Kinney, Michael J. (2011) ***The communal nursery area paradigm revisited: niche overlap versus niche separation among juvenile shark species of Cleveland Bay.*** **PhD Thesis, James Cook University.**

Kinney, Michael J. (2011) ***The communal nursery area paradigm revisited: niche overlap versus niche separation among juvenile shark species of Cleveland Bay*****. PhD thesis, James Cook University.**

The Communal Nursery Area Paradigm Revisited: Niche Overlap Versus Niche Separation Among Juvenile Shark Species of Cleveland Bay

Thesis submitted by
Michael J. Kinney (B.A. Integrative Biology)
University of California, Berkeley
College of Letters and Sciences
in August 2011

for the degree of Doctor of Philosophy
James Cook University, Queensland
School of Earth and Environmental Sciences

Statement of Originality

I declare that the contents of this thesis are original, except as acknowledged in the text. The material presented herein has not previously been submitted for a degree at this, or any other university.

Michael Kinney
August 31st 2011

Statement of Contribution by Others

Chapter 1
The introduction was my own work. My supervisor Dr. Colin Simpfendorfer proofread earlier versions of this chapter.

Chapter 2
This chapter was published in 2009 by the journal, Conservation Letters. I am the primary author and my supervisor Dr. Colin Simpfendorfer is the secondary author. This chapter is my own work. My supervisor assisted in refining the scope of this work and proofread earlier versions of this chapter and assisted in responding to review comments prior to its publication.

Chapter 3
The methods chapter was my own work. The construction and use of fisheries-independent sampling gear was aided by members of my research centre. I am grateful to all the volunteers whose assistance during field sampling trips was invaluable.

Chapter 4
Other members of my research centre assisted me in the collection of samples on both fisheries-dependent and independent sampling trips. All stomach content analysis and statistical analysis was conducted by me. My supervisors Dr. Colin Simpfendorfer and Dr. Andrew Tobin proofread earlier versions of this chapter.

Chapter 5
This chapter was published in 2011 by the journal, Marine Ecology Progress Series. I am the primary author and my supervisors Dr. Colin Simpfendorfer and Dr. Andrew Tobin, as well as Dr. Aaron Fisk, and Dr. Nigel Hussey are all co-authors. Other members of my research centre assisted me in the collection of samples on fisheries-independent sampling trips. I am grateful to the help and support provided by Dr. Aaron Fisk, and Dr. Nigel Hussey during my visit to their lab where I prepared and analysis my samples using their labs mass spectrometer. My supervisors Dr. Colin Simpfendorfer and Dr. Andrew Tobin, as well as Dr. Aaron Fisk, and Dr. Nigel Hussey all proofread earlier versions of this chapter and assisted me in responding to review comments prior to its publication.

Chapter 6
Other members of my research centre assisted me in the collection of data on fisheries-independent sampling trips. All data and statistical analyzes were conducted by me. My supervisors Dr. Colin Simpfendorfer and Dr. Andrew Tobin proofread earlier versions of this chapter.

Chapter 7
Other members of my research centre assisted me in the collection of data on fisheries-independent sampling trips. All data and statistical analyzes were conducted by me. My supervisor Dr. Colin Simpfendorfer proofread earlier versions of this chapter.

Chapter 8
The general discussion was my own work. My supervisor Dr. Colin Simpfendorfer proofread earlier versions of this chapter.

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

Acknowledgments

Firstly I would like to thank all my family and friends for their support during the last few years as I pursued my passion so far from home. Rather than attempting to list you all, and inadvertently omitting some of you I will simply write this statement to all of you. Your unconditional support has helped me immensely during my stay in Australia and over the course of my degree, and I can never thank you all enough. Despite moving halfway around the world I never felt isolated form the ones who care for and support me.

For generously providing me with a scholarship I would like to thank both the School of Earth and Environmental Science, and James Cook University. Without their financial assistance none of this would have ever been possible. I would also like to thank Professor Helene Marsh for all of her advice and assistance in attaining my school and university scholarship. I am indebted to you for all of your help during my studies, and for sheltering me during cyclone Yasi. I would like to thank Dr. Mark Hamann for all of his support and advice, tutoring for your practicals was always a pleasure and I am profoundly grateful to you for providing me the opportunity to visit the Torres Straits and participate in your green sea turtle research, it was a fantastic experience.

I am extremely thankful to all of the members of the Fishing and Fisheries Research Centre, your assistance in the office, lab, and field made this project possible, and I could not have asked for a better group to work with over the course of my degree. I would also like to thank the countless volunteers who braved the “treacherous” waters of Cleveland Bay at all hours of the day and night, not only did your assistance make this project possible but your boundless enthusiasm made it fun.

Above all others in Australia I would like to thank my primary supervisor, Dr. Colin Simpfendorfer for giving me the opportunity to move out to Australia and pursue my doctorate in such a fascinating field. Thanks for always being approachable and allowing me the freedom to develop and conduct this research, without your assistance this project would have never been possible. I know I have grown and prospered under your supervision and for that I am forever grateful.

Dedication

This thesis is dedicated to my parents. Without their unconditional love, support and encouragement none of this would have been possible. You have always instilled in me the confidence and desire to pursuer my dreams, wherever they lead. No son could have asked for a better mother and father, thank you.

List of Publications and Presentations Relevant to the Thesis

Kinney MJ, Simpfendorfer CA (2009) Reassessing the Value of Nursery Areas to Shark Conservation and Management. Conserv Lett 2:53-60

Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA (2011) Communal or Competitive? Stable Isotope Analysis Provides Evidence of Resource Partitioning within a Communal Shark Nursery. Mar Ecol Prog Ser 439:263-276

Kinney MJ, Simpfendorfer CA (2009) Preliminary Results of the Reassessment of a Purported Communal Shark Nursery in Cleveland Bay, Queensland Australia (poster presentation) Australian National Network in Marine Science Conference on Marine Science in Tropical, Temperate and Southern Oceans 2009, Hobart, Tasmania, Australia

Kinney MJ, Tobin AJ, Simpfendorfer CA (2010) Reassessing a Purported Communal Shark Nursery in Cleveland Bay, Queensland Australia (oral presentation) The American Elasmobranch Society Joint Meeting of Ichthyologists and Herpetologists 2010, Providence, Rhode Island, United States of America

Abstract

The ecology of multiple sympatric juvenile shark species inhabiting a single common, or 'communal', nursery environment during early life was the focus of this thesis. Previous work on these communal shark nurseries hypothesized a number of potential advantages gained by young sharks via their use, including greater protection from predation compared to single species shark nurseries, and an abundance of dietary resources which allowed sympatric species to feed and grow to maturity with limited competition despite high levels of dietary overlap. Almost twenty years have passed since the establishment of these original hypotheses, and yet little subsequent work has been done on communal shark nurseries to test them, resulting in the persistence of these original hypotheses in numerous current scientific works. This thesis endeavors to reassess the ecology of the originally defined communal shark nursery of Cleveland Bay, in northern Queensland, Australia, with primary aims including: an evaluation of spatial, temporal, and dietary niche partitioning between sympatric species; an investigation into the potential protective advantages gained through communal nursery areas use; and finally an assessment into the potential place that communal nursery area conservation could play in the larger picture of shark management.

Sampling of shark populations occurred both on commercial fishing boats (fisheries-dependent) and on research vessels (fisheries-independent). Fisheries-depended efforts focused principally on the determination of dietary resource use through the collection of stomach contents from euthanized sharks, while fisheries-independent efforts centered on the collection of catch data to determine spatial and temporal variation in abundance.

Additionally, tissue samples for stable isotope analysis were collected from sharks and teleosts captured during fisheries-independent activities. Tissue samples were used in combination with stomach content data to explore issues of dietary resource partitioning among various shark and teleost species within the nursery environment.

Of the thirteen juvenile shark species captured in Cleveland Bay, six of them were found to use the area as a nursery: *Carcharhinus fitzroyensis, Rhizoprionodon acutus, Carcharhinus amboinensis, Carcharhinus sorrah*, and *Carcharhinus limbatus/tilstoni*. Two additional species, *Sphyrna mokarran*, and *Sphyrna lewini*, were also potentially using the area as a nursery, although data for these species were limited. Off the six species found to use the bay as a nursery area, niche partitioning was apparent between each of them to varying degrees. Dietary resource partitioning among sharks revealed three general groups: 1) *R. acutus* and *R. taylori*, 2) *C. fitzroyensis,* and *C. sorrah*, and 3) *C. amboinensis*, and *C. limbatus/tilstoni*. Across all three groups of sharks the diets of each species contained a large proportion of small teleost prey, but the families of the most prevalent prey varied between groups, and species. Stable isotope values indicated a wide range of primary carbon sources which were partitioned between individual shark species adding further evidence to the hypothesis of partitioned dietary resources. Spatial and temporal separation was also apparent between the juvenile sharks in Cleveland Bay with species occupying different areas of the bay, under diverse environmental conditions, often indicating unique seasonal patterns. For example, species such as *C. sorrah*, occurred most frequently in the deeper, exposed waters of the bay, while the majority of other species inhabited varying areas among the shallows. Seasonal patterns suggested that species such as *C. amboinensis* occurred predominantly during the summer, while other species, such as *R. acutus* and *C. limbatus/tilstoni,* occurred more often during the winter and spring.

Despite the general pattern of spatial and temporal separation displayed among the sympatric juvenile sharks of Cleveland Bay, discrete species rich areas were also identified in both the shallow, 0-5 meter, and slightly deeper, 5-10 meter, waters of the bay. These species-rich areas indicate that juvenile sharks of several species, while segregated over much of their range within the nursery, can sometimes be found inhabiting the same specific areas, potentially sheltering from predators, or adverse environmental conditions, or exploiting dietary resources in more exposed sections of the bay. Therefore, these species-rich aggregations may provide juvenile sharks within communal nursery areas additional protective benefits not available to sharks in single species nurseries where such aggregations do not occur, or occur at a reduced scale.

The findings of this thesis have improved our understanding of communal shark nursery areas by revealing them to be highly diverse environments, both in terms of species composition, and patterns of individual species' habitat and dietary resource use. Contrary to original assessments, it is likely that a delicate balance of resource partitioning strategies, rather than an overabundance of resources, is what allows several juvenile shark species to utilize the same nursery environment. The understanding, and maintenance, of this balance is imperative to the management of these important early life environments. With concerns over the proliferation of identified shark nursery environments potentially leading to unmanageably vast conservation areas, communal shark nurseries could provide a useful alternative where juvenile sharks of several species could be protected via the management of a single discrete area.

Table of Contents

Table of Figures

CHAPTER 3

CHAPTER 4

Chapter 5

Chapter 6

Chapter 7

Table of Tables

Chapter 4

CHAPTER 5

Chapter 6

Chapter 7

1 Chapter 1.

General Introduction

1.1 Elasmobranchs

Within the class Chondrichthyes (cartilaginous fishes) is the subclass Elasmobranchii that includes skates and rays (batoidea), and sharks (selachii). I will use the term ‘shark’ to imply all living members of the Class Chondrichthyes that are not batoids or chimaeras. The taxonomy of chondrichthyan fishes is not fully understood, hence the discrepancy of between 2 to 6 superorders within the subclass Elasmobranchii (Last & Stevens 2009). Discussions of taxonomy are beyond the scope of this work and are mentioned here only to give a frame of reference to this research. In this thesis the conventional view of two superorders (Squalomorphi, and Galeomorphi) was followed (Compagno 2002). Within the superorder Galeomorphi (galeomorph sharks) is the order Carcharhiniformes (ground or whaler sharks) which is the largest order of sharks containing eight families, Carcharhinidae (requiem sharks), Hemigaleidae (weasel sharks), Leptochariidae (barbeled houndshark), Proscylliidae (finback cat sharks), Pseudotriakidae (false cat shark), Scyliorhinidae (cat sharks), Sphyrnidae (hammerhead sharks), and Triakidae (hound sharks), there are over 270 species within these eight families (Nelson 1994, Last & Stevens 2009). The sharks within the families Carcharhinidae and Sphyrnidae are the primary focus of this work; these families contain some of the most recognizable sharks in the ocean, including *Carcharhinus melanopterus*, *Galeocerdo cuvier*, *Carcharhinus leucas*, and all species of hammerheads.

Sharks, in general, have relatively slow growth rates, low fecundity, and late age at maturity, making them particularly susceptible to anthropogenic threats such as over-fishing (Springer 1967, Hoenig & Gruber 1990, Bonfil 1994, 1999, Musick 1999b, Schlacher et al. 2005). There are, however, substantial variations from this generalized life history strategy among species. Of the 54 species in the family Carcharhinidae there are those such as *Rhizoprionodon taylori* that grow to just over half a meter in length and reach maturity after only one year (Simpfendorfer 1993), while others such as *Carcharhinus obscurus* can attain lengths of over three and a half meters and, in the case of females, take 17-23 years to reach maturity (Simpfendorfer et al. 2002). Within the eight species of the family Sphyrnidae some species, such as *Sphyrna tiburo,* grow to less then a meter and take approximately 2 years to mature (Parsons 1993), while others, such as *Sphyrna lewini*, can reach lengths of three and a half meters and, according to some estimates, take up to 15 years to mature (Piercy et al. 2007).

The majority of sharks inhabiting the world's oceans occur on the continental shelves, from inshore waters to depths of about 200 meters, with the greatest abundance and diversity occurring in tropical and sub-tropical waters (Compagno 1990). This close proximity to land has often brought sharks into contact with humans, mostly to the detriment of sharks (DeMaster et al. 2001). The exploitation of sharks has varied over the years from early use of shark liver oil in the nineteen hundreds as a source of vitamin A, to the use of shark fins as aphrodisiacs and as a delicacy in shark-fin soup. More recently, extracts from shark cartilage are being investigated for potential tumour suppression benefits as well as alternative cancer treatment possibilities (Lee & Langer

, Gingras et al. 2000, Hassan et al. 2005). Additionally shark flesh has been, and still is, used for food in many parts of the world.

1.2 Exploitation of the Seas and of Sharks

As early as the thirteenth century negative impacts caused by overfishing were recognized by some in western society. Callum Roberts writes in *The Unnatural History of The Sea*: "In 1289, Philip IV of France banned the use of a dozen different kinds of nets and barrier traps and imposed seasonal restrictions on two other methods of [freshwater] fishing." Philip's proclamation read:

> "Today each and every river and waterside of our realm, large and small, yields nothing due to the evil of the fishers and the devices of [their] contriving, and because the fish are prevented by them from growing to their proper condition, nor have the fish any value when caught by them, nor they any good for human consumption, but rather bad…"

Remarkably, even six centuries later the understanding of the impacts of fishing in freshwater environments had no influence on fishing practices at sea. Humans believed that marine organisms were virtually immune to anthropogenic effect:

> "…animals living in the water, especially the sea waters, are protected from the destruction of their species by Man. Their multiplication is so rapid and their means of evading pursuit or traps are so great that there is no likelihood of his being able to destroy the entire species of any of these animals."
>
> -Jean Baptiste Lamarck (1809)

Only within recent decades have humans become aware of the vulnerability of ocean ecosystems and their own capacity to affect the species within them.

> "…continuing with business as usual, i.e. accommodating subsidy-driven overcapacity without bothering about externalities … would lead, in addition to further depletion of biodiversity, to intensification of 'fishing down marine food web', which ultimately involves the transformation of marine ecosystems into dead zones"
>
> -(Pauly 2009)

While it is now generally agreed that human-induced pressures have resulted in the decline of some coastal shark populations, to what degree is still highly contested. For example, Camhi (1999), Baum et al. (2003), and Myers et al. (2007) have estimated declines of up to 87% in Atlantic sharks over the past 20 years, but inconsistent fishing gear and species identification, along with selective use of available data by some researchers, have led other authors to claim that such estimates are distorted or exaggerated (e.g. Burgess et al. 2005a, b). Despite such discrepancies declining shark populations are still a point of concern.

There are many possible reasons for declining shark populations, including poorly managed shark-targeted fisheries (Olsen 1959, Walker 1998, Musick et al. 2000, FAO 2002), by-catch from non-target fisheries (Bonfil 1994, FAO 2002), shark meshing programs designed to remove large coastal sharks from popular bathing beaches (van der Elst 1979, Dudley & Cliff 1993, Dudley 1997, Stevens et al. 2000a, Dudley & Simpfendorfer 2006), and human infringement on critical coastal habitats (Barker & Schluessel 2005). Shark by-catch estimates alone have grown from 271,800 tonnes in 1950 to 828,364 tonnes in 2000 (FAO 2002). However, considering the extensive underreporting of shark by-catch, global catches could be more than double the recorded amount (Bonfil 1994, Pauly 2009). These pressures, made worse by rapidly improving fishing technology, globalization of consumer markets, and the decline of many teleost fisheries, have increased both the demand and availability of shark products (Barker & Schluessel 2005).

Along with the continued exploitation of sharks has come ever improving and expanding scientific knowledge, and in more recent times, increased public awareness of the embattled status of many shark populations. These factors in turn have led to the current climate in which shark conservation is seen as an important global marine management goal (FAO 1999, Stevens et al. 2000a, Barker & Schluessel 2005, Stevens et al. 2005b, Pauly 2009). In step with global initiatives, Australia has listed shark research and conservation as one of its top marine management priorities. As a member of the United Nation's Food and Agriculture Organization (FAO) Australia has created a National Plan of Action for the Conservation and Management of Sharks (Shark-Plan) (SAG & Lack 2004) which looks to address issues of shark by catch, inadequate species identification, and data deficiency for shark stock assessments, among others.

In Queensland, the Great Barrier Reef Marine Park Authority (GBRMPA) lists quantifying the level of shark catch, both commercial and recreational, as a critical information need (GBRMPA 2005). Other agencies such as the Queensland Department of Employment, Economic Development and Innovation (DEEDI) are currently funding projects that analyze the catch of the inshore finfish fishery which includes a number of shark species. Support from both national and state level agencies have helped make shark species inhabiting the waters surrounding Australia some of the most researched in the world (Stevens et al. 2005a). Still, much about sharks, including those around Australia, remains unknown, and even historically well-established theories such as nursery area use in early life, have begun to change based on new evidence and more rigorous study (i.e. Heithaus 2007, Heupel et al. 2007, Knip et al. 2010).

1.3 Shark Nursery Areas and Communal Nursery Areas

While Meek (1916) initially described shark nurseries nearly a century ago, most shark researchers rely on the nursery area theories developed by Springer (1967). Springer, who discussed the supposed benefits provided by nursery habitats, based his characterization of the typical shark nursery on a hypothetical shark species that was intended to represent the general life history strategy of a large number of ecologically similar sharks. Though Springer never explicitly outlined which ecological traits should be used to qualify habitats as nursery areas, his preliminary observations became the basis for the prevailing shark nursery area paradigm (Heupel et al. 2007). In particular, three basic concepts originating from Springer's hypothesis have been perpetuated by later studies. First, adult males rarely, if ever, enter the nursery areas of their own species (Hobson 1963, Olsen 1984, Castro 1989, Branstetter 1990, Compagno 1990, Morrissey & Gruber 1993, Simpfendorfer & Milward 1993). Second, mature females only enter nursery areas when they are gravid and at full term, and stop feeding once they reach the nursery grounds (Olsen 1984, Compagno 1990, Castro 1993, Morrissey & Gruber 1993, Simpfendorfer & Milward 1993). Third, food is not a limiting factor for young sharks within the nursery, and they stay in the vicinity of the nursery grounds while feeding and growing during their formative years (Branstetter 1990, Salini et al. 1992, Castro 1993, Simpfendorfer & Milward 1993, Van der Molen & Caille 2001, Rechisky & Wetherbee 2003). The first two observations both relate to the protective advantages afforded to young sharks within nurseries since large sharks are their only important predators (Springer 1967), while the third relates to the general productivity of nursery environments. These three tenants formed the heart of the dominant nursery area paradigm that has largely persisted to the present.

In 1993, the concept of ‘communal shark nursery areas’ entered the literature when Simpfendorfer & Milward (1993) reported eight shark species utilizing Cleveland Bay off the east coast of Queensland, Australia as a nursery. That same year Bull’s Bay, off the coast of South Carolina in the United States, was described as a similar nursery used by nine shark species (Castro 1993). Evidence of dietary overlap among the sharks in these areas was thought to indicate that food resources were not limiting and, due to the multi-species makeup of these nurseries, their protective nature was expanded, compared to that of single species nurseries, since the adult populations of many shark species would avoid their own nursery areas. Thus, these studies of communal shark nurseries relied on the same assumptions applied to shark nursery areas in general. Since these original works little research has focused on communal shark nursery areas, and subsequently the initial hypotheses of their advantages have persisted in the scientific literature relatively unchanged and unchallenged.

With concerns of declining shark populations communal nursery areas could potentially be an important component of current and future shark management plans, allowing for the protection of several species in relatively small, discrete areas. However, before this can happen a more rigorous approach must be applied to communal nursery areas to investigate how several sympatric juvenile shark species are able to use the same nursery environment, and what benefits or drawbacks might they incur through the use of a communal rather than a single species nursery.

1.4 Overall Study Aims and Thesis Structure

As part of a comprehensive approach to characterizing the ecology of communal shark nursery areas this thesis will focus on the reassessment of Cleveland Bay as a communal shark nursery area, and more generally, on the ecology of communal shark nursery areas as a whole. This study has three primary objectives: (1) to determine the level of niche overlap compared to niche separation among the shark species in this nursery, with attention to dietary, spatial, and temporal resources; (2) to determine if adult sharks avoid their own nurseries, thus providing increased protection from predation to young sharks as suggest by early communal nursery studies; and (3) based on the research findings, discuss the relative advantages and disadvantages of communal nurseries compared to single species nurseries and the potential role that communal nurseries could play in shark conservation.

This thesis is broken down into eight chapters, each of which deals with a specific aspect of the overall theme of my work concerning the ecology of shark nursery areas, or more specifically, communal shark nursery areas. Each chapter is written as a stand alone work that includes an independent introduction which reviews relevant literature and identifies the overall aims of the chapter as well as its own methods section, when relevant, which highlights the specific approach, or approaches, used. This is in addition to the overall introduction and methods chapters presented in the first few chapters of the thesis. Chapters 1 and 2 are essentially both introduction chapters, with Chapter 1 providing a brief introduction to sharks, nursery areas, and broad conservation issues, while Chapter 2 focuses more on nursery areas and their overall value to shark conservation efforts. Chapter 3 describes the study site and includes the general methods outlining the overall approaches used to examine the ecology of shark nurseries during the course of this thesis. Chapters 4 through 7 each investigate different aspects of communal shark nursery area ecology such as dietary (Chapters 4-5), and spatiotemporal (Chapter 6) resource separation versus overlap, and patterns of species richness (Chapter 7). Finally, Chapter 8 provides a general discussion which compares past hypotheses of communal nursery areas with current data to determine how our scientific knowledge of these areas has changed and what role these kinds of shark nursery areas could play in current and future efforts to conserve shark populations.

2 Chapter 2.

Reassessing the Value of Nursery Areas to Shark Conservation and Management

---

2.1 Introduction

The life history traits of many shark species, including large body size, slow growth, late maturity, and low fecundity, makes them particularly vulnerable to overfishing and other anthropogenic threats (Musick et al. 2000, Frisk et al. 2005). Indeed, many shark populations have declined with respect to their pre-exploited biomass (Baum & Myers 2004, Shepherd & Myers 2005, Cortés et al. 2007), raising concern for their conservation and requiring the development of management planning.

The difficulty of managing adult sharks with expansive ranges, along with the tendency of some fisheries to apply teleost-based management to sharks, has at times steered strategies toward the protection of younger age classes, particularly neonates and young juveniles. The widespread application of such management strategies, which emphasize increasing recruit survival to boost populations, raised interest in so-called ‘essential fish habitat’ (NOAA 1996). For sharks, essential fish habitat has mostly centered on the identification of discrete inshore nursery areas used by early life stages in the belief that these stages were vital for population stability and recovery (Bonfil 1997). Such belief stemmed from the teleost type of management model, of which the protection of young individuals within nursery habitats is a standard principle. As a result of the NOAA 1996 mandate, which required the identification of essential fish habitat in all fisheries management plans in the U.S., shark nursery area research increased (McCandless et al. 2007).

Greater focus on identifying shark nurseries as essential fish habitat generated a push for nurseries to be designated marine protected areas (MPAs) (Bonfil 1999). The ideal MPA design provides protection for all life stages of the species of concern (Bonfil 1999), which is impractical for the majority of shark species because they are wide-ranging. Instead, MPAs could be used to protect some sharks during certain life stages, such as younger age classes within nursery areas (Bonfil 1999, Roberts 2000, Heupel & Simpfendorfer 2005b). While this option has been examined theoretically for a number of nursery areas (Heupel & Simpfendorfer 2005b, Garla et al. 2006b), implementation of MPAs in such areas has been limited (Bonfil 1999, Heupel & Simpfendorfer 2005b).

MPA designation for shark nursery areas has lagged due partly to confusion over which habitats constitute true 'nurseries'. As Heupel et al. (2007) point out, for several decades there was a lack of standardized criteria to differentiate between nursery and non-nursery habitat, resulting in the identification of large coastal stretches as nurseries, often based solely on the presence of neonates, juveniles, or both (Castro 1993, Simpfendorfer & Milward 1993, Hammerschlag & Fallows 2005, Blackburn et al. 2007). The subsequent addition of nursery area sub-categories such as primary, secondary (Bass 1978), and communal (Simpfendorfer & Milward 1993) further complicated the debate regarding what constitutes a nursery. The large geographic area and number of these purported shark nurseries would render protective measures (i.e. MPAs) extraordinarily expansive, costly and complicated (Heupel et al. 2007). A more refined definition for shark nurseries was necessary to avoid labeling vast areas as nurseries and diluting the ability to protect the most valuable areas (Beck et al. 2001). In response, Heupel et al. (2007) recently outlined three basic criteria designed to standardize the classification of shark nursery areas and identify those of greatest importance: (1) that sharks are more commonly encountered in the area than in other areas, (2) that sharks have a tendency to remain or return for extended periods, and (3) that the area or habitat is used repeatedly across years.

With some improvement in the identification, mapping, and in some cases protection, of nursery areas, little attention has been given to the practical value of nurseries to the recovery of harvested shark populations. I examined the importance of shark nurseries in the wider context of shark population recovery and management by discussing the relative importance of neonates and young juveniles (i.e. those stages that occur in nursery areas) to population recovery, and by reviewing the possible repercussions of focusing conservation efforts on nursery-using early life stages while adult populations remain comparatively undermanaged. While it is recognized that not all shark species use nursery areas in early life (Heupel *et al.* 2007) this review will focus on those species that do.

2.2 How Important are Young Sharks for Population Persistence?

Demographic models can illustrate how various factors affect the intrinsic rate of population increase in long-lived, slow-growing marine species (Musick 1999a).

Elasticity/sensitivity analyzes within these models estimate how a population's intrinsic rate of increase is affected by various mortality rates at selected life stages. For example, Gallucci et al. (2006) used an age-structured Leslie matrix model for *Rhizoprionodon taylori* and *Squalus acanthias* and found that the survival of juveniles nearing maturity was proportionately more important to population maintenance than the survival of any other age class. Studies on other species such as *Dipturus batis* (Brander 1981) obtained similar results. Additionally, three separate studies published in a single volume (Musick 1999b) came to similar conclusions for four different shark species (Cortés 1999b, Heppell et al. 1999, Simpfendorfer 1999). Each of the previous studies found that neonate (age 0-1) survival had relatively little influence on the overall population growth rate. Brewster-Geisz & Miller (2000) went so far as to model the "perfect nursery ground closure" where mortality for neonate *Carcharhinus plumbeus* was set at zero. Although the model's results showed that with 'perfect' nursery area protection, fishing pressure on the rest of the population could increase slightly while remaining sustainable; in reality the complete protection of early life stages to the point of zero mortality is clearly impossible. For most shark species, only neonates and young juveniles typically occupy nursery areas whereas larger juveniles nearing maturity tend to move away from nurseries, so Brewster-Geisz & Miller (2000) concluded that nursery closures or size limits which protect only neonates and young juveniles are unlikely to promote population recovery; effective management must involve protection for older age classes along with nursery-using life stages.

In regard to the above demographic models, a brief discussion of stage-based and age-based modelling is prudent since both are drawn upon here as evidence. There has been debate regarding the appropriateness of using stage-based demographic models for sharks. Originally stage-based models were considered to allow demographic modelling of data-deficient species (Cortés 1999b, Miller et al. 2003). This, coupled with the hypothesis that small errors in parameter estimates for life-history tables could be magnified for long lived species (Brewster-Geisz & Miller 2000, Miller et al. 2003) led some authors to see stage-based models as a way around these limitations (Cortés 1999b, Brewster-Geisz & Miller 2000). Problems arise when stage-based models define a limited number of stages, (three or less), or do not include fixed-stage durations which can lead to inaccurate elasticity calculations and questionable estimates of population recovery times (Mollet & Cailliet 2003). Of the demographic models mentioned above, only two are stage-based (Cortés 1999b, Brewster-Geisz & Miller 2000). Both include fixed-stage durations and define more then three stages, thus avoiding the two major pitfalls identified in stage-based demographic models of shark populations. Conclusions derived from these stage-based models, while potentially not exactly the same as those from age-based models, are generally in agreement. There is still debate over the appropriateness of stage-based demographic modelling of sharks; however, that is beyond the scope of this review.

For nursery-using sharks, the above demographic studies illustrate the potential limitations of management based on nursery conservation. For example, Simpfendorfer (1999) found that for *Carcharhinus obscurus* the most important age class in terms of maintaining a positive intrinsic rate of population increase was that of large juveniles nearing maturity. Estimates place the age at maturity for *C. obscurus* around 17-22 years for females (220-250), and 20-23 years for males (230-243 cm) (Simpfendorfer et al.

). This places older juveniles of the species far outside the age and size range of individuals normally recorded within nurseries. Indeed, Castro (1993) found the typical size range of *C. obscurus* within a nursery was between 101-104 cm. This demonstrates that the age classes identified as essential for maintaining a positive intrinsic rate of population increase (i.e. older juveniles) in the aforementioned demographic models are not the same age classes inside nursery areas (i.e. neonates and younger juveniles), which has considerable ramifications for shark management priorities. Unfortunately, continued emphasis on the importance of protecting nurseries tends to overshadow the evidence that, for many species, such an approach would not benefit the most important age classes in terms of population stability and recovery.

The shark fishery for *Galeorhinus galeus* in southern Australia is an example of a management strategy with a heavy nursery component. The commercial shark fishery in southern Australia that began in the 1920s focused primarily on *G. galeus* and to a lesser extent on *Mustelus antarcticus*. Concerns over the collapse of the fishery date back to the 1950s (Olsen 1959), and in the 1960s, numerous bays around Tasmania that had been identified as important nursery habitats for *G. galeus* and *M. antarcticus* were protected. Despite these efforts, by the late 1980s *G. galeus* populations had been severely depleted (see Punt et al. 2000 for a detailed discussion of declining catch rates of *G. galeus*). In response, an interim management plan was introduced that further restricted access to these nurseries in an attempt reduce the incidental mortalities considered to hinder the population's recovery capacity (Williams & Schaap 1992). During the 1990s, an investigation into the *G. galeus* nursery areas around Tasmania revealed that juvenile numbers within the nurseries had plummeted since Olsen's (1959) original observations.

Whereas Olsen could handline up to 80 juveniles a day in the period 1948-1952, in 1992 no school sharks were caught in 23 hours of fishing in the same location and using the same technique (Stevens & West 1997). Concurrently, the standardized catch rate for *G. galeus* declined by over 50% from 1983 to 1997 (Punt et al. 2000). Thus, despite nursery-focused protective measures that had been in place for around 30 years, *G. galeus* populations had declined to the point of fishery collapse because fishing of adults had continued unsustainably over the same period. Nursery area management in the absence of effective protection for mature individuals led to declining numbers of pups until managed areas contained so few pups that there classification as nurseries was unwarranted.

Following the decline of *G. galeus* populations, the Southern Shark Fishery switched focus to the less profitable, but evidently more sustainable *M. antarcticus*. Prince (1992) attributed the apparent sustainability of the *M. antarcticus* fishery to the fact that only certain sized sharks were vulnerable to the fishery. He characterized this as a 'gauntlet fishery', in which only a subset of the population is exposed to fishing pressure. Subsequent demographic models helped refine this explanation by revealing that fishing effort focused on particular age classes, specifically the youngest age classes, could yield sustainable fisheries for certain shark species. In his demographic model of *C. obscurus* in a western Australian fishery, Simpfendorfer (1999) found that up to 64.6% of the youngest age class could be removed without decreasing the intrinsic rate of populations increase, as long as fishing did not occur on any other age class. This contrasted with a maximum of 4.3% sustainable removal when fishing effort is spread across all age classes. If considered on a simple biomass extracted basis the taking of a small proportion of larger animals may be preferable, the use of yield per recruit analysis would provide improved information in this situation. However, for the *C. obscurus* fishery the smallest individuals achieve a significantly greater price and so maximizes economic yield. This indicates the complexity of gauntlet fisheries since many factors including biology of the species and economics of the fishery will impact the effectiveness of such a strategy.

Prince (2005) came to a similar conclusion regarding the removal of young individuals for why the fishery for *G. galeus* collapsed but the fishery for *M. antarcticus* succeeded in southern Australia. *Galeorhinus galeus* were fished throughout the year and across all age classes, leading to rapid declines wherever they where fished intensively. Conversely, a combination of gear selectivity and age-specific swimming patterns, which increased the probability of mesh entanglement for younger individuals (Stevens & West 1997), led to the fishery for *M. antarcticus* selectively targeting mostly the younger age classes. Subsequently, the term ‘gauntlet fishery’ was modified to define fisheries that focus effort on younger age classes while leaving adult populations relatively unfished (Prince 2005).

The usefulness of gauntlet-style fisheries for sharks relates to the shape of their stock-recruitment curve (the relationship between the number of recruits and the number of mature breeders). Whereas teleost stock-recruitment curves typically have high curvature which translates to high recruitment even at low population sizes, shark stock-recruitment curves typically have limited curvature, meaning recruitment is strongly related to the size of the breeding population. Thus, for sharks any removal of the breeding population has a proportionally greater and longer-lasting effect on population size than a similar removal would have on a teleost population. Gauntlet fisheries therefore attempt to restrict fishing to younger age classes in recognition of the importance of maintaining sufficient breeding population sizes. The two most reliable methods for achieving this are to use highly size-selective gear, such as gillnets, or to confine fishing to areas where only the young age classes are typically found, which in many cases would be nurseries (Simpfendorfer 1999).

There is, however, an inherent danger in applying gauntlet fisheries to nursery areas due to the numerous ways existing nurseries are defined. Under the original definition of shark nurseries, Springer (1967) assumed that all nurseries were of equal recruitment value to the population. More recently, Beck (2001) redefined nursery area concepts for fish, establishing the idea of differential value to a population; that is, certain areas may be more valuable to population recruitment than others, and that only those with above-average contributions to the breeding population should be considered nursery areas. Beck's process for establishing the relative value of individual areas was complex, requiring extensive research over prolonged periods. Heupel et al. (2007) simplified this process for sharks when they revised the definition of shark nurseries to areas with high juvenile abundances across years (high in comparison to surrounding areas), relating this high abundance to high recruitment value for adult populations, therefore allowing a straightforward assessment of its importance. If gauntlet fisheries are established within nurseries that provide a uniquely high proportion of recruitment to the target population, this could put the population in danger of decline. Thus, before a gauntlet fishery is implemented, the recruitment value of target nurseries as well as the relative importance of other valuable nurseries for the species must be determined. It is also paramount to understand what rate of exploitation is sustainable, while younger age class my be able to support proportionally more fishing pressure then older age classes, the concentrated nature of a nursery must be recognized. Without proper management a gauntlet fishery may still quickly over-harvest young sharks and lead to a population decline.

The young age classes of some shark species are candidates for sustainable gauntlet fisheries because they can withstand proportionally higher rates of exploitation relative to older age classes. For other species, conserving neonates and young juveniles that reside in nursery areas will still play an important part in population stability, especially for nursery-using species that mature quickly. To date, only the fishery for *M. antarcticus* in southern Australia and the fishery for *C. obscurus* in western Australia exist as scientifically established examples of sustainable gauntlet fisheries, and seemingly little effort has focused on identifying other species for which such fisheries would be plausible. Instead, management continues to focus on the identification and protection of nursery areas as a strategy for stabilizing declining shark populations, despite strong evidence that such broad strategies overlook the importance of species-specific life history traits.

2.3 Possible Consequences of Nursery-Centric Management

It is not surprising that the different life history strategies among sharks make some species much more susceptible to over-exploitation than others. The same is true for conservation; protective measures that enhance the recovery of one shark species may be ineffective for other species, or even detrimental. Worryingly, nursery protection is a strategy often intended to promote the recovery of large-bodied, long-lived, and late-maturing shark species, but could prove more beneficial to those species that are comparatively smaller-bodied, shorter-lived, and earlier-maturing. Consider *Negaprion brevirostris* for which elasticities of large juveniles approaching maturity are higher than all other age classes (Frisk et al. 2005). Age validation studies indicate an average age at maturity of around 12 years (Brown & Gruber 1988). Extensive nursery area work on *N. brevirostris* conducted at Bimini, Bahamas indicates maximum residency periods in nurseries of around four years for juvenile *N. brevirostris* (Dibattista et al. 2007). As with *C. obscurus*, these findings suggest that protection of nursery areas alone would overlook the older juvenile age class that occurs outside of the identified nursery areas and instead protect the proportionately less important (in regards to population stability/recovery) neonate and young juvenile stages.

It should be noted that the Frisk et al. (2005) stage-based model for *N. brevirostris* included stage durations but only defined three stages. While Hoenig & Gruber (1990) produced an age-based model for *N. brevirostris* its lack of elasticity or sensitivity calculations precludes its usefulness in this case. However, the findings of Frisk et al. (2005) are in agreement with age-based models for biologically similar species, and while its limited number of stages reduces confidence, its use here remains appropriate in terms of its management implication.

The inconsistent suitability of nursery area protection is made apparent when *N. brevirostris* is compared to a smaller, more rapidly maturing shark species such as

Mustelus canis. Whereas the older juveniles of *N. brevirostris* typically reside outside nursery areas for around 7-8 years before reaching maturity, *M. canis* attain maturity 6 to 18 months after leaving the nursery (Compagno et al. 2005). Species like *C. obscurus* or *N. brevirostris* would thus spend more time outside protected nurseries before reaching maturity than would species like *M. canis*. This disproportionately exposes the post-nursery life stages of later-maturing species to greater risk of mortality before they can reproduce.

High mortality rates for these older juveniles, coupled with the continued exploitation of adults, inevitably leads to a reduction in the number of pups found within nursery areas. Again, this effect would be more pronounced for those species that are slower-growing, longer-lived, and attain maturity at a later age, while for species like *M. canis* the probability of surviving to maturity and successfully breeding at least once is comparatively greater.

These findings about the limited value of nursery-focused conservation-strategies are not limited to sharks, but have been identified in other long-lived marine species as well. For example, *Caretta caretta* (loggerhead turtle) is a large-bodied, slow-growing, late maturity species for which demographic models have identified the importance of older juveniles in maintaining a positive intrinsic rate of population increase. Heppell et al. (1996b) concluded that the loss of only a few hundred subadult and adult females each year could lead to extinction of the eastern Australian *C. caretta* in less then a century. Investigations into headstarting (the captive rearing of hatchlings from eggs collected in the wild) for marine turtles has revealed that attempts to boost the number of young turtles artificially has little to no effect on the population (Heppell *et al.* 1996a). Similar to Brewster-Geisz & Miller (2000) for *C. plumbeus*, Crowder et al. (1994) modelled the effects of 100% first year survival for *C. caretta*. Their model predicted that even at this extraordinary survival rate, the model population continued to decline. Later models for various marine turtle species (Chaloupka 2002, Mazaris et al. 2006) have come to similar conclusions in regards to the importance of subadult and adult individuals for population persistence.

2.4 Implications for Shark Management

Nursery areas are not stand-alone systems; the effects of depleted adult populations have direct effects on them due to the strong link between breeding population size and recruitment. Management strategies must include plans for the protection of both young age classes in nursery areas and older members of the population beyond nurseries. Similar to *C. caretta*, while the subadult and adult populations are the most important age classes in terms of maintaining a positive intrinsic rate of population increase there is still a strong positive relationship between first year survival and population persistence. Additionally, it is not hard to image that the functional elimination of coastal nursery areas though habitat destruction could push populations to a tipping point where suitable nursery areas become a limiting factor. Therefore, management must attempt to apply appropriate conservation measures to both year one individuals and older juveniles. For shark populations especially, managers must recognize the varied importance of these age classes and understand that while each is important for population persistence, management strategies must reflect the proportionally greater importance of older juveniles. More time- and resource-intensive, species-specific management should be a goal for shark conservation, at least for those species whose populations are depleted to the point where their intrinsic rate of population increase is in danger of becoming negative. This approach is important not simply because conservation efforts can disparately affect various species as previously discussed, but also because grouping species can mask local disappearances and declines. We must confront the idea that nursery area protection alone is typically not enough to ensure the stability of exploited, or recovery of depleted, shark populations. Instead, shark management must acknowledge both the diverse array of shark life history strategies, and the relative importance of different habitats to the various life stages of each species.

Implementing MPAs for species that show some site fidelity, such as reef-inhabiting sharks, may be a useful approach in certain cases (Bonfil 1999, Garla et al. 2006a, Garla et al. 2006b). However, for species thought to be fished at unsustainable rates, MPAs must be coupled with reductions in fishing capacity to avoid simply displacing effort to other sites (Fogarty & Murawski 1998). For species that lack site fidelity altogether or in all but the earliest age classes, maximum size limits may be beneficial as a way of protecting actively breeding individuals or those near breeding age, (i.e. maximum size limits that are less then the size at maturity), if this suits their particular life histories (Simpfendorfer 1999, Prince 2005). These are just some of the management options available to protect individuals approaching maturity. Again, management decisions must be made on a species-by-species basis and strategies will vary depending on a species' life history and level of conservation concern.

Nurseries designated for protection should be refined in accordance with more substantial criteria (Heupel et al. 2007) allowing managers to prioritize nurseries that contain higher neonate and young juvenile populations, have longer residency periods and are repeatedly used across years.

2.5 Conclusion

This chapter examined the importance of nursery areas to the management and recovery of shark populations. There is increasing information available demonstrating that well-protected and managed nursery areas are likely to provide little overall benefit to populations in the absence of management for other age classes. Demographic models and fisheries experience indicate that management focused on older juveniles (those that live outside nursery areas) and mature individuals may be most beneficial. Management plans must recognize the relative importance of various age classes to reverse the declining trends observed in some shark populations. While protecting nursery areas may not be able to conserve shark populations on their own, they remain an important component of broader shark management strategies.

3 Chapter 3.

Study Area and Methodology

3.1 Study Site

Cleveland Bay lies just off of Townsville on the north-east coast of Queensland. It covers an area of approximately 225km² from -19°10 to -19°19'S to 146°50 to 147°01'E. The bay is shallow throughout, only reaching a depth of ~15 meters as it becomes open sea. Most of the seabed has a slope of approximately 0.7 m/km (Hardy 1991). The Bay is bounded on the west by Townsville, on the north by Magnetic Island, and Cape Cleveland on the east (Figure 3.1). The benthic environment of the bay is predominantly seagrass and soft mud with some smaller areas of coastal reefs. For a more detailed analysis of the sediment types in Cleveland Bay see Cruz-Motta & Collins (2004). Additionally, seagrass habitats within Cleveland Bay have been expanding since the original Department of Primary Industries and Fisheries study, conducted between 1984 and 1988, which showed that the main concentration of seagrass within the bay was inside the 5 meter depth contour (Grech & Coles 2010). Current seagrass data indicates that now much of the bay contains seagrass beds; a model of present seagrass coverage indicating that although fluctuations occur during the wet (January to April) and dry (May to December) seasons, much of the bay is covered in seagrass during the whole of the year (Grech & Coles 2010). Tidal variation within the bay can be as high as 4.2m. There are four primary freshwater inputs into Cleveland Bay: Ross River and Ross Creek to the west, and Crocodile and Alligator Creeks to the south. Mangroves dominate the southern shore of the bay as well as the tidal sections of the four major waterways. During the summer, heavy rains can trigger large freshwater outflows from these waterways causing significant drops in the bay's salinity, from an average of 39.1 ‰ ± a standard error of 0.4 in the dry season to 36.3 ‰ ± 1.6 in the wet season (Figure 3.2a). Average surface water temperature in the bay can fluctuate from 30.6 °C ± 0.5 during the wet season to 22.4 °C ± 0.2 during the dry (Figure 3.2b), and average secchi depths (which can be used as a proxy for turbidity) can vary from 1.4 m ± 0.2 in the spring to 2.8 m ± 0.5 in winter (Figure 3.2c). All measurements of temperature, salinity, and secchi depth were collected at every location where sampling for sharks occurred.

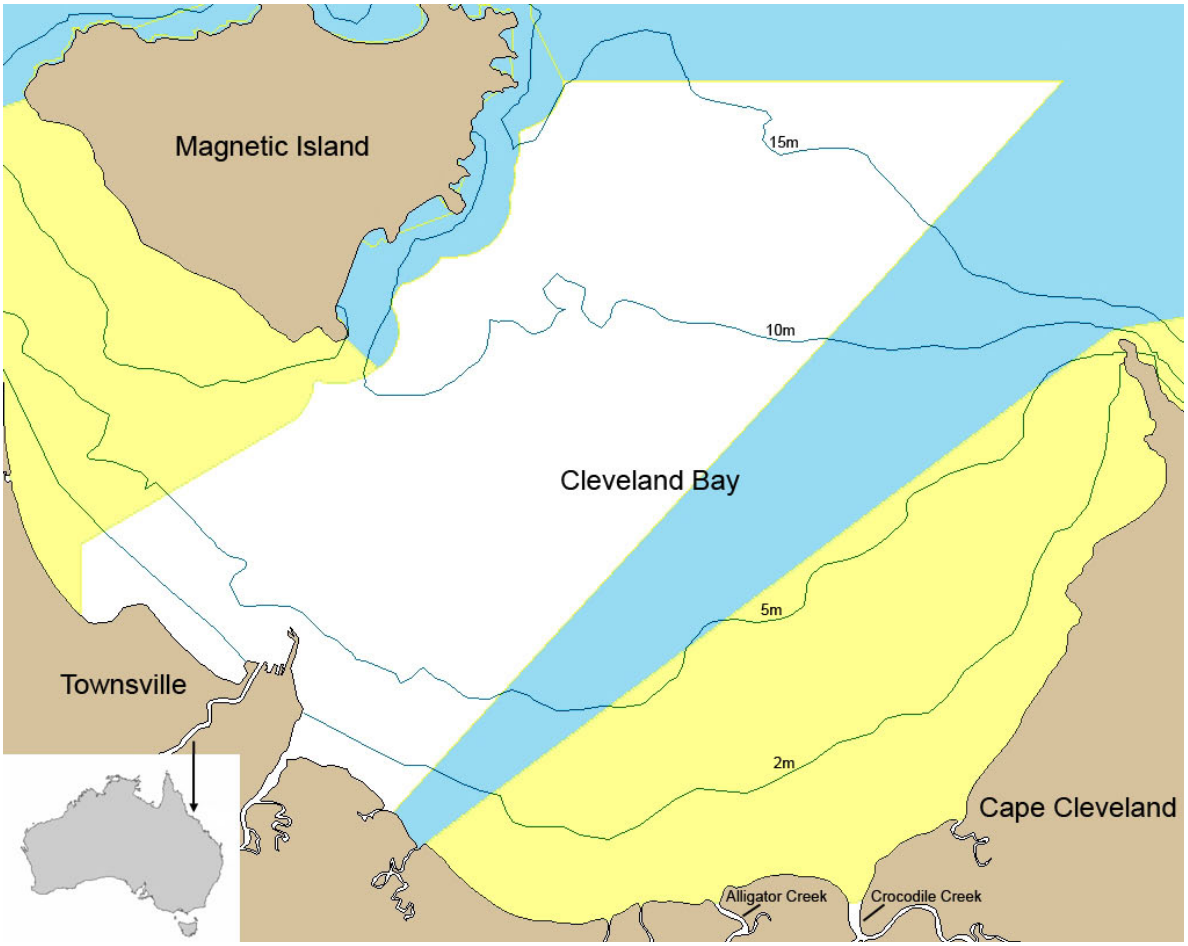
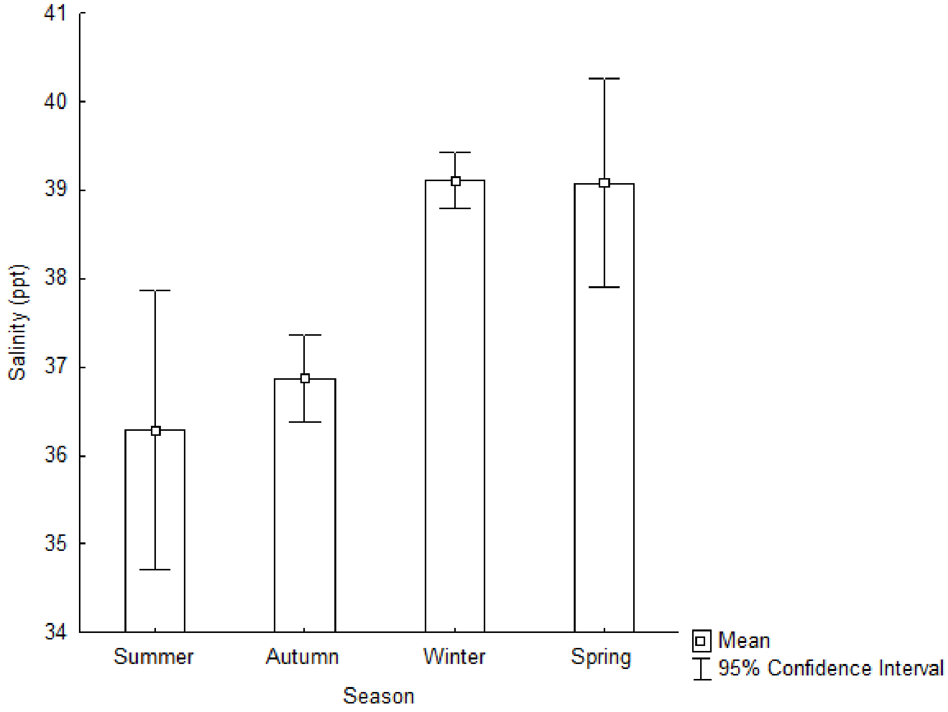
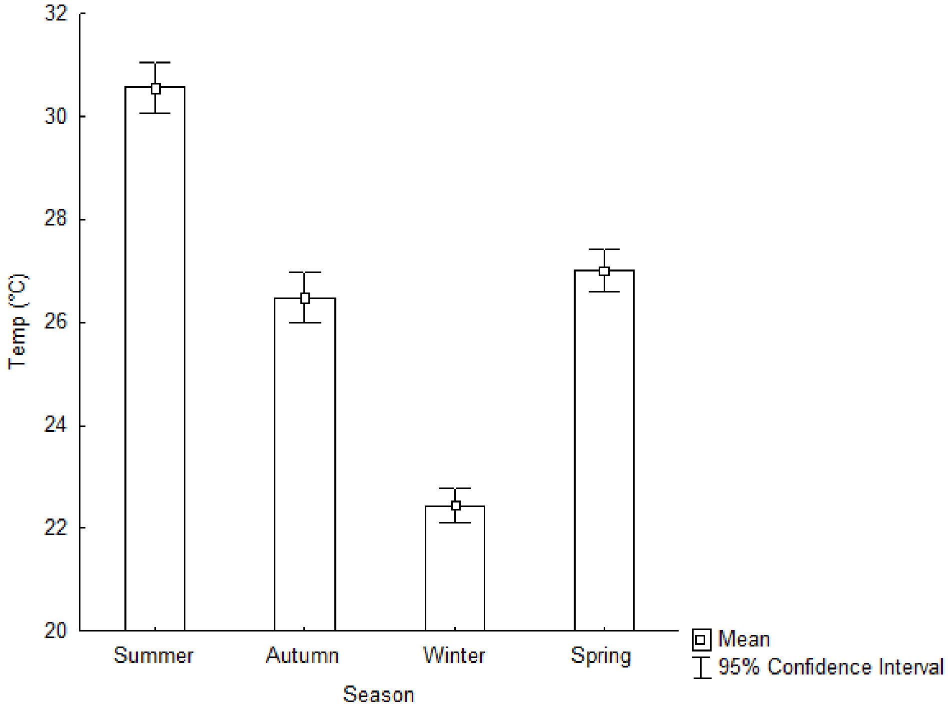


Figure 3.1: Map of Cleveland Bay with GBRMPA Conservation Park Zones marked in yellow, Townsville shipping channel in white, and isobaths delineated every 5 meters.

a)


41
40
39
38
37
36
35
34
Salinity (ppt)
Summer
Autumn
Winter
Spring
Season
Mean
95% Confidence Interval

b)


32
30
28
26
24
22
20
Temp (°C)
Summer
Autumn
Winter
Spring
Season
Mean
95% Confidence Interval

c)

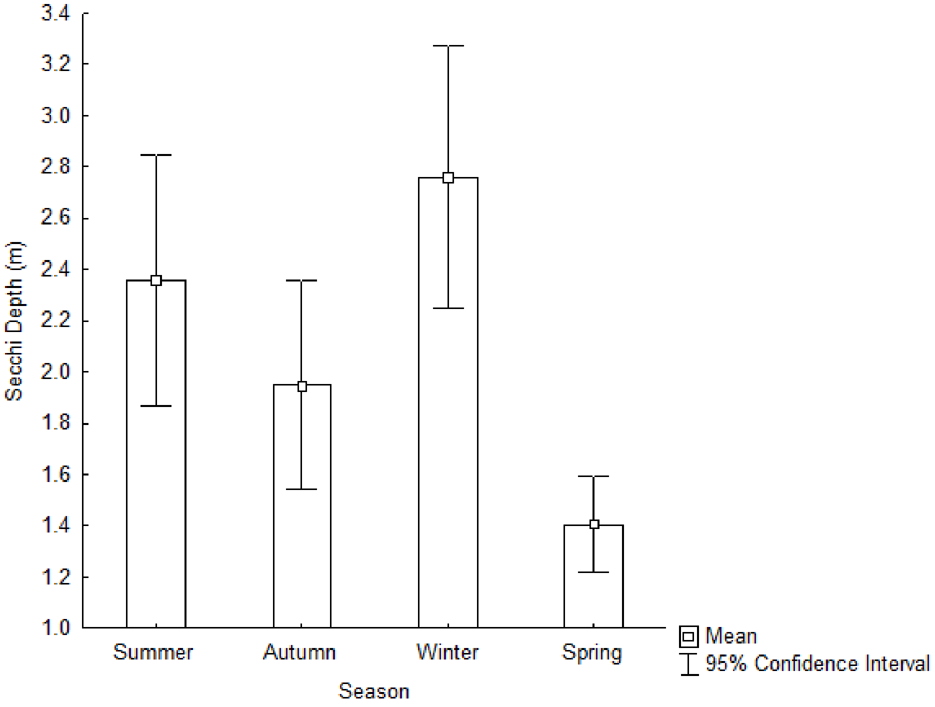


Figure 3.2a-c: Average a) salinity (ppt), b) temperature (°C), and c) secchi depth (meters) recorded in Cleveland Bay across seasons during fisheries independent sampling trips, with the wet season spanning the spring and summer, and dry season covering autumn and winter.

3.2 Sampling Design

Sampling for this project included field work onboard university research vessels (fisheries-independent) and commercial fishing boats (fisheries-dependent). Fisheries-independent sampling was used to gather ecological information regarding the sharks within Cleveland Bay as well as tissue samples from a select size range of certain species for stable isotope analysis, while fisheries-dependent sampling mainly provided stomach contents for the analysis of dietary overlap.

3.2.1 Fisheries-Independent

The fisheries independent sampling design within Cleveland Bay was intended to allow the identification of both spatial and temporal variation in catch rates among the young sharks inhabiting the bay. For these reasons sampling effort was spread among the four seasons: 1) summer (December-February), 2) autumn (March-May), 3) winter (June-August), and 4) spring (September-November) and across four distinct depth strata identified as: 1) foreshore (0-1.9 m), 2) seagrass strata (2-5 m), 3) soft bottom strata, below the seagrass strata (5-10 m), and 4) offshore (depths greater then 10 meters that are removed from the general nursery area). A combination of longlines and gillnets were used in an attempt to avoid the size limitation of each gear type, with longlines tending to capture larger sharks whereas gillnets typically catch smaller individuals, depending on mesh size.

A map of the bay was overlaid with transects based on lines of longitude (each transect was 30 seconds apart on a degrees minutes second scale), transects were used as a guide to identify general fishing areas for a sampling trip (Figure 3.3). Every transect was assigned a number and a random number generator was used to select which transects would be sampled on any given sampling trip, weather permitting. Sampling trips were conducted both during the day and night but most trips began at sunrise and ended in the late afternoon or early evening.

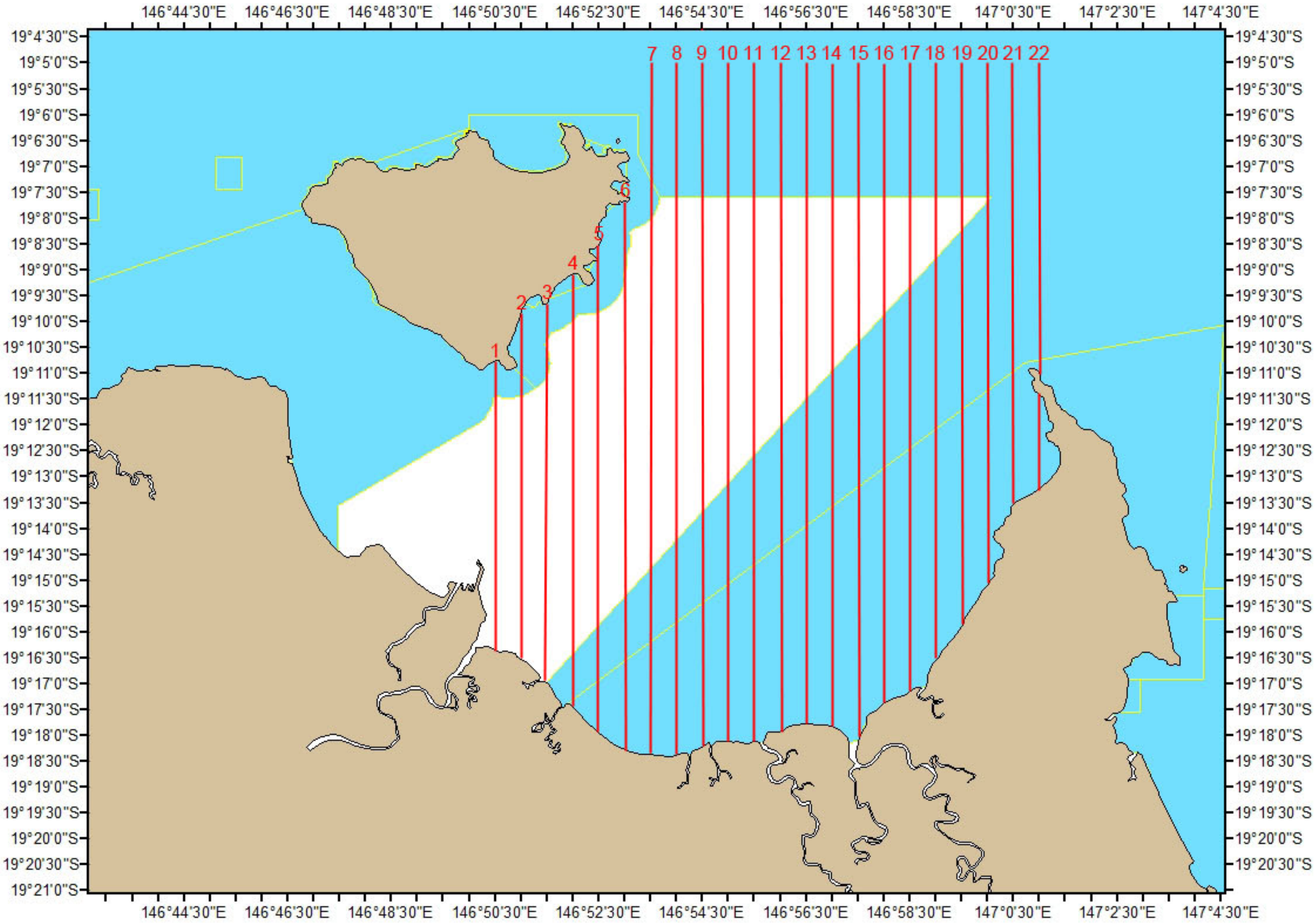


Figure 3.3: Map of Cleveland Bay overlaid with numbered transect lines which are based on lines of longitude. Transect line numbers were randomly chosen on sampling days and were used as a general guide for fishing effort.

Permits were obtained from both the Great Barrier Marine Park Authority (GBMPA), and the Department of Primary Industries and Fisheries (DPI&F) allowing work to be conducted in the protected yellow zones within Cleveland Bay. Unfortunately, a permit allowing gillnetting within the yellow zone covering much of the foreshore of Cleveland Bay was not obtained and so gillnetting effort in depth categories 1 and 2 where confined to the shallow waters just west of the protected yellow zone.

3.2.2 Longlining

Two longlines were constructed for this project and used simultaneously during sampling trips into Cleveland Bay. Both longlines consisted of an 800 meter long main line of 8 mm diameter nylon rope that was anchored at both ends. Main floats were attached to both ends for retrieval of the gear and marker floats were placed every 200 meters along the main line to indicate the lines location to other boaters (Figure 3.4). Five meter long gangions were attached to the main line approximately every ten meters. Gangions were constructed of 3.5 meters of 4mm diameter polyester rope attached to the main line by a stainless steel 5' shark clip. The polyester rope was then attached to a 1.5 meter long 1.8 mm diameter nylon coated wire leader by a stainless steel swivel. The wire leader then terminated in either a 14/0 or 16/0 galvanized circle hook (Figure 3.5).

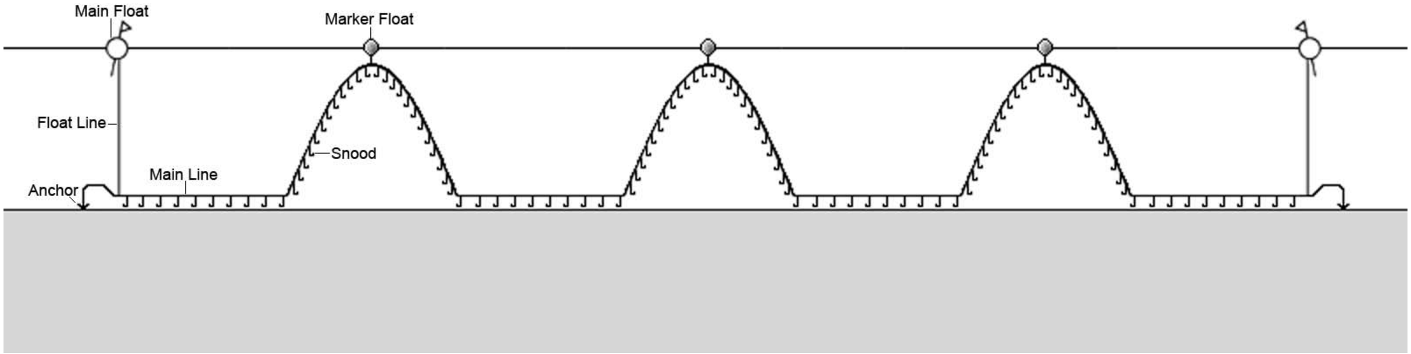


Figure 3.4: Diagram of fisheries independent longline sampling gear.

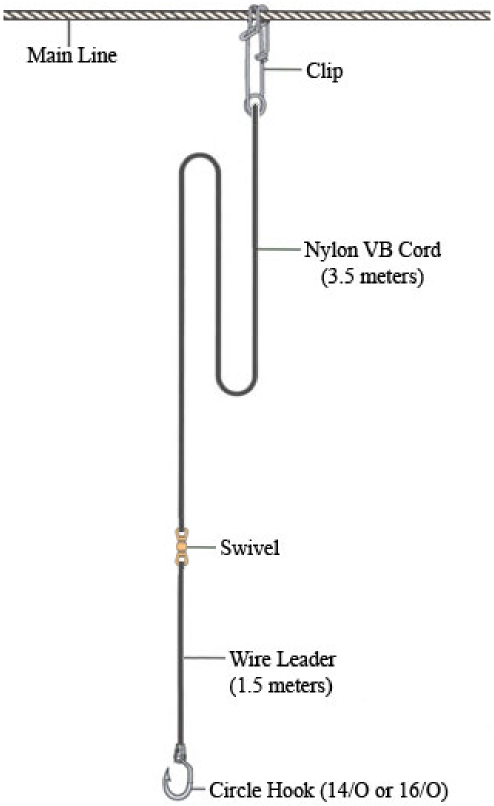


Figure 3.5: Diagram of gangion construction.

Each longline sampling trip normally involved setting between four or six longlines that were each left to soak for approximately one hour. Longlines were set parallel to the prevailing wind direction. In the absence of wind lines were set perpendicular to shore. Longlines were set over the stern of the boat and hauled over the bow. Common baits were *Mugil cephalus* (sea mullet), *Eleutheronema tetradactylum* (blue threadfin), and *Nemipterus bipunctatus* (butterfly bream). Fresh bait was used whenever possible in preference to frozen but frozen bait constituted the majority of longline set bait.

3.2.3 Gillnetting

A single 300 meter long 40 ply monofilament nylon mesh gillnet was constructed for this project. The net was hung on a 6 mm nylon float line with floats attached every 154 cm and weighted down by a 140 gram per meter lead line. The mesh size was 4.5 cm and the net height was 33 mesh drops.

Both ends of the gillnet were attached to piles of lead core rope that acted as non fixed anchors. Each end of the net was marked by a main float, and in shallow waters where the net reached the surface small white marker floats were attached to alert boat traffic of the nets position (Figure 3.6).

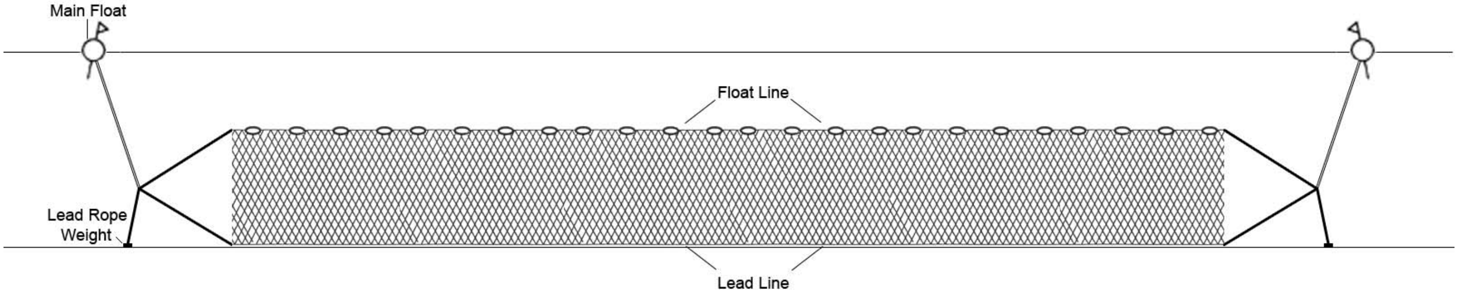


Figure 3.6: Diagram of fisheries independent gillnet sampling gear.

Gillnets were set and hauled over the bow, parallel to the prevailing wind direction. In the absence of wind nets were set perpendicular to shore. Netting trips typically consisted of four 30 to 60 minute sets.

3.2.4 Data Collected on Fisheries-Independent Sampling Trips

The goal of the fisheries-independent sampling was to tag and release all captured animals alive. All sharks were tagged with a plastic Rototag through the first dorsal fin which was marked with a unique id number on one side, and contact information for the project on the other. Sharks which measured over one meter in length where typically fitted with a "Superflexitag" where as smaller sharks received a standard "Rototag". Although uncommon, specimens that died during sampling were marked and returned to the lab.

3.2.5 Biological Measurements

Live captured elasmobranchs on longlines were brought to the side of the boat by pulling in the snood on which they were hooked and securing the tail using a two meter long nylon rope. Animal which were deemed small enough to be directly handled were restrained and brought on board, while larger animals were examined over the side of the boat. Live captured elasmobranchs in gillnets were hauled over the bow of the boat and freed from entangling mesh while being restrained. Once the sharks were properly restrained several biological measurements were taken:

a. Species ID – species identification were based on descriptions outlined in Sharks and Rays of Australia (Last & Stevens 1994, 2009).
b. Fork length – taken from the tip of the nose along the dorsal surface of the specimen to the fork in the caudal fin, measured to the nearest millimeter.
c. Stretched total length – with the upper lobe of the caudal fin stretched out straight the measurement is taken from the tip of the nose along the dorsal surface of the specimen to the tip of the upper lobe of the caudal fin.

d. Sex – male or female was determined by the presence or absence of claspers.
e. Clasper calcification – only recorded for males, a categorical observation of whether claspers were calcified (mature), not calcified (immature), or partially calcified (nearing maturity).
f. Clasper length – claspers were measured from the connection point of the anal fin to the tip of the clasper; measurements were made to the nearest millimeter.
g. Umbilical scar – a categorical observation of whether a specimen's umbilical scar was open, closed (healed), or partially closed (partially healed).
h. Release condition – a subjective measure of the condition of the animal upon release based on a scale from one to five (Hueter et al. 2006). One would be an animal who vigorously swam off immediately following release whereas five would be an animal who even after extensive revival efforts showed little sign of active swimming once released.
i. Hook details – the hook location, and size were recorded for all captured elasmobranchs, as well as whether or not the specimen was bleeding from the wound created by the hook.

3.2.6 Stable Isotope Samples

Seven elasmobranch and three predatory teleosts were sampled for stable isotope analysis. The seven elasmobranch species chosen were those most likely to use Cleveland Bay as a nursery based on their numerical dominance in the catch. The three species of teleosts were selected based on high catch numbers but also due to their piscivorous diets and large maximum size, factors which could potentially make them an addition source of dietary competition to young elasmobranchs using the area as a nursery. Tissue samples were collected from elasmobranchs and teleosts within a restricted size range. In general the lower limit for elasmobranchs was set at the size when the umbilical scar was completely healed and the upper limit was set at sizes prior to maturity. For teleosts tissue samples were taken from the largest captured individuals of the target species. Three different tissue types were collected from all sampled animals:

a. Muscle – extracted from just behind the first dorsal fin in sharks, and immediately adjacent to the dorsal fin in teleosts. Samples were stored in individually labeled 3ml Eppendorf safe-lock microcentrifuge tube which was then placed on ice until they could be frozen in the lab.
b. Blood plasma – taken from the caudal vein just anterior to the tail in both sharks and teleosts, blood plasma was separated from whole blood samples in the field using a portable centrifuge for approximately 90 seconds. An Eppendorf automatic 100-1000 μL pipette was used to remove the resultant plasma layer into a labeled 3ml Eppendorf safe-lock microcentrifuge tube which was then stored on ice until it could be frozen in the lab.
c. Red blood cell – centrifuged and separated in the same method as blood plasma, red blood cells were also stored in labeled 3ml Eppendorf safe-lock microcentrifuge tubes which were stored on ice until returned to the lab.

3.2.7 Environmental Parameters

For every set, data regarding the chemical and physical conditions of the sea were recorded as well as positional data. Seven environmental parameters were measured or recorded during each gear set:

a. Set start and end depth – water depth was taken form a depth sounder to the nearest 0.1 m at the start and end of each set.
b. Set start and end latitude / longitude – latitude and longitude were taken from either a hand held GPS or the boats onboard GPS plotter at both the start and end of each set.
c. Sea surface temperature – surface temperature was measured to the nearest 0.1°C by either a hand held digital thermometer or the boats onboard thermometer at the end of each set.
d. Sea surface salinity – water samples were collected at the end of each set and salinity was determined using a Refractometer.
e. Water turbidity – a Secchi disk was used to determine water turbidity to the nearest 10 centimeters
f. Wind strength – was estimated based on observations made during each set
g. Cloud cover – was estimated as percent sky cover at the end of each set.

3.2.8 Fisheries-Dependent

Fisheries observers were placed on commercial fishing vessels operating in the Townsville area to allow for the collection of stomach contents from captured elasmobranch and teleost species. The same biological measures taken for fisheries-independent caught specimens (3.2.5) were recorded for fisheries-dependent specimens.

Additionally, specimens were dissected to obtain stomach contents, which were bagged and placed on ice for later analysis in the lab.

4 Chapter 4.

Observations of Dietary Resource Partitioning by Sympatric Sharks and Predatory Teleosts in a Near Shore Nursery Environment

4.1 Introduction

The use of discrete inshore shallow water areas as nurseries by juvenile sharks is well documented in the scientific literature (e.g. Springer 1967, Williams & Schaap 1992, Castro 1993, Simpfendorfer & Milward 1993, Stevens & West 1997, Heupel & Simpfendorfer 2005b, Bethea et al. 2006, Blackburn et al. 2007, Heithaus 2007, McCandless et al. 2007, Merson & Pratt 2007, Skomal 2007, Carlson et al. 2008, DeAngelis et al. 2008, Froeschke et al. 2010b). Shark nursery area research has repeatedly drawn upon the hypothesis established by Springer (1967) to describe the ecology of these areas. Springer's hypothesis was intended to represent a typical shark nursery area, using a hypothetical shark species which could represent the general life history strategy of a large number of ecologically similar sharks. In particular, one of the major observations of his hypothesis was that food within a nursery is not a limiting factor for young sharks, and that young sharks can therefore remain in the vicinity of the nursery grounds while feeding and growing during their formative years, an observation which persisted in many subsequent works (Branstetter 1990, Salini et al. 1992, Castro 1993, Simpfendorfer & Milward 1993, Van der Molen & Caille 2001, Heupel & Hueter 2002, Rechisky & Wetherbee 2003).

The idea that shark nursery areas are, by definition, productive habitats that provide ample resources to juvenile sharks became a central idea in the conventional shark nursery area hypothesis. Even early on, however, the prevailing assumption of high food availability within shark nursery areas, based mainly on qualitative observations, was challenged by more quantitative studies. Gruber (1982), for example, found that juvenile lemon shark growth rates in Florida Bay were four times slower than those of lemon sharks fed to satiation in the laboratory. He postulated that the growth lag of the lemon sharks in the bay was due to intraspecific competition for food, in complete opposition to Springer's (1967) claim that resources in nursery areas must be abundant. Yet despite this early evidence that food could be a limiting factor for nursery-dependent young sharks, Springer's hypothesis retained its influence.

Nevertheless, more and more studies have begun to find slow growth rates or weight loss in juveniles that inhabit nursery areas. In Kane'ohe Bay, Hawaii, Bush et al. (2002) found reduced growth rates in juvenile *S. lewini* and suggested that the sharks were unable to obtain sufficient food resources within the nursery. Lowe (2002) and Duncan & Holland (2006) provided supplemental evidence of weight loss in the same population of *S. lewini* pups using tag recapture methods. Both studies suggest that weight loss might be due to a lack of food resources in the bay, the inadequate foraging abilities of the young sharks, or both. Recently, Hussey et al. (2009) provided evidence of maternal head-starting in newborn sharks in the form of enlarged livers. They postulate that these liver reserves are used by the young sharks in the first few weeks or months of life while they orientate themselves in their environment and develop their foraging skills. While this explains some of the weight loss as a natural occurrence, the authors state that the observed weight loss was likely a combination of expending the provisioned maternal head-start along with competition and limited prey availability. Other studies have found high mortality rates of young sharks in nursery areas, often attributing this is part to a lack of sufficient food resources (Manire & Gruber 1993, Duncan & Holland 2006). In Terra Ceia Bay, Florida, Heupel & Simpfendorfer (2002) found mortality rates of up to 90% for juvenile C. limbatus, attributing most of these deaths to natural causes including predation, starvation, and disease, as well as some unnatural causes such as fishing.

These findings, combined with dietary nursery studies, provide strong evidence that the view of nursery areas as highly protective and resource abundant reserves for young sharks is antiquated and no longer fits much of the current data (Heupel et al. 2007). They also raise interesting questions as to the nature of multi-species, or 'communal' shark nursery areas. The ecological pressures of these areas are often overlooked as they have been assumed to display the same characteristics of the single-species nursery area hypothesis discussed above (Castro 1993, Simpfendorfer & Milward 1993). There have been few studies that specifically target communal shark nursery areas for evidence of resource partitioning among juveniles. White et al. (2004) and White & Potter (2004) found some evidence of resource partitioning among three species of sharks and one ray species that share a nursery area in Shark Bay, Western Australia. However, because these studies only used traditional stomach content analysis, they were unable to obtain information on fine-scale dietary separation between the examined species. Additionally, Bethea et al. (2004) looked at dietary and spatial overlap among four species of nursery utilizing sharks and found that dietary overlap was high for similar sized sharks.

However, they also found that spatial overlap was not high and so postulated that sharks were overcoming competition for dietary resources by partitioning the resources of time or space.

The focus of this chapter and the next will be on the dietary overlap of the most abundant shark species inhabiting the established communal shark nursery area of Cleveland Bay (Simpfendorfer & Milward 1993) in Northern Queensland, Australia. This chapter will center on findings derived from traditional stomach content analysis, while the following chapter (Chapter 5) will combine stomach content data with the more modern method of stable isotope analysis to overcome some of the shortcomings of the former method while also complementing some of its stronger points. Stable isotope analysis will help elevate issues such as the snapshot nature of stomach content samples (Pinnegar & Polunin 1999, Pinnegar et al. 2001, Bearhop et al. 2004, MacNeil et al. 2005), large sample size requirements (Cortés 1997, 1999a, Estrada et al. 2005, MacNeil et al. 2005), the persistence of hard structures like cephalopod beaks and crustacean shells (Wilson et al. 1985), the preponderance of empty stomachs and unidentifiable prey items (Cortés 1997), and the frequent necessity of euthanatizing study animals (Heupel & Simpfendorfer 2010). While stomach content data will help identify possible prey families which may drive differences between species seen in stable isotopes data as well as clarify the extensiveness of individual species carbon values by indicating the breadth of a species diet. Combining stomach content analysis with stable isotope analysis therefore may provide a more detailed portrait of the dietary overlap and trophic positioning of the sharks inhabiting communal nursery areas in relation to each other.

4.2 Materials and Methods

4.2.1 Study Site

Large sample sizes are required to quantify dietary overlap between shark species using traditional stomach content analysis, often necessitating sample collection from commercial fishing operations. As commercial fishing restrictions apply across a large portion of Cleveland Bay, fisheries-dependent samples were collected from a wider area stretching from Halifax Bay through Cleveland Bay to maximize sampling. These bays are located adjacent to each other along the northeast coast of Queensland (Figure 4.1) and contain broadly similar habitats. There is little reason to suspect that the diet of sharks within Cleveland Bay will differ markedly from the diet of sharks in Halifax Bay since each bay contains similar habitats and, based on trawls conducted during this project, similar prey communities (Kinney unpublished data). For consistency with other chapters the study area will still be referred to as Cleveland Bay with the knowledge that additional samples were also collected from Halifax Bay.

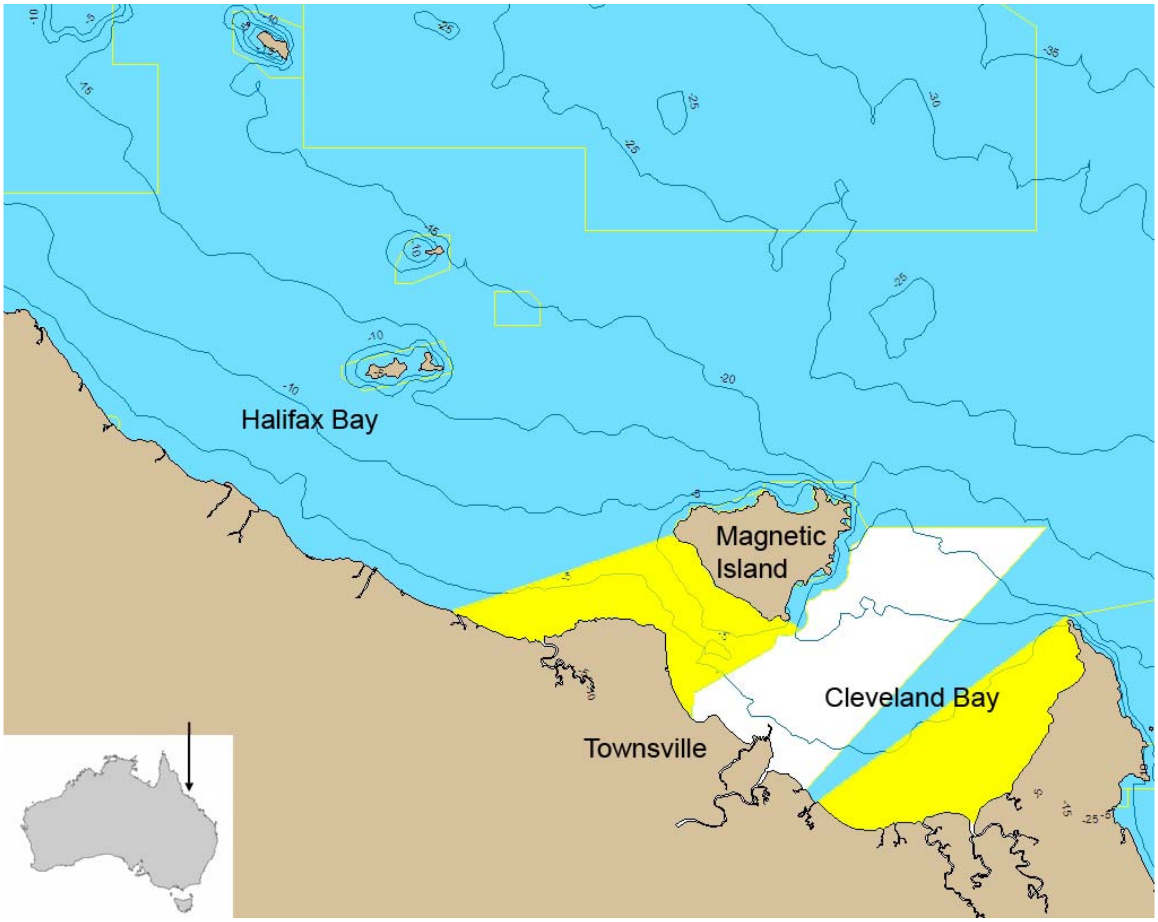


Figure 4.1: Map of Halifax and Cleveland Bay with Great Barrier Reef Marine Park Authority (GBRMPA) Conservation Park Zones marked in yellow and isobaths delineated every 5 meters. Yellow zones indicate areas where commercial fishing is not allowed and recreational fishing is restricted to hook and line only.

4.2.2 Sampling

Stomach contents were collected from commercial fishing vessels in Cleveland and Halifax Bay by onboard observers who recorded catch and effort details of the Queensland commercial inshore gillnet fishery (Harry et al. 2011). All shark species, and one select species of teleosts (used to examine the potential of dietary overlap between sharks and teleosts in the study area) were processed in the same way. Landed sharks and teleosts were identified to species, measured (for sharks: precaudal length (PCL): nose to precaudal notch, fork length (FL): nose to caudal fin fork, and stretched total length (STL): nose to tip of the upper lobe of the caudal fin, for teleosts only fork and stretched total length were measured), sexed, and provided with a unique identification number via a two part paper tag. Stomachs were extracted from dead individuals and place whole into plastic sample bags which were placed on ice and transported back to the lab. Since the aim of this study was to quantify dietary overlap among juveniles efforts were made to restrict sampling as much as possible to only juvenile sharks. However, due to the gear used by commercial fishers captured juveniles tended to represent larger sized juveniles; the smallest juveniles were often missed by the nets and so unsampled. Therefore conclusions based solely on stomach content data were made cautiously and with extensive comparison to all relevant dietary literature.

In the lab, stomach samples were thawed and fullness, on a scale of 1-4 (1 = <26%, 2 = 26%-50%, 3 = 51%-75%, and 4 = >75% full), was recorded before the contents were removed. Contents were washed over a sieve and identified to the lowest possible taxonomic level (typically family), counted, weighted, measured to the nearest millimeter, and assessed for digestive state [(1-4) 1 = >75%, 2 = 75%-51%, 3 = 50%-26%, and 4 = <26% flesh remaining]. Contents that were difficult to identify were photographed and reanalyzed later with assistance from experts for more accurate identification.

Stomachs that either contained no prey items or that had evidence of regurgitation were not used in subsequent dietary analyzes. Additionally, stomachs collected from either *C. tilstoni* or *C. limbatus* were grouped together for the purposes of this study due to the inability to accurately distinguish these two species in the field (Lavery & Shaklee 1991).

4.2.3 Data Analysis

In order to determine whether a sufficient sample size had been reached for determining the entire dietary breadth of each of the examined species, cumulative prey curves were constructed using PRIMER v6 (Clarke & Warwick 2001, Clarke & Gorley 2006). Using the method described in Bizzarro et al. (2007) linear regressions were conducted on the best fit lines generated for the last four points of each species cumulative prey curves. The slops of these lines were statistically compared to zero using a Student's t-test, if slopes were not significantly different, ($p > 0.05$), than curves were deemed to have reached an asymptote and sample size was sufficient to explain a species dietary breadth.

Diet composition was analyzed using the Index of Relative Importance (IRI) (Pinkas et al. 1971), which consists of three quantitative measurements: the frequency of occurrence (F_o), the numerical composition (N_c), and the mass composition (W_c).

$$\mathrm{IRI} = (N_c + W_c)\, F_o$$

The percent Index of Relative Importance (%IRI) was also calculated using: the percent of the total number of stomachs containing a certain prey item ($\%F_o$), the total number of items of a specific prey group or category expressed as a percentage of the total number of prey items found ($\%N_c$), and the wet weight of each specific prey group expressed as a percentage of the total wet weight of all specific prey items found ($\%W_c$).

$$\%\mathrm{IRI} = (\%N_c + \%W_c)\%F_o$$

By expressing IRI values as a percentage, %IRI values between individual prey groups could be compared (Cortés 1997).

Ordinations of dietary data were completed using the multivariate statistical software PRIMER. Analysis of dietary weight data (W_c) in PRIMER was broken into species groups and then into years of capture (2007-2009). Dietary data were randomly allocated into groups of 5 individuals of the same species that were caught during the same year. This method of pooling the dietary data of individuals has been advocated as a way of avoiding certain pitfalls inherent in shark dietary work, such as the low number of prey items contained in one stomach compared to the number of prey items recognized in the dietary study (White et al. 2004, Taylor 2007). Weight data were first standardized and then fourth root transformed before resemblance matrices were constructed using the Bray-Curtis similarity coefficient (Clarke & Warwick 2001). Multi-dimensional scaling (MDS) was performed on these matrices to allow the identification of overlap between species. MDS plots were used to visualize the relationship between examined species diets, with species that shared similar diets appearing more closely clustered in the plot, while species with dissimilar diets separated from each other. A two-way crossed analysis of similarities (ANOSIM) was run in order to identify whether differences in diet existed between investigated species and additionally between years. Similarity percentages (SIMPER) were then used to identify which prey species drove the similarities and dissimilarities between each predator species indicated by the ANOSIM and MDS results.

Index of relative importance calculations were carried out in R v2.8 (R Development Core Team 2008). A script was compiled to allow the reading in of basic dietary info, shark species, tag number, prey frequency of occurrence (F_o), prey numerical composition (N_c), and prey mass composition (W_c), and to output IRI and %IRI values.

Both %IRI and weight data (W_c) were used to investigate dietary overlap of predatory species in Cleveland Bay. By grouping weight data and dividing groups into years, more detailed analysis could be carried out on species with adequate sample sizes. Both shark and teleost species that were sampled more rarely were left out of analyzes that focused solely on prey weight since they often appeared as outliers in MDS plots. %IRI values allowed for the comparison of more species then weight data since %IRI values factor in frequency of occurrence and number of individual prey items. Dietary data for each species were collected and analyzed to produce one data point per species which could be compared on a MDS plot. A cut off of at least ten stomachs with identifiable prey items was used to avoid high plot stress levels caused by species with very low sample sizes, this cut off eliminated four of the original twelve sampled species leaving seven sharks and one teleost species for comparison. Due to the use of frequency of occurrence and numerical data former outliers to the weight data where brought into %IRI plots, however %IRI produced only one data point per species. If %IRI values are calculated at the same scale as prey weight data groups, (i.e. five individuals grouped together instead of one group for an entire species), in an attempt to increase the number of data points, the frequency of occurrence and numerical components of the %IRI calculations become subservient to weight data values, whereupon %IRI calculations add little to original prey weight data analysis. Both methods were therefore used and the results compared so that both a detailed analysis of the more heavily sampled species, and a more general comparison involving a greater number of species, could be presented.

4.3 Results

A total of 1,071 stomachs from twelve species were collected (Table 4.1), of which 461 (43%) contained at least one prey item. All species averaged a high number of empty stomachs (57.1% ± 14% SD). A total of 46 different prey family groups were identified and 1,070 individual prey items were examined. The majority of investigated stomachs containing prey items, (an average of 66.9%), fell into the lowest fullness category, while only 4% of stomachs ranked as full on average (Table 4.2). Most prey items were in a highly digested state with 87.1% on average recorded as digestive state 3 or 4 (Table 4.3).

Table 4.1: Summary of species sampled for stomach content analysis. All size measurements were based on stretched total lengths (STL). Average size at maturity is given to indicate maturity status of captured individuals. Estimated sizes at maturity are averages based on females drawn from (Stevens & Wiley 1986, Stevens & McLoughlin 1991, Compagno et al. 2005). All but three species average sizes fall well below their species average size at maturity indicating that the majority of captured animals were juveniles.

Species	# of Total Stomachs	# of non Empty Stomachs	% Empty Stomachs	# of Prey Items	Avg. Prey Items per Stomach	Sampled Size Range (mm)	Avg. Size ± SD (mm)	Avg. Size at Maturity (mm)	# Females	# Males
Carcharhinus amboinensis	33	14	57.6%	23	1.2	649 - 2400	1027 (± 311)	2125	18	15
Carcharhinus brevipinna	51	10	80.4%	28	2.2	455 - 2830	1043 (± 379)	2100	25	26
Carcharhinus dussumieri	36	10	72.2%	16	1.2	439 - 915	808 (± 94)	725	16	20
Carcharhinus fitzroyensis	25	7	72.0%	9	1.1	550 - 1280	741 (± 215)	850	15	10
Carcharhinus macloti	19	8	57.9%	12	1.2	729 - 910	808 (± 49)	890	4	15
Carcharhinus sorrah	224	94	58.0%	310	1.6	505 - 1700	950 (± 162)	925	118	106
Carcharhinus tilstoni/limbatus	309	121	60.8%	236	1.6	518 - 1930	852 (± 276)	1125	162	147
Eleutheronema tetradactylum	30	21	30.0%	35	1.2	385 - 660	511 (± 56)	-	13	17
Rhizoprionodon acutus	130	66	49.2%	105	1.3	379 - 909	676 (± 150)	750	50	80
Rhizoprionodon taylori	46	19	58.7%	46	2	400 - 885	648 (± 108)	450	31	15
Sphyrna lewini	132	70	47.0%	152	1.6	350 - 4660	991 (± 652)	1700	43	89
Sphyrna mokarran	36	21	41.7%	98	2.4	870 - 4280	1618 (± 593)	2175	21	15

Table 4.2: Summary of stomach fullness information for all twelve shark species.

	Stomach Fullness			
Species	0-25% Full	25-50% Full	50-75% Full	100% Full
C. tilstoni/limbatus	74.4%	12.4%	9.9%	3.3%
C. sorrah	51.1%	22.3%	13.8%	12.8%
S. lewini	48.6%	32.9%	17.1%	1.4%
R. acutus	54.5%	19.7%	19.7%	6.1%
S. mokarran	33.3%	38.1%	23.8%	4.8%
R. taylori	68.4%	26.3%	5.3%	0.0%
C. amboinensis	71.4%	7.1%	14.3%	7.1%
C. brevipinna	100.0%	0.0%	0.0%	0.0%
C. dussumieri	50.0%	20.0%	30.0%	0.0%
C. macloti	75.0%	12.5%	0.0%	12.5%
C. fitzroyensis	85.7%	14.3%	0.0%	0.0%

Table 4.3: Digestive state of prey items for all twelve shark species.

	Digestive State of Prey Item			
Species	1	2	3	4
C. tilstoni/limbatus	3.3%	6.6%	17.4%	72.7%
C. sorrah	24.5%	14.9%	28.7%	31.9%
S. lewini	2.9%	5.7%	12.9%	78.6%
R. acutus	4.5%	4.5%	19.7%	71.2%
S. mokarran	4.8%	23.8%	23.8%	47.6%
R. taylori	0.0%	5.3%	21.1%	73.7%
C. amboinensis	0.0%	14.3%	14.3%	71.4%
C. brevipinna	0.0%	10.0%	10.0%	80.0%
C. dussumieri	0.0%	10.0%	10.0%	80.0%
C. macloti	0.0%	0.0%	0.0%	100.0%
C. fitzroyensis	0.0%	0.0%	0.0%	100.0%

State 1 (100-76% flesh remaining), state 2 (75-51% flesh remaining), state 3 (50-26% flesh remaining), state 4 (25-1% flesh remaining).

Cumulative prey curves did not reach asymptotes for species included in this study ($p < 0.001$) (Figure 4.2); thus I was unable to determine the complete dietary breadth of these species. This limitation, however, did not preclude my main objective of comparing the prevalence of the most commonly ingested prey items across species in order to investigate levels of potential dietary overlap between sharks and teleosts within a communal shark nursery, much like Simpfendorfer & Milward (1993). As with Simpfendorfer & Milward (1993) detailed analysis of food resource partitioning was not possible with stomach content data alone and so further, more advanced investigations of resource partitioning are reserved for Chapter 5 when stomach content data is coupled with stable isotope data.

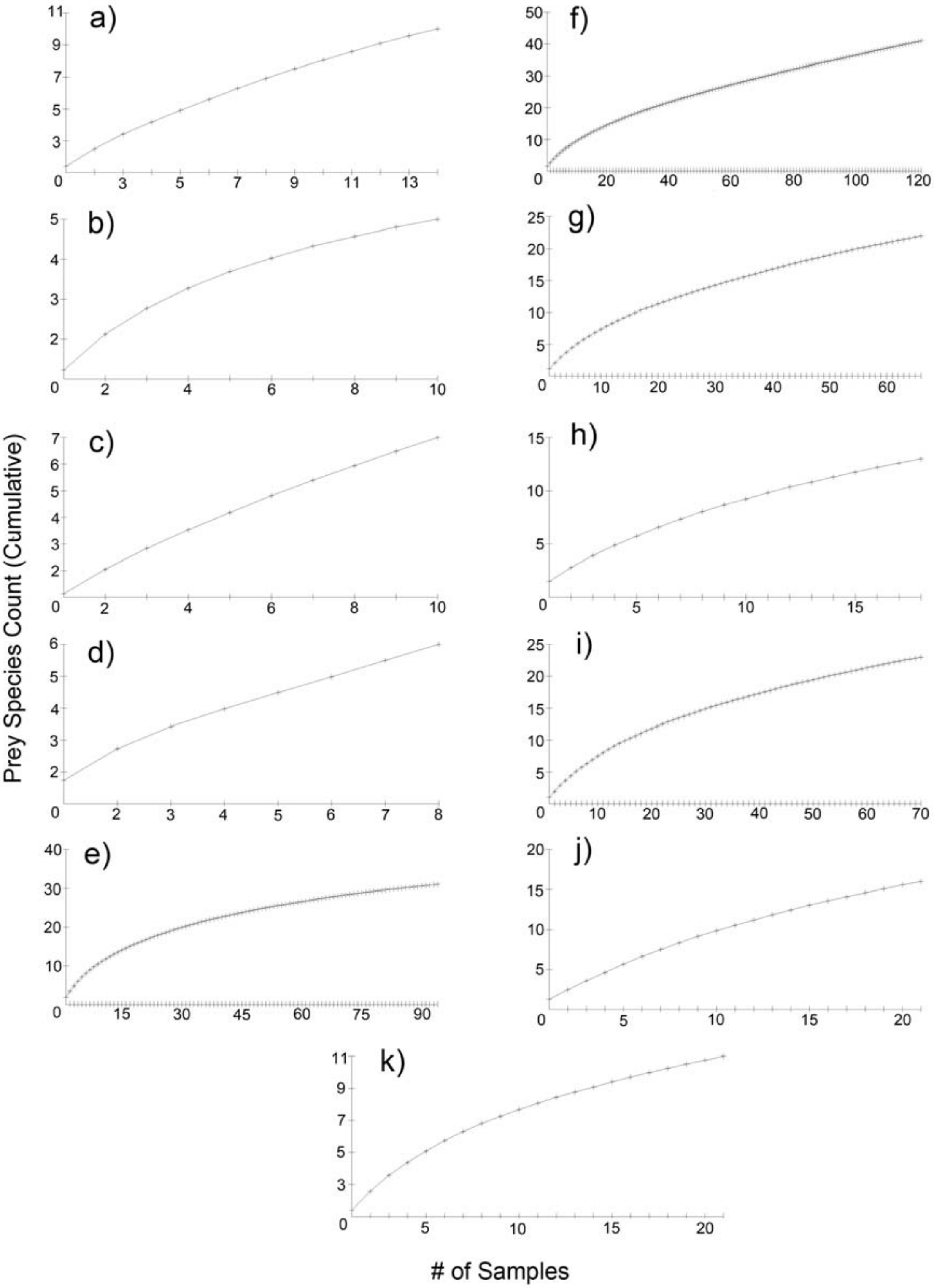


Figure 4.2: Cumulative prey curves for a) *Carcharhinus amboinensis*, b) *Carcharhinus brevipinna*, c) *Carcharhinus dussumieri*, d) *Carcharhinus macloti*, e) *Carcharhinus sorrah*, f) *Carcharhinus limbatus/tilstoni*, g) *Rhizoprionodon acutus*, h) *Rhizoprionodon taylori*, i) *Sphyrna lewini*, j) *Sphyrna mokarran*, and k) *Eleutheronema tetradactylum*. Order of stomachs was permutated 999 times to avoid bias. Due to large differences in sample sizes between species axis scales vary.

4.3.1 Dietary Weight Results

Initially, diet data from all twelve sampled species across all three sampling years were analyzed with MDS plots. However, data outliers caused by limited sample sizes of some species impaired the ability to detect patterns in the data and inflated plot stress levels (which are estimates of the accuracy of produced plot), thus the four most commonly sampled species (*C. tilstoni/limbatus, Carcharhinus sorrah, Sphyrna lewini, and Rhizoprionodon acutus*) in regards to sample size (121[across both species], 94, 70, and 66 stomachs containing prey) were sub-sampled from the larger group of twelve species for more detailed analysis. A MDS plot of these sub-sampled species indicated possible differences between their diets, but again high plot stress levels hampered accurate estimation of the differences in diet within this species assemblage possibly owing to differences in diets across sampling years (Figure 4.3).

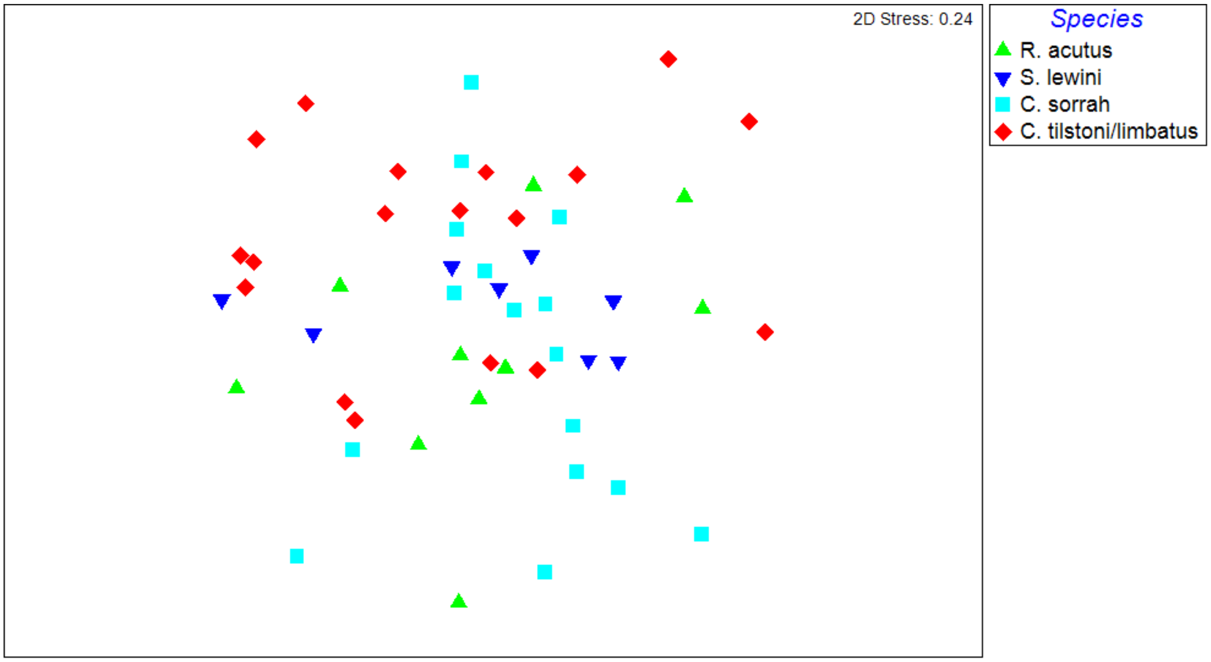


Figure 4.3: MDS ordination of the Bray-Curtis resemblance matrix derived from prey species weight data of the four most commonly sampled shark species in terms of number of non-empty stomachs examined

from 2007-2009. Stress levels are over 0.2 which is considered high, and remain high even in 3D plot. Year labels were excluded from this graph due to the inability to view the results when year labels were present. Each point represents a pool of five random individuals from a given species.

Year and species were both significant factors contributing to differences in shark diets (ANOSIM p< 0.01). For species groups, differences were greatest between *R. acutus* and both *C. sorrah* and *C. tilstoni/limbatus,* as well as *S. lewini* and *C. sorrah*; while for year groups, the greatest difference was between 2007 and 2009 data according to pairwise testing (Table 4.4). Further analyzes were separated by year so that diets of the species assemblage for each year could be examined independently since ANOSIM results identified year as a significant factor.

Table 4.4: Pairwise results from two-way crossed ANOSIM with species and year as factors. **a)** Results of tests for differences across species groups. **b)** Results of tests for differences across species groups. (* mark significant results; note that not all groups with significance levels less then 5% are marked as significant since R statistic values must also be high; otherwise significance can simply be an artifact of excessive statistical power do to the number of possible permutations)

Pairwise Tests (a)

Species Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed
R. acutus **/** *S. lewini*	0.226	11.7	3600	999	116
R. acutus **/** *C. sorrah*	0.453	0.1	240240	999	0
R. acutus **/** *C. tilstoni/limbatus*	0.41	0.1	1633632	999	0
S. lewini **/** *C. sorrah*	0.451	0.3	105840	999	2
S. lewini **/** *C. tilstoni/limbatus*	0.28	1.4	160160	999	13
C. sorrah **/** *C. tilstoni/limbatus*	0.314	0.2	129489360	999	1

Pairwise Tests (b)

Year Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed
2007 **/** 2008	0.267	0.6	499458960	999	5
2007 **/** 2009	0.644	0.1	352800	999	0
2008 **/** 2009	0.359	0.5	4804800	999	4

MDS plots based on diet data of *C. sorrah* in 2007 clearly separate from the other three species, *S. lewini*, *C. tilstoni/limbatus* and *R. acutus*. *Sphyrna lewini*, *C. tilstoni/limbatus* and *R. acutus* display some overlap but *S. lewini* can still be easily separated from the other two species (Figure 4.4a). SIMPER analysis of 2007 dietary data shows that *C. tilstoni/limbatus, R. acutus,* and *S. lewini* diets are dominated by unidentifiable fish, which explains the general clustering seen in the MDS plot. *Sphyrna lewini* has two prey categories in addition to unidentifiable fish, Sillaginidae [0.58 Similarity or dissimilarity/standard deviation (Sim/SD)], and Penaeidae (0.58 Sim/SD), which contribute to its overall diet; this explains the ability to separate that species from *C. tilstoni/limbatus* and *R. acutus*. *Carcharhinus sorrah* diet is dominated by teleosts from the families Leiognathidae (12.09 Sim/SD), and Haemulidae (1.31 Sim/SD) which is demonstrated by its separation from all other species. The MDS plot for 2008 displays a less defined but still evident separation of the four species. The cause of this less defined separation can be traced back to the abundance of unidentifiable fish in stomach contents of each species. The separation between *C. tilstoni/limbatus* and *R. acutus* is the clearest (supported by ANOSIM results Table 4.4) with *C. sorrah* and *S. lewini* occupying the space between these species in the plot (Figure 4.4b). Diet data from 2009 were sparser than in either of the pervious years and a clear pattern is not evident in the MDS plots (Figure 4.4c). SIMPER analysis again reveals unknown fish as the main cause of the general overlap of all four species despite differences in their most important prey family.

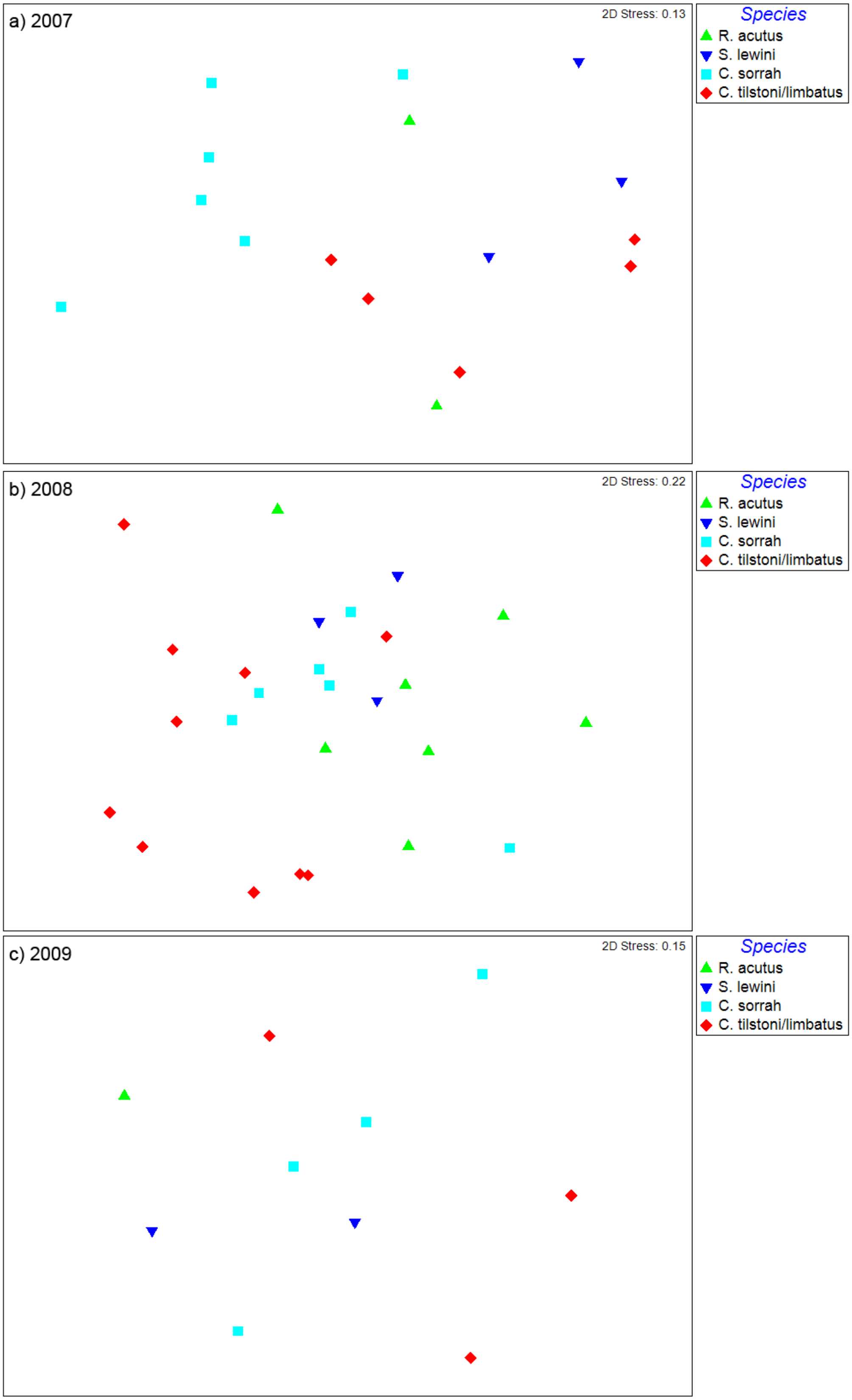


Figure 4.4a-c: MDS ordination of the Bray-Curtis resemblance matrices derived from 2007-2009 prey species weight data of the four most commonly sampled shark species in terms of number of non-empty stomachs examined.

4.3.2 Index of Relative Importance Results

Results from %IRI calculations agree with top prey categories identified for *C. sorrah, R. acutus, S. lewini,* and *C. tilstoni/limbatus* in SIMPER analysis based on weight data, as well as in raw data seen in (Table 4.5) through (Table 4.12). The MDS plot identified species that were generally caught at larger sizes, [*Carcharhinus amboinensis*, and *Sphyrna mokarran*, (Table 4.1)], as separate from other shark species (Figure 4.5). Additionally, *Eleutheronema tetradactylum*, the only teleost species, plotted outside of the general cluster of inshore sharks since, of its top prey categories only Trichiuridae was shared with any shark species. *Carcharhinus sorrah* also appeared somewhat separate to other examined species. The general overlap of the remaining species is not unexpected; as indicated by analysis of prey species weight data in PRIMER, however these species do still differ in their top prey categories.

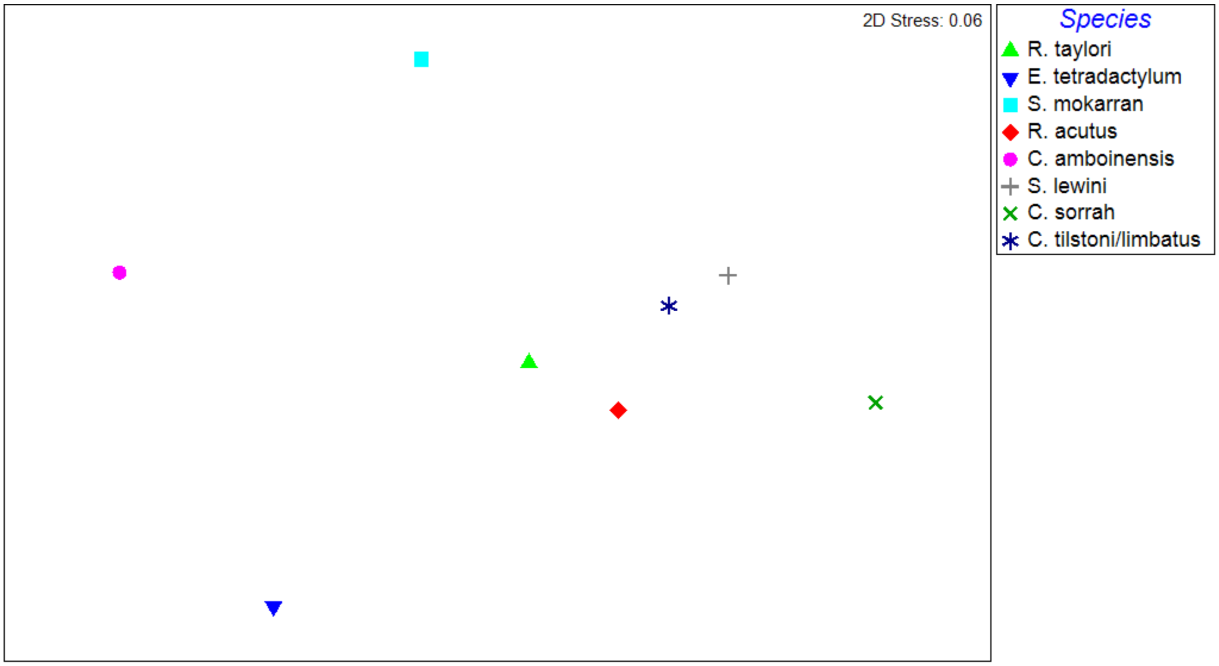


Figure 4.5: MDS plot of %IRI data from all species with more then ten stomachs containing identifiable prey items.

Table 4.5: Index of relative importance data for *R. taylori* (non empty stomachs n=19).

Prey itmes	$\%N_c$	$\%W_c$	$\%F_o$	%IRI
Clupeidae (Herring spp.)	10.9	19.7	18.2	10.1
Engraulidae (Anchovy spp.)	4.3	5	4.5	0.8
Leiognathidae (Ponyfish spp.)	34.8	22.3	4.5	4.7
Mullidae (Goatfish spp.)	2.2	2.5	4.5	0.4
Polynemidae (Threadfin spp.)	2.2	3.3	4.5	0.4
Scombridae (Mackerel spp.)	2.2	14.1	4.5	1.3
Unknown teleost spp.	43.5	33.2	59.1	82.3

%Fo is the percent of the total number of stomachs containing a certain prey item, %Nc is the total number of items of a specific prey group or category expressed as a percentage of the total number of prey items found, %Wc is the wet weight of each specific prey group expressed as a percentage of the total wet weight of all specific prey items found, and %IRI is the percentage of relative importance for each prey family group.

Table 4.6: Index of relative importance data for *E. tetradactylum* (non empty stomachs n=21).

Prey itmes	%N_c	%W_c	%F_o	%IRI
Carangidae (Trevally spp.)	2.9	2.3	3.7	0.4
Drepanidae (Sicklefish spp.)	2.9	0.7	3.7	0.3
Engraulidae (Anchovy spp.)	11.4	11.2	11.1	4.9
Penaeidae (Prawn spp.)	17.1	18.4	11.1	7.7
Terapontidae (Striped Grunter spp.)	2.9	0.6	3.7	0.3
Trichiuridae (Hairtail spp.)	17.1	43.6	22.2	26.4
Unknown teleost spp.	45.7	23.2	44.4	60

See Table 4.5 for descriptive caption.

Table 4.7: Index of relative importance data for *S. mokarran* (non empty stomachs n=21).

Prey itmes	%N_c	%W_c	%F_o	%IRI
Callionymidae, Draconettidae (Dragonet spp.)	1	0.5	2.9	0.1
Clupeidae (Herring spp.)	2	1.5	5.7	0.5
Crustaceans (Crab spp.)	3.1	0.1	8.6	0.7
Haemulidae (Sweetlip and Grunter spp.)	1	24.7	2.9	1.9
Hydrophiidae (Sea Snake spp.)	2	5.1	5.7	1.1
Leiognathidae (Ponyfish spp.)	2	0.1	2.9	0.2
Penaeidae (Prawn spp.)	1	0.2	2.9	0.1
Platycephalidae (Flathead spp.)	3.1	1.7	2.9	0.4
Psettodidae (Halibut spp.)	1	19	2.9	1.5
Rhinidae, Rhinobatidae, etc. (Ray spp.)	6.1	13.5	11.4	5.8
Serranidae (Cod spp.)	1	2.1	2.9	0.2
Soleidae, Bothidae, etc. (Flat Fish spp.)	4.1	5.6	5.7	1.4
Trichiuridae (Hairtail spp.)	4.1	6.5	5.7	1.6
Unknown teleost spp.	68.4	19.4	37.1	84.5

See Table 4.5 for descriptive caption.

Table 4.8: Index of relative importance data for *R. acutus* (non empty stomachs n=66).

Prey itmes	%N_c	%W_c	%F_o	%IRI
Callionymidae, Draconettidae (Dragonet spp.)	1	2.9	1.3	0.1
Clupeidae (Herring spp.)	11.4	18.2	11.5	9
Engraulidae (Anchovy spp.)	1	0.5	1.3	0.1
Haemulidae (Sweetlip Spp.)	1	1.2	1.3	0.1
Hydrophiidae (Sea Snake spp.)	2.9	1.5	3.8	0.4
Leiognathidae (Ponyfish spp.)	8.6	5.4	9	3.3
Loliginidae (Squids)	3.8	5.9	3.8	1
Mugilidae (Mullet spp.)	1	2.5	1.3	0.1
Mullidae (Goatfish spp.)	1	1.7	1.3	0.1
Penaeidae (Prawn spp.)	9.5	4.1	10.3	3.7
Scombridae (Mackerel spp.)	1	10.7	1.3	0.4
Soleidae, Bothidae, etc. (Flat Fish spp.)	21	16	12.8	12.6
Synodontidae (Saurida spp.)	1	0.2	1.3	0.1
Unknown teleost spp.	36.2	29.2	39.7	69

See Table 4.5 for descriptive caption.

Table 4.9: Index of relative importance data for *C. amboinensis* (non empty stomachs n=14).

Prey itmes	%N_c	%W_c	%F_o	%IRI
Carcharhinidae (Shark spp.)	4.3	60.8	5	6.2
Crustaceans (Crab spp.)	4.3	0.3	5	0.4
Engraulidae (Anchovy spp.)	8.7	1.8	5	1
Hydrophiidae (Sea Snake spp.)	21.7	5	25	12.7
Polynemidae (Threadfin spp.)	4.3	1	5	0.5
Triacanthidae, Triacanthodidae (Tripodfish spp.)	4.3	0.6	5	0.5
Unknown teleost spp.	52.2	30.5	50	78.7

See Table 4.5 for descriptive caption.

Table 4.10: Index of relative importance data for *S. lewini* (non empty stomachs n=70).

Prey itmes	%N_c	%W_c	%F_o	%IRI
Callionymidae, Draconettidae (Dragonet spp.)	0.7	0.1	1.1	0.1
Clupeidae (Herring spp.)	10.5	5.2	10.9	5.8
Crustaceans (Crab spp.)	2.6	0.3	2.2	0.2
Hydrophiidae (Sea Snake spp.)	0.7	0.1	1.1	0.1
Leiognathidae (Ponyfish spp.)	3.9	1.8	4.3	0.8
Loliginidae (Squids)	4.6	11.8	6.5	3.6
Mullidae (Goatfish spp.)	2	1.2	2.2	0.2
Penaeidae (Prawn spp.)	11.2	7.2	14.1	8.8
Scombridae (Mackerel spp.)	2	53.7	3.3	6.3
Sillaginidae (Whiting spp.)	4.6	3.1	5.5	0.7
Soleidae, Bothidae, etc. (Flat Fish spp.)	0.7	0.3	1.1	0.1
Spirulidae (Cuttlefish spp.)	3.9	1.4	6.5	1.2
Synodontidae (Saurida spp.)	1.3	4.2	2.2	0.4
Unknown teleost spp.	49.3	9.4	35.9	71.7

See Table 4.5 for descriptive caption.

Table 4.11: Index of relative importance data for *C. sorrah* (non empty stomachs n=94).

Prey itmes	%N_c	%W_c	%F_o	%IRI
Apogonidae (Apogon spp.)	0.3	0	0.6	0.1
Carangidae (Trevally spp.)	2.2	6.3	2.4	0.4
Clupeidae (Herring spp.)	8.7	11.2	11.2	9.4
Gerridae (Gerres spp.)	2.9	6.2	2.5	1
Haemulidae (Sweetlip Spp.)	8.4	16.1	6.2	6.4
Leiognathidae (Ponyfish spp.)	20.3	12.5	11.8	16.4
Loliginidae (Squids)	1.9	1.5	3.7	0.5
Menidae (Moonfish spp.)	0.6	0.8	1.2	0.1
Mullidae (Goatfish spp.)	7.7	8.6	5	3.4
Penaeidae (Prawn spp.)	5.1	1.9	7.5	2.2
Polynemidae (Threadfin spp.)	1	2.5	1.9	0.3
Sciaenidae (Croaker and Jewfish spp.)	1	5.2	1.9	0.5
Sillaginidae (Whiting spp.)	2.6	1.7	3.1	0.6
Soleidae, Bothidae, etc. (Flat Fish spp.)	0.6	0.1	1.2	0.1
Spirulidae (Cuttlefish spp.)	1	2.1	1.9	0.2
Terapontidae (Striped Grunter spp.)	1.6	4.6	2.5	0.7
Tetraodontidae (Toadfish spp.)	1	1	1.2	0.1
Unknown teleost spp.	30.2	15.5	29.8	57.6

See Table 4.5 for descriptive caption.

Table 4.12: Index of relative importance data for *C. tilstoni/limbatus* (non empty stomachs n=121).

Prey itmes	%N_c	%W_c	%F_o	%IRI
Ariidae (Catfish spp.)	1.3	0.3	2.2	0.1
Carangidae (Trevally spp.)	1.6	7.6	2.8	0.3
Clupeidae (Herring spp.)	14.4	14.7	10.9	6.5
Engraulidae (Anchovy spp.)	0.4	0.2	0.7	0.1
Gerridae (Gerres spp.)	0.8	3.2	1.4	0.1
Leiognathidae (Ponyfish spp.)	9.3	4.2	5.1	1.4
Loliginidae (Squids)	11	13.6	7.2	3.6
Mullidae (Goatfish spp.)	3	2	1.4	0.1
Penaeidae (Prawn spp.)	1.3	1.2	2.2	0.1
Polynemidae (Threadfin spp.)	3.8	7.6	5.8	1.4
Scombridae (Mackerel spp.)	2.1	8.7	2.9	0.6
Synodontidae (Saurida spp.)	0.8	4.9	1.4	0.2
Unknown teleost spp.	48.3	30.1	52.9	85.5

See Table 4.5 for descriptive caption.

The nature of standard stomach content analysis often leads to unknown teleosts representing the dominant prey category for a given predatory species. This information is useful at a basic level for identifying each of the above eight species as piscivorous, but the high proportion of unknown species found in stomachs can often overshadow the importance of other identifiable prey categories. Therefore data concerning the top prey categories for each of the eight species is presented here both with and without unknown teleosts as a dietary category (Figure 4.6 and Figure 4.7).

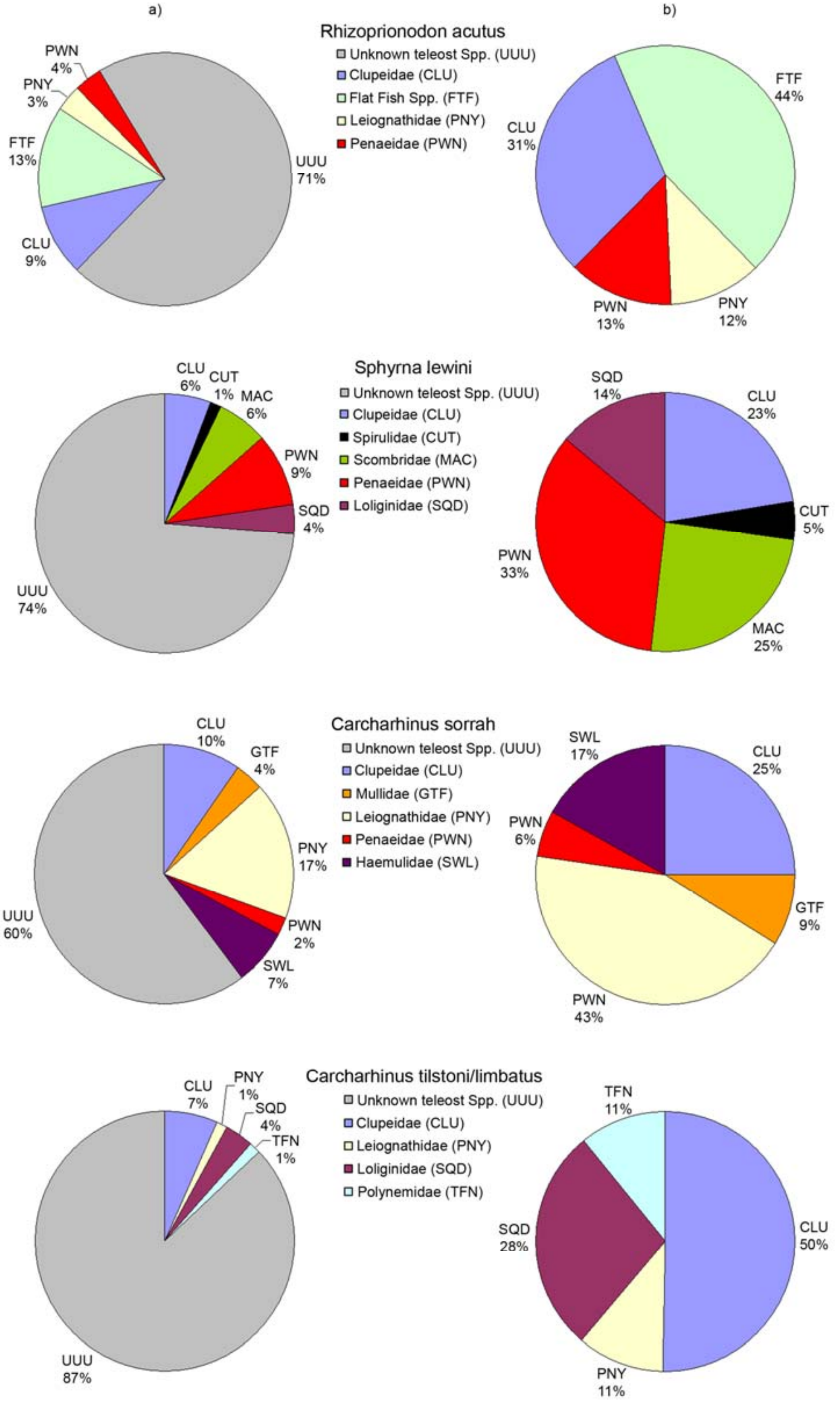


Figure 4.6: Index of relative importance pie charts for top four shark species in terms of number of non empty stomachs examined. Column (a) includes unidentified teleost as a prey category, while column (b) excludes unidentified teleost.

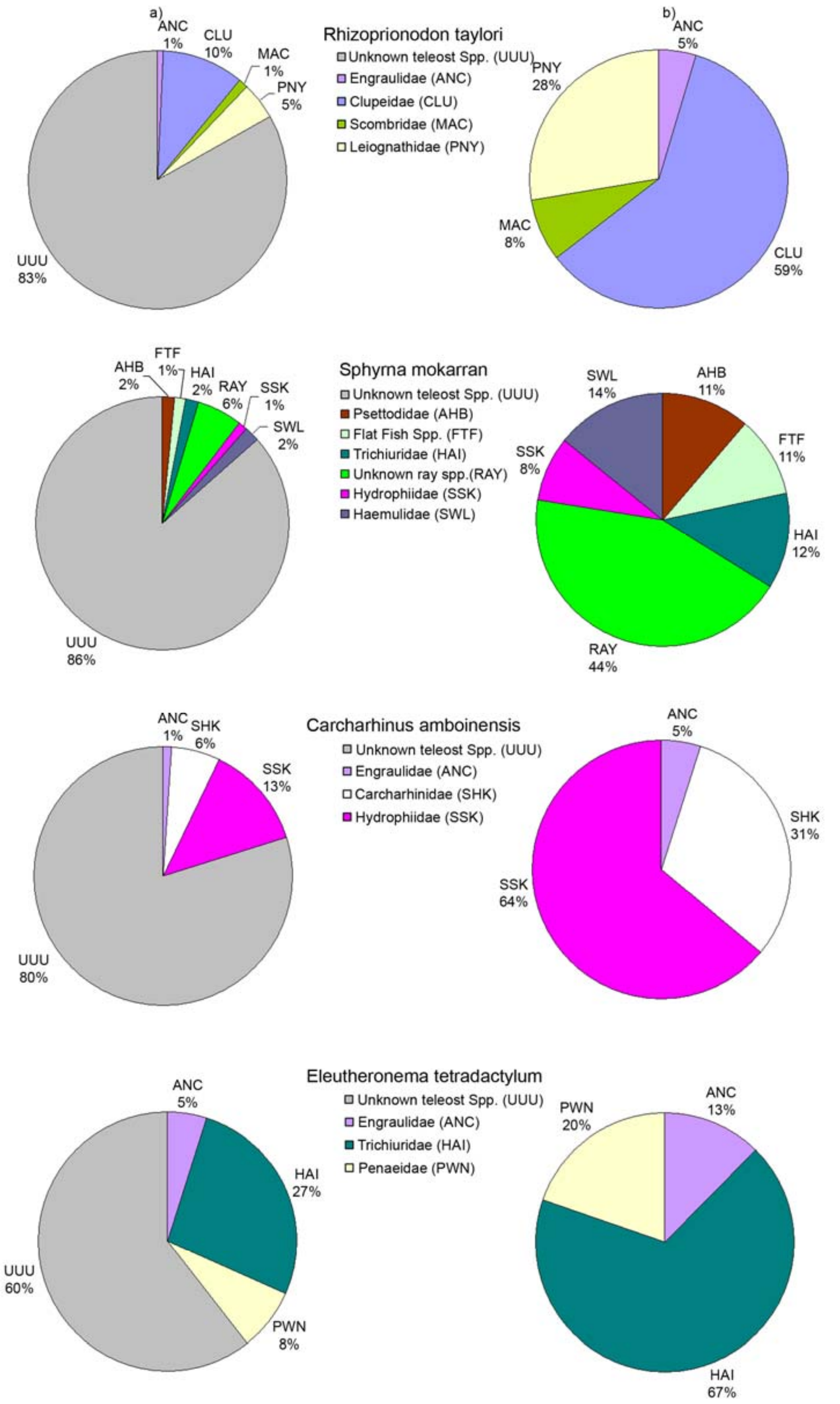


Figure 4.7: Index of relative importance pie charts for additional three shark and one teleost species included in %IRI MDS plot. Column (a) includes unidentified teleost as a prey category, column (b) exclude unidentified teleost.

4.4 Discussion

Stomach content analysis indicates a degree of dietary separation between shark species that contrasts with the original investigations of communal nurseries (Castro 1993, Simpfendorfer & Milward 1993). Early research into communal shark nurseries suggested that the high resource availability in productive inshore environments would preclude the need for resource partitioning between juvenile sharks. My data indicates that certain prey categories are important dietary components to a number of different shark species, much like Simpfendorfer & Milward's (1993). However, the order of importance and percent contribution to the overall diet of these prey categories differs among species. Simpfendorfer & Milward's (1993) conclusions favored a more traditional stance of abundant resources precluding competition and differences in percent contribution of certain important prey categories was not seen as enough evidence to break from tradition and claim resource partitioning. Coupling my stomach content data with findings derived from stable isotopes (Chapter 5) affords me the ability to further probe these dietary differences and establish more clearly that resource partitioning is identifiable within the nursery environment of Cleveland Bay. However this chapter will focus principally on identifying and discussing the primary prey families found in the stomachs of frequently encountered shark species while a more detailed analysis of resource partitioning will be presented in Chapter 5.

Stomach content results suggest that species of a similar size and morphology have a greater degree of dietary overlap than larger species or those with highly divergent morphologies. For example, the diets of *Rhizoprionodon taylori*, *R. acutus*, and *C.*

tilstoni/limbatus were all more similar to each other than to other larger species such as *C. amboinesis* and *S. mokarran*, a finding which has been echoed in other similar studies (Ellis et al. 1996, Platell et al. 1998, Bethea et al. 2004, Paterson & Drouillard 2006). This may represent similarities in foraging locations for similarly sized species, or gape limitations which precludes smaller predators from consuming certain larger prey items.

4.4.1 Individual Species Diets

Carcharhinus amboinesis

Demersal fish and other elasmobranchs were identified as important prey in the diet of *C. amboinesis*. Research on the diet of this species has often suffered from limited sample size; e.g. Stevens & McLoughlin (1991) obtained 35 individuals, Taylor (2007) sampled 31, and the present study captured a total of 33. However, results for each study as well as my own are in general agreement over the main prey categories which constitute a large portion of this species diet. The overall diet of this species showed little overlap with other investigated species indicating a relatively unique diet in relation to other sharks in Cleveland Bay.

Carcharhinus sorrah

Teleosts were the dominant prey for *C. sorrah*, especially Leiognathids, Clupeids, and Penaeidae. Differing ratios of these three prey categories were found among shark species of a similar size, including *C. tilstoni/limbatus, R. acutus, R. taylori, and S. lewini* and, along with the prevalence of unidentifiable teleosts, account for the general overlap seen in MDS plots of these five species. Despite this general overlap, the importance of these three prey categories differed for each of the five listed species, and each species exploited other significant unique prey categories. For instance, Haemulidae and Mullidae were significant prey categories for *C. sorrah* but did not appear in the %IRI calculations for any of the other four species, indicating that a general prey basis may be used by several shark species but each also exploits one or a few unique prey species, potentially reducing overall competition for dietary resources. My findings of a teleost based diet dominated by a few abundant species is corroborative of previous work carried out on *C. sorrah* in Cleveland Bay (Simpfendorfer & Milward 1993) and in a review of shark diets by Cortés (1999a).

Carcharhinus tilstoni/limbatus

The diet of *C. tilstoni/limbatus* was highly piscivorous which correlates well with the extensive body of work concerning the diets of these species (Dudley & Cliff 1993, Simpfendorfer & Milward 1993, Cortés 1999a, Heupel & Hueter 2002, Bethea et al. 2004, Taylor 2007). Despite sampling over 300 individuals, the prevalence of unidentified teleosts in the stomach contents (%IRI value of >80%) as well as the high percentage of empty stomachs (>60%) made the identification of important prey categories for these species difficult. Clupeidae and Loliginidae were the only two prey categories that made up more then 1% of the %IRI calculations for these species, indicating potential dietary overlap with *C. sorrah*, *R. acutus, R. taylori, and S. lewini*. The small size and generally poor conditions of stomach contents for *C. tilstoni/limbatus* suggests that periods between feeding were long and that often prey was not consumed whole but rather bitten into smaller pieces before consumption (Taylor 2007). It is also important to note that spatial investigations on *C. tilstoni/limbatus* (Chapter 6) identified difficulties in modelling these two species together, suggesting that future work concerning spatial and temporal resource partitioning, as well as dietary resource partitioning, would benefit from separating these species if possible.

Eleutheronema tetradactylum

Although the diet of *E. tetradactylum* was also highly piscivorous, the teleost family that dominated its stomach contents, Trichiuridae, was found in the stomach of only one other species—that of *S. mokarram*. Other than Trichiuridae, *E. tetradactylum* and *S. mokarram* did not share any major prey categories. Previous work on the diet of *E. tetradactylum* in the waters of Northern Queensland indicate similar findings of a teleost dominated diet supplemented by prey from the family Penaeidae (Salini et al. 1990). My stomach content results indicated little dietary overlap between *E. tetradactylum* and other examined shark species; however, samples taken from larger individuals would be necessary in order to rule out dietary overlap completely.

Sphyrna mokarran

Like most species the diet of *S. mokarran* was dominated by teleosts, with the majority of them unidentifiable. The single largest identifiable prey category however was rays, a category which was unique to *S. mokarran*. *Sphyrna mokarran* larger average size in the catch, 50 cm longer than all other captured species, may help to explain its general separation from other investigated species. My results are consistent with other dietary studies (Stevens & Lyle 1989), indicating that much like *C. amboinesis*, *S. mokarran* diet is significantly different from other species investigated in Cleveland Bay.

Rhizoprionodon acutus, *Rhizoprionodon taylori*, and *Sphyrna lewini*

As stated above, the diets of *R. acutus*, *R. taylori*, and *S. lewini* were all closely related with the diet of *C. sorrah*, and *C. tilstoni/limbatus*. Each of these species showed high %IRI values for Leiognathids, Clupeids, and Penaeidae, although in differing ratios. My results for these species corroborated with the dietary literature for each, indicating the consistency of my results with other established studies (Stevens & Lyle 1989, Simpfendorfer 1993, Simpfendorfer 1998, Bush & Holland 2002, Lowe 2002, Bush 2003, White et al. 2004, Last & Stevens 2009). As described above, it seems that a general overlap in main prey categories is displayed by *C. sorrah, C. tilstoni/limbatus, R. acutus*, *R. taylori*, and *S. lewini*, however each species also exploits one or a few unique prey categories, which may be an indication of partitioning in order to reduce overall competition for dietary resources.

Stomach content results indicate that communal shark nurseries are intricate communities where limited resources are divided between resident species in order to allow diverse arrays of inhabitants to utilize the same general area while reducing competition. This is a much different view than that of the traditional communal nursery area hypothesis which assumes abundant resources and thus a limited need for resource partitioning strategies (Simpfendorfer & Milward 1993). However, the limitations of stomach content analysis as mentioned in this chapter (i.e. the prevalence of unidentifiable prey items and empty stomachs), highlights the importance of utilizing other approaches, such as DNA analysis of stomach contents (Barnett et al. 2010) or stable isotope analysis, to validate results. Chapter 5 will utilize stable isotope analysis along with results from this chapter to allow for a more robust assessment of resource partitioning strategies among the sympatric shark species using Cleveland Bay as a nursery, much like (Paterson & Drouillard 2006) did for sympatric species of teleost in the Detroit River, USA.

5 Chapter 5.

Communal or Competitive? Stable Isotope Analysis Provides Evidence of Resource Partitioning within a Communal Shark Nursery

---

5.1 Introduction

The use of discrete inshore shallow water areas as nurseries by juvenile sharks has been established in the scientific literature since the mid twentieth century (Springer 1967). Over time many aspects of the original shark nursery area hypothesis have been altered, omitted, or added to, but the central paradigm has persisted. One of the longest standing tenants of the nursery area paradigm is the hypothesis of resource abundance—the idea that young sharks can remain in the nursery while feeding and growing for the first few years of life with little to no competition (Branstetter 1990, Salini et al. 1992, Castro 1993, Simpfendorfer & Milward 1993).

More recent shark nursery area studies are finding evidence countering the hypothesis of nursery area resource abundance. Evidence of slow growth rates (Bush & Holland 2002, Lowe 2002, Duncan & Holland 2006) and high mortality rates of young sharks in nursery areas, attributed in part to a lack of sufficient food resources (Manire & Gruber 1993, Duncan & Holland 2006). In the Gulf of Mexico, mortality rates of up to 90% for juvenile *Carcharhinus limbatus* within Terra Ceia Bay, Florida, were attributed to natural mortality, including predation, starvation, and disease (Heupel & Hueter 2002, Heupel & Simpfendorfer 2002). These findings provide strong evidence that the view of nursery areas as protective, resource abundant reserves for young sharks is outdated and no longer fits much of the current data (Heupel et al. 2007).

While evidence of resource limitations within single species nursery areas is mounting, few studies have investigated resource partitioning among co-occurring shark species (Salini et al. 1992, Platell et al. 1998, Bethea et al. 2004, White et al. 2004), with only Bethea et al. (2004) focusing specifically on juveniles in these areas. Although these studies have found some evidence of resource partitioning, several limitations inherent to stomach content analysis have made determining broad-scale resource partitioning difficult. These include: the snapshot nature of stomach content data (Pinnegar & Polunin 1999, Pinnegar et al. 2001, Bearhop et al. 2004, MacNeil et al. 2005), the persistence of hard structures like cephalopod beaks and crustacean shells (Wilson et al. 1985), and in the case of animals such as sharks the preponderance of empty stomachs and unidentifiable prey items (Cortés 1997). These limitations often necessitate large sample sizes (Cortés 1997, 1999a, Estrada et al. 2005, MacNeil et al. 2005) which are often not feasible either due to simple project logistics or concerns over a species conservation status (Heupel & Simpfendorfer 2010). These problems are compounded further when an investigation seeks to understand the diet of a select size or age range; for example the diet of young sharks within nursery areas.

One way to address the limitations of stomach content analysis is through the use of naturally occurring stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). This technique has emerged as a powerful alternative or complementary tool for assessing the feeding ecology of organisms (Domi et al. 2005). The approach is based on the principle that the stable isotope ratios in consumer tissues can be related in a predictive way to those in their diet (DeNiro & Epstein 1978, 1981). Values of $\delta^{13}C$ can be used to track sources of primary carbon, as $\delta^{13}C$ shows relatively little (~1‰ per trophic level) change between trophic levels from primary producers up through apex predators (Peterson & Fry 1987, Hobson & Welch 1992). As such, $\delta^{13}C$ can be a useful indicator of sources of primary productivity in simple systems where at least two isotopically distinct sources are present (Hobson et al. 1995). Enrichment of ^{15}N occurs at a rate of approximately 2-4‰ of $\delta^{15}N$ with each step up in trophic level (Peterson & Fry 1987, Michener & Schell 1994, Post 2002), making it possible to model an organism's relative trophic position within a given ecosystem.

Stable isotope analysis (SIA) provides many benefits over traditional stomach content analysis: (1) it represents assimilated, not just ingested, prey items (Bearhop et al. 2004, Domi et al. 2005); (2) isotopic values represent long term feeding behaviors (from months to years depending on the tissue analyzed) (Domi et al. 2005, MacNeil et al. 2005, MacNeil et al. 2006); (3) sampling multiple tissues can provide distinct timeframes due to differences in tissue turnover rates (Kurle & Worthy 2002, MacNeil et al. 2005); and (4) samples from several different tissues can be obtained without the need to euthanize animals. Stable isotope analysis therefore provides a useful tool to investigate questions such as dietary resource partitioning within communal shark nursery areas.

While a number of SIA studies have been carried out on the structure of marine food webs (Hobson & Welch 1992, Michener & Schell 1994, Hobson et al. 2002), and focusing on specific teleost species (Thomas & Cahoon 1993, Das et al. 2000, Harvey et

, Cunjak et al. 2005, Perga & Gerdeaux 2005, Schlacher et al. 2005), little research has been published on SIA for sharks. These include a handful of field studies that focus on sharks and rays (Fisk et al. 2002, Estrada et al. 2003, Domi et al. 2005, MacNeil et al. 2005, Estrada et al. 2006, Kerr et al. 2006, McMeans et al. 2009), with only three laboratory studies: MacNeil et al. (2006) which assessed variable uptake and elimination of carbon and nitrogen isotopes in the tissues of freshwater ocellate river stingrays (*Potamotrygon motoro*); Hussey et al. (2010a) which looked at diet-tissue discrimination factors in large sharks held under semi-controlled conditions; and Logan and Lutcavage (2010) who investigated the effects of diet switching on captive sandbar sharks (*Carcharhinus plumbeus*).

This study utilized SIA of multiple tissues representing variable integration periods to assess the extent of dietary resource partitioning by seven of the most commonly occurring juvenile shark species, as well as three large predatory teleost species, within an established communal shark nursery area (Simpfendorfer & Milward 1993). The juvenile shark species examined were distributed throughout the nursery, displayed varying degrees of spatial and temporal overlap, and rarely left the nursery during early life (Chapter 6). Therefore, comparisons of stable isotope values between species were not compromised by spatial or temporal factors specific to any one section of the bay.

5.2 Materials and Methods

5.2.1 Study Site

Cleveland Bay is situated east Townsville on the north-east coast of Queensland, covering an area of approximately 225km² from 19°10 to 19°19'S to 146°50 to 147°01'E. For a detailed description of the bay please refer to section 3.1 of Chapter 3.

5.2.2 Field Sampling for Stable Isotope Tissues

Multiple tissue samples were collected from seven species of sharks and three species of teleost inhabiting Cleveland Bay during fisheries independent sampling trips from November 2008 to May 2010 (Table 5.1). While juvenile sharks of other species were caught during sampling, the seven species investigated here are the most likely species to use Cleveland Bay as a nursery based on their numerical dominance in the catch. Sampled animals were captured using longlines and gillnets deployed throughout the bay. For a detailed description of the construction and use of longlines and gillnets during this project please refer to sections 3.2.2 and 3.2.3 of Chapter 3. All captured shark and teleost species were identified, measured (total length: nose to tip of the upper lobe of the caudal fin), sexed, sampled for SIA (muscle and blood), tagged and released.

Table 5.1: Details of sampled animals used to examine stable isotope signatures of sympatric sharks and predatory teleost species in Cleveland Bay. Target size range is based on total length (CUS: closed umbilical scar) and was chosen to avoid juvenile sharks whose stable isotope values are confounded by maternal investment (Olin et al. 2011). All lengths are in mm with (± SD).

Species	n	# Males	# Females	Fork Length (mm)	Total Length (mm)	Target Size Range (mm)	Range of Capture Dates
Rhizoprionodon taylori	11	1	10	492 (± 24)	604 (± 28)	>400	15/04/2009 - 4/11/2009
Carcharhinus fitzroyensis	9	3	6	686 (± 135)	849 (± 155)	CUS-900	30/04/2009 - 28/02/2010
Carcharhinus macloti	10	10	0	642 (± 36)	794 (± 55)	CUS-800	3/11/2009 - 28/02/2010
Rhizoprionodon acutus	9	7	2	596 (± 77)	740 (± 88)	>700	14/04/2009 - 4/11/2009
Carcharhinus amboinensis	10	4	6	798 (± 155)	992 (± 178)	CUS-1200	17/04/2009 - 24/02/2010
Carcharhinus sorrah	9	8	1	795 (± 106)	1000 (± 102)	CUS-900	18/11/2008 - 6/11/2009
Carcharhinus limbatus/tilstoni	11	5	6	808 (± 132)	997 (± 153)	CUS-1000	31/03/2009 - 11/12/2009
Lates calcarifer	11	-	-	-	659 (± 86)	>600	1/09/2009 - 2/02/2010
Eleutheronema tetradactylum	11	-	-	478 (± 71)	582 (± 81)	>400	1/09/2009 - 2/03/2010
Scomberomorus queenslandicus	10	-	-	426 (± 49)	470 (± 55)	>400	5/25/2010

5.2.3 Stable Isotope Tissue Sampling, Preparation and Analysis

Tissues examined for SIA in this study included muscle, blood plasma, and red blood cells. These tissues were selected based on differences in their turnover rates which represent a broad feeding time scale (estimated number of days to 95% diet equlibrium for muscle=422 days, blood=265 days; MacNeil et al. 2006), their comparability with other studies, and ease of collection using minor invasive methods. Muscle tissue was extracted from just behind the first dorsal fin in sharks, and immediately adjacent to the dorsal fin in teleosts using a 4mm disposable biopsy punch. Blood was taken from the caudal vein just anterior to the tail in both sharks and teleosts using a heparinised needle and syringe. After collection blood samples were spun in a portable centrifuge in the field for approximately 90 seconds. Using an Eppendorf automatic 100-1000 µL pipette the resultant plasma and red blood cell layers were pipetted into individually labeled 3ml Eppendorf safe-lock microcentrifuge tubes. All samples were stored on ice during transport and immediately frozen (-20^{o}C) on return to the laboratory.

Tissue samples were collected from sharks and teleosts within a restricted size range. The lower limit for sharks was set at the size when the umbilical scar was completely healed to avoid the effect of maternal influence on stable isotope signatures of young animals (Hussey et al. 2010b, Vaudo et al. 2010, Olin et al. 2011). Maximum sizes for sampled sharks were based on sizes prior to maturity, to include only individuals likely to be using the habitat as a nursery. An exception to this maximum size limit was *R. taylori*, which attains maturity after one year and remains within nursery habitats throughout its life (Carlson *et al.* 2008). For this species any captured animals with healed umbilical scars were sampled. Teleost tissue samples were taken from the largest captured individuals of the target species in an effort to only sample individuals that have already shifted to a more piscivorous diets (Baker & Sheaves 2005). All tissue samples were freeze dried and then ground to a powder using hand-held polypropylene pellet pestles.

Within animal tissues, lipids are reportedly depleted in ^{13}C relative to proteins and carbohydrates (Post et al. 2007). Variations in lipid content among organisms and tissue types can potentially lead to more negative δ^{13}C values creating misleading stable isotope results unless corrected (Post et al. 2007). The focus of my study on comparing stable isotope values between sharks and teleosts inhabiting the same coastal environment necessitated the extraction of lipids in order to avoid this potential source of error. A collaborative work which provides a more through examination of the effects of lipid extract on shark tissue can be found in Appendix 1. All tissues were lipid extracted in the same manner (see below) and results are based on lipid extracted values.

Lipid extraction (LE) was undertaken following a modified Bligh & Dyer (1959) method. Powdered tissue samples were combined with 5ml of 2:1 chloroform-methanol then placed in a water bath (30° C) for 24 hours. Upon removal from the water bath, LE tissue samples were agitated for 30 seconds, centrifuged for 3 minutes, then decanted. A second addition of 5ml of 2:1 chloroform-methanol was then added followed by another round of agitating and centrifuging before the final decant. The resulting tissue pellet was left to dry overnight in a fume hood. Once dry, between 400-600 µg of the powered LE tissue sample was weighed out into tin capsules and both stable carbon and nitrogen isotope ratios and total percent carbon (C) and percent nitrogen (N) were determined by a continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA) equipped with an elemental analyzer (Costech, Valenica, CA, USA). Due to low percent carbon and nitrogen encountered when using LE plasma (Bailey McMeans, personal communication), 1,000-1,200 µg of LE plasma samples were used.

Stable isotope ratios are expressed in δ notation as deviations from standards in parts per thousand (‰) according to the following:

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

in which X is ^{13}C or ^{15}N, R_{sample} is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ and $R_{standard}$ represents the ratio for the respective standard. The standard reference material was Pee Dee Belemnite carbonate for CO_2 and atmospheric nitrogen for N_2. Replicate analyzes of NIST (National Institute of Standards and Technology) standard bovine muscle (NIST 8414, n = 67) and an internal lab standard (Tilapia, *Oreochromis niloticus*, muscle, n = 67) yielded a precision (i.e. one standard deviation) of 0.15‰ and 0.24‰ for $\delta^{15}N$ and 0.06‰ and 0.09‰ for $\delta^{13}C$, respectively.

5.2.4 Stomach Content Collection and Analysis

Concurrent to the fisheries independent sampling for stable isotopes a number of fisheries dependent observer trips were conducted to gather stomach content data from sharks captured aboard commercial fishing boats operating in the Queensland inshore gillnet fishery. Stomach contents were used to complement stable isotope findings by identifying important prey categories as well as to reinforce assessments of generalist or specialist feeding strategies identified via variations in mean isotopic values. Stomach contents were removed from landed sharks and stored frozen for transportation. In the laboratory, stomach contents were washed over a sieve, identified to the lowest possible taxonomic level, counted, weighted, assessed for digestive state [(0-4) with higher numbers indicating a more digested state], and total length measured to the nearest millimeter. Diet composition was analyzed using the percent Index of Relative Importance (%IRI) (Pinkas et al. 1971), which combines three quantitative measurements: percent frequency ($\%F_o$), percent number ($\%N_c$) and percent weight ($\%W_c$).

$$\%IRI = (\%N_c + \%W_c)\%F_o$$

By expressing IRI values as a percentage (%IRI), values between individual prey groups are standardized (Cortés 1997). %IRI values were compared to SIA data to confirm conclusions derived from the nursery assemblage stable isotope profiles.

5.2.5 Statistical Analysis

Least squares linear regressions were used to assess the effect of increasing shark body size on $\delta^{15}N$ and $\delta^{13}C$ values to ensure that body size was not the driving force behind species-specific variations in stable isotope values. For $\delta^{13}C$ and $\delta^{15}N$ values, isotope bi-plots were graphed for all ten species (seven shark and three teleost) to show the range of values displayed within the Cleveland Bay community. Data were normally distributed and so a factorial MANOVA was used to asses if the differences between species and sample tissue types were significant, and univariate analysis was used to test if differences were significant for either carbon or nitrogen separately across all examined species and tissue types. A Post hoc Tukey's HSD test for homogenous groups was undertaken to establish groupings of species which showed statistically significantly different carbon or nitrogen values (Cherel et al. 2008).

5.3 Results

Over 300 tissue samples were collected and analyzed for stable isotopes from 101 captured individuals (69 sharks, 32 teleosts), across ten species. Capture locations ranged across Cleveland Bay and other than *L. calcarifer*, examined species were not found exclusively in any one area. Least square linear regressions found that $\delta^{15}N$ and $\delta^{13}C$ values did not vary systematically with total length for any of the seven sampled shark species (Table 5.2a-c), identifying that there was no confounding species-specific effect of size on $\delta^{15}N$ or $\delta^{13}C$ values. Data from tag recapture and fisheries independent catch (Chapter 6), as well as passive acoustic monitoring (Simpfendorfer, C.A., unpublished data) collected concurrent to stable isotope samples, identified patterns of continued residency in Cleveland Bay during early life stages of examined species. Each species was therefore considered as a homogeneous group with tissue stable isotope values representative of their diet in the nursery habitat of Cleveland Bay.

Table 5.2a-c: Results summary of linear regressions examining the effect of size on $\delta^{15}N$ and $\delta^{13}C$ values.

a) Muscle

Species	$\delta^{15}N$			$\delta^{13}C$		
	r	p	Slope	r	p	Slope
R. taylori	0.468	0.204	0.010	-0.099	0.818	-0.003
C. fitzroyensis	0.336	0.416	0.001	-0.353	0.391	-0.001
C. macloti	-0.335	0.345	-0.002	-0.577	0.333	-0.003
R. acutus	-0.586	0.097	-0.002	0.613	0.079	0.005
C. amboinensis	-0.629	0.051	-0.002	0.358	0.31	0.003
C. sorrah	0.606	0.063	0.003	0.373	0.289	0.005
C. limbatus/tilstoni	-0.484	0.132	-0.003	-0.028	0.934	0.000

b) Plasma

Species	$\delta^{15}N$			$\delta^{13}C$		
	r	p	Slope	r	p	Slope
R. taylori	0.086	0.801	0.001	-0.004	0.991	0.000
C. fitzroyensis	0.438	0.238	0.001	0.178	0.648	0.001
C. macloti	-0.615	0.058	-0.003	0.634	0.067	0.010
R. acutus	-0.230	0.552	-0.001	-0.319	0.403	-0.002
C. amboinensis	-0.259	0.471	-0.001	0.512	0.130	0.003
C. sorrah	0.481	0.159	0.002	0.288	0.453	0.002
C. limbatus/tilstoni	-0.549	0.080	-0.003	0.062	0.855	0.000

c) Red Blood Cells

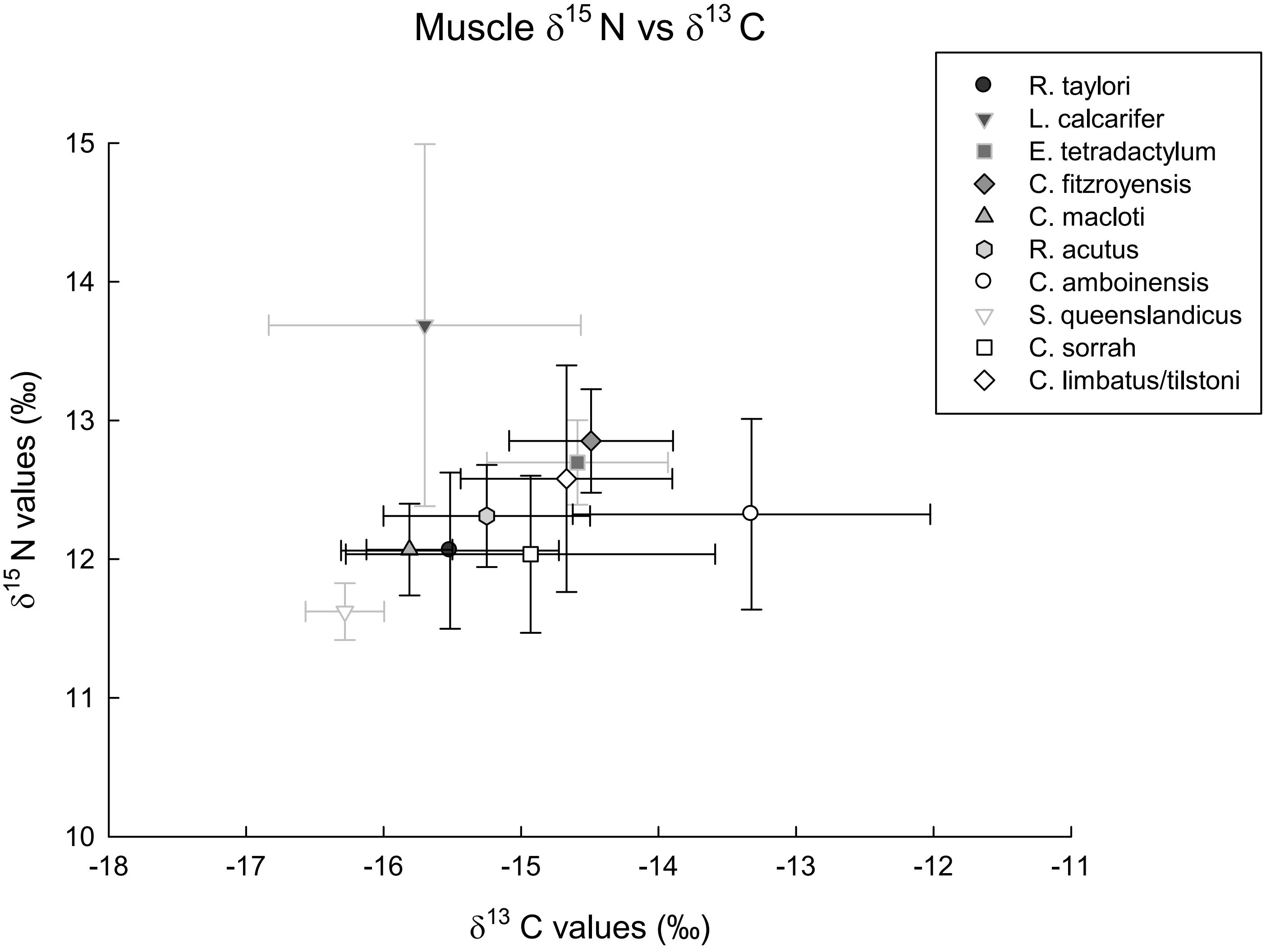
Species	$\delta^{15}N$			$\delta^{13}C$		
	r	p	Slope	r	p	Slope
R. taylori	0.165	0.628	0.002	-0.242	0.474	-0.001
C. fitzroyensis	0.359	0.342	0.001	0.059	0.88	0.000
C. macloti	-0.390	0.265	-0.002	-0.526	0.119	-0.003
R. acutus	0.268	0.486	0.001	-0.175	0.653	-0.001
C. amboinensis	-0.209	0.563	0.000	0.192	0.594	0.001
C. sorrah	0.050	0.897	0.000	0.489	0.266	0.007
C. limbatus/tilstoni	-0.383	0.245	-0.001	-0.150	0.66	-0.001

5.3.1 Sympatric Shark and Predatory Teleosts Species Stable Isotope Values

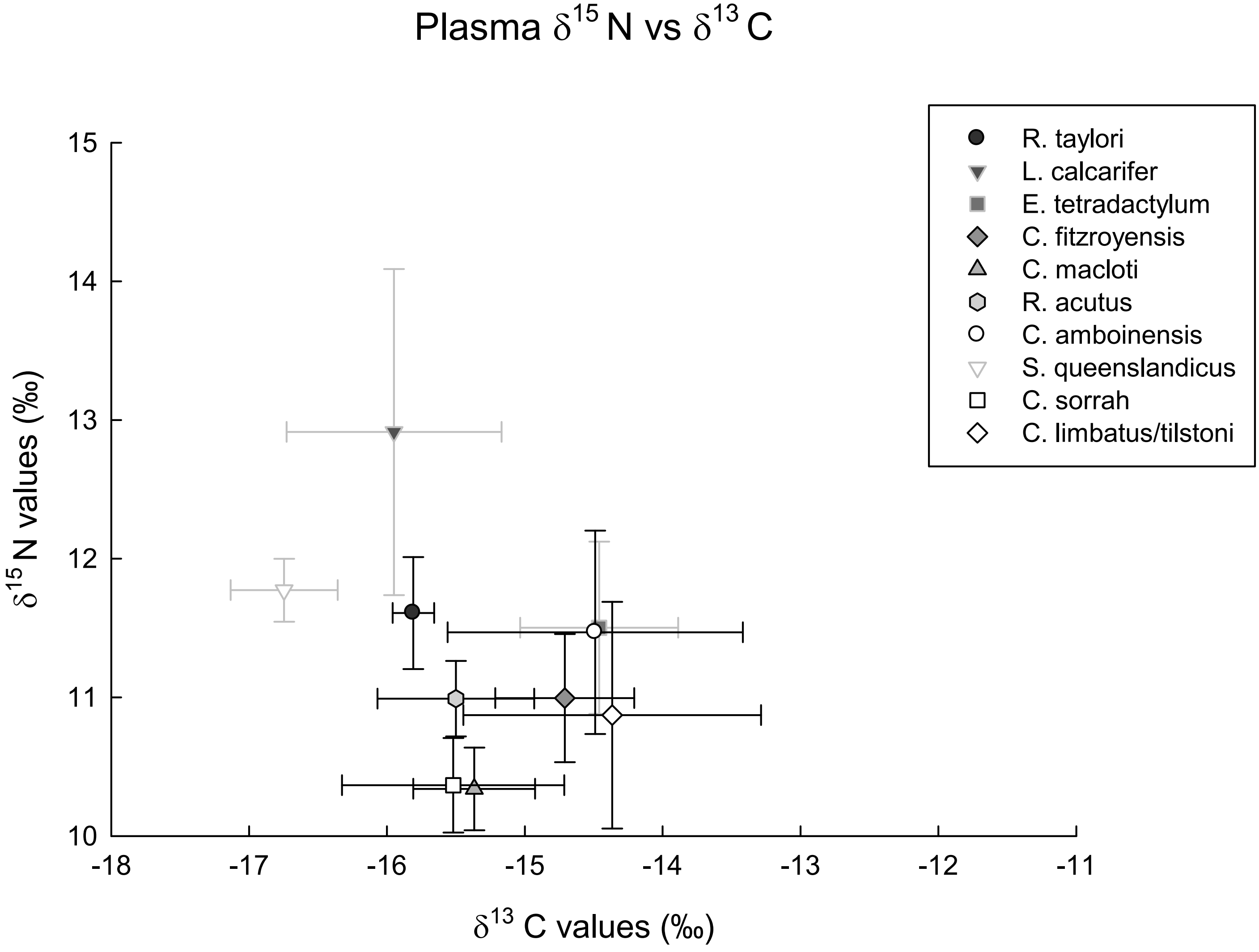
Average $\delta^{13}C$ values spanned a wide range (-13.3 ‰ to -17.1 ‰) across predator species of Cleveland Bay (Figure 5.1a-c, Appendix 2), indicating a broad prey base supported by a number of carbon sources. Variance of $\delta^{13}C$ means for individual species was diverse and varied by tissue type. Some species displayed high variance across multiple tissue types, such as *Carcharhinus amboinensis* and *Carcharhinus limbatus/tilstoni*, while other species, such as *Rhizoprionodon taylori*, showed minimal variance (Figure 5.1a-c, Appendix 2). Species with highly variant carbon values were likely feeding on multiple carbon sources while species with tighter carbon values most likely specialize on a smaller number of prey items (Layman et al. 2007, Newsome et al. 2009).

Values of $\delta^{15}N$ had a smaller range of average species values than $\delta^{13}C$ for all tissue types examined (from 10.3 ‰ to 13.7 ‰) (Figure 5.1a-c, Appendix 2), indicating that species in the bay were feeding on a wide range of prey species which likely occupy a similar trophic position with similar $\delta^{15}N$ values. Variance in $\delta^{15}N$ values for all tissue types was highest for *Lates calcarifer*, while species such as *Carcharhinus sorrah* and *Scomberomorus queenslandicus* showed the least variance (Figure 5.1a-c, Appendix 2). Similar to carbon, highly variant nitrogen isotope values indicated that a species diet was more diverse than a species with a less varied value.

a).


Muscle δ^{15}N vs δ^{13}C
R. taylori
L. calcarifer
E. tetradactylum
C. fitzroyensis
C. macloti
R. acutus
C. amboinensis
S. queenslandicus
C. sorrah
C. limbatus/tilstoni
δ^{15}N values (‰)
15
14
13
12
11
10
-18
-17
-16
-15
-14
-13
-12
-11
δ^{13}C values (‰)

b).


Plasma δ^{15}N vs δ^{13}C
R. taylori
L. calcarifer
E. tetradactylum
C. fitzroyensis
C. macloti
R. acutus
C. amboinensis
S. queenslandicus
C. sorrah
C. limbatus/tilstoni
15
14
13
12
11
10
δ^{15}N values (‰)
-18
-17
-16
-15
-14
-13
-12
-11
δ^{13}C values (‰)

c).

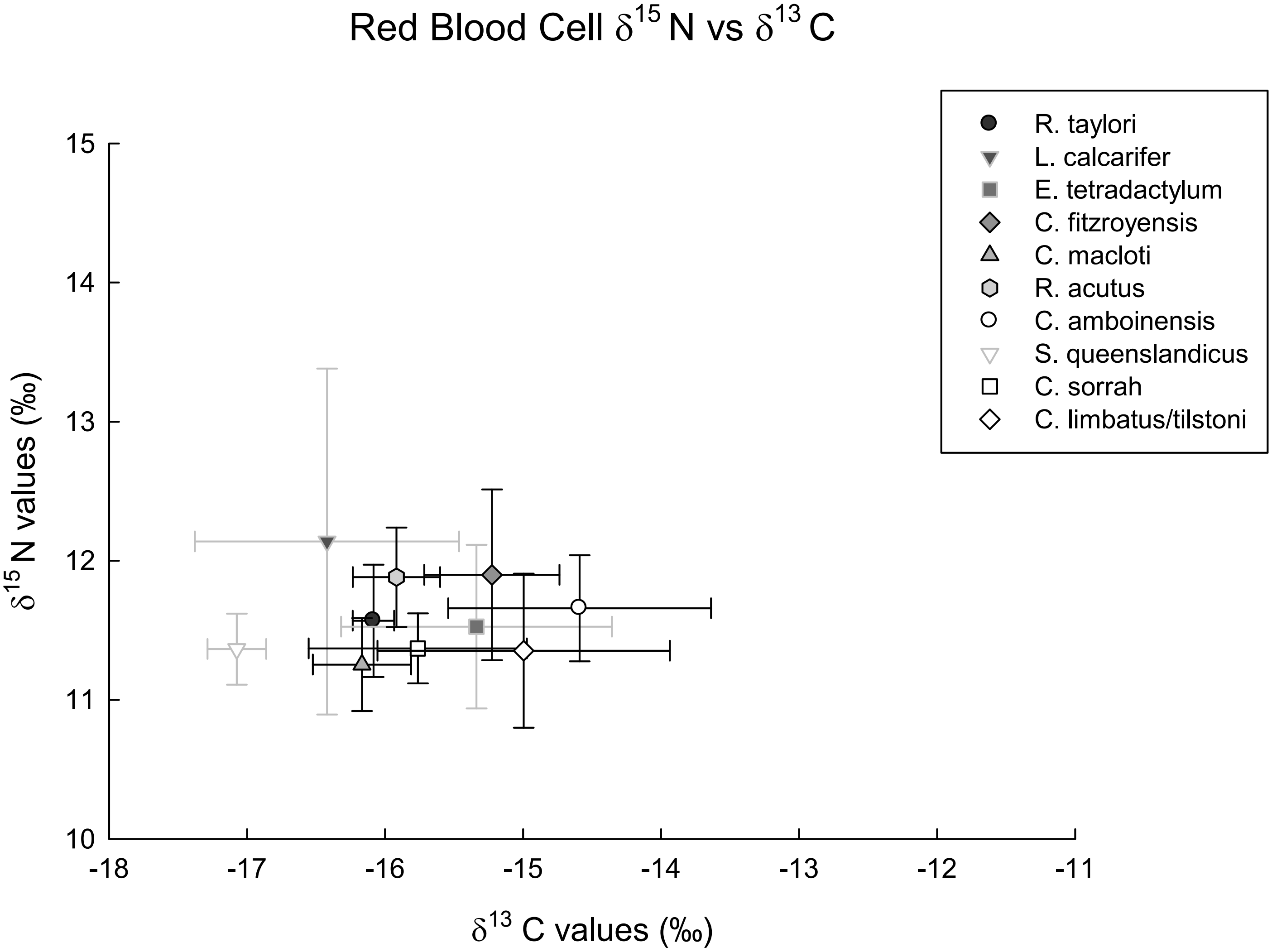

Red Blood Cell δ^{15}N vs δ^{13}C

Figure 5.1a-c: Mean (± SD) of all species δ13C and δ15N. Symbols with gray lines indicate teleost species.

All seven sympatric shark species and three predatory teleost species from Cleveland Bay showed statistically significant differences in their overall isotopic values (MANOVA, Wilks' lambda, $F_{18,542} = 21.65$, $p < 0.0001$), as did all tissue types ($F_{4,542} = 59.79$, $p < 0.0001$). In univariate analyzes, both δ^{13}C ($F_{9,272}= 22.11$, $p < 0.0001$) and δ^{15}N ($F_{9,272} = 17.60$, $p < 0.0001$) values were significantly different between all examined species, as were $\delta^{13}C$ ($F_{2,272}$ = 19.59, $p < 0.0001$) and $\delta^{15}N$ ($F_{2,272}$ = 83.10, $p < 0.0001$) values for all tissue types.

Post-hoc Tukey's HSD test for homogenous groups broke the ten species into five groups for $\delta^{13}C$ means, and three groups for $\delta^{15}N$ means (Table 5.3a-b). The $\delta^{13}C$ groups showed some overlap, which was to be expected considering the observed range of $\delta^{13}C$ standard deviations (Table 5.3a). *Scomberomorus queenslandicus* and *L. calcarifer* formed the smallest group. Overlap in the remaining four groups was largely attributed to two species, *Carcharhinus fitzroyensis* and *C. sorrah*, which displayed broad $\delta^{13}C$ values. This indicated that the diet of these two species was more generalized allowing them to bridge three of the four remaining groups. *Lates calcarifer*, *R. taylori*, *Carcharhinus macloti*, and *Rhizoprionodon acutus* formed one group (Table 5.3a: Group 1), while *Eleutheronema tetradactylum*, *C. limbatus/tilstoni* and *C. amboinensis* formed another (Table 5.3a: Group 2). The remaining two groups were composed of the two bridging species (*C. fitzroyensis* and *C. sorrah*), along with two minor bridging species, *R. acutus* and *E. tetradactylum*, whose $\delta^{13}C$ values spanned across two groups (Table 5.3a: Groups 3-4). Of the three teleost species, only *S. queenslandicus* separated completely from the seven shark species. These post-hoc groups showed that sharks in Cleveland Bay displayed a wide range of $\delta^{13}C$ values, but within that range there were distinct species assemblages supported by different primary carbon sources, while a few species exploited a wide range of carbon sources.

Table 5.3a-b: Results of post hoc Tukey's HSD test for homogenous groups: a) Shark and teleost species grouped by mean δ^{13}C values, indicating the range of exploited carbon sources, b) Shark and teleost species grouped by mean δ^{15}N values, identifying trophic level differences between species. Groupings based on mean values across all sampled tissue types.

a)

Species	δ^{13} C Mean	Group 1	Group 2	Group 3	Group 4	Group 5
S. queenslandicus	-16.7					****
L. calcarifer	-16.0	****				****
R. taylori	-15.8	****				
C. macloti	-15.6	****				
R. acutus	-15.6	****		****		
C. sorrah	-15.4	****		****	****	
C. fitzroyensis	-14.8		****	****	****	
E. tetradactylum	-14.8		****		****	
C. limbatus/tilstoni	-14.7		****			
C. amboinensis	-14.1		****			

b)

Species	δ^{15} N Mean	Group 1	Group 2	Group 3
C. macloti	11.2		****	
C. sorrah	11.3		****	
C. limbatus/tilstoni	11.6	****	****	
S. queenslandicus	11.6	****	****	
R. acutus	11.7	****	****	
R. taylori	11.7	****	****	
C. amboinensis	11.8	****		
C. fitzroyensis	11.9	****		
E. tetradactylum	11.9	****		
L. calcarifer	12.9			****

The post hoc Tukey's HSD test for homogenous groups of δ^{15}N values separated the ten species into three groups with considerable overlap (Table 5.3b). The first group contained all shark species except *C. macloti* and *C. sorrah*, and all teleost species except *L. calcarifer* (Table 5.3b: Group 1). The second group was similar to group one except that it included *C. macloti* and *C. sorrah* while eliminating *C. amboinensis*, *C. fitzroyensis*, and *E. tetradactylum* (Table 5.3b: Group 1). The third and final group contained only *L. calcarifer* (Table 5.3b: Group 3). These δ^{15}N groupings indicated that the examined species in Cleveland Bay showed a high degree of overlap in δ^{15}N values which was not surprising considering the range of nitrogen values across all species and tissue types was only 3.4‰ (Figure 5.1a-c), while trophic levels are typically separated by between 2-4‰.

5.3.2 Index of Relative Importance Profiles

A total of 742 stomachs were collected and examined from five shark species for which I also collected stable isotope samples and that fell within my defined size parameters. The %IRI calculations revealed a wide array of prey items in the diet of all species, however individual species displayed more specialized diets then others (Appendix 3). *Rhizoprionodon acutus*, *C. sorrah*, and *C. limbatus/tilstoni* all displayed broad δ^{13}C values and each fed on a wide variety of prey categories; *R. acutus* (13), *C. sorrah* (17), and *C. limbatus/tilstoni* (12, Appendix 3). In contrast, *R. taylori* which showed little variation in δ^{13}C values also had a small number of prey categories in its stomach contents (accepting the low sample size for this species) with only six identified categories (Appendix 3).

5.4 Discussion

The results of my study provide quantitative evidence of dietary resource partitioning among young sharks of several species within a communal nursery area. What was once considered an environment with abundant dietary resources with limited resource partitioning appears instead to be a competition rich area where young sharks partition resources amongst themselves, as well as other predatory teleost species. Highly clustered $\delta^{15}N$ species values indicated that both the juvenile sharks and teleosts in the bay were feeding at similar trophic positions. However, the range of $\delta^{13}C$ values among species indicated that within that trophic level there were several different source pathways with distinct carbon signatures. Differences in the variance of $\delta^{15}N$ and $\delta^{13}C$ means among species also indicated that certain sharks and teleosts displayed a more generalist diet, while others were more specialized, providing yet another possible avenue by which dietary resources could be partitioned. The $\delta^{15}N$ and $\delta^{13}C$ values of some teleost species overlapped with the seven shark species, suggesting that these teleosts are a source of potential competition in addition to the inter- and intra-specific competition among sharks. This added competitive element may make niche partitioning, at least in terms of dietary resources, a more advantageous option for young sharks.

The $\delta^{15}N$ values of young sharks in Cleveland Bay were highly clustered, ranging only ~ 3.6‰ across all tissue types (with 2-4‰ the difference between trophic levels) indicating that these sharks were all feeding within the same trophic level. The $\delta^{15}N$ values of two of the sampled predatory teleost species, *E. tetradactylum* and *S. queenslandicus*, displayed overlap in $\delta^{15}N$ values with sharks in the bay indicating that these species were likely feeding within the same tropic guild. Only *L. calcarifer* differed significantly from the examined sharks, displaying an inflated $\delta^{15}N$ value which may indicate feeding at a higher trophic level, or may simply be a reflection of the lower diet tissue discrimination factor of sharks [2.3‰ (Hussey et al. 2010a)] compared to teleosts [3.0‰ (Vanderklift &

) or ~2.5‰ (Caut et al. 2009)]. A further explanation for the enriched $\delta^{15}N$ values of *L. calcarifer* could be due to a unique feature of their capture location. All sampled *L. calcarifer* were captured on the sand flats adjacent to the discharge point of a tertiary treated sewage pipe at the southern end of the bay. *Lates calcarifer* found on the flats display little movement out of the area based on findings from tracking work (Amos Maplestone, personal communication). The enrichment of localized food sources and the limited movements displayed by *L. calcarifer* in the area likely result in the observed high $\delta^{15}N$ values for this species (Schlacher et al. 2005). Apart from *L. calcarifer*, few sharks were captured near this discharge point despite extensive fishing efforts in the area, and none were found to reside in the area over extended periods (Chapter 6).

Tukey's HSD test for homogenous groups separated the examined species into only three groups based on $\delta^{15}N$ values. The overlap between these groups was extensive, with *L. calcarifer* the only species that displayed significantly different values. Based on $\delta^{15}N$ values alone, the dietary overlap of juvenile sharks and predatory teleosts may be high in communal shark nursery areas such as Cleveland Bay. Stable isotope studies on coexisting teleost species have found similar results with $\delta^{15}N$ values indicating feeding within a single trophic level (Thomas & Cahoon 1993, Paterson & Drouillard 2006). These results also agree with the prevailing communal nursery area research that suggests high dietary overlap among sharks based on stomach content analysis (Castro 1993, Simpfendorfer & Milward 1993).

The $\delta^{13}C$ values of the sharks and teleosts covered a similar range to $\delta^{15}N$ of ~ 3.8‰ across all tissue types, but because $\delta^{13}C$ has a smaller diet tissue discrimination value $\delta^{13}C$ results indicate several primary carbon sources were exploited by the study species. Three of the five groups identified by the post hoc Tukey's HSD test for homogenous groups displayed minimal overlap while the remaining two groups contained species whose values bridged between groups. The broad range of $\delta^{13}C$ values displayed across all species, as well as the five groups identified in the Tukey's test, provide strong evidence in favor of a nursery environment that is partitioned in terms of basal dietary resources. This is in agreement with stable isotope studies on coexisting teleost species which found similar $\delta^{15}N$ values, but variable $\delta^{13}C$ values which were attributed to resource partitioning between species occupying similar trophic positions in the same habitat (Nagelkerken & van der Velde 2004, Paterson & Drouillard 2006). Thomas & Cahoon (1993) investigated five species of reef-associated teleosts and found that while each of the species seemed to occupy the same trophic position, their $\delta^{13}C$ values indicated at least two supporting trophic pathways, one planktonic and the other benthic.

My results, indicating a wide range of $\delta^{13}C$ values among my study species, conflicts with the established communal shark nursery area paradigm (Simpfendorfer & Milward 1993). Instead of an environment where resource partitioning is limited due to abundant resources, my findings indicated that young sharks in communal nursery areas partition the resources of the area amongst themselves as well as other predatory species such as large teleosts. This suggests that food resources may not be as abundant as was once thought and that resource partitioning is a strategy employed to reduce competition. My findings, along with other recent research on communal shark nursery areas [e.g. Bethea et al. (2004) who similarly suggest that juvenile sharks within nursery areas may be partitioning resources on both temporal and spatial scales], further strengthen the claim that the prevailing shark nursery area paradigm—whether applied to single species or communal shark nursery areas—is outdated and no longer fits much of the current data.

The variance in δ^{13}C values displayed by some species possibly indicates another approach to dietary niche separation employed by sharks and teleosts in Cleveland Bay. Species which had more variable δ^{13}C values, such as *L. calcarifer*, *R. acutus*, *C. sorrah*, C. amboinensis, and C. limbatus/tilstoni, are potentially feeding on a wide variety of prey species, typifying a more generalist diet (see Wetherbee et al. 1990 for a review of shark feeding strategies). This feeding strategy enables these species to exploit a variety of food sources opportunistically. Alternatively, species such as *S. queenslandicus*, *R. taylori*, and *C. macloti* exhibited lower variation in δ^{13}C values indicating that these species were likely feeding on a more specialized diet. This may allow them to avoid or reduce competitive interactions by specializing on a small number of prey species that can be exploited more successfully than their potential competitors (Mihuc 1997), or focus on more abundant prey species for which competition is lower, or it may be as a result of being outcompeted necessitating feeding on non preferred prey items (Baird et al. 1992). However, caution is warranted when using variation around stable isotope means as a measure of generalist versus specialist feeding strategies. Although, this methods potential has been discussed (Bearhop et al. 2004), variation in consumers stable isotope values could be driven by variation at the prey level. I used stomach contents to deal with this issue, which is discussed below.

Values of %IRI serve to validate the division of examined sharks into these groups by providing a quantitative number of prey groups for each species. Groups of generalist and specialist species identified by the two methods agree well for all species except *C. amboinensis*. *Carcharhinus amboinensis* exhibit some of the more varied $\delta^{13}C$ values among examined shark species; however, stomach content analysis revealed only six prey categories (accepting the low sample size for this species), about half the number of categories compared to other species classified as generalists (*R. acutus*, *C. sorrah*, and *C. limbatus/tilstoni*) (Appendix 3). Only when examined more closely do these findings reveal the nature of *C. amboinensis* diet. In contrast to the other shark species which typically feed on relatively similar prey items (teleosts from families including Clupeidae, Mullidae, and Leiognathidae), *C. amboinensis* feed on a wide range of prey, from teleost families (Engraulidae and Polynemidae), to sea snakes (Hydrophiidae), and other sharks (Carcharhinidae). These prey may occupy similar trophic positions during certain periods of their lives but are likely supported by different primary carbon sources. In essence, *C. amboinensis* exhibit a generalist $\delta^{13}C$ signature but are actually feeding on relatively few prey items that are isotopically dissimilar, making it more likely that this species is a specialist predator despite its varied $\delta^{13}C$ values. It would be easy to assume that with highly varied $\delta^{13}C$ values a species is likely feeding on a number of prey items and is probably a generalist. However, as shown, this one dimensional approach can be misleading and it is important to validate stable isotope results whenever possible with stomach content data.

Despite the utility of my SIA approach to questions of shark nursery area feeding strategies, this method does have a limitation. The persistence of stable isotope values from adult females in their young precludes the sampling of neonates, preventing the exploration of dietary resource partitioning among the youngest animals in the nursery. However, feeding success in these neonate sharks is generally low, as demonstrated by measured weight loss in young sharks (Duncan & Holland 2006) attributed to the utilization of parental reserves stored in their livers (Hussey et al. 2010b). This would mean that results gathered from neonate animals would be unlikely to reveal dietary resource strategies which relate to competition or resource partition in the nursery. Additional drawbacks include identifying accurate levels of nitrogen fractionation, and different diets leading to similar stable isotope values, or vice versa. With further study these issues can be resolved, however, until then, it is important to recognize these limitations when considering conclusions derived from stable isotopes.

5.5 Conclusion

Stable isotope analysis is a powerful tool that can greatly improve our understanding of ecological communities. Through comparing the stable isotope values of multiple tissues within variable integration periods from multiple shark and teleost species within a known communal shark nursery I was able to elucidate important information on species resource partitioning strategies. Understanding how different species utilize the dietary resources within important habitats such as nursery areas is a key component in identifying how best to manage and protect these areas (Heithaus 2007).

Nursery area management, if implemented properly (Heupel et al. 2007, Kinney & Simpfendorfer 2009), has the potential to be a powerful tool for shark conservation. Future investigations into nursery areas, that incorporate SIA, could provide more detailed knowledge about inter- and intra-species resource use which is often missing from current management efforts. Coupling this technique with investigations of other resource use strategies within a nursery, such as temporal or spatial habitat usage, could greatly improve our understanding and ability to mange these environments. This knowledge would be particularly valuable to inform management of communal nursery areas in order to provide strategic protection for multiple co-occurring shark species while avoiding the need to protect vast coastal stretches.

6 Chapter 6.

Spatial and Temporal Segregation Among Sympatric Shark Species in a Communal Shark Nursery

---

6.1 Introduction

The segregation of populations based on age class has been observed for a large number of marine species (Robertson & Duke 1987, Blaber et al. 1995, McCandless et al. 2007). Typically this separation allows for the exploitation of different food sources or habitat types, offering potential benefits to growth, fitness, protection from predation, or a myriad of other factors (Beck et al. 2001). Many shark species in particular display such separation, with juveniles segregating into early life habitats often labeled as nursery areas (McCandless et al. 2007). The original hypothesis of shark nurseries revolved around three central concepts: 1) adult males rarely, if ever, enter the nursery areas of their own species; 2) mature females only enter nursery areas when they are gravid and at full term, and stop feeding once they reach the nursery grounds; and 3) food is not a limiting factor for young sharks within the nursery (Springer 1967). In essence, a nursery area used by a single shark species was assumed to represent that species' fundamental niche during the nursery-utilizing period of its life; (i.e. the entire environmental range that the species is capable of utilizing in the absence of competition) (Hutchinson 1957). Over the years, the original hypothesis of nursery area dynamics has been altered and expanded in order to keep pace with new scientific findings. Most recently, Heupel et al.

(2007) developed stricter criteria for defining an area as a shark nursery in an attempt to mitigate concerns that, with the designation of so many areas as nurseries, taking measures to protect such habitats would mean the management of excessively vast coastal stretches. Additionally, concerns over the effectiveness of conservation efforts focused on nursery areas have arisen due to evidence suggesting that the protection of later life stages may be more critical in terms of population recovery (Kinney & Simpfendorfer 2009). This is not to suggest that nursery areas don't have a role in the recovery of shark populations, but rather that more appropriate nursery area research and management strategies are needed in order to integrate these habitats into a more viable approach to shark conservation.

One particular area of shark nursery area research that has received little attention is that of *communal* shark nurseries. Originally defined in the literature by Simpfendorfer and Milward (1993), communal nursery areas are discrete nurseries where the young of multiple shark species reside while feeding and growing to maturity. Simpfendorfer and Milward's conception of communal nurseries stipulated a resource rich area which lacked competition between resident species or predation from adult sharks that avoid the area due to the presence of their own juveniles. Thus, much like the prevailing single species shark nursery area hypothesis, communal shark nurseries were assumed to represent the fundamental niche of all resident juvenile shark species. However, these conclusions were based principally on the analysis of stomach contents which identified broad dietary overlap, and the predominance of juveniles in gillnet catches. Since this original work, few studies have directly investigated the potential niche partitioning strategies of shark communities inhabiting communal nurseries, with only a handful looking at habitat partitioning (Michel 2002, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008) and even fewer focused on dietary resource partitioning (Bethea et al. 2004, White et al. 2004). Other studies have also unintentionally identified communal shark nursery areas (McCandless et al. 2007, Froeschke et al. 2010a) but were not focused on understanding how the areas functioned as communal nurseries. Nonetheless, these studies have begun to alter our understanding of communal shark nurseries and the shark species residing within them.

Communal nursery areas have potential as conservation habitats where management could benefit several shark species in one area, possibly reducing the need for costly widespread conservation efforts across multiple single-species nurseries. Limiting the resources required to manage shark nursery areas would allow for greater resources to be directed at later life stages while engendering a more comprehensive approach to shark management. This spread of conservation strategies is crucial for maintaining, and in some cases recovering, shark stocks around the world (Kinney & Simpfendorfer 2009). However, while communal nurseries represent an alluring alternative in shark nursery conservation, we still know very little about the ecology of these areas.

If communal nursery areas are to be considered as an alternative to single species nursery protection, it will be valuable to have a better scientific understanding of how several species are able to use the same nursery environment, and whether resources really are abundant enough to negate competition, as was suggested by the original communal nursery area hypothesis. I hypothesized that counter to the established hypothesis (Simpfendorfer & Milward 1993), young sharks within communal nursery areas do display, to differing extents, patterns of spatiotemporal resources partitioning. In other words, the original assessment of communal nursery areas representing the fundamental niche of resident juvenile species it is more likely that due to resource partitioning strategies young sharks within communal nursery areas are more likely inhabiting their realized niche, i.e. the part of the fundamental niche in which a species actually occurs as a result of competition (Hutchinson 1957). Additionally, I propose that if adult sharks are present within communal nurseries overlap between the realized niches of adults and juveniles of the same species will be low potentially due to several factors including food-risk tradeoffs exercised by juveniles (Heupel & Hueter 2002, Heithaus 2004, Heupel et al. 2007), and dilution (Connell 2000) due to the greater number of juvenile sharks able to inhabit a communal nursery which is partitioned into a number of realized niches. The results of this study can help to provide a greater understanding of communal shark nursery dynamics which may be useful in the management and conservation of nursery-utilizing shark species.

6.2 Materials and Methods

6.2.1 Study Site

Cleveland Bay lies just off of Townsville on the north-east coast of Queensland, covering an area of approximately 225km² from 19°10'S to 19°19'S and from 146°50'E to

147°01'E (Figure 6.1). For a detailed description of the bay please refer to section 3.1 of Chapter 3.

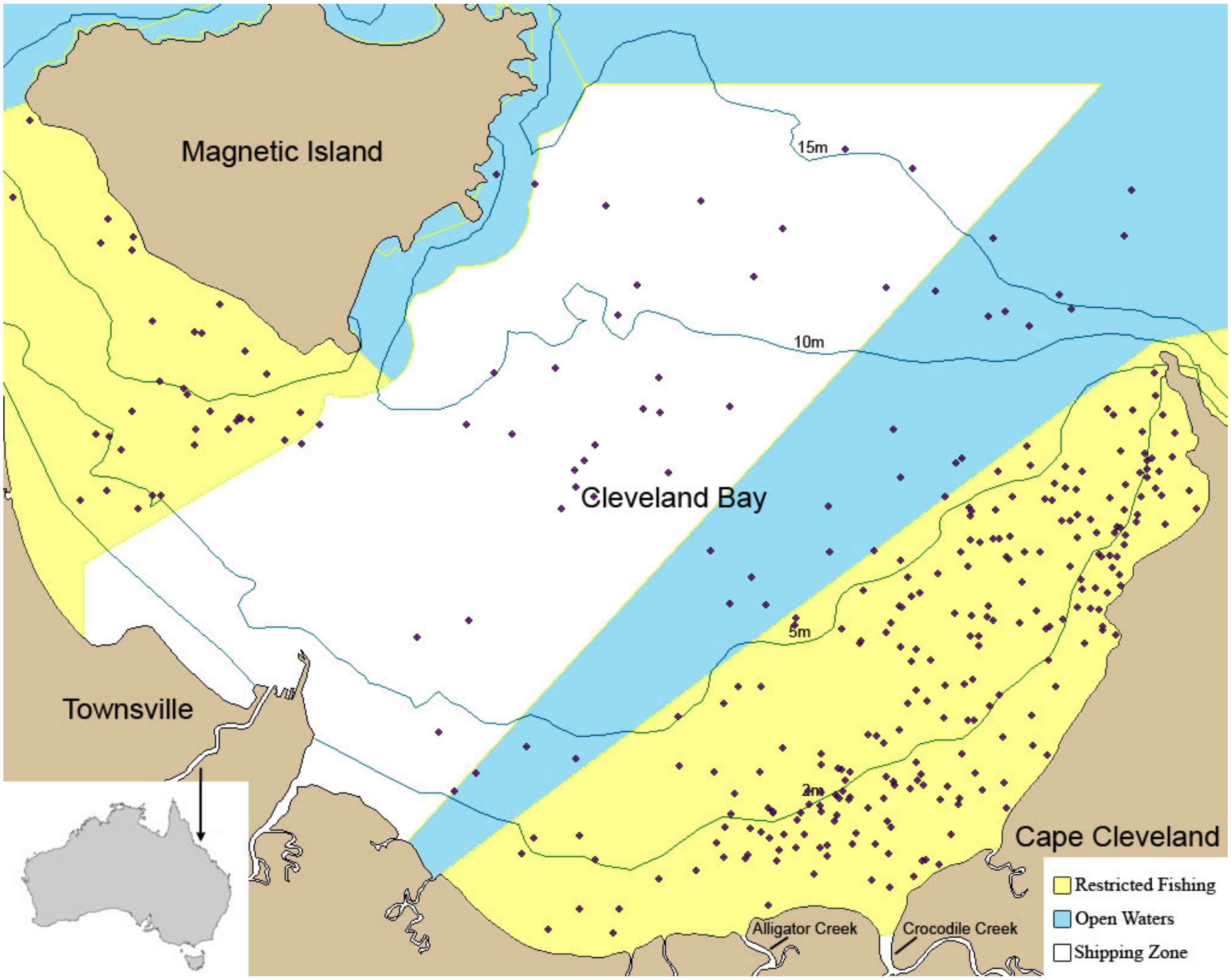


Figure 6.1: Map of Cleveland Bay with GBRMPA Conservation Park Zones marked in yellow, Townsville shipping channel in white, and isobaths delineated at 2, 5, 10, and 15 meters. Dots represent locations where longlines were deployed during the project**.**

6.2.2 Sampling

Nine of the most commonly captured shark species, mainly from the families Carcharhinidae and Sphyrnidae, were collected from the waters of Cleveland Bay from January 2008 to December 2009, using longlines in depths from less then one meter to more then fifteen meters. For a detailed description of the construction and use of longlines during this project please refer to section 3.2.2 of Chapter 3.

All captured sharks were identified to species, measured (precaudal length (PCL): nose to precaudal notch; fork length (FL): nose to caudal fin fork; and stretched total length (STL): nose to tip of the upper lobe of the caudal fin), sexed, tagged with a plastic Rototag through the first dorsal fin and released.

6.2.3 Catch Per Unit Effort Weighted 95% Kernel Densities

Set locations were recorded as the midpoint for each logline and plotted using ArcGIS 9.3. Catch per unit effort (CPUE) for each species was calculated for each recorded set location using 100 hook hours as the standard effort unit for CPUE calculations. The catch of each species was then split into mature and immature individuals and CPUE was determined for each. *Carcharhinus amboinensis* were the only exception because only one individual above this species' size at maturity was captured during the project and so analysis of adult CPUE was excluded (Figure 6.2f). For males, maturity status was assessed directly by observing presence or absence of calcified claspers—animals with non-calcified or only partially calcified claspers were identified as juveniles, while calcified claspers identified adults. Female maturity status was assessed based on measured total body lengths compared to estimates from sizes at maturity drawn form the literature (Stevens & Wiley 1986, Stevens & McLoughlin 1991, Compagno et al. 2005). Sampled blacktip sharks could have been either of the two species known to inhabit the study area (*Carcharhinus limbatus* or *Carcharhinus tilstoni*). Differentiating between the two species in the field was extremely difficult as the only established differences are the number of vertebrae and specific genetic disparities (Lavery & Shaklee 1991). For this paper size at maturity for *C. tilstoni* was used due to the dominance of this species in subsampled vertabr counted catch.

Individual capture locations were unsuited to assessments of species spatial usage scales and degrees of overlap. Kernel densities facilitated the conversion of capture locations points to polygons thus assisting in the assessment of individual species spatial properties. Kernel density estimates were calculated from the CPUE weighted catch locations for the juveniles and adults of each study species resulting in a utilization distribution (Van Winkle 1975) for each. Utilization distributions were used to create 95% kernel density to identify areas within the study site which represent the main areas used by a given species and maturity state. A smoothing factor of 400 meters was used for kernel density estimates since all set locations were midpoints with 400 meters of longline extending out from them. Estimated 95% kernel densities were mapped using Hawth's Tools in ArcGIS. Once mapped, the areas covered by each species' 95% kernels (km^2) were calculated, as was the percent overlap with every other species. Percent overlap values were divided into three categories: low (0 – 33% overlap), moderate (34 – 66% overlap), and high (67-100% overlap).

6.2.4 Drivers of Species Occurrence and Distribution

Individual species distributions were analyzed for their relationship to select predictors using boosted regression trees (BRT). Nine predictors (Table 6.1) were selected for their likely functional relevance to the distribution of shark species. Selection of variables was influenced in part by previous work using BRT to identify relevant factors to the distribution of several shark species (Froeschke et al. 2010a). Salinity and temperature were both measured at the surface (< 2 meters) at the terminal end of longlines upon full deployment of the gear. Secchi depth, (a proxy for turbidity), was also measured at the terminal end of longline sets. Set depth was measured at the beginning and end of each line and these measures were averaged to give an indication of depth across the set. Categorical depth (depth strata) was included for two reasons: to test the effect of distance from shore, and because the chosen depth categories represent different available habitats within the bay. The four depth categories were based on isobath lines (Figure 6.1): 1) foreshore 0-2 meters deep, 2) intertidal mud flats 2-5 meters, 3) subtidal seagrass beds 5-10 meters, and 4) deep waters >10 meters deep. Mangrove proximity was measured in ArcGIS as the distance form longline set midpoints to the edge of the nearest mapped mangrove stand. Probability of seagrass coverage was estimated using model predictions sourced from Grech & Coles (2010); differences in seagrass coverage predicted by the model between the wet and dry season--September through February and March through August respectively--were accounted for by using wet season seagrass predictions for sharks caught during this season, and vice versa for the dry season. In order to identify and potentially remove non-informative predictor variables all BRT models were run twice, once with the full set of predictors and once with a reduced set created by using the simplification script in the ‘gbm’ library. Results from both models were compared and the model with the highest predictive performance used; if differences between the two models were insignificant the full model was used.

Table 6.1: Predictors used in boosted regression tree models.

Variable	Description	Mean	Range
Secchi Depth (m)	Surface water transparency, assessed using a secchi disk	1.8	0.2-11
Temperature (°C)	Surface temperature at terminal end of longline set	26.6	19.9-34.2
Mangrove Proximity (km)	Distance in km's from set location to nearest mapped mangroves	3.5	0.2-13.2
Average Set Depth (m)	Average of depths measured at each end of longline sets	3.9	0.5-15.9
Salinity (ppt)	Surface salinity at terminal end of longline set	33.2	19.9-34.2
Seagrass Probability (%)	Modelled probability of seagrass cover at set location	0.5	0-0.69
Depth Strata	Categorical depths based on isobath contours	-	-
Season	Season sample occurred	-	-
Year	Year sample occurred	-	-

Boosted regression trees produce a large number of relatively simple tree models and combine them adaptively to optimize predictive performance (Elith et al. 2006, Leathwick et al. 2006, Leathwick et al. 2008). Each regression tree is based on a series of binary splits constructed from supplied predictor variables (Hastie et al. 2001). This technique allows for the fitting of complex non-linear relationships and often has superior predictive performance when compared to more widely utilized techniques for investigating species-habitat relationships such as generalized linear and additive models (Elith et al. 2006, Leathwick et al. 2006, Elith et al. 2008, Leathwick et al. 2008, Parisien & Moritz 2009). Some of the advantages of using BRTs are that predictor variables can be continuous or categorical, the model can handle missing or outlier values, and transformations do not affect the model outcomes. Modelled results can also be output into simple-to-navigate fitted functions that depict the influence of predictor variables on, in the case of this paper, the probability of occurrence of a given shark species. The relative importance of predictor variables can also be determined using BRTs. Each variable's influence is scaled to 100 indicating that variables with higher values have a stronger influence on the response variable. Model predictive performance can also be estimated using receiver operator characteristic curve (ROC) values. Values for ROC estimate the degree to which fitted values discriminate between observed presences and absences (Parisien & Moritz 2009). Values of ROC range from 0.5 to 1, where 1 indicates perfect discrimination of probabilities between presence and absence, and 0.5 indicates that model performance in no better than random (Froeschke et al. 2010a). Typically models with ROC values of 0.7 or higher are considered "useful" (Swets 1988, Pinkerton et al. 2010). This represents a potential drawbacks of BRT use, species with limited data, or which are very wide ranging may only be caught sporadically and BRT results will therefore likely not be useful with ROC values less than 0.7. For these kinds of species BRT results will be an unreliable source on which to base conclusion.

Boosted regression trees have recently been used to look at ecological questions across broad scales (Elith et al. 2006, De'ath 2007, Leathwick et al. 2008, Froeschke et al. 2010a). This has mainly been due to their predictive power and ability to map out a species' probability of occurrence across a large spatial scale. For this paper, however, I combine boosted regression tree results with the more traditional method of kernel density analysis in order to examine the question of niche separation between sympatric species of young sharks within the spatially restricted environment of a single 'communal nursery' area. This approach shifts the use of boosted regression trees away from a broad scale predictive technique to a more restrictive scale where the descriptive powers of BRT analysis can be used to help understand the physical drivers behind observed spatial usage patterns identified by kernel densities.

Analyzes were carried out in R (version 2.8.1, R Development Core Team, 2008) using the 'gbm' library supplemented with functions from Elith et al. (2008). All models were fit to allow interactions using a tree complexity of three and a learning rate of 0.005, 0.001, or 0.0005. Differences in learning rates reflect the differences in total catch between species, with rarer animals typically requiring slower learning rates. All learning rates were chosen to produce models which generated between 1,000 and 2,000 trees, which is likely to be optimal (Elith et al. 2008). As with kernel density estimates, two models were run for each species (one on juveniles and one on adult) in order to allow for differences in occurrence patterns between mature and immature animals to be examined.

6.2.5 Effects of Season on Species Occurrence

In order to more closely examine the possible effect of season on the occurrence of shark species in Cleveland Bay, two one-way ANOVAs were run - one on juveniles and one on adults - using log transformed CPUE for each species as the dependent variable and season as a categorical predictor. Grouping catch by season reduced the number of zeros in the data allowing for the use of a non zero inflated statistical approach. Despite the inclusion of season in BRT models, other component variables of season, such as water temperature and salinity, often lead to season receiving a relatively low ranking in fitted functions. Examining season independently allowed me to identify the effects that seasonal changes have on species occurrence, and whether or not species display significantly different seasonal patterns which would suggest some level of temporal separation.

6.3 Results

A total of 314 longline sets resulted in the capture and tagging of 990 elasmobranchs during the course of this study (January 2008 – January 2010). The nine species investigated in this paper were the most commonly captured shark species within Cleveland Bay, accounting for ~ 69 % of the total catch (682 individuals), and comprise both juveniles and adults (Figure 6.2a-h). The majority of species size frequencies were dominated by juveniles, however, some species such as *Carcharhinus fitzroyensis*, and *C. limbatus/tilstoni* were dominated by smaller, younger juveniles, while other species such as *Rhizoprionodon acutus*, and the two hammerhead species (*Sphyrna mokarran* and *Sphyrna lewini*) were dominated by larger, older juveniles. This discrepancy in juvenile size frequencies between species is likely due to gear limitations, with juveniles of species with small sizes at birth unlikely to be captured by longlines, or potentially Cleveland Bay not acting as a nursery for certain species, an issue which will be returned to later.

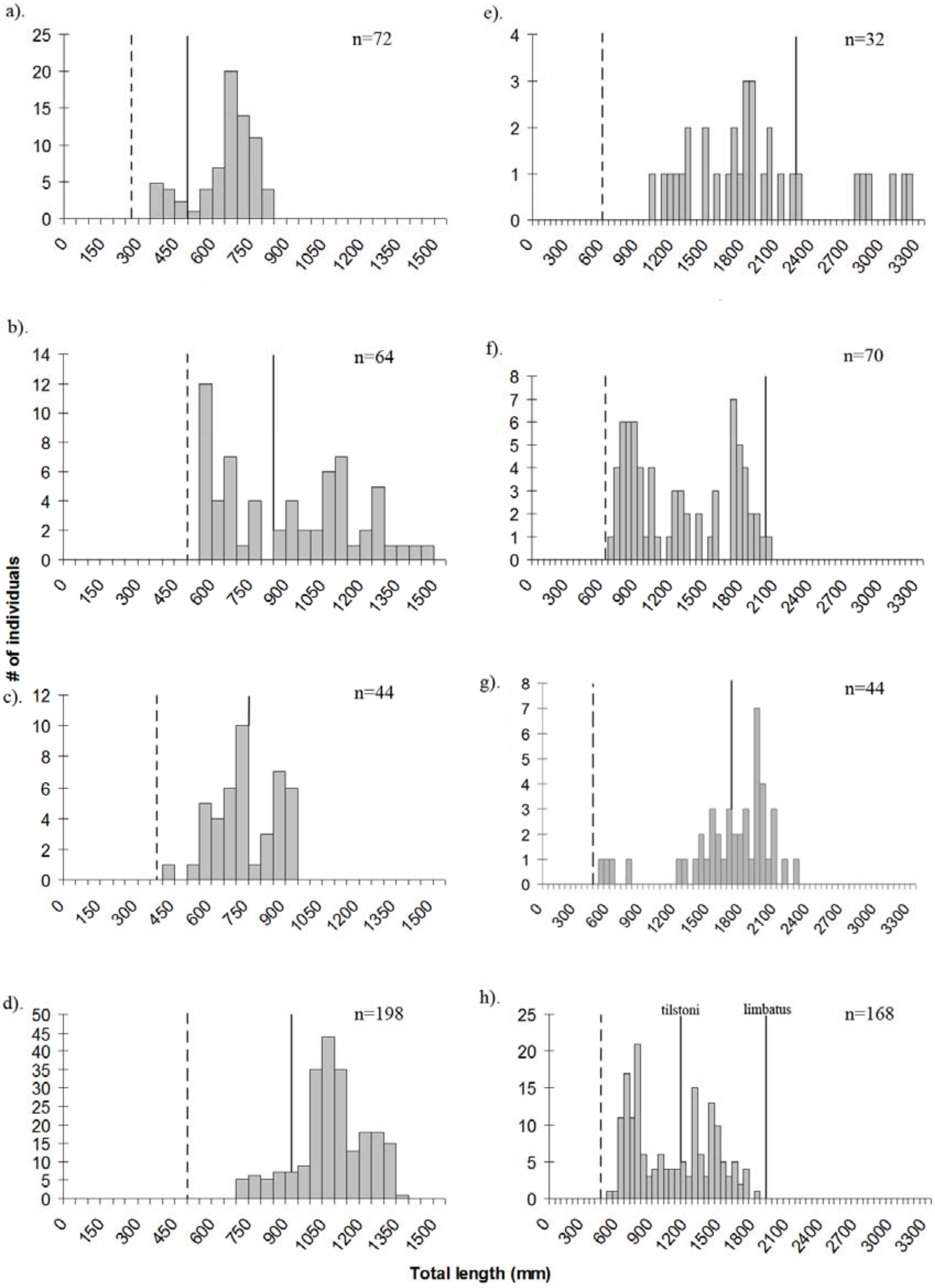
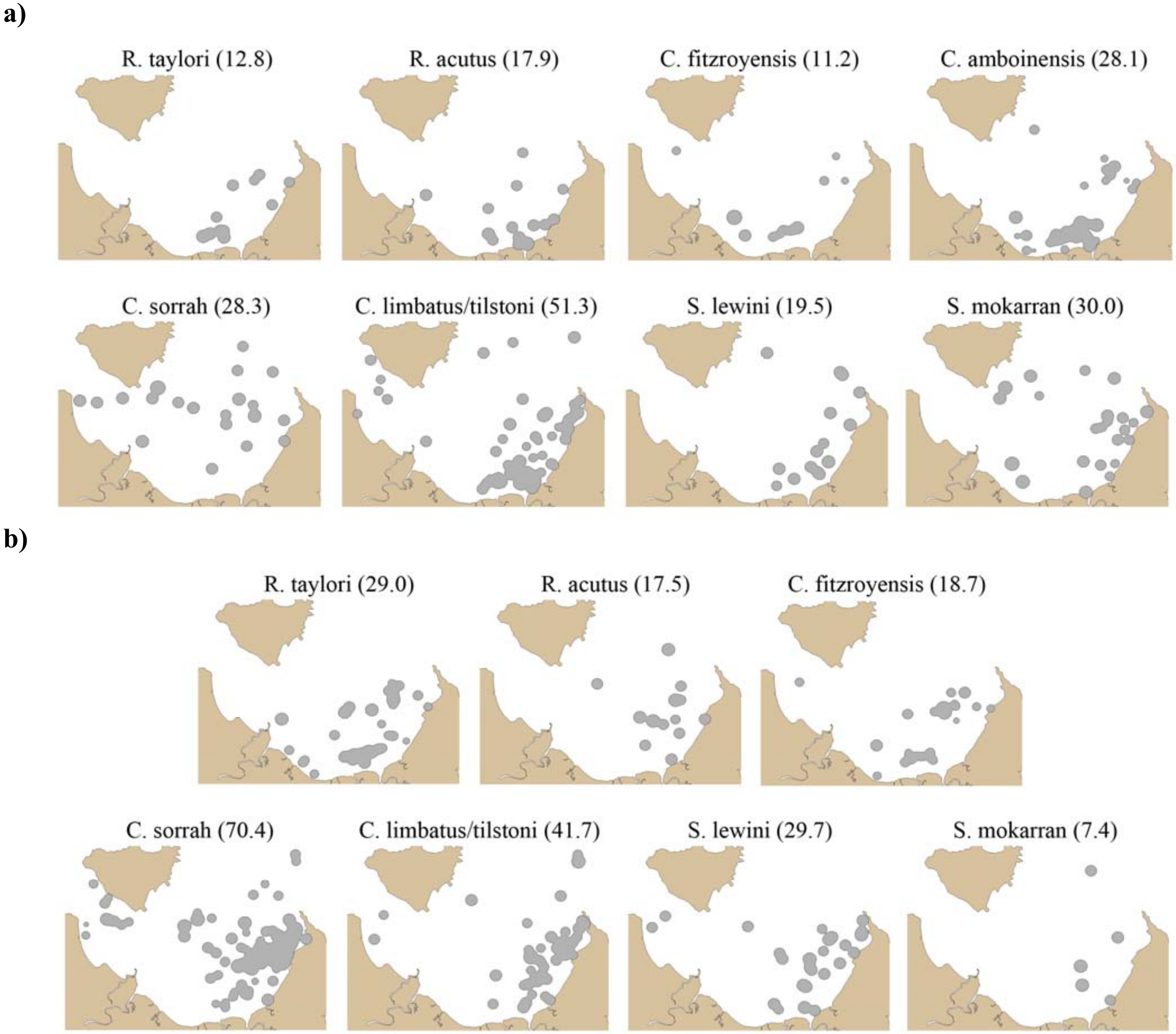


Figure 6.2a-h: Length frequency histograms of (a) Rhizoprionodon taylori, (b) Carcharhinus fitzroyensis, (c) Rhizoprionodon acutus, (d) Carcharhinus sorrah, (e) Sphyrna mokarran, (f) Carcharhinus amboinensis, (g) Sphyrna lewini, (h) Carcharhinus limbatus/tilstoni. Dotted lines indicate estimated size at birth and solid lines an average of male and female estimated size at maturity. Estimated sizes at birth and maturity are drawn from (Stevens & Wiley 1986, Stevens & McLoughlin 1991, Compagno et al. 2005).

6.3.1 Kernel Densities

Estimated 95% kernel density areas averaged 27.6 km^2 (± 16.6) across all nine focal species (Figure 6.3a-b). Adult *Carcharhinus sorrah*, and adult and juvenile *C. limbatus/tilstoni*, displayed extensive ranges comprising 70.4 km^2, 41.7 km^2 and 51.3k m^2 , respectively, which explains the high standard deviation in average 95% kernel areas. Most other species showed ranges of approximately 20 km^2 (mean area of all species 95% kernel density excluding adult *C. sorrah*, and adult and juvenile *C. limbatus/tilstoni* was 20.8 ± 8 km^2).

Mapped 95% kernel densities for the majority of juveniles were concentrated in shallow waters (< 5 m) predominantly in the mangrove lined southern section of the bay near creek and river mouths (Figure 6.3a). However, within this general section of the bay the kernel densities for each species occupied slightly different areas. Conversely, the kernel density of juvenile *C. sorrah* was much more diffuse than other focal species and showed no evidence of higher concentrations in the shallow waters of the bay. Adult 95% kernel densities were typically more dispersed than examined juveniles, although the majority of species still showed higher concentrations in the shallow waters of the bay (< 5 m) (Figure 6.3b). Contrary to juveniles however, adults of most species were concentrated more heavily near Cape Cleveland on the rocky eastern edge of the bay rather than near the river and creek mouths along the mangrove lined southern shore. Interestingly, the kernel density for adult *C. sorrah* displayed a much higher concentration in shallow waters then did juveniles for that species.



a)

R. taylori (12.8)
R. acutus (17.9)
C. fitzroyensis (11.2)
C. amboinensis (28.1)
C. sorrah (28.3)
C. limbatus/tilstoni (51.3)
S. lewini (19.5)
S. mokarran (30.0)

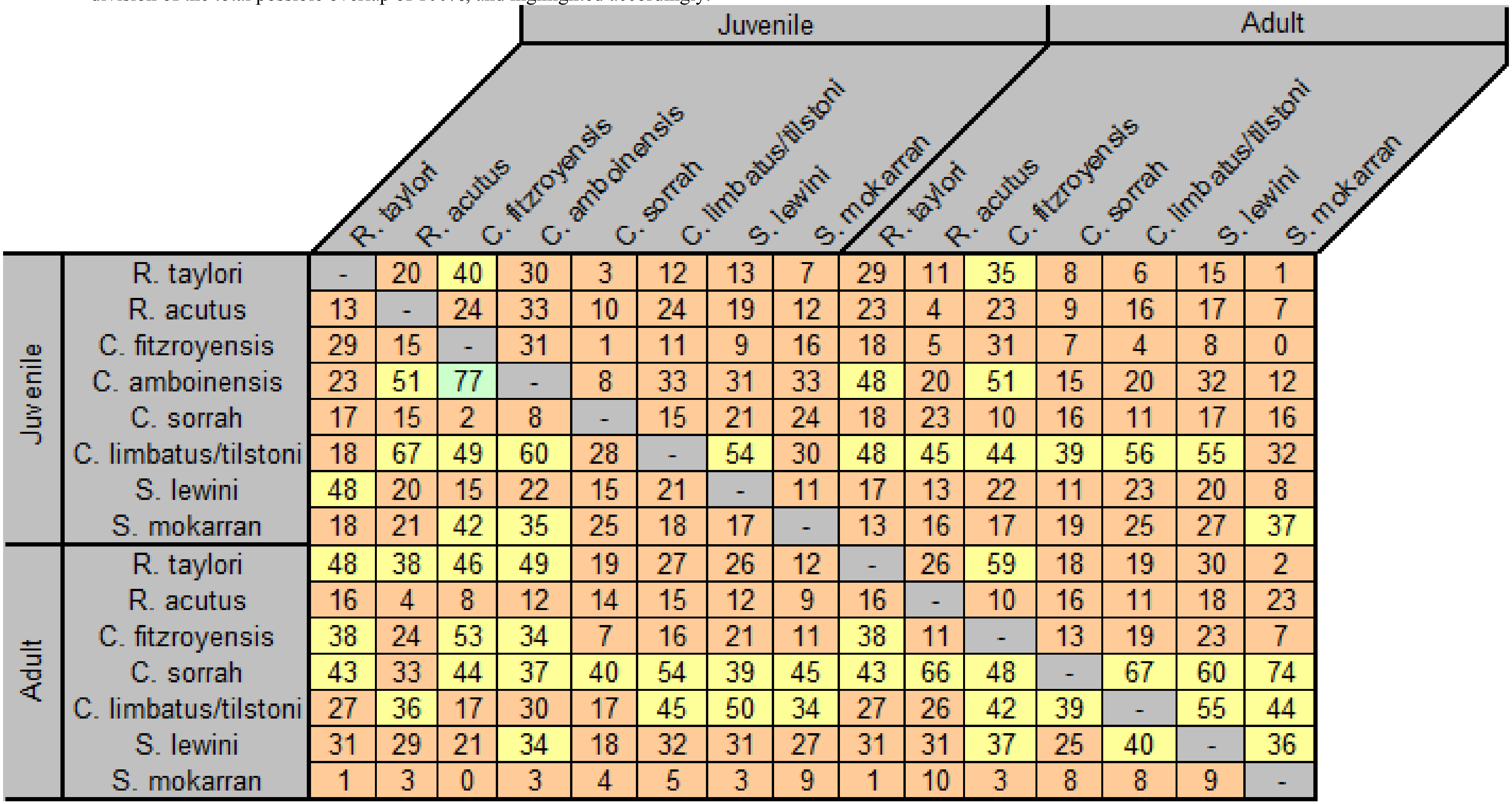
b)

R. taylori (29.0)
R. acutus (17.5)
C. fitzroyensis (18.7)
C. sorrah (70.4)
C. limbatus/tilstoni (41.7)
S. lewini (29.7)
S. mokarran (7.4)

Figure 6.3a-b: (a) Juvenile 95% kernel densities, (b) adult 95% kernel densities. Values following species names are total kernel areas in km2.

Average percent overlap between all examined species was low (24% ± 17), as was percent overlap among juveniles (24% ± 17), and adults (28% ± 20), when considered separately (Table 6.2). No two species shared a high percentage of overlap with each other, as was illustrated by the mapped 95% kernel densities. A number of species displayed moderate overlap with adult *C. sorrah* and adult and juvenile *C. limbatus/tilstoni*, while these three species themselves displayed low percent overlap with other examined species.

Table 6.2: Percent overlap between species calculated 95% kernel densities. Table can be read as the percentage of kernel overlap of species along the top with species along the side. Percent overlap values have been separated into three basic categories: high (green), mid (yellow), and low (red), based on an even division of the total possible overlap of 100%, and highlighted accordingly.

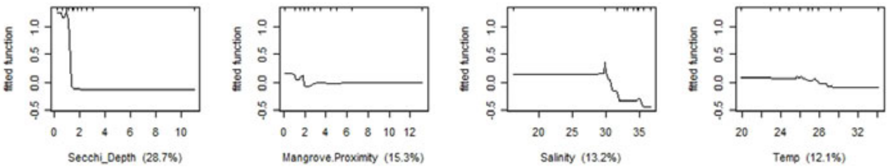


		Juvenile								Adult						
		R. taylori	R. acutus	C. fitzroyensis	C. amboinensis	C. sorrah	C. limbatus/tilstoni	S. lewini	S. mokarran	R. taylori	R. acutus	C. fitzroyensis	C. sorrah	C. limbatus/tilstoni	S. lewini	S. mokarran
Juvenile	R. taylori	-	20	40	30	3	12	13	7	29	11	35	8	6	15	1
	R. acutus	13	-	24	33	10	24	19	12	23	4	23	9	16	17	7
	C. fitzroyensis	29	15	-	31	1	11	9	16	18	5	31	7	4	8	0
	C. amboinensis	23	51	77	-	8	33	31	33	48	20	51	15	20	32	12
	C. sorrah	17	15	2	8	-	15	21	24	18	23	10	16	11	17	16
	C. limbatus/tilstoni	18	67	49	60	28	-	54	30	48	45	44	39	56	55	32
	S. lewini	48	20	15	22	15	21	-	11	17	13	22	11	23	20	8
	S. mokarran	18	21	42	35	25	18	17	-	13	16	17	19	25	27	37
Adult	R. taylori	48	38	46	49	19	27	26	12	-	26	59	18	19	30	2
	R. acutus	16	4	8	12	14	15	12	9	16	-	10	16	11	18	23
	C. fitzroyensis	38	24	53	34	7	16	21	11	38	11	-	13	19	23	7
	C. sorrah	43	33	44	37	40	54	39	45	43	66	48	-	67	60	74
	C. limbatus/tilstoni	27	36	17	30	17	45	50	34	27	26	42	39	-	55	44
	S. lewini	31	29	21	34	18	32	31	27	31	31	37	25	40	-	36
	S. mokarran	1	3	0	3	4	5	3	9	1	10	3	8	8	9	-

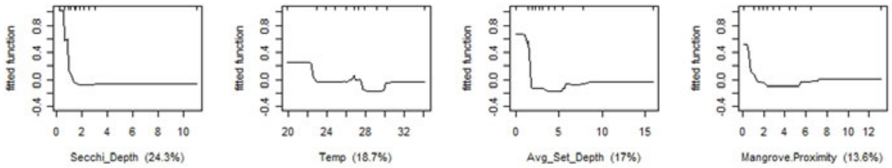
6.3.2 Boosted Regression Tree Occurrence Profiles

Fitted functions of the most influential predictors of species occurrence were complex and non-linear for all species (Figure 6.4a-h and Figure 6.5a-g). The majority of species' ROC values suggested good predictive performance (>0.7), excepting *S. lewini* (adult: 0.63, juvenile: 0.70), *S. mokarran* (adult: 0.69, juvenile: 0.65), and *C. limbatus/tilstoni* (adult: 0.62, juvenile: 0.60) (Table 6.3).

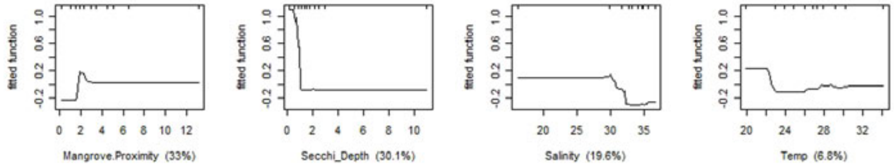
a). R. taylori (Juvenile)



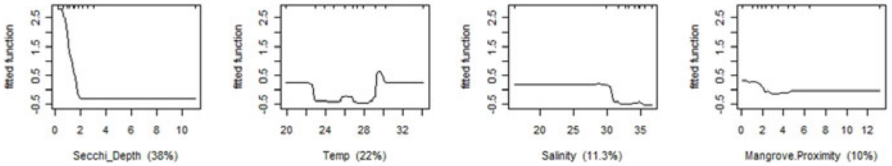
b). R. acutus (Juvenile)



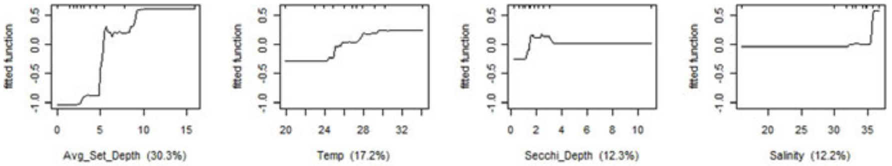
c). C. fitzroyensis (Juvenile)



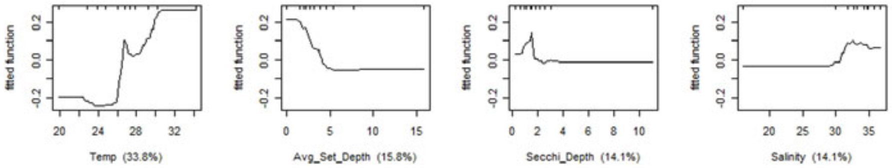
d). C. amboinensis (Juvenile)



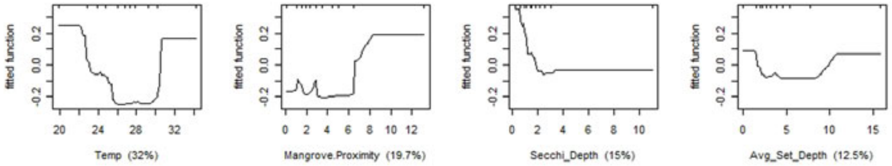
e). C. sorrah (Juvenile)



f). C. limbatus/tilstoni (Juvenile)



g). S. lewini (Juvenile)



h). S. mokarran (Juvenile)

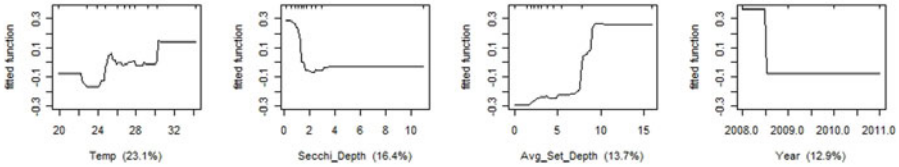
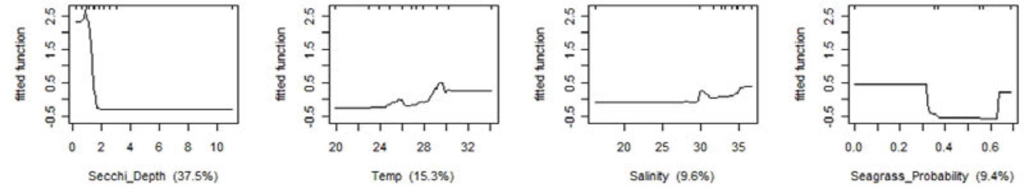
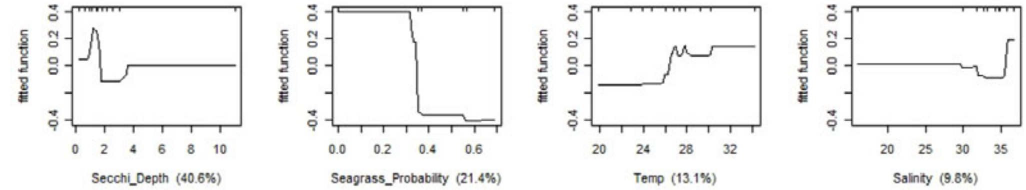


Figure 6.4a-h: Fitted functions from boosted regression trees relating the probability of juvenile shark occurrence to environmental parameters. Graphs (a-h) depict the four most influential predictor variables for all eight examined shark species. Higher values along the y-axis indicate greater probability of occurrence. Percentage values under graphs indicate the relative importance of each predictor variable scaled to 100. The deciles of the distribution of the predictors are indicated by tick marks along the top of each plot. Predictor variable codes and units are as per Table 1.

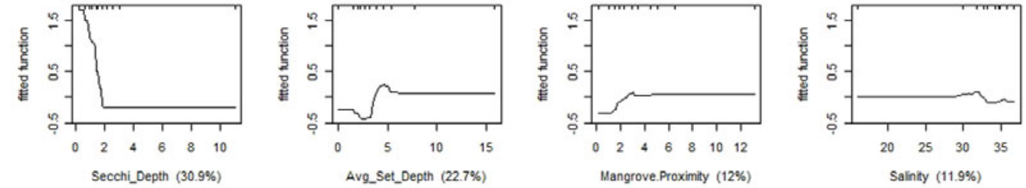
a). R. taylori (Adult)



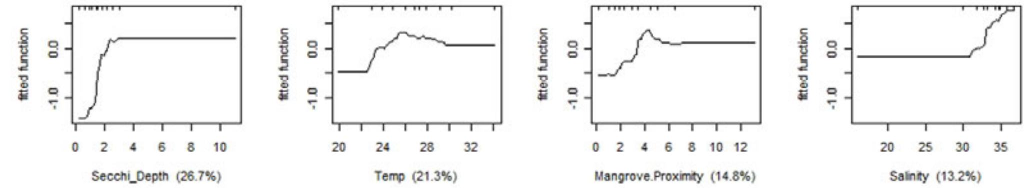
b). R. acutus (Adult)



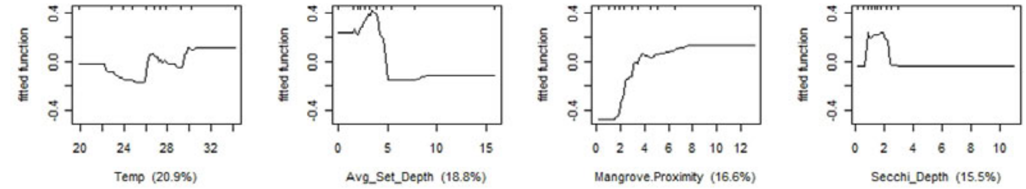
c). C. fitzroyensis (Adult)



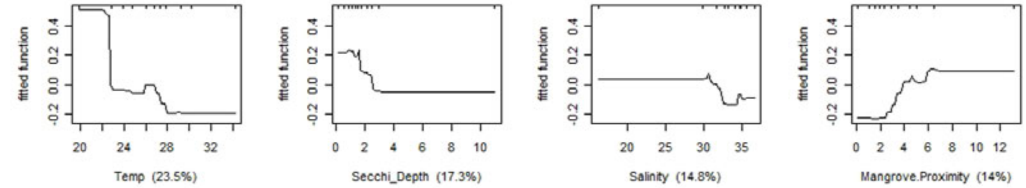
d). C. sorrah (Adult)



e). C. limbatus/tilstoni (Adult)



f). S. lewini (Adult)



g). S. mokarran (Adult)

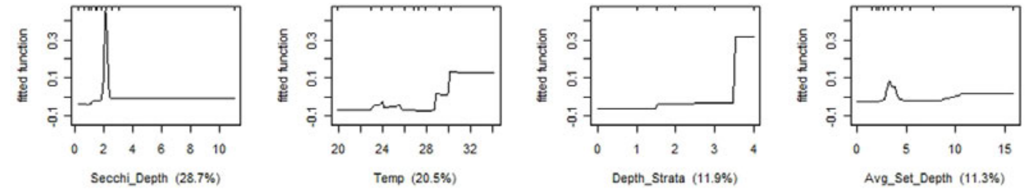


Figure 6.5a-g: Fitted functions from boosted regression trees relating the probability of adult shark occurrence to environmental parameters. Graphs (a-g) depict the four most influential predictor variables for seven of the eight examined shark species, *Carcharhinus amboinensis* were excluded due to the rarity of mature individuals in the catch. Higher values along the y-axis indicate greater probability of occurrence. Percentage values under graphs indicate the relative importance of each predictor variable scaled to 100. The deciles of the distribution of the predictors are indicated by tick marks along the top of each plot. Predictor variable codes and units are as per Table 1.

Table 6.3: Boosted regression tree receiver operator characteristic curve (ROC) values. Values of ROC range from 0.5 to 1, where 1 indicates perfect discrimination of probabilities between presence and absence, and 0.5 indicates that model performance in no better than random. Models with ROC values of 0.7 or higher are considered "useful" and are marked by an *. Model tc = tree complexity, model lr = learning rate.

	Juveniles				Adults			
Species	Model tc	Model lr	# of Trees	ROC	Model tc	Model lr	# of Trees	ROC
R. taylori	3	0.001	1200	0.73*	3	0.003	1500	0.85*
R. acutus	3	0.001	1150	0.71*	3	0.0005	1100	0.72*
C. fitzroyensis	3	0.0005	1800	0.72*	3	0.001	1800	0.76*
C. amboinensis	3	0.002	1600	0.85*	3	-	-	-
C. sorrah	3	0.001	1600	0.8*	3	0.0015	2000	0.75*
C. limbatus/tilstoni	3	0.0005	1250	0.60	3	0.001	1400	0.63
S. lewini	3	0.0003	1800	0.64	3	0.0005	1400	0.61
S. mokarran	3	0.0005	1650	0.60	3	0.0003	1200	0.65

Across all 15 models, two key factors had the greatest influence over species occurrences: secchi depth (i.e. turbidity) and temperature (Figure 6.6). Together these two factors ranked as the most influential predictors of species occurrence across 13 of 15 models. Juvenile *C. sorrah* and juvenile *C. fitzroyensis* were the only exceptions, with average set depth (30.3%) the most influential predictor for *C. sorrah*, and mangrove proximity (33%) the most influential predictor for *C. fitzroyensis*.

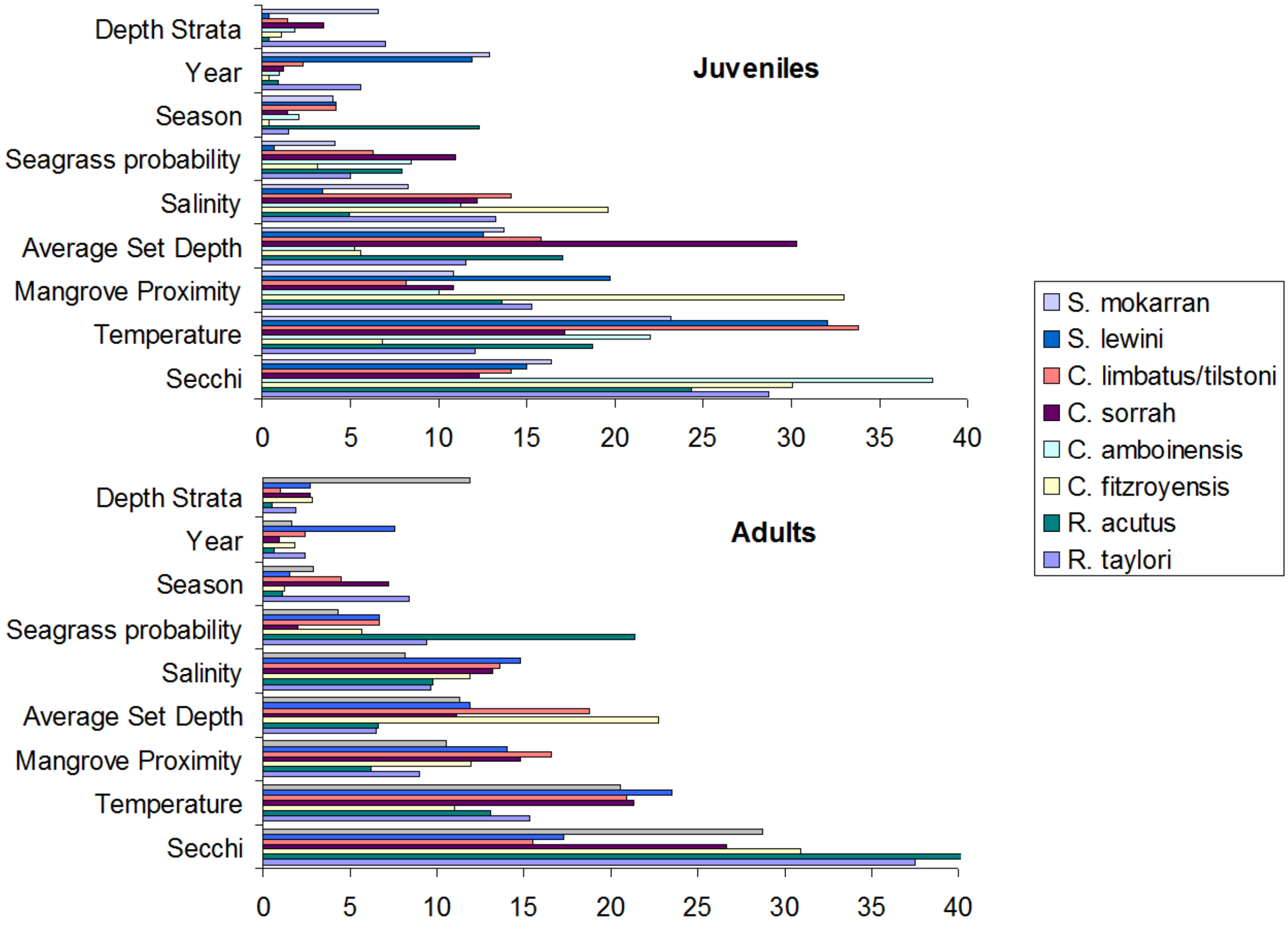


Figure 6.6: Percent contribution of environmental and temporal variables predicting presence or absence of seven adult, and eight juvenile shark species.

The correlation between the tested factors of season, temperature, salinity, and secchi depth were statistically significant in all but one case (Table 6.4). However, BRTs largely ignore non-informative predictors when fitting trees. Additionally, measures of relative influence produced by the models quantify the importance of predictors, and irrelevant ones have a minimal effect on prediction (Elith et al. 2008). Fitted functions showed little difference between full models and simplified ones, and no increase in model predictive performance, indicating that BRT's were successful in ignoring non informative predictors. Thus, for consistency of examined variables between tested species, results from full models were used in this study.

Table 6.4: Correlation of boosted regression tree environmental predictors with the temporal predictor of season. Significant results ($p < 0.05$) are marked with an *.

	Season	Temperature	Salinity	Secchi Depth
Season	-			
Temperature	-0.523*	-		
Salinity	-0.058	-0.490*	-	
Secchi Depth	0.299*	-0.181*	0.129*	-

Among the most influential factors, a few key values indicated clear divisions between tested species. For example, models for secchi depth indicated higher probabilities of occurrence at secchi depths near or below two meters for all examined species except juvenile *C. sorrah*. This finding supports the spatial patterns displayed by kernel densities which identified juvenile *C. sorrah* as the only species which predominated in the deeper, less turbid waters of the bay removed from shore. The relationship between examined species and temperature was more complex, but as with secchi depth a key value emerged which divided the species occurrence profiles into two groups--roughly half the models indicating higher probabilities of occurrence at temperatures above 29°C, and half indicating higher probabilities of occurrence at temperatures below 29°C. What is most interesting about this is that temperatures over 29°C were never measured outside of the summer months of December, January, and February (Figure 6.7). Thus, despite the inclusion of season in BRT models, the comparatively greater influence of correlated factors (as evident by their higher ranking) such as temperature, secchi depth, and salinity led to model predictions which were more strongly influenced by these factors and relegated the influence of season to the position of a non-informative predictor that the models largely ignored.

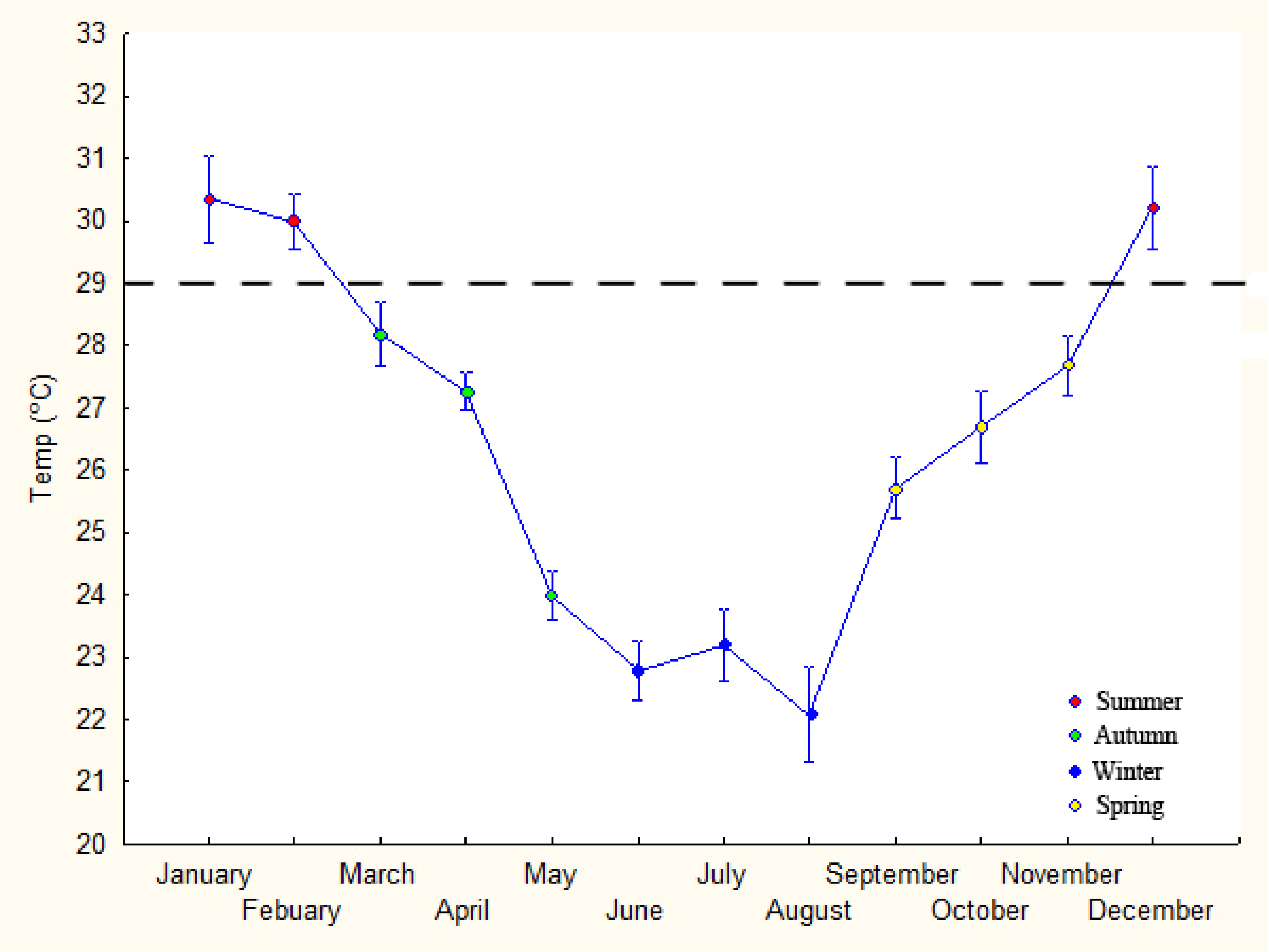


Figure 6.7: Average water surface temperatures plotted by month with 29 °C indicated by a horizontal dashed line. Seasons are denoted by color, with red circles identifying summer, green circles autumn, blue circles winter, and yellow circles spring. Vertical bars denote 0.95 confidence intervals.

6.3.3 Seasonal ANOVA Results

One-way ANOVA’s indicated that the occurrences of five species life stages (3 juveniles, 2 adults) were significantly influenced by season (Table 6.5). Juvenile *R. acutus*, and *C. limbatus/tilstoni*, as well as adult *C. sorrah* each displayed significantly increased probabilities of occurrence during the spring, while juvenile *Carcharhinus amboinensis* and adult *Rhizoprionodon taylori* occurred more frequently in the summer. Species which displayed a significant seasonal effect were graphed and compared with BRT temperature results. All species which showed significantly increased CPUE during the summer matched species whose BRT identified higher probabilities of occurrence above 29°C and vice versa for species below 29°C (Figure 6.8a-b). The only exception to this pattern were juvenile *C. limbatus/tilstoni* which displayed high catch during spring but had a BRT temperature profile which indicated a summer peak, but as ROC results for this species’ model indicate low predictive performance, BRT findings for juvenile *C. limbatus/tilstoni* must be interpreted with caution. Seasonal ANOVA results indicate that while factors such as temperature, secchi depth, and salinity predominated in the ranking of BRT, the correlated temporal factor of season was also an important influence on several shark species in Cleveland Bay.

Table 6.5: Results of one way ANOVAs on juvenile and adult log transformed catch per unit effort data (CPUE measured in 100 hook hours), and season. Species with CPUEs which were significantly affected ($p < 0.05$) by season are marked with an *.

Species	Juveniles		Adults	
Multivariate Results	$F_{24,879}$	p	$F_{24,879}$	p
	2.255*	0.001*	2.189*	0.001*
Univariate Results	$F_{3,313}$	p	$F_{3,310}$	p
R. taylori	0.507	0.678	6.108*	0.001*
R. acutus	4.854*	0.003*	0.9	0.442
C. fitzroyensis	1.225	0.301	0.755	0.52
C. amboinensis	5.017*	0.002*	-	-
C. sorrah	0.961	0.411	4.123*	0.007*
C. limbatus/tilstoni	2.695*	0.046*	0.511	0.675
S. lewini	0.638	0.591	1.751	0.157
S. mokarran	0.927	0.428	0.585	0.626

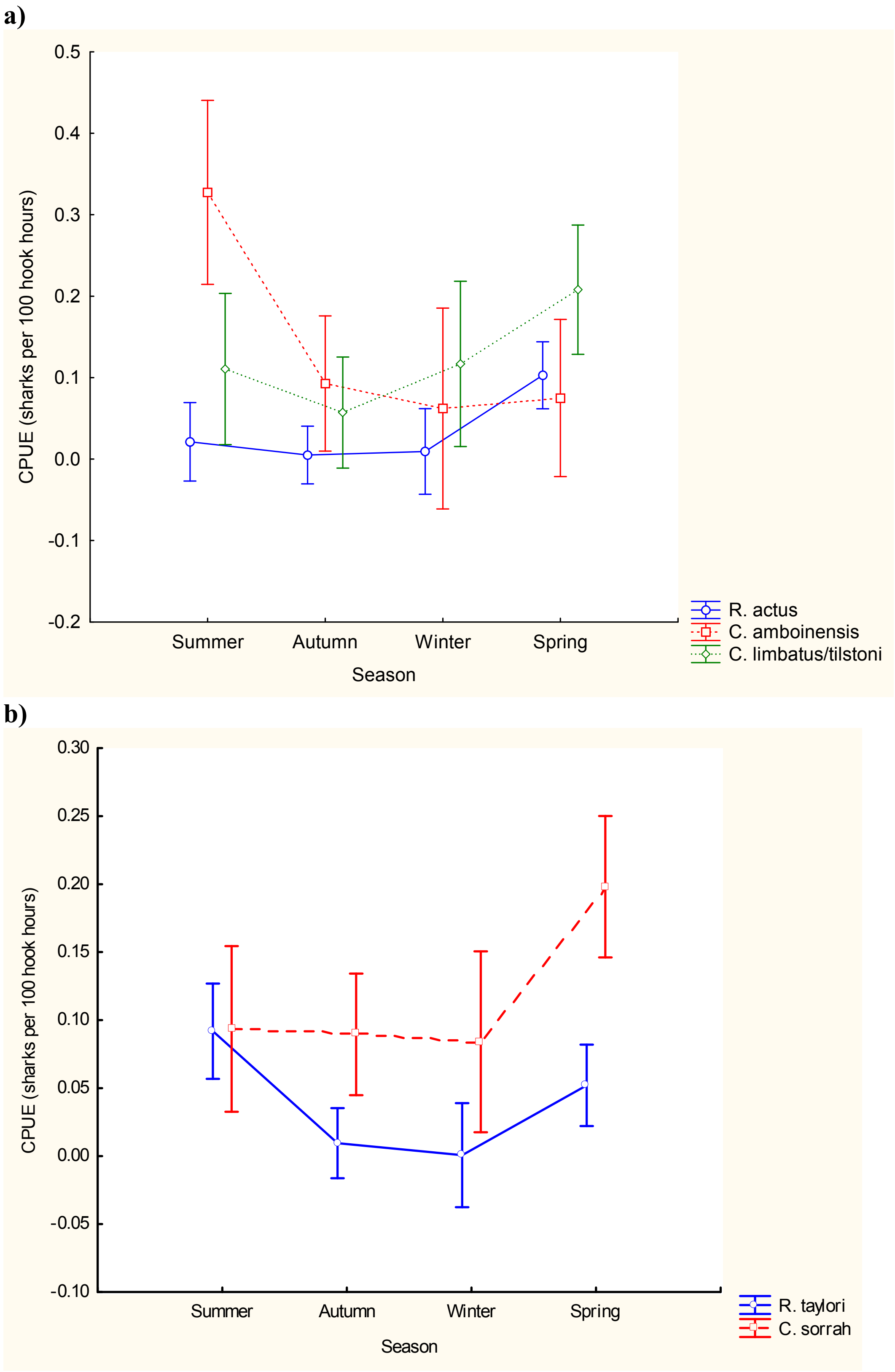


Figure 6.8a-b: Log transformed seasonal catch per unit effort of a) juveniles, and b) adults which were significantly influenced ($p < 0.05$) by season. Vertical bars denote 0.95 confidence intervals.

6.4 Discussion

Low percentage overlap between shark species' kernel densities and unique species-specific BRT occurrence profiles provides evidence of a communal nursery environment that is more segregated than originally proposed by Simpfendorfer & Milward (1993). The prevalence of adult sharks captured on baited longlines indicated that adults of many species are common in Cleveland Bay. However, differences in the 95% kernel densities of adults and juveniles did signify that juveniles of most species occupy the more sheltered shallow waters in the southern and south-eastern sections of the bay, and had low levels of overlap with adults of the same species. Spatial, and in some cases temporal niche separation appeared common among the sympatric juvenile shark species inhabiting the bay, indicating that the majority of species are occupying a reduced realized niche, a finding which has been echoed for nurseries containing more than one species along the coasts of the Caribbean (Pikitch et al. 2005, DeAngelis et al. 2008), and the Indian Ocean (White & Potter 2004) to name a few. These reduced realized niches highlight the importance of scale when identifying a nursery. Defining a nursery at the appropriate scale could benefit management by distinguishing discrete areas where management could be most effective, while avoiding the labeling of expansive areas containing sparsely used habitats. Additionally, determining the appropriate scale of a nursery will facilitate more accurate comparisons between nurseries.

The predominance of low percent overlap between the 95% kernel densities of juvenile sharks in the southern and south-eastern sections of Cleveland Bay indicated that the spatial overlap of individual species was limited, and that species' realized niches are spatially segregated within the nursery. The limited general overlap between juveniles could potentially be interpreted as a number of small single species nursery areas which exist within a single bay. This again identifies the importance of scale when considering nursery environments. Of key importance here when determining if Cleveland Bay represents one communal nursery or several single species nurseries are the presence of empty or sparkly used areas between individual species nurseries, and species rich areas. If Cleveland Bay represents one communal nursery there will be few if any empty areas and some areas where species overlap and several species can be found regularly. If the bay is a number of individual single species nurseries there should be some empty environments and little to no species rich areas since the nurseries will exist largely independently from one another. Evidence of few empty areas existing between species predominant areas of occurrence, as well as the presence of some species rich environments (discussed in more detail in Chapter 7), suggests that Cleveland Bay represents a communal nursery and not a number of smaller individual species nurseries.

Adult kernel densities for each species generally covered larger areas than their juvenile counterparts. However, percent kernel density overlap with juveniles was still low, indicating that although adults were prevalent in Cleveland Bay they did not predominately occur in the same areas as juveniles. This was also evident when comparing BRT profiles, specifically for mangrove proximity, between adults and juveniles. The majority of species' juveniles displayed higher probabilities of occurrence near mangroves as compared to adults, and mapped mangrove distribution showed mangroves occurring predominately along the more sheltered shallow waters near the southern and south-eastern shores of the bay. Overall, low overlap between juveniles is likely a result of fitness-maximizing behaviors allowing juveniles of several sympatric species to use the same general nursery area while maintaining high fitness levels potentially through competitive displacement (DeBach 1966, Case et al. 1994, Pyle et al. 1999, Stewart et al. 2002). Low overlap between juveniles and adults, and the smaller average kernel density areas of juveniles is likely a means of predation avoidance employed by young sharks in the nursery area of the bay, as adult sharks are the only significant predators of juvenile sharks (Springer 1967, Cortés 1999a). While my findings differ from the original assessment of Cleveland Bay, which assumed high spatial overlap due to limited resource partitioning (Simpfendorfer & Milward 1993), my results are in agreement with more recent works carried out on other nursery areas inhabited by multiple species (Michel 2002, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008), all of which have identified varying degrees of spatial segregation among species.

Despite the presence of adult sharks in Cleveland Bay throughout much of the year, low levels of kernel overlap indicate that juveniles and adults predominately occupy different areas within the bay, however kernel estimates alone provide little information as to why. Based on BRT profiles it is possible that much of this spatial division is driven by differences in environmental conditions. However, this separation of adults and juveniles is not true for all species. For example, juvenile *C. sorrah* predominate in deeper waters near the center of Cleveland Bay, an area frequented by the adults of several species. In a study off northern Australia Stevens et al. (2000b) also found that the smallest captured *C. sorrah* were caught both inshore and offshore, where as the smallest individuals of other examined species where found only inshore. This variation is likely the result of alternative early life history strategies where species balance the tradeoffs of reduced predation and resource availability (Branstetter 1990, Heithaus 2007). The majority of examined juveniles appear to opt for the protection provided by the shallow turbid waters at the southern and south-eastern ends of the bay, despite the apparent dietary resource partitioning observed among them (Kinney et al. 2011). In contrast, juvenile *C. sorrah* may be opting for the greater resource availability provided by reduced competition with other juveniles in the central waters of the bay, in lieu of increased protection from predation in the more sheltered waters at the southern and south-eastern ends of the bay. The increased presence of adults in these central waters is unlikely to reduce the availability of dietary resources to juvenile *C. sorrah* since, as reported in Stevens et al. (2000b) *C. sorrah* likely undergo an ontogenetic change in feeding depth helping to separate their prey from that of adults. Additionally, it is likely that adults are more apt to take larger prey which are unavailable to juvenile *C. sorrah* due to gape size limitations. This division in early life history strategies within a single communal nursery indicates the spatiotemporal complexity of these coastal systems as well as the importance of obtaining species-specific data in order to understand the ecology of these diverse environments.

Turbidity and temperature were identified as the predominant environmental factors structuring the distributions of sharks within Cleveland Bay. High turbidity (secchi depths < 2 m) positively correlated with increased probabilities of occurrence in BRT models for all species except *C. sorrah*. Highly turbid waters are often seen as beneficial to juvenile sharks within nurseries as a means of protection from predation, and along with shallow depths constitute key factors of nursery area use according to the established nursery area paradigm (Springer 1967, Brewer et al. 1995, Paterson & Whitfield 2000, Pekcan-Hekim & Lappalainen 2006). *C. sorrah* may forgo the potential benefits of highly turbid shallow inshore waters, as mentioned above, to avoid the need for resource partitioning with other sympatric shark species, or alternatively *C. sorrah* may simply be less tolerant to turbid water conditions and so may be forced into deeper clearer areas.

Temperatures above or below 29°C were an important divide between species occurrences. Several studies have indicated the advantages of temperature for growth and reproduction for many aquatic species (e.g. Wood & McDonald 1997, Gibson et al. 2002, Perry et al. 2005), confirming the importance of temperature as an ecological resource. My results suggest that a potential driver of resource partitioning in shark species could be temperature; for some species this indicated temporal separation by using Cleveland Bay during different seasons (a pattern which is obviously driven by several environmental factors, but was significantly correlated with temperature in this study). While for others it indicated a key physical driver which influenced spatial differences observed in kernel densities. The importance of temperature for sharks within nurseries has been demonstrated previously (Simpfendorfer et al. 2005, Froeschke et al. 2010a), and in the case of communal nurseries areas, temperature appears to be an important factor that influences the observed niche separation among juveniles.

The partitioning of the bay based on the seasonal shifts of influential physical factors such as temperature highlights an important difference between nursery areas such as Cleveland Bay in the tropics, and those typically found in temperate, or subtropical waters. The majority of shark nursery areas identified in temperate areas, such as many of those identified in McCandless et al. (2007), tend to act as nurseries for only a portion of the year, with the typical pattern involving an emigration away from the area during the colder winter months after abrupt declines in water temperature (Heupel 2007). This migration away from the protected waters of the nursery is primarily attributed to juveniles seeking out warmer deeper waters during the winter and only returning to shallow coastal nurseries when temperatures have risen to a suitable level. Cleveland Bay on the other hand, with its less abrupt temperature shift from summer (average 30.6 °C) to winter (average 22.4 °C), continues to act as a nursery year round but for an altered suite of species, with *C. limbatus/tilstoni*, *R. acutus*, and *C. amboinensis* found predominantly in the spring and summer, while the juveniles of species like the *C. fitzroyensis* appear to be more common during autumn and winter. This constrained temperature range allowing continued use by a changing suite of juvenile shark species may explain why tropical nurseries like Cleveland Bay are able to act as communal nurseries for several species, and why, to date, communal shark nursery areas appear predominantly in tropical, and occasionally sub-tropical environments (Michel 2002, Bethea et al. 2004, White et al. 2004, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008). While not all tropical shark nursery areas are communal nurseries, for example Bimini in the Bahamas, or Atol das Rocas in Brazil, both of which act as nurseries for lemon sharks (*Negaprion brevirostris)* (Gruber et al. 2001, de Freitas et al. 2009). The often higher diversity of shark species found in tropical environments compared to temperate ones might be another factor which contributes to communal nurseries being more likely in the tropics.

The reduced area of the bay identified by kernel density analysis as important to nursery-utilizing species, in comparison to the overall size of the bay, highlights the importance of scale in nursery area research. When an area is found to contain juveniles of one or a number of species, commonly the entire area (often a bay, lagoon, or reef environment) is defined as a nursery (e.g. Castro 1993, Feldheim et al. 2002, Parsons & Hoffmayer 2005, Duncan & Holland 2006, Merson & Pratt 2007). The original assessment of Cleveland Bay similarly classified the entire bay as a nursery (Simpfendorfer & Milward 1993). My results clearly indicate that for the majority of species, only the shallow waters in the southern and south-eastern sections of the bay are used extensively by juvenile sharks as a nursery, greatly reducing the scale of the originally defined nursery area of Cleveland Bay, a finding which has been echoed by other studies on individual species such as *C. amboinensis* in Cleveland Bay (Knip et al. 2011a, Knip et al. 2011b). The appropriate scale is important when identifying a nursery, not only to reduce the target area of management efforts, thus reducing management costs, but also to more accurately define the boundaries of a nursery area, as opposed to other environments where juveniles may simply be passing through on limited forays. Froeschke et al. (2010b) highlights the importance of properly defining the scale of a nursery and suggests the use of temporal stability of high-density regions as a means of classifying nurseries, a method used by Fodrie & Levin (2008) in studies of teleost nurseries and Heupel et al. (2007) in a review of shark nurseries, where areas are observed over years to assess if they retain their high densities. In the case of Cleveland Bay, sampling spread across the entire 225 km^2 of the bay over two years, suggests that the majority of species' juveniles reside in the approximately 80 km^2 in the southern and south-eastern sections of the bay. As a result, for the majority of species this would be the appropriate scale of a Cleveland Bay communal shark nursery based on this idea of temporally stable high density regions.

Some of the limitations of this study include the difficultly of determining accurate BRT profiles or kernel densities for infrequently captured species (e.g. *S. lewini* and *S. mokarran*), or species which proved problematic to differentiate in the field (e.g. *C. limbatus/tilstoni*). Species with low catch rates produced models with low accuracies and disparate kernel densities which hampered the interpretations of results. *Sphyrna lewini*, and *S. mokarran* were an example of this, with low ROC values for BRT models (0.69 and 0.65 for adult and juvenile *S. mokarran*, and 0.63 and 0.7 for adult and juvenile *S. lewini*). These animals also showed disparate kernel densities which rendered it difficult to assess their use of Cleveland Bay as a nursery. However, previous work by Simpfendorfer & Milward (1993), as well as ongoing work in Cleveland Bay (Simpfendorfer unpublished data) have reported higher catch rates for these species than those found during the course of this study. Therefore the significance of Cleveland Bay as a nursery for both *S. mokarran* and *S. lewini* remains unclear and warrants further investigation. Alternatively, *R. taylori* seem unlikely to utilize Cleveland Bay as a nursery, due to the low catch of small juveniles in the area. This finding agrees with recent evidence suggesting that juveniles of this species do not use nursery areas in the traditional sense (Heupel et al. 2007, Knip et al. 2010). Despite this, Cleveland Bay likely still represents an important environment for *R. taylori* but is unlikely to benefit their recruitment as significantly as it does for species for which Cleveland Bay is a nursery.

Species which were difficult to distinguish in the field, such as *Carcharhinus limbatus/tilstoni*, potentially confounded modelling and mapping results when the two species were grouped together. Low performance of BRT models (ROC = 0.60) despite the abundant catch of these animals, indicates that modelling *C. limbatus and C. tilstoni* together instead of independently was ineffective, and each species likely exhibits a distinct occurrence profile. Hence, calculating the 95% kernel density of these species together is likely the cause of their large kernel areas as both juveniles and adults. These results highlight the danger in assuming that morphologically similar species are also ecologically similar, a sentiment that has been expressed in other studies such as Tillett et al. (2011) concerning *Carcharhinus leucas* and *C. amboinensis* in northern Australia. Future studies would benefit from the separation of morphologically similar species prior to analysis.

Through the use of boosted regression trees and kernel density analysis I have been able to derive robust results which identify Cleveland Bay as a nursery environment that is partitioned both spatially and temporally by sympatric juvenile shark species. Counter to the original assessment of Cleveland Bay as a communal nursery with low levels of resource partitioning (Simpfendorfer & Milward 1993), my analyzes show that both spatial and temporal resource partitioning are apparent among juveniles in the bay, leading to a number of realized niches for individual species that reduce the potential for competition within the nursery. Despite the diverse array of realized niches, a few key physical factors--mainly turbidity, temperature, and the proximity of mangroves--appear to strongly influence occurrence patterns of all species in the nursery, results which agree with Taylor (2007) for sharks in Moreton Bay, Southeastern Queensland Australia.

Changes to these key factors could greatly affect the community of sharks found in the bay. Hence the maintenance of these environmental conditions should be considered by managers as an important component of any conservation effort.

Communal nurseries provide an attractive, cost-effective alternative to managing single-species nurseries due to the concentration of several species' juveniles in a single, discrete area (Kinney & Simpfendorfer 2009). However, the divisions between individual species niches indicate that a delicate balance, rather than an overabundance of resources, is likely what allows these areas to function as communal nurseries. The maintenance of this balance, through the protection of key areas and physical factors, will be instrumental in creating viable communal nursery area management.

7 Chapter 7.

Drivers of Species Richness in Near Shore Shark Communities: Implications for Nursery Area Management and Conservation

---

7.1 Introduction

Investigations into varying patterns of marine species richness and diversity have gained increased interest with the recognition of the global imperative for biodiversity conservation. These investigations have occurred across vastly different geographic scales; from global (Poore & Wilson 1993, Gray 1997, Gaston 2000, Sala & Knowlton 2006), to specific islands, ocean shelfs (Shackell & Frank 2003, Leathwick et al. 2006), individual reefs, and bays (Nagelkerken et al. 2001, Gratwicke & Speight 2005). Such studies have predominantly aimed at identifying important areas for conservation and management, or generating baseline data to assist in environmental monitoring. In addition, several authors have compared observed patterns of marine species richness with environmental factors in order to examine the underling influence of these factors (e.g. Nagelkerken et al. 2000, White & Potter 2004, Leathwick et al. 2006, DeAngelis et al. 2008). Such studies provide baseline information useful for measuring the effects of alterations of important environmental factors, which can assist in prioritizing strategies aimed at maintaining environmental integrity for conservation goals. These investigations are especially useful in coastal environments, where the possibility of anthropogenic alteration of environmental conditions is high (DeMaster et al. 2001, Jackson et al. 2001, Jennings et al. 2008, Knip et al. 2010), and where the young of many marine species spend their formative years (Beck et al. 2001), making coastal environments focal points for conservation and management actions.

The concept of prioritizing spatially restricted key conservation areas has become increasingly popular in the wider conservation biology community (Pressey et al. 1993, Mittermeier et al. 1998, Myers et al. 2000, Roberts et al. 2002, Brooks et al. 2006), and such an approach could be of particular interest to elasmobranch conservation, as the young of many species inhabit shallow coastal waters that serve as nurseries (Heupel et al. 2007). Estimated declines of more than 90% for some elasmobranch species over the past two decades (Shepherd & Myers 2005, Myers et al. 2007) have resulted in conservation efforts receiving increased attention. Such efforts have often focused on nurseries in attempts to increase recruit survival and so boost populations, a strategy originating from many teleost based management plans (Kinney & Simpfendorfer 2009). However, recent concerns regarding the feasibility of managing vast areas identified as nurseries (Heupel et al. 2007), as well as the questionable value of nursery area conservation in the absence of more effective management for older individuals (Kinney & Simpfendorfer 2009), have brought this teleost-centric conservation approach into question. While shark nursery area protection is still considered an important component of effective shark management, the aforementioned studies argue that care needs to be taken in identifying areas as nurseries to ensure their significance, thus limiting the total area required to protect the maximum number of species, unfortunately, to date such an approach has rarely been used in elasmobranch conservation.

One strategy that could be beneficial for achieving effective shark nursery area conservation, while limiting the spatial scope required to manage such areas, would be to identify discrete, species-rich areas for young sharks which could potentially provide valuable nursery habitat to several species. In the past, areas which served as nurseries for multiple shark species were identified as communal nursery areas (Castro 1993, Simpfendorfer & Milward 1993). These areas were seen as discrete nurseries where the young of multiple shark species could reside while feeding and growing to maturity. Since these original studies, the term 'communal nursery' has been used less often in the scientific literature, with more recent studies opting to simply refer to them as nurseries used by several species. Regardless of the terminology, only a handful of studies have focused on nursery areas used by more than one species, investigating subjects such as habitat (Michel 2002, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008) and dietary resource use (Bethea et al. 2004, White et al. 2004). Little attention, however, has been directed at assessing the potential value of these areas to provide important nursery habitat for several species while limiting the management scale necessary to afford such protection.

Here I present results of an analysis comparing patterns of shark species richness with relevant environmental predictors within a bay identified broadly as a communal shark nursery (Simpfendorfer & Milward 1993). Richness was chosen in preference to other measures of diversity since the total number of species being considered was low (6 species). My primary focus was on patterns of juvenile richness, however adult species richness was also investigated in order to examine the separation between juveniles and adults, and to investigate the physical factors that may influence observed patterns of different life history stages. My aims were to identify discrete, species-rich areas within multi species shark nurseries, and the environmental predictors that influenced the use of these areas. Ultimately my goal was to develop simple criteria that could be added to the established approach for assessing single species shark nursery areas as described by Heupel et al. (2007), in order to expand the usefulness of this approach to nursery areas used by more than one shark species. This revised approach could be used to prioritize shark nurseries, or areas within them, for conservation, and to assist in limiting the spatial scale of indentified shark nursery areas, thus avoiding concerns of producing a seemingly insurmountable management task.

7.2 Materials and Methods

7.2.1 Study Site

Cleveland Bay lies just off of Townsville on the north-east coast of Queensland, covering an area of approximately 225 km² from 19°10’S to 19°19’S and from 146°50’E to 147°01’E (Figure 7.1). For a detailed description of the bay please refer to section 3.1 of Chapter 3.

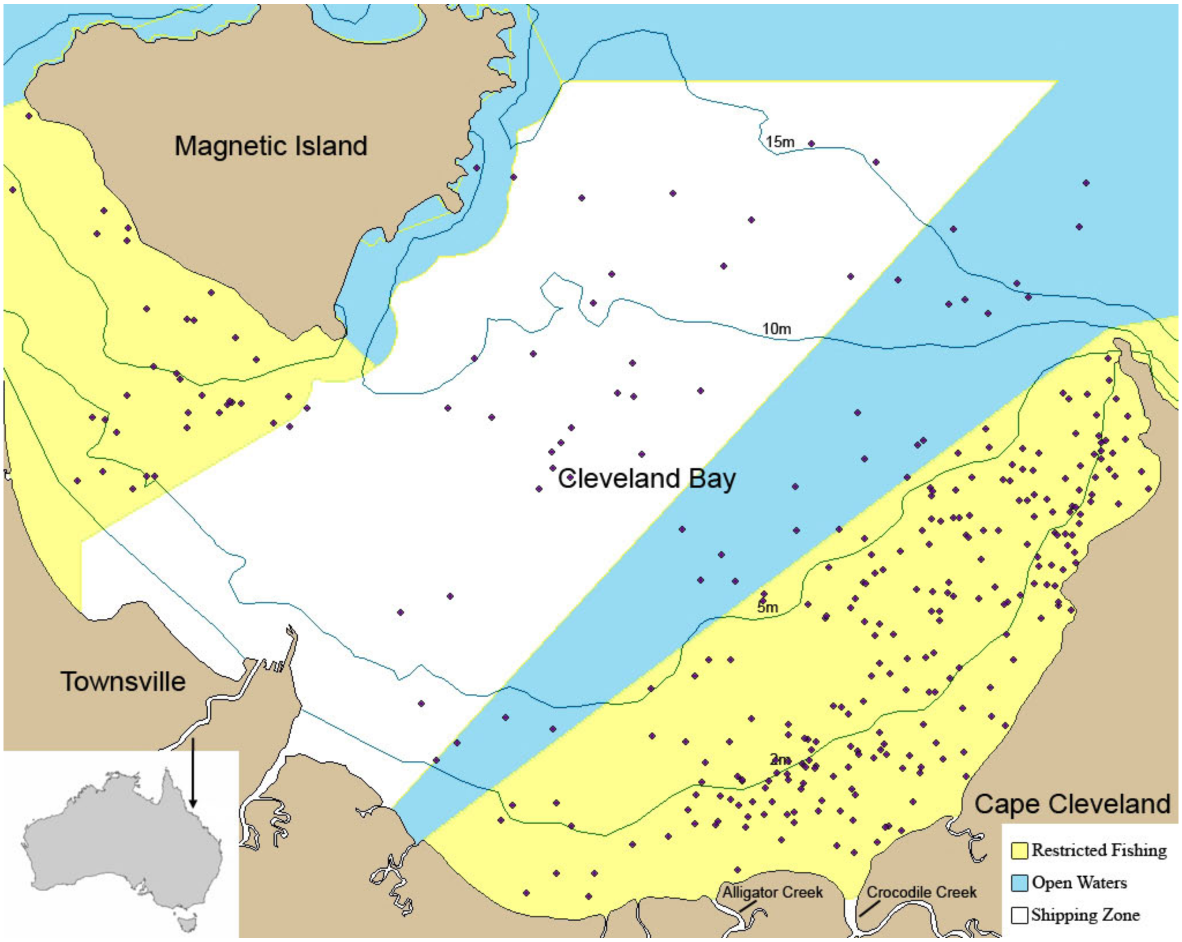


Figure 7.1: Map of Cleveland Bay with GBRMPA Conservation Park Zones marked in yellow, Townsville shipping channel in white, and isobaths delineated at 2, 5, 10, and 15 meters. Dots represent locations where longlines were deployed during the project.

7.2.2 Sampling

A total of eighteen shark species, mainly from the families Carcharhinidae and Sphyrnidae, were collected from the waters of Cleveland Bay from January 2008 to December 2009 using longlines in depths from less then one meter to more then fifteen meters. For a detailed description of the construction and use of longlines during this project please refer to section 3.2.2 of Chapter 3. All captured sharks were identified to species, sexed, tagged with a plastic Rototag through the first dorsal fin, measured (precaudal length (PCL): nose to precaudal notch, fork length (FL): nose to caudal fin fork, stretched total length (STL): nose to tip of the upper lobe of the caudal fin), and released.

Juveniles of twelve species were captured during the course of this study; however my primary interest was focused on patterns of species richness for juveniles that use Cleveland Bay as a nursery. Therefore, employing the three criteria recently established by Heupel et al. (2007) to identify nursery utilizing species, I narrowed my study to those species whose juveniles: (1) occurred more often in the bay than in other areas, 2) tended to remain in the area for extended periods of weeks or months, and 3) repeatedly used the bay across years. Juvenile *Carcharhinus amboinensis, Carcharhinus fitzroyensis, Carcharhinus sorrah, Carcharhinus limbatus/tilstoni, and Rhizoprionodon acutus* met all three nursery criteria (Table 7.1), allowing me to focus efforts on understanding the species richness patterns displayed by these nursery utilizing species, instead of more transient species occasionally found in the bay. Due to an inability to distinguish *Carcharhinus limbatus* from *Carcharhinus tilstoni* in the field, these two species were treaded as one. Adults were investigated for their potential overlap and possible predation on juveniles, adults having been identified as the only significant predators of juvenile sharks (Springer 1967, Cortés 1999a). Although adult sharks from sixteen species were captured during the project only the adults' from some of the larger species were examined in adult species richness models. This brought the total number of adult species down to twelve in the final model. (Table 7.1).

Table 7.1: Shark species caught in Cleveland Bay, (n = number caught, # of sets = the number of longlines sets which captured at least one shark of the indicated species). Species are organized based on number caught in each of the three categories. Only six of the twelve captured juvenile shark species were used in analysis of juvenile species richness in order to focus my analysis on species which were using Cleveland Bay as a nursery (excluded species are listed under "Juveniles – not used in analysis"). All captured species of adult sharks were used in adult species richness analysis.

Species	n	# of sets	Nursery Area Criteria		
Juveniles			1	2	3
Carcharhinus limbatus/tilstoni	102	53	x	x	x
Carcharhinus amboinensis	69	53	x	x	x
Carcharhinus fitzroyensis	37	24	x	x	x
Carcharhinus sorrah	30	21	x	x	x
Rhizoprionodon acutus	27	15	x	x	x
Juveniles - not used in analysis					
Sphyrna mokarran	25	23		x	x
Sphyrna lewini	19	13		x	x
Rhizoprionodon taylori	12	10		x	x
Galeocerdo cuvier	6	5			x
Stegostoma fasciatum	3	3			x
Carcharhinus dussumieri	1	1			x
Chiloscylium punctatum	1	1			x
Adults					
Carcharhinus sorrah	168	104			
Carcharhinus limbatus/tilstoni	66	43			
Carcharhinus fitzroyensis	27	11			
Sphyrna lewini	25	27			
Carcharhinus macloti	12	8			
Carcharhinus melanopterus	9	5			
Carcharhinus dussumieri	8	7			
Sphyrna mokarran	7	5			
Carcharhinus amboinensis	1	1			
Carcharhinus leucas	1	1			
Hemipristis elongata	1	1			

7.2.3 Species Richness Mapping

Locations for each longline deployment, and all shark species captured on each line, were recorded. The number of unique species captured on individual longlines was summed to give a species richness value for each. Since these data were spatially dispersed, predictive mapping in ArcGIS 9.0 was used to produce a continuous layer of species richness which could be overlaid on a map of the bay to identify patterns of species richness. Kriging (a spatial prediction methodology) can be used to predict species richness in regions with no data that are proximate to areas with observed data (Johnston et al. 2003). Ordinary kriging is the most well known and widely used form of kriging employed by ecologists; it relies on the spatial correlation structure of data to determine the weighting values used to estimate unsampled locations. Indicator kriging follows a similar approach, except that it makes no assumption of normality and is essentially a non-parametric counterpart to ordinary kriging (Moyeed & Papritz 2002). Indicator kriging was therefore appropriate for this study because catch data for sharks are often zero-inflated and thus highly positively skewed, which, coupled with the small number of richness categories, made transforming the data to achieve normality unfeasible. Instead of assuming a normal distribution at each estimate location, indicator kriging builds a cumulative distribution function at each point based on the behavior and correlation structure of indicator transformed data points in the surrounding area (Johnston et al. 2003). To achieve this, indicator kriging needs one or a series of threshold values between the smallest and largest data values in the set. These threshold values, often referred to as indicator kriging cut-offs, are used to numerically build the cumulative distribution function of the estimation point. For my purposes, a cut-off of greater than one was established in order to separate the data into areas with one or less species present from those with more than one species present. Indicator kriging then estimated the probability that the estimation point is above or below the threshold value and uses these probabilities to create an interpolation map which visually depicts patterns of species richness. Standard error maps were produced in ArcGIS using geostatistical analyst to calculate standard errors for both adults and juveniles (Johnston et al. 2003).

Adults were more wide ranging than juveniles and were encountered across a wider area of the bay, causing kriged maps of adult species richness to display higher standard error values. In order to avoid misrepresenting richness data, both juvenile and adult richness maps were cropped in ArcGIS based on standard error estimates. Areas of the bay which were sparely sampled, or which produced limited catch data, displayed high standard errors and were removed from kriged species richness maps. This removal improved confidence in interpolation maps by avoiding the estimation of areas which had limited data.

7.2.4 Boosted Regression Tree Modelling

Boosted regression trees (BRT) were used to evaluate the effect of physical factors on patterns of species richness in the bay. Boosted regression trees produce a large number of relatively simple tree models and combine them adaptively to optimize predictive performance (Elith et al. 2006, Leathwick et al. 2006, Leathwick et al. 2008). This technique allows for the fitting of complex non-linear relationships and often has superior predictive performance when compared to more widely utilized techniques for investigating species-habitat relationships, such as generalized linear and additive models (Elith et al. 2006, Leathwick et al. 2006, Elith et al. 2008, Leathwick et al. 2008, Parisien & Moritz 2009). Modelled results are output into simple-to-navigate fitted functions that depict the influence of predictor variables on, in the case of this paper, the probability of high species richness. The relative importance of predictor variables can also be determined using BRT. Each variable’s influence is scaled to 100 indicating that variables with higher values have a stronger influence on the response variable.

Boosted regression trees have recently been used to look at ecological questions across broad scales (Elith et al. 2006, De'ath 2007, Leathwick et al. 2008, Froeschke et al. 2010a). This is mainly due to their predictive power and ability to map out species richness, or individual species probabilities of occurrence, across large spatial scales. For this paper, however, I utilize the descriptive power of BRT at a finer scale; along with results derived from indicator kriging, these techniques allowed me to map patterns of species richness as well as make predictions as to the physical factors which potentially drive these patterns. Boosted regression tree analyzes were carried out in R (version 2.81, R Development Core Team, 2008) using the ‘gbm’ library supplemented with functions from Elith et al. (2008). Models were fit to allow interactions using a tree complexity of 3 and a learning rate of 0.002. This learning rate was chosen to produce models which generated between 1,000 and 2,000 trees, which is considered optimal (Elith et al. 2008).

Nine predictors (Table 7.2) were selected for their potential functional relevance to the distribution of shark species (and hence species richness). Selection of variables was influenced in part by previous work using boosted regression trees (BRT) to identify relevant factors to the distribution of several shark species (Froeschke et al. 2010a). Salinity and temperature were both measured at the surface (< 2 meters) at the terminal end of longlines upon full deployment of the gear using a refractometer and digital thermometer respectively. Secchi depth, (a proxy for turbidity), was also measured at the terminal end of longline sets using a secchi disk. Set depth was measured at the beginning and end of each line using the boats depth sounder, these measures were averaged to give an indication of depth across the set. Categorical depth (depth strata) was included for two reasons: to test the effect of distance from shore, and because the chosen depth categories represent different available habitats within the bay. The four depth categories were based on isobath lines (Figure 1): 1) foreshore 0-2 meters deep, 2) intertidal mud flats 2-5 meters, 3) subtidal seagrass beds 5-10 meters, and 4) deep waters >10 meters deep. Mangrove proximity was measured in ArcGIS as the distance form longline set midpoints to the edge of the nearest mapped mangrove stand. Mangrove cover was assessed using the Australia New Zealand Land Information Council's coastal waterways geomorphic habitat shapefile (ANZLIC 2009). Probability of seagrass coverage was estimated using model predictions sourced from Grech & Coles (2010); differences in seagrass coverage predicted by the model between the wet (September-February) and dry season (March-August) were accounted for by using wet season seagrass predictions for sharks caught during this season, and vice versa for the dry season. Month and year were also included to assess if species richness varied significantly within these time periods.

Table 7.2: Physical factors used in boosted regression tree models.

Variable	Description	Mean	Range
Secchi Depth (m)	Surface water transparency, assessed using a secchi disk	1.8	0.2-11
Temperature (°C)	Surface temperature at terminal end of longline set	26.6	19.9-34.2
Mangrove Proximity (km)	Distance in km's from set location to nearest mapped mangroves	3.5	0.2-13.2
Average Set Depth (m)	Average of depths measured at each end of longline sets	3.9	0.5-15.9
Salinity (ppt)	Surface salinity at terminal end of longline set	33.2	19.9-34.2
Seagrass Probability (%)	Modelled probability of seagrass cover at set location	0.5	0-0.69
Depth Strata	Categorical depths based on isobath contours	-	-
Season	Season sample occurred	-	-
Year	Year sample occurred	-	-

7.2.5 Physical Factor Mapping

In addition to interpolation maps of species richness, I generated maps of select physical factors examined in my BRT modelling. These maps are not dynamic as they are aggregate over the two years of sampling during the project and so could only represent factors which were relatively stable over time (secchi depth, mangrove cover, etc.). Physical factor maps included maps of secchi depth, depth contours of the bay, mangrove lined shores, and seagrass coverage for both the dry and wet season (Figure 7.2). These maps of modelled BRT physical factors allow a visual assessment of some of the tested factors, facilitating the comparison of kriged species richness data and BRT modelled physical factors.

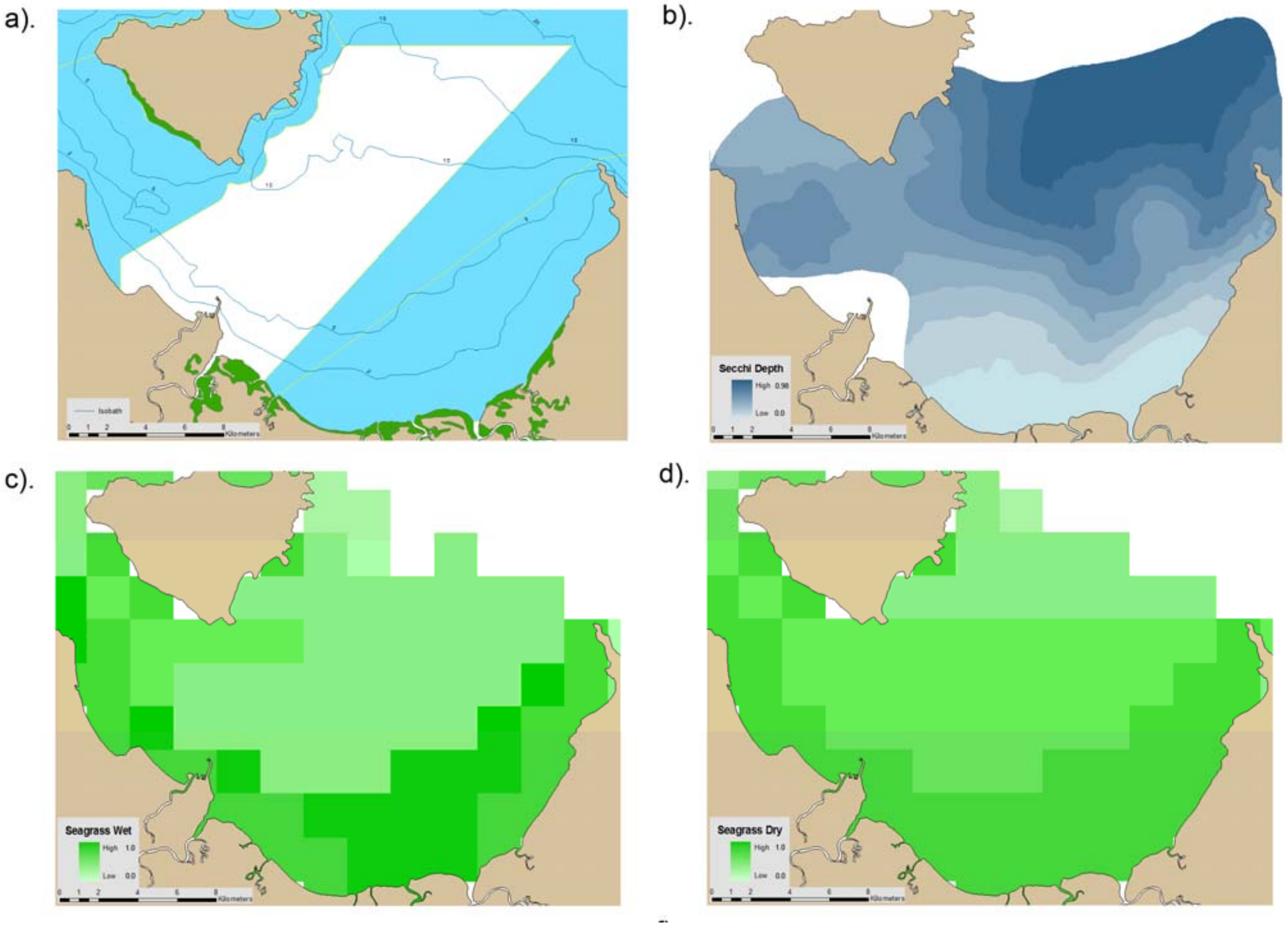


Figure 7.2a-d: Select mapped physical factors used in boosted regression tree (BRT) modelling. Standard error maps were produced for each factor and used to crop maps. Areas of the bay which were sparely sampled and so produced high standard errors were removed from kriged interpolation maps. a) Bathememetry of the bay; lines indicate isobath divisions at 2, 5, 10, 15, and 20 meters. Dark green shore lines identify mangroves. b) Interpolated map of secchi depth (kriging cutoff set at 1.5 meters); darker colors indicate higher visibility. c-d) Mapped probabilities of seagrass coverage during the wet (c) and dry (d) seasons.

7.3 Results

A total of 314 longline sets resulted in the capture and tagging of 990 elasmobranchs during the course of this study (January 2008 – January 2010). Juveniles from the six species identified as using Cleveland Bay as a nursery, along with all captured species of adult sharks, accounted for ~69 % of the total catch (682 individuals). The greatest number of different juvenile shark species captured on any one longline was four, while for adults, species richness on a single longline peaked at six. Mapped juvenile species richness indicated two distinct areas of high richness (Figure 7.3a). Richness was highest in the shallow southern waters of Cleveland Bay near the mangrove lined shores, while a comparatively less rich "secondary" juvenile species-rich location occurred in the deeper central section of the bay. Adult species richness peaked in the central waters of the bay in virtually the same location as the secondary area of juvenile species richness, while near the coast adult species richness was consistently low (Figure 7.3b). These divisions between areas of adult and juvenile species richness reinforce the hypothesis of segregation between life stages of sharks using nurseries.

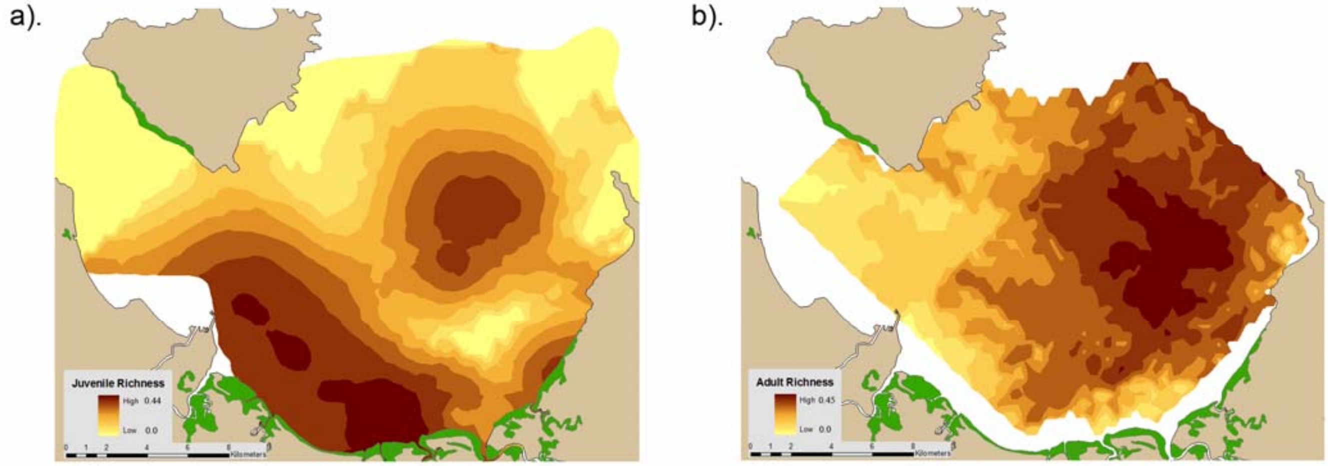


Figure 7.3a-b: Species richness interpolation maps derived by indicator kriging for a) juveniles, and b) adults. Indicator kriging cut-offs for both juveniles and adults were set at values over one, so that maps identify areas with higher or lower probabilities of capturing more than one species of shark. Standard error maps were produced and used to crop species richness interpolation maps. Areas of the bay which were sparely sampled, or which produced limited catch data and so high standard errors were removed from kriged richness maps.

Fitted functions from BRT identified secchi depth (a proxy for turbidity), temperature, seagrass probability, and mangrove proximity as the four most influential predictors of species richness for both juveniles and adults (Figure 7.4). For juveniles, fitted functions identified turbidity and temperature as the two dominant factors influencing species richness (Figure 7.5a). Juvenile richness was highest in areas with high turbidity and temperatures (< 2 m secchi depth and > 30° C). Secchi depths of less than two meters were commonly recorded in the shallow water of the bay; however, water surface temperatures above 30° C were not recorded outside of summer months (December-February), indicating that juvenile species richness peaked in the shallow southern waters of the bay during the summer. Apart from water temperature and turbidity, species richness BRT fitted functions also indicate a positive relationship between juvenile species richness, mangrove proximity, and seagrass probability. Areas with the highest juvenile species richness were those in close proximity to mangroves (< 2 km) and with high modelled probabilities of seagrass cover (> 60 %). Physical factor maps concurred with BRT findings; areas identified through indicator kriging as containing the highest species richness for juveniles included those located predominately closer to mangroves, with high seagrass probabilities, and increased turbidity (Figure 7.2). Although more removed from the mangrove lined coast, the secondary area of juvenile species richness was correlated with an area of increased turbidity, as compared to shrouding waters at the same depth. This spike in turbidity is likely an important factor in the areas status as a secondary area of juvenile species richness.

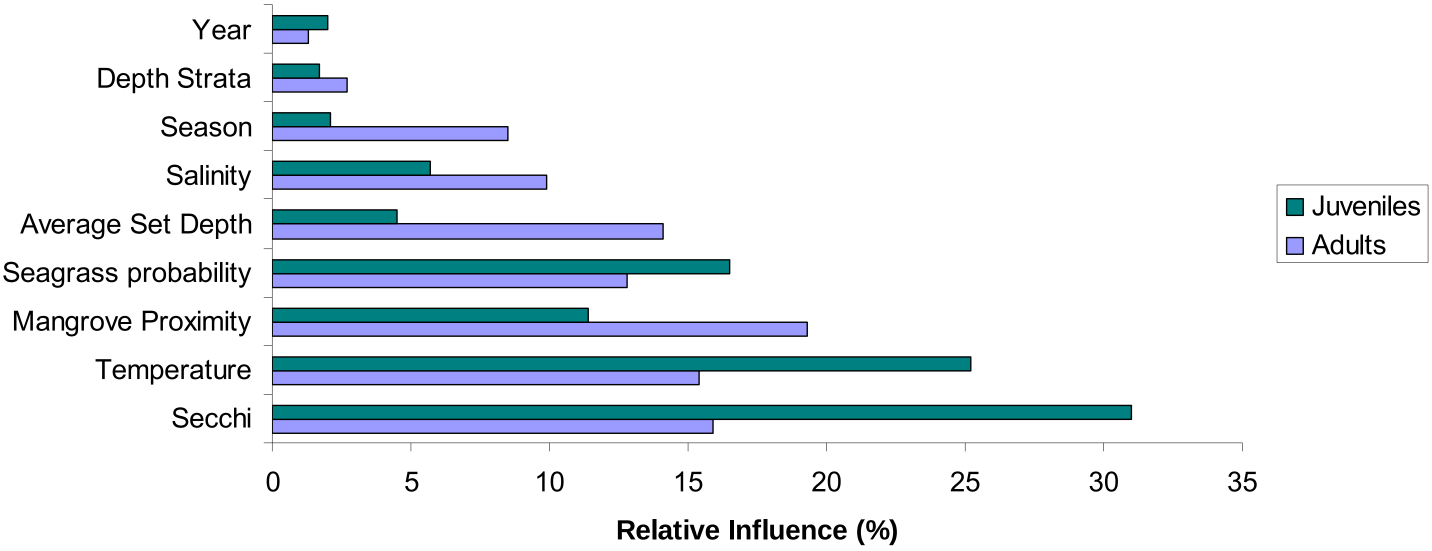
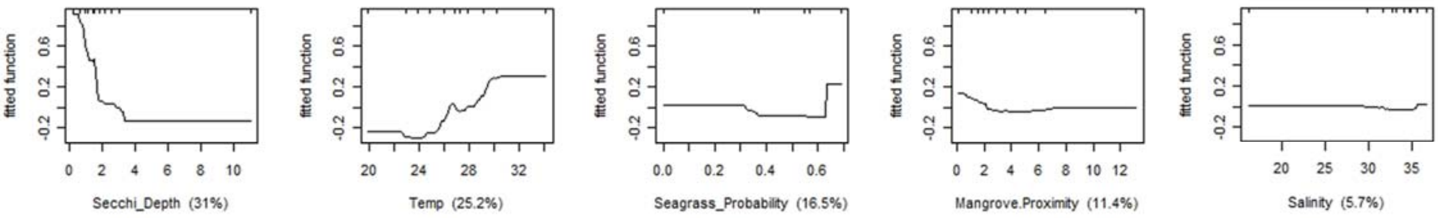


Figure 7.4: Average contributions (%) of examined physical factors in boosted regressions tree models for juvenile and adult shark species richness. Factors are ranked in ascending order based on average overall contribution.

In contrast, adult fitted functions indicated high adult species richness in areas away from mangroves (~ 5 km), with low probabilities of seagrass cover (< 40 %), lower turbidity (~2 m secchi depth). and cooler water temperatures (approximately 25°-29° C) in the slightly deeper central regions of the bay (Figure 7.5b). These findings, as well as the low ranking of set depth (4th most influential factor) suggest that clearer, cooler waters are more important than overall depth since in the shallow waters near Cape Cleveland where these conditions predominate, adult species richness is higher than areas of similar depth near the southern end of the bay where turbidity and water temperatures rise. Again, BRT findings related well to mapped physical factors which identified species-rich areas for adults as those further from mangroves with comparatively lower turbidity, and decreased probabilities of seagrass cover, in relation to areas where juvenile richness was highest (Figure 7.2).

a). Juvenile species richness



b). Adult species richness

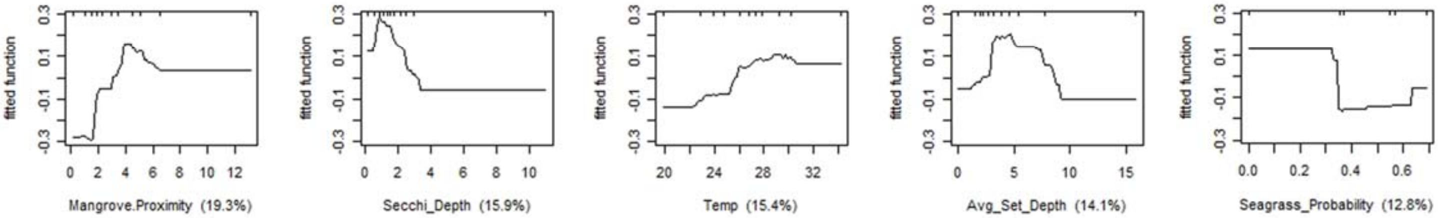


Figure 7.5a-b: Fitted functions of the five most influential physical factors produced from boosted regression trees run on: a) juvenile, and b) adult species richness data. Higher values along the y-axis indicate greater probability of higher species richness. Percentage values under graphs indicate the relative importance of each predictor variable scaled to 100. The deciles of the distribution of the predictors are indicated by tick marks along the top of each plot. Predictor variable codes and units are listed in Table 7.2.

7.4 Discussion

For multi species shark nursery areas a diverse array of niches are important in order to allow sympatric species juveniles to use the same nursery while limiting competition for resources (Michel 2002, Bethea et al. 2004, White et al. 2004, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008). However, my results have indicated that resource partitioning in these environments is coupled with a degree of species overlap, identified by discrete areas of species richness. These species-rich areas are important components of multi species nurseries, and likely of enhanced conservation significance due to their use by the young of several species. The identification and understanding of these species-rich locations could help managers to establish minimum sized areas that could be considered essential for the effective management of multi species shark nurseries.

The division between areas of adult and juvenile richness fits generally with the established nursery area paradigm concerning the limited presence of adults in nursery areas. However, the hypothesis that adults refrain from entering nursery areas and thus avoid shallow water environments (Springer 1967), something that has been reiterated in later works (e.g. Branstetter 1990, Castro 1993, Simpfendorfer & Milward 1993), is not supported by my findings. Results from BRT rank water depth as only the fourth most influential factor on adult shark species richness, and the greatest species richness of adult sharks occurs in waters only five meters deep. This suggests that physical factors other than, or in addition to, depth play an important role in the separation of adults and juveniles in coastal waters, and that adults are not necessarily avoiding shallow water areas.

The importance of physical factors such as turbidity and temperature to juvenile sharks in nursery areas has been observed not only for the sharks in Cleveland Bay, but also for several other shark species in nurseries around the world (White & Potter 2004, Ortega et al. 2009, Froeschke et al. 2010a). Turbidity often peaks in shallow water areas where sediments, disturbed by swell, wind, or tidal actions, become suspended in the water column (Jing & Ridd 1996). It has been suggested that the elasmobranch eye may undergo ontogenetic shifts to accommodate changes in its optical environment (Cohen et al. 1990, Litherland et al. 2009) such that juvenile sharks may be more suited to see in turbid environments than adults. The combination of shallow waters and high turbidity creates an environment which is seldom frequented by adults, where juvenile sharks are less exposed to predation, much like the southern waters of Cleveland Bay. Increased temperature in these waters may also act as a kind of thermal resource, potentially offering benefits to growth and fitness (Magnuson et al. 1979). Several studies have indicated the advantages of beneficial temperatures for many aquatic species (e.g. Wood & McDonald 1997, Gibson et al. 2002, Perry et al. 2005), including sharks (e.g. Hight & Lowe 2007), confirming the importance of temperature as an ecological resource. It is also possible however, that temperatures in these areas are high enough to become suboptimal and detrimentally affect the metabolic rates of sharks, if this is the case it may be that juvenile sharks' trade less than ideal temperatures for greater protection from predation (Heithaus 2007). Regardless, areas of high turbidities, shallow waters, and increased temperatures provide an important refuge for young sharks within Cleveland Bay where adult sharks are less likely to be found.

Apart from turbidity and water temperature, juvenile shark species richness in Cleveland Bay displayed a positive relationship with close mangrove proximity and high seagrass probability. These findings related well to several other nursery studies, focused both on sharks and teleosts, which have found strong correlations between the presence of juveniles and the proximity of mangroves and seagrass beds. Nagelkerken et al. (2001) found that teleost abundance and species richness of nursery aged individuals were high in areas covered by seagrass, and in areas close to mangroves; however, species richness and general abundance were highest in areas that contained both seagrass beds *and* mangroves. Nagelkerken et al. (2001) concluded that proximity to both seagrass beds and mangroves were important parameters for young teleosts in nurseries and that together these environments produced an added beneficial effect and played an important role in the early life of many marine fish species. Pikitch et al. (2005), in a study at Glover's reef off of Belize in Central America, came to a similar conclusion concerning the young of several shark species, as did DeAngelis et al. (2008) for *Negaprion brevirostrisand* and C. limbatus in a nursery off of the United States Virgin Islands. Additionally White & Potter (2004) investigated several species of sharks in Shark Bay Western Australia and found that the highest catch rates and greatest richness of shark species was found in seagrass beds, although they were unable to look a the combined effect of seagrass beds near mangroves. The additive effect of mangrove lined shores and seagrass beds likely relates to both increased prey availability and refuge areas for young sharks (Morrissey & Gruber 1993a, White et al. 2004, White & Potter 2004, DeAngelis et al. 2008). In Cleveland Bay young sharks may refuge in shallow, turbid, seagrass beds, while exploiting both prey in the seagrass and those forced to abandon the shelter of nearby mangrove roots as the tide drops. Together, turbidity, depth, seagrass cover, mangrove proximity, and temperature create a favorable environment for juvenile sharks where they can refuge from predators, exploit available prey, and gain potential growth and fitness benefits provided by advantageous water temperatures.

The observed correlations between the above physical factors and juvenile shark species richness indicated the importance of these combined elements to sharks in nurseries, and also highlighted the advantages gained by juvenile sharks within nurseries, generally supporting the hypothesized advantages assumed in early nursery area work (Springer 1967), although not for the same reasons. However, the secondary area of juvenile species richness identified in interpolation maps did not share all of the same physical factors, and likely did not therefore provide the same advantages. The secondary area was in deeper waters more removed from mangrove lined shores, had lower probabilities of seagrass cover, and overlapped heavily with identified areas of high adult shark species richness. Concurrent work focused on species-specific niche partitioning strategies identified at least one species-- *Carcharhinus sorrah*--that contributed considerably to the secondary peak in juvenile species richness (Chapter 6). Utilizing the deeper central waters of the bay during early life, it was postulated that *C. sorrah* were potentially avoiding competition with juveniles from other sympatric shark species, much like *Carcharhinus perezi* at Glover's reef (Pikitch et al. 2005). Another likely component of the secondary area of juvenile species richness is occasional foraging trips by the juveniles of various shark species into these more exposed waters. It has been observed with *Carcharhinus limbatus* in Florida (Heupel & Hueter 2002), that young sharks sheltering in one area occasionally venture into more exposed locations to exploit alternative dietary resources. The sustained presence of juvenile *C. sorrah*, as well as occasional foraging trips by other sympatric species, is one potential reason for the secondary peak in juvenile species richness. Unfortunately, data regarding the geographic distribution of dietary resources were not available for my study and so could not be included in my models. Although this secondary area appeared in deeper waters where adults are more commonly encountered, the turbidity of the area was greater than surrounding waters of a similar depth. This areas heightened turbidity may be a contributing factor to the increased juvenile species richness observed. High turbidity and greater numbers of juvenile sharks from various species compared to surrounding waters may potentially providing some degree of protection for young sharks in these deeper, more exposed waters. Further work into the importance of this secondary species-rich area of Cleveland Bay is necessary to confirm its role and support my hypotheses.

Identifying areas within multi species nurseries which support the richest communities of juvenile shark species effectively helps focus nursery area management on the key areas and physical factors most important to nursery-utilizing species. These species-rich areas can be seen as minimum starting points from which conservation efforts can be developed. Unfortunately, even the most recent criteria established to help identify shark nurseries were designed primarily to assist in the identification of single species nurseries (Heupel et al. 2007), and can do little to assist in the identification of areas of increased important to several species. This is not surprising since the majority of research directed at shark nurseries has been focused on discrete areas used by one species of shark (Rechisky & Wetherbee 2003, Heupel & Simpfendorfer 2005a, Duncan & Holland 2006, Heupel et al. 2006, Heupel & Simpfendorfer 2008), as opposed to areas which act as nurseries for several shark species. Applying the criteria established for single species nursery area identification to every species in a multi species nursery would be a means of distinguishing nurseries for each species individually. However, without an investigation into areas which support the greatest species richness, this method may overlook key areas which are important to several species and may therefore be of increased conservation significance.

While patterns of species richness may not be fundamental to the identification of an area as a nursery, recognition of species rich habitats will be an important consideration for managers looking to protect communal nurseries. This is not to suggest that only areas which display high species richness are important in terms of nursery area use; but rather, species rich areas could provide a means of efficiently prioritizing a minimum sized area that could be considered essential to effectively manage an environment which functions as a shark nursery for multiple species.

With concerns over the rapidly expanding spatial scale of identified shark nursery areas, as well as their questionable conservation importance without simultaneous management of older individuals, shark nursery areas used by multiple species may provide an advantageous alternative to single species nursery conservation. Such nurseries could allow for the protection of several species within a limited spatial scale, easing concerns of identifying overly vast areas, as well as freeing up resources that could be directed at managing older individuals outside nurseries. However, before such an approach can be put into practice further research into the comparative contributions of single species and multi species shark nurseries to adult shark populations will be necessary.

Much like current efforts to protect global biodiversity, it must be recognized that in shark nursery area management, resources are limited and must be focused in order to achieve the best possible conservation results. Utilizing the Heupel et al. (2007) shark nursery criteria while also considering species richness patterns could prove valuable in identifying key areas within multi species shark nurseries that merit increased conservation consideration, limiting the expense of nursery area protection, thus contributing to a more focused and cost effective approach to shark management.

8 Chapter 8.

A Reassessment of Communal Shark Nurseries: Benefits, Drawbacks, and Conservation Potential

---

8.1 Introduction

'Communal' is a term used to describe something that is shared by, or common to, a group, and typically refers to a beneficial relationship. The term 'communal shark nursery', when first coined, reflected this meaning, and was used to describe nursery environments which afforded beneficial attributes to multiple species of resident juvenile sharks (Simpfendorfer & Milward 1993). At the time of the term's inception, Springer's (1967) paradigm concerning the benefits of nursery areas to young sharks was well established in the scientific literature. Three key observations comprise the core of this prevailing paradigm, each of which has been reiterated in numerous subsequent studies. These include: (1) adult males rarely, if ever, enter the nursery areas of their own species (Hobson 1963, Olsen 1984, Castro 1989, Branstetter 1990, Compagno 1990, Morrissey & Gruber 1993a, Simpfendorfer & Milward 1993); (2) mature females only enter nursery areas when they are gravid and at full term, and stop feeding once they reach the nursery grounds (Olsen 1984, Compagno 1990, Castro 1993, Morrissey & Gruber 1993a, Simpfendorfer & Milward 1993), both important aspects of the hypothesis since adult sharks are considered the only significant predators of juvenile sharks (Springer 1967, Cortés 1999a); and (3) food is not a limiting factor for young sharks within the nursery, and they stay in the vicinity of the nursery grounds while feeding and growing until reaching maturity (Branstetter 1990, Salini et al. 1992, Castro 1993, Simpfendorfer & Milward 1993). These observations, however, were created in reference to areas used by a single shark species. Therefore, when communal nurseries were discovered, Springer's nursery area hypothesis was extended to them, with one significant alteration--if the adults of a species are assumed not to enter into their own nursery areas to feed, than a communal nursery, with its diversity of species, was hypothesized to benefit from several species' adults avoiding the same nursery environment, thus further reducing the risk of predation for resident juvenile sharks (Simpfendorfer & Milward 1993).

Since Simpfendorfer & Milward (1993) only a handful of studies have focused on communal nurseries, investigating subjects such as habitat (Michel 2002, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008) and dietary resource use (Bethea et al. 2004, White et al. 2004). With findings of resource partitioning indicating a limited supply of spatial and dietary resources, evidence is mounting that the benefits derived from communal nursery area use may not be as great as originally hypothesized.

Utilizing supporting evidence from the scientific literature as well as this original research conducted in Cleveland Bay--the first area to be defined as a communal shark nursery (Simpfendorfer and Milward 1993)--I attempt to determine the potential ecological benefits or drawbacks that might be associated with communal shark nursery use. My findings could have significant impacts on the importance of communal nurseries in current and future shark conservation efforts.

8.2 Evaluating the Original Communal Nursery Area Hypotheses

8.2.1 Reduced Predation

Based on the original shark nursery area hypothesis (Springer 1967), adult sharks should generally avoid their own nursery areas, with adult females only entering when gravid and about to give birth. Therefore, predation within a nursery should be lower than outside of it, i.e. juvenile mortality rates due to predation should be relatively low. Contrary to this, several studies within nursery areas have found surprisingly high mortality rates, such as 85 - 93% for *Sphyrna lewini* in Hawaii (Duncan & Holland 2006), 61 – 92% for *Carcharhinus limbatus* in Florida (Heupel & Simpfendorfer 2002), and 38 – 65% for *Negaprion brevirostris* in the Bahamas (Gruber et al. 2001). While it is difficult to identify exact causes of mortality, each of the above studies indicated natural mortality from predation as a contributing source of high mortality rates within shark nurseries. Unfortunately, the focus on juvenile catches during these studies limited the landings of adult animals, principally through the effective utilization of juvenile targeting fishing methods such as small hook hand lines (Duncan & Holland 2006), rod and real (Heupel & Simpfendorfer 2002), or small mess gillnets (Gruber et al. 2001). This limitation made direct identification of predator species difficult. However, several studies, including my own, have recorded the catch of adult male and female sharks on baited lines within nursery areas of their own species, indicating that these animals do indeed feed while on their own nursery grounds (Clarke 1971, Rountree & Able 1996, Merson & Pratt 2001, Duncan & Holland 2006). Therefore, if mortality rates are high and adult sharks have been found feeding within their own nursery areas, the protective advantage gained by young sharks inhabiting nurseries becomes a question of whether adults are found more often inside nurseries than outside of them, and potentially, whether juveniles gain a more effective means of avoiding predation while in nursery areas.

High mortality rates and the catch of adults on baited longlines within shark nursery areas, while suggestive, does not confirm whether the presence of adults *within* nurseries is greater than, or even equal to, their presence outside of them. In Cleveland Bay, therefore, I used longlining to explore patterns of adult and juvenile presence throughout the entire bay (Chapter 6), including the shallow protected waters historically found to act as a nursery (Simpfendorfer & Milward 1993), and the deeper, more exposed waters which are, according to the established shark nursery hypothesis, less likely to represent a nursery environment. My findings indicate that adults, while present in the shallows, predominantly occur separately from juveniles in the deeper more exposed waters of the bay. This does, to an extent, support the hypothesis that adults tend to avoid nursery areas, or at least core refuges within nurseries, and therefore juveniles are gaining some protective advantages through there use. However, I did not find evidence in support of the premise that adult sharks differentiate, and so avoid, their own species' nurseries as opposed to those of other species. Indeed, the adults of resident juvenile species were captured as often as non residents. This suggests that the hypothesized protective benefits of communal nursery area use may not be as high as originally thought and that communal and single species nurseries may, in fact, provide comparable protective advantages.

Many studies have identified shallow depths as a predominant protective advantage afforded to juvenile sharks in nursery areas (Springer 1967, Branstetter 1990, Castro 1993, Simpfendorfer & Milward 1993). While depth does seem to play an important part in the separation of adults and juveniles, my investigation of Cleveland Bay found that a number of other physical factors, such as temperature, turbidity, salinity, and bottom type, also influence the use of inshore nursery areas by juvenile sharks, sometimes more than depth, a finding which has been supported by other nursery area studies (Morrissey & Gruber 1993a, White & Potter 2004, Pikitch et al. 2005, Simpfendorfer et al. 2005, DeAngelis et al. 2008, Ortega et al. 2009, Froeschke et al. 2010a). Of the many factors considered in these investigations, the most consistent factors that appear to have a significant influence on the occurrence of juveniles in nurseries are temperature, turbidity, and bottom type. Together these factors influence both the presence of juveniles within nursery areas, as well as the limited occurrence of adults (Chapter 6). These kinds of environmental divisions are likely an important consideration in the protection juvenile sharks gain from nursery area use.

Where several species utilize the same nursery environment and require, or perhaps tolerate, a range of environmental conditions, many species have been observed to carve out unique ecological niches in response to competition (Bethea et al. 2004, White et al. 2004, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, DeAngelis et al. 2008). A communal nursery whose habitats and resources are partitioned into a number of diverse niches is, theoretically, able to maintain a larger population of juvenile sharks than an un-partitioned single species nursery, in which the number of sharks is restricted by individuals competing over a smaller, or less diverse, resource pool. Unfortunately, it is difficult to find direct comparisons in the scientific literature of juvenile shark populations between similarly sized single species nurseries and communal nurseries. In this absence, parallels can be drawn from studies of fish abundances between temperate and tropical waters. Tropical waters, with their greater diversity of prey species, have been found to support larger communities of both herbivorous and predatory fish compared to more temperate systems (Hobson 1994, Meekan & Choat 1997). Greater prey diversity in tropical waters supports the development of unique dietary niches, with some generalist and some more specialist feeders, facilitating the partitioning of dietary resources amongst sympatric species (de Mérona et al. 2003, Winemiller et al. 2008). Meanwhile, consumers in more temperate waters, where prey diversity is lower, tend to be mostly generalists (Hobson 1994) making it difficult for sympatric species to inhabit the same area without engaging in detrimental levels of competition. Since their establishment in the scientific literature (Simpfendorfer & Milward 1993), communal shark nursery areas have been found principally in tropic or subtropical waters, all of which support diverse prey bases (Michel 2002, Bethea et al. 2004, White et al. 2004, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008). The diversity of prey in these areas would allow greater niche diversity, and so increased abundances of predatory sharks, compared to areas with lower prey diversity and fewer predatory niches, i.e. single species nurseries in temperate waters. Of course this does not mean that all shark nursery areas in tropical waters act as communal nurseries (i.e. Morrissey & Gruber 1993b), but rather that communal nurseries are more likely to occur, or perhaps are even restricted to occurring, in tropical environments.

If larger populations of juvenile sharks are present within a nursery area, predation risk to the individual drops--i.e. reduced per capita mortality rates for aggregated prey, a hypothesis which has been demonstrated for prey which must be targeted individually (such as sharks) as opposed to smaller less mobile prey which can be taken in large numbers via a single attack (such as plankton) (Connell 2000). Aggregation behavior has been observed within shark nursery areas for several species including *Sphyrna lewini*, *Carcharhinus perezi, Negaprion brevirostris, Carcharhinus limbatus,* and others (Clarke 1971, Gruber et al. 1988, Holland et al. 1993, Simpfendorfer & Milward 1993, Merson & Pratt 2001, Lowe 2002, Heupel & Simpfendorfer 2005a, Garla et al. 2006b). The protective advantages of these types of aggregations have been identified in each case. In Cleveland Bay, I analyzed the locations of species aggregations by exploring species richness (Chapter 7). Two primary locations within the bay displayed high juvenile shark species richness--one in the shallow, sheltered waters near the coastline, and another in the comparatively deeper, less sheltered waters of the bay. The first area makes logical sense as a sheltered place where young sharks can refuge from potential predators. However, the more exposed waters seemed an unlikely place to find rich juvenile shark communities. It is possible that the deeper, less sheltered waters of the bay represent a rich feeding area where juveniles from several species are able to exploit different food resources from those available in the more protected shallow waters of the bay (Chapter 7). It may also be, that juveniles frequent these deeper areas during times of adverse environmental conditions in the more sheltered shallow waters of the bay (Knip et al. 2011b). Whether for access to richer feeding grounds, or refuge from adverse conditions, juveniles may be able to offset some of the predation risks associated with these more exposed waters by sheltering in aggregations comprised of several species. Access to these high risk areas for juveniles within communal nurseries would therefore be less perilous than for juveniles in nurseries which contain fewer individuals, and so, smaller aggregations.

8.2.2 Abundant Resources

The concept of abundant dietary resources within shark nurseries was originally based on the assumed richness of coastal environments (Springer 1967, Bass 1978, Branstetter 1990), or, in the case of communal nurseries, a limited pool of evidence suggesting overlapping prey species in stomach contents which was interpreted as an abundance of resources (Simpfendorfer & Milward 1993). The hypothesis of plentiful food supplies within shark nurseries has persisted until relatively recently (Heupel et al. 2007). However, utilizing a combination of stable isotopes and stomach content analysis, I was able to determine that young sharks within Cleveland Bay partition dietary resources as a result of competition among sympatric species (Kinney et al. 2011). Other studies have identified similar findings of dietary resource partitioning within nurseries containing more than one shark species (Bethea et al. 2004, White et al. 2004). With partitioning of available dietary resources a population of sharks can potentially grow larger than in areas with fewer dietary niches where population sizes are constrained by a less diverse prey base. This constricted prey base could force species into competitive interactions for a single or limited number of ecological niches thus limiting predator population sizes.

Resource partitioning among species within communal shark nurseries goes beyond dietary resources, as both spatial and temporal separation are also apparent among juvenile sharks (Michel 2002, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008). This new evidence suggests that early hypotheses concerning the limited existence of dietary, spatial, and temporal resource partitioning strategies among juvenile sharks within communal nurseries were perhaps an overly simplistic view of the ecology of these areas. However, the strict separation of species via resource partitioning is an equally inadequate hypothesis. While resource partitioning among juveniles in communal nursery areas is apparent, some degree of overlap, as discussed above regarding species richness, appears to be an important benefit of communal nursery use. Such overlap could potentially allow for greater protection from predation, or access to high risk resources, or a combination of the two (Chapter 7).

8.2.3 Benefits and Drawbacks

It has been argued that nursery area use can include tradeoffs; e.g. some species use nurseries that have limited resources but provide increased protection from predation, while others inhabit resource rich nurseries that are more exposed and so have comparatively high levels of predation (Branstetter 1990, Gruber et al. 2001, Heithaus 2007). Often these tradeoffs are tied to a species' life history (Branstetter 1990), with smaller, faster growing species benefiting from more exposed nurseries which provide them with ample resources that allow rapid growth out of the vulnerable juvenile stage. In contrast, slower growing species benefit from protected nurseries where they can safely reside during a longer early life stage. I propose that communal nurseries have the potential to provide a combination of the two. When juveniles of several species inhabit one communal nursery area but exploit unique niches, the total number of young sharks able to use the nursery without reduced fitness levels due to competition is theoretically greater than a comparatively sized single species nursery. As discussed in the above section, this increased number of juveniles within communal nurseries allows for larger aggregations of sharks, which in turn limits the risk of predation to the individual. This reduction in predation allows juvenile sharks to utilize more exposed, potentially resource rich waters while maintaining a degree of protection from predation greater than that offered by its ambient environment. In a sense, communal nursery areas may blur the distinction between nurseries that predominantly offer resources versus those that offer protection. However, future work examining advantages to growth rates and survivorship within single species nurseries compared to communal ones will need to be carried out in order to validate these hypotheses.

Unfortunately, the diversity of prey species which seem to be required to maintain juvenile shark populations within communal nurseries largely limits them to more tropical waters, as evidenced by the locations of identified shark nurseries which support several species' juveniles (Michel 2002, Bethea et al. 2004, White et al. 2004, White & Potter 2004, Pikitch et al. 2005, Yokotaa & Lessa 2006, Wiley & Simpfendorfer 2007, DeAngelis et al. 2008). This does potentially exclude temperate and cold water shark species from inhabiting communal nurseries, although further research will be necessary to confirm this. However, for species capable of utilizing communal nurseries, the benefits to juveniles (as discussed here) are potentially greater than those gained through single species nursery area use.

8.3 Communal Nursery Areas and the Larger Picture of Shark Conservation

Over the years an extensive body of research has arisen focused on shark nurseries (See Heithaus 2007, Heupel et al. 2007, McCandless et al. 2007 for reviews). However, until relatively recently, little attention had been paid to the overall value of nursery area conservation in the recovery of exploited shark populations (Kinney & Simpfendorfer 2009). It appears that for some species, even total protection of their nurseries would do little to stem the tide of population decline without sufficient protection for older individuals residing outside nurseries. While this may seem an argument for the abandonment of nursery area conservation efforts, the interpretation of these data must be made cautiously. The key is to understand the connection between adult and juvenile populations--just as protecting nursery areas while ignoring older individuals leads to population declines, so too does protecting adults while ignoring nursery areas. A balanced strategy is what is needed for effective shark conservation; yet this is inherently difficult.

Juvenile sharks and nursery areas are some of the more well studied and understood aspects of shark biology and ecology. The reasons for this are that, in general, adult shark populations are wider ranging, more mobile, and less concentrated than their juvenile counterparts. The most comprehensive studies conducted on adult sharks to date have been carried out on particular concentrations of individuals in repeatedly used feeding or mating grounds (Klimley & Nelson 1984, Heyman et al. 2001, Arauz & Antoniou 2006, Domeier & Nasby-Lucas 2007, Hearn et al. 2010), or in unique habitats that contain more site attached species such as reef sharks (Garla et al. 2006a, Garla et al. 2006b, Papastamatiou et al. 2009, Field et al. 2011). For the most part, adult populations are logistically difficult and expensive to study, while juveniles, residing in coastal nursery areas, allow for easy access to denser populations providing a comparatively cheap and simple alternative. Additionally, nursery areas provide a discrete environment which can be identified and protected, while adults inhabit more open waters that can span multiple jurisdictional boundaries and economic exclusion zones. In international waters, where sharks are taken commonly as by-catch (Bonfil 1994, FAO 2002), traditional conservation and management approaches such as protected areas and catch quotas often prove too costly, or difficult to enforce (Barker & Schluessel 2005). Despite the difficultly involved in studying adult shark populations it is clear that without increased knowledge and more effective management at adult stages, efforts to conserve juvenile populations in nursery areas will largely be unsuccessful (Kinney & Simpfendorfer 2009).

The disproportionate focus of current conservation efforts on shark nursery areas has led to vast coastal areas being defined as shark nurseries. With so many areas identified as nurseries for one species or another, often with limited supporting evidence, the total area of identified shark nurseries is rapidly becoming unmanageable (Heupel et al. 2007). Heupel et al. (2007) confronted this problem by establishing more restrictive criteria which could be used to refine nursery area identification to those areas that truly provide beneficial nursery environments to young sharks. This research further builds upon such work by highlighting the potential importance of communal shark nursery areas. Communal nurseries are capable of supporting diverse communities of juvenile sharks in limited, discrete areas. The protection of one communal nursery area could potentially benefit several species of sharks on a more manageable spatial scale than the protection of each species individually within single species nurseries. Additionally, as discussed above, communal nurseries may provide additional protection and increased access to dietary resources via species aggregations, making them valuable nursery environments for those species capable of using them, i.e. tropical species. For more temperate water shark species which are potentially unable to benefit from communal nursery use, or species which are simply not found within communal nurseries, single species nursery area protection remains an important management component.

More restrictive identification criteria as well as increased focus on communal shark nurseries will not only help make shark nursery area management more efficient and feasible, but it could also increase available conservation resources for adult shark management. The reduced cost and effort needed to conserve smaller total shark nursery assets could potentially assist managers in targeting shark populations outside of nurseries. This would require a multinational approach, similar to the international shark plans already adopted by several countries (FAO 1999, also see Barker & Schluessel 2005 for an overview of international mechanisms adopted for the protection and management of shark resources since 1994). Additionally, greater effort could be placed on developing more selective gears which limit the by-catch of shark species in longline fisheries. In particular, a more active role in regulating the catch of threatened and endangered species should be a priority. For example, techniques for determining the species of disembodied shark fins have already been developed and can be used to identify illegally harvested shark fins (Shivji et al. 2005, Wong et al. 2009, Johnson 2010). Essentially, shark conservation is a global issue which will require extensive resources and manpower in order to succeed, and like all large projects, resources must be properly targeted to provide the greatest benefit with the least waste. Communal shark nurseries can provide managers with a useful means of refining nursery area conservation to protect multiple species without the drawback of identifying vast unmanageable areas.

8.4 Future Research Directions

My research has provided an increased understanding of communal shark nursery areas by clarifying some of the misconceptions and highlighting the benefits associated with them. The prevalence of resource partitioning among sympatric shark species indicates that a delicate balance, rather than an overabundance of resources, is likely what allows these areas to function as communal nurseries. This balance is also an important factor which allows large populations of juvenile sharks to utilize a single nursery, something which underpins the potential benefits gained by young sharks within communal nurseries. Future research focused on comparing the community structure of various communal nurseries could be useful in identifying the level of consistency between different areas. For example, do all communal nursery areas function in the same way, with diverse species partitioning resources and gaining protection from beneficial conditions and large populations? Or, do ecological benefits vary depending on the species within, or the location of, the nursery? Further work concerning species aggregations could help elucidate drivers behind such behavior and increase our understanding of species interactions within communal nurseries. Additionally, stable isotope research on the prey communities that support communal shark nursery areas could help establish individual species niche widths and lead to a better understanding of the food web within these environments.

8.5 Conclusion

My original research, supported by additional findings in the literature, demonstrates that communal shark nurseries do provide beneficial or "communal" attributes to the juvenile sharks that use them, although not for the reasons originally proposed. Communal nurseries may thus provide a cost-effective management alternative to the protection of vast single species shark nursery areas. Further work is needed to determine whether results from Cleveland Bay are applicable to communal nurseries in general; however, the inclusion of communal nurseries in shark management plans could prove important in balancing conservation efforts between juvenile and adult populations.

References

ANZLIC (2009) Queensland coastal waterways geomorphic habitat mapping, Version 2 (1:100 000 scale digital data).

Arauz R, Antoniou A (2006) Preliminary results: Movements of scalloped hammerhead sharks (*Sphyrna lewini*) tagged in Cocos Island National Park, Costa Rica. Memoria: Primer Seminario Taller Sobre el Estado del Conocimiento de la Condrictio fauna de Costa Rica. pp 8–9 (in Spanish).

Baird RW, Abrams PA, Dill LM (1992) Possible indirect interactions between transient and resident killer whales: Implications for the evolution of foraging specializations in the genus Orcinus. Oecologia 89:125-132

Baker R, Sheaves M (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. Mar Ecol Prog Ser 291:197-213

Barker MJ, Schluessel V (2005) Managing global shark fisheries: Suggestions for prioritizing management strategies. Aquat Conservat Mar Freshwat Ecosyst 15:325-347

Barnett A, Redd KS, Frusher SD, Stevens JD, Semmens JM (2010) Non-lethal method to obtain stomach samples from a large marine predator and the use of DNA analysis to improve dietary information. J Exp Mar Biol Ecol 393:188-192

Bass AJ (1978) Problems in studies of sharks in the southwest Indian Ocean. In: Hodgson ES, Mathewson RF (eds) Sensory Biology of Sharks, Skates and Rays. Office of Naval Research, Department of the Navy, Arlington, VA

Baum JK, Myers RA (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecol Lett 7:135-145

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the Northwest Atlantic. Science 299:389-392

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: A novel approach using stable isotope analysis. J Anim Ecol 73:1007-1012

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633-641

Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol-Prog Ser 268:245-264

Bethea DM, Hollensead LD, Carlson JK (2006) Shark nursery grounds and essential fish habitat studies. In. Report to NOAA Fisheries, Highly Migratory Species Office, Panama City, FL

Bizzarro J, Robinson H, Rinewalt C, Ebert D (2007) Comparative feeding ecology of four sympatric skate species off central California, USA. Environ Biol Fish 80:197-220

Blaber SJM, Brewer DT, Salini JP (1995) Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the gulf of Carpentaria, Australia. Estuarine, Coastal and Shelf Science 40:177-193

Blackburn JK, Neer JA, Thompson BA (2007) Delineation of bull shark nursery areas in the inland and coastal waters of Louisiana. In: McCandless CT, Kohler NE, Pratt

HL (eds) Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States, Book Symposium 50. American Fishers Society, Bethesda, Maryland

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Physiol Pharmacol 37:911-917

Bonfil R (1994) Overview of world elasmobranch fisheries. FAO Fisheries Technical Paper 341:1-119

Bonfil R (1997) Status of shark resources in the southern Gulf of Mexico and Caribbean: Implications for management. Fish Res 29:101-117

Bonfil R Marine protected areas as a shark fisheries management tool. In: Seret B, Sire JY (eds). Proc Proceedings of the 5th Indo-Pacific Fish Conference Noumea, 1997. Societe Francaise d'Ichtyologie, Paris and Istitut de Recherche pour le Developement, Paris

Brander K (1981) Disappearance of common skate *Raia batis* from Irish Sea. Nature 290:48-49

Branstetter S (1990) Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In: NOAA Tech Rep 1990, Book NMFS

Brewer DT, Blaber SJM, Salini JP, Farmer MJ (1995) Feeding ecology of predatory fishes from Groote-Eylandt in the Gulf of Carpentaria, Australia, with special reference to predation on penaeid prawns. Estuar Coast Shelf Sci 40:577-600

Brewster-Geisz KK, Miller TJ (2000) Management of the sandbar shark, *Carcharhinus plumbeus*: Implications of a stage-based model. Fish Bull 98:236-249

Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL (2006) Global biodiversity conservation priorities. Science 313:58-61

Brown CA, Gruber SH (1988) Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. Copeia 1988:747-753

Burgess GH, Beerkircher LR, Cailliet GM, Carlson JK, Cortes E, Goldman KJ, Grubbs RD, Musick JA, Musyl MK, Simpfendorfer CA (2005a) Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? Fish 30:19-26

Burgess GH, Beerkircher LR, Cailliet GM, Carlson JK, Cortes E, Goldman KJ, Grubbs RD, Musick JA, Musyl MK, Simpfendorfer CA (2005b) Reply to "Robust estimates of decline for pelagic shark populations in the Northwest Atlantic and Gulf of Mexico". Fish 30:30-31

Bush A (2003) Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks, *Sphyrna lewini*, in Kane'ohe Bay, O'ahu, Hawai'i. Environ Biol Fish 67:1-11

Bush A, Holland K (2002) Food limitation in a nursery area: Estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834) in Kane'ohe Bay, O'ahu, Hawai'i. J Exp Mar Biol Ecol 278:157-178

Camhi M (1999) Sharks on the line II: An analysis of Pacific state shark fisheries, Vol. National Audubon Society, Living Oceans Program, Islip, NY

Carlson JK, Heupel MR, Bethea DM, Hollensead LD (2008) Coastal habitat use and residency of juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*). Estuaries Coasts 31:931-940

Case TJ, Bolger DT, Petren K (1994) Invasions and competitive displacement among house geckos in the tropical Pacific. Ecology 75:464-477

Castro JI (1989) The biology of the golden hammerhead, *Sphyrna-Tudes*, off Trinidad. Environ Biol Fish 24:3-11

Castro JI (1993) The shark nursery of Bulls Bay, South-Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fish 38:37-48

Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors (Δ15N and Δ13C): The effect of diet isotopic values and applications for diet reconstruction. J Appl Ecol 46:443-453

Chaloupka M (2002) Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. Ecol Model 148:79-109

Cherel Y, Le Corre M, Jaquemet S, Menard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: New information from stable isotopes. Mar Ecol Prog Ser 366:281-291

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial

Clarke KR, Warwick RM (2001) Change in marine communities: An approach to statistical analysis and interpretation, 2nd edition.

Clarke TA (1971) The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. Pac Sci 25:133-144

Cohen JL, Hueter RE, Organisciak DT (1990) The presence of a porphyropsin-based visual pigment in the juvenile lemon shark (*Negaprion brevirostris*). Vision Res 30:1949-1953

Compagno LJV (1990) Alternative life-history styles of cartilaginous fishes in time and space. Environ Biol Fish 28:33-75

Compagno LJV (2002) Sharks of the world. An annotated and illustrated catalogue of shark species known to date., Vol 2. FAO, Rome

Compagno LJV, Dando M, Fowler S (2005) Princeton field guides: Sharks of the world, Vol. Princeton University Press, Princeton, New Jersey

Connell SD (2000) Is there safety-in-numbers for prey? Oikos 88:527-532

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. Can J Fish Aquat Sci 54:726-738

Cortés E (1999a) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707-717

Cortés E (1999b) A stochastic stage-based population model of the sandbar shark in the western north Atlantic. In: Musick JA (ed) Life in the Slow Lane: Ecology and Conservation of Long Lived Marine Animals. American Fisheries Society Symposium 23., Bethesda, Maryland.

Cortés E, Brown CA, Beerkircher LR (2007) Relative abundance of pelagic sharks in the western north Atlantic Ocean, including the Gulf of Mexico and Caribbean Sea. Gulf Caribb Res 19:135-145

Crowder LB, Crouse DT, Heppell SS, Martin TH (1994) Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecol Appl 4:437-445

Cruz-Motta JJ, Collins J (2004) Impacts of dredged material disposal on a tropical soft-bottom benthic assemblage. Mar Pollut Bull 48:270-280

Cunjak RA, Roussel JM, Gray MA, Dietrich JP, Cartwright DF, Munkittrick KR, Jardine TD (2005) Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. Oecologia 144:636-646

Das K, Lepoint G, Loizeau V, Debacker V, Dauby P, Bouquegneau JM (2000) Tuna and dolphin associations in the north-east Atlantic: Evidence of different ecological niches from stable isotope and heavy metal measurements. Mar Pollut Bull 40:102-109

De'ath G (2007) Boosted trees for ecological modeling and prediction. Ecology 88:243-251

de Freitas RHA, Rosa RS, Wetherbee BM, Gruber SH (2009) Population size and survivorship for juvenile lemon sharks (Negaprion brevirostris) on their nursery grounds at a marine protected area in Brazil. Neotrop Ichthyol 7:205-212

de Mérona B, Vigouroux R, Horeau V (2003) Changes in food resources and their utilization by fish assemblages in a large tropical reservoir in South America (Petit-Saut Dam, French Guiana). Acta Oecol 24:147-156

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United States Virgin Islands: Evidence of habitat partitioning by two shark species. Mar Ecol-Prog Ser 358:257-271

DeBach P (1966) The competitive displacement and coexistence principles. Annu Rev Entomol 11:183-212

DeMaster DP, Fowler CW, Perry SL, Richlen MF (2001) Predation and competition: The impact of fisheries on marine-mammal populations over the next one hundred years. J Mammal 82:641-651

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495-506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341-351

Dibattista JD, Feldheim KA, Gruber SH, Hendry AP (2007) When bigger is not better: Selection against large size, high condition and fast growth in juvenile lemon sharks. J Evol Biol 20:201-212

Domeier M, Nasby-Lucas N (2007) Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). Mar Biol 150:977-984

Domi N, Bouquegneau JM, Das K (2005) Feeding ecology of five commercial shark species of the Celtic Sea through stable isotope and trace metal analysis. Mar Environ Res 60:551-569

Dudley SFJ (1997) A comparison of the shark control programs of New South Wales and Queensland (Australia) and KwaZulu-Natal (South Africa). Ocean & Coastal Management 34:1-27

Dudley SFJ, Cliff G (1993) Some effects of shark nets in the Natal nearshore environment. Environ Biol Fish 36:243-255

Dudley SFJ, Simpfendorfer CA (2006) Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978-2003. Mar Freshw Res 57:225-240

Duncan KM, Holland KN (2006) Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. Mar Ecol-Prog Ser 312:211-221

Elith J, Graham CH, Anderson RP, Dudik M, others a (2006) Novel methods improve prediction of species distributions for occurrence data. Ecography 29:129-151

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802-813

Ellis JR, Pawson MG, Shackley SE (1996) The comparative feeding ecology of six species of shark and four species of ray (elasmobranchii) in the north-east Atlantic. J Mar Biol Assoc U K 76:89-106

Estrada JA, Lutcavage M, Thorrold SR (2005) Diet and trophic position of Atlantic bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen isotope analysis. Mar Biol 147:37-45

Estrada JA, Rice AN, Lutcavage ME, Skomal GB (2003) Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. J Mar Biol Assoc U K 83:1347-1350

Estrada JA, Rice AN, Natanson LJ, Skomal GB (2006) Use of isotopic analysis of vertebrae in reconstructiong ontogenetic feeding ecology in white sharks. Ecology 87:829-834

FAO (1999) International plan of action for the conservation and management of sharks. In, Rome

FAO (2002) Yearbook: Fishery statistics: Capture production 2000. In: 90/1 FFS (ed) Food and Agricultural Organization for the United Nations, Rome

Feldheim KA, Gruber SH, Ashley MV (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. Proceedings of the Royal Society of London Series B: Biological Sciences 269:1655-1661

Field I, Meekan M, Speed C, White W, Bradshaw C (2011) Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. Coral Reefs 30:61-71

Fisk AT, Tittlemier SA, Pranschke JL, Norstrom RJ (2002) Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of Greenland sharks. Ecology 83:2162-2172

Fodrie FJ, Levin LA (2008) Linking juvenile habitat utilization to population dynamics of California halibut, Vol 53. American Society of Limnology and Oceanography, Waco, TX, ETATS-UNIS

Fogarty MJ, Murawski SA (1998) Large-scale disturbance and the structure of marine systems: Fishery impacts on Georges Bank. Ecol Appl 8:S6-S22

Frisk MG, Miller TJ, Dulvy NK (2005) Life histories and vulnerability to exploitation of elasmobranchs: Inferences from elasticity, perturbation and phylogenetic analyses. J Northwest Atl Fish Sci 35:27-45

Froeschke J, Stunz GW, Wildhaber ML (2010a) Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar Ecol Prog Ser 407:279-292

Froeschke JT, Stunz GW, Sterba-Boatwright B, Wildhaber ML (2010b) An empirical test of the 'shark nursery area concept' in Texas bays using a long-term fisheries-independent data set. Aquat Biol 11:65-76

Gallucci VF, Taylor IG, Erzini K (2006) Conservation and management of exploited shark populations based on reproductive value. Can J Fish Aquat Sci 63:931-942

Garla RC, Chapman DD, Shivji MS, Wetherbee BM, Amorim AF (2006a) Habitat of juvenile Caribbean reef sharks, *Carcharhinus perezi*, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. Fish Res 81:236-241

Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006b) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: The potential of marine protected areas for conservation of a nursery ground. Mar Biol 149:189-199

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220-227

GBRMPA (2005) Research needs for protection and management of the Great Barrier Reef Marine Park. In, Townsville

Gibson RN, Robb L, Wennhang H, Burrows MT (2002) Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. Mar Ecol Prog Ser 229:233-244

Gingras D, Renaud A, Mousseau N, Béliveau R (2000) Shark cartilage extracts as antiangiogenic agents: Smart drinks or bitter pills? Cancer Metastasis Rev 19:83-86

Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J Fish Biol 66:650-667

Gray JS (1997) Marine biodiversity: Patterns, threats and conservation needs. Biodivers Conserv 6:153-175

Grech A, Coles RG (2010) An ecosystem-scale predictive model of coastal seagrass distribution. Aquat Conserv 20:437-444

Gruber SH (1982) Role of the lemon shark, *Negaprion brevirostris* (Poey) as a predator in the tropical marine environment: A multidisciplinary study. Fla Sci 45:46-75

Gruber SH, de Marignac JRC, Hoenig JM (2001) Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. Trans Am Fish Soc 130:376-384

Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. Bull Mar Sci 43:61-76

Hammerschlag N, Fallows C (2005) Galapagos sharks (*Carcharhinus galapagensis*) at the Bassas da India atoll: First record from the Mozambique Channel and possible significance as a nursery area. S Afr J Sci 101:375-377

Hardy TA (1991) Impact on Townsville's beaches of proposed extension to the Port of Townsville. In: Townsville Port Authority draft impact assessment study, eastern harbour expansion (Appendix E 13), Townsivlle

Harry AV, Tobin AJ, Simpfendorfer CA, Welch DJ, Mapleston A, White J, Williams AJ, Stapley J (2011) Evaluating catch and mitigating risk in a multispecies, tropical, inshore shark fishery within the Great Barrier Reef World Heritage Area. Mar Freshw Res 62:710-721

Harvey CJ, Hanson PC, Essington TE, Brown PB, Kitchell JF (2002) Using bioenergetics models to predict stable isotope ratios in fishes. Can J Fish Aquat Sci 59:115-124

Hassan ZM, Feyzi R, Sheikhian A, Bargahi A, Mostafaie A, Mansouri K, Shahrokhi S, Ghazanfari T, Shahabi S (2005) Low molecular weight fraction of shark cartilage can modulate immune responses and abolish angiogenesis. Int Immunopharmacol 5:961-970

Hastie T, Tibshirani R, Friedman JH (2001) The elements of statistical learning: Data mining, inference, and prediction. Springer, New York

Hearn A, Ketchum J, Klimley A, Espinoza E, Peñaherrera C (2010) Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos Marine Reserve. Mar Biol 157:1899-1915

Heithaus MR (2004) Predator-Prey Interactions. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Florida

Heithaus MR (2007) Nursery areas as essential shark habitats: A theoretical perspective. In: McCandless CT, Kohler NE, Pratt HL (eds) Shark nursery grounds of the Gulf of Mexico and east coast waters of the United States. American Fisheries Society Symposium, Bethesda, MD

Heppell SS, Crowder LB, Crouse DT (1996a) Models to evaluate headstarting as a management tool for long-lived turtles. Ecol Appl 6:556-565

Heppell SS, Crowder LB, Menzel TR (1999) Life table analysis of long-lived marine species with implications for conservation and management. In: Musick JA (ed) Life in the slow lane: Ecology and conservation of long lived marine animals. American Fisheries Society Symposium 23., Bethesda, Maryland.

Heppell SS, Limpus CJ, Crouse DT, Frazer NB, Crowder LB (1996b) Population model analysis for the loggerhead sea turtle, *Caretta caretta*, in Queensland. Wildl Res 23:143-161

Heupel MR (2007) Exiting Terra Ceia Bay: Examination of cues stimulating migration from a summer nursery area. In: McCandless CT, Kohler NE, Pratt HL (eds) Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States. American Fisheries Society, Bethesda MD, pp. 265-280

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: Concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287-297

Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Mar Freshw Res 53:543-550

Heupel MR, Simpfendorfer CA (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Can J Fish Aquat Sci 59:624-632

Heupel MR, Simpfendorfer CA (2005a) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar Biol 147:1239-1249

Heupel MR, Simpfendorfer CA (2005b) Using acoustic monitoring to evaluate MPAs for shark nursery areas: The importance of long-term data. Mar Tech Soc J 39:10-18

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat Biol 1:277-289

Heupel MR, Simpfendorfer CA (2010) Science or slaughter: Need for lethal sampling of sharks. Conserv Biol 24:1212-1218

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. Environ Biol Fish 76:47-67

Heyman WD, Graham RT, Kjerfve B, Johannes RE (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Mar Ecol-Prog Ser 215:275-282

Hight BV, Lowe CG (2007) Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? J Exp Mar Biol Ecol 352:114-128

Hobson E (1994) Ecological relations in the evolution of acanthopterygian fishes in warm-temperate communities of the northeastern Pacific. Environ Biol Fish 40:49-90

Hobson ES (1963) Feeding behavior in three species of sharks. Pac Sci 17:171-194

Hobson KA, Ambrose WG, Jr., Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from delta13C and delta15N analysis. Mar Ecol Prog Ser 128:1-10

Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon J-M, Fortier M (2002) A stable isotope ([delta]13C, [delta]15N) model for the North Water food web: Implications for evaluating trophodynamics and the flow of energy and contaminants. Deep Sea Research Part II: Topical Studies in Oceanography 49:5131-5150

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high arctic marine food web using delta-C-13 and delta-N-15 analysis. Mar Ecol-Prog Ser 84:9-18

Hoenig JM, Gruber SH Life-history patterns in the elasmobranchs: Implications for fisheries management. In: Pratt HL, Gruber SH, Taniuchi T (eds) NOAA Technical Report NMFS 90. Proc Elasmobranchs as living resources: Advances in the biology, ecology, systematics, and the status of the fisheries Proceedings of the second United States-Japan workshop

Holland KN, Wetherbee BM, Peterson JD, Lowe CG (1993) Movements and distribution of hammerhead shark pups on their natal grounds. Copeia:495-502

Hueter RE, Manire CA, Tyminski JP, Hoenig JM, Hepworth DA (2006) Assessing Mortality of Released or Discarded Fish Using a Logistic Model of Relative Survival Derived from Tagging Data. Trans Am Fish Soc 135:500-508

Hussey NE, Brush J, McCarthy ID, Fisk AT (2010a) [delta]15N and [delta]13C diet-tissue discrimination factors for large sharks under semi-controlled conditions. Comp Biochem Physiol Part A Mol Integr Physiol 155:445-453

Hussey NE, Wintner SP, Dudley SFJ, Cliff G, Cocks DT, Aaron MacNeil M (2010b) Maternal investment and size-specific reproductive output in carcharhinid sharks. J Anim Ecol 79:184-193

Hussey NE, Wintner SP, Dudley SFJ, Cliff G, Cocks DT, MacNeil MA (2009) Maternal investment and size-specific reproductive output in carcharhinid sharks. J Anim Ecol 9999

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harbor Symp Quant Biol 22:415-427

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-637

Jennings D, Gruber S, Franks B, Kessel S, Robertson A (2008) Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. Environ Biol Fish 83:369-377

Jing L, Ridd PV (1996) Wave-current bottom shear stresses and sediment resuspension in Cleveland Bay, Australia. Coastal Engineering 29:169-186

Johnson R (2010) The use of DNA identification in prosecuting wildlife-traffickers in Australia: Do the penalties fit the crimes? Forensic Science, Medicine, and Pathology 6:211-216

Johnston K, Ver Hoef JM, Krivoruchko K, Lucas N (2003) Using ArcGIS Geostatistical Analyst, Vol

Kerr L, Andrews A, Cailliet G, Brown T, Coale K (2006) Investigations of Δ14C, δ13C, and δ15N in vertebrae of white shark (Carcharodon carcharias) from the eastern North Pacific Ocean. Environ Biol Fish 77:337-353

Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA (2011) Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. Mar Ecol Prog Ser 439:263-276

Kinney MJ, Simpfendorfer CA (2009) Reassessing the value of nursery areas to shark conservation and management. Conserv Lett 2:53-60

Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: A refuging central-position social system. Behav Ecol Sociobiol 15:45-54

Knip DM, Heupel MR, Simpfendorfer CA (2010) Sharks in nearshore environments: Models, importance, and consequences. Mar Ecol Prog Ser 402:1-11

Knip DM, Heupel MR, Simpfendorfer CA, Moloney J (2011a) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Mar Ecol Prog Ser 425:233-246

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011b) Wet-season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. Mar Freshw Res 62:658-667

Kurle CM, Worthy GAJ (2002) Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal *Callorhinus ursinus*: Implications for dietary and migratory reconstructions. Mar Ecol-Prog Ser 236:289-300

Last PR, Stevens JD (1994) Sharks and rays of Australia, Vol. CSIRO Division of Fisheries., Australia

Last PR, Stevens JD (2009) Sharks and rays of Australia, Vol. CSIRO Publishing, Australia

Lavery S, Shaklee JB (1991) Genetic evidence for separation of two sharks, *Carcharhinus limbatus* and *C. tilstoni*, from Northern Australia. Mar Biol 108:1-4

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecol Lett 10:937-944

Leathwick JR, Elith J, Chadderton WL, Rowe D, Hastie T (2008) Dispersal, disturbance, and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. Journal Biogeography 35

Leathwick JR, Elith J, Francis MP, Hastie T, Taylor P (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. Mar Ecol Prog Ser 321:267-281

Lee A, Langer R (1983) Shark cartilage contains inhibitors of tumor angiogenesis. Science 221:1185-1187

Litherland L, Collin SP, Fritsches KA (2009) Visual optics and ecomorphology of the growing shark eye: A comparison between deep and shallow water species. J Exp Biol 212:3583-3594

Logan J, Lutcavage M (2010) Stable isotope dynamics in elasmobranch fishes. Hydrobiologia 644:231-244

Lowe CG (2002) Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kane'ohe Bay, O'ahu, HI. J Exp Mar Biol Ecol 278:141-156

MacNeil MA, Drouillard K, Fisk AT (2006) Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Can J Fish Aquat Sci 63:345-353

MacNeil MA, Skomal GB, Fisk AT (2005) Stable isotopes from multiple tissues reveal diet switching in sharks. Mar Ecol-Prog Ser 302:199-206

Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. Am Zool 19:331-343

Manire CA, Gruber SH A preliminary estimate of natural mortality of age-0 lemon sharks, *Negaprion brevirostris.* In: Branstetter S (ed) NMFS 115. Proc Conservation Biology of Elasmobranchs. NOAA (National Oceanic and Atmospheric Administration) technical report NMFS (National Marine Fisheries Service).

Mazaris AD, Broder B, Matsinos YG (2006) An individual based model of a sea turtle population to analyze effects of age dependent mortality. Ecol Model 198:174-182

McCandless CT, Kohler NE, Pratt HL (eds) (2007) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States, Vol Symposium 50. Am. Fish. Soc. Symp. 50, Bethesda, Maryland

McMeans BC, Olin JA, Benz GW (2009) Stable-isotope comparisons between embryos and mothers of a placentatrophic shark species. J Fish Biol 75:2464-2474

Meek A (1916) The migrations of fish. Edward Arnold, London

Meekan MG, Choat JH (1997) Latitudinal variation in abundance of herbivorous fishes: A comparison of temperate and tropical reefs. Mar Biol 128:373-383

Merson RR, Pratt HL (2001) Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. Environ Biol Fish 61:13-24

Merson RR, Pratt HL (2007) Sandbar shark nurseries in New Jersey and Ney York: Evidence of northern pupping grounds along the United States east coast. In: McCandless CT, Kohler NE, Pratt HL (eds) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Maryland

Michel M (2002) Environmental factors affecting the distribution and abundance of sharks in the mangrove estuary of the Ten Thousand Islands, Florida, USA. PhD PhD Thesis, University of Basel, Switzerland,

Michener RH, Schell DM (1994) Stable isotope ratios as tracers in marine and aquatic food webs. In: Lajtha K, Michener RH (eds) Stable isotopes in ecology and environmental science. Blackwell Scientific Publications, Oxford

Mihuc TB (1997) The functional trophic role of lotic primary consumers: Generalist versus specialist strategies. Freshw Biol 37:455-462

Miller TJ, Frisk MG, Fogarty MJ (2003) Comment on Mollet and Cailliet (2002): Confronting models with data. Mar Freshw Res 54:737-738

Mittermeier RA, Myers N, Thomsen JB, Da Fonseca GAB, Olivieri S (1998) Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conserv Biol 12:516-520

Mollet HÂ F, Cailliet GÂ M (2003) Reply to comments by Miller et al. (2003) on Mollet and Cailliet (2002): Confronting models with data. Mar Freshw Res 54:739-744

Morrissey JF, Gruber SH (1993a) Habitat Selection by Juvenile Lemon Sharks, Negaprion Brevirostris. Environ Biol Fish 38:311-319

Morrissey JF, Gruber SH (1993b) Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 2:425-434

Moyeed R, Papritz A (2002) An empirical comparison of kriging methods for nonlinear spatial point prediction. Mathematical Geology 34:365-386

Musick JA (1999a) Ecology and conservation of long-lived marine animals. In: Musick JA (ed) Life in the slow lane: Ecology and conservation of long lived marine animals. American Fisheries Society Symposium 23., Bethesda, Maryland.

Musick JA (ed) (1999b) Life in the slow lane: Ecology and conservation of long-lived marine animals, Vol. Am. Fish. Soc. Symp. 23

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). Fish 25:9-13

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846-1850

Nagelkerken I, Dorenbosch M, Verberk WCEP, Morinière ECdl, Velde Gvd (2000) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: Patterns in biotope association, community structure and spatial distribution. Mar Ecol Prog Ser 202:175-192

Nagelkerken I, Kleijnen S, Klop T, van der Brand RACJ, Cocheret de la Morinière E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats : A comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar Ecol Prog Ser 214:225-235

Nagelkerken I, van der Velde G (2004) Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. Mar Ecol Prog Ser 274:153-159

Nelson JS (1994) Fishes of the world, Vol. John Wiley & Sons, Inc., New York

Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961-974

NOAA (1996) Magnusen-Stevens fishery conservation and management act, as amended through Oct. 11, 1996. In: NOAA tech memo NMFS-F/SPO-23. National Marine Fisheries Service, Silver Spring, MD

Olin JA, Hussey NE, Fritts M, Heupel MR, Simpfendorfer CA, Poulakis GR, Fisk AT (2011) Maternal meddling in neonatal sharks: Implications for interpreting stable isotopes in young animals. Rapid Commun Mass Spectrom 25:1-9

Olsen AM (1959) The status of the school shark fishery in south-eastern Australian waters. Mar Freshw Res:27

Olsen AM (1984) Synopsis of biological data on the school shark, *Galeorhinus australis*. FAO Fisheries Synopsis 139, 42

Ortega L, Heupel M, Beynen P, Motta P (2009) Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary. Environ Biol Fish 84:361-373

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90:996-1008

Parisien MA, Moritz MA (2009) Environmental controls on the distribution of wildfire at multiple spatial scales. Ecol Monogr 79:127-154

Parsons GR (1993) Age determination and growth of the bonnethead shark *Sphyrna tiburo*: A comparison of two populations. Mar Biol 117:23-31

Parsons GR, Hoffmayer ER (2005) Seasonal changes in the distribution and relative abundance of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the north central Gulf of Mexico. Copeia:914-920

Paterson AW, Whitfield AK (2000) Do shallow-water habitats function as refugia for juvenile fishes? Estuarine, Coastal and Shelf Science 51:359-364

Paterson G, Drouillard K (2006) Quantifying resources partitioning in centrachids with stable isotope analysis. Limnol Oceanogr 51:1038-1044

Pauly D (2009) Beyond duplicity and ignorance in global fisheries. Sci Mar 73:215-224

Pekcan-Hekim Z, Lappalainen J (2006) Effects of clay turbidity and density of pikeperch (*Sander lucioperca*) larvae on predation by perch (*Perca fluviatilis*). Naturwissenschaften 93:356-359

Perga ME, Gerdeaux D (2005) 'Are fish what they eat' all year round? Oecologia 144:598-606

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912-1915

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293-320

Piercy AN, Carlson JK, Sulikowski JA, Burgess GH (2007) Age and growth of the scalloped hammerhead shark, Sphyrna lewini, in the north-west Atlantic Ocean and Gulf of Mexico. Mar Freshw Res 58:34-40

Pikitch EK, Chapman DD, Babcock EA, Shivji MS (2005) Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). Mar Ecol-Prog Ser 302:187-197

Pinkas LM, Oliphant S, Iverson ILK (1971) Foot habits of albacore, bluefin tuna and bonito in Californian waters. California Fish and Game Bulletin 152:1-105

Pinkerton MH, Smith ANH, Raymond B, Hosie GW, Sharp B, Leathwick JR, Bradford-Grieve JM (2010) Spatial and seasonal distribution of adult *Oithona similis* in the Southern Ocean: Predictions using boosted regression trees. Deep Sea Research Part I: Oceanographic Research Papers 57:469-485

Pinnegar JK, Campbell N, Polunin NVC (2001) Unusual stable isotope, fractionation patterns observed for fish host-parasite trophic relationships. J Fish Biol 59:494-503

Pinnegar JK, Polunin NVC (1999) Differential fractionation of delta C-13 and delta N-15 among fish tissues: Implications for the study of trophic interactions. Funct Ecol 13:225-231

Platell ME, Potter IC, Clarke KR (1998) Resource partitioning by four species of elasmobranchs (Batoidea : Urolophidae) in coastal waters of temperate Australia. Mar Biol 131:719-734

Poore GCB, Wilson GDF (1993) Marine species richness. Nature 361:597-598

Post D, Layman C, Arrington D, Takimoto G, Quattrochi J, Montaña C (2007) Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179-189

Post DM (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83:703-718

Pressey RL, Humphries CJ, Margules CR, Vane-Wright RI, Williams PH (1993) Beyond opportunism: Key principles for systematic reserve selection. Trends Ecol Evol 8:124-128

Prince JD (1992) Stock assessment and fisheries management in the southern shark fishery: An independent perspective. In: Authority AFM (ed) SharkFAG Doc, Canberra

Prince JD (2005) Gauntlet fisheries for elasmobranchs - the secret of sustainable shark fisheries. J Northw Atl Fish Sci 35:407-416

Punt AE, Walker TI, Taylor BL, Pribac F (2000) Standardization of catch and effort data in a spatially-structured shark fishery. Fish Res 45:129-145

Pyle P, Schramm MJ, Keiper C, Anderson SD (1999) Predation on a white shark (*Carcharodon carcharias*) by a killer whale (*Orcinus orca*) and a possible case of competitive displacement. Mar Mamm Sci 15:563-568

R Development Core Team (2008) R: A language and environment for statistical computing R Foundation for Statistical Computing Vienna, Austria

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fish 68:113-128

Roberts CM (2000) Selecting marine reserve locations: Optimality versus opportunism. Bull Mar Sci 66:581-592

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280-1284

Robertson A, Duke N (1987) Mangroves as nursery sites: Comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Mar Biol 96:193-205

Rountree RA, Able KW (1996) Seasonal abundance, growth, and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary. Fish Bull 94:522-534

SAG, Lack M (2004) National plan of action for the conservation and management of sharks (Shark-plan). In. Australian Government Department of Agriculture, Fisheries and Forestry

Sala E, Knowlton N (2006) Global marine biodiversity trends. Annual Review of Environment and Resources 31:93-122

Salini JP, Blaber SJM, Brewer DT (1990) Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. Mar Biol 105:363-374

Salini JP, Blaber SJM, Brewer DT (1992) Diets of sharks from estuaries and adjacent waters of the north-eastern Gulf of Carpentaria, Australia. Aust J Mar Freshw Res 43:87-96

Schlacher TA, Liddell B, Gaston TF, Schlacher-Hoenlinger M (2005) Fish track wastewater pollution to estuaries. Oecologia 144:570-584

Shackell NL, Frank KT (2003) Marine fish diversity on the Scotian Shelf, Canada. Aquat Conservat Mar Freshwat Ecosyst 13:305-321

Shepherd TD, Myers RA (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. Ecol Lett 8:1095-1104

Shivji MS, Chapman DD, Pikitch EK, Raymond PW (2005) Genetic profiling reveals illegal international trade in fins of the great white shark, *Carcharodon carcharias*. Conserv Genet 6:1035-1039

Simpfendorfer CA (1993) Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori,* from north Queensland, Australia. Environ Biol Fish 36:233-241

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

Simpfendorfer CA (1999) Demographic analysis of the dusky shark fishery in southwestern Australia. In: Musick JA (ed) Life in the slow lane: Ecology and conservation of long lived marine animals. American Fisheries Society Symposium 23., Bethesda, Maryland.

Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. Estuaries 28:78-85

Simpfendorfer CA, McAuley RB, Chidlow J, Unsworth P (2002) Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. Mar Freshw Res 53:567-573

Simpfendorfer CA, Milward NE (1993) Utilization of a tropical bay as a nursery area by sharks of the Families Carcharhinidae and Sphyrnidae. Environ Biol Fish 37:337-345

Skomal GB (2007) Shark nursery areas in the coastal waters of Massachusetts. In: McCandless CT, Kohler NE, Pratt HL (eds) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Maryland

Springer S (1967) Social organization of shark populations. In: P.W. G, Mathewson RF, D.P. R (eds) Sharks, skates, and rays. John Hopkins Press, Baltimore

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000a) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476-494

Stevens JD, Lyle JM (1989) Biology of three hammerhead sharks (*Eusphyra blochii, Sphyrna mokarran and S. lewini*) from Northern Australia. Mar Freshw Res 40:129-146

Stevens JD, McLoughlin KJ (1991) Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. Australian Journal of Marine & Freshwater Research 42:151-199

Stevens JD, Simpfendorfer CA, Francis M (2005a) Southwest Pacific, Australasia and Oceania. In: Sharks, rays and chimaeras: The status of the chondrichthyan fishes.

IUCN/SSC Shark Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK

Stevens JD, Walker TI, Cook SF, Fordham SV (2005b) Threats faced by chondrichthyan fish. In: Fowler S, Cavanagh RD, Camhi M, Burgess G, Caille G, Fordham S, Simpfendorfer C, Musick J (eds) Sharks, rays and chimaeras: The status of the chondrichthyan fishes. The World Conservation Union (IUCN), Gland, Switzerland

Stevens JD, West GJ (1997) Investigations of school and gummy shark nursery areas in south eastern Australia. In: FRDC Project 93/061. CSIRO Marine Research: Hobart.

Stevens JD, West GJ, McLoughlin KJ (2000b) Movements, recapture patterns, and factors affecting the return rate of carcharhinid and other sharks tagged off northern Australia. Mar Freshw Res 51:127-141

Stevens JD, Wiley PD (1986) Biology of 2 commercially important carcharhinid aharks from northern Australia. Aust J Mar Freshw Res 37:671-688

Stewart KM, Bowyer RT, Kie JG, Cimon NJ, Johnson BK (2002) Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. J Mammal 83:229-244

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285-1293

Taylor S (2007) Population structure and resource partitioning among carcharhiniform sharks in Moreton Bay, southeast Queensland, Australia. PhD, University of Queensland,

Thomas CJ, Cahoon LB (1993) Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. Mar Ecol-Prog Ser 95:19-24

Tillett BJ, Meekan MG, Field IC, Hua Q, Bradshaw CJA (2011) Similar life history traits in bull (*Carcharhinus leucas*) and pig-eye (*C. amboinensis*) sharks. Mar Freshw Res 62:850-860

van der Elst RP (1979) Proliferation of small sharks in the shore based natal sport fishery. Environ Biol Fish 4:349-362

Van der Molen S, Caille G (2001) Bahia Engano: a north Patagonian nursery area for the smoothhound shark *Mustelus schmitti* (Carcharhiniformes : Triakidae). J Mar Biol Assoc U K 81:851-855

Van Winkle W (1975) Comparison of several probabilistic home-range models. J Wildl Manag 39:118-123

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet δ^{15}N enrichment: A meta-analysis. Oecologia 136:169-182

Vaudo JJ, Matich P, Heithaus MR (2010) Mother–offspring isotope fractionation in two species of placentatrophic sharks. J Fish Biol 77:1724-1727

Walker TI (1998) Can shark resources be harvested sustainably? A question revisited with a review, of shark fisheries. Mar Freshw Res 49:553-572

Wetherbee BM, Gruber SH, Cortes E (1990) Diet, feeding habits, digestion, and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. NOAA Tech Rep NMFS:17-28

White WT, Platell ME, Potter IC (2004) Comparisons between the diets of four abundant species of elasmobranchs in a subtropical embayment: Implications for resource partitioning. Mar Biol 144:439-448

White WT, Potter IC (2004) Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Mar Biol 145:1023-1032

Wiley TR, Simpfendorfer CA (2007) The ecology of elasmobranchs occurring in the Everglades National Park, Florida: Implications for conservation and management. Bull Mar Sci 80:171-189

Williams H, Schaap AH (1992) Preliminary results of a study into the incidental mortality of sharks in gill-nets in two Tasmanian shark nursery areas. Aust J Mar Freshw Res 43:237-250

Wilson RP, La Cock GD, Wilson MP, Mollagee F (1985) Differential digestion of fish and squid in jackass penguins, *Spheniscus demersus*. Ornis Scandinavica 16:77-79

Winemiller KO, Agostinho AA, Caramaschi EP (2008) Fish ecology in tropical streams. In: Dudgeon D (ed) Tropical stream ecology. Academic Press, Amsterdam, Netherlands

Wong EHK, Shivji MS, Hanner RH (2009) Identifying sharks with DNA barcodes: Assessing the utility of a nucleotide diagnostic approach. Molecular Ecology Resources 9:243-256

Wood CM, McDonald DG (eds) (1997) Global warming: Implications for freshwater and marine fish, Vol. Cambridge University Press, Cambridge

Yokotaa L, Lessa RP (2006) A nursery area for sharks and rays in northeastern Brazil. Environ Biol Fish 75:349-360

1 Appendix 1.
All Species δ 13C and δ 15N Values

Species	Tissue Type	n	δ ^{13}C	δ ^{15}N	C:N
R. taylori	Muscle	11	-15.52 (± 0.79)	12.06 (± 0.56)	3.27 (± 0.11)
	Plasma	11	-15.81 (± 0.15)	11.61 (± 0.40)	3.80 (± 0.04)
	Red Blood	11	-16.08 (± 0.15)	11.57 (± 0.40)	3.43 (± 0.05)
L. calcarifer	Muscle	11	-15.70 (± 1.13)	13.69 (± 1.31)	3.29 (± 0.08)
	Plasma	11	-15.95 (± 0.78)	12.91 (± 1.18)	3.69 (± 0.06)
	Red Blood	11	-16.42 (± 0.96)	12.14 (± 1.24)	3.48 (± 0.29)
E. tetradactylum	Muscle	11	-14.59 (± 0.66)	12.70 (± 0.30)	3.30 (± 0.08)
	Plasma	11	-14.46 (± 0.57)	11.50 (± 0.62)	3.77 (± 0.06)
	Red Blood	11	-15.34 (± 0.98)	11.53 (± 0.59)	3.63 (± 0.21)
C. fitzroyensis	Muscle	9	-14.49 (± 0.60)	12.85 (± 0.37)	3.19 (± 0.12)
	Plasma	9	-14.71 (± 0.50)	10.99 (± 0.46)	3.76 (± 0.04)
	Red Blood	9	-15.23 (± 0.49)	11.90 (± 0.61)	3.36 (± 0.05)
C. macloti	Muscle	10	-15.81 (± 0.31)	12.07 (± 0.33)	3.36 (± 0.07)
	Plasma	10	-15.37 (± 0.44)	10.34 (± 0.30)	3.83 (± 0.07)
	Red Blood	10	-16.17 (± 0.36)	11.25 (± 0.33)	3.44 (± 0.07)
R. acutus	Muscle	9	-15.25 (± 0.75)	12.31 (± 0.37)	3.24 (± 0.07)
	Plasma	9	-15.50 (± 0.57)	10.99 (± 0.27)	3.81 (± 0.07)
	Red Blood	9	-15.92 (± 0.32)	11.88 (± 0.36)	3.38 (± 0.05)
C. amboinensis	Muscle	10	-13.32 (± 1.30)	12.32 (± 0.69)	3.22 (± 0.26)
	Plasma	10	-14.49 (± 1.07)	11.47 (± 0.73)	3.72 (± 0.05)
	Red Blood	10	-14.59 (± 0.95)	11.66 (± 0.38)	3.36 (± 0.05)
S. queenslandicus	Muscle	10	-16.28 (± 0.29)	11.62 (± 0.21)	3.27 (± 0.05)
	Plasma	10	-16.75 (± 0.39)	11.77 (± 0.23)	3.72 (± 0.07)
	Red Blood	10	-17.07 (± 0.21)	11.36 (± 0.26)	3.59 (± 0.06)
C. sorrah	Muscle	9	-14.93 (± 1.34)	12.04 (± 0.57)	3.31 (± 0.14)
	Plasma	9	-15.52 (± 0.81)	10.37 (± 0.34)	3.84 (± 0.06)
	Red Blood	9	-15.76 (± 0.79)	11.37 (± 0.25)	3.47 (± 0.04)
C. limbatus/tilstoni	Muscle	11	-14.67 (± 0.77)	12.58 (± 0.82)	3.40 (± 0.07)
	Plasma	11	-14.37 (± 1.08)	10.87 (± 0.82)	3.74 (± 0.11)
	Red Blood	11	-15.00 (± 1.06)	11.35 (± 0.55)	3.45 (± 0.08)

Appendix 2: Summary of δ15N, δ13C and C:N values with (mean ± SD) of examined shark and teleost species in Cleveland Bay across all tissue types

2 Appendix 2.
Species Stomach Content %IRI Calculations

Shark Species	Prey Items	%Nc	%Wc	%Fo	%IRI
R. taylori (n=46)	Engraulidae (Anchovy spp.)	7.7	7.5	11.1	4.4
	Clupeidae (Herring spp.)	19.2	29.5	44.4	56.3
	Mullidae (Goatfish spp.)	3.8	3.7	11.1	2.2
	Scombridae (Mackerel spp.)	3.8	21	11.1	7.2
	Leiognathidae (Ponyfish spp.)	61.5	33.4	11.1	27.4
	Polynemidae (Threadfin spp.)	3.8	4.9	11.1	2.5
R. acutus (n=130)	Engraulidae (Anchovy spp.)	1.5	0.7	2.1	0.2
	Clupeidae (Herring spp.)	17.9	25.7	19.1	28.7
	Callionymidae, Draconettidae (Dragonet spp.)	1.5	4.1	2.1	0.4
	Soleidae, Bothidae, etc. (Flat Fish spp.)	32.8	22.6	21.3	40.7
	Mullidae (Goatfish spp.)	1.5	2.4	2.1	0.3
	Synodontidae (Saurida spp.)	1.5	0.3	2.1	0.1
	Scombridae (Mackerel spp.)	1.5	15.1	2.1	1.2
	Mugilidae (Mullet spp.)	1.5	3.5	2.1	0.4
	Leiognathidae (Ponyfish spp.)	13.4	7.7	14.9	10.9
	Penaeidae (Prawn spp.)	14.9	5.8	17	12.2
	Loliginidae (Squids)	6	8.3	6.4	3.2
	Hydrophiidae (Sea Snake spp.)	4.5	2.1	6.4	1.5
	Haemulidae (Sweetlip Spp.)	1.5	1.7	2.1	0.2
C. amboinensis (n=33)	Engraulidae (Anchovy spp.)	18.2	2.5	10	5
	Carcharhinidae (Shark spp.)	9.1	87.5	10	23.5
	Crustaceans (Crab spp.)	9.1	0.4	10	2.4
	Hydrophiidae (Sea Snake spp.)	45.5	7.2	50	64.1
	Polynemidae (Threadfin spp.)	9.1	1.5	10	2.6
	Triacanthidae, Triacanthodidae (Tripodfish spp.)	9.1	0.9	10	2.4
C. sorrah (n=224)	Apogonidae (Apogon spp.)	0.5	0.1	0.9	0.2
	Gerridae (Gerres spp.)	4.1	7.3	3.5	2.2
	Clupeidae (Herring spp.)	12.4	13.3	15.9	21.9
	Sciaenidae (Croaker and Jewfish spp.)	1.4	6.1	2.7	1.2
	Spirulidae (Cuttlefish spp.)	1.4	2.5	2.7	0.6
	Soleidae, Bothidae, etc. (Flat Fish spp.)	0.9	0.1	1.8	0.1
	Terapontidae (Striped Grunter spp.)	2.3	5.4	3.5	1.4
	Mullidae (Goatfish spp.)	11.1	10.2	7.1	8.1
	Menidae (Moonfish spp.)	0.9	0.9	1.8	0.2
	Leiognathidae (Ponyfish spp.)	29	14.8	16.8	39.5
	Penaeidae (Prawn spp.)	7.4	2.2	10.6	5.5
	Loliginidae (Squids)	2.8	1.8	5.3	1.3
	Haemulidae (Sweetlip Spp.)	12	19	8.8	14.6
	Polynemidae (Threadfin spp.)	1.4	3	2.7	0.6
	Tetraodontidae (Toadfish spp.)	1.4	1.1	1.8	0.2
	Carangidae (Trevally spp.)	2.3	0.2	1.8	1
	Sillaginidae (Whiting spp.)	3.7	2.1	4.4	1.4

C. limbatus/tilstoni (n=309)	Engraulidae (Anchovy spp.)	0.8	0.3	1.5	0.1
	Gerridae (Gerres spp.)	1.6	4.6	3.1	0.8
	Ariidae (Catfish spp.)	2.5	0.4	4.6	0.5
	Clupeidae (Herring spp.)	27.9	21	23.1	45.1
	Mullidae (Goatfish spp.)	5.7	2.8	3.1	1.1
	Synodontidae (Saurida spp.)	1.6	7	3.1	1.1
	Scombridae (Mackerel spp.)	4.1	12.5	6.2	4.1
	Leiognathidae (Ponyfish spp.)	18	6	10.8	10.4
	Penaeidae (Prawn spp.)	2.5	1.7	4.6	0.8
	Loliginidae (Squids)	21.3	19.5	15.4	25.1
	Polynemidae (Threadfin spp.)	7.4	10.8	12.3	8.9
	Carangidae (Trevally spp.)	1.6	9.1	3.1	1.7

Appendix 3: Percent index of relative importance values (%IRI) based on stomach content analysis of commercially caught sharks.