 13.8 respectively. Plasma $\delta^{13}C$ and $\delta^{15}N$ ranged from -16.8 to -13.7 and 8.3 to 12.7 respectively. An insufficient number of males were captured in RE and UP to investigate the effect of sex on $\delta^{13}C$ and $\delta^{15}N$ in these bays (Table 5.2).

Stretched total length had a small, inconsistent, and mostly insignificant influence on *R. taylori* $\delta^{13}C$ and $\delta^{15}N$. Linear Bayesian regression analysis showed only BG muscle $\delta^{13}C$ (median, 95% credibility intervals; 0.006, 0.004 - 0.008), BG plasma $\delta^{13}C$ (median, 95% credibility intervals; 0.003,0.0006 - 0.006 $\delta^{13}C$), CB muscle $\delta^{13}C$ (median, 95% credibility intervals; 0.005, 0.0007 - 0.009) , CB plasma $\delta^{13}C$ (median 95% credibility intervals; 0.003, 0.0008 - 0.005), and RE muscle $\delta^{13}C$ (median 95% credibility intervals; 0.006, 0.001 - 0.01) had a

Table 5.2. *Rhizoprionodon taylori* male (M) and female (F) sample size, combined stretch total length in mm (STL mm), and δ^{13}C and δ^{15}N tissue range (mean ± SD) from Repulse Bay (RE), Upstart Bay (UP), Bowling Green Bay (BG), Cleveland Bay (CB), and Rockingham Bay (RO).

Bay	M	F	STL (mm)	Muscle δ^{13}C	Muscle δ^{15}N	Plasma δ^{13}C	Plasma δ^{15}N
RE	1	20	595-755 (699±41)	-16.6 - -14.5 (-15.5±0.5)	12.0-13.4 (12.7±0.4)	-16.7 - -14.7 (-15.6±0.5)	10.2-12.7(11.9±0.8)
UP	0	11	674-780 (714±35)	-16.0 - -14.2 (-15.2±0.5)	11.1-12.3 (11.6±0.5)	-15.9 - -14.5 (-15.1±0.5)	9.19-11.4 (10.4±0.8)
BG	18	37	462-753 (641±68)	-16.6 - -12.8 (-15.3± 0.7)	10.6-13.2 (12.0±0.6)	-16.7- -13.7 (-15.4±0.6)	9.6-12.0 (11.1±0.7)
CB	7	28	415-744 (650±80)	-18.1 - -13.3 (15.04±1.0)	10.7-13.5 (12.5±0.6)	-16.5 - -14.2 (-15.2±0.5)	8.3-12.3 (11.0±0.9)
RO	4	20	625-755 (678±38)	-17.0 - -14.5 (-15.8±0.6)	11.6-13.8 (12.7±0.5)	-16.8- -14.5 (-16.0±0.5)	10.0-12.5 (11.6±0.6)

significantly positive relationship with STL. Only BG plasma $\delta^{15}N$ was significantly correlated with *R. taylori* STL (median 95% credibility intervals; 0.003, 0.0 - 0.005). Sex also had an inconsistent effect on *R. taylori* $\delta^{13}C$ and $\delta^{15}N$. Female muscle and plasma $\delta^{13}C$ from BG and muscle from CB was significantly higher than male $\delta^{13}C$ (Fig. 5.2). However, there was no significant difference in $\delta^{13}C$ between sexes in RO or plasma tissue from CB. There was no significant difference in $\delta^{15}N$ between sexes for muscle or plasma tissue (Fig. 5.2). As a result of the inconsistent effect of sex on $\delta^{13}C$ and $\delta^{15}N$ and the small, uneven sampling of males between locations, males were excluded from between bay $\delta^{13}C$ and $\delta^{15}N$ comparisons.

When compared to the primary produces, female *R. taylori* muscle and plasma $\delta^{13}C$ values fell within range of the combined benthic and pelagic $\delta^{13}C$ values of their respective capture locations. Sample bay accounted for 33.0% and 38.2% of the estimated variance components (% standard deviation) in muscle and plasma $\delta^{13}C$, respectively. The results of the Bayesian ANOVA showed female *R. taylori* muscle $\delta^{13}C$ from UP, BG, and CB was significantly higher than muscle $\delta^{13}C$ values from RO (Fig. 5.1b). Muscle $\delta^{13}C$ from CB was also significantly higher than muscle $\delta^{13}C$ from RE. Female *R. taylori* plasma $\delta^{13}C$ in UP, BG, and CB was significantly higher than plasma $\delta^{13}C$ from RO and RE (Fig. 5.1b). It was not possible to differentiate between the $\delta^{13}C$ values of individuals captured in UP, BG and CB for either muscle or plasma. These results show there was a high degree of similarity in *R. taylori* $\delta^{13}C$ between adjacent bays (i.e. those within 100 km), while *R. taylori* from more distant bays (> 100 km separation) had less similar $\delta^{13}C$ values. Overall, differences in *R. taylori* $\delta^{13}C$ between locations were more pronounced in plasma than muscle.

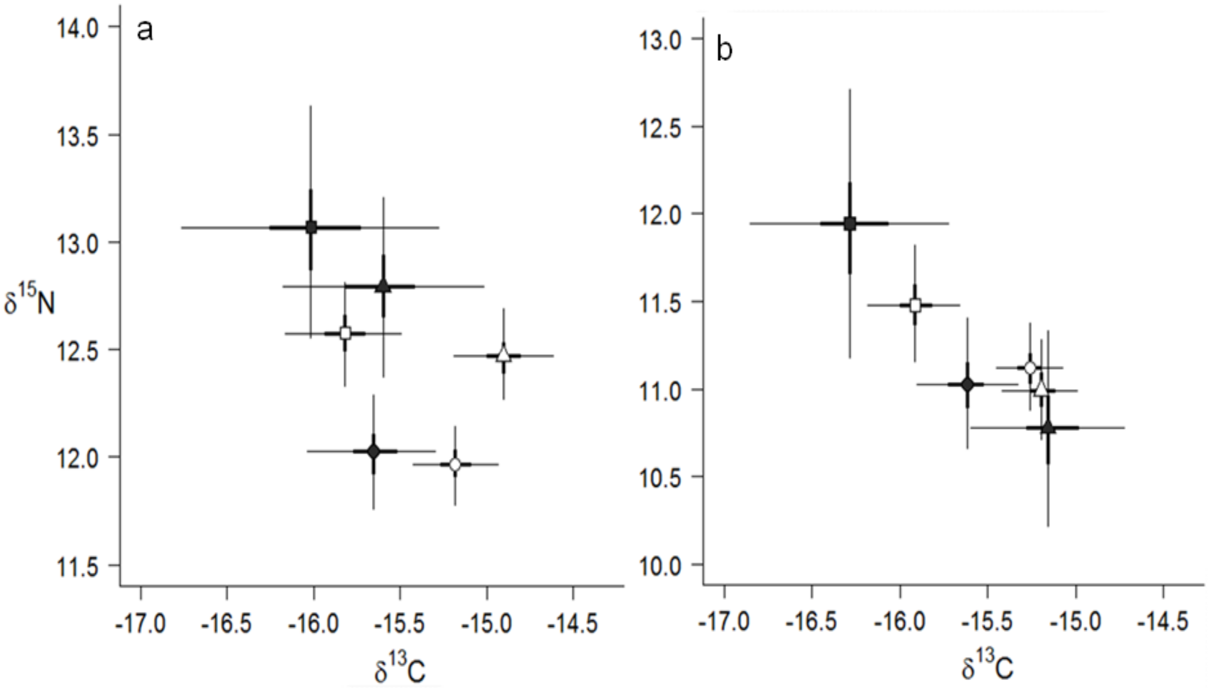

Fig. 5.2. Median δ13C and δ15N values of Bayesian ANOVA of female (white) and male (dark grey) *Rhizoprionodon taylori* for muscle (a) and plasma (b) tissue in Bowling Green Bay (●), Cleveland Bay (▲) and Rockingham Bay (■). Black lines show 50% and 95% credibility intervals of posterior draws.

The results of the Bayesian ANOVA showed sample bay accounted for 45.6% and 45.1% of the estimated variance components (% standard deviation) in muscle and plasma δ^{15}N, respectively. Female *R. taylori* muscle δ^{15}N from RE and RO was significantly higher than muscle δ^{15}N from BG and UP (Fig. 5.1b). Female *R. taylori* plasma δ^{15}N from RE was also significantly higher than plasma δ^{15}N in UP, BG and CB. Plasma δ^{15}N from RO was significantly higher than plasma δ^{15}N in UP. Muscle and plasma δ^{15}N values from UP, BG and CB closely overlapped. The differences in *R. taylori* δ^{13}N between sample bays were more pronounced in plasma than muscle. Similar to the δ^{13}C analysis, δ^{15}N analysis showed that *R. taylori* from more distant bays (> 100 km separation) had more distinct δ^{15}N values.

Linear Bayesian correlation analysis indicated significant positive correlation between muscle and benthic δ^{13}C values based on location (Table 5.3). However, correlation between muscle and pelagic δ^{13}C was not significant. Plasma δ^{13}C was significantly positively correlated with pelagic δ^{13}C values; however correlation between plasma and benthic δ^{13}C was not significant. None of the δ^{15}N tissue-primary producer geographic correlations were significant. Although not all correlations between tissues and study site δ^{13}C and δ^{15}N based on location were significant, the geographic patterns in female *R. taylori* δ^{13}C and δ^{15}N were similar to the geographic patterns in benthic and pelagic δ^{13}C and δ^{15}N. Shark, benthic and pelagic δ^{13}C values from UP, BG, and CB were often significantly higher than the δ^{13}C values in RE and RO. Similarly, shark, benthic, and pelagic samples from RE and RO had the highest δ^{15}N values compared to UP, BG, and CB. These results suggest that individuals in RE and RO did not forage extensively in the centralized bays within the study area.

Table 5.3. Results of linear Bayesian correlation analysis between the $\delta^{13}C$ and $\delta^{15}N$ of *Rhizoprionodon taylori* and the benthic and pelagic producers across sample bays. ρ defined the correlation parameter. Correlations were considered significant if the 95% credibility intervals (CIs) of the posterior draws did not overlap with 0.

Isotope	Comparison	Median ρ value	95% CIs ρ value
$\delta^{13}C$	Benthic-Muscle	0.815	0.063 - 0.996
$\delta^{13}C$	Pelagic-Muscle	0.626	-0.262 - 0.992
$\delta^{13}C$	Benthic-Plasma	0.723	-0.081 - 0.0991
$\delta^{13}C$	Pelagic-Plasma	0.825	0.123 - 0.998
$\delta^{15}N$	Benthic-Muscle	0.383	-0.503 - 0.960
$\delta^{15}N$	Pelagic-Muscle	0.661	-0.239 - 0.994
$\delta^{15}N$	Benthic-Plasma	0.700	-0.1452 - 0.996
$\delta^{15}N$	Pelagic-Plasma	0.603	-0.278 - 0.996

5.4 Discussion

The results of this Chapter suggest that female *R. taylori* did not forage between areas that are more than 100 km a part on the Queensland coast over short periods of time (~ 6 months). Less pronounced geographic differences in *R. taylori* muscle $\delta^{13}C$ and $\delta^{15}N$ compared to plasma could indicate individuals foraged between more distant bays (> 100 km) over six months to one year. However, *R. taylori* muscle $\delta^{13}C$ and $\delta^{15}N$ also reflected the geographic trends in benthic and pelagic $\delta^{13}C$ and $\delta^{15}N$ values. Therefore, while some *R. taylori* likely foraged between more distant bays, most may have spent extended periods of time (~ 1 year) near their respective capture locations. Therefore, these results suggest *R. taylori* may not make long distance movements(> 100 km) over a period of time spanning approximately six months to one year.

The regional movement patterns demonstrated by *R. taylori* contrasts with the regional movement patterns of the Atlantic sharpnose shark, *R. terraenovae*, which has a similar life history (Loefer and Sedberry 2003) and nearshore residency patterns (see Chapter 4;Carlson *et al.* 2008). In contrast to *R. taylori, R. terraenovae* is known to move broadly over short periods of time (Kohler *et al.* 1998; Carlson *et al.* 2008; Suárez-Moo *et al.* 2013). Tag and recapture data of *R. terraenovae* from the Gulf of Mexico showed one individual travelled 169 km in 35 days, and another individual travelled 322 km in 228 days (Carlson *et al.* 2008). Given the biological and behavioural similarities between *R. taylori* and *R. terraenovae*, it was anticipated that *R. taylori* would exhibit similar large-scale regional movement patterns. Instead, female *R. taylori* appeared to be similar to the closely related milk shark, *R. acutus*, another small-bodied, fast-growing species that has a similar geographic range to *R. taylori* (Last and Stevens 2009). Although data on the movement and site fidelity of *R. acutus* are limited, stock structure analysis indicates this species exhibits moderate site fidelity with some long distance movements (Ovenden *et al.* 2011; Schroeder 2011).

Although muscle and plasma $\delta^{13}C$ and $\delta^{15}N$ values suggest limited regional foraging and dispersal of *R. taylori*, the results do not necessarily indicate long-term residency within individual bays. Female *R. taylori* sampled from adjacent, central bays (UP, BG, and CB) had indistinguishable plasma and muscle $\delta^{13}C$ values. The $\delta^{15}N$ values of *R. taylori* from UP, BG, and CB were all relatively low and closely overlapped, particularly in plasma. There are several possible explanations for the similarity in values between these locations. The first is that similarity in isotopic baselines between UP, BG, and CB resulted in similar isotope values for sharks feeding in those areas. A second explanation is that *R. taylori* captured in UP, BG, and CB regularly moved between and fed within these bays, thus accumulating similar isotope profiles. The observed similarity could be the result of a combination of these two explanations. Acoustic tracking from Chapter 4 indicated *R. taylori* move between CB and BG, therefore, it is likely that the similar isotope values in sharks sampled in UP, BG, and CB were, at least in part, the result of regular movement between these neighbouring areas.

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

It has been suggested that small-bodied, fast growing, productive sharks use multiple nearshore areas because it increases individual access to resources (Heupel *et al.* 2007; Carlson *et al.* 2008; Knip *et al.* 2010). The limited regional range indicated by *R. taylori* isotope values in this chapter suggests that sufficient resources to support *R. taylori* survival, growth, and annual reproduction were located within 100 km of capture locations. Regional dispersal may have also been limited by the high energetic cost associated with long-range movement (Roff 1988; Nøttestad *et al.* 1999; Alerstam *et al.* 2003). Therefore, female *R. taylori* movement patterns may represent an energetic balance between maximising the benefits of using multiple bays and minimising the reciprocal costs of long-distance movement. As a result, *R. taylori* may serve as an important ecological link between bays < 100 km apart, but may not be as significant a link between more distant bays (> 100 km) over approximately 6-12 months. However, it should be noted that SIA in sharks is not temporally refined enough to detect sporadic or short-term long-range dispersal (Logan and Lutcavage 2010; Kim *et al.* 2012). Individuals may have travelled to more distant bays but if *R. taylori* did not forage in those bays, isotope analysis would not be able to detect the presence of *R. taylori* in those areas. Moreover, although *R. taylori* in CB had higher $\delta^{13}C$ values compared to other populations, several individuals had low $\delta^{13}C$ values relative to locally available $\delta^{13}C$ sources and the majority of the population. This could suggest longer range movement into areas with lower $\delta^{13}C$ source values, such as RE and RO. Therefore, this work cannot rule out the possibility that *R. taylori* made occasional long-range movements.

There was also insufficient data to assess male movement patterns and it is possible that male *R. taylori* exhibit different movement patterns.

The regional movement patterns demonstrated by female *R. taylori* may provide resilience to local (i.e. single bay) fluctuations in environmental conditions. For example, the results of Chapter 4 indicated *R. taylori* in CB select for seagrass habitat over other primary habitats. Individuals may have been selecting for seagrass because that habitat is typically abundant in small prey (Jackson *et al.* 2001; Gillanders 2006). Local declines in seagrass could negatively affect *R. taylori* access to resources. However, the results of Chapter 4 and 5 suggest individuals move between areas within 100 km. The ability to move into different nearby bays to exploit adequate resources may be a successful survival strategy. By moving between different locations, *R. taylori* are "buffered" against unproductive conditions in one bay by potentially more productive conditions in another bay (Yates *et al.* 2012). Thus, the use of multiple locations may help to stabilize the *R. taylori* population (Secor *et al.* 2009; Yates *et al.* 2012). However, without more detailed information on resource availability in each area and the dietary patterns of *R. taylori*, it is difficult to say how changes in any one area may affect the population.

The variability in environmental δ^{13}C and δ^{15}N values may have been the result of variable amounts of freshwater input into each bay. Freshwater runoff into nearshore areas, primarily from rivers, reduces the δ^{13}C value in the environment (Boutton 1991; Hobson 1999). Freshwater has lower δ^{13}C because it contains ^{13}C depleted CO_2 derived from the decomposition of terrestrial organic matter (Boutton 1991; Hobson 1999). RO and RE typically have high to moderate amounts of freshwater input respectively (see Chapter 3). This may explain why RE and RO baseline samples had lower δ^{13}C compared to the other locations. Higher δ^{15}N in RE and

RO may be the result of large expanses of sugarcane farms in the area in combination with high rates of freshwater input (Thorburn *et al.* 2011 and refs therein). Nitrogen runoff from fertilizer used on these farms may have drained into RE and RO and the surrounding areas, resulting in higher local δ^{15}N. It should be noted that because zooplankton and phytoplankton were not separated prior to analysis, comparisons of pelagic δ^{15}N values between bays may be biased as a result of different amounts of zooplankton being collected from each sample location. If certain bays had a higher volume of zooplankton, the baseline pelagic δ^{15}N values reported for those bays would be artificially high in comparison to other locations (Montoya 2008). However, the similar geographic pattern in δ^{15}N demonstrated by benthic and pelagic samples suggest that the presence of zooplankton in the samples did not obviously bias the results. As δ^{13}C trophic discrimination factors are relatively small, it was unlikely that different amounts of zooplankton between locations would affect the interpretation of the δ^{13}C results.

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

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

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

Chapter 6

Geographic and Temporal Variation in the Trophic Ecology of a Small-bodied Shark

6.1 Introduction

Lethal effects of sharks on prey populations via direct predation is 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 through 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 trophic ecology 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 (see Chapter 2; Terraube *et al*. 2011). 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*. 2012a). The two most commonly used isotopes are δ^{13}C (^{13}C/^{12}C) and δ^{15}N (^{15}N/^{14}N) as they provide complementary information on species dietary patterns (Shiffman *et al*. 2012). The δ^{13}C in animal tissues increases in relatively small amounts between prey and predators but more obviously 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 δ^{13}C can be used to estimate the carbon sources of a consumer (DeNiro and Epstein 1978; Peterson and Fry 1987). In contrast, δ^{15}N values predictably increase from prey to predator (Deniro and Epstein 1981; Peterson and Fry 1987). As a result, δ^{15}N in animal tissues can be used to estimate the trophic position of an individual (Post 2002). The δ^{13}C and δ^{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 estimate the dietary specialisation of a population in a given area and/or a species as a 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 δ^{13}C and δ^{15}N from different tissues can be used to evaluate changes in dietary sources 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).

Chapters 4 and 5 established that *Rhizoprionodon taylori* is best defined as a species with a low degree of habitat specialisation; however, *R. taylori* has demonstrated a strong preference for seagrass habitat, potentially because seagrass is typically highly productive and abundant in small teleost prey. 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). Chapter 5 showed *R. taylori* move between bays < 100 km apart, but more distant populations are likely separated for approximately one year. It is possible that *R. taylori* in different locations may have distinct diets resulting in unique relationships with local environments. Geographically distinct populations of marine mammals (e.g. *Mirounga leonine*; 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 chapter was to define the trophic ecology 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 (seagrass, macroalgae, and plankton) 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 chapter will improve understanding of the diets of small-bodied sharks and how this species may respond to variability in environmental conditions.

6.2 Data Analysis

The combined findings of Chapters 4 and 5 indicated female *R. taylori* captured in UP, BG, and CB probably move between these areas over the course of at least one year. Thus UP, BG, and CB likely represent a single potential feeding area for *R. taylori* captured in any one of these bays. The results of the acoustic analysis in Chapter 4 support the conclusion that *R. taylori* move between these locations. Chapter 5 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), which included UP, BG, and CB (Fig. 6.1). 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 (see Chapter 5). *Rhizoprionodon taylori* plasma δ^{13}C and δ^{15}N turnover was estimated to take approximately 6 months while muscle was estimated to take one year (see Chapter 5).

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

The Likelihood

$$y_{ij} \sim Normal(\mu + \alpha_i , \sigma^2) \qquad (6.1)$$

The Priors

$$\mu \sim Normal(0, 10^{-6}) \qquad (6.2a)$$

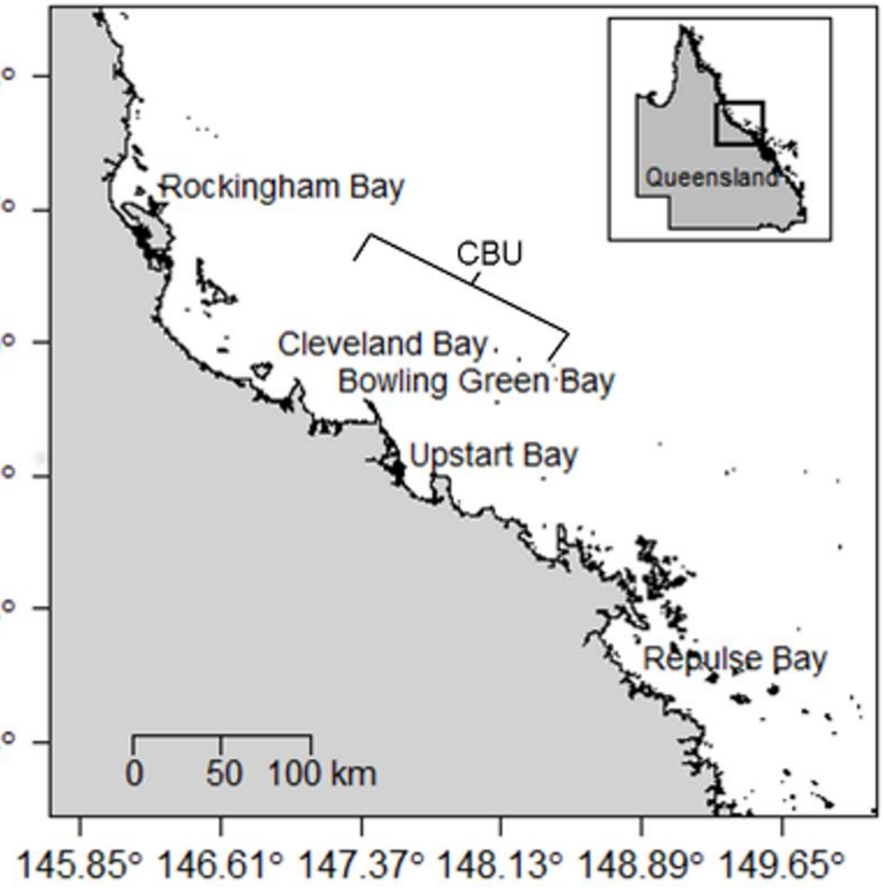

Fig. 6.1. Map of stable isotope sampling region indicating the five sampling locations and three designated feeding areas, Rockingham Bay, Cleveland Bay Unit (CBU), and Repulse Bay for *Rhizoprionodon taylori*. Inset indicates location along the north Queensland coast, Australia.

$$\alpha_i \sim Normal(0, 10^{-6}\ ) \qquad (6.2b)$$

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 was also used to test for differences between sample areas in δ^{13}C and δ^{15}N in muscle and plasma. Results of Chapter 5 showed that animal size had limited and inconsistent effects on *R. taylori* δ^{13}C and δ^{15}N. Therefore, size was not included in this analysis.

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

$$TP_{individual} = TP_{baseline} + \frac{\delta 15\mathrm{N}_{indvidual} - \delta 15\mathrm{N}_{baseline}}{3.2} \qquad (6.3)$$

Where $TP_{baseline}$ and $\delta 15\mathrm{N}_{baseline}$ were the known TP and median δ^{15}N value of environmental baselines (based on the results of Bayesian analysis). Seagrass δ^{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 a combination of phytoplankton and zooplankton.

Rhizoprionodon taylori δ^{13}C and δ^{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 δ^{13}C and δ^{15}N values within a group (i.e. sample area) to represent maximum niche breath (Layman *et al*. 2007), and (2) Bayesian standard ellipses (SEA$_b$) which incorporate the 40% densest δ^{13}C/δ^{15}N data points within a group 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 (Jackson *et al*. 2011) in R version 3.0.2 (R Development Core Team, 2013). 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 access each applied version of the models.

6.3 Results

6.3.1 Study Site δ^{13}C and δ^{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 δ^{13}C range than RO and RE samples (Table 6.1). The CBU also had a slightly larger range of δ^{15}N values.

Table 6.1. The δ^{13}C and δ^{15}N range (mean ± SD) of combined pelagic and benthic samples from each sample area, Repulse Bay (RE), Cleveland Bay Unit (CBU), and Rockingham Bay (RO).

Sample area	Sample size	δ^{13}C range	δ^{15}N range
RE	17	-23.28 - -15.15 (-19.9 ± 2.5)	1.33-6.22 (5.5 ± 1.4)
CBU	64	-20.54- -8.44 (-15.9 ± 3.9)	0.62-6.78 (3.4 ± 1.7)
RO	20	-21.46- -12.05 (-17.7 ± 2.9)	2.94-7.26 (4.6 ± 1.3)

Rockingham Bay and RE had relatively similar baseline δ^{13}C and δ^{15}N ranges. Benthic samples had higher δ^{13}C values than pelagic samples in all areas (Fig. 6.2a). In contrast, pelagic samples had higher δ^{15}N values than benthic samples in all areas. CBU benthic and pelagic samples had higher δ^{13}C than RO and RE samples. RE and RO had higher δ^{15}N values than CBU samples.

6.3.2 Shark δ^{13}C and δ^{15}N

One hundred and sixteen female *R. taylori* were sampled from across the three sample areas (Table 6.2); sizes ranged from 543 to 780 mm (mean ± SE = 681 ± 5.0). *Rhizoprionodon taylori* δ^{13}C and δ^{15}N followed similar geographical patterns to environmental isotope baselines (Fig. 6.2b). Plasma and muscle δ^{13}C from female *R. taylori* captured in CBU was higher than the δ^{13}C values in RO and RE. Plasma and muscle δ^{15}N from *R. taylori* in RE and RO was higher than the δ^{15}N in CBU. The trophic position of each *R. taylori* sample population spanned more than one trophic level (~ 3.2‰) and indicated each population was composed of secondary and/or tertiary consumers (Table 6.2). Trophic position varied between tissues but less so between locations. 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. *Rhizoprionodon taylori* in RE had a lower range of TPs than *R. taylori* in RO and CBU.

Isotopic niche breadth of *R. taylori* varied between locations and tissues. Analysis of muscle δ^{13}C and δ^{15}N indicated the CBU population had the largest isotopic niche (Fig. 6.3a). However, credibility intervals of niche breadth calculations indicated that the CBU population only had a significantly larger isotopic niche than *R. taylori* in RE (Fig. 6.3c). Analysis of plasma δ^{13}C and δ^{15}N revealed all three populations had similar niche breadth sizes, although CBU was still the

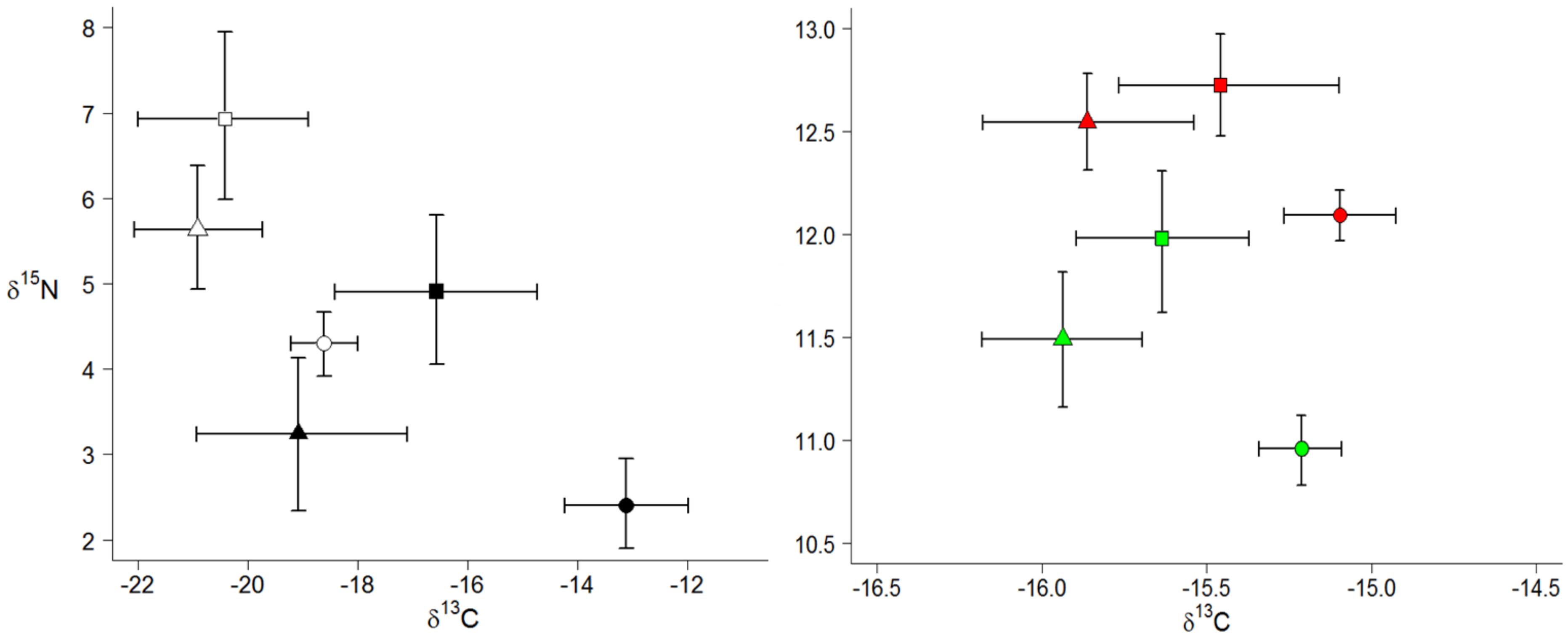

Fig. 6.2. Median δ^{13}C and δ^{15}N results of Bayesian ANOVA of (a) benthic (black) and pelagic samples (white), and *Rhizoprionodon taylori* muscle (red) and plasma (green) in Repulse Bay (■), the Cleveland Bay Unit (●) and Rockingham Bay. Black lines show 95% credibility intervals of posterior draws.

Table 6. 2. Total catch, δ^{13}C range, δ^{15}N range, trophic position (TP) range and mean with standard error (SE) of female *Rhizoprionodon taylori* in each sample area (Area), Repulse Bay (RE), Cleveland Bay Unit (CBU), and Rockingham Bay (RO).

Area	Total Catch	Tissue	δ^{13}C range	δ^{15}N range	TP Range	Mean TP ±SE
RE	20	Muscle	-16.6 - -14.5	11.94-13.39	3.2-4.1	3.7 ± 0.04
		Plasma	-16.7 - -14.7	10.19-12.66	2.7-3.9	3.5 ± 0.05
CBU	76	Muscle	-18.1 - -13.3	10.57-13.35	3.6-4.9	4.3 ± 0.02
		Plasma	-16.5- - 13.7	8.33-12.34	2.9-4.6	3.9 ± 0.03
RO	20	Muscle	-17.0 - -14.5	11.64-13.76	3.6-4.8	4.2 ± 0.05
		Plasma	-16.8- -14.5	9.92-12.52	3.1-4.4	3.8 ± 0.05

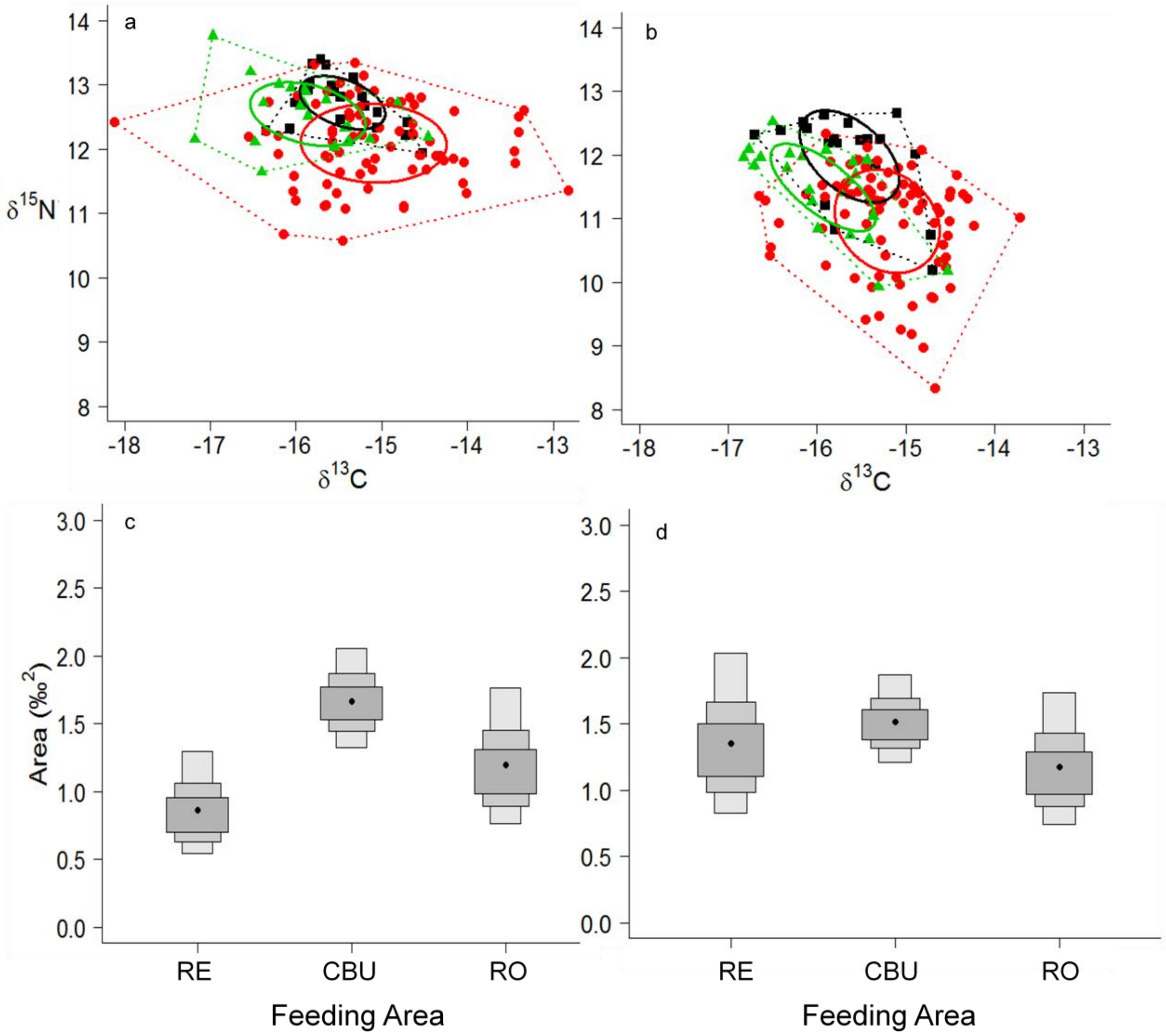

Fig. 6.3. Isotopic niche breadth of *Rhizoprionodon taylori*. Convex hulls of total niche width of muscle (a) and plasma (b) are dotted lines. Bayesian Standard Ellipses (SEA$_b$) isotope niches are shown for Repulse Bay (RE; ■/black), Cleveland Bay Unit (CBU; •/red), and Rockingham Bay (RO; ▲/green). 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.

largest (Fig. 6.3b,d). Isotopic niche size remained relatively constant in CBU and RO between muscle and plasma. In contrast, the niche breadth of *R. taylori* in RE substantially increased from muscle to plasma. This large increase in RE niche breadth was primarily the result of an increase in the range of *R. taylori* δ^{15}N in that area.

Pelagic and benthic contributions to *R. taylori* diet varied between locations (Fig. 6.4). In CBU the mixing model showed that the diet was split equally between benthic and pelagic sources for both muscle and plasma. In contrast, the diets of *R. taylori* in RE and RO were primarily composed of benthic sources. The constrained credibility intervals of the RE plasma mixing model (Fig. 6.4a) strongly indicates benthic prey were the primary dietary source in this area more recently. 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.

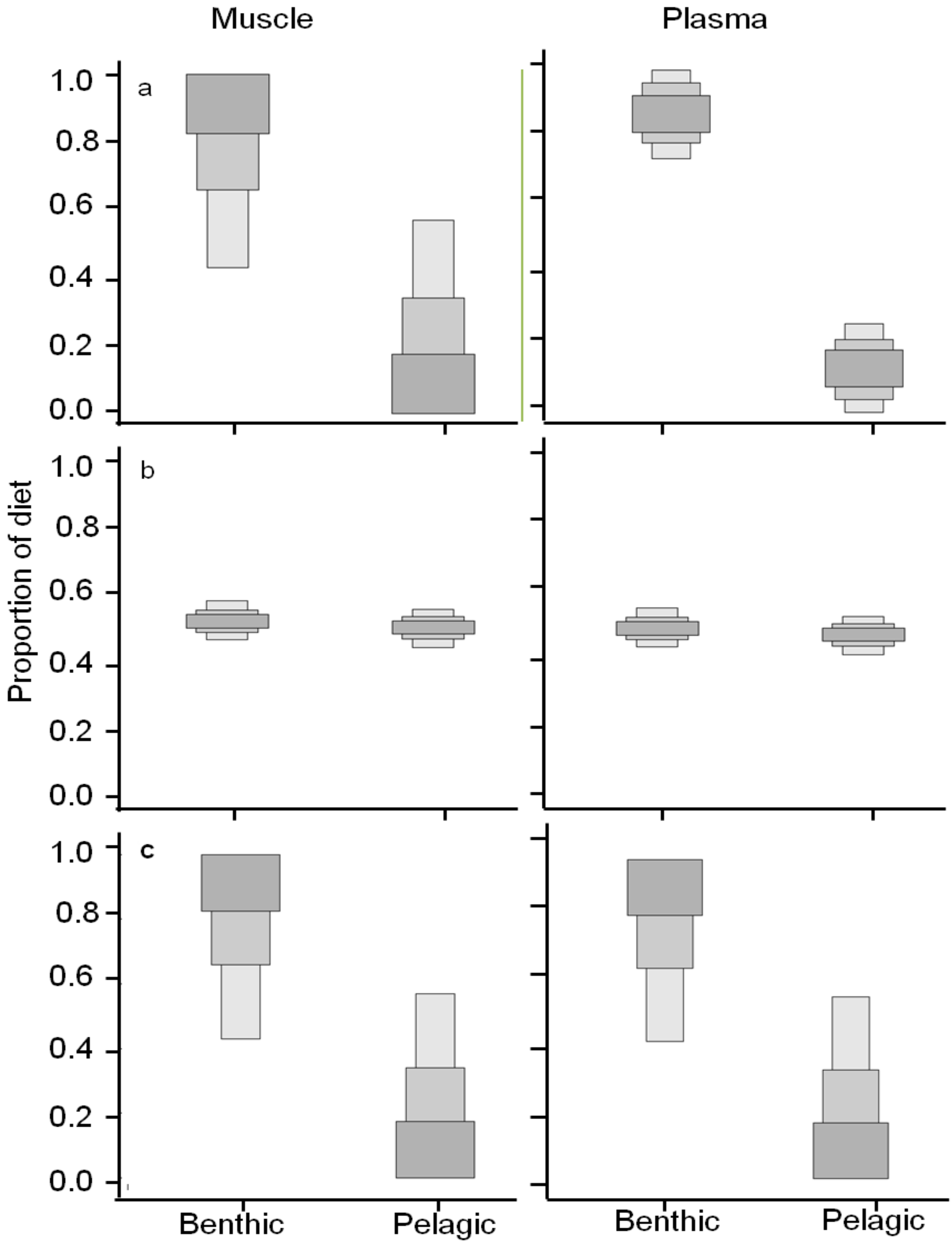

Fig. 6.4. Proportional contributions of benthic and pelagic food web sources to *Rhizoprionodon taylori* diet using a two-source Bayesian mixing model for plasma and muscle tissue in a) Repulse Bay, b) Cleveland Bay Unit, and c) Rockingham Bay. Shaded boxes are 50, 75, 95 (from dark to light grey) credibility intervals of posterior draws of SEA_b.

Discussion

Small-bodied, highly productive, moderately mobile predators such as *R. taylori* (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 as predator and prey items (Lundberg and Moberg 2003). Geographic and/or temporal changes in the diet of species like *R. taylori* can provide valuable information on species ecological roles in different marine communities, species vulnerability to environmental change, and indicate variation in environmental conditions between areas. Therefore, data on the diet of small-bodied species is critical to a better understanding of marine ecosystems.

Chapter 4 showed *R. taylori* selected for nearshore seagrass habitat, potentially because this habitat is highly productive and abundant in suitable prey. As a result, it was expected that benthic or seagrass-based prey would represent a large component of *R. taylori* diet. Results of this chapter have confirmed benthic sources are a significant and in some areas a majority contributor to *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 Cleveland Bay 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 Chapter. An even division of prey types in *R. taylori* diet in Cleveland Bay is also consistent with mixing model results within the CBU, supporting the accuracy of these results. Therefore, although the analysis present in this chapter is not a direct measure population specialisation (see Chapter 2), 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 specialisation, at least at a population level (Matich *et al*. 2010).

The broad dietary niche and range of trophic positions exhibited by *R. taylori* collectively across all sampling regions is similar to other species within this genera such as the Atlantic sharpnose shark *Rhizoprionodon terraenovae* (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 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 smooth-hound, *Mustelus schmitti,* (Belleggia *et al*. 2012), the lemon shark *Negaprion brevirostris* (Cortés and Gruber 1990), the sandbar shark *Carcharhinus plumbeus* (McElroy *et al*. 2006), and the starrspotted-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 *R. taylori* consume a wide range of prey they will most likely consume prey that is highly abundant or most beneficial to them 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 Cleveland Bay 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. However, it should be noted it is unlikely all possible δ^{13}C and δ^{15}N dietary sources were accounted for in RO and RE. In Chapter 5 it was established that although *R. taylori* in RO and RE were spending large periods of time feeding in their respective capture sites, they were probably moving into other nearby areas. Therefore, benthic and pelagic sampling in RO and RE did not fully account for the dietary δ^{13}C and δ^{15}N available to *R. taylori* sampled in those areas, particularly over the time span incorporated by muscle tissue. This would bias the results of the mixing models and may help to explain why there were large credibility intervals in mixing model outputs from RE and RO. Therefore, the results of the RO and RE muscle mixing models, and the implications they have for geographic variation in diet, should be interpreted with caution.

The geographic variation in isotope niche breadth may have also been due to variable patterns in selection or prey abundance. The *R. taylori* in CBU had a broad diet composed of an equal mix of benthic and pelagic prey, while *R. taylori* in RE and RO had smaller niche breadths and fed primarily on benthic prey. The less specialised diet of *R. taylori* in the CBU could result in a larger isotopic niche. However, it is also possible that the differences in niche breadth are due to differences in isotopic baselines between locations. The CBU had the largest range in baseline δ^{13}C and δ^{15}N values. If *R. taylori* were opportunistic and/or broad predators, presumably the isotopic niche of *R. taylori* would increase as the range in baseline δ^{13}C and δ^{15}N values also increased. This would be most obvious in tissues with shorter turnover times (i.e. plasma). 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 δ^{13}C and δ^{15}N values of local sources.

There was also moderate geographic variation in female *R. taylori* δ^{15}N and trophic position. Most of this variability is likely due to variability in δ^{15}N at the base of the food chain as shark tissues exhibited similar geographic trends in δ^{15}N as environmental baselines. The higher δ^{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 (see Chapter 5). However, trophic position calculations, which accounted for variation in δ^{15}N baselines, found *R. taylori* in RE were consuming prey at lower trophic positions than in other areas. This could indicate there is a lower abundance of higher trophic level prey in RE compared to RO and CBU. It is also possible that lower trophic level prey was abundant or beneficial in RE and thus formed a larger component of local diet. However, differences in trophic level were small and warrant further investigation, potentially using stomach content analysis. Overall, the differences in diet between locations suggest prey availability likely varies between locations and that *R. taylori* may have different effects on prey structure in each area.

Comparisons between muscle and plasma isotope values suggested there was some 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 one 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 the 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 chapter indicate that *R. taylori* has a low degree of dietary specialisation and is 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 (see Chapter 5), spatial and temporal variation in *R. taylori* diet may not only indicate differences in local prey biodiversity, but also that this species has unique effects on distinct local ecosystems. For that reason, this study emphasises the importance of examining the trophic ecologyof 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 a species with low habitat and likely dietary specialisation, *R. taylori* is probably resilient to environmental change, particularly at a local level.

Chapter 7

Movement Ecology of a Nearshore, Medium-bodied Shark, the Creek Whaler *Carcharhinus fitzroyensis*

7.1 Introduction

Nearshore areas are highly productive and dynamic environments that often contain a diverse range of habitat types, such as seagrass meadows, mangroves, and rocky and/or sandy substrate (Robertson and Duke 1987; Beck *et al.* 2001). As a result of this productivity and diversity, nearshore areas function as important foraging and nursery grounds for many shark species (Heupel *et al.* 2007; Knip *et al.* 2010).However, nearshore ecosystem health and biodiversity is in a state of global decline (Suchanek 1994; Lotze *et al.* 2006) due to numerous anthropogenic influences, including coastal pollution (Shahidul Islam and Tanaka 2004), inshore fishing (Blaber *et al.* 2000), and climate change (Harley *et al.* 2006). Consequently, there is a need to determine how environmental change affects nearshore marine species.

The majority of shark research in nearshore areas has investigated the habitat use of large-bodied species that use these areas as nursery grounds (e.g. Rechisky and Wetherbee 2003; Ortega *et al.* 2009; DiGirolamo *et al.* 2012). Nearshore areas provide juvenile sharks with protection from predators and in some cases productive foraging grounds (Branstetter 1990; Castro 1993). As a result, juveniles of large-bodied species are often highly resident to nearshore areas (e.g. Knip *et al.* 2011a). In contrast, large-bodied adults use substantially larger amounts of space, spend more time offshore, and may only use specific nearshore areas for short periods of time for foraging or pupping (Feldheim *et al.* 2002; Grubbs 2010). Considerably less data are available on the nearshore habitat use of smaller coastal species, such as the small-bodied milk shark *Rhizoprionodon acutus* (maximum total length 100 cm) or the medium-bodied nervous shark *Carcharhinus cautus* (maximum total length 150 cm) (Last and Stevens 2009). Medium- bodied species (max TL < 1500 mm) in particular have received little focused study. In contrast to large-bodied sharks, small- and medium-bodied species use nearshore areas consistently throughout their lives as juveniles and adults (Knip *et al.* 2010).

Limited work suggests nearshore species exhibit a variety of movement and habitat use strategies. For example, the Australian sharpnose shark *Rhizoprionodon taylori* and Atlantic sharpnose shark *R. terraenovae* have large coastal home ranges with individuals using a wide array of habitats (Carlson *et al.* 2008; Chapter 4). In contrast, the spottail shark *Carcharhinus sorrah* exhibits high site fidelity to single nearshore embayments with some individuals using small home ranges and consistent habitats (Knip *et al.* 2012a). Different strategies will likely affect the fitness of sharks in nearshore ecosystems.

The purpose of this chapter was to define the movement and habitat use patterns of *Carcharhinus fitzroyensis* in a nearshore area, compare movement strategies to sharks of other size categories, and evaluate its vulnerability to environmental change. Passive acoustic telemetry was used to determine *C. fitzroyensis* residency, space use, habitat selection and specialisation. Results of this chapter will lead to a better understanding of how medium-bodied coastal sharks use nearshore habitats relative to other species groups.

7.2 Data Analysis

7.2.1 Residency

Presence was evaluated each day. Individuals were deemed present if they were detected two or more times in the array in a given day. Residency was determined using a residency index that calculated the number of days an individual was present in the array as a proportion of the total days monitored (e.g. Abecasis and Erzini 2008; Werry *et al*. 2014). The index ranged from 1 to 0, indicating high to low residency, respectively. An ANCOVA was used to test for differences in residency between sample years with STL as a covariate. Individuals that were present in the bay for less than 14 days total were excluded from space use and habitat analysis.

7.2.2. Space use

Individual positions were estimated using the mean position algorithm described by Simpfendorfer et al. (2002) to determine individual centre of activity (COA) locations. The COA represented a weighted mean position for each 30 minute interval an individual was detected in the array. COA locations were used to calculate individual monthly activity space as 50% and 95% kernel utilisation distributions (KUDs) using the *adehabitatHR* package in R version 3.0 (Calenge 2006). To prevent overestimation of KUD size, KUD calculations incorporated an impassable boundary that represented the Cleveland Bay coastline. KUD calculations used a smoothing parameter of 0.008. A linear mixed effects model was used to determine if 50% and 95% KUD size was affected by animal size, month and/or diel period. To account for repeated measures in the data, individual was incorporated as a random factor in the resultant models. Models were computed using the *nlme* package in R (Pinheiro *et al*.

2013). Models were compared using Akaike information criterion with a small sample size bias correction (AICc) where models with the lowest AICc were considered to be the most significant drivers of KUD size. Akaike weights were also calculated to facilitate model assessment (Wagenmakers and Farrell 2004).

7.2.3 Habitat selection

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

The proportion of time spent in each habitat by individuals was compared to habitat availability using Strauss's (1979) linear selectivity index (L_i) to determine if *C. fitzroyensis* were selecting for or avoiding habitats:

$$L_i = r_i - p_i \tag{7.1}$$

where r_i was the proportion of habitat *i* used and p_i was the proportion of habitat *i* available in the study site. $L_i < 0$ indicated negative selection or avoidance. $L_i > 0$ indicated positive selection. $L_i = 0$ indicated the habitat was neither positively nor negatively selected for and was used opportunistically (Strauss 1979). The mean of resident individual L_i values was calculated for each year and each two week time period within each year to assess population habitat selection over time. A chi-squared goodness-of-fit test was used to determine if the proportion of time spent in each habitat by the resident population relative to habitat availability was significantly different, and hence if mean annual selection was significant.

7.2.4 Habitat niche breadth

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

$$FT = \sum_{i=1}^{R} (p_i q_i)^{1/2} \tag{7.2}$$

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

A variation of equation (7.2) was used to calculate individual niche overlap (Arlettaz 1999):

$$FT = \sum_{i=1}^{R} (p_{ik} q_{ik})^{1/2} \tag{7.3}$$

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

7.3 Results

Sixteen *C. fitzroyensis* (3 male, 13 female) were released with acoustic transmitters in Cleveland Bay between February and September 2012. Size ranged from 679 to 1370 mm STL (mean ± SE = 943 ± 48.9). All individuals were caught and released on the eastern side of Cleveland Bay. Five *C. fitzroyensis* were not detected or died following release and were excluded from analysis. One immature female was recaptured and collected by a local commercial fisherman 36 km north of the original release location approximately two weeks after release. These individuals were also excluded from analysis. The remaining 10 *C. fitzroyensis* (1 male, 9 female) were monitored in Cleveland Bay from September 2012 to May 2014. Size and clasper state indicated the male was immature. Size indicated seven females were mature and two were immature. Size ranged from 679 to1109 mm (mean ± SE = 945 ± 54.2).

7.3.1 Residency

Individuals were present in Cleveland Bay for 1 to 452 days (mean ± SE = 205 ± 53) (Fig. 7.1). Three individuals left the array within two weeks of release and did not return within the monitoring period. The residency index ranged from 0.002-0.74 (mean ± SE = 0.34 ± 0.09). There was no significant relationship between residency and size (ANCOVA, $F_{(1,18)} = 0.1616$, $P > 0.05$) or sample year (ANCOVA, $F_{(1,18)} = 0.1379$, $P > 0.05$). There was no clear seasonal pattern in presence except for one mature female that exhibited a seasonal pattern in presence.

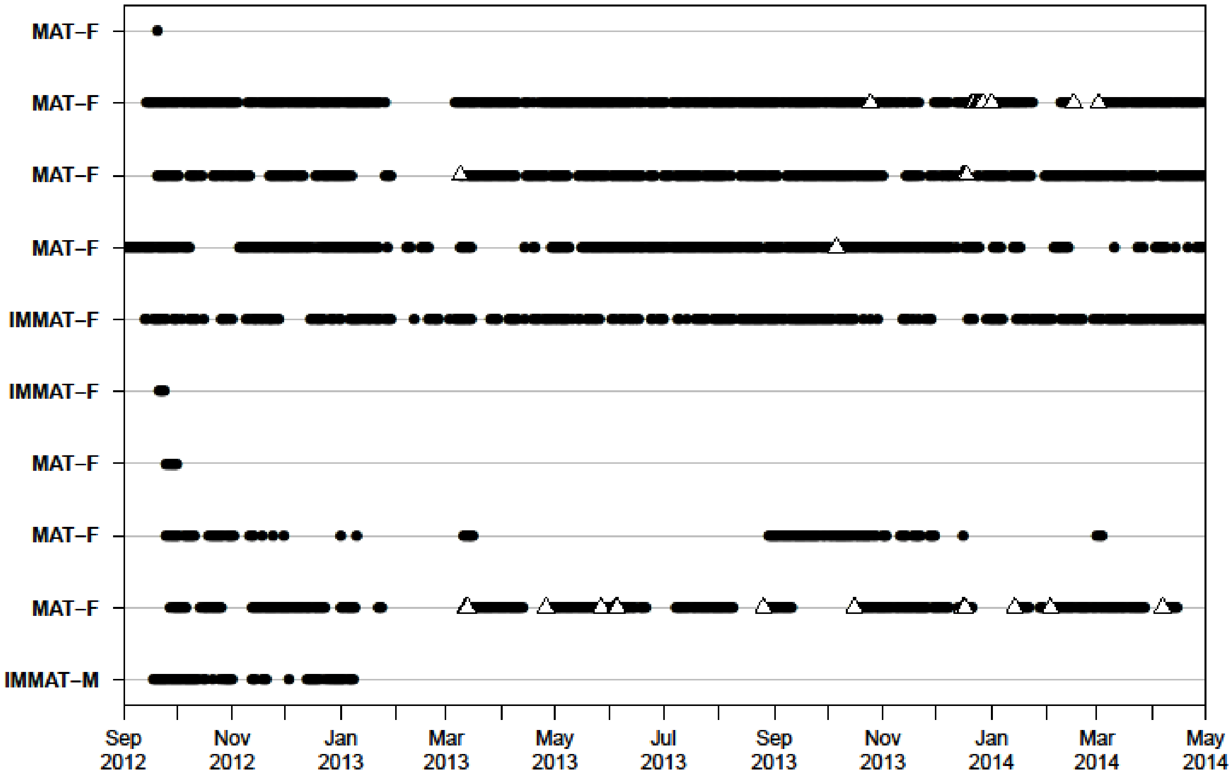

Fig. 7.1. Daily presence of *Carcharhinus fitzroyensis* released with acoustic transmitters in Cleveland Bay in 2012- 2014. Individuals are identified by maturity (mature=MAT, immature=IMMAT) and sex (male=M, female=F). Detections in Cleveland Bay are indicated by black circles. Additional detections in Bowling Green Bay are indicated by white triangles.

This individual was consistently present from September to December in 2012 and 2013, was present for several weeks in April 2013 and 2014, and was never detected between May and August during any year of the study.

Four mature female *C. fitzroyensis* were detected on receivers in Bowling Green Bay. These individuals were some of the most highly resident to Cleveland Bay. Two were only detected in Bowling Green Bay for single days before returning to Cleveland Bay. However, the two other females made brief excursions lasting approximately one week into Bowling Green Bay throughout the monitoring period.

7.3.2 Space Use

With the exception of one individual, all resident individuals exclusively used the eastern side of Cleveland Bay. Individual monthly activity space ranged from 2.6 to 19.8 km^2 (mean ± SE =10.6 km^2 ± 0.3) for 50% KUDs and 9.1 to 81.9 km^2 (mean ± SE = 47.9 km^2 ± 1.0) for 95% KUDs. The best possible model to explain both 50% and 95% KUD size included month and diel period as factors (Table 7.1). Shark length appeared to have little or no effect on KUD size and the model that only included size as a factor was worse than the null model for both 50% and 95% KUDs. This indicates immature and mature individuals utilized similar amounts of space within the bay. KUD size was larger during the day than at night for both 50% and 95% KUDs (Fig. 7.1). The influence of month on KUD size was most prominent in May and August (Fig. 7.2). In May, there was a distinct increase in 50% and 95% KUD size compared to all other months of the year. In contrast, August 50% and 95% KUD size was considerably smaller than all other months. KUD locations also fluctuated on a monthly basis according to this pattern. In August, activity space was centralized adjacent to the south-eastern creek mouths in Cleveland Bay (Fig. 7.3). During the rest of the year, but most

Table 7.1. Effect of animal size, month and diel period on creek whaler *Carcharhinus fitzroyensis* 50% and 95% kernel utilisation distribution (KUD) size (km^2). Degrees of Freedom (df), Akaike's information criterion correction (AICc), ΔAICc, and Akaike weights (W) values are given for each model. AICc values are marked with an * if models were significantly different from the null model using a likelihood ratio test. The best fit models are **bolded**.

Model	df	50% KUD AICc	95% KUD AICc	50% KUD ΔAICc	95% KUD ΔAICc	50% KUD W	95% KUD W
KUD ~ 1	3	1127.2	1624.2	81.79	102.98	0.00	0.00
KUD ~ Size	4	1136.0	1631.4	90.62	109.97	0.00	0.00
KUD ~ Size+Diel	5	1131.0	1624.2	85.60	102.77	0.00	0.00
KUD ~ Size+Month	15	1064.3*	1539.3*	18.91	17.93	0.00	0.00
KUD ~ Month	14	1054.3*	1532.1*	8.87	10.72	0.012	0.05
KUD ~ Month+Diel	15	**1045.4***	**1521.4***	0.00	0.00	0.982	0.969
KUD ~ Diel	4	1122.2*	1617.2*	76.79	95.82	0.00	0.00
KUD ~ Size+Month+Diel	16	1055.4*	1528.6*	10.02	7.19	0.007	0.027

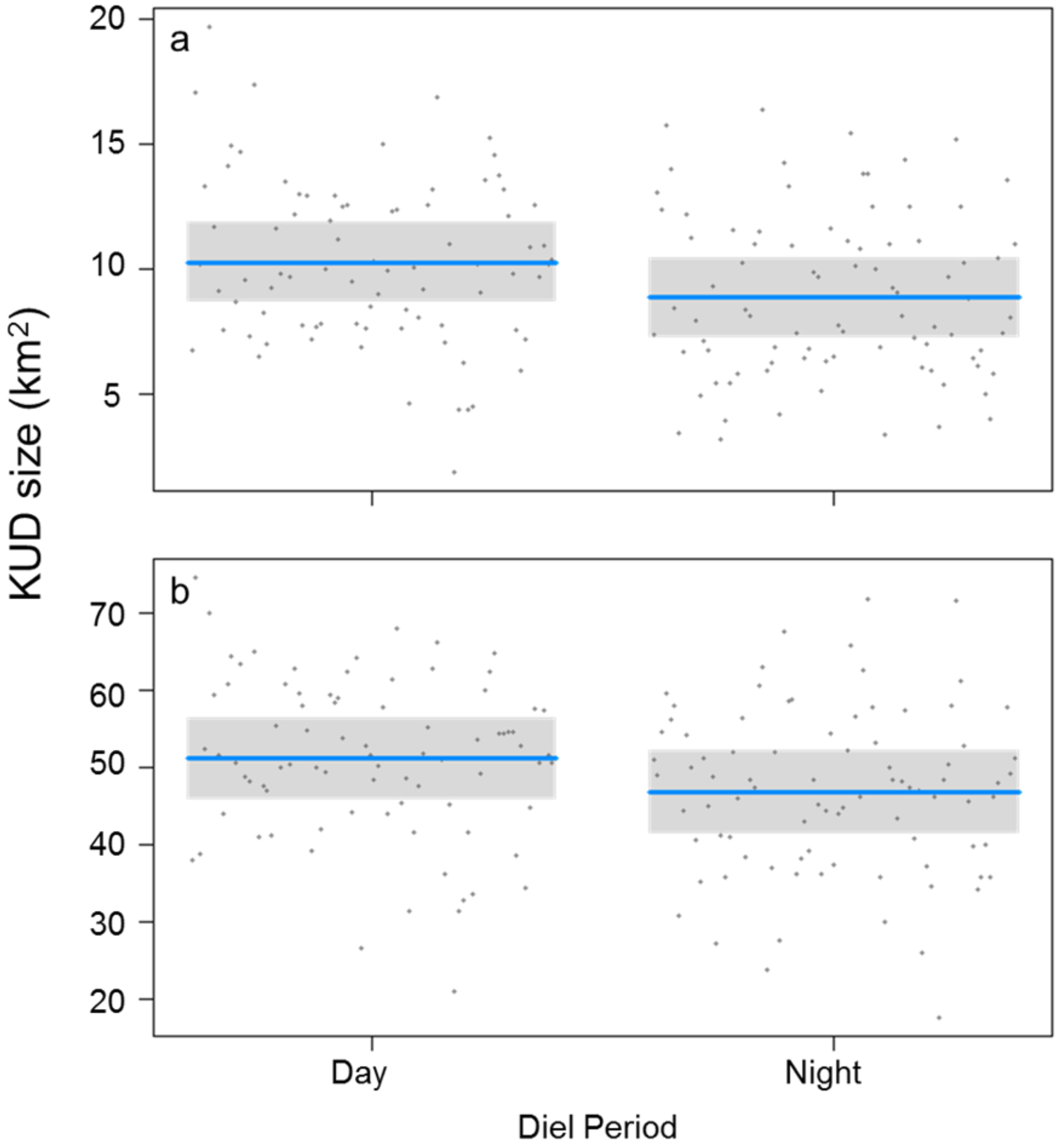

Fig.7.2. Effect of Diel period on (a) 50% and (b) 95% kernel utilisation size (km^2) of *Carcharhinus fitzroyensis*. Blue bars are mean predicted value of linear mixed effect model output, grey bands are 95% confidence intervals of model output.

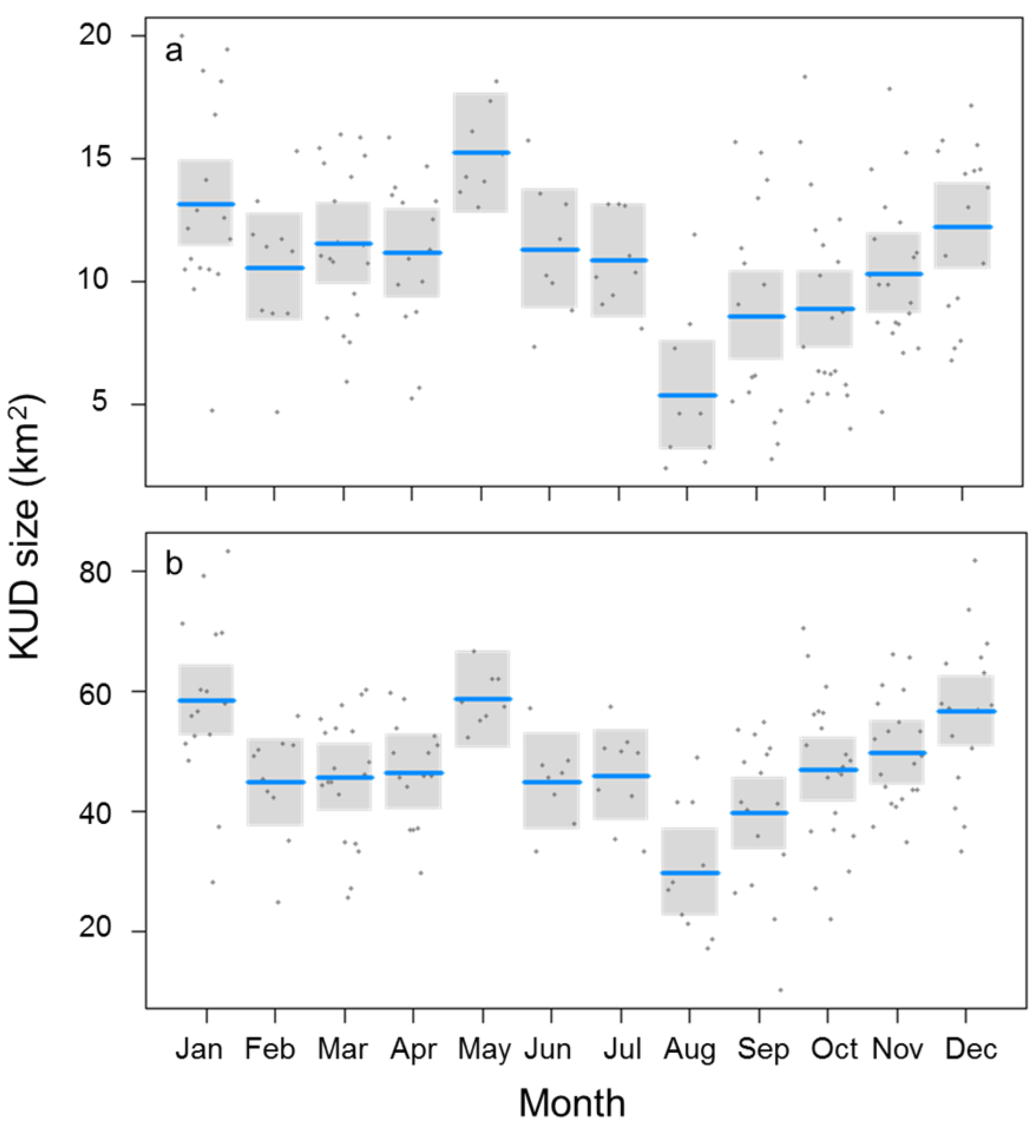

Fig.7.3. Effect of Month on 50% (a) and 95% (b) kernel utilisation size (km^2) of *Carcharhinus fitzroyensis*. Blue bars are mean predicted value of linear mixed effect model output, grey bands are 95% confidence intervals of model output.

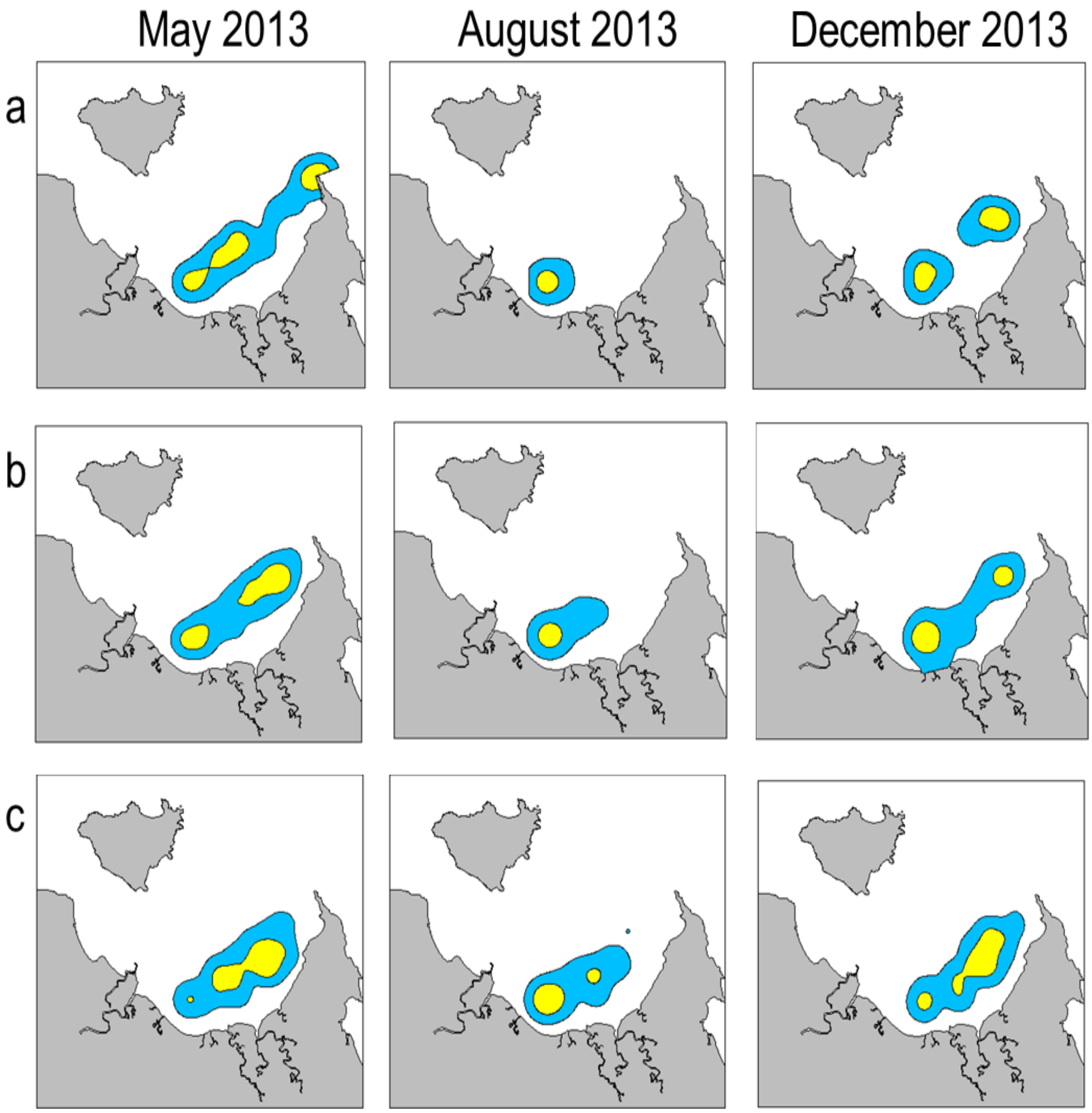

Fig.7.4. Monthly activity spaces of (a) one immature and (b, c) two mature *Carcharhinus fitzroyensis* in Cleveland Bay in May 2013, August 2013 and December 2013. Each panel shows the 95% (blue fill) and 50% (yellow fill) kernel utilisation distributions.

notably in May, KUD positions were more widely spread throughout the eastern half of the bay. The monthly pattern in KUDs location was observed in immature and mature individuals.

7.3.3 Habitat Selection and Specialisation

Individuals were detected in all five habitat types; however, the majority of time was spent in seagrass habitat (Table 7.2). There was no significant difference in time spent in each habitat between immature and mature individuals (Chi-squared test, X^2_{16}=20.00, $P > 0.05$). As a result, all individuals were grouped for habitat selection and specialisation analysis. Mean individual Strauss selection values for the entire monitoring period indicated *C. fitzroyensis* selected for seagrass habitat, used outer bay mud substrate opportunistically, and avoided reef, mudflat and sand inshore habitats (Fig. 7.5). A Chi-squared goodness of fit test indicated selection was significant (X^2_4=144.758, $P < 0.05$). Mean fortnightly Strauss index values showed that selection for seagrass was consistently positive throughout the monitoring period (Fig. 7.6). Selection for outer bay habitat was highly variable and fluctuated between positive and negative selection. There was no apparent seasonal pattern in the selection of outer bay mud substrate; however, individuals selected for outer bay habitat less often in the second year of the study. Mudflat, reef, and sandy inshore habitats were consistently avoided over time.

Mean individual niche breadth for *C. fitzroyensis* was moderate and ranged from 0.70 to 0.77 (mean ± SE = 0.73 ± 0.03). Mean individual niche overlap was large and ranged from 0.91 to 1 (mean ± SE = 0.97 ± 0.03), indicating resident *C. fitzroyensis* used nearly identical proportions of the same habitats.

Table 7.2. Mean and standard error of time spent in each habitat by mature and immature *Carcharhinus fitzroyensis* in Cleveland Bay, measured as a percent (%) with standard error (SE).

Habitat Type	Time Spent ± SE Mature	Time Spent ± SE Immature
Seagrass	72.9 ± 3.5	72.7 ± 6.26
Outer bay mud substrate	20.4 ± 4.4	20.0± 2.7
Reef	0.09 ± 0.1	0.0 ± 0.0
Sandy inshore	1.6 ± 1.2	0.19 ± 0.19
Intertidal mudflat	5.0 ± 2.5	7.11 ± 3.69

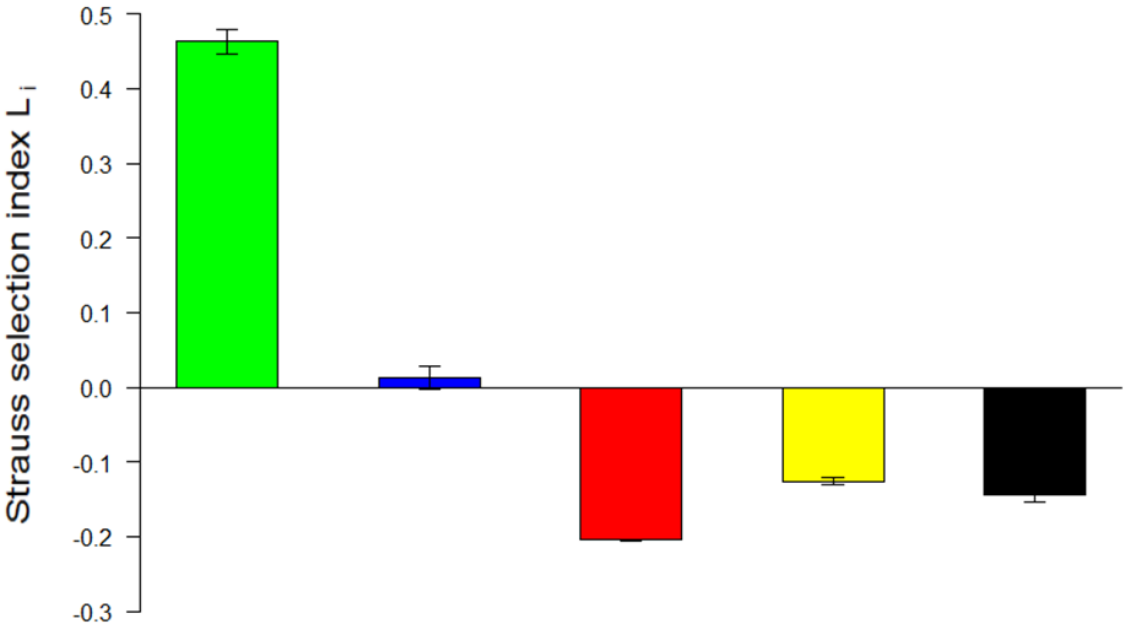

Fig.7.5. Mean Strauss linear selection index values of seagrass (green), outer bay mud substrate (blue), reef (red), sandy inshore (yellow) and intertidal mudflat (black) habitats by *Carcharhinus fitzroyensis* in Cleveland Bay between September 2012 to May 2014. Bars indicate standard error.

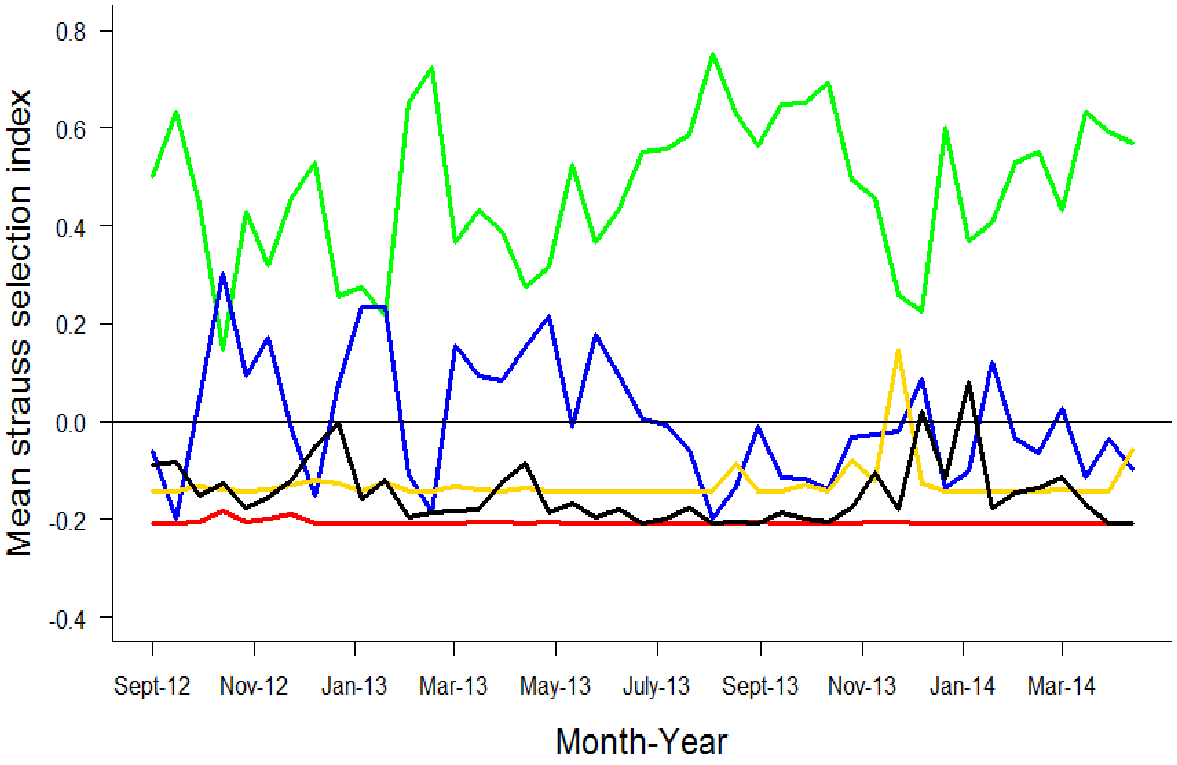

Fig. 7.6. Mean fortnightly individual Strauss linear selection values of *Carcharhinus fitzroyensis* in Cleveland Bay for seagrass (green), outer bay mud substrate (blue), reef (red), sandy inshore (yellow) and intertidal mudflat (black).

7.4 Discussion

Similarity in immature and mature *C. fitzroyensis* residency, space use, and habitat use patterns suggests individuals share nearshore resources. High individual niche breadth overlap and consistent habitat selection patterns exhibited by the sample population showed that there was limited individual variability in habitat use. All individuals almost exclusively used seagrass habitats and to a lesser extent outer bay mud substrate habitats. The shared use of nearshore areas by mature and immature individuals is consistent with other small- and medium-bodied coastal species, such as *R. acutus* (Henderson *et al.* 2006; Schroeder 2011), *R. terraenovae* (Carlson *et al.* 2008), *R. taylori* (Chapter 4 and 5), *C. sorrah* (Knip *et al.* 2012a), and the grey-smooth hound shark *Mustelus californicus* (Ebert 2003; Espinoza *et al.* 2011). However, in contrast to *C. fitzroyensis*, many small-bodied coastal species use a wide array of habitats. For example, *R. taylori*, *R. terraenovae*, and *M. californicus* all exhibited low residency to single nearshore areas (Carlson *et al.* 2008; Espinoza *et al.* 2011; Chapter 4). *Rhizoprionodon taylori* and *R. terraenovae* also used a variety of habitats in nearshore embayments (Carlson *et al.* 2008; Chapter 4). Although *C. sorrah* displayed high residency and site fidelity to single nearshore habitats, individuals also demonstrated a high degree of spatial segregation and individual variability in habitat use (Knip *et al.* 2012a; Knip *et al.* 2012c). Unlike *C. fitzroyensis*, *C. sorrah* demonstrated no habitat preference at the population level. Instead, the residency and habitat use patterns exhibited by *C. fitzroyensis* are more similar to those exhibited by juveniles of large-bodied species. Juveniles of large-bodied species, such as the pigeye shark *Carcharhinus amboinensis*, the bull shark *Carcharhinus leucas*, and the lemon shark *Negaprion brevirostris*, are highly resident to nearshore areas and often use the same habitats and home ranges for long periods of time (Heupel *et al.* 2010; Murchie *et al.* 2010; Knip *et al.* 2011a). Therefore, the results of this study demonstrate that

C. fitzroyensis used a combination of residency and movement strategies previously reported in small- and large-bodied species.

The long term use of seagrass exhibited by the *C. fitzroyensis* population suggests this habitat had sufficient resources to support the majority of the population over long periods of time. Consistent use of nursery areas by large-bodied sharks is in part motivated by high nearshore productivity and prey availability (Castro 1993), Seagrass habitats are usually highly productive and contain relatively large populations of small fish and bottom dwelling prey (Orth *et al.* 1984; Edgar and Shaw 1995; Jackson *et al.* 2001). Therefore, seagrass habitat may be excellent foraging grounds for *C. fitzroyensis*. Moreover, consistent use of seagrass habitat on the eastern side of Cleveland Bay could result in greater familiarity with the distribution of resources in that area (Kuba *et al.* 2010; Schluessel 2014). Increased resource availability and better knowledge of resource distribution could make it highly beneficial for immature and mature *C. fitzroyensis* to remain in the eastern side of the bay over long periods of time. It should be noted that some of the highly resident *C. fitzroyensis* individuals made occasional excursions into Bowling Green Bay and the habitats used during those excursions could not be precisely determined. However, Bowling Green Bay is dominated by mud substrate and seagrass habitats (Furnas 2003; GBRMPA 2011) Therefore, when individuals were in Bowling Green Bay it is likely they were utilizing habitats similar to those used in

It is possible that the close association with seagrass habitat and the eastern half of the bay demonstrated by *C. fitzroyensis* was due to bias in catch distribution. Fishing effort was concentrated in the eastern portion of the bay. Therefore the high residency to that area may have been the by-product of where individuals were captured (Knip *et al*. 2012). However, fishery independent and dependent sampling throughout Cleveland Bay revealed that *C. fitzroyensis* has been almost exclusively captured on the eastern side of the bay (Simpfendorfer, unpublished data). Therefore, tracking and activity space data are likely representative of how this species uses space within Cleveland Bay and are not the result of sampling bias. Fishery independent catch data from northern Australia also showed this species is often caught in mud substrate habitats and/or in areas with high potential for benthic growth (Simpfendorfer, unpublished data; GBRMPA 2011). Therefore, results from coastal catch data supports the conclusion that seagrass is one of the primary habitats used by *C. fitzroyensis*.

Long-term residency by immature *C. fitzroyensis* may also have been influenced by life history (Heupel *et al.* 2007). As previously discussed, juveniles of large-bodied species exhibit high site fidelity to nearshore areas because these areas can provide protection from predators (Castro 1993). Although *C. fitzroyensis* is potentially a productive species, it reaches sexual maturity five to six years later than small-bodied species and generally gives birth to smaller litters (Last and Stevens 2009; Smart *et al.* 2013). Therefore, high residency to shallow nearshore areas may provide some beneficial protection for immature *C. fitzroyensis* from large-bodied predators (Heithaus 2007). This may also explain why, similar to large-bodied species, neonate *C. fitzroyensis* have been observed in shallow habitats and expand their range as they grow (Harry *et al.* 2011).

While seagrass habitat was the principal habitat used by *C. fitzroyensis*, moderate habitat specialisation values and selection analysis indicate seagrass habitat was used in conjunction with outer bay mud substrate. Use of outer bay mud substrate was highly variable over time and lack of seasonality in selection suggests this habitat was not used in response to seasonal abiotic changes in the environment. Selection of outer bay habitat could represent occasional foraging excursions in this habitat. Although outer bay habitats were available on both sides of

Cleveland Bay, *C. fitzroyensis* rarely use outer bay habitats on the western side of the bay. This would suggest that, regardless of why outer bay habitat was used, individuals preferred to remain in close proximity to seagrass habitat. Consistent avoidance of sandy inshore, reef and mudflat habitat suggests these habitats were not suitable for *C. fitzroyensis.*

This study also revealed there was individual variability in presence. A few individuals spent less than two weeks in the bay, suggesting broader movements occur in a portion of the population. Further evidence of broad movement came from an individual that was recaptured 36 km from Cleveland Bay a few weeks after release. Individual variability in presence has been reported in other elasmobranchs, such as the medium-bodied *C. sorrah* (Knip *et al.* 2012a) and the cownose ray *Rhinoptera bonasus* (Collins *et al.* 2007). The low residency exhibited by some *C. fitzroyensis* are more similar to the movement patterns exhibited by small-bodied species such as *R. terraenovae* (Carlson *et al*. 2008). Therefore, some *C. fitzroyensis* individuals may have used more transitory strategies to gain greater access to a wider range of resources, such as prey and potential mates.

The space use patterns exhibited by *C. fitzroyensis* may have also been motivated by prey availability. The short-term change in activity space and location observed in August and May suggests a biotic or behavioural stimulus that caused changes in distribution to occur over a short period of time. If *C. fitzroyensis* were responding to changes in abiotic factors, changes in space use would likely mimic the more gradual pattern of changes in bay temperature and salinity. Therefore, the short term change in space use may have been a response to a short-lived biotic factor, such as a change in prey location and abundance. Diel patterns in space use may also be linked to foraging behaviour. Larger day time activity spaces suggest *C. fitzroyensis* were more active during the day and may be primarily diurnal feeders. This contrasts with what has been found in other elasmobranchs that typically utilize small core areas during the day and move more widely at night for feeding (Sundström *et al.* 2001; Cartamil *et al.* 2003; Garla *et al.* 2006b).

The results of this study have shown that *C. fitzroyensis* exhibited resource use and movement strategies that are often associated with both small- and large-bodied species. While immature and mature age classes shared space and resources, the population was highly resident to the bay. As previously discuss, the high residency displayed by some individuals may be highly beneficial.. However, the habitat use strategies of *C. fitzroyensis* could make them more vulnerable to environmental change. The regular movement of small-bodied sharks between different bays and/or habitats often means they are resilient to local environmental change (Knip *et al.* 2010; Yates *et al.* 2012). However, the high residency and strong association with seagrass habitat makes *C. fitzroyensis* vulnerable to local nearshore environmental change, specifically deterioration of seagrass habitat. Seagrass habitat abundance and biodiversity is under threat of decline from numerous human activities, including dredging (Walker and McComb 1992; Erftemeijer and Lewis III 2006), excessive nutrient deposition (McGlathery 2001; Ralph *et al.* 2006), chemical contamination such as herbicides (Haynes *et al.* 2000), and the effects of climate change (Orth *et al.* 2006; Hughes *et al.* 2008; Waycott *et al.* 2009). As immature and mature individuals share space and resources, declines in seagrass availability would likely affect all age classes within the population. This chapter has demonstrated that medium-bodied coastal species use nearshore habitats differently compared to other size classes of sharks. Moreover, the movement patterns of medium-bodied species could increase their vulnerability to environmental alterations. Therefore, future research should strive to increase understanding of medium-bodied species and the evolutionary causes, costs, and benefits of their behaviours.

Chapter 8

General Discussion

8.1 Conclusions and Implications

Nearshore areas are highly dynamic, productive environments that contain key habitats for many marine species, including sharks (Beck *et al.* 2001; Knip *et al.* 2010). However, nearshore areas are exposed to a variety of destructive anthropogenic influences, such as human development, pollution, and inshore fishing (Lotze *et al.* 2006; Bulleri and Chapman 2010; Breen *et al.* 2014). Consequently, nearshore shark species may be susceptible to population decline as a result of environmental change. Therefore, data on the residency, space use, resource selection, and specialisation of nearshore sharks are critical to species management. However, varying definitions of shark resource use, specifically resource specialisation, have limited research in this area. Without a consistent, widely applicable definition to describe the resource use of shark species, researchers are unable to compare results and may misinterpret findings. The definition for shark resource specialisation proposed in Chapter 2 provides a conceptual context for measuring and interpreting shark resource specialisation in a variety of circumstances. The “requirements only” (Peterson *et al.* 2011) definition of niche breath proposed by Hutchinson (1957) best suits the current technological constraints of marine research and most directly addresses the primary questions of most resource use investigations. Moreover, the definition provided uses a continuum model for species comparison that more accurately reflects the role of species in nature. The definition is also flexible enough to incorporate unique environmental circumstances and scales that vary between studies and species. As a result, specialisation and vulnerability can be considered at a scale and context appropriate to the focal species and environment. By applying a consistent but widely applicable definition for shark resource specialisation it was possible to assess and compare the diet, habitat use, and level of specialisation of *R. taylori* and *C. fitzroyensis*.

Based on the collective findings of Chapters 4, 5, and 6, *R. taylori* is best described as a species with a low degree of resource specialisation that is adaptive to local environmental change. Results showed that *R. taylori* used different habitats and embayments, which is consistent with other small-bodied species. The diet of *R. taylori* included prey from seagrass and plankton food chains. Geographic variation in *R. taylori* diet also suggested that populations were foraging opportunistically. Thus, if a particular bay or habitat was in decline, it is likely that *R. taylori* could move into another bay or habitat and successfully use the resources there. Previous work has also shown that *R. taylori* is a highly productive species (Simpfendorfer 1992b). The combination of *R. taylori* movement patterns, diet, and productivity mean this species would be resilient to nearshore environmental change. However, large-scale decreases in seagrass availability may affect *R. taylori* behaviour. Stable isotope analysis revealed *R. taylori* had a smaller coastal range than was expected based on the movement of similar small-bodied species (e.g. *Rhizoprionodon terraenovae*) (Carlson *et al.* 2008; Kohler *et al.* 1998). Dietary analysis also suggested seagrass habitat was important for *R. taylori* throughout its range. Therefore, although small-bodied coastal species are often considered less vulnerable to environmental change, loss of seagrass over a broad spatial scale could be problematic for *R. taylori*. If there was a decline in seagrass availability and/or benthic productivity across multiple bays, *R. taylori* may have to use different habitats (e.g. sandy inshore) more often and/or expand its range to ensure sufficient access to resources. Prey abundance in seagrass would decline with loss of habitat, and as a result *R. taylori* may need to increase consumption of prey from plankton food chains. A reduction in seagrass availability and/or benthic productivity may also affect population fitness, but this would be dependent on other factors such as competition for reduced resources.

In contrast to *R. taylori*, the resource use patterns of *C. fitzroyensis* suggested this species has a moderately high degree of habitat specialisation. Immature and mature *C. fitzroyensis* demonstrated consistent selection for seagrass habitat and high residency to Cleveland Bay. Although there was some individual variability in presence and evidence for long range movement, the majority of individuals exhibited high residency. Coastal catch records also suggest that *C. fitzroyensis* prefers mud substrate and seagrass habitats throughout its range (Simpfendorfer unpublished data). Therefore, unlike *R. taylori*, there is little evidence to suggest that *C. fitzroyensis* would be able to efficiently use other habitats if seagrass habitats were no longer available. These results indicate that *C. fitzroyensis* may be vulnerable to population decline as a result of nearshore change, in particular the destruction of seagrass habitat. Therefore, although both species occupy nearshore areas throughout their lives and exhibit a preference for seagrass habitat, the differences in habitat use and movement indicate that *C. fitzroyensis* is more vulnerable to environmental change than *R. taylori*.

As discussed in Chapters 4 and 7, differences in movement strategies may be a result of contrasting life histories. The small-bodied *R. talyori* is a highly productive, fast-growing species (Simpfendorfer 1992b; Last and Stevens 2009). Due to its small size, *R. taylori* is vulnerable to predation inside and outside of nearshore areas (see Chapter 4), and thus may ultimately benefit from moving between embayments to gain access to more resources. In comparison, *C. fitzroyensis* is slower-growing and less productive (Lyle 1987; Smart *et al*.

2013), therefore it may derive greater benefit from residency in highly productive habitats, similar to juveniles of large-bodied sharks (e.g. Conrath and Musick 2010). However, differences in movement patterns observed between these species are likely based on a variety of complex biological factors that require further investigation.

Research in Cleveland Bay has shown that nearshore sharks can exhibit a diverse range of movement and resource use strategies (Knip *et al*. 2011; Knip,*et al*. 2012; Chin *et al*. 2013). These strategies will affect species exposure and vulnerability to environmental change. Movement and resource use data can also be used to identify key habitats and locations for different populations and species. Improved knowledge of the resource selection and specialisation of nearshore shark species will result in a better understanding of species and enhance management strategies. For example, both *R. taylori* and *C. fitzroyensis* preferred seagrass habitat. As such, protection of seagrass will likely be an important consideration in spatial management of these species if required. This dissertation also demonstrated that the resource use patterns of immature and mature individuals may affect the population’s overall response to change. For example, consistent use of seagrass by immature and mature *C. fitzroyensis* suggests that both groups will be negatively affected by declines in seagrass availability. Therefore it is important to consider movement and habitat use across multiple age classes to gain a population level understanding of resource requirements.

This dissertation has demonstrated the importance of defining the movement and resource use patterns of sharks in nearshore areas. Species resource use patterns are highly diverse and dependent on life history and environmental circumstance. Species that are more specialised (i.e. *C. fitzroyensis*) will likely prove more vulnerable to environmental change or degradation than species that have a low degree of resource specialisation (i.e. *R. taylori*). However, as demonstrated by *R. taylori*, even species that have a low degree of specialisation may be negatively affected by changes to the environment. As human development in coastal areas increases, the level of resource specialisation exhibited by species will be a critical component of habitat and species management plans.

8.2 Future Research

Although the work described in this dissertation has increased understanding of nearshore sharks, it has also highlighted topics that require further study. It is still unclear how changes in abiotic factors such as water temperature, oxygen content, or salinity affect *R. taylori* and *C. fitzroyensis* habitat use and movement. The use of sandy inshore habitat by *R. taylori* was correlated with changes in freshwater input into Cleveland Bay, however this correlation was inconsistent among individuals. It is possible that movement into sandy habitats was not a physiological response to changes in freshwater input but the result of another driver. For example, some *R. taylori* may have moved into sandy inshore areas to give birth. Therefore, having more detailed knowledge of how species respond to changes in environmental factors and what role biological drivers play is important to understanding population level movements and vulnerabilities.

As discussed in Chapter 3, isotope analysis is not commonly used to study the movement of sharks. This is in part due to limiting factors such as long turnover times in tissues (Logan and Lutcavage 2010). Studies that have used isotopes to examine the movement of sharks have primarily investigated movement at broad or coarse spatial scales (e.g. Abrantes and

Barnett 2011; Carlisle *et al.* 2012). However, the techniques used in Chapter 3 to assess the annual range of *R. taylori* demonstrated that isotopes can be used to define movement at regional scales in relatively high detail. In future, isotope analysis could be used to gain a better understanding of shark movement as well as diet.

Due to its relative rarity, it was not possible to sample sufficient *C. fitzroyensis* for stable isotope movement and diet analysis. However, knowledge of *C. fitzroyensis* broader scale movements and diet would greatly enhance our current understanding of this species. For example, isotope analysis could be used to determine if seagrass or benthic food chains are the primary contributor to *C. fitzroyensis* diet, as the telemetry data suggests. Previous isotope analysis in Cleveland Bay suggests that *C. fitzroyensis* has higher $\delta^{13}C$ values than *R. taylori* and several other species of sharks and teleosts (Kinney *et al*. 2011). This could indicate *C. fitzroyensis* feeds from benthic or seagrass food chains more often than *R. taylori*. This interpretation is supported by the telemetry results in Chapters 4 and 7, which demonstrated *C. fitzroyensis* used seagrass habitats more consistently than *R. taylori*. However, the sample size of *C. fitzroyensis* in the previous study was small (n=9; Kinney *et al*. 2011), therefore further study is needed to comprehensively assess *C. fitzroyensis* diet. Given that *C. fitzroyensis* was highly resident to Cleveland Bay, the inclusion of additional isotopes in analysis, such as sulphur, may improve assessment of coastal movement and habitat use (Connolly *et al.* 2004). The potential for more distinct coastal patterns in $\delta^{34}S$ compared to $\delta^{13}C$ and $\delta^{15}N$ would make it easier to detect *C. fitzroyensis* movement between embayments, even over long periods of time. Including tissues that have relatively fast isotope turnover rates, such as liver (MacNeil *et al.* 2006), would also make it possible to detect seasonal changes in *C. fitzroyensis* diet. Plasma and muscle turnover rates in medium-bodied sharks would likely be too slow to detect changes in diet between seasons (Logan and Lutcavage 2010; Kim *et al.* 2012).

Movement and residency patterns exhibited by *R. taylori* were mostly consistent with those exhibited by other small-bodied sharks (Carlson *et al.* 2008; Espinoza *et al.* 2011). Collectively, these results suggest that small-bodied sharks are generally highly mobile and use a wide array of habitats. However, the results of Chapter 7 suggest that medium-bodied species exhibit unique nearshore movement and habitat use strategies compared to small- and large-bodied sharks. Medium-bodied species may exhibit resource use and movement patterns better suited to their biological traits. Unfortunately, there has been little research on the movement of medium-bodied nearshore sharks. The results of this dissertation indicate that more focused study on medium-bodied species is required as these species likely have a distinct relationship with the environment and specific vulnerabilities to change. Future work should also focus on developing theoretical explanations for medium-bodied shark behaviour.

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