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ABUNDANCE, DISTRIBUTION, AND HABITAT USE OF SHARKS IN TWO NORTHEAST FLORIDA ESTUARIES

by

Michael Philip McCallister

A thesis submitted to the Department of Biology

in partial fulfillment of the requirements for the degree of

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Abstract

Sharks are considered top predators in many marine ecosystems, and can play an important role in structuring those communities. As a result, it is necessary to understand the factors that influence their abundance and distribution. This is particularly important as fishery managers develop fishery management plans for sharks that identify areas that serve as essential fish habitat (EFH). This includes nursery habitat where sharks are born and juveniles spend the early part of their life. However, our understanding of shark habitat use in the northeast Florida waters is limited. The goal of this thesis was to characterize the abundance and distribution of sharks in northeast Florida estuaries, and to examine the effect of abiotic and biotic factors affecting shark habitat use. A bottom longline survey conducted from 2009 – 2011 indicated that 11 shark species use the estuarine waters of northeast Florida during summer months. Atlantic sharpnose (*Rhizoprionodon terraenovae*), blacktip (*Carcharhinus limbatus*), bonnethead (*Sphyrna tiburo*), and sandbar sharks (*Carcharhinus plumbeus*) were the most abundant species and made up 87.1% of the total catch. Month, bottom water temperature, and depth were the most important factors determining the presence and abundance of these species. This study also examined the role of prey abundance in determining the abundance of Atlantic sharpnose sharks. The probability of catching an Atlantic sharpnose shark, and the abundance of Atlantic sharpnose sharks, were most influenced by site. Neither potential prey abundance nor preferred prey abundance were not significant factors effecting Atlantic sharpnose abundance. This may be a result of prey sampling not providing an accurate measure of the true availability of prey resources. Other factors, such as predation risk, may better explain habitat use patterns of Atlantic sharpnose sharks. Continued sampling will give a better understanding of the factors influencing shark habitat use in this area.

Introduction

In 1996, the U.S. Congress re-authorized Magnuson-Steven's Act as the Sustainable Fisheries Act (Magnuson-Stevens Act, 1996), and included a provision that required fishery managers to identify essential fish habitat (EFH). Since then, there have been increased efforts to characterize EFH for managed species (e.g., Sedberry et. al., 2001), as well as to examine the importance of EFH in developing ecosystem management plans (e.g., Lindeman et. al., 2000; Rosenberg et. al., 2000; Friedlander, 2001). Of particular importance in their role as EFH are nearshore estuarine and marine ecosystems (e.g. seagrass meadows, marshes, and mangroves) that serve as nursery habitat. The role of these ecosystems has been examined extensively (see Beck et. al. 2001 for a review) because of their high levels of productivity and ability to support increased abundance and diversity of marine organisms (Beck et. al., 2003), and the selective advantages they provide during early life history stages (e.g. Gibson, 1994; Nagelkerken et. al. 2002).

In the last decade, there has been increasing concern over the global decline in shark populations and its effects (e.g., Baum et. al., 2003; Myers et. al., 2007; Baum and Blanchard, 2010; Ferretti et. al., 2010). In particular, there is concern about the susceptibility of many shark populations to overexploitation as a result of overfishing (Musick et. al., 2000). In the United States, this has prompted fishery managers to develop specific fishery management plans (FMPs) that identify and characterize EFH in order to protect healthy shark populations and rebuild declining ones (NMFS 1999, 2003, 2006). This has resulted in numerous studies that have identified the presence of shark nursery habitats in coastal waters of the U.S., and characterized

the environmental and habitat preferences for sharks that use them (e.g. Branstetter, 1990; Grubbs et. al., 2007a; McCandless et. al. 2007a). While identification of potential shark nursery habitat is important, it is equally important to understand how and why sharks utilize these areas. Although shark nurseries are generally thought to provide abundant food resources and decreased predation risks (Branstetter, 1990; Castro, 1993), it has recently been suggested that selection of nursery habitat may be driven by tradeoffs between growing quickly in high risk areas with ample resources, or growing slowly in low risk areas with limited resources (Heithaus, 2007). However, few studies have examined this and our understanding of the factors that influence selection and use of nursery habitat is limited. Thus, further research is necessary to manage these areas and preserve the attributes that make them essential to sharks (Heithaus, 2007).

The purpose of this project was to gather critical data on the use of northeast Florida's nearshore and estuarine waters as shark nursery habitat and examine the factors that control selection and use of that habitat. The first two objectives of this thesis were to: 1) characterize the abundance and distribution of shark species in two northeast Florida estuaries, Cumberland Sound and Nassau Sound, and 2) identify and delineate habitat preferences for sharks within these estuaries, and identify potential EFH and nursery habitat. The third objective of this thesis was to examine the effect of prey abundance on habitat selection for sharks.

Chapter 1

Abundance, distribution, and identification of potential nursery habitat for sharks in northeast Florida waters

1.1 Introduction

Congress' reauthorization of the Magnuson-Stevens Fishery Conservation and Protection Act (MSA) in 1996 affirmed the widely accepted notion that Essential Fish Habitat (EFH) plays a critical role in the life-history of many marine organisms. According to the MSA, essential fish habitat is defined as "those waters and substrate necessary to fish for spawning, feeding, breeding, or growth to maturity," and should include habitats used at any portion of the species' life cycle (Magnuson-Stevens Act, 1996). Of particular importance in their role as EFH are nearshore estuarine and marine ecosystems (e.g. seagrass meadows, marshes, and mangroves) that serve as nursery habitats, providing a selective advantage for juveniles. For sharks, this may include increased prey abundance and decreased risk of predation (Branstetter, 1990; Castro, 1993).

The shark nursery concept was first put forth by Springer (1967), who described shark nurseries as discrete parts of a species range where parturition occurs and/or juvenile sharks spend the early part of their lives. Shark nurseries were further defined by Bass (1978) by distinguishing between primary and secondary nurseries. According to Bass's definition, primary nursery habitats are those areas where young sharks are born and spend up to the first

year of their life, while secondary nursery habitats are where slightly older but not yet mature individuals occur. Although these definitions have been well accepted, and the concept of shark nursery habitat is well established, clear criteria that can be used to identify nursery areas have been lacking. More recently, the shark nursery concept was re-examined by Heupel et al. (2007), who proposed a definition with three criteria that could be used to quantitatively identify shark nursery habitat: 1) juvenile sharks are more commonly encountered in the area than in others, 2) juvenile sharks will remain or return to these areas over an extended period of time, and 3) the area will be utilized repeatedly across years compared to other areas.

Concern about the susceptibility of shark populations to overfishing (FAO, 2000) has prompted U.S. fishery managers to develop specific fishery management plans (FMPs) for sharks (NMFS 1999, 2003, 2006). A critical component of these management plans is the identification of essential fish habitat (NMFS, 1999). Recognizing the importance of nursery habitat to the success of shark populations, fishery managers have developed FMPs that require the identification and delineation of suitable nursery habitat. This has resulted in numerous ongoing and detailed studies examining the presence of shark nurseries in most of the major estuaries along the Atlantic and Gulf Coasts of the U.S. (see McCandless et. al., 2007b). However, close examination of the scientific literature reveals a noticeable gap in knowledge regarding shark habitat along the East Coast of the US (Fig. 1). Specifically, there have been no studies to examine the presence of shark nursery habitat in northeast Florida.

In 2009, the University of North Florida (UNF) established an annual shark abundance survey to examine shark populations in the coastal and estuarine waters from the Florida-Georgia border to St. Augustine, FL. The goal of this project was to gather critical data on the use of northeast Florida's nearshore and estuarine waters as shark nursery habitat. Using data collected

from 2009 – 2011 during the UNF shark abundance survey, this paper characterizes the abundance and distribution of juvenile shark species in two northeast Florida estuaries, Cumberland Sound and Nassau Sound, and identifies and delineates EFH for juvenile sharks within these estuaries.

1.2 Study Site

Cumberland and Nassau Sounds are located in northeast Florida (Fig. 2) on the northern and southern boundaries of Nassau County, respectively, and are part of the Nassau – St. Mary's Water Basin. Cumberland Sound is located at the mouth of the St. Mary's River between Cumberland Island, GA and Amelia Island, FL. Nassau Sound is situated between Amelia Island and Big Talbot Island at the confluence of Sister's Creek and the Nassau and Amelia Rivers. Both of these estuaries can be considered healthy, with the last water quality assessment of the Nassau – St. Mary's Water Basin classifying the bodies of water that feed into Cumberland Sound as Class III surface waters (suitable for maintaining a healthy, well balanced population of fish and wildlife) and those that enter Nassau Sound as Class II surface waters (suitable for shellfish harvest and propagation) (FLDEP, 2007).

1.3 Methods

Shark Abundance Survey

Longline sampling was conducted in the nearshore and estuarine waters of Cumberland (Fig. 3a) and Nassau (Fig. 3b) Sounds from late April through November, with the most extensive sampling effort occurring from May – September. Each region was sampled weekly via bottom longline fishing. The longline consistsed of a single 300-m #8 braided nylon

mainline, anchored at both ends and marked with two buoys, containing50 gangions, each composed of a 1m 90-kg test monofilament leader, size 120 stainless steel longline snap, 4/0 swivel, and a 12/0 barbless circle hook baited with Atlantic mackerel (*Scomber scombrus*). Initially sets were allowed to soak for one hour; however, after the second week the soak time was reduced to 30 minutes to reduce animal mortality. Five to six sets were fished each day, and the location of each set was selected haphazardly. Environmental data was collected at each sampling location after the longline was set. Bottom water temperature (^{o}C), salinity ($^{o}/_{oo}$), and dissolved oxygen (mg/L) were measured using an YSI-85. Water depth (m) was recorded at the beginning and end of each set. The average depth for each set was calculated and used in all analyses.

All sharks caught during the survey were identified to species, and relevant biological data, including sex, length (cm), weight (kg), life stage, and umbilical scar status were recorded. Length measurements were taken for pre-caudal length (PCL), fork length (FL), total length (TL), and stretched total length (STL). Life stage was classified as either young-of-the-year (YOY; umbilical scar present), juvenile (not yet mature), or mature. Males were considered mature if the claspers were calcified and by comparing recorded lengths to previously published lengths at maturity. Female maturity was determined by comparing to previously published lengths at maturity. Status of YOY sharks was classified based on the degree of umbilical scar healing using the criteria described by Aubrey and Snelson (2007): 1) umbilical remains present, 2) open or fresh scar, 3) partially open, some healing, 4) well healed, scar visible, and 5) no scar present. All sharks caught alive were tagged in the dorsal fin with a numbered roto-tag provided by NOAA Fisheries Service, and released. The release condition for all animals was categorized using “vitality codes” established by Manire et al. (2001).

Data Analysis

Since the majority of hooks were recovered without bait, soak time was not included in calculations of catch rates. Catch rates were expressed as catch per unit effort (CPUE), and was calculated as the number of sharks per 50 hooks. Overall CPUE was calculated on a monthly basis for all sharks caught in Cumberland and Nassau Sound. Trends in abundance were examined by calculating average monthly CPUE from 2009 – 2011.

Two types of analysis were used to examine the effect of environmental data on shark catch. Due to the large number of sets that caught no sharks, catch data was split into presence/absence and abundance data. Presence/absence data was generated by determining whether or not each set caught at least one shark. Sets that caught zero sharks were then removed and abundance data was generated for each set that caught at least one shark. Analyses were performed using these data for all shark species combined, as well as the four most abundant shark species. Logistic regression models (SAS v. 7.0) were performed using presence/absence data to determine which environmental factors had the greatest influence on whether sharks were present in the study site or not. Factors included in the analysis included month, water depth, bottom water temperature, salinity, dissolved oxygen, and interactions between these factors. For each model run, factors that were not significant were removed until the final model included only those factors which were significant. Factors were determined to be significant if $p \leq 0.05$. For all sets that caught at least one shark, general linear models (GLMs) (SAS v. 7.0) were used to determine which factors had the greatest influence on the abundance of sharks. The same factors that were used in the logistic regressions were also used in the GLMs, and only factors that were found to be significant were included in the final models.

Species-specific accounts were presented for all shark species caught during the survey. These include overall monthly abundance, sex specific length-frequency plots, and percent of catch by maturity. Species-specific accounts were provided in order of overall abundance. The three species with the lowest abundance were discussed together.

1.4 Results

Overall

A total of 310 longline sets were made in Cumberland Sound (n=147) and Nassau Sound (n=163) from 2009 – 2011. A total of 622 sharks were caught, representing 11 species (Table 1), with an average of two sharks caught per set. Species composition included all four species of the small coastal shark complex (SCS), the Atlantic sharpnose (*Rhizoprionodon terraenovae*), bonnethead (*Sphyrna tiburo*), blacknose (*Carcharhinus acronotus*), and finetooth (*Carcharhinus isodon*); five species from the large coastal shark complex (LCS), blacktip (*Carcharhinus limbatus*), sandbar (*Carcharhinus plumbeus*), scalloped hammerhead (*Sphyrna lewini*), spinner (*Carcharhinus brevipinna*), and lemon (*Negaprion brevirostris*); as well as the nurse shark (*Ginglymostoma cirratum*) and the smooth dogfish (*Mustelus canis*). All 11 species were caught in Cumberland Sound and 9 of the 11 species were caught in Nassau Sound, and with the exception of the blacknose, all species were caught in greater numbers in Cumberland Sound compared to Nassau Sound. Of the 622 sharks that were caught, the Atlantic sharpnose shark (n=348), blacktip shark (n=95), bonnethead shark (n=63), and sandbar shark (n=36), were the four most abundant species and accounted for 87.1% of the total catch (Table 1).

The average CPUE for all sharks from 2009 - 2011 was 1.60 sharks 50-hooks^{-1} (SD = 1.12). Annual average CPUE was highest for 2010 (2.15 sharks 50-hooks^{-1}). Figure 4 shows the

trends in average monthly CPUE for all sharks from 2009 – 2011. Average monthly CPUE increased from 0.18 sharks 50-hooks^{-1} in April to a maximum of 3.27 sharks 50-hooks^{-1} in July. After July, monthly CPUE decreased steadily through the late summer and fall until October.

Environmental Analysis

Sharks were caught in Cumberland and Nassau sounds in a wide range of environmental conditions. Mean values, and ranges, for environmental variables for all longline sets, all species combined, and each individual species are presented in Table 2. Logistic regressions were performed to examine the effect of environmental variables on the presence/absence data for all species combined and the four most abundant species. Significant factors were found in the models for each of the four most abundant species and for all species combined (Table 3). When looking at all shark species combined, month, bottom temperature, and their interaction were all highly significant factors ($p < 0.0001$) associated with the presence/absence of sharks. Sharks were present from late spring (end of April) through fall (early November) and were caught in waters from 19.1 – 36.2°C. Month, bottom temperature, and their interaction were also found to be significant factors in the model for Atlantic sharpnose sharks with bottom temperature being highly significant ($p < 0.01$). Atlantic sharpnose were present in water temperatures from 20 – 36.2°C (Table 2). Significant factors that influenced the presence/absence of blacktips were also month and bottom temperature, with depth nearly significant ($p = 0.0535$). Blacktips were present from May – September in water temperatures from 22.6 – 36.2°C. Dissolved oxygen was the only significant factor affecting the presence/absence of bonnetheads. The presence of sandbar sharks was significantly affected by month and depth, with depth being highly significant ($p < 0.01$). Sandbar sharks were present in all months of the survey, and were caught in water 4 – 11m deep.

General linear models (GLMS) were run to examine the effect of environmental variables on the abundance of all shark species combined and the four most abundant species. Results from the GLMs produced significant models for Atlantic sharpnose sharks, blacktip sharks, and all shark species combined (Table 4). Depth, bottom temperature, dissolved oxygen, and the interaction between bottom temperature and dissolved oxygen all had a significant effect on shark abundance when all species were combined, with bottom temperature being the most significant. Shark abundance was higher in warm, deep waters, with moderate levels of dissolved oxygen, and for sets that caught more than the average number of sharks/set (2 <) average depth, bottom temperature, and dissolved oxygen were 6.4m, 27.8^{o}C, and 5.0mg/L respectively. The only significant factor in the GLM for Atlantic sharpnose sharks was bottom temperature ($p = 0.0056$); *R. terranovae* were most abundant in waters 24.8 – 31^{o}C (mean = 28.2^{o}C). The GLM for blacktip sharks was the most complex. Depth, bottom temperature and dissolved oxygen were each significant factors, as well as the interactions between these variables (Table 4). Most sharks were caught in water 4 – 8m deep, with bottom temperatures ranging from 25 – 30^{o}C and dissolved oxygen content of 3 – 6mg/L.

Atlantic sharpnose

Atlantic sharpnose sharks (n=348) were the most abundant species caught in the study site and accounted for 55.9% of the total catch. Individuals were caught in all months of the survey except for April, with the highest number of sharks caught between May and September (Figure 5). Lengths of captured Atlantic sharpnose sharks ranged from 31-102cm TL, and sex specific length-frequency data can be seen in Figure 6. Mature sharks made up 57% of the total catch and were most abundant in May and June. They had a mean length of 89.0cm TL (range = 72-101cm TL), and a mean weight of 3023.9g (SD=627.6g). Young-of-the-year individuals

made up 37% of the total catch and were present from May –September with greatest abundances occurring in July and August. Mean length was 40.9cm TL (range = 31-48cm TL) and mean weight was 331.3g (SD = 151.9g). All YOY individuals that were caught had umbilical scars that were mostly healed or well healed; none were found with umbilical remains or fresh/open umbilical scars. Juveniles made up only 6% of the total catch, and were caught between June and October. The few juveniles that were caught had a mean length of 58.0cm TL (range = 49-66.5cm TL) and a mean weight of 1055.2g (SD = 199.5g). The overall sex ratio of females to males was 1:4.03, and was significantly different from a 1:1 ratio ($\chi^2 = 122.88$, $p < 0.0001$) with males (n=274) making up 78.8% of the catch. Of the 68 females caught most were YOY and juvenile individuals. A single mature female (95cm TL) was caught in Nassau Sound on May 19, 2010. This was a pregnant female, and she gave birth to three full-term pups while on the line.

Blacktip

Blacktip sharks (n = 95) were the second most abundant species caught in the survey and accounted for 15.3% of the total catch. This was the most abundant species in the large coastal shark complex (LCS) that was caught. Individuals were only present from May to September, and the greatest abundance of animals was seen between June and August (Figure 7). Individuals ranged in size from 56 – 173cm TL, and included YOY, juvenile, and mature individuals (Fig. 8). The male to female sex ratio was 1:1.3, and did not differ significantly from a 1:1 expected ratio ($\chi^2 = 1.32$, $p = 0.251$). The survey caught primarily YOY (57%) and juvenile (38%) individuals. Young-of-the-year blacktips were present from May – August, with the greatest abundance occurring from July – August. YOY individuals had a mean length of 64.1cm TL (range = 56 – 71cm TL) and an average weight of 1861.3g (SD = 365.6g). Umbilical

scars in various stages of healing (fresh to well healed) were observed on all YOY blacktips. Juveniles, present from May – September, had a mean length of 87.2cm TL (74 – 122cm TL) and weight of 5866.4g (SD = 2466.4g). Only five mature blacktips (3 males, 2 females) were caught during the survey, ranging in size from 144 – 173cm TL (mean = 152.8cm TL).

Bonnethead

A total of 63 bonnetheads were caught from 2009 – 2011. This was the third most abundant species caught during the survey and comprised 10.1% of the total catch. Bonnetheads were present from May – October, with the majority of animals caught in the summer (Figure 9). Bonnetheads were captured at lengths ranging from 41 – 118cm TL. Sex specific length-frequency data can be seen in Figure 10. The male to female sex ratio was 1:4.45, and was significantly different than 1:1 ($\chi^2 = 22.82$, $p < 0.0001$). Mature bonnetheads were most abundant from June – August, and comprised 80% of the catch. Individuals ranged in size from 75 – 118cm TL (mean = 100cm TL), had an average weight of 5176.8g (SD = 1968.4g), and were mostly female. Very few juvenile (n = 8) and YOY (n = 4) bonnetheads were captured. Juveniles had a mean length of 68.1cm TL (range = 60 – 77cm TL) and mean weight of 1292.3g (SD = 167.7g). YOY ranged in size from 45 – 52cm TL (mean = 47.9cm TL) and weighed an average of 437.5g (SD = 85.4g).

Sandbar

A total of 36 sandbar sharks were caught in Cumberland and Nassau sound and made up 5.8% of the total catch. This species was caught in all months of the survey, with a slightly higher abundance in mid-summer (Figure 11). Sandbar sharks caught during the survey ranged in size from 56 – 161cm TL, and length-frequency distributions for male and female sandbar sharks can be seen in Figure 12. The overall sex ratio was not significantly different from 1:1 (χ^2

= 1.82, p = 0.1773). Young-of-the-year (n = 8) and juvenile (n = 26) sharks dominated the catch, and only a single mature sandbar (male, 161cm TL) was caught. Juvenile sharks, present in all months, had a mean size of 99.7cm TL (range = 71 – 130cm TL) and mean weight of 4309.1g (SD = 785.6g). Young-of-the-year sharks, present from June – August and in October, had a mean size of 62.9cm TL (range = 57 – 72cm TL) and mean weight of 1757.7g (SD = 615.2g).

Scalloped Hammerhead

A total of 22 scalloped hammerheads (3.5%) were captured during the survey, all of which were YOY or juvenile individuals. Scalloped hammerheads were only present in summer months (Figure 13). Sharks ranged in size from 50 – 102cm TL and the sex ratio was significantly different from 1:1 (χ^2 = 6.86, p = 0.0088, Fig. 14). Juvenile sharks ranged in size from 57 – 102cm TL (n = 17, mean = 78.6cm TL). Mean size of YOY sharks (n = 5) was 53.5cm TL (range = 50 – 56.5cm TL).

Finetooth

Finetooth sharks (n = 19) were caught in all months of the survey (Figure 15) and comprised 3.1% of the total catch. Lengths of captured finetooth sharks ranged from 58 – 145cm TL (Figure 16), and the sex ratio was significantly different from a 1:1 ratio (χ^2 = 6.72, p = 0.0095) with males (n = 15) being most commonly caught. Juveniles made up 72% of all finetooth sharks caught and had a mean size of 75.7cm TL (range = 60 – 84cm TL) and a mean weight of 2759.3g (SD = 1027.2g). Three mature finetooth were caught, 2 males (135 and 145cm TL) and 1 female (156cm STL). A single YOY finetooth (57.5cm TL) was caught in August and had a well healed umbilical scar.

Blacknose

Only 15 blacknose sharks (2.4%) were caught in the survey from 2009 – 2011. Blacknose sharks were present in summer months, with most animals being caught in June (Figure 17). Blacknose sharks caught during the survey ranged in size from 80 – 125cm TL (Figure 18), and the 2:1 male to female sex ratio was not significant (χ^2 = 1.06, p=0.303). All but one of the sharks were mature individuals with a mean size of 112.4cm TL, and mean weight of 8482.1g (SD = 1913.1g).

Spinner

A total of 11 spinner sharks were caught in Cumberland and Nassau Sound. All sharks were caught in July and August. Lengths of captured spinner sharks ranged from 66 – 93cm TL, and an equal number of males (n = 6) and females (n = 5) were caught (Figure 19). Of the 11 sharks caught, 10 were YOY individuals with mostly healed or well healed umbilical scars. Mean size and weight of YOY spinners was 70.5cm TL (range = 66 – 74cm TL) and 2041.2g (SD = 226.8g).

Other Species

The nurse shark (n=9), lemon shark (n=3), and smooth dogfish (n=1) combined to make up 2.1% of the total catch and were the three least abundant species encountered during the survey. All nurse sharks caught in the survey were juvenile individuals and ranged in size from 148-195cm STL (mean 168.2cm STL) (Figure 20). Of the three lemon sharks caught, data was only able to be recorded for two of them. Both were juvenile females, 140 and 155cm TL, and were both caught on June 15, 2010. A single, female smooth dogfish was caught in May 2011 in Cumberland Sound.

Tag-Recapture Data

A total of 419 sharks were tagged in Cumberland and Nassau sound from 2009 – 2011, and 18 were recaptured, for a recapture rate of 4.3% (Table 5). Of the 18 sharks recaptured, 17 were initially tagged in Cumberland Sound and 1 in Nassau Sound. The longest time at liberty was 411 days for a mature male Atlantic sharpnose tagged in Cumberland sound in May 2010 and recaptured in Cumberland Sound in June 2011 at a distance of 2.6km from where it was tagged. The longest distance traveled was 190.5km for a mature male sharpnose tagged in Cumberland Sound and recaptured off Cape Canaveral, FL. One shark, an Atlantic sharpnose, was tagged in Cumberland Sound and recaptured 14 days later in Nassau Sound having traveled ~21km. Fifteen of the 18 recaptured sharks were caught less than 10km from where they were initially tagged. All 10 YOY and juvenile sharks that were recaptured were re-caught the same year they were tagged.

1.5 Discussion

This study represents the first attempt to characterize the abundance and distribution of shark populations in the nearshore and estuarine waters of northeast Florida. Eleven different species were caught from 2009 – 2011, including species in both the small coastal (SCS) and large coastal (LCS) shark management units. This suggests that the estuarine waters of Cumberland and Nassau Sounds support a high diversity of shark species. Although there are no similar studies from northeast Florida to provide a direct comparison, these results are similar to studies from South Carolina (Ulrich et. al., 2007) and, in particular, Georgia (Belcher and Jennings, 2010). Eight of the species caught during this study were also caught in the study by Belcher and Jennings (2010) in Georgia. The four most abundant species that accounted for

87.1% of the total catch in this study, Altantic sharpnose, blacktip, bonnethead, and sandbar sharks, were also the four most abundant species identified in estuarine waters of Georgia and accounted for 96.1% of the total catch (Belcher and Jennings, 2010).

Results from the logistic regressions and general linear models provide a summary of the environmental factors that affect the presence and abundance of shark species in northeast Florida estuaries. The presence of sharks in Cumberland and Nassau sounds was affected most by month and/or bottom temperature. Although sharks were caught in all months of the survey, no sharks were caught in waters with a bottom temperature below 19°C, and sets that caught sharks were slightly warmer (mean = 27.2°C) than sets that did not (mean = 25.6°C). Also, the lowest abundance of sharks, and lowest CPUE, were seen in months at the beginning (April) and end (October and November) of the survey period. This suggests that the presence of sharks in northeast Florida estuaries is seasonal, and that movement into the estuaries occurs at a minimum, or threshold, temperature. This is consistent with findings for sharks in other coastal nurseries as well. Temperature was the driving factor for the movement of sandbar sharks into nurseries in both Delaware Bay (Merson and Pratt, 2001) and Chesapeake Bay (Grubbs et. al., 2007b). Castro (1993) and Ulrich et. al. (2007) documented the presence of sharks in South Carolina estuaries after water temperatures reached ~19-20°C.

Results from this survey suggest that the estuarine waters of Cumberland and Nassau Sound serve as nursery habitat for Atlantic sharpnose and blacktip sharps, and possibly for bonnethead sharks as well. High catches of YOY Atlantic sharpnose with healing umbilical scars in summer months, particularly July and August, suggests that this area serves as a primary nursery with immigration into the nursery occurring in early summer. This is consistent with findings from the northwest Gulf of Mexico (Carlson and Brusher, 1999). The capture of a

pregnant female in late May also supports this premise. The high abundance of YOY blacktips with visible umbilical scars, as well as juveniles, suggests that Cumberland and Nassau Sound act as both a primary and secondary nursery. Limited tag return data suggests that blacktips utilize these estuaries throughout the summer months, until moving offshore in the fall. A similar pattern was seen for juvenile blacktip sharks in Terra Ceia Bay by Heupel and Hueter (2001, 2002).

The overall low abundance of bonnetheads during this survey can likely be attributed to gear bias. Environmental constraints prevented consistent and reliable use of gillnets as part of the survey. On the few occasions where a gillnet was used, the catch consisted almost completely of bonnethead sharks (McCallister, unpublished data). This is not surprising as other studies of shark nurseries that used longline gear have reported low catches of bonnetheads (e.g. Ulrich et. al., 2007; Belcher and Jennings, 2010), while studies that have used nets reported much higher catches (e.g. Gurshin et. al. 2007). Despite low catches, however, the presence of pregnant females and a few YOY individuals with healed umbilical scars suggests these waters likely serve as nursery habitat in some respect.

It has been suggested that merely noting the presence of pregnant females and/or high abundance of young-of-the-year and juvenile sharks in an area does not mean an area is a nursery, or functions as critical habitat (Heithaus, 2007). Instead, Heupel et. al. (2007) proposed using well defined criteria that could be tested to provide a quantitative assessment of whether an area serves as nursery habitat. Though they were not used directly in this study, data from this survey appear to provide preliminary support for two of the three criteria. Tag return data from four blacktips tagged in Cumberland Sound and recaptured less than 7km from their initial location after 1 – 2 months at liberty, suggests that sharks remain in the area for extended periods

of time. Also, the fact that YOY and juvenile individuals of the four most abundant species were caught in each year of the survey, suggests that Cumberland and Nassau Sound are used across multiple years. Continued sampling within these regions, as well as expanding the survey to surrounding areas, will enable further testing of these criteria.

Given the current need to identify Essential Fish Habitat (EFH) and incorporate this information into fishery management plans (NMFS, 1996), studies that identify and describe shark nursery habitat are increasing. Although nursery grounds have already been identified and well studied for some the species caught during this survey (e.g. Grubbs et. al., 2007; Ulrich et. al. 2007) many of these species are considered to be highly migratory, thus, identifying potential nursery habitat throughout their range will provide a more detailed account of the location of potential EFH for use by fishery managers. This is the first study to identify and describe potential nursery habitat for young-of-the-year and juvenile sharks in northeast Florida waters. Given the lack of information on shark habitat use in these waters, and the presence of commercial shark fisheries within this region (Trent et. al., 1997), as well as a large recreational fishing presence, it is important that these areas be described. The data reported in this paper represents the first three years of an ongoing shark abundance survey in northeast Florida waters. Further research is needed to provide more species specific data on shark nursery habitat use in this region, including predator-prey relationships, movement patterns within nurseries, and species interactions.

1.6 Acknowledgements

This work was funded through a grant from the National Oceanic and Atmospheric Association National Marine Fisheries Service Cooperative Atlantic States Shark Pupping and Nursery Survey Program. Additional financial support was provided by 2 Graduate Scholar Grants awarded by the

University of North Florida Graduate Program. The University of North Florida Biology Department provided the vessels and vehicles used during this study. Tags and tagging equipment was provided by NOAA/NMFS division of Highly Migratory Species. Special thanks go out to my dedicated volunteers, especially Brenda Anderson, Amanda Breakey, Arianne Leary, Rachel Smith, and Christina Walker, without whom it would have been impossible to run trips. This research was conducted under the authorization of Florida Fish and Wildlife Conservation Commission Special Activity License # SAL-09-1136A-SR.

Table 1-1. Species composition and total abundance for all sharks caught in Cumberland and Nassau Sound from 2009 – 2011. Numbers in parentheses are percent of the total catch. Species are sorted in order of overall abundance (most abundant to least abundant). CS = Cumberland Sound, NS = Nassau Sound. Species listed in italics represent 87.1% of the total catch of all sharks.

	Year - Location								
	2009		**2010**		**2011**		**Total**		
Species	**CS**	**NS**	**CS**	**NS**	**CS**	**NS**	**CS**	**NS**	**Overall**
Atlantic Sharpnose	60 (52.6%)	28 (54.9%)	86 (61.4%)	60 (57.7%)	81 (51.6%)	33 (58.9%)	227 (55.2%)	121 (57.3%)	348 (55.9%)
Blacktip	18 (15.8%)	14 (27.4%)	21 (15%)	16 (15.4%)	19 (12.1%)	7 (12.5%)	58 (14.1%)	37 (17.5%)	95 (15.3%)
Bonnethead	18 (15.8%)	5 (9.8%)	12 (8.6%)	10 (9.6%)	14 (8.9%)	4 (7.1%)	44 (10.7%)	19 (9%)	63 (10.1%)
Sandbar	13 (11.4%)	1 (2%)	4 (2.9%)	3 (2.9%)	14 (8.9%)	1 (1.8%)	31 (7.5%)	5 (2.4%)	36 (5.8)
Scalloped Hammerhead	2 (1.8%)	0 (0%)	7 (5%)	4 (3.8%)	7 (4.5%)	2 (3.5%)	16 (3.9%)	6 (2.8%)	22 (3.5%)
Finetooth	2 (1.8%)	0 (0%)	2 (1.4%)	5 (4.8%)	7 (4.5%)	3 (5.4%)	11 (2.7%)	8 (3.8%)	19 (3.1%)
Blacknose	0 (0%)	3 (5.9%)	2 (1.4%)	5 (4.8%)	2 (1.3%)	3 (5.4%)	4 (1%)	11 (5.2%)	15 (2.4%)
Spinner	0 (0%)	0 (0%)	2 (1.4%)	0 (0%)	9 (5.7%)	0 (0%)	11 (2.7%)	0 (0%)	11 (1.8%)
Nurse	0 (0%)	0 (0%)	2 (1.4%)	1 (1%)	3 (1.9%)	3 (5.4%)	5 (1.2%)	4 (1.9%)	9 (1.4%)
Lemon	1 (<1%)	0 (0%)	2 (1.4%)	0 (0%)	0 (0%)	0 (0%)	3 (<1%)	0 (0%)	3 (<1%)
Smooth Dogfish	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (<1%)	0 (0%)	1 (<1%)	0 (0%)	1 (<1%)
Total	114	51	140	104	157	56	411	211	622

Table 1-2. Environmental conditions inhabited by sharks caught in Cumberland and Nassau Sound from 2009 – 2011. Means and ranges (in parentheses) are given. Species are listed in order of abundance. DO = dissolved oxygen

Species	Depth (m)	Bottom Temp. (^oC)	Salinity ($^o/_{oo}$)	DO (mg/L)
All longline sets	6.1 (1.8 - 14.3)	26.6 (17.3 - 36.2)	33.4 (24.2 - 37.7)	5.2 (2.96 - 9.58)
All species	6.0 (1.8 - 12.8)	27.2 (19.1 - 36.2)	33.5 (24.2 - 37.7)	5.2 (2.96 - 9.58)
Atlantic sharpnose	6.1 (1.8 - 12.8)	27.4 (20.1 - 36.2)	33.3 (24.2 - 37.7)	5.2 (3.18 - 9.58)
Blacktip shark	5.3 (2.3 - 11.8)	28.1 (22.6 - 36.2)	33.1 (24.2 - 36.8)	5.1 (3.1 - 8.77)
Bonnethead	5.8 (1.8 - 12.0)	27.8 (20.9 - 31.0)	33.3 (24.2 - 37.0)	4.6 (2.96 - 6.40)
Sandbar	7.9 (4 – 12)	26.0 (19.7 - 30.8)	32.7 (27.4 - 36.6)	5.1 (3.33 - 6.5)
Scalloped hammerhead	7.4 (3.3 - 12.8)	27.8 (24.7 - 31.0)	33.7 (29.6 - 36.2)	4.9 (3.27 - 9.58)
Finetooth	5.5 (3.0 - 12.0)	26.6 (19.1 - 31.0)	33.1 (25.3 - 36.4)	4.7 (3.21 - 6.05)
Blacknose	6.5 (2.3 - 10.7)	27.1 (24.6 - 29.0)	33.7 (29.3 - 36.6)	5.1 (4.13 - 6.52)
Spinner	7.3 (5.1 - 10.7)	28.2 (26.6 - 29.6)	34.6 (29.2 - 36.6)	4.4 (3.27 - 6.30)
Nurse	8.4 (4.5 - 11.8)	28.5 (27.3 - 31.0)	34.6 (29.4 - 36.7)	4.5 (3.72 - 5.21)
Lemon	7.9 (3.0 - 9.5)	28.3 (19.7 - 30.7)	34.6 (33.4 - 35.5)	4.5 (3.62 - 6.10)
Smooth dogfish	6.2 -	24.2 -	35.2 -	5.62 -

Table 1-3. Logistic regression results and significance associated with factors used in the models to examine the effect of environmental factors on the presence/absence of sharks in Cumberland and Nassau Sounds. Interactions between variables are denoted by terms joined by * in the model parameters. MO = month, D = depth, BT = bottom temp., SAL = salinity, DO = dissolved oxygen. Significance was determined at $p \leq 0.05$, and significant factors are in bold.

Species	Model	Intercept	Factors
All sharks	MO+BT+BT*MO	p < 0.0001	**MO, p = 0.0002** **BT, p < 0.0001** **MO*BT, p < 0.0001**
Atlantic sharpnose	MO+BT+BT*MO	p = 0.0014	**MO, p = 0.0275** **BT, p = 0.0008** **MO*BT, p = 0.0136**
Blacktip	MO+D+BT	p = 0.0001	**MO, p = 0.0213** D, p = 0.0535 **BT, p < 0.0001**
Bonnethead	MO+D+BT+SAL+DO	p = 0.2907	MO, p = 0.9577 D, p = 0.9277 BT, p = 0.3125 SAL, p = 0.2359 **DO, p = 0.0010**
Sandbar	MO+D	p < 0.0001	**MO, p = 0.0269** **D, p =0.0012**

Table 1-4. Results from general linear models used to examine the effect of environmental factors on the abundance of sharks in Cumberland and Nassau Sounds. Model significance and the significance of individual model variables are presented. Interactions between variables are denoted by terms joined by * in the model parameters. MO = month, D = depth, BT = bottom temp., SAL = salinity, DO = dissolved oxygen. Significance was determined at $p \leq 0.05$, and significant factors are in bold.

Species	Model	Model Sig.	Factors
All sharks	D+BT+SAL+DO+BT*DO	p < 0.0001	**D, p = 0.0342**
			BT, p = 0.0077
			SAL, p = 0.0764
			DO, p = 0.0398
			BT*DO, p = 0.0347
Atlantic sharpnose	D+BT	p = 0.093	D, p = 0.1251
			BT, p = 0.0056
Blacktip	D+BT+SAL+DO+BT*D*DO+ BT*D+BT*DO+D*DO	p = 0.0011	**D, p = 0.0007**
			BT, p = 0.0107
			SAL, p = 0.0823
			DO, p = 0.0130
			BT*D*DO, p = 0.0008
			BT*D, p = 0.0005
			BT*DO, p = 0.0108
			D*DO, p = 0.0010

Table 1-5. Shark recaptures from 2009 – 2011 for Cumberland and Nassau Sound. Days refer to the number of days at liberty between initial capture and recapture; distance (km) is the straight-line distance between location tagged and location recaptured. CS = Cumberland Sound, NS = Nassau Sound, M = male, F = female, YOY = young-of-the-year.

Species	Sex	Maturity	Date Tagged	Location Tagged	Location Recaptured	Days	Distance (km)
Atlantic Sharpnose	M	Mature	7/1/2009	CS	NS	14	20.6
Atlantic Sharpnose	M	Mature	8/5/2009	CS	CS	326	2.6
Atlantic Sharpnose	M	Mature	8/5/2009	CS	Daytona Beach	224	190.5
Atlantic Sharpnose	M	Mature	8/5/2009	CS	CS	32	2.1
Atlantic Sharpnose	M	Mature	8/17/2009	CS	CS	4	3.9
Atlantic Sharpnose	M	Mature	5/4/2010	CS	CS	411	3.5
Atlantic Sharpnose	M	Mature	5/10/2010	CS	CS	13	2.5
Atlantic Sharpnose	M	Mature	5/25/2011	CS	CS	352	3.7
Blacktip	M	Juvenile	7/15/2009	CS	CS	63	3.1
Blacktip	F	YOY	7/15/2009	CS	CS	71	7.3
Blacktip	F	Juvenile	9/9/2009	CS	CS	39	7
Blacktip	M	Juvenile	6/2/2010	NS	Little Talbot Island	100	18.1
Blacktip	F	Juvenile	5/20/2011	CS	CS	63	0.9
Bonnethead	F	Mature	5/6/2010	CS	Fernandina Beach	23	7.3
Bonnethead	F	YOY	7/13/2011	CS	CS	4	3.8
Sandbar	M	YOY	7/22/2011	CS	CS	30	2.7
Sandbar	M	YOY	8/11/2011	CS	CS	9	1.9
Spinner	M	YOY	8/5/2011	CS	CS	13	1.7

Figure 1-1.

Map redacted. Paper copy available upon request to home institution

Figure 1-2

Map redacted. Paper copy available upon request to home institution

Figure 1-3

Map redacted. Paper copy available upon request to home institution

b)

Map redacted. Paper copy available upon request to home institution

Figure 1-4.

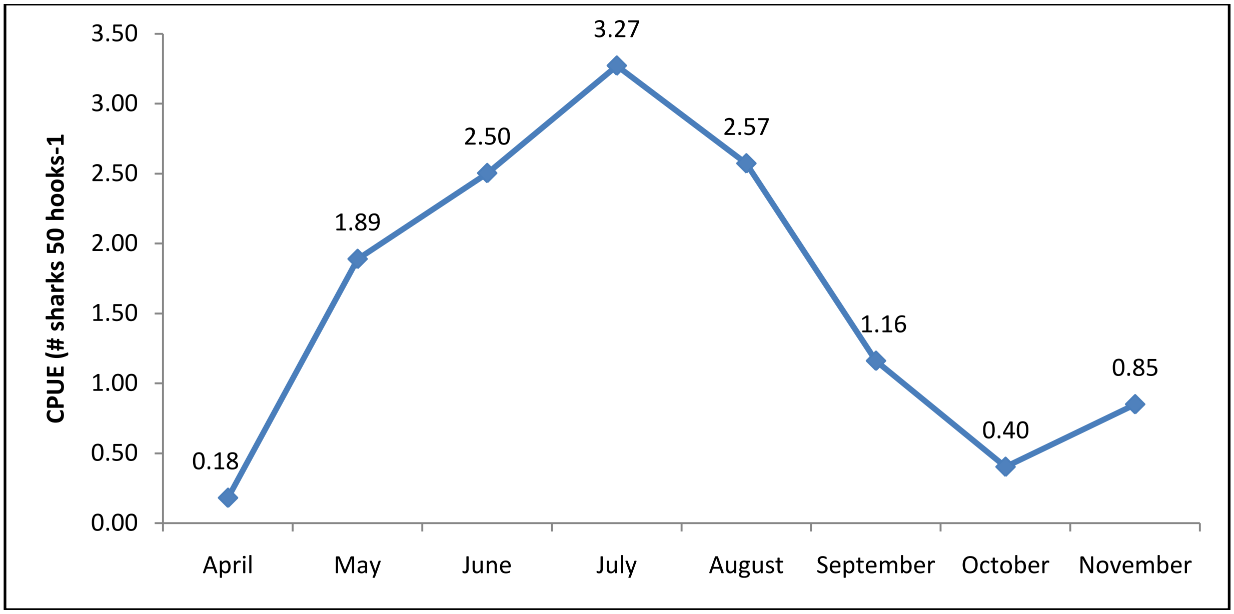
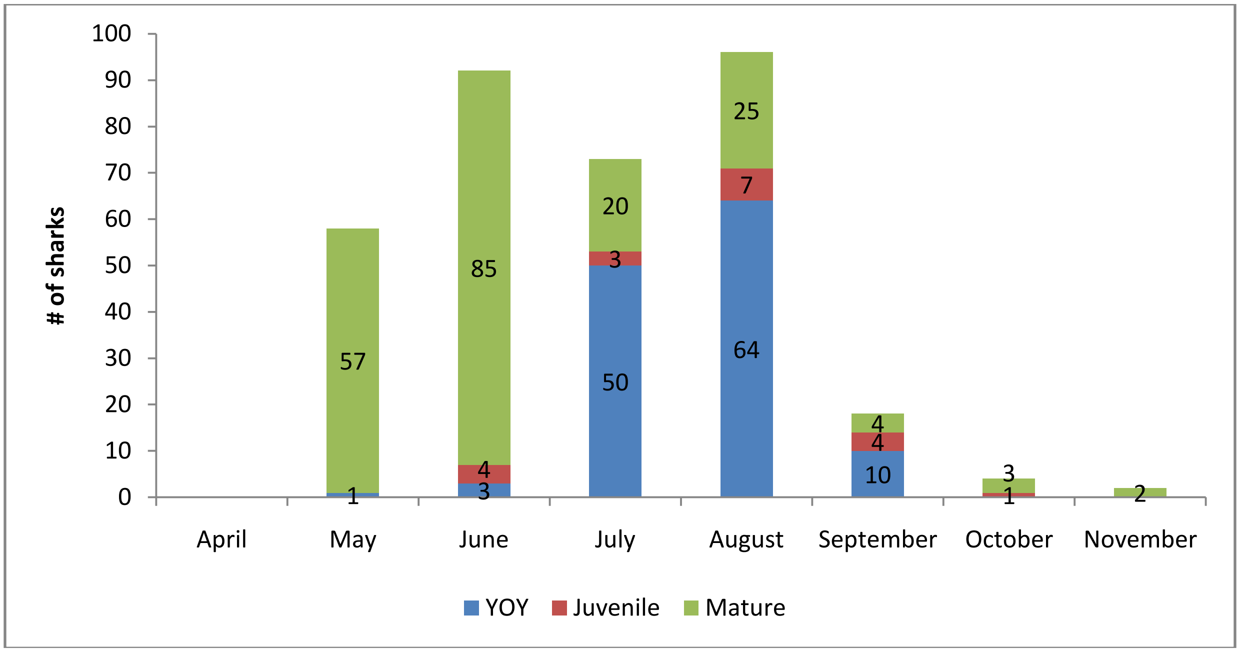
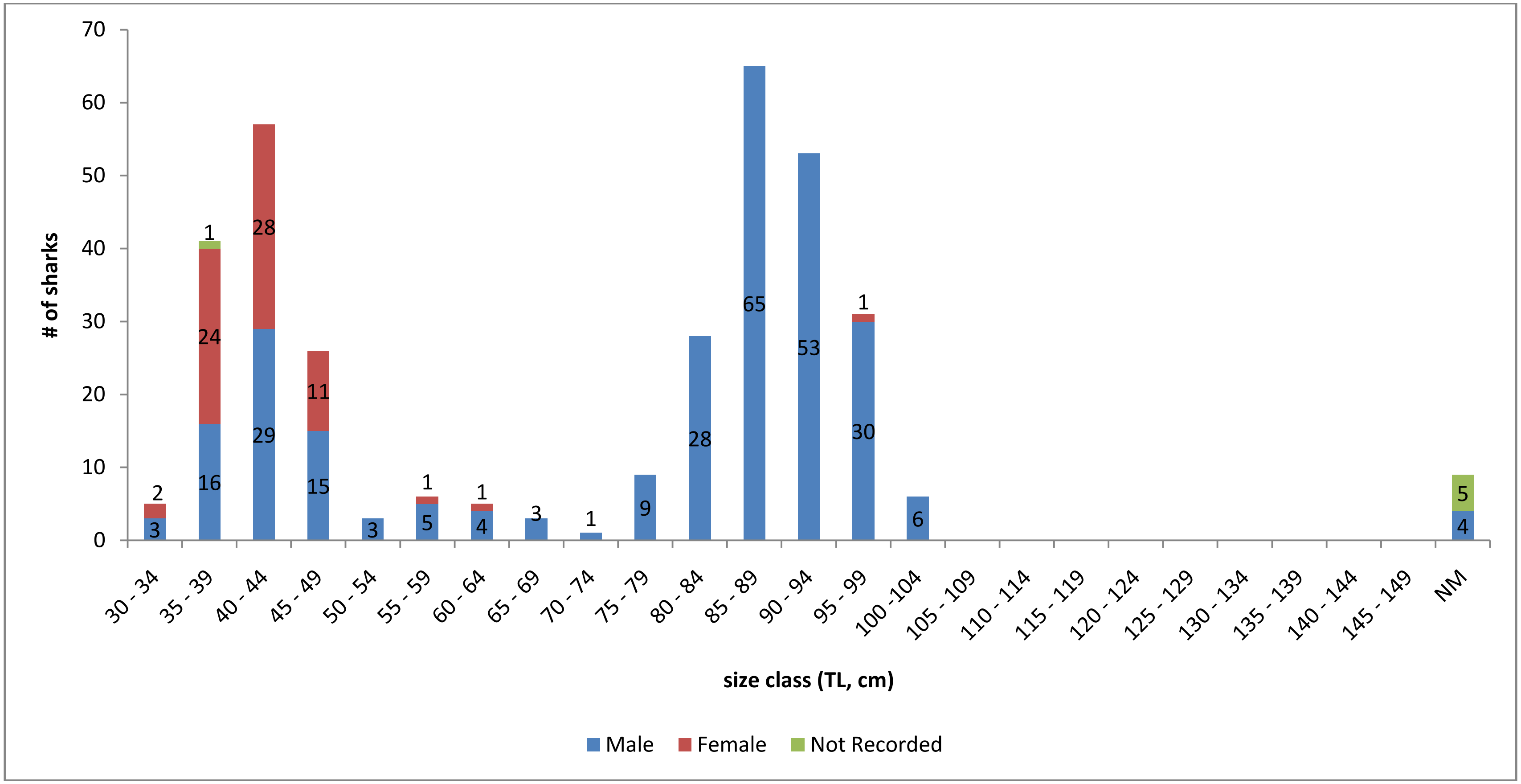

CPUE (# sharks 50 hooks-1
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
0.18
1.89
2.50
3.27
2.57
1.16
0.40
0.85
April
May
June
July
August
September
October
November

Figure 1-5.



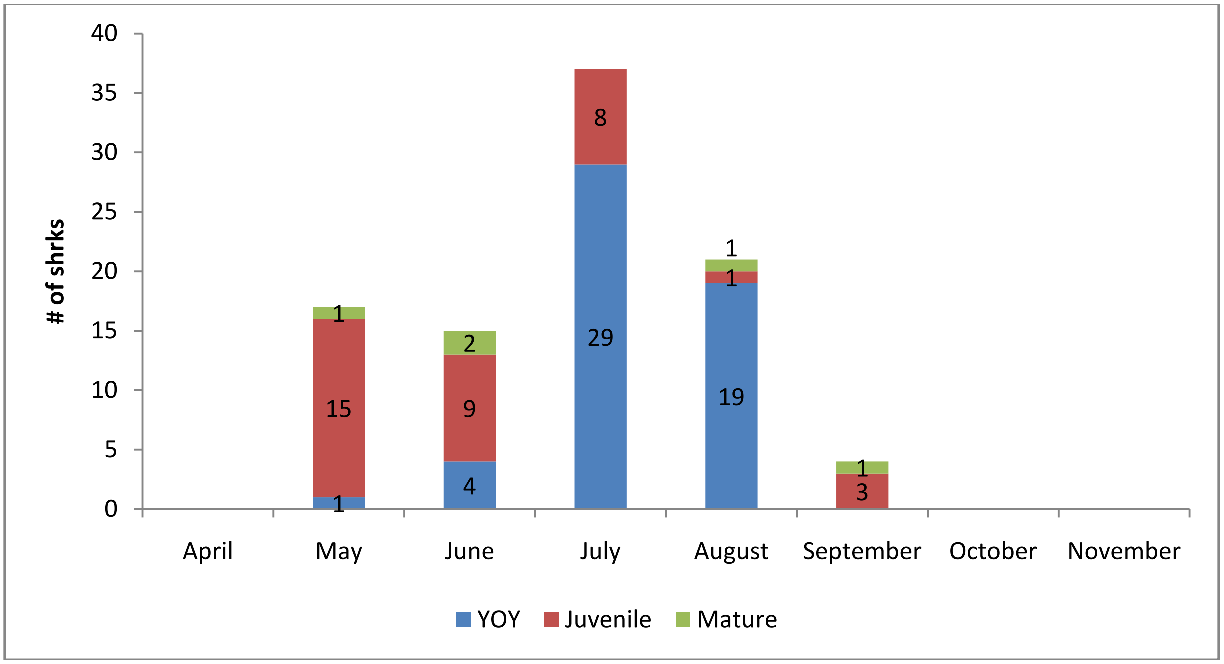
100
90
80
70
60
50
40
30
20
10
0
# of sharks
57
1
85
4
3
20
3
50
25
7
64
4
4
10
3
1
2
April
May
June
July
August
September
October
November
YOY
Juvenile
Mature

Figure 1-6.



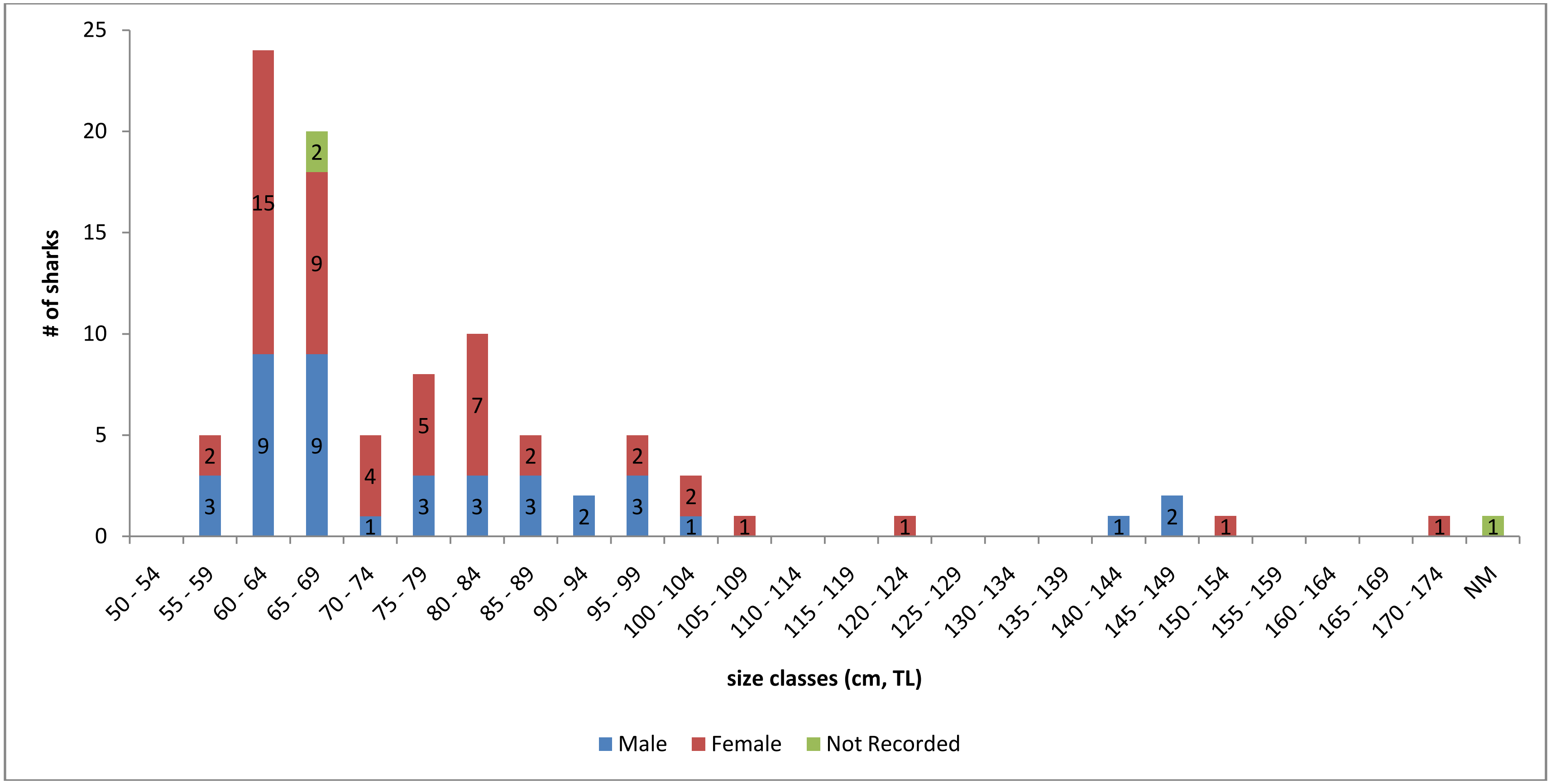
# of sharks
70
60
50
40
30
20
10
0
2
3
1
24
16
28
29
11
15
3
1
5
1
4
3
1
9
28
65
53
1
30
6
5
4
30 - 34
35 - 39
40 - 44
45 - 49
50 - 54
55 - 59
60 - 64
65 - 69
70 - 74
75 - 79
80 - 84
85 - 89
90 - 94
95 - 99
100 - 104
105 - 109
110 - 114
115 - 119
120 - 124
125 - 129
130 - 134
135 - 139
140 - 144
145 - 149
NM
size class (TL, cm)
Male
Female
Not Recorded

Figure 1-7.



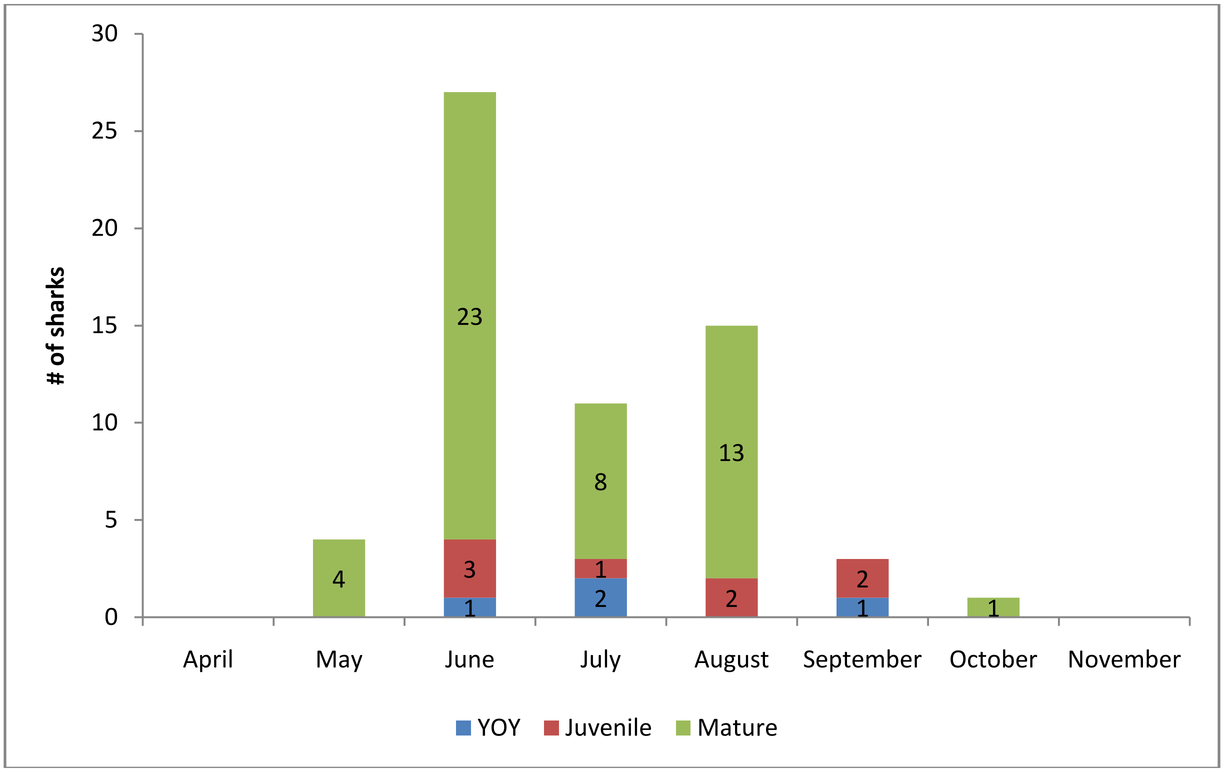
# of shrks
40
35
30
25
20
15
10
5
0
April
May
June
July
August
September
October
November
1
15
1
2
9
4
8
29
1
1
19
1
3
YOY
Juvenile
Mature

Figure 1-8.



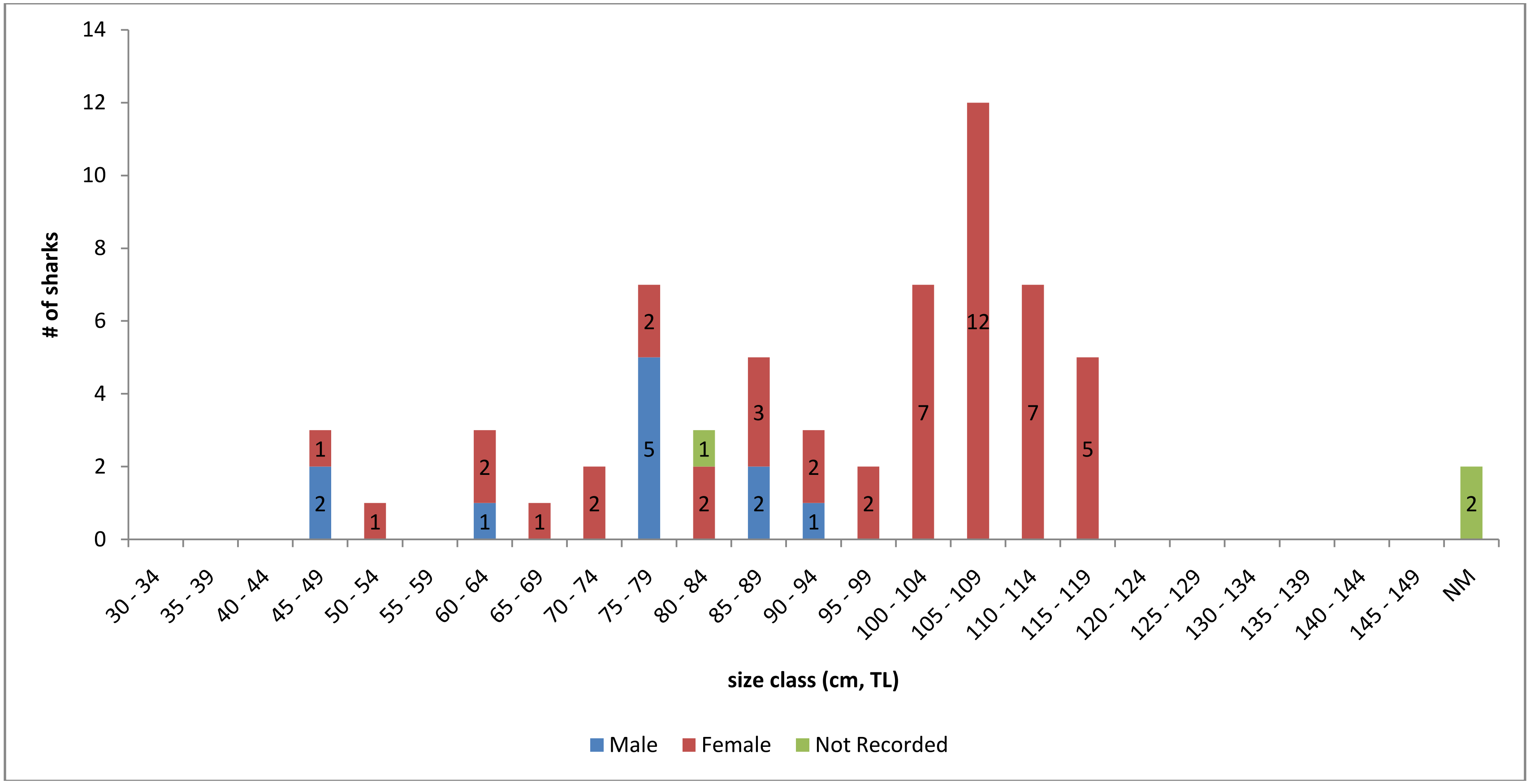
25
20
15
10
5
0
# of sharks
3
2
9
15
9
9
2
1
4
3
5
3
7
3
2
2
3
2
1
2
1
1
1
2
1
1
1
50 - 54
55 - 59
60 - 64
65 - 69
70 - 74
75 - 79
80 - 84
85 - 89
90 - 94
95 - 99
100 - 104
105 - 109
110 - 114
115 - 119
120 - 124
125 - 129
130 - 134
135 - 139
140 - 144
145 - 149
150 - 154
155 - 159
160 - 164
165 - 169
170 - 174
NM
size classes (cm, TL)
Male
Female
Not Recorded

Figure 1-9.



# of sharks
30
25
20
15
10
5
0
23
8
13
4
3
1
2
2
2
1
1
1
April
May
June
July
August
September
October
November
YOY
Juvenile
Mature

Figure 1-10.


14
12
10
8
6
4
2
0
# of sharks
1
2
1
2
1
1
2
2
5
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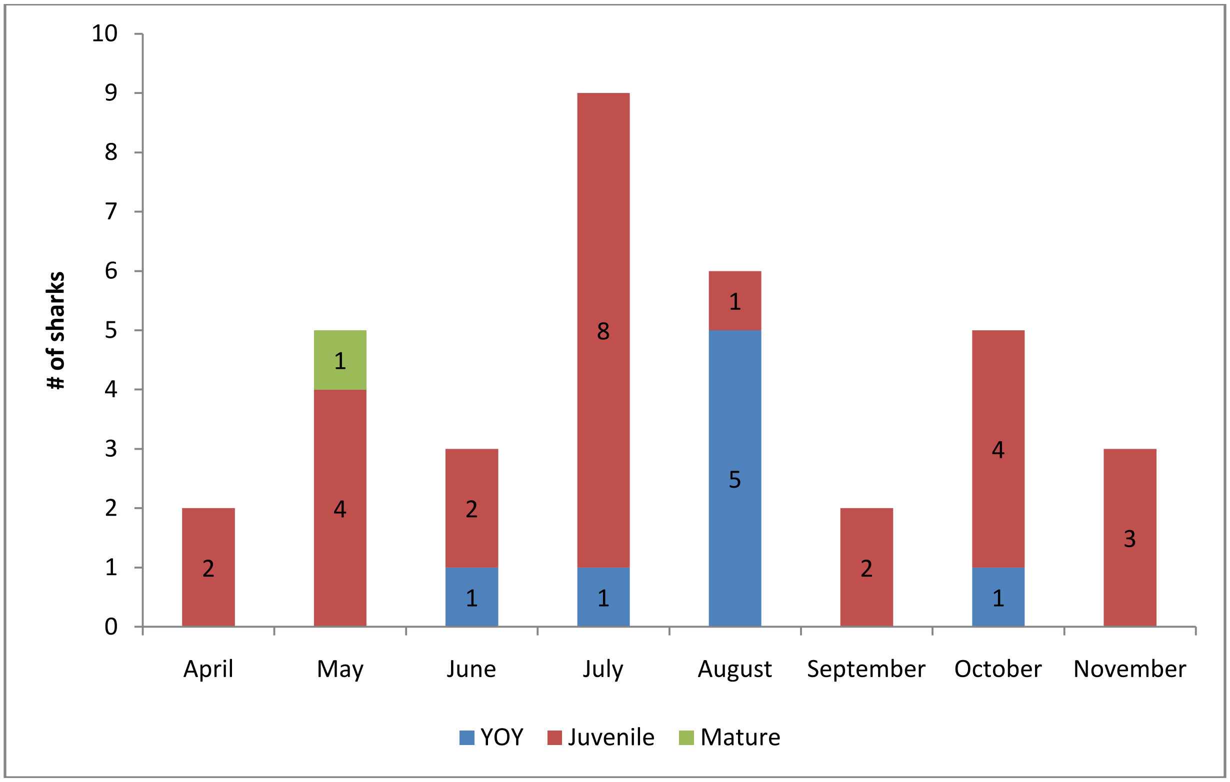
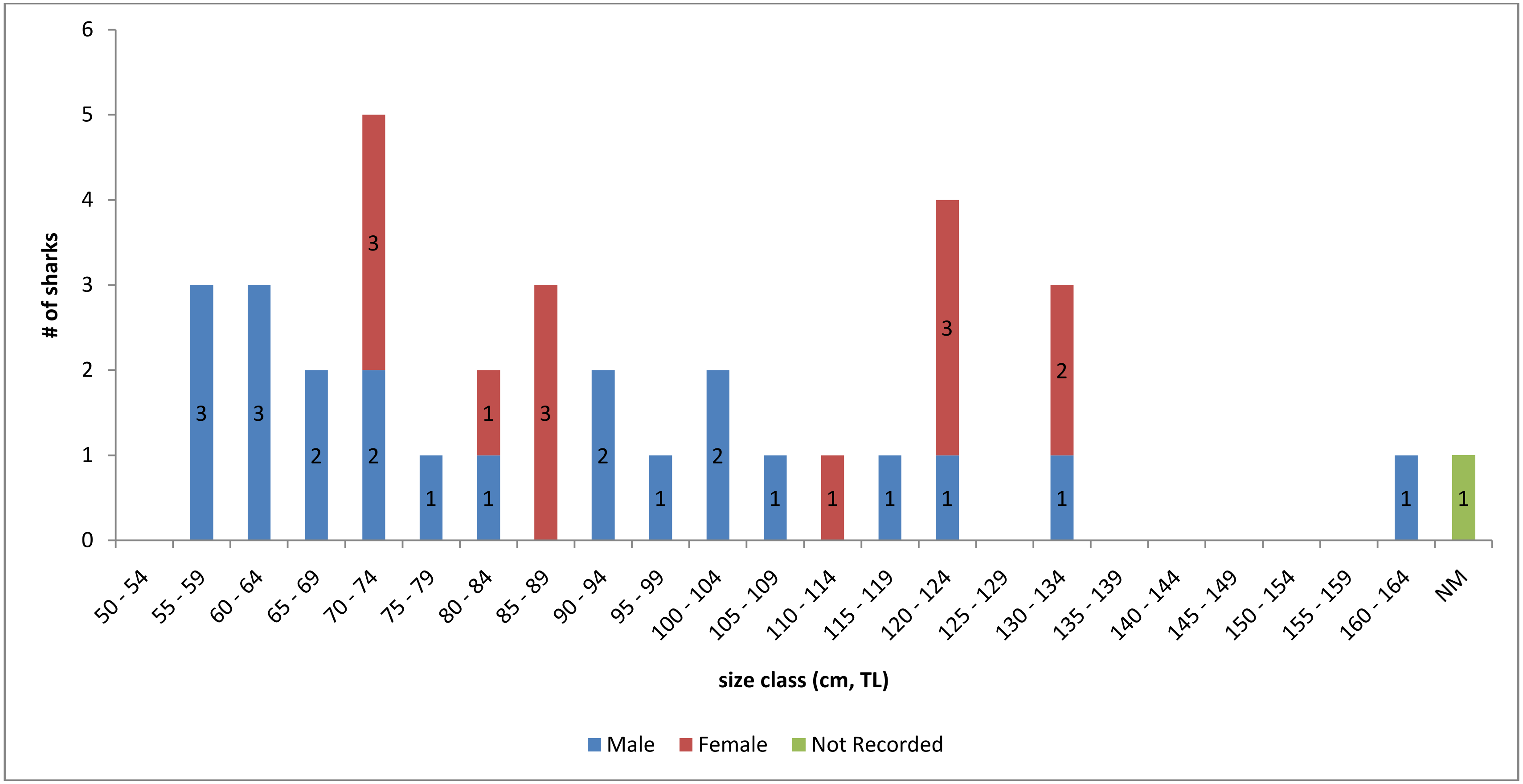
2
3
2
2
1
2
7
12
7
5
2
30 - 34
35 - 39
40 - 44
45 - 49
50 - 54
55 - 59
60 - 64
65 - 69
70 - 74
75 - 79
80 - 84
85 - 89
90 - 94
95 - 99
100 - 104
105 - 109
110 - 114
115 - 119
120 - 124
125 - 129
130 - 134
135 - 139
140 - 144
145 - 149
NM
size class (cm, TL)
Male
Female
Not Recorded

Figure 1-11.



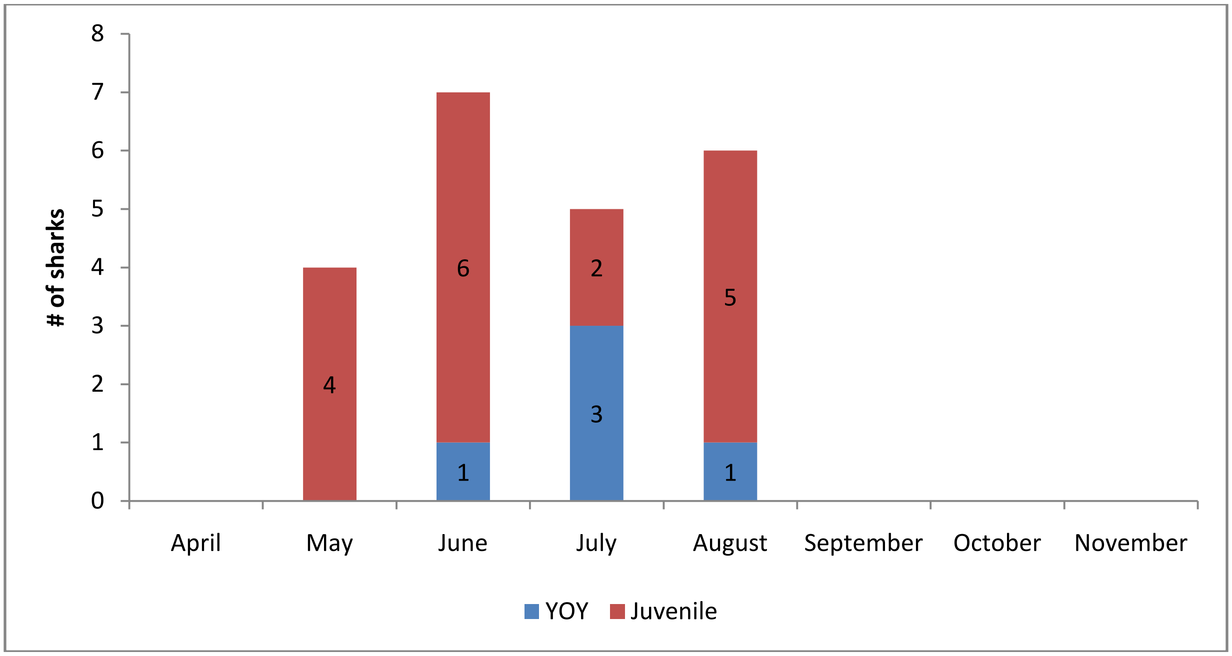
10
9
8
7
6
5
4
3
2
1
0
# of sharks
2
1
4
2
1
8
1
1
5
2
4
1
3
April
May
June
July
August
September
October
November
YOY
Juvenile
Mature

Figure 1-12.



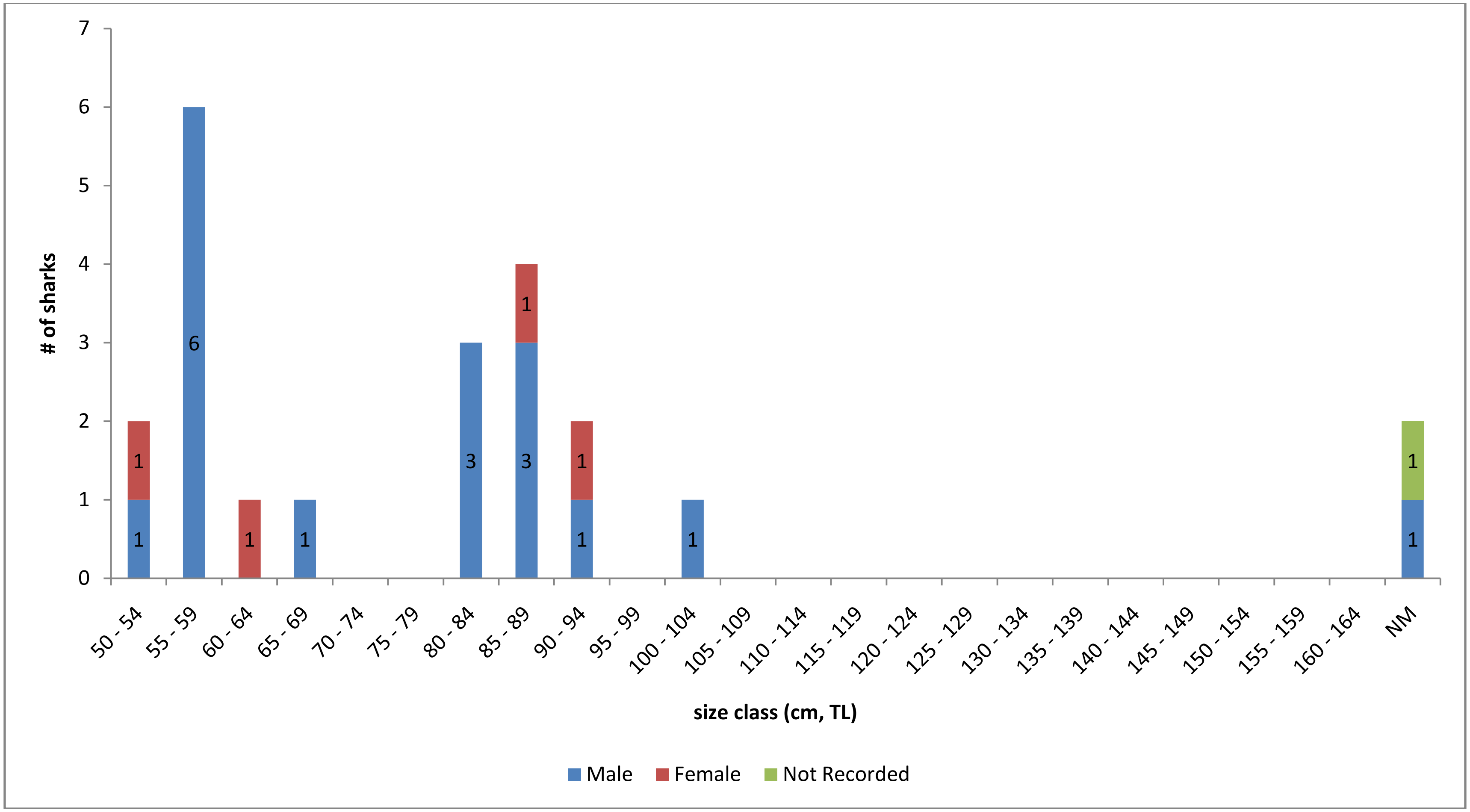
# of sharks
0
1
2
3
4
5
6
3
3
2
3
2
1
1
1
3
2
1
2
1
1
1
3
1
2
1
1
1
50 - 54
55 - 59
60 - 64
65 - 69
70 - 74
75 - 79
80 - 84
85 - 89
90 - 94
95 - 99
100 - 104
105 - 109
110 - 114
115 - 119
120 - 124
125 - 129
130 - 134
135 - 139
140 - 144
145 - 149
150 - 154
155 - 159
160 - 164
NM
size class (cm, TL)
Male
Female
Not Recorded

Figure 1-13.



8
7
6
5
4
3
2
1
0
# of sharks
4
6
1
2
3
5
1
April
May
June
July
August
September
October
November
YOY
Juvenile

Figure 1-14.



7
6
5
4
3
2
1
0
# of sharks
6
1
1
3
3
1
1
1
1
1
1
1
50 - 54
55 - 59
60 - 64
65 - 69
70 - 74
75 - 79
80 - 84
85 - 89
90 - 94
95 - 99
100 - 104
105 - 109
110 - 114
115 - 119
120 - 124
125 - 129
130 - 134
135 - 139
140 - 144
145 - 149
150 - 154
155 - 159
160 - 164
NM
size class (cm, TL)
Male
Female
Not Recorded

Figure 1-15.

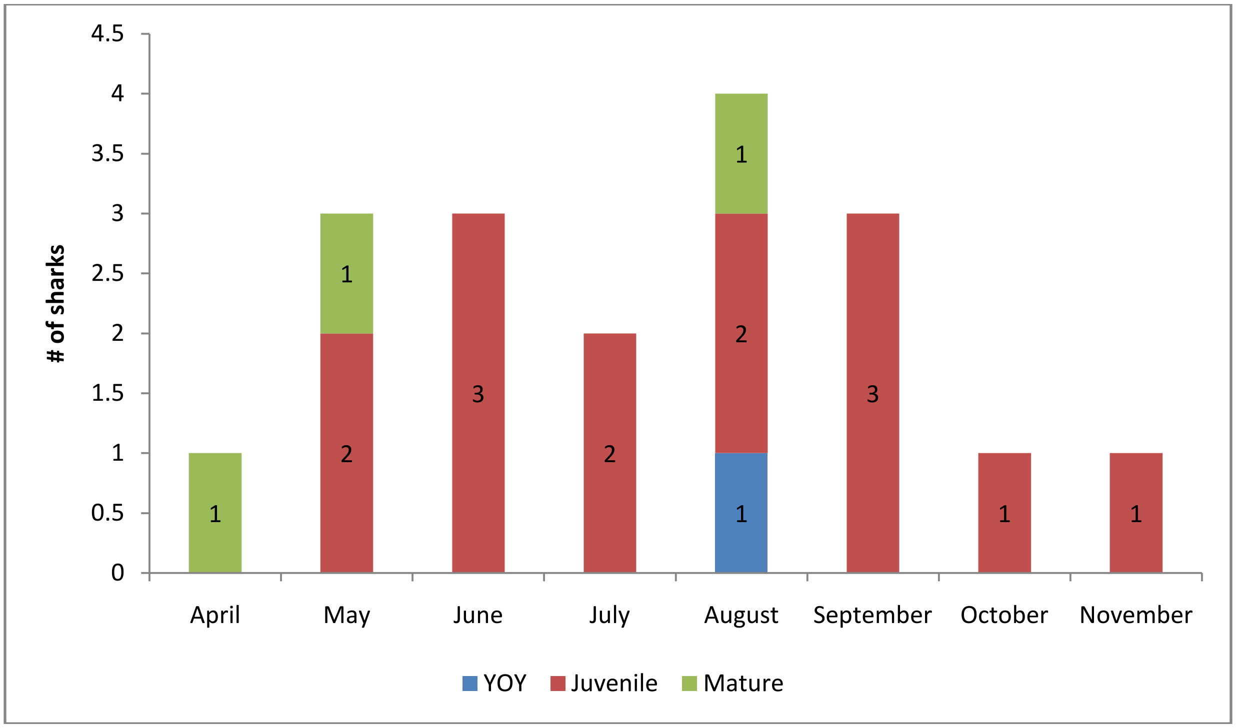
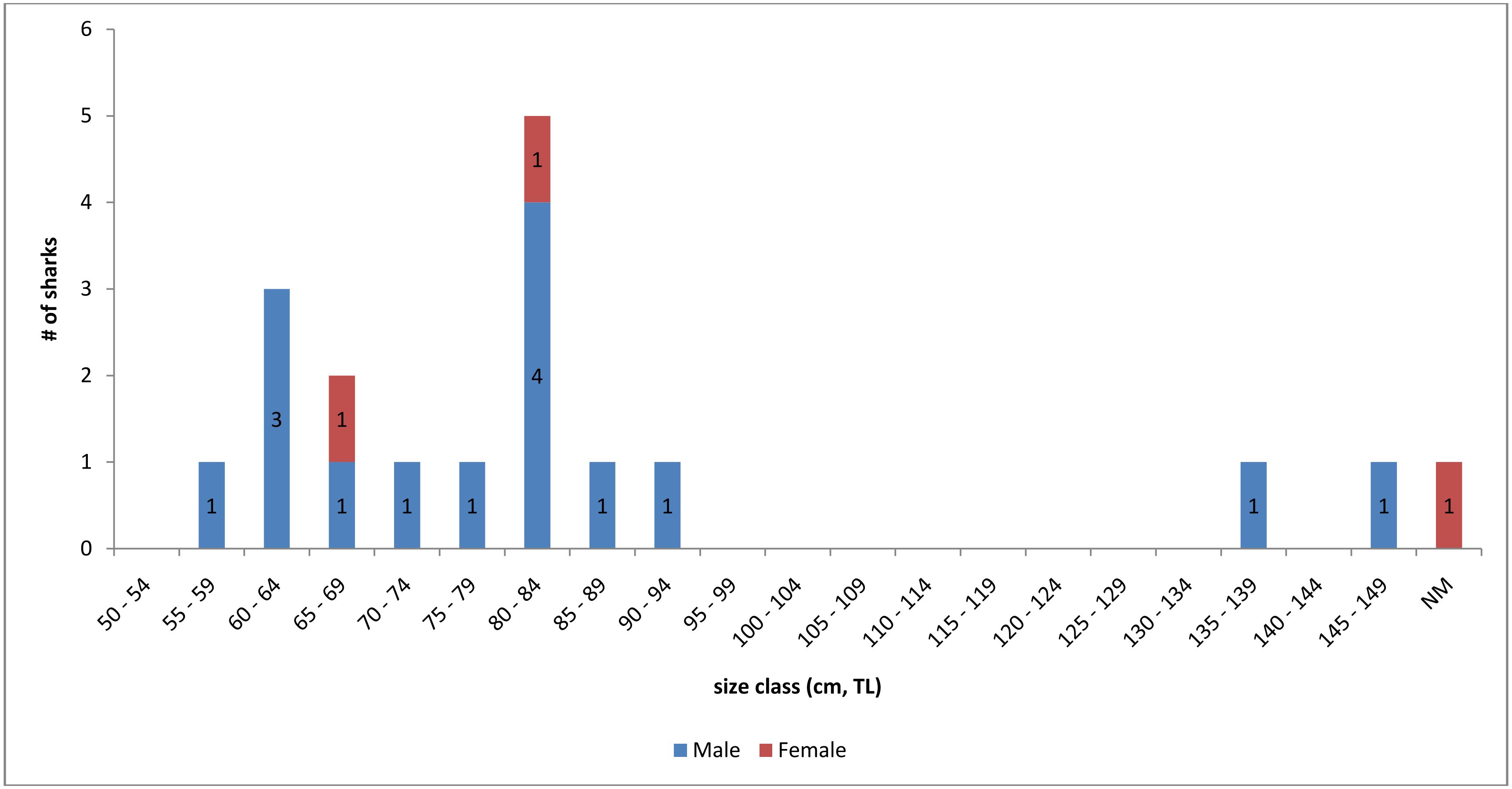
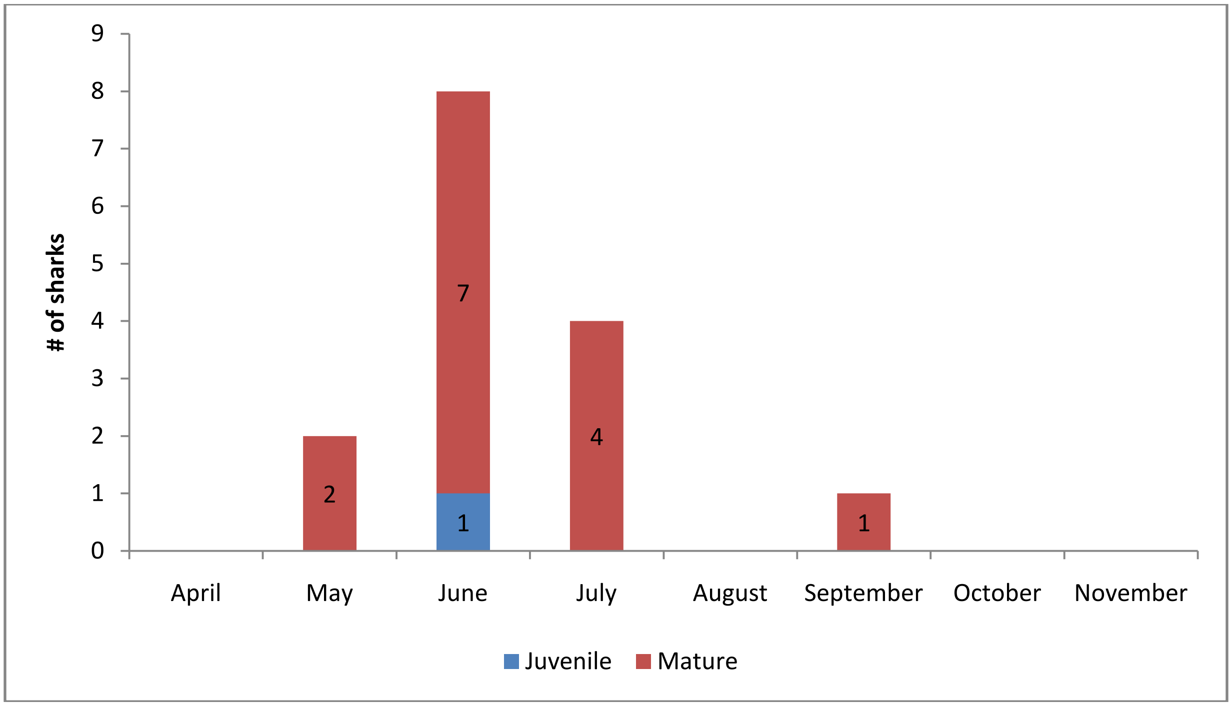

4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
# of sharks
1
2
1
3
2
1
2
1
3
1
1
April
May
June
July
August
September
October
November
YOY
Juvenile
Mature

Figure 1-16.



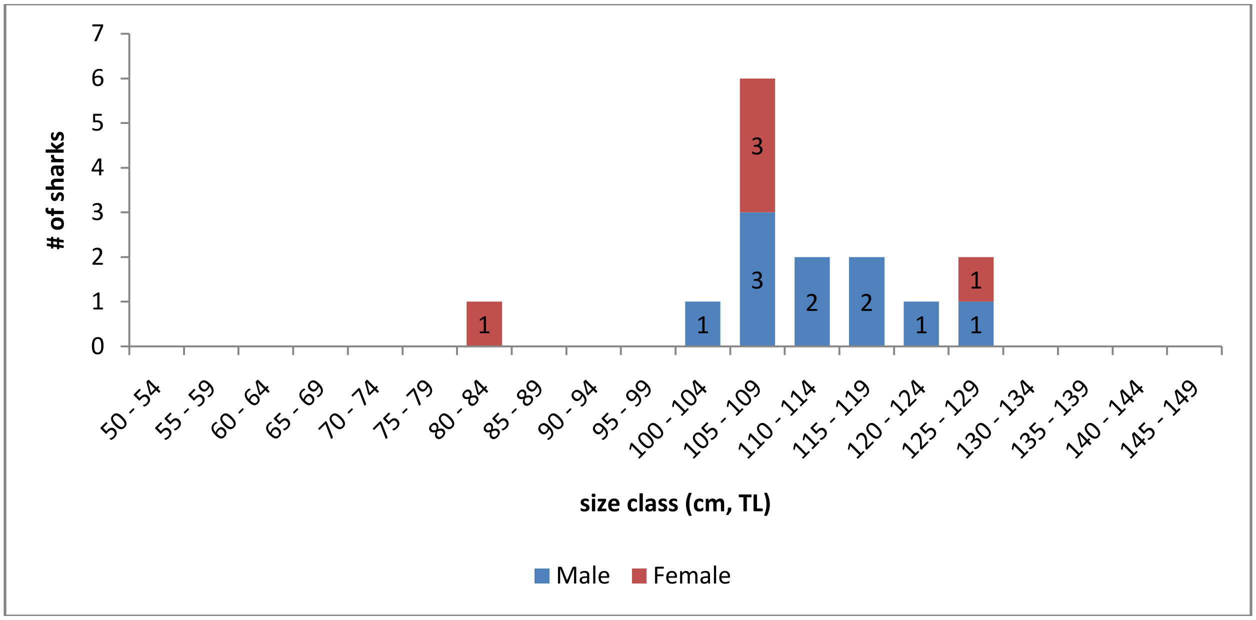
6
5
4
3
2
1
0
# of sharks
1
3
1
1
1
1
4
1
1
1
1
1
1
1
50 - 54
55 - 59
60 - 64
65 - 69
70 - 74
75 - 79
80 - 84
85 - 89
90 - 94
95 - 99
100 - 104
105 - 109
110 - 114
115 - 119
120 - 124
125 - 129
130 - 134
135 - 139
140 - 144
145 - 149
NM
size class (cm, TL)
Male
Female

Figure 1-17.



# of sharks
9
8
7
6
5
4
3
2
1
0
7
4
2
1
1
April
May
June
July
August
September
October
November
Juvenile
Mature

Figure 1-18.



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4
3
2
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# of sharks
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1
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2
2
1
1
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55 - 59
60 - 64
65 - 69
70 - 74
75 - 79
80 - 84
85 - 89
90 - 94
95 - 99
100 - 104
105 - 109
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135 - 139
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145 - 149
size class (cm, TL)
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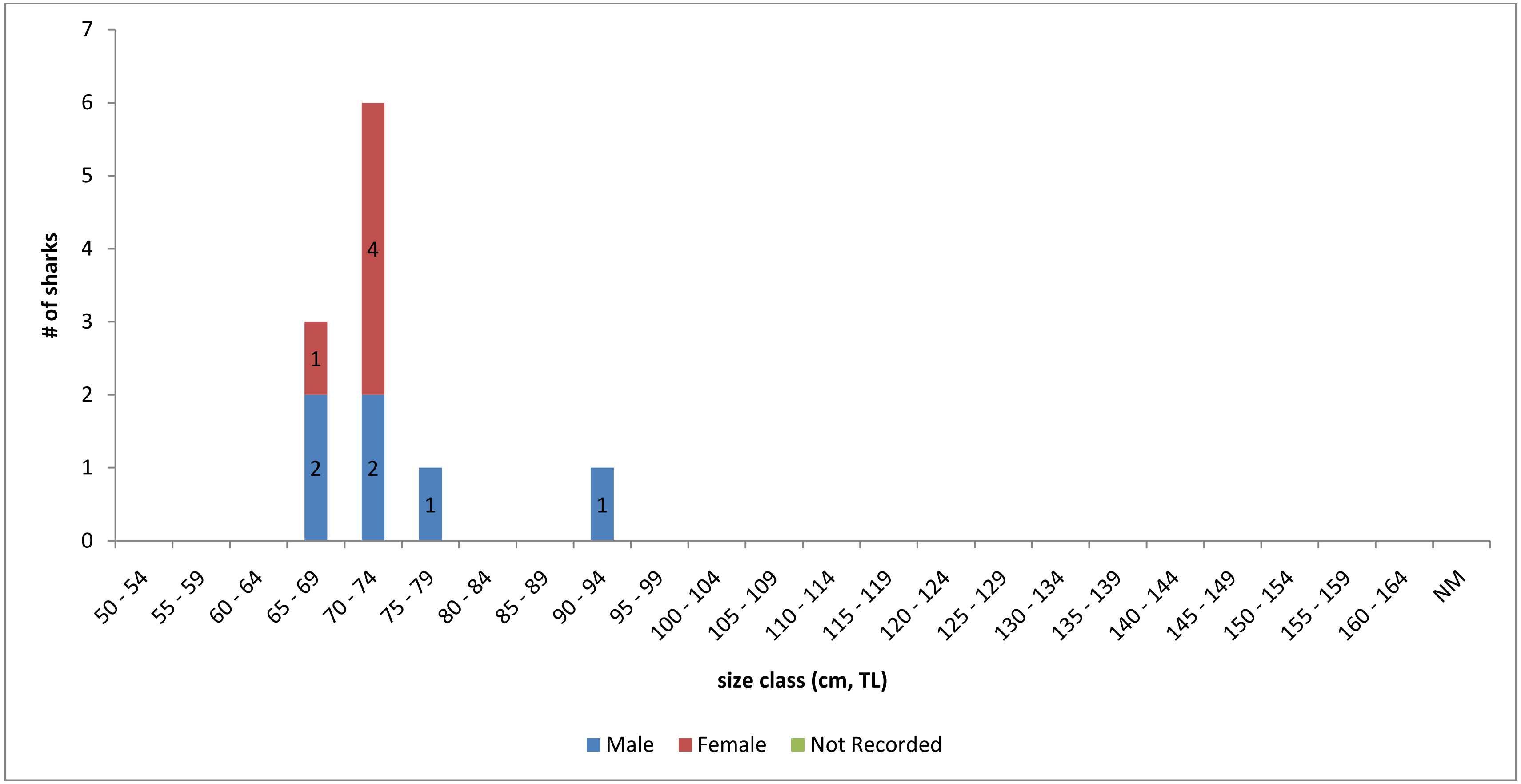
Female

Figure 1-19.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130 - 134
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NM
size class (cm, TL)
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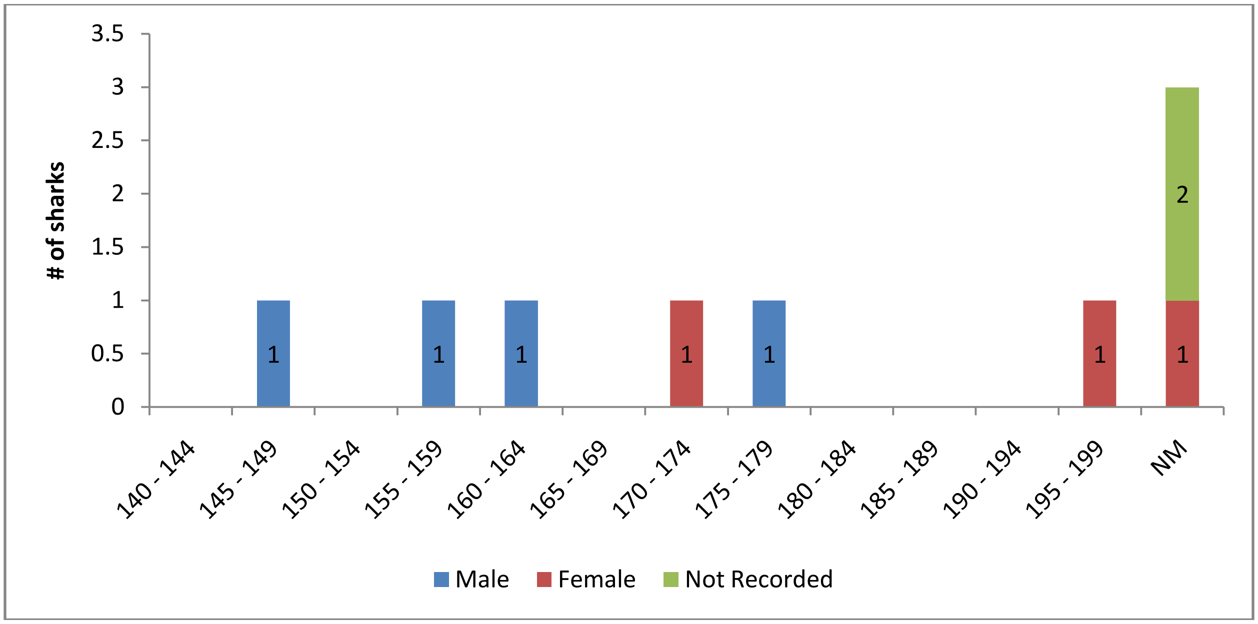
Female
Not Recorded

Figure 1-20.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145 - 149
150 - 154
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160 - 164
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175 - 179
180 - 184
185 - 189
190 - 194
195 - 199
NM
Male
Female
Not Recorded

Chapter 2

Do Measures of Prey Abundance Predict Habitat Selection for the Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*) in Two Northeast Florida Estuaries

2.1 Introduction

As top level predators, sharks can play an important role in structuring marine communities (Cortes, 1999). As a result, it is important to understand the factors that influence their abundance and distribution. More specifically, it is necessary to understand how abiotic and biotic factors influence patterns of habitat use. This is particularly important as fishery managers move toward more ecosystem based fishery management plans (Rosenberg et. al., 2000). For sharks, this includes fishery management plans aimed at identifying and protecting protect essential fish habitat (NMFS, 1999).

One factor that is thought to play an important role determining the abundance and distribution of predators is the abundance of their prey. This comes from the idea of the ideal free distribution (Fretwell and Lucas, 1970), which suggests that predators will distribute themselves evenly across habitats in proportion to the availability of their prey. Thus, areas with higher prey abundance can support higher abundance of predators, while areas of low prey abundance will support a lower abundance of predators. It is also possible, however, that the abundance of predators will not match that of their prey, particularly when prey species are highly mobile. Hugie and Dill (1994) suggested that predator avoidance by prey species would result in a mismatch between the abundance of predators and their prey. In this case, predators may choose to select habitat where the food of their prey is most abundant.

Studies that have examined the role of prey abundance on habitat selection in coastal sharks have been limited. Those studies that have been conducted provide conflicting evidence for the idea that shark abundance will match the abundance of their prey. In Shark Bay, Western Australia, tiger sharks were found to prefer shallow seagrass habitats where their prey was most abundant (Heithaus et. al., 2002). Conversely, Heupel and Heuter (2002) found no correlation between the amount of time sharks spent in different regions of Terra Ceia Bay, FL and the prey abundance in those regions. Similarly, in Florida Bay, USA, there was no link between shark abundance and fish abundance at small spatial scales within regions, but shark abundance was positively correlated with fish abundance at a regional scale (Torres et. al., 2006). Given the conflicting results of these studies, further research is needed to gain a better understanding of the role of prey abundance in determining shark abundance and habitat selection.

The Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) is a small coastal shark species found in coastal waters through the northwest Atlantic Ocean (Castro, 2011). In the United States it is managed as part of the small coastal shark (SCS) management unit (NMFS, 2006) and is the most abundant shark in U.S. Atlantic waters (Cortes, 2002). Because of this, numerous aspects of the biology of Atlantic sharpnose sharks, including its life history (Carlson and Baremore, 2003), diet and foraging ecology (Bethea et. al., 2004, 2006), and reproductive biology (Parsons, 1983) have been well studied. The high abundance of Atlantic sharpnose sharks in nearshore coastal waters makes this species a good model to use to examine the role of prey abundance on habitat selection.

The goal of this study was to provide a general characterization of the diet of Atlantic sharpnose sharks and to directly examine the effect of prey abundance on habitat selection of Atlantic sharpnose sharks in the estuarine waters of northeast Florida. Specifically, this study

characterized the diet of Atlantic sharpnose sharks to identify preferred prey items and examined the effect of overall prey abundance and preferred prey abundance on the abundance of Atlantic sharpnose sharks in two northeast Florida estuaries across multiple habitat types.

2.2 Methods

Animal sampling

Sampling for Atlantic sharpnose sharks was conducted in the nearshore and estuarine waters of Cumberland (Fig.1 a) and Nassau (Fig. 1b) Sounds from May to September during the years2010 and 2011. Sampling was conducted as part of the University of North Florida's annual shark abundance survey. Each region was sampled weekly using a 300m bottom longline that was anchored at both ends,marked with two buoys, and contained 50 gangions. Each gangion was comprised of a 1m 90-kg test monofilament leader, size 120 stainless steel longline snap, 4/0 swivel, and a 12/0 barbless circle hook baited with Atlantic mackerel (*Scomber scombrus*). Sets were allowed to soak for 30 minutes to reduce animal mortality. All Atlantic sharpnose sharks that were caught were measured, weighed, and the sex and maturity status were determined. Environmental data was collected at each sampling location after the longline was set. Water quality parameters including bottom water temperature (^{o}C), salinity ($^{o}/_{oo}$), and dissolved oxygen (mg/L) were measured using an YSI Model85 Salinity, Conductivity, Dissolved Oxygen & Temperature System. Water depth (m) was measured at the beginning and end of each set using a depth sensor mounted on the transom of the boat, and the average depth for each set was recorded. Habitat type was also recorded for each set, and was characterized as either creek or sound habitat. Sound habitat was designated as those areas in the main portion of

the estuary with a direct connection to the ocean. Creek habitat included all tidal creeks and rivers, and portions of the Intra-Coastal Waterway that fed into the sound.

Stomach Contents

Stomach contents were obtained from most Atlantic sharpnose sharks that were caught during the survey using a non-lethal stomach eversion technique described by McElroy (2009). Briefly, a shark was held on its back and pointed downward, positioning the mouth over a strainer (3-mm square mesh). A PVC pipe, appropriately sized to the mouth and pharynx of the shark, was inserted into the throat and the stomach past the cardiac sphincter. The pipe was then slowly removed to generate negative pressure, drawing the stomach into the pipe and down into the mouth. Stomach contents were collected with the strainer. Any food items that remained in the stomach or mouth were removed with forceps. Sharks were then tipped back to allow the stomach to return to its natural position, revived, and released. Stomach contents were then gathered from the strainer, placed in a labeled ziplock bag, and stored on ice until back in the lab. Samples were kept frozen until they could be analyzed.

Prey Abundance Sampling

Prey abundance data for Cumberland and Nassau Sound was obtained from the Florida Fish and Wildlife Conservation Commission's field lab in Jacksonville, FL. As part of their ongoing Fishery Independent Monitoring (FIM) Program, FWC collects data on the abundance and distribution of finfish and macro-invertebrates during monthly sampling trips to Cumberland and Nassau Sounds. Fish were sampled using three different sampling gears: a 21.3m bag seine, 123m bag seine, and 6.1m otter trawl. A detailed explanation of the FIM sampling protocol can be found in Solomon et. al. 2006.

Data Analysis

Since the majority of hooks were recovered without bait, soak time was not included in calculations of catch rates. Catch rates were expressed as catch per unit effort (CPUE), and was calculated as the number of sharks per 50 hooks. CPUE was calculated on a monthly basis for Cumberland and Nassau Sound. CPUE and raw abundance data for each month of sampling were used to describe trends in Atlantic sharpnose abundance in the two sounds during the sampling period. A mixed between-within subjects ANOVA (SPSS v. 18) was used to test for differences in catch rates between Cumberland and Nassau Sound and the two habitat types within each site. Significance was determined at an alpha level of 0.05.

Analysis of stomach contents collected from sharks was used to characterize the diet of Atlantic sharpnose sharks in Cumberland and Nassau Sound. Stomach contents were identified to the lowest possible taxon, counted, and weighed to the nearest 0.1g. Upon identification, stomach contents were grouped into six major prey categories: family Clupeidae (CLU), other pelagic teleosts (PEL), family Sciaenidae (SCI), other epibenthic teleosts (EPI), crustaceans (CRU), and other invertebrates (INV), and were based on the prey categories defined in Bethea et. al., 2004.

The contribution of each prey item to the diet was calculated using three relative measures of prey quantity (RMPQs): numerical index (%N, percent by number), gravimetric index (%W, percent by weight), and percent frequency occurrence (%FO). Percent by number (%N) was calculated as the number of individuals of a prey type divided by the total number individuals of all prey types from all stomachs multiplied by 100. Percent weight (%W) was calculated as the weight of individuals of each prey type divided by the total weight of individuals of all prey types from all stomachs multiplied by 100. Percent frequency occurrence

(%FO) was calculated as the number of stomachs containing a prey category divided by the total number of stomachs containing prey multiplied by 100 (Hyslop, 1980). The numerical and weight indices were calculated on a per stomach basis to provide mean and variability measures (Ferry and Cailliet, 1996), and are presented as $\overline{\%N}$, $\overline{\%W}$ ± SE. Diet composition was further described using the index of relative importance (IRI). Index of relative importance was calculated according to Pinkas et. al. (1971), with a modification for weight instead of volume: $IRI_i = (\%N + \%W) * \%FO$. It was expressed as a %IRI using the equation: $\%IRI_i = 100\ IRI_i / \sum IRI_i$, as per the recommendation of Cortes (1997). The percentage IRI was also calculated on a per stomach basis and presented as $\overline{\%\,IRI}$ ± SE. To allow for comparison to other studies, each of the RMPQs and $\overline{\%\,IRI}$ were also calculated for the six major prey categories. Unidentifiable prey items were not included in any of the analyses.

Cumulative prey curves were used to determine if a sufficient amount of stomachs had been obtained to accurately assess the diet. Cumulative prey curves were constructed by plotting the mean number of unique prey items against the cumulative number of non empty stomachs. The order in which stomachs were analyzed was randomized five times to prevent bias, and the mean number of unique prey items per stomach was plotted. An adequate sample size was assumed if the curve reached an asymptote (Ferry and Cailliet, 1996), which was determined using linear regression (Bizzarro et. al., 2007). The prey curve was assumed to have reach an asymptote if the slope of the line of last 4 points of the prey curve was not significantly different ($p > 0.05$) than a line of 5% slope (Bethea et. al., 2011). Prey curves were constructed for both Cumberland Sound and Nassau Sound, as well as for the two sites combined.

Data from FWC's FIM survey were used to describe the overall abundance of fish and macro-invertebrates in Cumberland and Nassau Sounds during the sampling period. Catch data

was used to generate two descriptive measures of prey abundance, potential prey catch per unit effort (PPCPUE) and preferred prey catch per unit effort (PCCPUE). Since three different gear types were used, the total area sampled (m^2) by each gear was combined to provide the total area sampled in a given habitat for a given month. Potential prey catch per unit effort was the total number of potential prey species captured per square meter of area sampled. Preferred prey catch per unit effort was the total number of preferred prey (identified from stomach content analysis above) per square meter of area sampled. Both PPCPUE and PCCPUE were calculated on a monthly basis for each habitat type in Cumberland and Nassau Sound. A mixed between-within subjects ANOVA (SPSS v. 18) was used to test for differences in potential prey CPUE and preferred prey CPUE between Cumberland and Nassau Sound and the two habitat types within each site. Since neither the PPCPUE nor PCCPUE data were normally distributed, the data were log-transformed and the mixed between-within subjects ANOVA was run using the $\log_{10}$ transformed data. Significance was determined at an alpha level of 0.05.

Models

Two levels of analysis were conducted to examine the effect of physical factors and prey abundance on the abundance of Atlantic sharpnose sharks in Cumberland and Nassau Sounds. All models used in these analyses were performed using SAS (v. 7.0). Final models were generated using backwards stepping to eliminate factors with the highest p-value until only significant factors remained. If a factor was not significant, but was part of a significant interaction, it was kept in the model. Significance was determined at an alpha level of 0.05.

In the first analysis, longline catch data for *R. terraenovae* from 2010 – 2011 was used to examine the effect of month, site, and habitat type on the presence/absence and abundance of *R. terraenovae*. To do this catch data was first split into presence/absence data and abundance data.

Presence/absence data was generated by determining if sharks were caught during individual sets. Sets that caught zero sharks were then removed and abundance data was generated for each set that caught at least one shark. A logistic regression model was performed using the presence/absence data to examine the effect of month, site, habitat type and all interactions on whether or not at least one shark was caught. Next, a general linear model (GLM) was performed using shark abundance data to examine the effect of month, site, habitat type, and all interactions on shark abundance. In the second level of analysis, a GLM was generated to examine the effect of site, habitat type, prey abundance, and all interactions on the abundance of *R. terraenovae*. Since prey abundance was only sampled on a monthly basis, shark abundance data, generated from the first level of analysis, was pooled monthly for each site and habitat type and mean monthly shark abundance was used in the model. Also, because PCCPUE, the measure of preferred prey abundance, is a subset of PPCPUE, the effect of each of these measures of prey abundance was modeled in separate models. For all GLMs, the final model was selected using backwards stepping and eliminating the factor with the highest p-value first.

2.3 Results

Shark Abundance

A total of 260 Atlantic sharpnose sharks were caught in Cumberland (n = 167) and Nassau (n = 93) Sounds during the sampling period (Table 1). Atlantic sharpnose CPUE in Cumberland Sound was low in May, increased in June and remained high through the summer, then declined in September (Figure 2). A similar pattern was also seen in Nassau Sound (Figure 3), although overall CPUE was lower than in Cumberland Sound. Results of the mixed between-within subjects ANOVA indicated there was no significant interaction between site and habitat

type (Wilks Lamda = 0.801, $F_{1,16}$ = 3.971, p = 0.064) and no significant effect of habitat type (Wilks Lambda = 0.787, $F_{1,16}$ = 4.325, p = 0.054) on Atlantic sharpnose CPUE. There was, however, a significant effect of site on Atlantic sharpnose CPUE (F_1 = 14.013, p < 0.005), with mean CPUE being significantly higher in Cumberland Sound than in Nassau Sound (Figure 4).

Diet Analysis

A total of 197 stomachs were examined from Atlantic sharpnose sharks caught in Cumberland and Nassau Sound. Of these, 107 stomachs (54.3%) contained prey items. For the 107 stomachs that contained prey items, 35 were from Nassau Sound and 72 were from Cumberland Sound. Stomach contents consisted of teleosts (5 orders, 6 families), crustaceans (mostly decapod shrimp), mollusks (cephalopods), and other invertebrates (Table 2).

Crustaceans were the most important major prey category found in the diet of Atlantic sharpnose sharks in Cumberland and Nassau Sounds (38.11 $\overline{\%IRI}$ and 36.28 $\overline{\%IRI}$, respectively; Figure 5). In both sites, identifiable crustaceans were comprised mostly of penaeid shrimps and other decapod shrimps (see Table 2). Sciaenid fish were the second most important prey category (24.99 $\overline{\%IRI}$ and 35.91 $\overline{\%IRI}$, respectively; Figure 5). In Cumberland Sound star drum (*Stellifer lanceolatus*) and croaker (*Micropagonias undualtus*) were the dominant species found in this prey category, while in Nassau Sound *S. lanceolatus* and spot (*Leiostomus xanthurus*) were most abundant (Table 2). When combined, these two prey categories made up more than 60% of the total diet in Cumberland Sound and 70% in Nassau Sound. Clupeids were the third most important prey category (18.77 $\overline{\%IRI}$ and 16.60 $\overline{\%IRI}$, respectively; Figure 5). Other pelagic teleosts, primarily anchovies (*Anchoa* spp., Table 2), were the fourth most important prey category (11.61 $\overline{\%IRI}$ and 9.50 $\overline{\%IRI}$, respectively; Figure 5). The remaining two major prey categories, other invertebrates and other epibenthic teleosts, contributed very little to the diet of

Atlantic sharpnose in Cumberland (4.91 $\overline{\%IRI}$, 1.61 $\overline{\%IRI}$) and Nassau (0.93 $\overline{\%IRI}$, 0.93 $\overline{\%IRI}$) (Figure 5).

Overall diet data for the two sites combined showed the same trends in the importance of each of the six major prey categories (Figure 5), with crustaceans and sciaenids being the two most important. These trends were also the same for each of the 3 RMPQs (Table 3). At the lowest possible taxonomic level the five most important prey items in the overall diet were clupeids (16.46 $\overline{\%IRI}$), *S. lanceolatus* (10.92 $\overline{\%IRI}$), Penaeid shrimps (7.76 $\overline{\%IRI}$), *L. xanthurus* (7.42 $\overline{\%IRI}$), and other crustaceans (6.07 $\overline{\%IRI}$); (Table 2).

Cumulative prey curves constructed for Cumberland and Nassau Sounds, indicated that a sufficient number of stomachs had had been examined in Cumberland Sound (Figure 6a) but not for Nassau Sound (Figure 6b). At the lowest taxonomic level, the slope of the best fit line of the last four points for Cumberland Sound ($b = 0.06$, $r^2 = 0.6$) and was significantly different from a line of 5% slope ($t = 0.287$, $p = 0.4$), where as for Nassau Sound the slope ($b = 0.38$, $r^2 = 0.96$) was significantly different from a line of 5% slope ($t = 6.24$, $p = 0.012$). When combined, however, the cumulative prey curve constructed for the overall diet indicated that a sufficient number of stomachs had been examined for precise diet analysis (Figure 6c). At the lowest taxonomic level, the slope of the best fit line of the last four points ($b = 0.16$, $r^2 = 0.8$) was not significantly different from a line of 5% slope ($t = 1.945$, $p = 0.195$). For this reason, only data from the overall diet analysis was used to identify preferred prey items.

Prey Abundance

Prey sampling in Cumberland Sound collected a total of 22,324 finfish and macro-invertebrates, representing 102 different species (Table 4a). In Nassau Sound a total of 31,377 finfish and macro-invertebrates were collected, representing 108 species (Table 4b). It should be

noted that FWC sampling only focuses on finfish and commercially important macro-invertebrates, and as a result abundance data on other invertebrate species (prey category INV; i.e., mollusks, polychaetes, etc.) were not available. In Cumberland Sound average monthly PPCPUE was highest in May in creek habitat and highest in July in sound habitat (Figure 7a). In Nassau Sound PPCPUE was fairly consistent across all months in creek habitat, but was highest in June in sound habitat (Figure 8a). Since crustaceans and sciaenids were the two most important prey categories in the diet based on the diet analysis, preferred prey CPUE (PPCPUE) was calculated using catch data for species in these two prey categories. In Cumberland Sound, PCCPUE was fairly consistent across months in the creek habitat, however, PCCPUE in sound habitat was low in May and June, peaked in July, and decreased in August and September (Figure 7b). In Nassau Sound PCCPUE was highest in May and slowly declined throughout the summer in creek habitat, while in sound habitat PCCPUE was low in May, peaked in June, and decreased through the end of the summer (Figure 8b).

Results of the mixed between-within subjects ANOVA for PPCPUE showed there was no significant interaction between site and habitat type (Wilks Lamda = 0.993, $F_{1,17} = 0.118$, $p = 0.735$). There was a significant effect of habitat type (Wilks Lambda = 0.778, $F_{1,17} = 4.853$, $p = 0.042$), with mean PPCPUE being higher in creek habitat than sound habitat (Figure 9). There was no effect of site on PPCPUE ($F_1 = 0.002$, $p = 0.965$). For PCCPUE, results from the mixed within-between subjects ANOVA showed that there was a significant interaction between site and habitat type (Wilks Lamda = 0.758, $F_{1,15} = 4.799$, $p = 0.045$), as well as a significant effect of habitat type on PCCPUE (Wilks Lamda = 0.681, $F_{1,15} = 7.037$, $p = 0.018$). PCCPUE was higher in creek habitat than sound habitat, and there was a greater change in PCCPUE between habitats in Nassau Sound than Cumberland Sound (Figure 10).

Modeling

The first level of analysis examined the effect of month, site, and habitat type on the presence and abundance of Atlantic sharpnose sharks. Results from the logistic regression showed that there was a significant effect of site on the presence/absence of Atlantic sharpnose sharks, as well as a significant interaction between month and habitat type (Table 5). A greater proportion of longline sets that caught at least one Atlantic sharpnose shark was greater in Cumberland Sound compared to Nassau Sound (Figure 11). Looking at the interaction between month and site, the probability of catch at least one Atlantic sharpnose shark was highest in sound habitat in May, June, August, and September, and higher in creek habitat in July (Figure 12). Results from the GLM showed that site was the only significant factor in determining the abundance of Atlantic sharpnose sharks ($F_1 = 6.12$, $p = 0.015$), with shark abundance being greater in Cumberland Sound compared to Nassau Sound.

The second level analysis examined the effect of site, habitat type, and prey abundance on Atlantic sharpnose abundance. Results from the GLMs were the same when both PPCPUE and PCCPUE were used in the model. In both cases the only significant factor in the model was site ($F_1 = 6.72$, $p = 0.015$). As in the first level of analysis, shark abundance was greatest in Cumberland Sound compared to Nassau Sound.

2.4 Discussion

The overall diet of Atlantic sharpnose sharks in Cumberland and Nassau Sounds indicated that this species feeds primarily on crustaceans and sciaenid fishes, with crustaceans being slightly more important than sciaenids (37.6 and 28.63 $\overline{\%\,IRI}$, respectively). This is consistent with findings from previous studies. In the north central Gulf of Mexico Drymon et.

al. (2011) showed that Atlantic sharpnose sharks fed primarily on teleost fishes (including croaker, *M. undulatus*) and crustaceans (including shrimps and portunid crabs). In the northeast Gulf of Mexico, Atlantic sharpnose fed heavily on crustaceans (mainly penaeid shrimps), sciaenids (mainly croaker), and clupeids (mainly *Brevoortia* spp.) (Bethea et. al. 2004, 2006). It should be noted, however, that in the studies by Bethea et. al. the diet was described for each life stage, and the overall importance of different prey varied by life stage. For example, young-of-the-year sharks fed primarily on crustaceans and sciaenids were of little importance, whereas mature sharks fed almost exclusively on sciaenids (Bethea et. al. 2006). That both crustaceans and sciaenids showed relatively similar $\overline{\%\,IRI}$ values in this study is likely a result of the diet of Atlantic sharpnose sharks being described across all life stages combined.

There was little difference in the diet of Atlantic sharpnose sharks caught in Cumberland Sound and Nassau Sound. In both regions, the two most important prey categories were crustaceans and sciaenids. This is not consistent with findings by Bethea et. al. (2006), which showed variation in the diet of Atlantic sharpnose sharks caught in two bays in the northeast Gulf of Mexico. These differences were attributed to differences in habitat structure and the availability of potential prey species associated with those habitats. The lack of variation in the diet between the two sites in this study has a few possible explanations. First, there is very little difference in the overall habitat structure between Cumberland and Nassau Sound. Both areas are characterized by extensive salt marsh creeks with mud bottom and oyster bars, and open sounds with muddy/sandy bottom (McCallister, personal observations). Second, prey sampling indicated that the availability of both potential and preferred prey species was not different between the two sites, and the species composition was also similar between sites. Finally, cumulative prey curves only indicated a sufficient number of stomachs had been sampled to

accurately describe the diet of sharks in Cumberland Sound. It is possible that the analysis of more stomachs from sharks in Nassau Sound that differences between the diets might appear.

Results from the models generated in the first level of analysis indicated that site had the greatest influence on the presence and abundance of Atlantic sharpnose sharks in Cumberland and Nassau Sound. Both the probability of catching at least one and the abundance of Atlantic sharpnose sharks was higher in Cumberland Sound than in Nassau Sound. Analysis of catch rates also showed that CPUE for Atlantic sharpnose sharks was also higher in Cumberland Sound. This is not surprising, as it would be expected for shark abundance to be higher where the probability of capture is greater, and that catch rates in those areas would be higher too. Regional differences in shark abundance have also been shown in southwest Florida (Simpfendorfer et. al., 2005), Florida Bay (Torres et. al, 2006), and the Indian River Lagoon system (Curtis, 2008).

Prey abundance did not have a significant effect on the abundance of Atlantic sharpnose sharks in Cumberland and Nassau Sounds, regardless of whether measures of potential prey abundance or preferred prey abundance were used. In both models where prey abundance was included as a predictive variable, it was removed from the model during backwards elimination of non-significant factors. As in the first level of analysis, site was the only factor to have a significant effect on the abundance of Atlantic sharpnose sharks. This is further supported by results from the analysis of shark and prey catch rates. While prey CPUE was higher in creek habitat than sound habitat, there was no effect of habitat type on CPUE of Atlantic sharpnose sharks. Similarly, there was no effect of site on prey CPUE, but sharpnose CPUE was higher in Cumberland Sound. The lack of effect of prey abundance on shark abundance is consistent with findings from other studies. In Terra Ceia Bay, FL, movement patterns of juvenile blacktip

sharks were not correlated with prey density (Heupel and Heuter, 2002). Similarly, juvenile scalloped hammerheads use the waters of Kane'ohe Bay, HI despite limited prey abundance and low foraging success (Duncan and Holland, 2006). In both of those studies it was suggested that predation risk, rather than prey abundance, played a more important role in determining the abundance of sharks.

Further support of the role of predation risk in determining the abundance of predators can be seen in Shark Bay, Western Australia. In Shark Bay, bottlenose dolphins modify their foraging behavior, feeding in habitats with lower prey densities when tiger sharks are present, due to the increased risk of predation by tiger sharks (Heithaus and Dill, 2002). Conversely, large tiger sharks do not face any predation risk in Shark Bay, and were shown to prefer habitats where their prey is more abundant (Heithaus et. al., 2002).

With a maximum total length of ~1m it is possible that predation risk may be influencing the abundance of Atlantic sharpnose sharks in this study. On multiple occasions Atlantic sharpnose sharks were caught with bite marks from larger sharks present, or only half of a shark was retrieved (McCallister, personal observations). Although predation risk may be influencing the abundance of Atlantic sharpnose sharks, it is unclear if differences in predation risk between the two sites explain the significant effect of site in models of shark abundance. Though not directly tested, large sharks that could be potential predators of *R. terraenovae* have been caught in both Cumberland and Nassau Sound (personal observations); however, further research is needed to accurately assess the risk of predation in each of these sites.

More recently it has been suggested that incorporating measures of prey abundance into models that predict marine predator abundance may not improve the predictive ability of those models. Torres et. al. (2008) found that models of dolphin habitat selection that included prey

abundance were not as powerful as those models that only incorporated environmental variables. One reason they suggest for this is the difficulty of surveying prey abundance on a small enough scale to show potential variability. Indeed, the main complication encountered in the current study was the different scales at which shark abundance and prey abundance were measured. Though collaborating with FWC to obtain data on the abundance of potential prey species eliminated the need to conduct our own prey sampling, given the sampling protocol used by FWC it was only possible to obtain measures of prey abundance on a monthly basis. As a result, measures of shark abundance had to be pooled monthly and the mean monthly abundance used when examining the effect of prey abundance. This likely resulted in the loss of variability in shark abundance within and between months. Also, with only a single monthly measure of prey abundance there was less chance to see changes in prey abundance during the month. This prevented the use of more complex models to examine the effect of prey abundance the by limiting the amount of factors that could be included in the model. Sampling prey abundance on a weekly basis, similar to the shark sampling, would allow for more rigorous statistical testing of the effect of prey abundance and other abiotic factors on shark abundance.

This study used a multi-faceted approach to examine the effect of prey abundance on habitat selection and abundance of Atlantic sharpnose sharks in two northeast Florida estuaries. While the results of this study suggest that prey abundance does not affect the abundance of Atlantic sharpnose sharks, analysis of stomach contents did show that sharks were feeding on prey species that were abundant in the region. Despite this, it appears that the abundance of Atlantic sharpnose sharks is likely driven by other factors besides prey abundance, though further research is needed. Future studies that aim to examine the effect of biotic and abiotic

factors on shark abundance should consider finer-scale sampling of prey abundance, as well as the inclusion of environmental variables and other potential predator- prey interactions.

2.5 Acknowledgements

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Table 2-1. Raw monthly abundance of Atlantic sharpnose sharks caught in a) Cumberland Sound and b) Nassau Sound from May – September 2010 and 2011.

a) Cumberland Sound

	May	June	July	August	September	Total
2010	22	36	14	14	-	86
2011	15	21	17	19	9	81
Total	37	57	31	33	9	167

b) Nassau Sound

	May	June	July	August	September	Total
2010	17	13	13	15	2	60
2011	4	10	10	9	0	33
Total	21	23	23	24	2	93

Table 2-2. Stomach contents from Atlantic sharpnose sharks from a) Cumberland Sound (n = 72), b) Nassau Sound (n = 35), and c) both sites combined (n = 107). Means are presented for %N, %W, and %IRI. SE = standard error.

	a) Cumberland Sound							**b) Nassau Sound**						
Prey Item	**%N**	**SE**	**%W**	**SE**	**%FO**	**%IRI**	**SE**	**%N**	**SE**	**%W**	**SE**	**%FO**	**%IRI**	**SE**
Pelagic Teleosts														
F. Clupeidae	14.12	3.90	15.03	4.19	16.67	14.78	4.02	14.29	5.02	18.62	6.37	25.71	19.15	6.00
Brevoortia sp.	1.39	1.39	1.39	1.39	1.39	1.39	1.39							
F. Engraulidae	1.39	1.39	1.39	1.39	1.39	1.39	1.39							
Anchoa sp.	5.56	2.53	4.63	2.40	6.94	4.91	2.44	5.48	2.49	6.44	3.79	14.29	5.98	3.02
F. Carangidae								2.86	2.86	2.86	2.86	2.86	2.86	2.86
F. Atherinidae														
Menidia sp.	2.08	1.54	2.70	1.90	2.78	1.64	1.41							
Epibenthic Teleosts														
F. Sciaenidae	1.04	0.77	1.06	0.75	2.78	0.49	0.41	0.71	0.71	0.40	0.40	2.86	0.09	0.09
B. chrysoura	0.69	0.69	1.23	1.23	1.39	0.26	0.26							
Cynoscion sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.43	1.43	2.70	2.70	2.86	0.70	0.70
L. xanthurus	3.47	1.80	3.25	1.85	5.56	3.40	1.85	15.24	6.01	14.85	5.99	17.14	15.04	6.00
M. undulatus	6.02	2.56	6.60	2.86	8.33	5.94	2.62	2.38	1.69	2.13	2.00	5.71	1.47	1.24
S. lanceolatus	9.26	2.89	8.70	3.08	13.89	10.99	3.39	10.71	4.55	8.48	4.69	17.14	10.08	4.62
F. Syngnathidae	1.39	1.39	1.39	1.39	1.39	1.39	1.39							
O. Anguilliformes								0.95	0.95	2.24	2.24	2.86	0.48	0.48
Unid. Teleosts	23.15	4.31	19.89	4.49	33.33	27.72	4.88	16.67	5.72	15.59	6.01	22.86	18.95	6.19
Arthropods														
C. Crustacea	5.32	2.49	6.80	2.96	6.94	5.39	2.50	7.38	3.53	6.32	3.70	14.29	6.88	3.61
O. Decopoda								4.52	3.04	3.15	2.86	8.57	3.40	2.87
F. Penaeidae	6.94	2.81	8.36	3.24	9.72	7.58	3.01	6.67	3.50	9.23	4.73	11.43	8.12	4.01

Table 2-2. Continued

Prey Item	a) Cumberland Sound							b) Nassau Sound						
	%N	SE	%W	SE	%FO	%IRI	SE	%N	SE	%W	SE	%FO	%IRI	SE
Unid. Decopod Shrimp	3.94	2.10	2.97	1.95	5.56	3.07	1.96	6.90	3.39	4.22	3.01	14.29	5.49	3.09
F. Portunidae	0.93	0.65	0.76	0.54	2.78	0.17	0.13							
O. ocellatus	0.35	0.35	0.48	0.48	1.39	0.04	0.04							
F. Xanthidae	1.39	1.39	1.39	1.39	1.39	1.39	1.39							
Unid. Anomura	3.47	1.80	3.49	1.97	5.56	2.40	1.54							
Unid. Thalassinidea	2.78	1.68	4.00	2.28	4.17	2.07	1.46							
O. Isopoda	1.39	0.98	0.25	0.21	2.78	0.25	0.18	0.95	0.95	0.32	0.32	2.86	0.10	0.10
Molluscs														
C. Cephalopoda	3.94	2.10	4.23	2.34	5.56	3.34	1.99	0.95	0.95	0.11	0.11	2.86	0.12	0.12
Other Inverts								1.90	1.49	2.33	1.73	5.71	1.10	0.90

Table 2-2. Continued

Prey Item	c) Combined Sites						
	%N	**SE**	**%W**	**SE**	**%FO**	**%IRI**	**SE**
Pelagic Teleosts							
F. Clupeidae	14.17	3.08	16.21	3.49	19.63	16.46	3.15
Brevoortia sp.	0.93	0.93	0.93	0.93	0.93	0.93	0.93
F. Engraulidae	0.93	0.93	0.93	0.93	0.93	0.93	0.93
Anchoa sp.	5.53	1.88	5.22	2.03	9.35	5.06	1.96
F. Carangidae	0.93	0.93	0.93	0.93	0.93	0.93	0.93
F. Atherinidae							
Menidia sp.	1.40	1.04	1.82	1.28	1.87	1.07	1.30
Epibenthic Teleosts							
F. Sciaenidae	0.93	0.57	0.85	0.52	2.80	0.28	1.09
B. chrysoura	0.47	0.47	0.83	0.83	0.93	0.12	0.91
Cynoscion sp.	0.47	0.47	0.88	0.88	0.93	0.07	0.92
L. xanthurus	7.32	2.35	7.05	2.36	9.35	7.42	2.31
M. undulatus	4.83	1.81	5.14	2.04	7.48	4.45	2.02
S. lanceolatus	9.74	2.44	8.63	2.57	14.95	10.92	2.07
F. Syngnathidae	0.93	0.93	0.93	0.93	0.93	0.93	0.93
O. Anguilliformes	0.31	0.31	0.73	0.73	0.93	0.06	0.88
Unid. Teleosts	21.03	3.45	18.49	3.59	29.91	25.37	3.30
Arthropods							
C. Crustacea	6.00	2.02	6.64	2.32	9.35	6.07	2.19
O. Decopoda	1.48	1.01	1.03	0.94	2.80	1.01	1.12
F. Penaeidae	6.85	2.20	8.65	2.66	10.28	7.76	2.34
Unid. Decopod Shrimp	4.91	1.79	3.38	1.63	8.41	3.68	1.72
F. Portunidae	0.62	0.44	0.51	0.36	1.87	0.08	1.09
O. ocellatus	0.23	0.23	0.32	0.32	0.93	0.02	0.69
F. Xanthidae	0.93	0.93	0.93	0.93	0.93	0.93	0.93
Unid. Anomura	2.34	1.22	2.35	1.33	3.74	1.44	1.50
Unid. Thalassinidea	1.87	1.14	2.69	1.54	2.80	1.30	1.57
O. Isopoda	1.25	0.72	0.27	0.18	2.80	0.21	1.01
Molluscs							
C. Cephalopoda	2.96	1.45	2.88	1.58	4.67	2.29	1.64
Other Inverts	0.62	0.49	0.76	0.57	1.87	0.19	1.01

Table 2-3. Diet composition by major prey category for the overall diet of Atlantic sharpnose sharks by mean percent number ($\overline{\%N}$), mean percent weight ($\overline{\%W}$), percent frequency occurrence (%FO), and mean index of relative importance ($\overline{\%IRI}$). Prey categories are listed in order of importance based on $\overline{\%IRI}$. SE = standard error.

Prey Category	$\overline{\%N}$	SE	$\overline{\%W}$	SE	% FO	$\overline{\%IRI}$	SE
CRU	35.22	4.51	35.28	4.76	50.54	37.60	4.64
SCI	28.67	4.30	27.18	4.46	41.94	28.63	4.35
CLU	18.28	3.76	19.82	4.07	23.66	18.03	3.78
PEL	11.38	3.06	11.38	3.20	15.05	10.88	3.06
INV	4.84	1.98	4.41	1.97	7.53	3.56	1.85
EPI	1.61	1.20	1.94	1.37	2.15	1.30	1.10

Table 2-4. Twenty-five most abundant prey species in a) Cumberland Sound and b) Nassau Sound as identified through prey sampling. Total abundance and percentage of catch are presented. Only the twenty-five most abundant species are presented, as the remaining species make up less than 2% and 5% of the catch in each sound, respectively.

a) Cumberland Sound			b) Nassau Sound		
Species	**N**	**%**	**Species**	**N**	**%**
Anchoa hepsetus	6704	37.99	Anchoa mitchilli	12055	38.42
Anchoa mitchilli	5306	30.07	Anchoa hepsetus	5813	18.53
Menidia menidia	1927	10.92	Menidia menidia	3059	9.75
Stellifer lanceolatus	1687	9.56	Penaeid Shrimps	1646	5.245881
Penaeid Shrimps	255	1.44	Membras martinica	1536	4.90
Chloroscombrus chrysurus	201	1.14	Mugil cephalus	852	2.72
Bairdiella chrysoura	182	1.03	Micropogonias undulatus	700	2.23
Harengula jaguana	106	0.60	Bairdiella chrysoura	548	1.75
Membras martinica	106	0.60	Trachinotus carolinus	493	1.57
Leiostomus xanthurus	102	0.58	Opisthonema oglinum	444	1.42
Mugil cephalus	91	0.52	Leiostomus xanthurus	410	1.31
Dasyatis sabina	88	0.50	Anchoa lyolepis	353	1.13
Lagodon rhomboides	84	0.48	Cynoscion spp.	330	1.05
Opisthonema oglinum	71	0.40	Mugil curema	305	0.97
Trinectes maculatus	58	0.33	Menticirrhus americanus	304	0.97
Callinectes similis	56	0.32	Stellifer lanceolatus	272	0.87
Paralichthys dentatus	43	0.24	Dasyatis sabina	157	0.50
Menticirrhus americanus	42	0.24	Trinectes maculatus	153	0.49
Pomatomus saltatrix	36	0.20	Callinectes sapidus	149	0.47
Portunus spp.	36	0.20	Harengula jaguana	134	0.43
Gymnura micrura	33	0.19	Eucinostomus spp.	123	0.39
Prionotus scitulus	30	0.17	Callinectes similis	113	0.36
Cynoscion spp.	25	0.14	Symphurus plagiusa	112	0.36
Micropogonias undulatus	25	0.14	Cynoscion nebulosus	89	0.28
Etropus crossotus	20	0.11	Fundulus heteroclitus	86	0.27

Table 2-5. Results of logistic regression modeling the effect of month, site, habitat type, and all interactions on the presence/absence of *R. terraenovae* in Cumberland and Nassau Sounds from May to Septmeber, 2010 – 2011. Significant values are presented in bold.

Factor	Significance
Overall Model Fit	**$p < 0.001$**
Month	$p = 0.1118$
Site	**$p = 0.0255$**
Habitat	$p = 0.3794$
Month*Habitat	**$p < 0.001$**

Figure 2-1.

Map redacted. Paper copy available upon request to home institution

Figure 2-2.

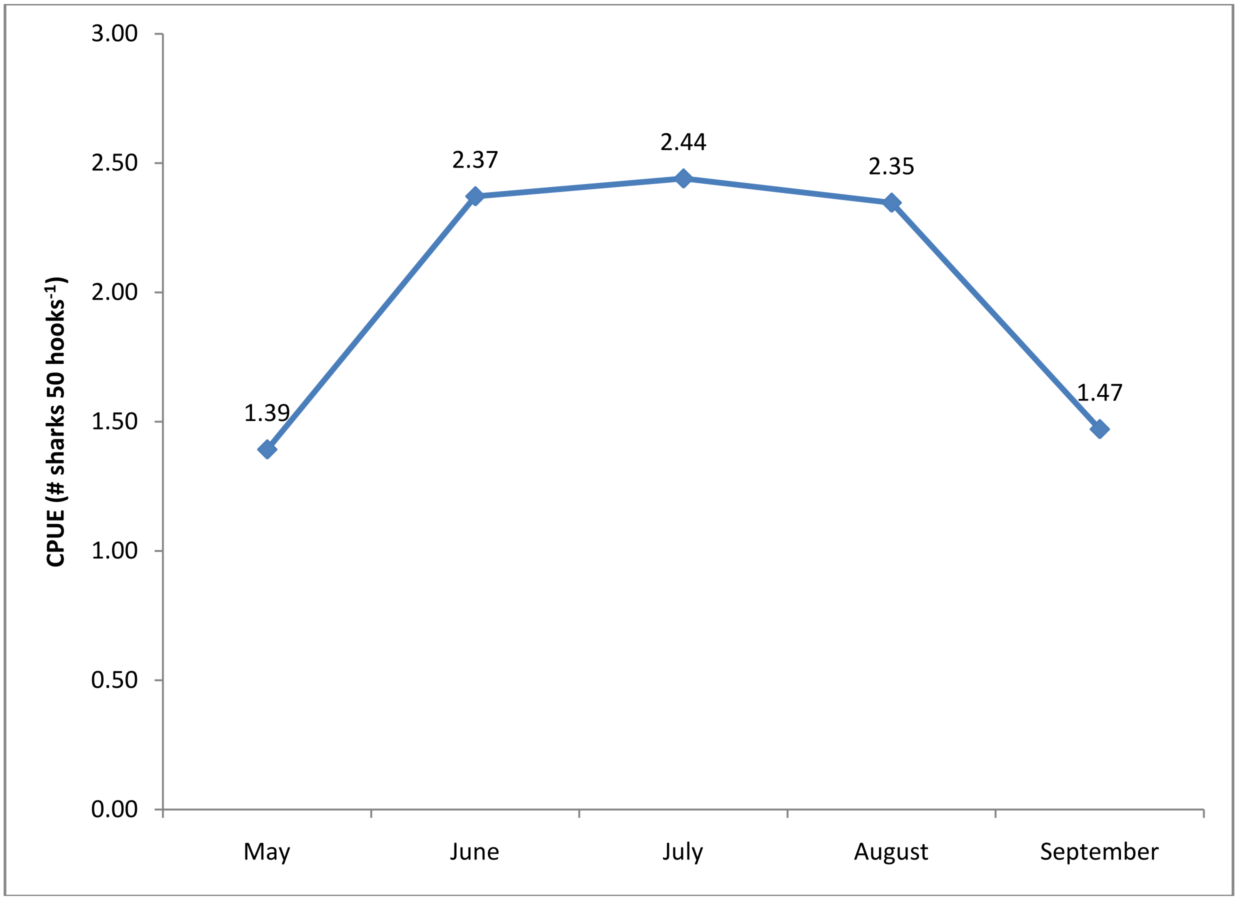

CPUE (# sharks 50 hooks-1)
3.00
2.50
2.00
1.50
1.00
0.50
0.00
1.39
2.37
2.44
2.35
1.47
May
June
July
August
September

Figure 2-3.

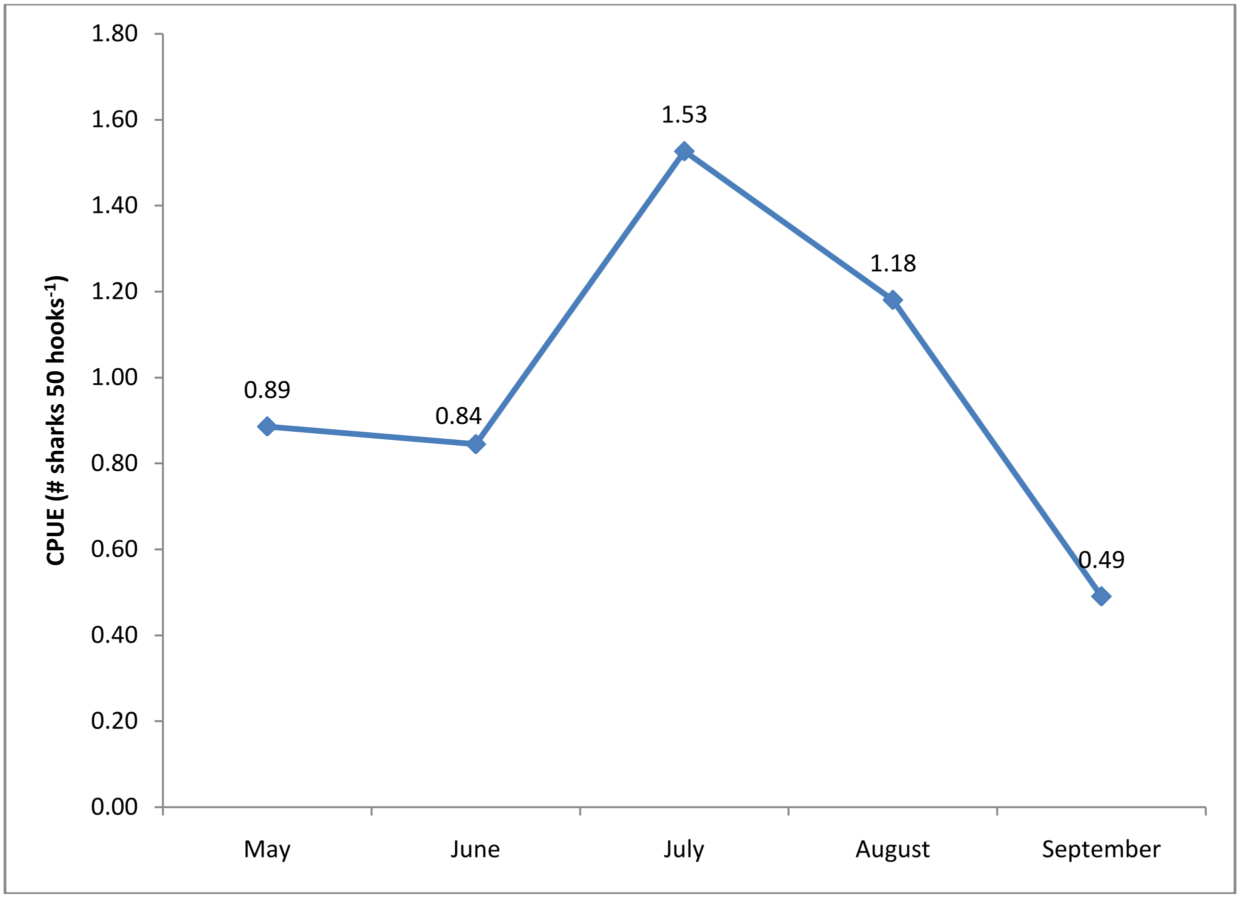

1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
CPUE (# sharks 50 hooks-1)
0.89
0.84
1.53
1.18
0.49
May
June
July
August
September

Figure 2-4.

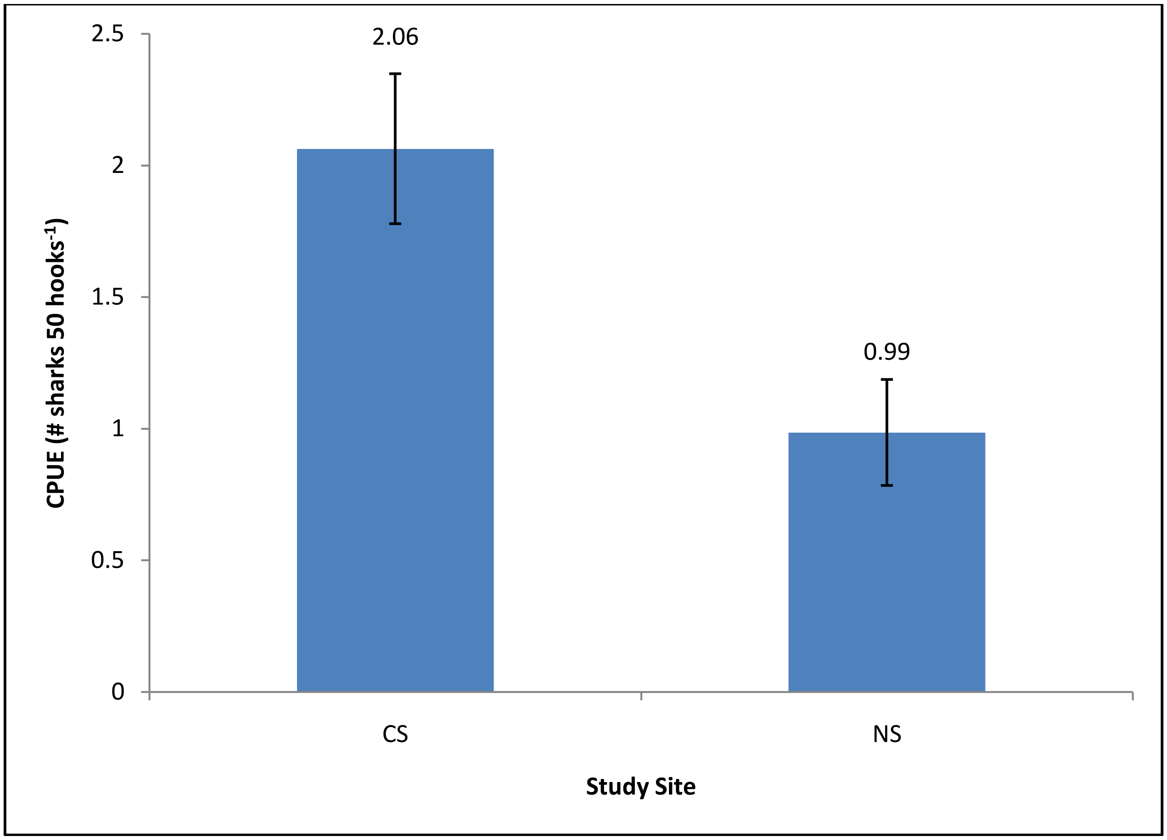


Figure 2-5.

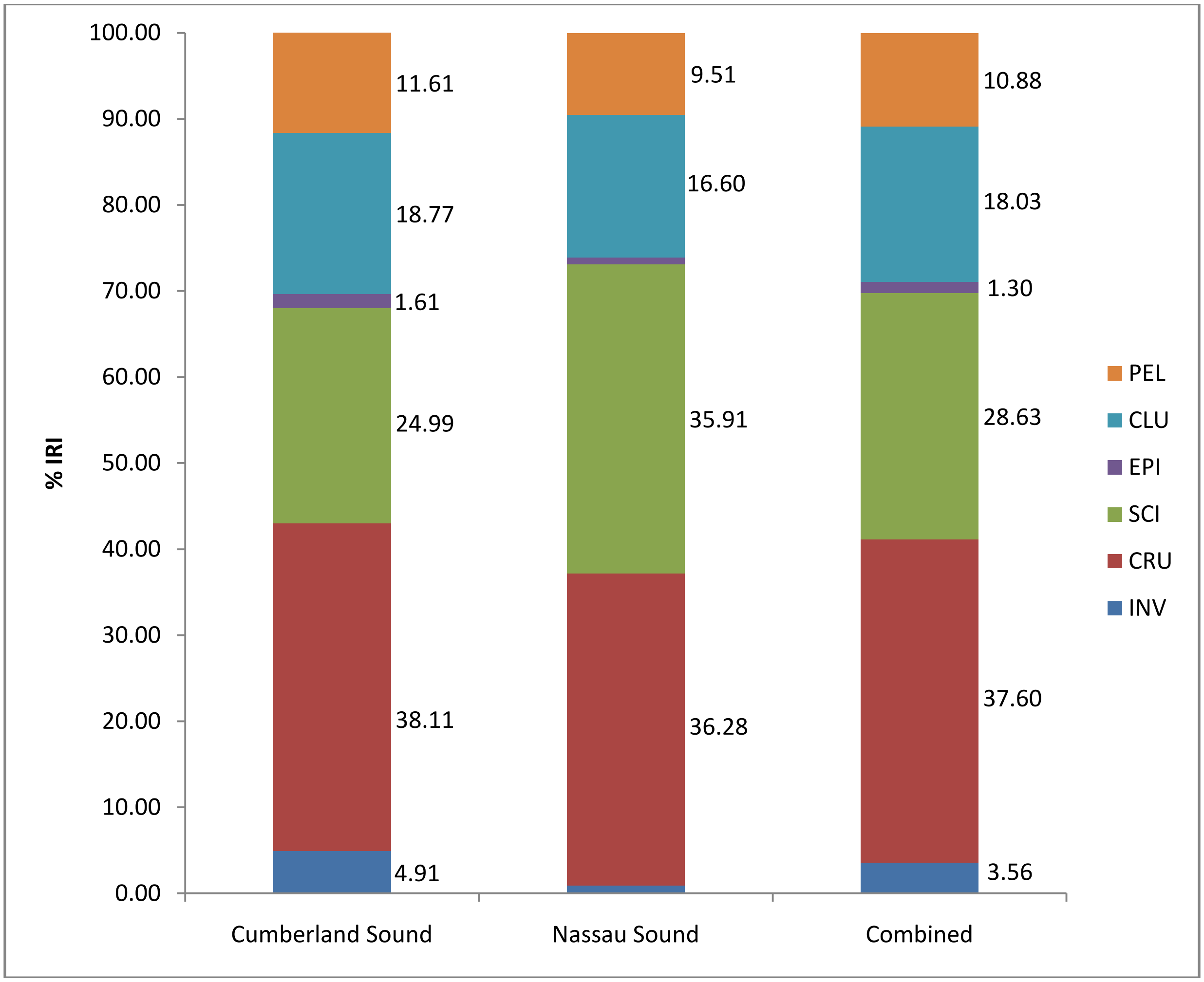
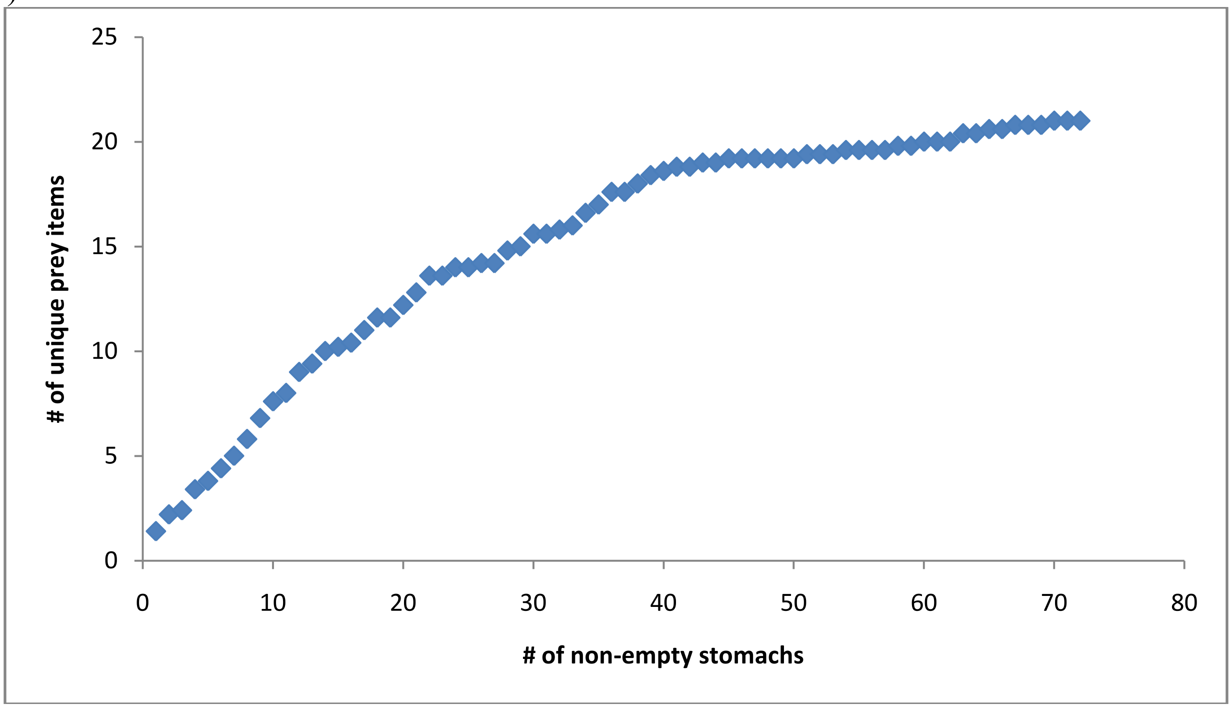

100.00
90.00
80.00
70.00
60.00
50.00
40.00
30.00
20.00
10.00
0.00
% IRI
11.61
18.77
1.61
24.99
38.11
4.91
9.51
16.60
35.91
36.28
10.88
18.03
1.30
28.63
37.60
3.56
Cumberland Sound
Nassau Sound
Combined
PEL
CLU
EPI
SCI
CRU
INV

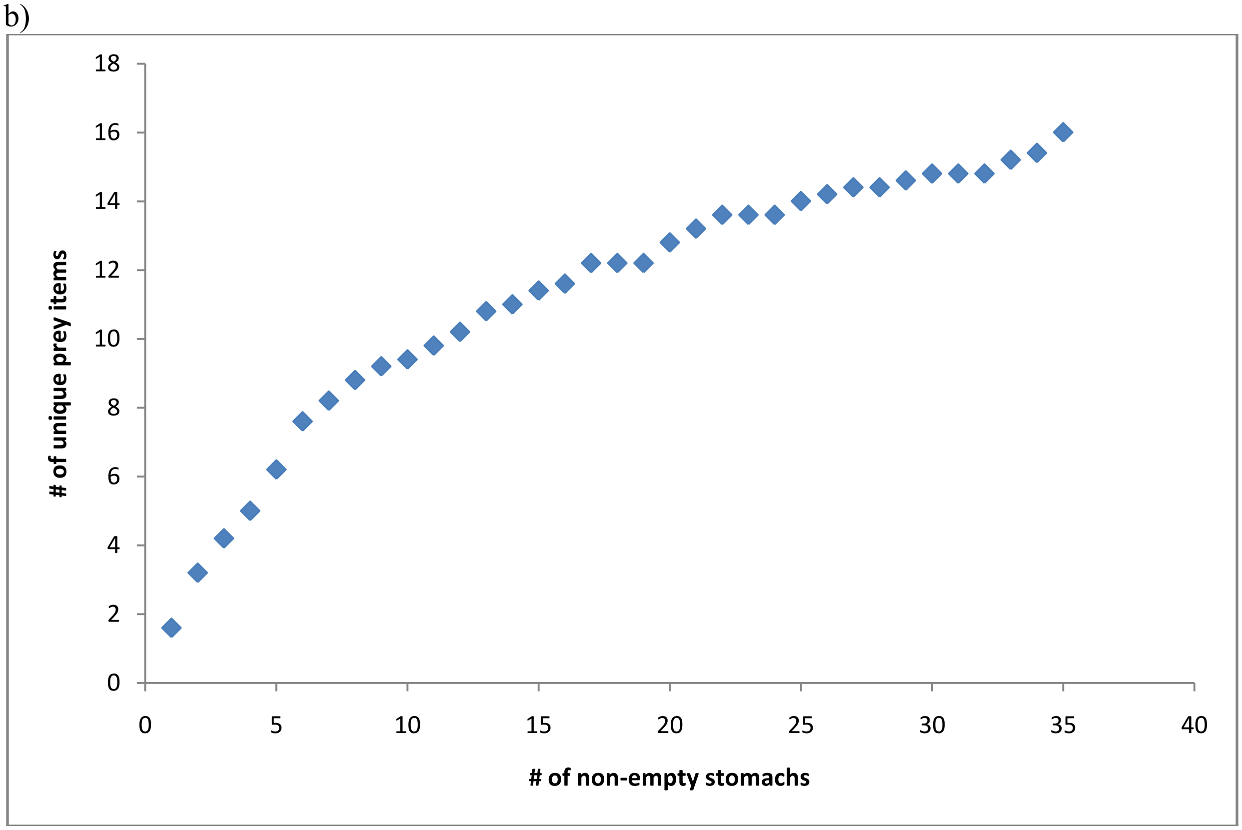
Figure 2-6.

a)



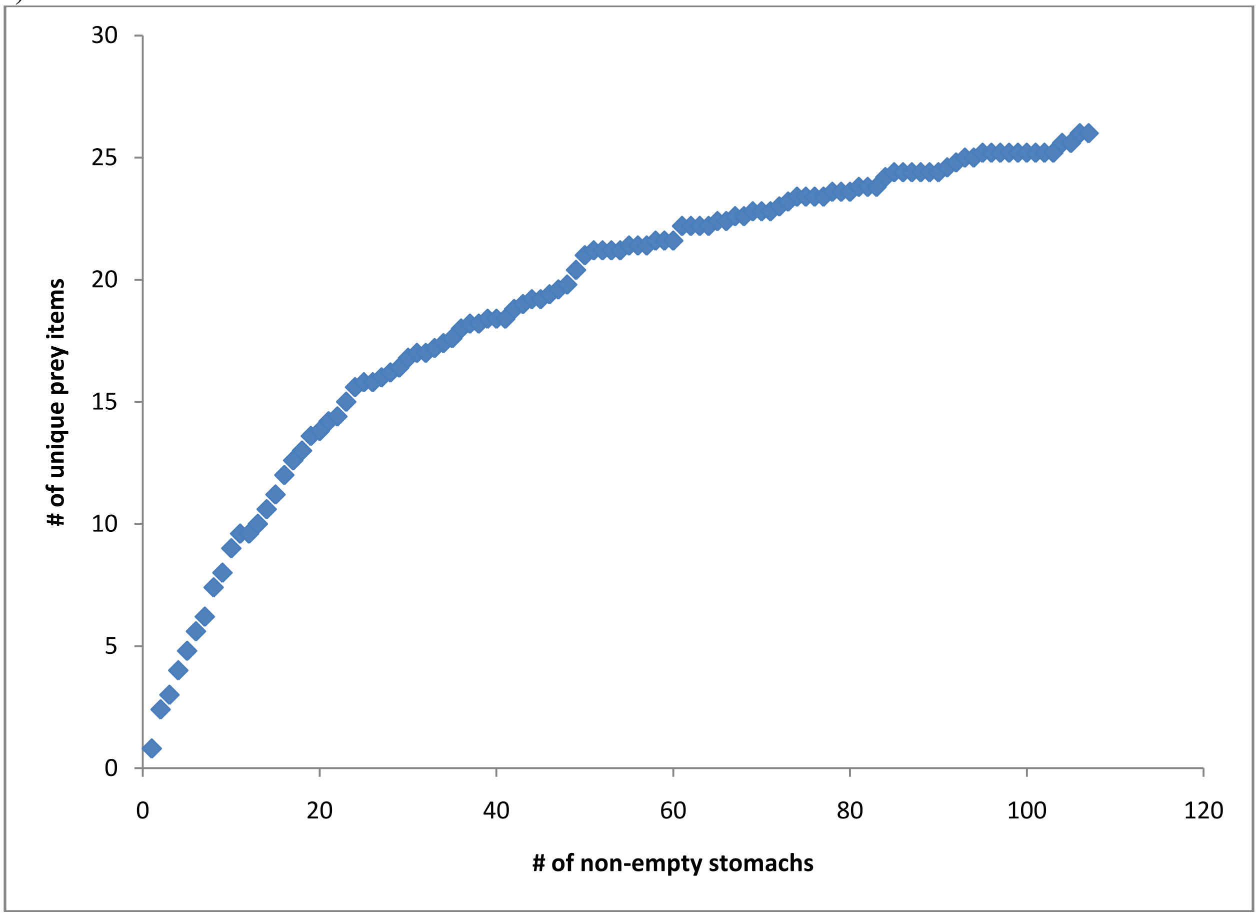
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
# of unique prey items
# of non-empty stomachs

b)



18
16
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30
35
40
# of unique prey items
# of non-empty stomachs

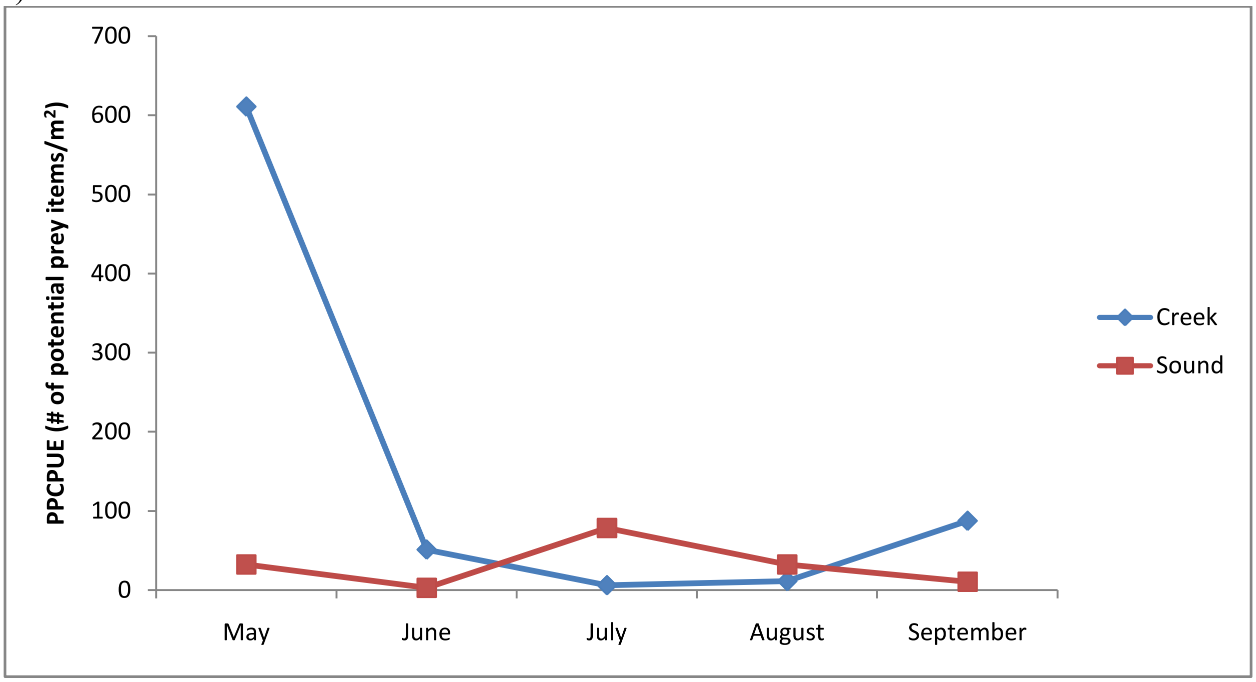
c)



30
25
20
15
10
5
0
# of unique prey items
0
20
40
60
80
100
120
# of non-empty stomachs

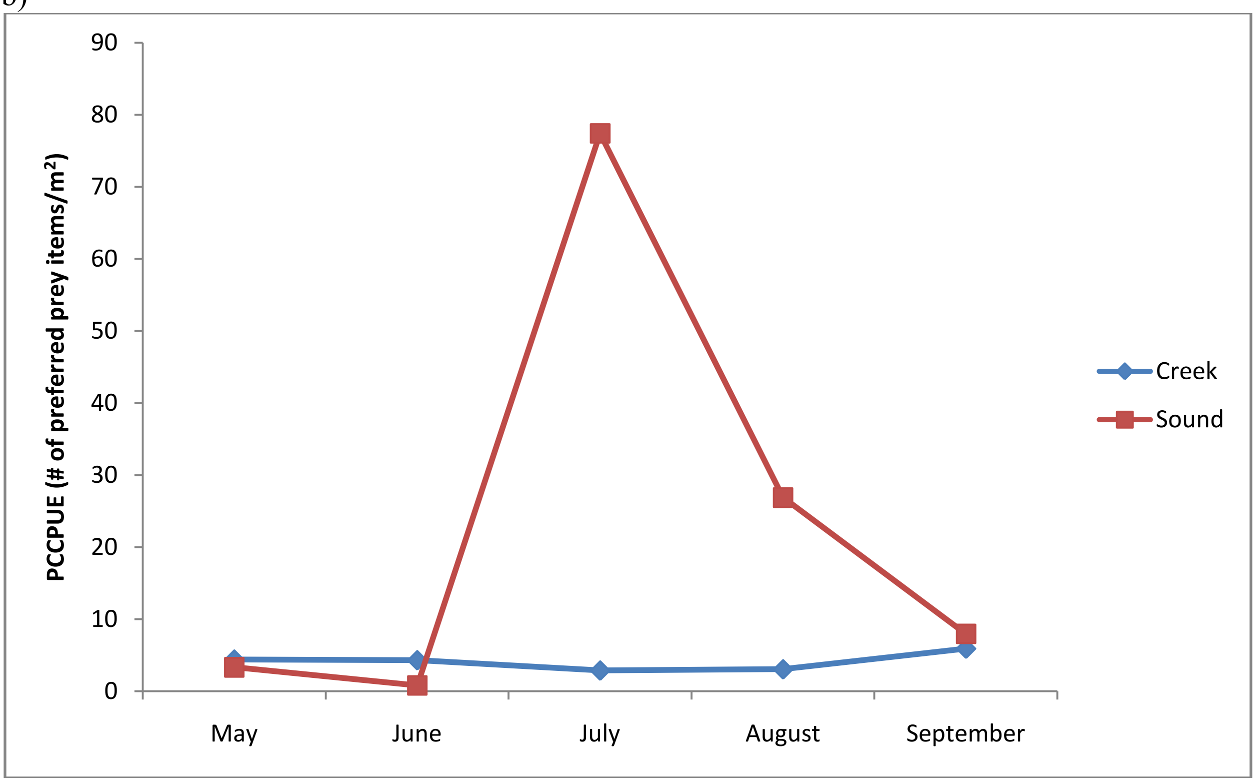
Figure 2-7.

a)



PPCPUE (# of potential prey items/m²)
700
600
500
400
300
200
100
0
May
June
July
August
September
Creek
Sound

b)



PCCPUE (# of preferred prey items/m²)
90
80
70
60
50
40
30
20
10
0
May
June
July
August
September
Creek
Sound

Figure 2-8.

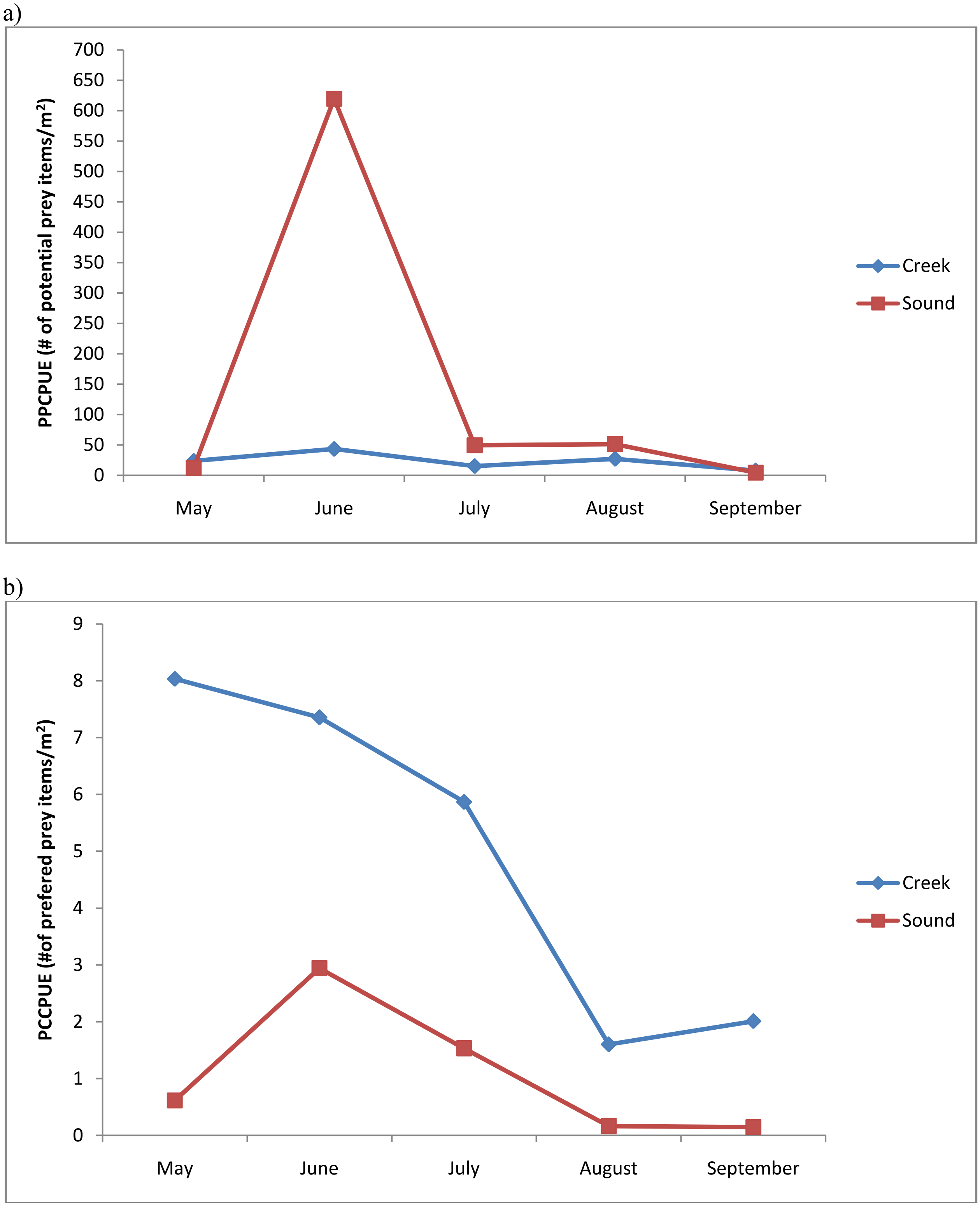

a)
700
650
600
550
500
450
400
350
300
250
200
150
100
50
0
PPCPUE (# of potential prey items/m²)
May
June
July
August
September
Creek
Sound
b)
9
8
7
6
5
4
3
2
1
0
PCCPUE (#of prefered prey items/m²)
May
June
July
August
September
Creek
Sound

Figure 2-9.

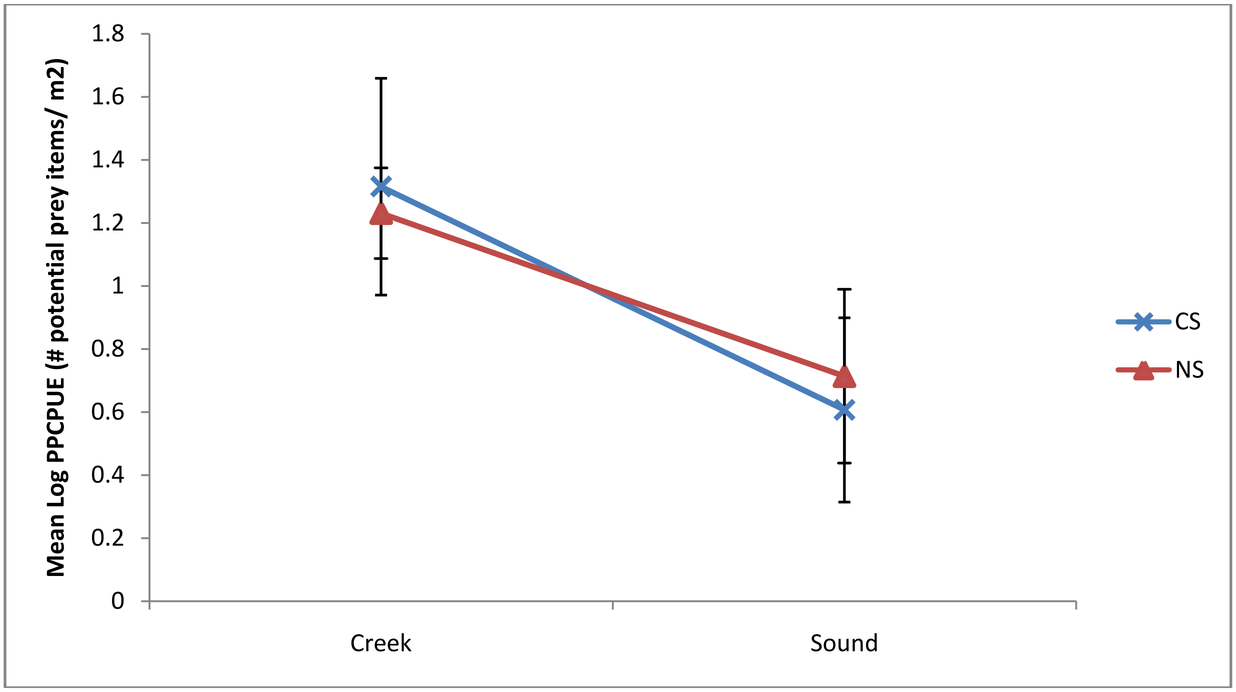
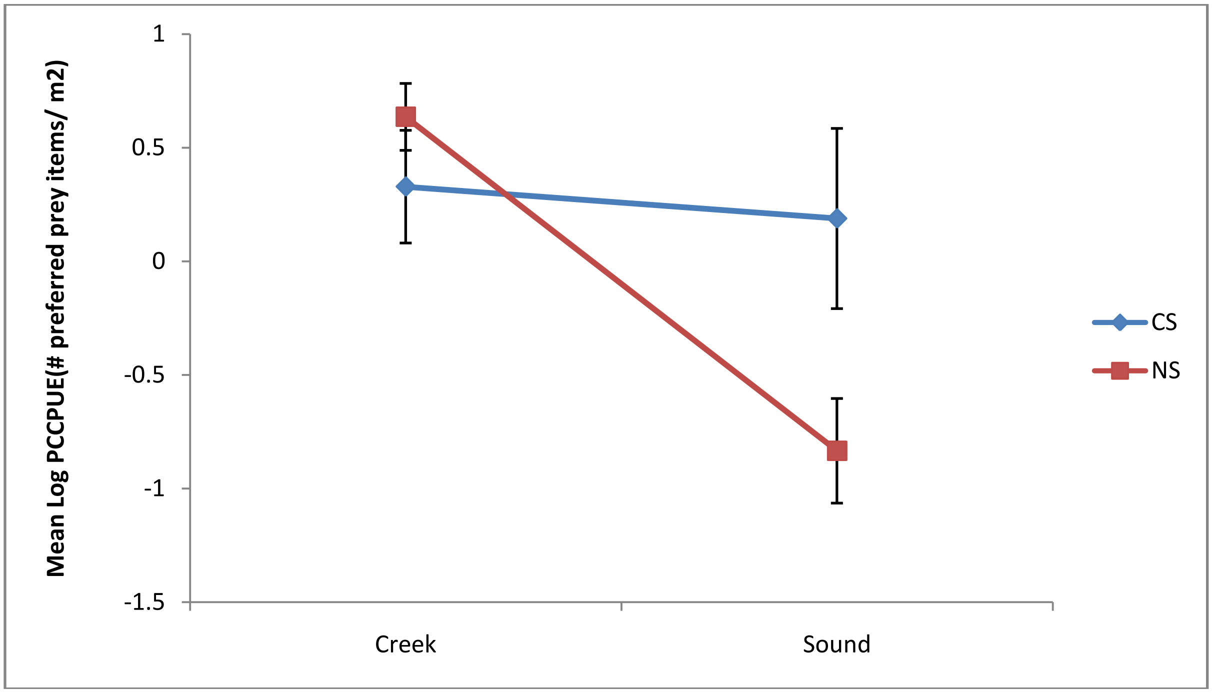

Mean Log PPCPUE (# potential prey items/ m2)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Creek
Sound
CS
NS

Figure 2-10.



Mean Log PCCPUE(# preferred prey items/ m2)
1
0.5
0
-0.5
-1
-1.5
Creek
Sound
CS
NS

Figure 2-11.

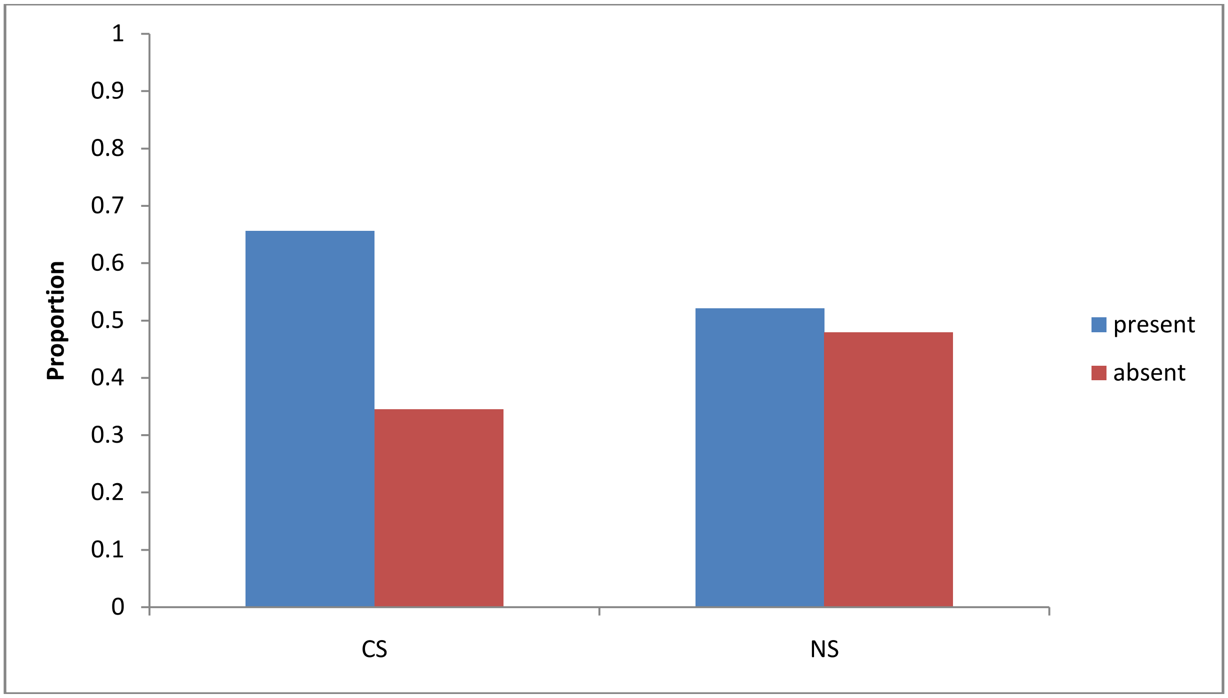
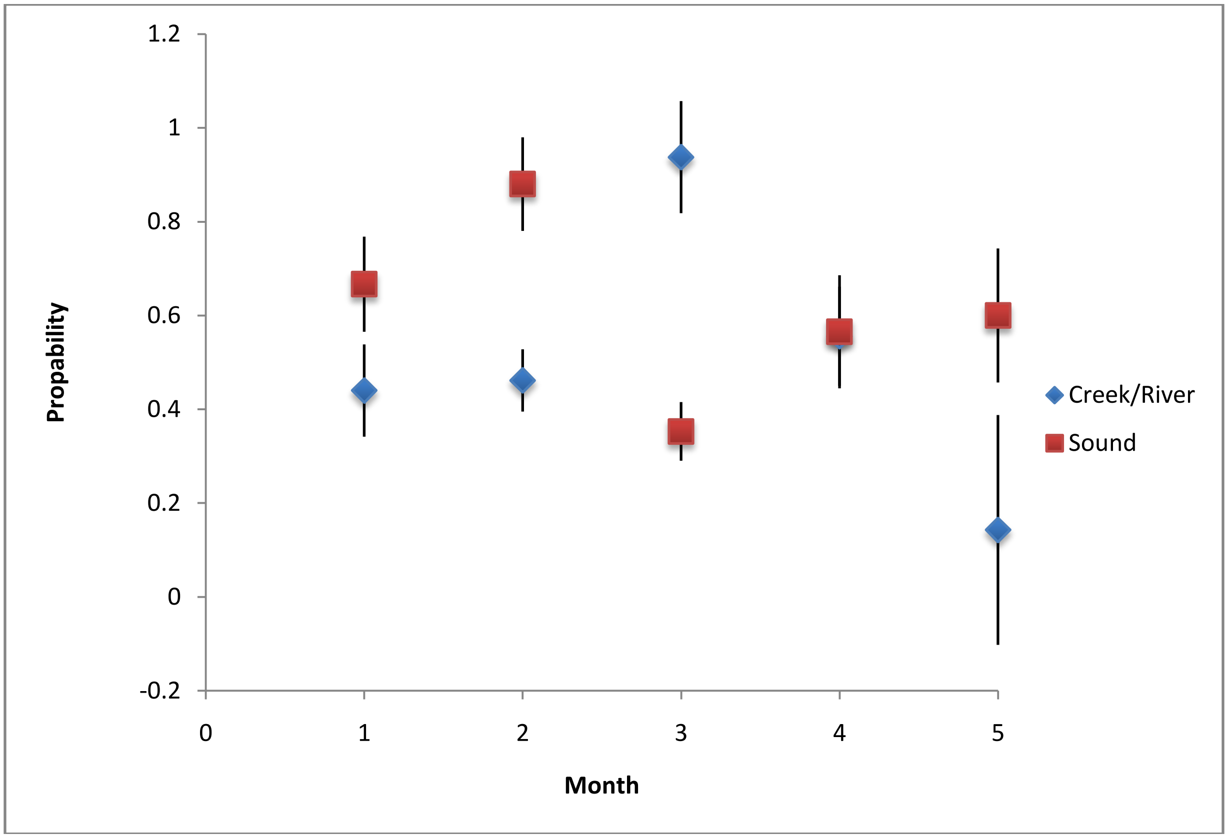


Figure 2-12.


1.2
1
0.8
0.6
0.4
0.2
0
-0.2
0
1
2
3
4
5
Month
Propability
Creek/River
Sound

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