What makes a house a home: Examining the relationship between growth and predation risk in a coastal elasmobranch, the lemon shark (*Negaprion brevirostris)*

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Abstract

Many shark species are known to use nursery grounds, though few use coastal habitats in the same manner as juvenile lemon sharks. Lemon sharks pup in shallow, coastal areas and although the reasons for this behaviour are unknown, the two most likely explanations are access to food and avoidance of predators. This thesis aimed to examine these ideas by testing the hypotheses that a) sites with high resource availability will yield high juvenile lemon shark abundance and b) an increase in predation risk will result in decreased juvenile lemon shark abundance and increased individual growth rates. Seine nets were set to capture juvenile lemon sharks and their fish prey. Drum lines were used to measure predator abundance outside of each of the nine study inlets, while ARCGIS mapping software was used to assess site-specific refuge availability across the entire tidal cycle. Juvenile lemon shark abundances correlated strongly with mojarra (*Gerres* spp*.)*, their preferred food item. Lemon sharks also showed a weak, but non-significant positive relationship with refuge availability, but not with predator abundance. Individuals in areas with high predator presence however, showed increased growth rates. Our data suggest that juvenile lemon shark populations exhibit frequency-dependent habitat selection with respect to prey availability. Moreover, the results indicate that of the variables studied, food availability primarily determined habitat quality in nursery grounds, with a less important role for predation pressure. If lemon shark populations are constrained by juvenile recruitment, appropriate management of their coastal nursery areas offer a powerful conservation tool.

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beach, from CEI to the OSC and from the hockey rink to the stone, I have enjoyed every second of my time at MUN. I can only hope that this project inspires future students to think outside the box.

Dedication

This thesis is dedicated to my parents, Bruce and Cherie Hamilton. They have stood as pillars of stability throughout my entire life and have provided me with unwavering motivation during my graduate career. Without them, I would not be the man I am today. Above all, they have bestowed upon me the means with which to succeed, a gift I will forever strive to become worthy of.

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Chapter 1

INTRODUCTION

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Introduction and Overview

According to the fossil record, sharks have inhabited the oceans for over 400 million years (Camhi et al., 1998). They have survived ice ages and large scale environmental shifts. However, since the inception of commercial fishing, global shark populations have declined as much as 89% for some species, largely because of commercial by-catch and finning (Hoenig and Gruber, 1990; Feldheim et al., 2002; Baum et al, 2003). As K-selected (slow life history) species with late maturity and low reproductive rates, sharks are difficult to fish sustainably (NMFS 2006; Feldheim et al. 2002; Gruber and Parks 2002) and are highly susceptible to other forms of human disturbance (e.g. habitat destruction). Many shark species act as apex predators in their respective environments, and removal of these animals can result in environmental degradation and trophic cascades (Myers et al. 2007; Heithaus et al. 2008).

Some areas of the world have been proactive in protecting shark populations. Island nations such as Palau and The Maldives recently passed legislation banning both shark capture and export in their territorial waters. In The Bahamas, long line fishing was banned in 1993 and in July 2011, legislation was passed banning all commercial shark exports, effectively turning over 264,000 square kilometers of territorial waters into a shark sanctuary. This type of legislation offers a template and precedent for many other coastal and non-coastal nations involved in shark fishing.

Shark populations also have the economic potential to generate significant financial revenues. Ecotourism involving sharks has increased throughout the past two decades and offers substantial profit by protecting current populations while simultaneously promoting species conservation (Topelko and Dearden, 2005). Similarly, these animals offer a service to the marine environment. By maintaining apex predator populations, marine ecosystems remain healthy and resilient and pay dividends to the natural environment often used for eco-tourism. However, many shark species have large home ranges and extensive migration routes, putting them in danger of capture when they leave protected areas. Even with protective measures in place, many coastal species, such as the lemon shark (*Negaprion brevirostris)*, remain at risk from tourism-driven coastal development (Feldheim, 2002; Jennings, 2008; DiBattista, 2010).

Beyond the looming threat of habitat loss, other factors affect juvenile sharks in their nursery habitats. Coastal inlets, used by multiple species as nurseries, offer access to elevated densities of potential prey items, while simultaneously providing protection from pelagic predators. However, a nursery habitat is a time dependent space because juveniles eventually require either more resource, or a different type of resource. The resulting niche shift will be directly affected by resource availability, what type of resource is needed, the level of competition found within each habitat, and, ultimately, the intensity of pressure exerted by external predators.

The effect of predation on the growth and development of individuals is an important component to consider when looking at aquatic ecosystems (Werner et al., 1983; Connell, 2002). High predation rates can lower growth rates by altering normal foraging patterns (Werner et al., 1983; Werner and Gillam, 1984). The relationship between growth and mortality risk has been examined previously in several shark species (Heithaus 2007; Heupel et al. 2007). In many cases, larger conspecifics often comprise the main predator within nurseries (Gruber et al., 2001; Freitas et al., 2009), but their effects on juvenile growth and distribution require further investigation. Equally important is the availability and distribution of potential prey items. Resource availability has been repeatedly shown as a major factor influencing habitat selection (Abrahams, 1989; Moody et al. 1996).

The way in which animals develop in their nursery environments often strongly reflects the stresses and influences around them (Hoenig and Gruber, 1990; Freitas et al., 2006). Within a complicated system, such as the marine environment, many wide-ranging factors can shape the ontogeny of the organisms within them. Two major factors that influence habitat quality are resource availability and mortality risk. Individual organisms are known to collect and integrate information regarding both factors and assess them in a continual balancing act (Biro et al. 2006). This balance manifests itself in patterns of distribution which are best interpreted with the aid of the ideal free distribution (Fretwell and Lucas, 1970) or optimal foraging theory (Pyke, 1977). Using these ideals provides a foundation for interpreting habitat quality and its impact on habitat selection. In doing so, we aim to understand how the tri-trophic relationship between coastal resources, juvenile sharks and larger predators will facilitate development of models to better understand how each of the aforementioned factors weighs into habitat selection by coastal shark species.

The lemon shark is a large-bodied, viviparous coastal species that spans the tropical regions of the Western Atlantic and Eastern Pacific (Schultz, 2008; Chapman et al., 2009). Like some other marine organisms, such as bonefish and turtles (Humston et al., 2005; Murchie, 2010), these animals exhibit natal site fidelity. This interpretation is based on evidence that juvenile lemon sharks remain within a small mangrove habitat for the first 3-6 years of life before slowly transitioning to sea grass beds and eventually the open ocean (Morrissey and Gruber, 1993; Murchie, 2010). During the juvenile stage, lemon sharks exhibit a small home range, which expands as they develop. The coastal mangrove habitats used by juvenile lemon sharks offer protection and access to food, which is vital for growth and survival (Simpfendorfer and Milward 1993; Gruber et al. 2001; Franks, 2007). Previous research has shown that lemon shark juveniles prey on small invertebrates and teleost species, such as mojarra (*Gerres* spp), as their main source of food (Newman et al. 2010). These teleost prey spend most of their lives in mangroves, which offer physical structure in the form of prop roots that likely aid in assuring higher survivorship. However, the relative distributions of juvenile lemon sharks and mojarra has yet to be fully understood. Mangrove inlets offer protection in the form of refuge, thereby affecting overlap with potential predators. By understanding distribution of juvenile lemon shark populations, we aim to model impacts that resource availability and predation risk have on the distribution and growth of this species.

Cape Eleuthera, on the south end of the island of Eleuthera, is characterized by a wide array of tidally influenced inlets of differing habitat quality. Though previous studies have examined nursery areas (Franks, 2007; Chapman et al., 2009), few have based analysis on nursery inlets. Study of habitat quality within mangrove habitats will enable a priori hypotheses about the effects of resource availability and mortality risk. Changing environmental parameters (Abrahams et al., 2007), interference competition or refuge availability may all potentially affect this dynamic. The impacts of food availability and its effect on growth may affect each habitat, and therefore each population (Dupuch et al. 2009) quite differently. Our goal is to understand how these organisms balance the information available to them and how that balance affects overall habitat use and selection.

The purpose of this study is to assess the quality of juvenile lemon shark nurseries with respect to individual growth, distribution and mortality risk. Because these animals depend on coastal nurseries for growth and survival during early juvenile life, it is important to understand how these factors may interact to shape habitat suitability (Werner and Gillam, 1984). Such knowledge will provide an index of how individuals select nursery habitat. Studying how trade-offs (i.e. growth and mortality) are balanced within each nursery will facilitate better understanding of the most important factors in the early life history of lemon sharks. We hypothesize that a) areas with high resource availability will support the highest abundance of juvenile lemon sharks and b) areas with high risk will exhibit lower abundances and higher growth rates.

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Co-authorship statement

The research described in this thesis was carried out by the author, Ian R Hamilton, who was responsible for data collection and analysis. Guidance for experimental design and analysis, as well as financial support, was provided by Mark Abrahams and Ian Fleming, who also made significant editorial contributions during the preparation of the chapters/manuscript. On-site project supervision and research support was provided by Edd Brooks, who also aided in securing financial assistance provided by the Cape Eleuthera Institute.

Chapter 2

Growth and Distribution Patterns of Juvenile Lemon Sharks in Mangrove Creek Ecosystems

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Abstract

Lemon sharks use coastal inlets (creeks) as nursery habitats, with females entering these creeks in the spring to give birth to live young that spend their first years of life in these locations. Although this phenomenon is well known, the mechanism behind habitat selection is not well understood. We reasoned that lemon sharks are selecting nursery habitats in a way that integrates resource availability as a major driver behind habitat selection. We therefore quantified population differences among nurseries and assessed how resource availability shapes patterns of use. Seine nets were used to capture and tag juvenile lemon sharks and potential prey items in nine mangrove inlets in southern Eleuthera Island, The Bahamas. We used a multiple mark-recapture technique to assess growth rates and distribution patterns of juveniles within our nine sites. Data indicate a strong relationship between lemon shark and prey abundance, with a particularly strong correlation between lemon sharks and mojarra (family *Gerres*) abundances. This distributional difference did not translate to differences in growth rate because specific growth rates differed little among the nine sites, with the exception of one location. Given the philopatric nature of juveniles, our results give way to the idea that both density-dependence and maternal site selection may play important roles in patterns of distribution.

Introduction

The lemon shark (*Negaprion brevirostris)* has been a model organism for studying and understanding the biology and life history of elasmobranchs for many decades. Given their biological attachment to coastal areas, this species allows for close examination of the many factors affecting the early life history of elasmobranchs, a critical characteristic in ongoing and future ecology and conservation biology. Lemon sharks are viviparous and give birth to live young which remain within shallow, mangrove-lined coasts. Previous research has demonstrated defined home ranges in juvenile lemon sharks within their natal site, and marked philopatry (Morrissey and Gruber, 1993; Feldheim et al, 2004; Chapman et al, 2009). Further work shows they have a dietary preference for mojarra (Family *Gerres;* Newman et al, 2010). Jennings (2008) showed marked decreases in growth in lemon sharks when mangrove stands were removed. Because lemon sharks spend much of their early life in these ecosystems, it is important to develop models to predict how individuals select habitat and what the subsequent effects will be on development. Nonetheless, current information is deficient regarding how resource availability impacts observed patterns of distribution and growth. Determining how these animals gather and use information in their natural environment requires a better understanding of the impacts of resource availability.

Mangrove ecosystems are important nursery grounds for elasmobranchs as well as many coral reef fish (Mumby et al, 2003; Mumby, 2005). These systems connect to transitional grounds such as sea grass beds and eventually coral reef systems. Conservation of elasmobranch species has often focused on preserving such critical habitats (Heupel et al, 2007), especially given the large home ranges and transmigratory behaviour of many elasmobranchs. Given the importance of these mangrove ecosystems to our model species, we aim for improved understanding of the fundamental relationships between juvenile lemon sharks and their teleost prey within these nursery systems.

A myriad of factors often influence habitat selection decisions. Animals often select habitats to optimize foraging success relative to potential risk (Moody et al. 1996). However, in many coastal marine ecosystems, physical refuge provided by the coastline minimizes encounter rate with predators while simultaneously providing a consistent source of prey. In systems where physical structure minimizes predation risk, resource availability and abiotic environmental suitability likely determine habitat utilization. Ecological theory, such as the ideal free distribution, describes how individuals will distribute themselves across habitats of varying resource quality. Ideal free distribution theory (Fretwell and Lucas, 1970) predicts that animals with perfect (ideal) knowledge about the distribution of their resources and are “free” to compete equally for access to them will distribute themselves proportionally to resource availability. Assessing populations of juvenile lemon sharks and teleost prey will aid in uncovering how resource availability affects the distribution patterns of this species within mangrove ecosystems. The information gathered will provide a fundamental understanding of how this species collects and utilizes information necessary in making habitat selection decisions.

We currently lack information on how this species functions within nursery areas and how they respond to varying levels of resource availability. Until now, very little research has focused on how prey populations drive the distribution and habitat selection of elasmobranchs. Our goal is to uncover mechanisms behind habitat selection and how these influence the distributions of juvenile elasmobranchs, in particular lemon sharks. We hypothesize that lemon shark populations in South Eleuthera are distributed with respect to food, resulting in negatively frequency-dependent distribution patterns. Therefore juvenile lemon sharks should make frequency-dependent habitat selection decisions to maximize individual access to food.

Methods

Study Location

The study was conducted on the south coast of Eleuthera, The Bahamas, which is characterized by numerous mangrove inlets. Mangrove systems provide nursery grounds for juvenile lemon sharks, as well as a vast array of coastal and reef fish and invertebrate species. This study focused on nine of these mangrove inlet systems (Fig. 2.1). Five of the creeks lay adjacent to the Exuma Sound, a deep water area laying approximately 1 km offshore. The remaining four creeks lay adjacent to Rock Sound, a shallow water sand bank stretching out 15 to 20 km offshore. These inlets are characterized by shallow water and fringing mangroves, which are influenced by semi-diurnal tides. Data regarding the physical features of each habitat can be found in table 2.1. Multiple mark-recapture of juvenile lemon sharks, as well as prey sampling were conducted within each of the inlet systems a minimum of four times throughout 2012 (see Appendix). No data were collected during October 2012 because of Hurricane Sandy.

Seining Procedure

Juvenile lemon sharks were targeted within their natal creeks and caught using a seine net. A 76 m Memphis Twine seine net, with 3.1 cm mesh, was used for standardized capture of both juvenile lemon sharks as well as fish prey found within each system. Seine nets were set in a standardized fashion across the mouth of each creek at high tide, and left for 4.5 hours (Fig. 2.2). For creeks with several distinct arms, nets were set at the sub creek level to allow equal sampling of the entire system. After 4.5 hours, during periods of lowest tide, fish were herded from the back of each inlet system towards the seine net. This process was used to maximize capture efficiency and minimize avoidance of the seine net by schooling teleost species. Once the fish were herded into the pocket of the net, we carefully encircled them with the arms of the seine. All captured lemon sharks were removed from the net and placed in a cooler for processing prior to release. Prey species captured within the seine net were counted and released. Any members of the mojarra or barracuda family were sub-sampled for fork length (FL) and total length (TL) prior to release.

Juvenile lemon shark tagging procedure

Once captured within the confines of the seine net, all juvenile lemon sharks were carefully transferred from the seine, using dip nets, to a large 60 L cooler for processing. Pre-caudal length (PCL), fork length (FL), total length (TL) and stretch total length (STL) measurements were taken. Juveniles were sexed and tagged with uniquely numbered external monofilament tags inserted into the dorsal fin and with AVID 12 mm Passive Integrated Transponder (PIT) tags inserted under the dorsal fins on the right side of the body using a small hypodermic needle. The redundant tag system allowed visual and sub-dermal identification of animals upon capture. All animals were weighed post-capture using a WeiHeng WHA-17 digital hanging scale. After sampling, each animal was carefully released outside the confines of the seine net back into the safety of the creek system.

Prey species collection

Following lemon shark processing, the other captured fish and invertebrate species were counted and a random sub sample of 10 barracuda (*Sphyraena barracuda*) and 10 mojarra (*Gerres* spp.) were measured for fork length (FL) and total length (TL). We collected these two species because both are considered major prey species of juvenile lemon sharks (Newman et al. 2010).

Statistical Analysis

a) Growth rate analysis

Specific growth rate was calculated from all recapture data using the standard formula (Jobling, 1983);

$$\text{Specific Growth Rate (SGR)} = (\text{Ln}\ (L2) - \text{Ln}\ (L1))/(T2\text{-}T1) * 100$$

Where L represents fork length (FL) at time of capture and T represents the number of days between recapture events. To quantify site-specific growth rates, a one-way ANOVA tested the effects of location on growth of juvenile lemon sharks. A Tukey post-hoc comparison of means then determined which environments differed significantly.

b) *Juvenile lemon shark and prey abundance analysis*

Catch per unit effort (CPUE) values were calculated for all species to formulate a mean abundance value for each location for further site-specific comparison. CPUE values were devised by calculating the number of animals caught per seine replicate. Captured animals were categorized at the species level and grouped into families. Prior to analysis, all juvenile lemon shark abundance data were log transformed (n+1) to account for zero capture events. Linear regression was used to compare prey abundance, and species-specific abundance, across all habitats.

Results

One hundred and twenty-six lemon sharks were captured with 52 recaptured. Of these, 28 were caught once and 24 caught twice or more. Only seven of the 52 recaptured animals (13%) were caught outside of their original tagging location. Of the captured juvenile sharks, 52 were female and 74 were male; individuals ranged in size from 49 to 100 cm FL. Juvenile lemon shark abundance differed significantly across the nine study sites (F = 178.85, df = 1, 8, p = 0.001). Four sharks caught were as large as or larger than 100 cm FL (100, 108, 117 and 133.5 cm) and were excluded from all analysis involving juveniles because they were considered sub-adults. All lemon shark specific capture data can be found in Table 2.2.

Recaptures outside of natal inlet

Of the 52 recaptured juvenile lemon sharks, 8 were recaptured in a location other than their original tagging location. Three of these individuals moved to areas with less food availability, whereas four individuals moved to areas with more available prey. One individual moved from its natal inlet to an inlet with high food availability, and was then recaptured again in its natal inlet. Five of the eight animals captured outside of their natal creek had moved to adjacent inlets, an average distance of 1.51 km. The three remaining individuals moved to non-adjacent creeks, with an average dispersal distance of 6.18 km. One of these individuals originally tagged in Plum Creek during 2011 was found several inlets down the coast at John Millers, a distance of 9.68 km. No tagged individuals moved between Exuma and Rock Sounds.

Site-specific growth

Because of the lack of recaptures in Hartford Creek, we excluded this system from the multi-site growth analysis. Very few animals were tagged (n = 4) and none of these animals were recaptured. We found significant differences in specific growth rate (Fig. 2.3) among the remaining study sites (ANOVA; F = 4.06; df = 7, 44; p = 0.002). However, a Tukey post-hoc comparison of means test separated Wemyss Bight Creek, with John Millers and Waterford Creeks forming a separate subgroup.

Distribution of resources

We collected a total of 8194 fish and invertebrates from 13 different families. Of these, the mojarra (*Gerres* spp.) (Fig. 2.4) made up 60% of the total number of fish captured (n = 4925), barracuda (*Sphyraena barracuda*) 8.5% (n=700) and bonefish (*Albula vulpes*) 18.7% (n = 1534). We observed significant differences in prey abundance across sites (F = 3.52; df = 8, 39; p = 0.004) however, only Kemps was found to differ significantly from Page and Hartford Creeks (Tukey post-hoc comparison of means test; $p < 0.05$) (Fig. 2.5). Mojarra abundance (F = 7.18; df = 8, 39; $p < 0.001$) and barracuda abundance (F=3.99; df = 8, 39; p = 0.002) also differed across sites. Average mojarra size was 12.6cm FL (±0.572 SE) whereas barracuda average size was 25.1cm FL (± 2.97 SE). However, neither genera differed significantly in size among sites (p = 0.412). Site-specific capture information of overall prey and mojarra abundance can be found in Table 2.2.

Distribution of juvenile lemon sharks vs. resources

Mean teleost prey abundance and lemon shark abundance were positively and significantly related (F =5.08; df = 1, 45; p = 0.029) (Fig. 2.6 A). However, site-specific analysis yielded a less significant result (F = 1.58; df = 1, 8; p = 0.26) (Fig 2.6 B). More specifically, juvenile lemon shark abundance was moderately and positively related to overall mojarra abundance (F = 20.72; df = 1, 45; p = 0.001), a known prey preference of juvenile lemon sharks (Fig. 2.7 A). However, juvenile lemon shark abundance also showed a non-significant site-specific relationship with mojarra (F = 1.47; df = 1, 8; p = 0.273) (Fig. 2.7 B). Finally, juvenile lemon shark abundance showed a non-significant relationship with both barracuda and bonefish abundances (p = 0.787; p = 0.648, respectively).

Discussion

Juvenile lemon sharks exhibit distinct site fidelity, a behaviour noted in this species and others (McKibben and Nelson, 1986; Correia, 1995; Vianna et al, 2013). As mentioned above, 87% of all recaptures were made at the original tagging location, suggesting a very strong site-fidelity mechanism in this species in our study systems. Given the varying geographic structure of the mangrove inlet systems on South Eleuthera, we hypothesize that this behaviour will result in differences in growth rate associated with variation in habitat quality (Fraser et al, 1999; Billman et al, 2011). Our results show a significant difference in growth rates, however, post-hoc testing suggests that this result is driven primarily by Wemyss Bight, with Waterford and John Millers Creeks adding minor variation. Juvenile lemon shark abundance also differed significantly across all the nine study sites, with more inter-site differences than for growth rates. By examining abundance of both juvenile lemon sharks and available prey items, juveniles seemed distributed among populations in a way consistent with ideal free distribution theory (Fretwell and Lucas, 1970; Sutherland, 1983; Abrahams, 1989; Hakoyama and Iguchi, 2001) based on the distribution of food. These data demonstrate that access to food in these nursery systems may be negatively frequency dependent.

Of particular interest is the fact that the distribution of juvenile lemon sharks is not necessarily a result of juvenile habitat selection but may instead be attributed to other factors, such as density-dependence survival or maternal site selection. Density-dependent survival has been shown to occur in this species (Gruber et al, 2001). It is therefore possible that these patterns have arisen due to density-dependent mortality driving patterns of abundance. Given the body of knowledge on the impacts of competition on individual growth and survival, lemon sharks in south Eleuthera may be directly impacted by either competition-saturated or competition-released locations. This variation in potential competition may then result in varying growth and distribution patterns similar to those found in this study.

Another potential factor is maternal site selection. The mechanisms behind reproductive site selection have long been studied in species such as birds, turtles and bony fish (Kolbe and Janzen, 2002; Citta and Lindberg, 2007; Camp et al., 2011; Crampton and Sedinger, 2011). However, neither the mechanism behind natal site selection, nor the scale over which it operates has ever been properly investigated in most shark species primarily because of their large home ranges and migratory behaviour that create logistical difficulties for such research (Manire and Gruber, 1990; Schultz, 2008). The coastal distribution of lemon sharks, however, affords an opportunity to explore this area of research and develop a better understanding of habitat selection behaviour. Previous research on genetic diversity suggests that adult female lemon sharks return to a specific home range, often thought to be their natal range, in order to pup (Feldheim et al, 2002, 2004, 2014; DiBattista et al, 2008). Based on our data, it is not unreasonable to suggest that the decision of where to place ones offspring may involve assessment of habitat quality, specifically the availability of potential food items. However, this insight needs to be taken lightly as many factors, such as density-dependence and competition may play as big, if not bigger, a roll in growth, survival and distribution patterns of juveniles.

Our results suggest that distribution of prey, specifically mojarra, can predict distributions of individual juvenile lemon sharks among populations. This information provides important insights into the early life history patterns observed in many coastal elasmobranchs. Our study has aimed to better understand how habitat quality is assessed and how this assessment manifests itself in habitat selection decisions. The results have shown that the distribution of juvenile populations is closely linked to that of their prey. However, this relationship is likely mediated by many factors such as competition, abiotic environmental condition or predation risk. Further assessment of coastal mangrove areas is necessary, due in large part to increasing coastal development, and will increase our understanding of mangrove ecosystems and highlight their importance to juvenile shark populations. Through our investigation into the dynamics of predator-prey interactions in juvenile lemon sharks, we provide a template for future research as well as providing a basis for better understanding the many factors affecting habitat quality and its impact on habitat selection decisions made by coastal elasmobranch species.

Tables

Table 2.1 – Site-specific habitat features for each of the nine mangrove inlet systems (lemon shark nurseries) studied

Inlet Name	Inlet Number	Inlet Mouth Diameter (m)	Bottom Type
Page	1	31.96	sand/rock
Kemps	2	61.32	sand/rock
Broad	3	176.14	sand
Starved	4	70.33	rock
Plum	5	48.19	sand
Waterford	6	42.87	sand
Wemyss Bight	7	89.34	sand
Hartford	8	37.61	sand
John Millers	9	33.37	sand

Table 2.2 Site-specific capture information for each of the nine mangrove inlets (lemon sharks nurseries) studied

Inlet Name	Inlet #	# Samples	# Juvenile lemon sharks captured	# recapture events	Mean prey biomass (fish/seine)	Mean mojarra biomass (fish/seine)
Page	1	7	26	14	76.71	50.29
Kemps	2	8	36	51	307.75	245.5
Broad	3	5	12	10	128	86.8
Starved	4	5	21	8	262	130.6
Plum	5	6	9	4	170	83
Waterford	6	4	4	2	67.25	35.5
Wemyss Bight	7	4	3	2	276.25	91.5
Hartford	8	4	6	0	48.25	15.75
John Millers	9	5	5	2	131.6	90.6

Figures

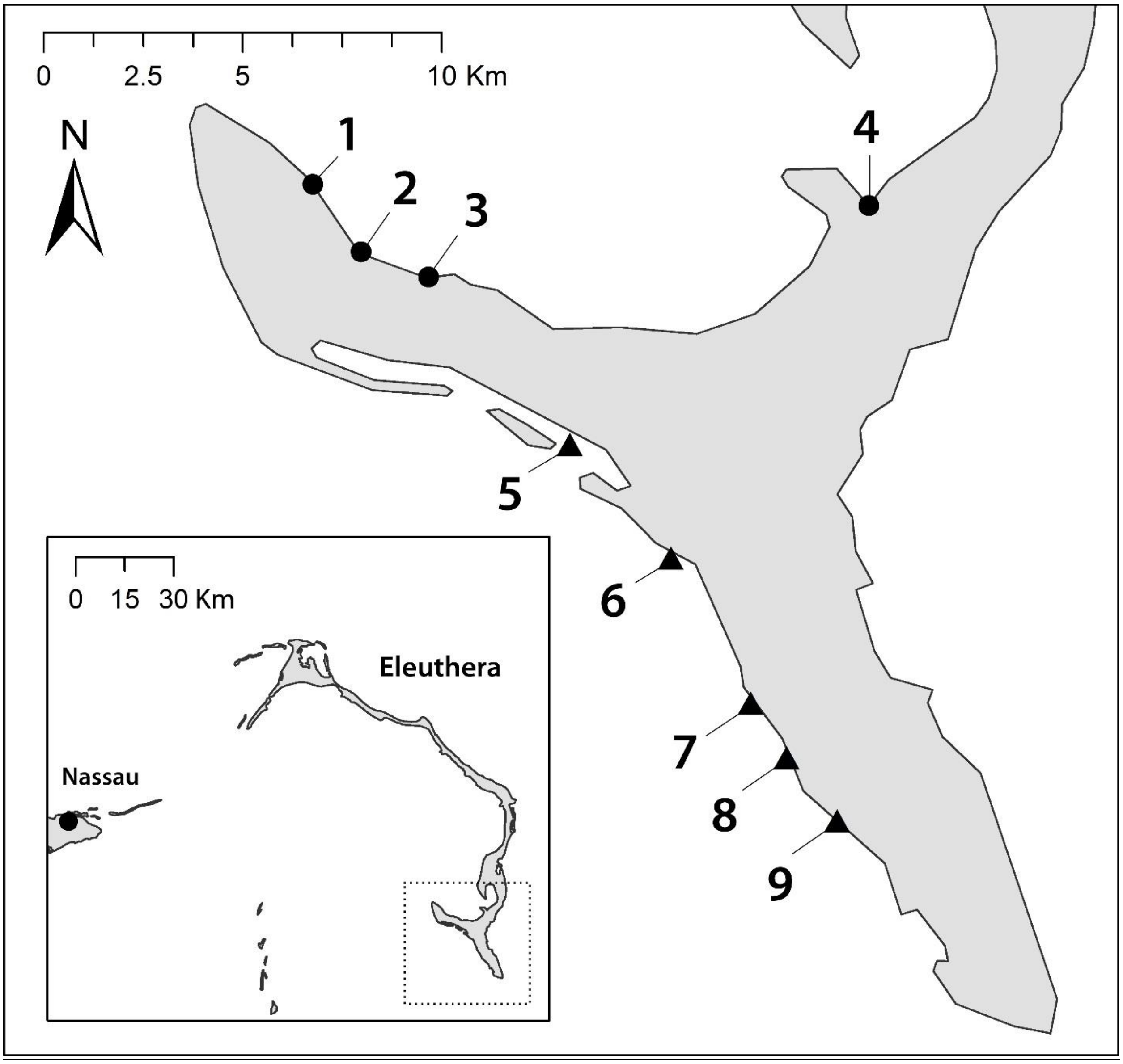

Figure 2.1: Map of the islands of New Providence and Eleuthera, The Bahamas. The large panel highlights the area of South Eleuthera, with circles showing the four Rock Sound nurseries and triangles representing the five Exuma Sound nurseries. Site legend: 1 = Page, 2 = Kemps, 3 = Broad, 4 = Starved, 5 = Plum, 6 = Waterford, 7 = Wemyss Bight, 8 = Hartford, 9 = John Millers.

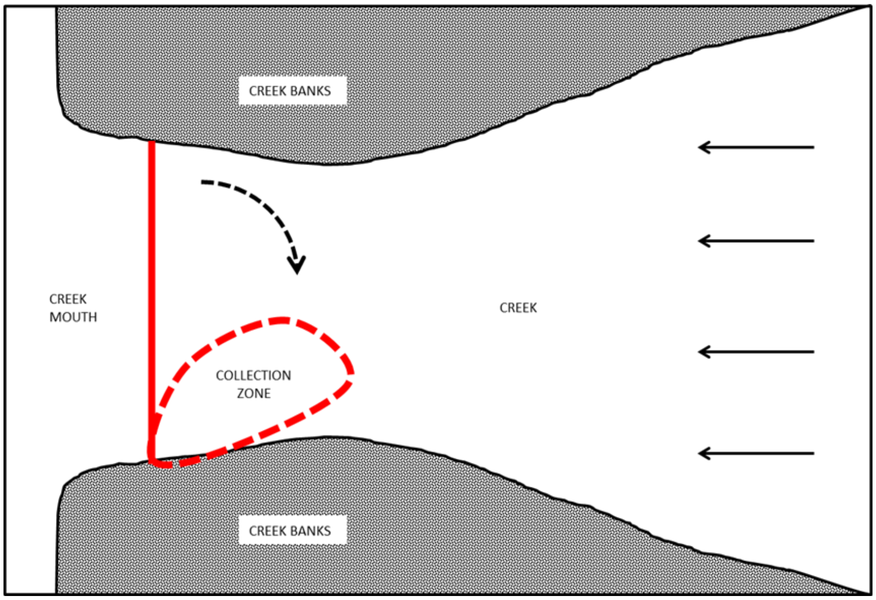

Figure 2.2: Figure outlining the standardized seining technique used to collect juvenile lemon shark and other fish and invertebrate species within each creek system. The solid red line represents the seine net used to capture samples. Solid arrows represent the path taken by researchers to herd fish towards the seine net. The dashed black line shows the direction of net closure. Red dashed line shows the collection zone used to contain captured animals.

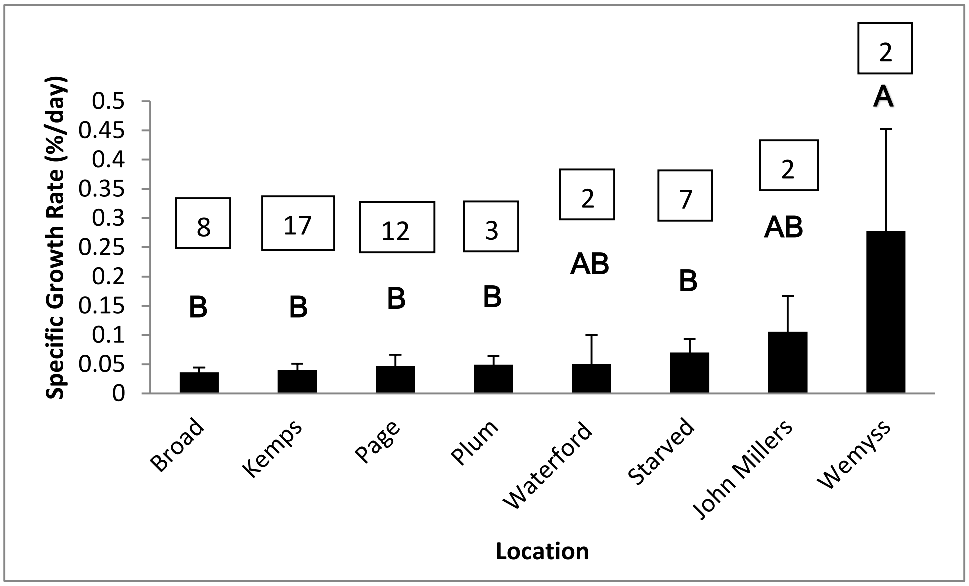

Figure 2.3: Mean (± 1 SE) site-specific growth of juvenile lemon sharks in each of nine creek systems on South Eleuthera, The Bahamas. Hartford Creek was excluded from analysis because of a lack of recaptures. ANOVA showed statistical significance (p = 0.002), however, a Tukey post-hoc comparison of means revealed that only Wemyss Bight differed significantly from the other sites. Boxed numbers above statistical groups show sample size of individuals included in growth rate analysis.

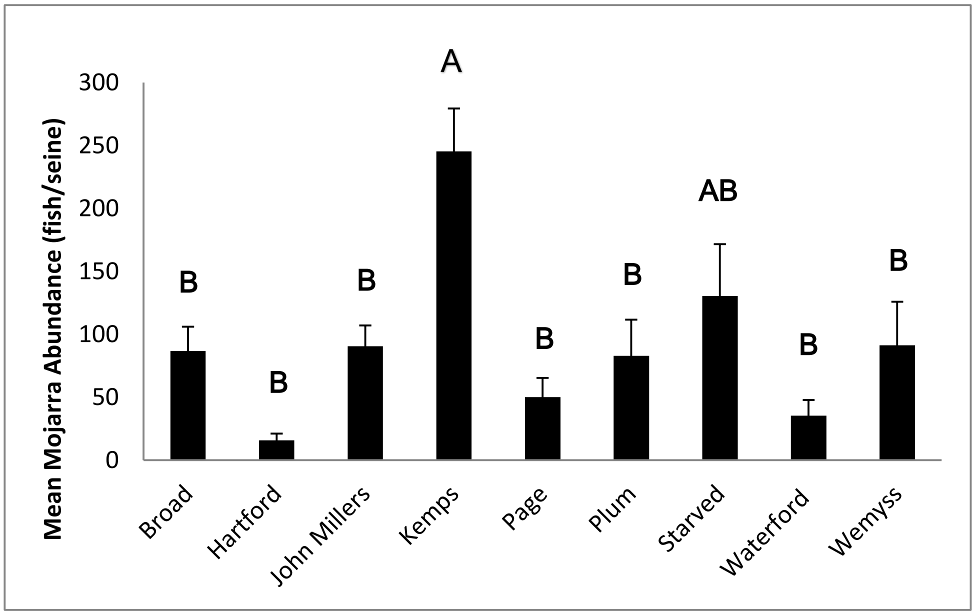

Figure 2.4: Mean (±1 SE) mojarra abundance in nine mangrove creeks of South Eleuthera, The Bahamas. Bars represent site-specific means calculated from seine net data. A one-way ANOVA showed statistical significance ($p < 0.001$). Tukey post-hoc comparison of means testing showed variation between several of the sites.

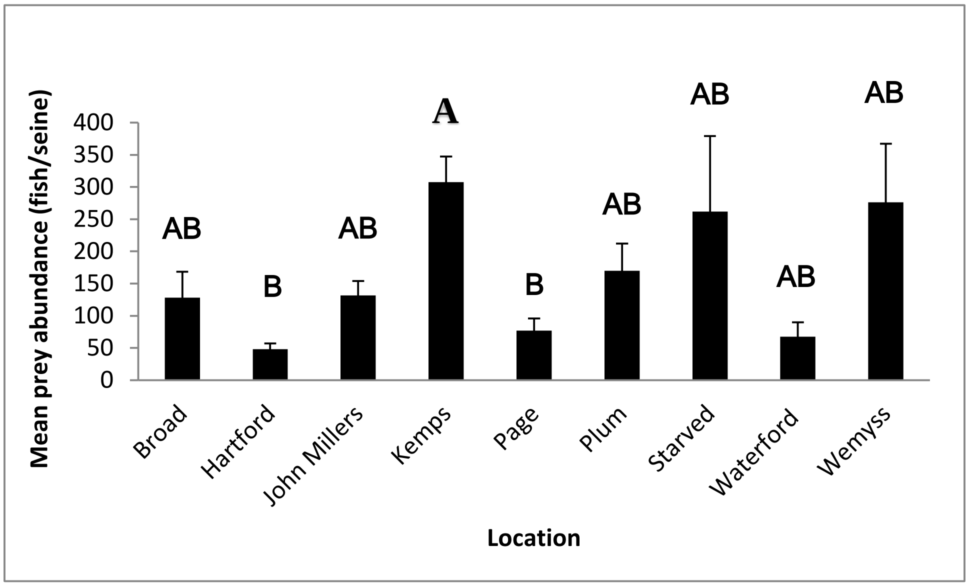

Figure 2.5: Mean (±1 SE) prey abundance available to juvenile lemon sharks in nine creek systems on South Eleuthera, The Bahamas. Thirteen families of fish were collected with biomass values calculated represented as total fish caught per seine replicate. One-way ANOVA showed statistical significance ($p = 0.004$). A Tukey post-hoc comparison of means test to determine sources of variation between sites showed three distinct subgroups.

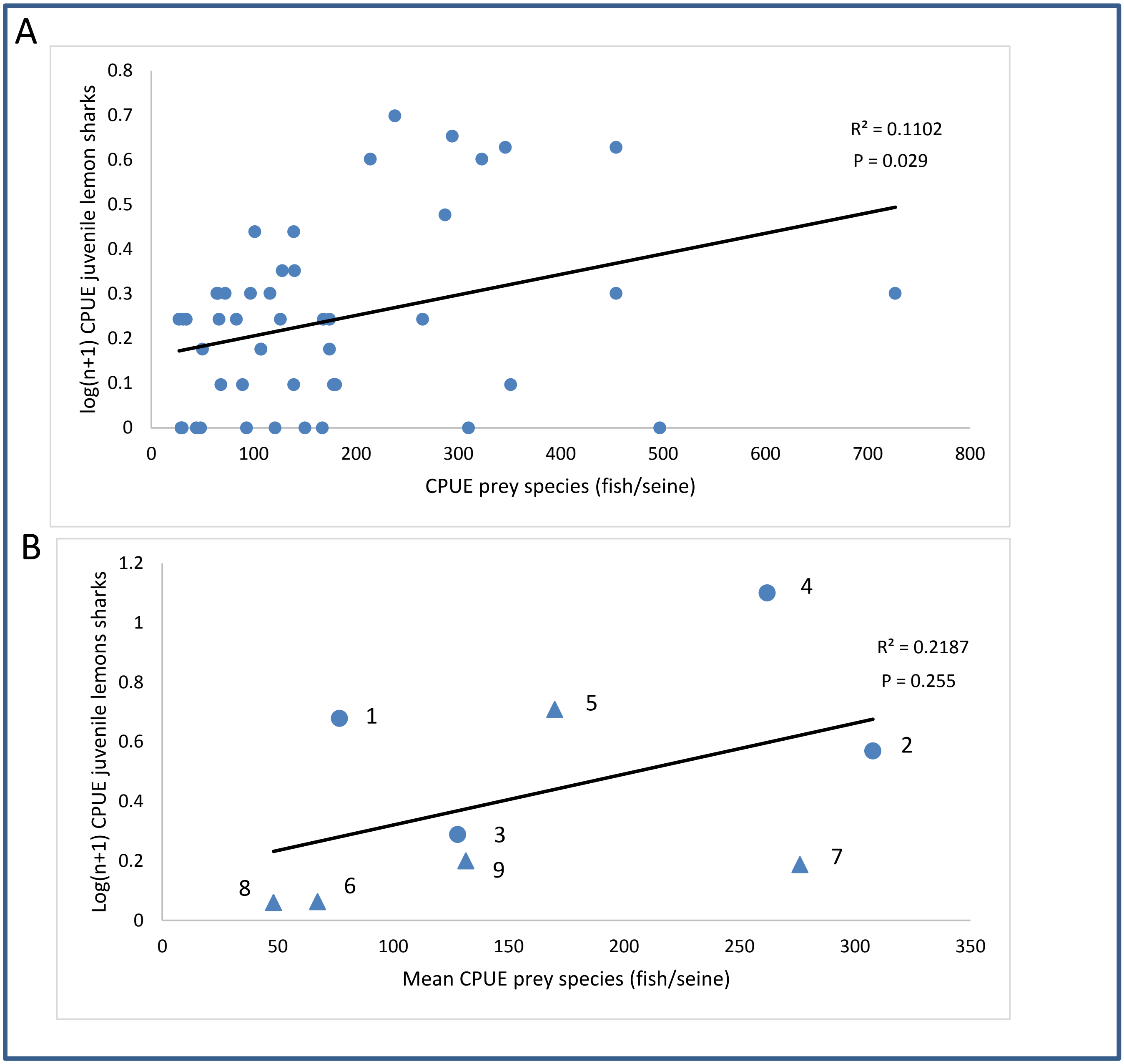

Figure 2.6: Juvenile lemon shark abundance compared to teleost prey abundance. A) Overall juvenile lemon shark abundance compared to mean teleost prey abundance and B) Site-specific comparison of juvenile lemon shark abundance and teleost prey abundance. Numbers and shapes correspond to sites outlined in Fig 2.1.

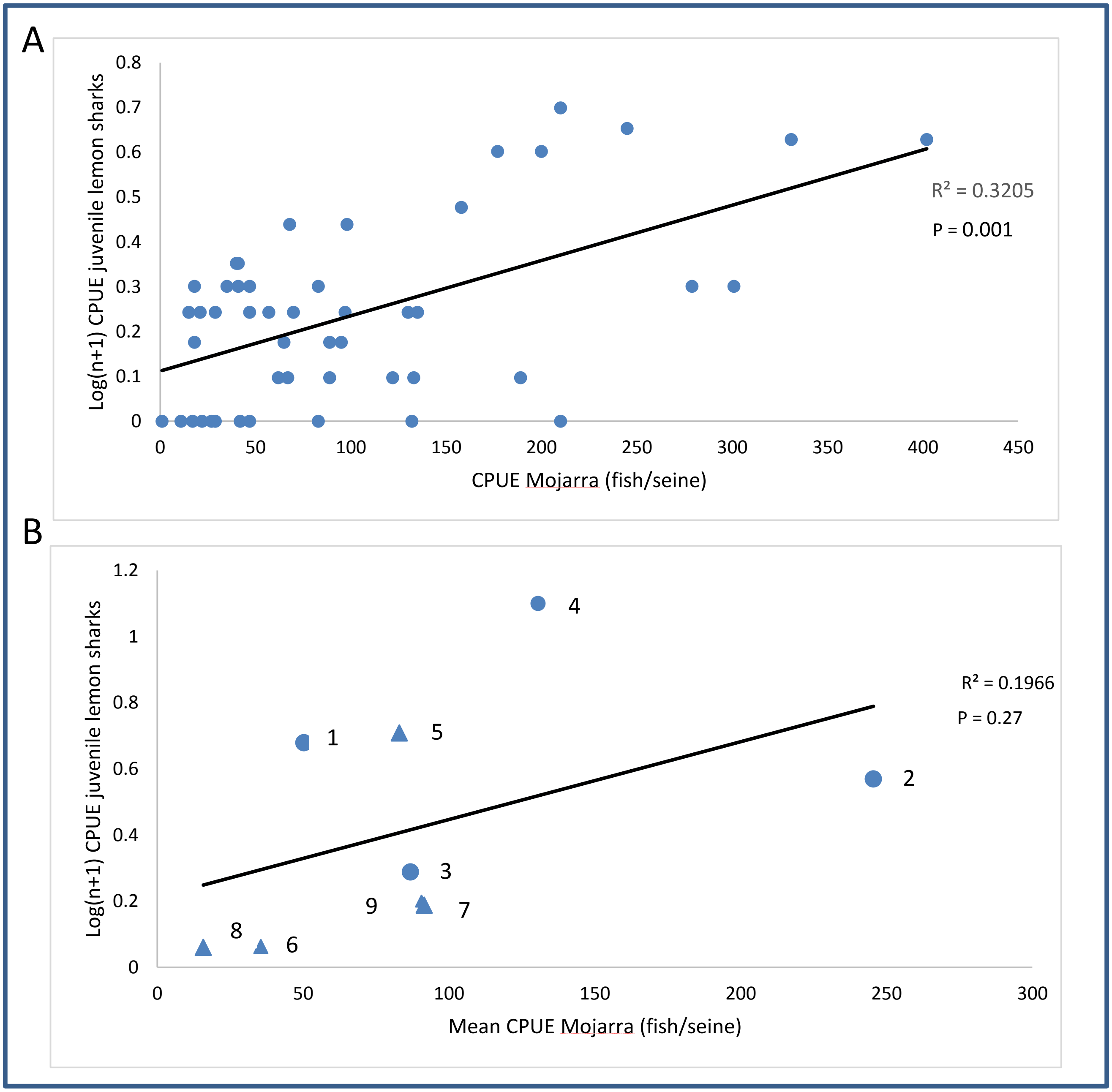

Figure 2.7 – Juvenile lemon shark abundance compared to mojarra abundance. A) Overall juvenile lemon shark abundance compared to mojarra abundance and B) Site-specific comparison of juvenile lemon shark abundance and mojarra abundance. Numbers correspond to sites outlined in Fig 2.1.

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Chapter 3

Examining the Effects of Predation Risk on Habitat Selection of Juvenile Lemon Sharks (*Negaprion brevirostris)*

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Abstract

Juvenile lemon sharks (*Negaprion brevirostris)* use fringing mangrove habitats during the first 3-6 years of life. Mangroves grow in shallow water areas with variable temperatures and dissolved oxygen levels that may create physiological refuges from predation for juvenile lemon sharks. This study sought to determine whether protection from predators was an important aspect of habitat quality. We hypothesized that juvenile lemon sharks a) are more abundant in areas with less predation risk and harsher abiotic conditions and b) make trade-offs between growth rate and mortality rate, resulting in increased growth rates within sites with higher levels of predation pressure. We collected field data from nine sites in South Eleuthera, The Bahamas to measure lemon shark growth rates and estimates of mortality rates at each location. Though results were not statistically significant, data suggest higher juvenile lemon shark abundances in areas with more physical vulnerability but, lower levels of predator encounter risk. High vulnerability sites also exhibited harsher environmental conditions, suggesting a possible physiological component to habitat selection. This information furthers our understanding of key parameters affecting habitat quality for juvenile lemon sharks, which can inform coastal habitat management decisions that promote the conservation of elasmobranchs.

Introduction

The impacts of risk in natural ecosystems affect the quality of any given habitat where predators are present. The way organisms behave under varying levels of predation can affect decisions regarding habitat use, foraging strategy, and subsequent interaction with predators. In their classic paper, Lima and Dill (1990) define predation risk as the product of the time an individual spends vulnerable to predators, the probability of predator encounter and the probability of escape given predator encounter. Assessing predator-prey interactions using these components allows determination of predator effects on their prey while simultaneously gaining insight into tactics prey species use to integrate this information into habitat selection decisions.

A strategy often used to manage risk involves selecting habitats inaccessible to predators, thus minimizing the amount of time an individual spends vulnerable to predation. These habitats, often referred to as refuges, can offer safety from predators through thermal, physical or physiological means (Sutton et al. 2007; Jachowski et al. 2012; Yamanaka, 2013). Many organisms seek refuge in areas inaccessible to their predators, based on either body size or physiological constraints (Chapman et al. 2002; Robb and Abrahams, 2002). This behaviour therefore converts safety into an environmental resource which must be managed along with prey resources in order to maximize individual fitness and survival. Though selection of predator free space can incur energetic cost, the benefit of reducing risk can be integrated into habitat selection decisions using the growth-mortality relationship (μ/g) proposed by Werner and Gilliam (1984).

Juvenile lemon sharks (*Negaprion brevirostris)* offer a model organism for studying risk effects in changing environments. This elasmobranch species uses shallow coastal inlets as nursery ground for the first 3-6 years of life (Chapman et al. 2009). These inlets are often mangrove lined and their roots provide physical protection from predators, such as tiger sharks (*Galeocerdo cuvier*), blacktip sharks (*Carcharhinus limbatus*), Caribbean reef sharks (*Carcharhinus perezi*) and most often, larger conspecifics (Guttridge et al. 2012). Given the shallow water, these locations can vary considerably in temperature and dissolved oxygen levels throughout the tide cycle (Ovalle et al. 1990; Wolanski et al. 1992).

The physical features of mangrove inlets provide juvenile lemon sharks with both physical protection from predation as well as an increased access to potential prey items. Previous work shows that prey species can use sub-optimal habitat, such as hypoxic areas, as a means of avoiding predators (Chapman et al. 2002; Anjos et al. 2008; Abrahams and Sloan. 2012). In many fish species, tolerance to hypoxia increases with body size. Adaptation or acclimation to hypoxia is mediated by expression of physiologically relevant genes, such as LDH-A, resulting in the release of lactate dehydrogenase (LDH) (Almeida-val et al. 2011). However, this relationship can also work in the opposite direction. Abrahams and Robb (2003) showed that hypoxia tolerance can scale inversely with body size as a result of either allometric scaling (e.g., the decrease in the ratio of gill size to body size) or fractal scaling (e.g., scale associated with complexities within circulatory systems). Assuming this relationship holds for lemon sharks, juveniles may use mangrove inlets as a physiological refuge because predators lack sufficient time to acclimate to the unique physical conditions found within these habitats. Given the frequency of environmental change within these systems, these habitats may offer both a benefit in the form of predation avoidance and resource availability, and a cost, in the form of physiological stress or changes in growth rates.

We use two of the three parameters proposed by Lima and Dill (1990) to quantify predation risk specific to individuals in each location and assess how risk is integrated in habitat selection decisions. We focused on mangrove inlets in The Bahamas because of their abundant juvenile lemon shark populations. Because each location fluctuates in abiotic condition throughout the tidal cycle, we collected physical data to understand how fluctuating environmental conditions may affect predator-prey relationships within our systems. By examining individual populations of juvenile lemon sharks, we aimed to determine how predation risk affects patterns of distribution and selection of natal habitat. We hypothesize that increased risk will result in decreased abundances of juvenile lemon sharks.

Methods

Study Location

The study was conducted in nine mangrove inlets on the island of Eleuthera (25.1000 °N, 76.1333 °W), which is a narrow island (120 km long and 1.6 km wide) located on the eastern border of The Bahamas (Fig. 3.1). Large parts of the inlets were lined with fringing red (*Rhizophora* mangle) and black mangroves (*Avicennia germinans*) and lay adjacent to either Rock Sound, a shallow water sand bank, or Exuma Sound, a deep water oceanic basin.

Fish capture and tagging

Assessment of the impacts of predation risk on habitat selection was conducted by implementing a multiple mark recapture of juvenile lemon sharks in each inlet of study. Juvenile lemon sharks were collected from each inlet using a seine net. Seine nets consisted of 76 m of 3.1 cm mesh with a floating top and lead-weighted bottom. Seine nets were set across the mouth of each inlet at high tide. After 4.5 hours, all fish were herded towards the seine net. Juvenile lemon sharks were removed first and measured for pre-caudal length (PCL), fork length (FL), total length (TL) and stretch total length (STL). Each individual was then sexed and tagged with an individually numbered external monofilament spaghetti tag and a uniquely coded internal 12 mm AVID PIT tag. Once tagged, individuals were weighed using a digital hanging scale and returned to the nursery. Each inlet was sampled a minimum of four times throughout 2012 (See appendix).

Drum Line Procedure

Predator abundances were assessed for all nine inlets using drum line fishing systems. A predator was defined as any animal larger than 130 cm total length of the following species: tiger sharks (*Galeocerdo cuvier*), blacktip sharks (*Carcharhinus limbatus*), lemon sharks (*Negaprion brevirostris*) and Caribbean reef sharks (*Carcharhinus perezi*). Drum lines consisted of a 20 kg concrete anchor attached to a large foam surface float via tar twine. A 5.5 m horizontal floating line was attached to the anchor line float by a PVC swivel mechanism, which led to another large float. A 1.4 m gangion baited with ca. 300g of bonito tuna (*Sarda sarda*) hung from the second float. The gangion consisted of an 8/0 snap-on connector crimped to 2 m of 300 kg test monofilament fishing line. The bottom 60 cm of the gangion was doubled over and crimped together to prevent bite-offs. A baited 16/0 circle hook was hung via 10 cm of 7x7 stainless steel aircraft cable to the terminal end of the gangion. This design minimized by-catch and allowed captured animals adequate room to encircle the vertical anchor line while remaining close to the surface for visual identification of capture.

Drum lines were set over high and low tide at each location every month. Upon deployment, three drums were set perpendicular to shore at each location. Drum line units were set at ca. 250 m increments starting at the mouth of each creek, extending out 500 m from shore. Each drum was set for four hours. After two hours, each drum was checked for predator capture and bait was either confirmed present or replaced. For analysis, total catch numbers were derived for each site because uniform sampling effort was expended at each location. Each inlet was sampled with 60 individual drum lines, spread evenly between high and low tide and equally across all 12 months of 2012, except October when Hurricane Sandy struck.

Habitat-specific Risk

Habitat specific risk was calculated using two parameters defined in Lima and Dill (1990) to describe predation risk. The original equation used was

$$P(\text{death}) = 1 - \exp(-\alpha d T) \tag{1}$$

where α represents the rate of encounter between predator and prey, d represents the probability of death given encounter and T represents the amount of time an individual spends vulnerable to predation.

The first parameter measured in this study, probability of encountering a predator (α), was estimated from drum line data used to calculate the number of predators captured outside each inlet. The second parameter, time spent vulnerable to predation (T), was broken down into two measures used to determine available refuges within each inlet. The first measure assessed periods above mid tide when environmental conditions allowed larger predators access to the inside of each inlet. Therefore, risk was inversely related to cover as measured by the creek-specific circumference to area ratio obtained from ARCGIS maps. The second measure assessed periods below mid tide. During these periods, it was assumed that the presence of depth refuges allowed juveniles to remain within each inlet at low tide, thereby eliminating the need to leave the nursery and increase the probability of encountering a predator. Risk was then determined by calculating the inlet-specific depth refuge availability. Depth refuges were considered to be any remaining pocket of water which remained at ≥1 m depth during low tide. Total vulnerability risk was calculated by combining the circumference: area ratio (high tide) with the depth refuge availability (low tide) to form a product representing the availability of physical refuge within each inlet.

Total predation risk was calculated as the combination of two factors; time spent vulnerable to predation (the product of high and low tide refuge availability measures) and probability of predator encounter in order to independently assess overall predation risk for each inlet independently.

Physical Environment

Two YSI data sondes (model 6920 V2 equipped with optical dissolved oxygen and temperature/conductivity probes) were deployed in the mouths of two differing systems; one in John Millers Creek, representing a high refuge (low risk) system, and one in Starved Creek, representing a low refuge (high risk) system. Each sonde measured temperature, salinity and dissolved oxygen levels every 30 minutes from May 11 through December 10, 2012. Sondes were placed at a high tide depth of 1 m, directly inside the mouth of the inlet to assure standardized data collection between low refuge and high refuge systems. Each unit was serviced every month to recalibrate probes, replace batteries and download sonde data to EcoWatch software.

Hypoxia thresholds were calculated from Carlson and Parsons (2001). During the above study, conditions were considered hypoxic at dissolved oxygen levels between 2.5 mg/L and 3.4 mg/L. Of the species examined in the study, the Florida smoothhound shark (*Mustelus norrisi*), which exhibits buccal pumping ability similar to lemon sharks, showed decreased swimming speeds and activity patterns during periods of hypoxia. Therefore, for our study, we considered 3.5mg/L the hypoxia threshold given that behaviour associated with hypoxia stress would likely occur at or below this standard level.

Results

Encounter risk analysis

In total, 51 predators of 4 different species were captured outside of the nine study systems. Of the predators captured, tiger sharks (*Galeocerdo cuvier*) made up 52.9% (n = 27) of the total number of predators captured, lemon sharks (*Negaprion brevirostris*) 17.6% (n = 9), blacktip sharks (*Carcharhinus limbatus*) 15.6% (n = 8) and Caribbean reef sharks (*Carcharhinus perezi*) 13.7% (n = 7). Sites adjacent to Exuma

Sound exhibited the highest predator pressures, with 76.5% of all predators being caught outside of these five inlet systems. Juvenile lemon sharks appeared in greater abundance in sites with lower predator presence, i.e. sites with lower encounter risk. However, this model was not statistically significant (F = 2.654; df = 1, 7; p = 0.154, Fig 3.2). Encounter risk was also compared to a) total teleost prey abundance and b) mojarra abundance, yielding non-significant results for both analyses ((a) F = 0.022; df = 1,7; p = 0.885; (b) F = 0.587; df = 1, 7; p = 0.468, respectively). Mean size distributions for all predatory species captured can be found in table 3.1.

Vulnerability risk analysis

Juvenile lemon sharks appeared in greater abundance in habitats with less refuge (Fig. 3.3), although this result was not statistically significant (F = 5.256; df = 1, 7; p = 0.062). Of the nine sites assessed, the four highest vulnerability risk inlets were all located adjacent to Rock Sound where minimal predator presence (encounter risk) was detected.

Abiotic environment assessment

Hypoxic conditions (dissolved oxygen levels < 3.5 mg/l) often occurred during the overnight low tide, and primarily in the system with higher levels of vulnerability risk (i.e. low refuge availability) as indicated (Fig. 3.4). Variations in dissolved oxygen levels were more extreme and more frequent in the location with high vulnerability risk. Dissolved oxygen in the low vulnerability location ranged from 2.82 to 10.83 mg/L whereas the high vulnerability location showed much greater fluctuations, ranging from 0.9 to 16.11 mg/L. Moreover, the high vulnerability location showed 113 periods of hypoxia from May to December, where the low risk area totalled only nine (Fig. 3.5). The average duration of hypoxic periods was also far longer in the high vulnerability location. In the low vulnerability location, periods of hypoxia lasted for an average of 1.88 hours (± 0.42 SD), where periods of hypoxia in the high vulnerability location averaged 4.2 hours (± 2.18 SD). As a result, the high vulnerability location was hypoxic for a greater percentage of the total sampling period (17%) than the low vulnerability location (0.6%; Fig. 3.6).

Discussion

These data demonstrate that predation risk, though clearly present in our systems, does not show strong correlation with the distribution of juvenile lemon sharks. However, juvenile lemon shark abundances tended to be highest in areas with high vulnerability risk (i.e. low refuge availability). Our previous work (See Chapter 2) shows that these nursery systems may be limited primarily by food availability. Until now little research has focused on predation risk and its effect on the quality of the habitat selected by juvenile elasmobranchs. We might reasonably expect high vulnerability risk sites to support abundant predators as a result of the potential for increased predator foraging efficiency. However, high vulnerability risk sites also had the lowest encounter pressure (i.e. low predator abundances). From a geographical perspective (Fig. 3.1), the Rock Sound nursery systems (sites 1-4) had low refuge and low encounter pressure whereas the Exuma Sound nurseries (sites 5-9), because of their proximity to deep water, had high encounter pressure while providing the most physical refuge.

In some cases, individuals will adopt a strategy of growing at a quicker rate to outgrow the preferred prey size of their predator (Werner et al. 1983), suggesting that growing faster and being larger can be advantageous. Conversely, research in Marquesas Cay, Florida, suggests that small size, likely driven by availability of mangrove refuge, is more advantageous for juvenile lemon sharks (Dibattista et al. 2007). This difference in growth could also link to higher levels of competition in refuge areas, resulting in decreased growth rates (Orrock et al. 2013). In many cases, prey species adapt life history strategies depending on the amount of direct predation pressure. Reznick et al (2001, 2008) have shown that riverine guppies can change life history strategy depending on the level of predation pressure. In this case, low predation locations show higher levels of somatic growth, whereas high predation locations show higher reproductive growth resulting in higher birth rates and lower mean body mass. As a result of their k-selected life history, juvenile lemon sharks cannot easily switch between somatic and reproductive growth in response to varying predation pressure. However, our data provide some evidence that they may utilize the growth-mortality (g/μ) relationship to maximize individual fitness and ensure higher survival rates.

Previous work has suggested several mechanisms, both physical and physiological, occur during selection of refuge habitat (Chapman et al. 2002; Anjos et al. 2008). From abiotic data collected in both a high and a low refuge site, our data show higher juvenile lemon shark abundance in locations characterized by harsher environmental conditions (dissolved oxygen, temperature). Semi-diurnal tides lead to constant change in these parameters within the nursery itself, forcing animals inside to either adapt or vacate to riskier habitats outside the confines of the nursery. Previous research has shown that larger predators require longer acclimation periods to hypoxic environments (Robb and Abrahams, 2003; Hedges, unpublished data; Abrahams and Sloan, 2012). Noting that conditions within our inlets change rapidly over time, opportunities for predator acclimation are short and infrequent, thereby offering a potential physiological refuge to juvenile lemon sharks. Although environmental (abiotic) fluctuations can pose a physiological cost to organisms living in these areas, they may prove advantageous to smaller animals as a result of allometric scaling issues that prevent larger predators from accessing juvenile habitats (Abrahams, 2006).

Mangrove inlet systems are known to vary strongly in both biotic and abiotic conditions (Peterson, 1990). The sampling sites in this study vary in mangrove cover, available depth refuge at low tide, as well as abiotic condition (see chapter 2). Previous research supports the idea that many teleost and elasmobranch species use mangrove habitats (Nagelkerken et al. 2000; Nagelkerken et al. 2001; Murchie et al. 2008), however, we found no significant relationship between juvenile lemon shark abundance and physical refuge availability. In high risk sites, predator encounter risk is low. However, these areas also offer less refuge to teleost prey of juvenile lemon sharks within the system. During periods of high tide, teleost prey of juvenile lemon sharks use mangrove refuges as cover, which simultaneously provide predator refuge to juvenile lemon sharks. Conversely, at low tide, these mangrove refuges are unavailable to small teleost prey, increasing potential foraging success for juvenile lemon sharks. Given this relationship, areas with high vulnerability risk may provide lemon sharks easier access to prey and, interestingly, a minimal amount of direct predator encounter risk. However, foraging success and potential growth rates may be mediated by site-specific density of both prey and intraspecific competition. Therefore, mangroves may be more important as a refuge for prey items of juvenile lemon sharks, rather than as a physical refuge for juvenile lemon sharks from larger predators. As a secondary benefit, if the abiotic condition of the inlets exclude predators, juvenile lemon sharks may only be at risk should they have to leave the nursery. Although food availability seems to drive these refuges, predator avoidance may represent a secondary benefit provided by the constant fluctuations in the abiotic conditions.

The trade-off between food and risk is an inevitable reality faced by many taxa (Lima and Dill, 1990; Moody et al. 1996). Juvenile lemon sharks in particular have been studied in order to gain insight into habitat use its importance as a tool for assessing nursery habitats (Heithaus 2007; Heupel et al. 2007). However, more investigation is needed to better understand how these two variables are balanced to maximize the growth-mortality (g/μ) relationship (Werner and Gilliam, 1984) and increase survival probability. This balance is invariably mediated by many other factors, both biotic and abiotic. We therefore sought to highlight the relationship between juvenile elasmobranchs and their predators and how this may be mediated by the physical environment. Our results provide insight into how this trade-off impacts individual ability to select specific habitat designed to maximize individual success.

This study aims to highlight the importance of nursery refuges to coastal elasmobranch species. Many elasmobranchs use inshore habitats for foraging, mating or pupping grounds. These areas are therefore necessary for the survival of the species in many stages of life. Further study of these habitats will not only increase our ecological knowledge, but reinforce its importance in managing coastal ecosystems.

Tables

Table 3.1 – Number and size distributions of predators captured off of the nine mangrove inlet systems (lemon shark nurseries) studied

Species	# captured	Mean FL size (cm)	SD
Blacktip shark (*C. limbatus*)	8	143	17.35
Caribbean Reef shark (*C. perezi*)	7	146	11.33
Lemon shark (*N. brevirostris*)	9	121	34.28
Tiger shark (*G. cuvier*)	27	155.39	32.64

Figures

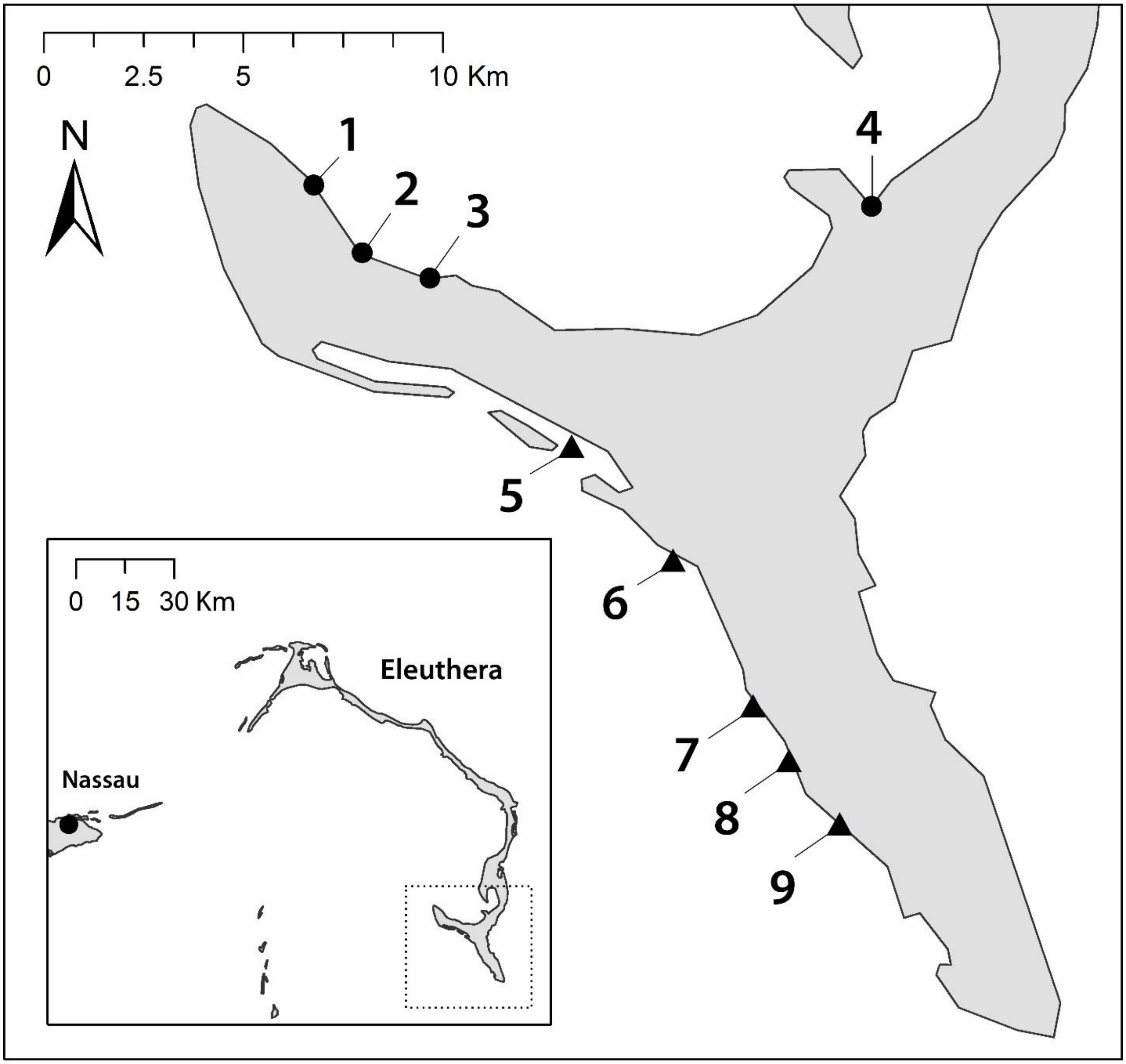

Figure 3.1 – Map of the east side of The Bahamas highlighting the islands of New Providence and Eleuthera. The large panel shows South Eleuthera, with numbered triangles highlighting the nine study sites. Sites 1-4 (circles) are located adjacent to Rock Sound, where sites 5-9 (triangles) are adjacent to the Exuma Sound. Site legend: 1 = Page, 2 = Kemps, 3 = Broad, 4 = Starved, 5 = Plum, 6 = Waterford, 7 = Wemyss Bight, 8 = Hartford, 9 = John Millers.

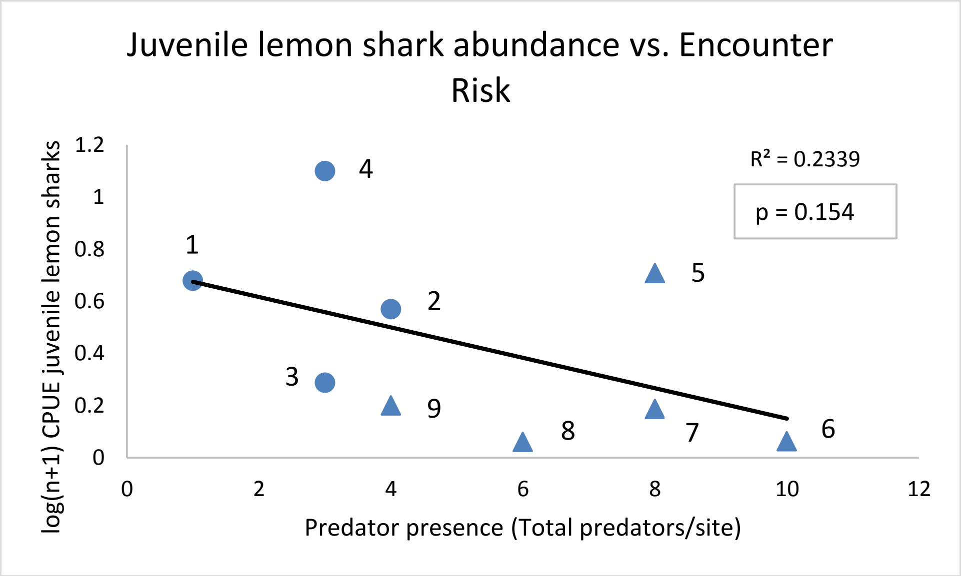

Figure 3.2 - Model used to predict lemon shark abundance (sharks/hr) as a function of predator presence (encounter risk). Circles represent inlets adjacent to Rock Sound. Blue triangles represent inlets adjacent to the Exuma Sound. Numbers correspond to site numbers listed in Fig. 3.1.

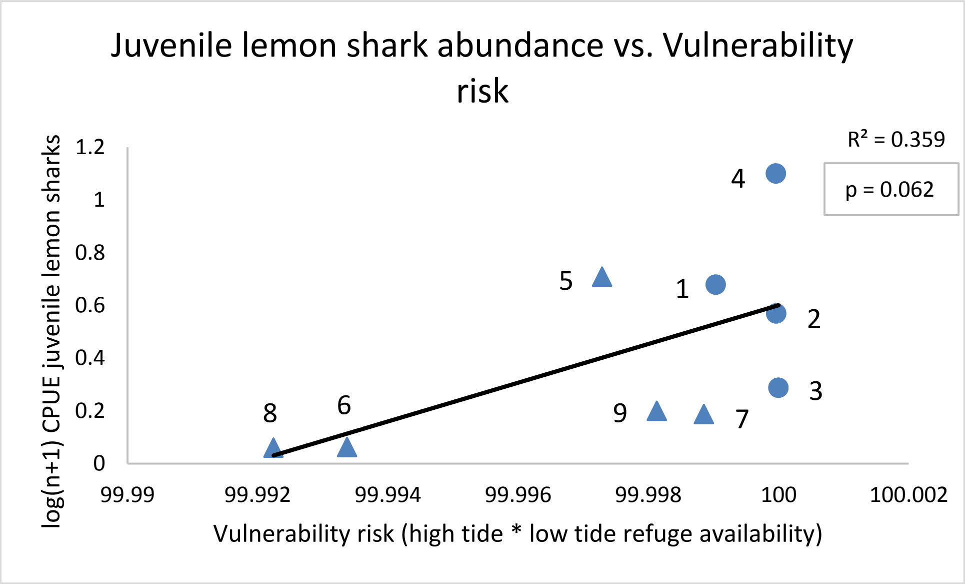

Figure 3.3 - Model used to predict lemon shark abundance as a function of vulnerability risk, a combined product of fringing mangrove cover and depth refuges available at each site. Circles represent the four sites located adjacent to Rock Sound. Blue triangles represent inlets adjacent to Exuma Sound. Numbers correspond to site numbers listed in Fig. 3.1.

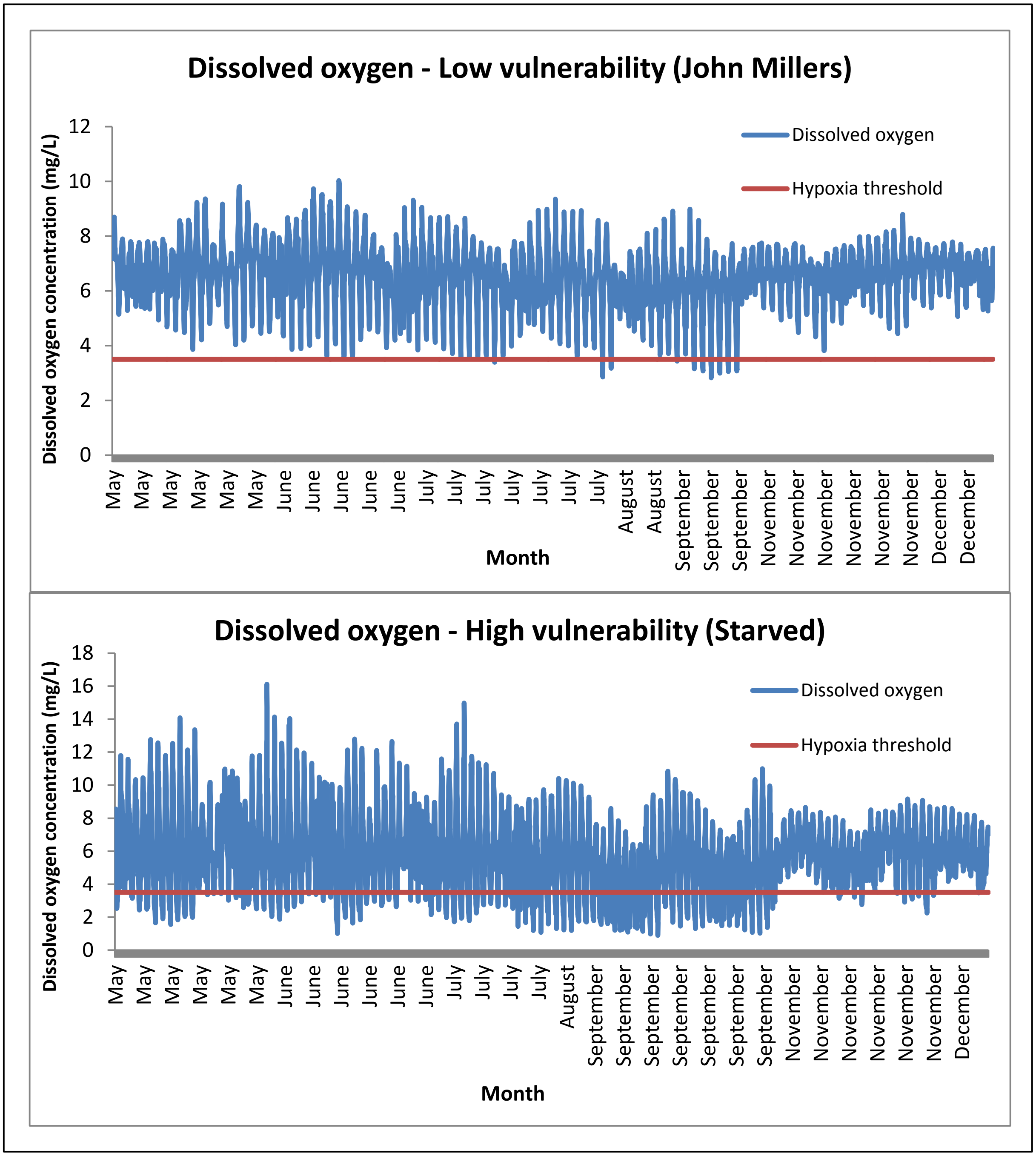

Figure 3.4 - Fluctuation in dissolved oxygen in both a low vulnerability (John Millers) and a high vulnerability (Starved) location throughout 2012. The red line depicts the theoretical hypoxia threshold derived from Carlson and Parsons (2001).

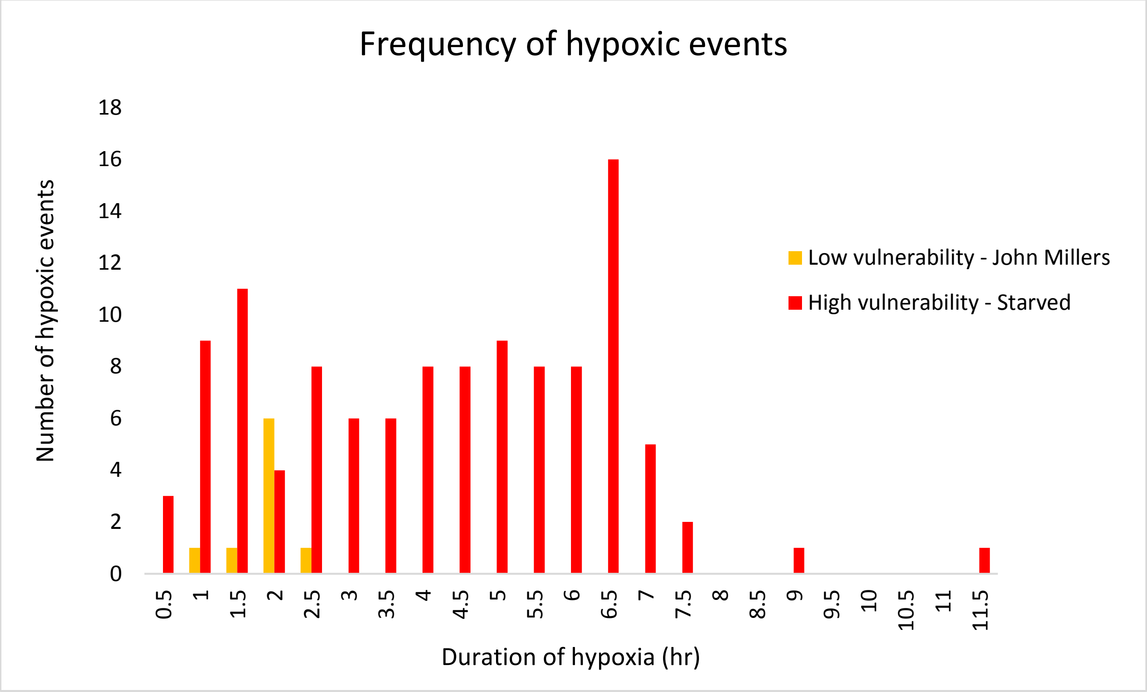

Fig 3.5 - Number of hypoxic events observed during the sampling period of May 11 through December 10, 2012. An event was defined as the period when dissolved oxygen levels dropped below 3.5 mg/L.

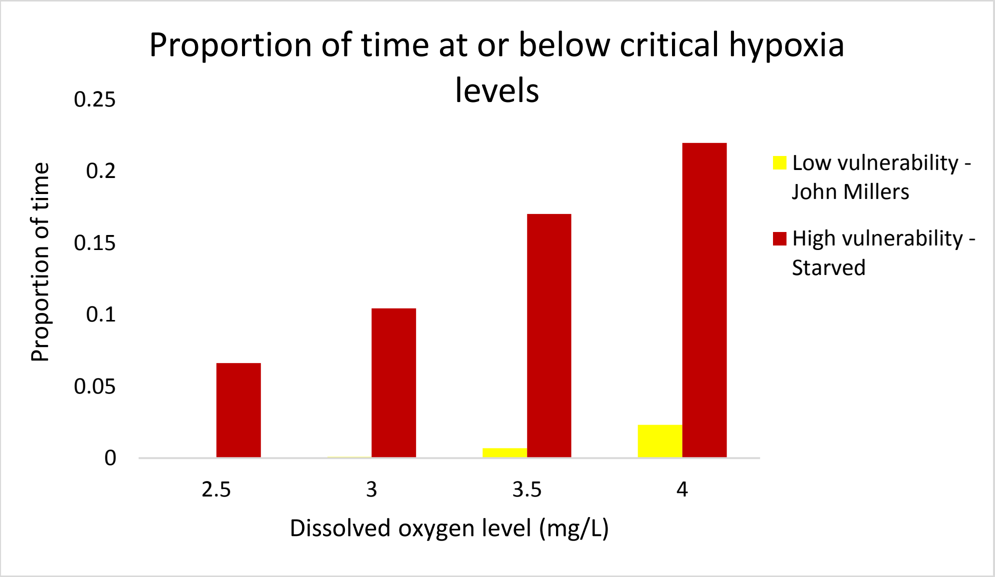

Fig 3.6 - Proportion of hypoxic time at each location. Dissolved oxygen levels were grouped using a frequency distribution into 0.5 mg/L categories to outline the proportion of time spent at or below each individual level

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Chapter 4

CONCLUSION

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Conclusion

This study presents several advances in ecological knowledge of the lemon shark. Until now, their association with their prey, and the resulting effect on their distribution, was relatively unclear. Our data suggest that coastal inlets used as nurseries are resource limited. These results indicate that juvenile lemon shark populations may exhibit frequency-dependent habitat selection, with a strong positive linear relationship between juvenile abundances and their major prey item, the mojarra (*Gerres* spp.) (Newman et al. 2010). The effects of predation risk were less clear but nonetheless provided further insight into risk effects on elasmobranchs. Our data suggested that juvenile lemon sharks were more abundant in areas with less physical refuge and lower levels of predator encounter risk. However, because these systems appear driven primarily by resource availability, we suggest that predation pressure has less effect on juvenile lemon sharks. Interestingly, our location with high vulnerability risk also showed far more extreme environmental conditions when compared with our low vulnerability site. These results provide insight into how these animals may weigh the costs and benefits of risk by using nurseries as a physiological refuge from predators (Robb and Abrahams, 2002). From our results, we can conclude that juvenile lemon sharks weigh both resource availability and risk, though not equally, in habitat selection decisions.

The need to understand ecological processes in elasmobranchs cannot be understated. Studies such as this increase our general ecological knowledge of elasmobranchs, but also provide insight into the mechanisms dictating patterns of life history. This study highlights important drivers of distribution patterns in juvenile elasmobranch species during early stages of life. We also provided a framework for better understanding the impacts of resource availability and predation risk. Many studies have called for a need to better understand how the food-risk trade-off impacts habitat use (Heithaus 2007; Heupel et al. 2007; Guttridge et al. 2012) The relationship between juvenile lemon sharks and their surrounding environment also implies a physiological component to risk management. This behaviour, also seen in bony fish, suggests that lemon sharks may take advantage of a body-size dependent physiological advantage as a means of managing risk from predators. Though much research has addressed movement patterns and home ranges (Morrissey and Gruber, 1993; Wetherbee et al. 2007), ours is the first study investigating how resource availability and predation risk, as potentially affected by physiology, shape distribution patterns and natal habitat selection in lemon sharks.

The use of coastal nurseries is not a behaviour specific to elasmobranchs. Many areas inhabited by sharks also offer vital recruitment and development grounds for a variety of coastal and reef species (Nagelkerken et al. 2000). Mangrove inlets facilitate prey development and therefore act as an important source of resource for many predator species. These areas also act as a transitional ground for many teleost species, thereby affecting the overall habitat quality of bordering sea grass beds and coral reef systems. Many of these areas are now under threat from anthropogenic development with clear effects on many coastal species (Feldheim and Edren, 2002; Jennings et al. 2008). Through the conservation of these important nursery areas, future marine management can protect mangrove habitats and their resident species.

This study demonstrated the important balance between resource availability and predation risk to juvenile lemon sharks within mangrove systems. The data collected provide valuable insight into the mechanisms behind habitat selection. By assessing distribution and growth patterns within the context of the growth-mortality relationship (μ/g), we have provided a template for understanding population level changes in a coastal elasmobranch species. Through this relationship, we are able to develop a foundation for understanding the complexities of early life history. From a theoretical perspective, our study provided insights into the scale on which lemon sharks gather information and assess the quality of a habitat. This research provides a framework for further developing our knowledge of the ecological trade-offs made by juvenile elasmobranchs and how resource management manifests itself in habitat selection decisions. Though issues such as habitat loss remain a threat, studies such as this highlight the importance of many coastal areas and act as a tool for furthering our ability to manage sustainable use of marine environments.

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Appendix

Location	Sampling dates (2012)
Starved creek	March 23, May 8, July 14, August 28, September 10
Broad creek	March 21, June 13, June 29, July 17, November 23
Kemps creek	March 5, April 18, May 4, May 14, June 28, July 14, August 2, September 24
Page creek	March 5, April 16, May 14, May 31, June 28, August 2, September 27
Plum creek	April 18, May 18, July 1, July 31, September 13, September 17
Waterford creek	March 6, July 20, August 16, November 29
Wemyss Bight creek	March 28, June 4, July 3, November 16
Hartford creek	March 28, May 21, September 28, November 13
John Millers creek	March 8, April 19, May 21, June 6, November 30

Appendix Table 1 – Sampling dates for each of the nine mangrove inlets assessed.