ABSTRACT

Bethea, Dana Michelle. Foraging ecology of the early life stages of four shark species (*Rhizoprionodon terraenovae, Carcharhinus limbatus, Carcharhinus isodon,* and *Carcharhinus brevipinna*) in Apalachicola Bay, Florida. (Under the supervision of Jeffrey A. Buckel)

As top predators, sharks have an important role in marine ecosystems in relation to populations of fish and invertebrates at lower trophic levels. Fishery management plans stress the need for an ecosystem approach, but few quantitative data on the foraging ecology of sharks have been published. Results from a literature review found that shark species close in taxonomic relation have high diet overlap. Stomach contents and catch data of early life stages of Atlantic sharpnose (*Rhizoprionodon terraenovae*), blacktip (*Carcharhinus limbatus*), finetooth (*Carcharhinus isodon*), and spinner sharks (*Carcharhinus brevipinna*) taken from fishery independent surveys in Apalachicola Bay, Florida, April-October 1999-2002 were examined to test for resource competition. All species are capable of taking teleost prey from birth, though Atlantic sharpnose and blacktip sharks show an ontogenetic shift in diet. Young-of-the-year Atlantic Sharpnose sharks feed mainly on shrimp, juveniles on sciaenids, and adults on clupeids. Young-of-the-year blacktip sharks feed mainly on sciaenids, whereas juveniles feed on clupeids. The primary prey of young-of-the-year and juvenile finetooth and spinner sharks is menhaden. Eight of ten size-selectivity tests showed neutral selection. Atlantic sharpnose and finetooth sharks consume relatively small-sized prey (over 60% <20% of their length) compared to teleost piscivores while blacktip sharks consume relatively larger prey (58% >20% of their length). Regardless of maturity state and species, diet overlap is high for species-life stage combinations that are similar in size; however, species-life stages did not show significant overlap in habitat use. One possible interpretation is that prey categories shared by similar-sized species are not limiting, but competition may exist for available habitat resources. More intensive monitoring is needed to fully understand temporal and spatial habitat use patterns among these early life stages. Quantifying the links among these sharks and the links between these sharks and resource species are critical for ecosystem modeling and a key step to a broader approach in fisheries management.

FORAGING ECOLOGY OF THE EARLY LIFE STAGES OF FOUR SHARK SPECIES (*RHIZOPRIONODON TERRAENOVAE, CARCHARHINUS LIMBATUS, CARCHARHINUS ISODON, AND CARCHARHINUS BREVIPINNA)* IN APALACHICOLA BAY, FLORIDA.

by
DANA M. BETHEA

A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the requirements for the
Degree of Master of Science

ZOOLOGY

Raleigh

2003

APPROVED BY:

_________________________	_________________________	_________________________
Peter S. Rand Department of Zoology	Jason A. Osborne Department of Statistics	John K. Carlson External Member

____
Jeffrey A. Buckel
Department of Zoology
Chair of Advisory Committee

BIOGRAPHY

Education

August 2001 – May 2003 North Carolina State University Raleigh, NC
Master of Science, Department of Zoology/Statistics Minor, (Expected) May 2003

August 2000 – May 2001 University of West Florida Pensacola, FL
Master of Science, Department of Biology

August 1995 – August 1999 University of Southern Mississippi Hattiesburg, MS
Bachelor of Science, Department of Biology/General Honors, August 1999

Professional Experience

August – May, 2003 Center for Marine Sciences & Technology Morehead City, NC
NC State Graduate Research Assistant

May – August, 2002 NOAA/National Marine Fisheries Service Panama City, FL
Shark Population Assessment Group Graduate Student Cooperative

January – May, 2002 North Carolina State University Raleigh, NC
NC State Graduate Research Assistant

August – December, 2001 North Carolina State University Raleigh, NC
NC State Graduate Student Teaching Assistant, FW423L – Intro. to Fisheries Management Lab
NC State Graduate Student Teaching Assistant, ZO420 – Intro. to Fisheries Management Lecture
NC State Graduate Student Teaching Assistant, ZO421 – Physiology Lecture

May – August, 2001 NOAA/National Marine Fisheries Service Panama City, FL
Shark Population Assessment Group Graduate Student Cooperative

January – May, 2001 University of West Florida Pensacola, FL
UWF Graduate Student Teaching Assistant, BIO1010L – Intro. to Biology Lab
UWF Graduate Student Teaching Assistant, ZOO4254L – Marine Invertebrate Zoology Lab

August – December, 2000 University of West Florida Pensacola, FL
UWF Graduate Student Teaching Assistant, BIO1010L – Intro. to Biology Lab
UWF Graduate Student Teaching Assistant, ZOO1010L – Intro. to Zoology Lab

August 1999 – August, 2000 NOAA/National Marine Fisheries Service Panama City, FL
Shark Population Assessment Group Intern

Publications

Carlson, J.K., E. Cortés, and D.M. Bethea (2003). Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. Fishery Bulletin 101:281-292.

Professional Activities

"Resource partitioning in four juvenile shark species in Apalachicola Bay, Florida" – Oral presentation at American Fisheries Society 132nd Annual Meeting Baltimore, MD August 18-22, 2002.

“Resource partitioning in four juvenile shark species in Apalachicola Bay, Florida” – Oral presentation at 5th Annual Zoology Graduate Student Symposium North Carolina State University Raleigh, NC March 27, 2002.

“Resource partitioning in four juvenile shark species in Apalachicola Bay, Florida” – Poster presentation at American Fisheries Society 25th Annual Larval Fish Conference Sandy Hook, NJ August 8-13, 2001.

“Population dynamics of the finetooth shark, *Carcharhinus isodon*, in the northeast Gulf of Mexico” – 2001 Annual Meeting of American Society of Ichthyologists and Herpetologists and American Elasmobranch Society July 5-10, 2001.

NOAA/National Marine Fisheries Service Red Snapper/Shark Longline Research Cruise aboard RV Gordon Gunter June 6-20, 2000.

Computer Experience
ArcGIS; Ecological Methodology and EcoSim ecological applications software; Endnote reference database software; Microsoft Access, Microsoft Excel, Microsoft Powerpoint, and Microsoft Word; SAS and Statistica statistical software; SigmaPlot graphing software; Adobe Photoshop 7.0

Awards Received
NC State Student Fisheries Society Travel Award – summer 2002; UWF Graduate Student Scholarly and Creative Activity Grant – spring 2001

Professional Memberships
American Elasmobranch Society; American Fisheries Society; American Society of Ichthyologists and Herpetologists; Ecological Society of America; NC State Zoology Graduate Student Association

ACKNOWLEDGEMENTS

Above all, I wish to thank John Carlson, Enric Cortés, and Ivy Baremore of the Shark Population Assessment Group at the National Marine Fisheries Service in Panama City, FL. Also, a special thank you goes to my major professor, Jeffrey Buckel. Thank you for giving me this opportunity and supporting me through the process. It has been an incredible experience.

I want to thank the 2001 and 2002 Shark Population Assessment Group interns, Lise Damange, Corrin Flora, Lori Hale, Scott Sherril-Mix, Michelle Satterwhite, and Jennifer Smith, for countless hours of assistance in the field and wetlab. It was long, dirty, and sometimes painful work. I appreciate all your help. I also want to thank the reef fish research biologists at the National Marine Fisheries Service in Panama City, FL, especially John Brusher, Linda Lombardi-Carlson, Doug DeVries, and Gary Fitzhugh, for aiding with the identification of finfish, invertebrate, and plant. And, thank you to Bill Blake and Steve Matthews for putting the boat and trailer back together every time we managed to tear it apart.

Thank you to the biology department at the University of West Florida, where this research initiated, and the zoology department at NC State University, where it was completed. Thank you to my committee members, Peter Rand and Jason Osborne, for their valuable comments and suggestions. A special thanks goes to the personnel and staff at the Center for Marine Sciences and Technology in Morehead City, NC, especially Jim Morley and Nate Bachelor, for the friendship and words of advice. Thank you to Troy Tuckey at the Florida Marine Research Institute Apalachicola Field Laboratory in Eastpoint, Florida, for providing additional prey abundance data. And, thank you to Fred Scharf at UNC Wilmington for providing assistance with quantile regression analysis.

I am truly grateful to my mother, father, and sister for loving and believing in me, no matter which road I choose to take. And lastly, I wish to thank my best friend and soul mate, Alex Dutton, for his unfailing love, patience, and understanding. We made it, babe. Now, let's get on with the rest of our life.

TABLE OF CONTENTS

TABLE OF CONTENTS (Cont'd)

LIST OF TABLES

LIST OF TABLES (Cont'd)

LIST OF FIGURES

DIET OVERLAP IN ELASMOBRANCHS: A REVIEW

1.1 INTRODUCTION

Species assemblages are a reflection of the way resources are partitioned within a community. Studies of resource partitioning are important tools for describing the potential for interactions within and between species. Organisms may partition their environment for several reasons, including interspecific competitive interactions and avoidance of predators (Schoener 1974; Crowder 1990).

There are three main resource dimensions along which niche partitioning can occur: trophic, spatial, and temporal. Ross (1986) concluded that trophic differences are likely to play a more important role in determining resource partitioning in teleost fishes. Because of the high trophic levels found for sharks (Cortés 1999), dietary partitioning may not be a driving force in structuring elasmobranch assemblages. Because of their similarities in trophic level, species to species interactions between elasmobranchs are likely to show high diet overlap regardless of taxonomic relation. Although dietary overlap among elasmobranchs may be high overall, differences may exist among the major aquatic habitats of the world. A prediction would be that temperate assemblages would have higher dietary overlap than tropical assemblages because of niche specialization.

This review was initiated prior to the field portion of my thesis research to identify general patterns in elasmobranch feeding ecology that would aid in hypothesis development. No studies have provided a review of the literature on diet overlap of elasmobranchs. Herein, I review the literature on diet overlap in elasmobranchs, and, more specifically: 1) test for biologically significant diet overlap in elasmobranch families, 2) test for differences in dietary overlap values estimated for closely related (within the same family) and distantly related (between different families) species, and 3) test for the effects of biogeographic region on diet overlap.

1.2 METHODS

1.2a Literature Review.

The diet reference database compiled by Dr. Enric Cortés at the National Marine Fisheries Service in Panama City, Florida, was used to identify comparative foraging papers. Additional references were found through Cambridge Scientific Abstracts. The last literature search was performed in March 2001 and studies published since then are not included.

For quantitative diet analysis, two types of studies were targeted: resource partitioning studies in which diet overlap was already calculated, and comparative feeding ecology studies in which diet overlap was not measured. Diet overlap was calculated for all studies (See section 1.2c). Literature was categorized based on biogeographic region where the study took place. Single-species studies were not included in this review because diet overlap calculations between studies would be biased by prey availability.

1.2b Quantitative Diet Analysis.

Quantitative diet compositions were calculated using the following eight food categories (modified from Cortés 1999): teleost fishes, cephalopods, molluscs, crustaceans, other invertebrates, other marine vertebrates, plants, and chondrichthyan fishes (Table 1.1). These categories were assumed to be narrow enough to properly represent the diet composition of each species of elasmobranch (Cortés 1999). When data were available on ontogenetic shifts in diet, separate juvenile and adult diet compositions were calculated and reported. When data on spatial or temporal patterns were available (i.e., diet of a particular species from two different areas reported), these were also used to calculate separate compositions. No qualitative data were used in this review.

The single indices of frequency of occurrence (%O), percent by number (%N), and percent weight (%W) of each prey item are commonly used in dietary analysis studies. Each of these measures gives specific information about the feeding habits of the predator. One of the more widely used compound indices is the index of relative importance (IRI=%O(%N+%W)). It has been argued that this method cancels out bias by incorporating bulk, amount, and occurrence into a single measure (Cortés 1997). To make comparisons among different food types easier, Cortés (1997) suggests that IRI values be expressed as percentages (%IRI). For this review, the %IRI was calculated when possible. Alternatively, single indices (%W or %V, %O, or %N) were used in the calculation of diet overlap values.

1.2c Diet Overlap Comparisons.

There are several measures available to determine niche overlap. The most common measure of niche overlap is Schoener's overlap index, but it is biased under changing number of resources and sample size (Smith and Zaret 1982). Krebs (1999a) argued that Horn's index of overlap has nearly zero bias at all sample sizes. Because of a large range of sample sizes, diet overlap was measured using Horn's index of niche overlap (Horn 1966). Symmetric diet overlap matrices were created using Ecological Methodology v5.1 software (Krebs 1999b). Horn's index of niche overlap is calculated as:

$$R_o = (S\ (p_{ij} + p_{ik})\log(p_{ij} + p_{ik}) - S\ p_{ij} \log p_{ij} - S\ p_{ik} \log p_{ik}) / 2 \log 2$$

where,

R_o = Horn's index of niche overlap for species *j* and *k*

p_{ij} = proportion resource *i* is of the total resources used by species *j*

p_{ik} = proportion resource *i* is of the total resources used by species *k*

Index values range from 0 (no overlap) to 1.0 (complete overlap). Index values equal to or greater than 0.6 are considered "biologically significant" (Pianka 1976).

Family Comparisons. To characterize niche overlap patterns of families of elasmobranchs, diet overlap values of unique pairs of species within the same family were used to calculate a mean family overlap value (MFOV). Based on preliminary data analysis, sample sizes of >4 unique pairings greatly reduced the variance of the sample (Figure 1.1). To reduce variability, only families with >4 unique species pairings were used when calculating a MFOV. Diet overlap estimates for species pairs were compared among the families using an analysis of variance approach. A Tukey HSD was used for *post-hoc* comparisons.

Mean diet overlap for closely related (within the same family) and distantly related (between different families) species were compared. Here, the values used to get an MFOV for a family were compared to diet overlap estimates for pairs of species not in the same family. Because ANOVA assumptions could not be met using transformation and sample sizes were low, a Mann-Whitney U test was used to compare diet overlap estimates for species pairs between the two groups (Zar 1999).

Regional Comparisons. The average annual surface temperature of the area where the study took place determined biogeographic region. Study sites with average surface temperatures from 15-25 ^{o}C were considered tropical/subtropical while those with average surface temperatures below 15 ^{o}C were considered subtropical/temperate (Lalli and Parsons 1999). Biogeographic comparisons tested for differences in diet overlap values between regions (e.g., tropical/subtropical v. subtropical/temperate) by family. Again, only families with >4 unique species pairings were used when calculating a mean regional family overlap value (MRFOV). The two regions were compared using a Mann-Whitney U test (Zar 1999).

1.3 RESULTS

1.3a Literature Review.

A total of 21 studies were reviewed for this paper, including 83 species in 15 families of the subclass Elasmobranchii (Table 1.2). A total of 129 diets were described in 4 resource partitioning studies (Table 1.3) and 17 comparative feeding ecology studies (Table 1.4).

1.3b Quantitative Diet Analysis.

Standardized diet compositions calculated for the species included in this paper can be found in Tables 1.3 and 1.4.

Teleost fish were the most common prey item found in elasmobranch stomachs. Teleost fish were found in 95% of the species and made up more than half of the diet in 65% of the species examined. Crustaceans were found in the stomachs of 81% of the species. Cephalopods were in the diets of 59% of the species, molluscs in 39%, and other invertebrates in 33%. Elasmobranch species constituted some proportion of the diet in 11% of the species. Other marine vertebrates, including sea birds, sea turtles, sea snakes, and marine mammals, were found in the stomachs of 4% of the species. Only 4% of the species stomachs contained plant material.

1.3c Diet Overlap Comparisons

Overlap values were generally high for elasmobranchs. Overlap matrices for resource partitioning studies can be found in Tables 1.5-1.8 and in Tables 1.9-1.25 for comparative feeding ecology studies.

Family Comparisons. MFOVs were compared for 5 families of elasmobranchs (those with >4 unique pairings; Figure 1.2). MFOVs were greater than 0.6 for all 5 families (in order from highest to lowest overlap): Triakidae (0.985), Rajidae (0.859), Carcharhinidae (0.831), Scyliorhinidae (0.776), and Squalidae (0.751). There were differences among the 5 families ($F=2.60$, $df=4,244$, $p=0.037$); however, multiple comparison tests showed no significant difference (Tukey HSD, $p>0.05$).

In all 5 families, diet overlap was higher for within family comparisons than for between family comparisons (Figure 1.3). For 4 of the 5, the difference was significant (Mann-Whitney U, $p<0.05$); there was no significant difference for the within versus between comparison for Squalidae ($U=387$, $p=0.107$; Figure 1.3d).

Regional Comparisons. Regional comparison were limited to two families: Carcharhinidae and Squalidae (Figure 1.4). All mean regional family overlap values (MRFOVs) were higher than 0.6. Though marginal, Carcharhinidae showed significantly higher overlap in the tropical/subtropical region ($U=719$, $p=0.041$; Figure 1.4a). Squalidae showed the hypothesized occurrence of lower dietary overlap in tropical/subtropical regions, but was not significant ($U=139$, $p=0.420$; Figure 1.4b).

1.4 DISCUSSION

In this review, there was little evidence of diet partitioning in elasmobranchs. For two elasmobranch families no generalized differences in diet overlap were found with respect to biogeographic region.

1.4a Family Comparisons.

The majority of species to species comparisons within families of elasmobranchs had high diet overlap. If all elasmobranchs occupy high trophic levels, then high diet overlap within a family would be expected. However, diet specialization was seen at the family level. For example, triakids fed predominately on crustaceans (Talent 1982; Ellis et al. 1996; Gelsleichter et al. 1999); whereas, teleost fish were the most common prey item for carcharhinids (Smale 1991; Stevens and McLoughlin 1991; Salini et al. 1992; Gelsleichter et al. 1999). Like teleosts, exploitation of different resources may have had a role in shaping shark assemblages.

The differences in trophic levels among elasmobranch families are shown by lower diet overlap for comparisons made between species in different families. As in teleosts (Ross 1986), elasmobranchs species that were distantly related showed less resource overlap than species that were closely related. For example, the diet overlap of triakid species and carcharhinid species was low. However, species to species comparisons for triakids and skates (e.g., Rajidae) and triakids and guitarfish (e.g., Rhinobatidae) led to high diet overlap. This is likely due to the fact that these species are all benthic predators (Talent 1982; Ellis et al. 1996). When developing hypotheses in elasmobranch resource partitioning studies, taxonomic relatedness and foraging habitat should be taken into consideration. For example, I would predict higher diet overlap among species in the field portion of my thesis because all are within the same family.

Species to species comparisons within other families may show greater diet separation. Diet overlap was examined for species to species comparisons in only 5 out of the 42 described families of elasmobranchs. Families not examined here may show different trends in resource partitioning. For example, species in Sphyrnidae have very different diets. *Sphyrna tiburo* in the eastern Gulf of Mexico feed almost entirely on crustaceans (Cortés et al. 1996), *S. lewini* in the central Pacific take a mix of teleosts and crustaceans (Clarke 1971), *S. tudens* in the Caribbean take mostly crustaceans supplemented by teleosts (Castro 1989), and *S. mokarran* in the southwest Indian prey almost exclusively on elasmobranchs (Cliff 1995). Additionally, *S. zygaena* in the southwest Indian show an ontogenetic shift in diet, taking mostly cephalopods as juveniles and teleost fish as adults (Smale 1991). Given this, the MFOV for Sphyrnidae would likely have been low.

1.4b Regional Comparisons.

Pooling at the broad level of region also led to high diet overlap values. Additionally, significant differences in diet overlap did not exist between biogeographic regions for Carcharhinidae and Squalidae. This agrees with what Ross (1986) found for trophic separation of teleosts in seven global habitats. Although the difference was not significant, Squalidae diet overlap was higher in subtropical/temperate regions compared to tropical/subtropical regions. This may result from niche specialization in the tropics for squalids.

1.4c Limits to the Literature.

This review was limited by several factors. Compared to the teleost literature, there are few quantitative studies within the elasmobranch literature that examine the diet of more than one species. Ross (1986) reviewed 233 teleost resource partitioning studies, an order of magnitude higher than what was included in this review. In addition, the prey categories used in this review may be too broad to properly represent elasmobranch diets. Over half of the studies (11 out of 21) reported unidentifiable fish comprising >50% of the diet of at least one study species. Categorizing prey simply as "teleost fish" could lead to overestimating diet overlap as some elasmobranch species may show specialization with this category (e.g., epibenthic teleosts vs. pelagic teleosts). The regional categories may also be too broad. For example, *Sphyrna tiburo* in the southern Gulf of Mexico feed mostly on cephalopods (Parsons 1987) while those in the eastern Gulf of Mexico feed on crustaceans (Cortés et al. 1996). The high diet overlap values reported here may also be biased by low sample size of stomachs; the median number of stomachs examined in this review was 43 and the average was 109. For example, Snelson and Williams (1981) reported the diets of Atlantic stingray (*Dasyatis americana*) and lemon sharks (*Negaprion brevirostris*) from the east coast of central Florida based on a sample size of 8 and 10, respectively.

1.4d Teleosts versus Elasmobranchs.

Consistently high diet overlap values such as the ones reported here are not seen in teleosts possibly because the teleost literature is more thorough (e.g., greater sample sizes and finer resource dimensions). There are 350 known species of sharks, and 450 known species of skates and rays. In contrast, there are 23,600 teleosts. Elasmobranchs are generally limited in their distribution compared to teleosts. Most elasmobranchs are found in relatively shallow temperate and particularly subtropical and tropical marine waters (Compagno 1984); whereas, teleost fish can be found in nearly all aquatic habitats (Helfman et al. 1999). All elasmobranchs are carnivorous, taking live prey or scavenging recently dead prey. Teleosts use plant material in all of its forms, including phytoplankton, cyanobacteria, algae, detritus, and vascular plants and their seeds (Wootton 1999, Helfman et al. 1999). Teleosts are the most diversified taxon of all vertebrates, having radiated into more niches than all of the other vertebrates combined (Helfman et al. 1999). Elasmobranch species take similar resources, but competition for those resources may not be as strong or may be nonexistent as compared to how competition influenced the evolution of teleosts.

Table 1.1. Prey categories used to calculate standardized diet compositions and diet overlap. Modified from Cortés (1999).

Code	Species Group
FISH	Teleost fishes (demersal and pelagic)
CEPH	Cephalopods (squids and octopuses)
MOL	Molluscs (all molluscs, excluding cephalopods)
CRUST	Crustaceans (shrimp, crabs, prawns, and lobsters)
INV	Other invertebrates (all invertebrates except molluscs and crustaceans, including zooplankton)
VERT	Other vertebrates (seabirds, sea turtles, sea snakes, and marine mammals)
PL	Plants (marine plants and algae)
CHOND	Chondrichthyan fishes (sharks, skates, rays, and chimaerids)

Table 1.2. Orders and families of elasmobranchs examined in this study.

	Order	Family
Sharks	Carcharhiniformes	Carcharhinidae
		Triakidae
		Hemigaleidae
		Sphyrnidae
		Scyliorhinidae
		Odontaspididae
	Orectolobiformes	Ginglymostomidae
		Hemiscyllidae
	Squatiniformes	Squatinidae
	Squaliformes	Squalidae
Skates & Rays	Myliobatiformes	Dasyatidae
		Myliobatidae
	Rajiformes	Rajidae
		Urolophidae
	Rhinobatiformes	Rhinobatidae

Table 1.3. Diet compositions of elasmobranchs from resource partitioning studies. MED = Mediterranean, NEA = northeast Atlantic, NWA = northwest Atlantic, SWP = southwest Pacific. Numbers (N) are presented as J = juvenile and A = adult. Habitat is presented as MS = middle slope and US = upper slope. %IRI = index of relative importance on a percent basis. See Table 1.1 for prey category definitions.

Study & Location	Family	Species	N (J)	N (A)	Habitat	Method	FISH	CEPH	MOL	CRUST	INV	VERT	PL	CHOND
McEachran et al. (1976)	Rajidae	*Raja erinacea*		785		%IRI	0.86	0	0.56	50.09	48.49	0	0	0
Subtrop/temperate	Rajidae	*R. ocellata*		441		%IRI	12.15	0	4.29	18.67	64.89	0	0	0
	Rajidae	*R. radiata*		313		%IRI	14.69	0	6.08	26.45	52.78	0	0	0
	Rajidae	*R. senta*		107		%IRI	0.74	0	25.67	55.45	18.14	0	0	0
Carrasson et al. (1992)	Squalidae	*Centroscymnus coelolepis*		17	MS	%IRI	15.60	77.00	0	0	2.80	0	0	0
Trop/subtropical	Squalidae	*C. coelolepis*	69		MS	%IRI	5.40	79.33	0	15.27	0	0	0	0
	Scyliorhinidae	*Galeus melastomus*		19	US	%IRI	25.02	19.36	0.10	54.92	0.60	0	0	0
	Scyliorhinidae	*G. melastomus*	41		US	%IRI	7.47	0.20	0	91.32	0	0	0	0
	Scyliorhinidae	*G. melastomus*		18	MS	%IRI	27.69	30.82	0	40.89	0.60	0	0	0
	Scyliorhinidae	*G. melastomus*	21		MS	%IRI	52.19	12.18	0	35.43	0.20	0	0	0
Ellis et al. (1996)	Triakidae	*Mustelus asterias*		46		%IRI	1.86	0	0	97.40	0.74	0	0	0
Subtrop/temperate	Triakidae	*Galeorhinis galeus*		46		%IRI	77.70	18.92	0	0	3.38	0	0	0
	Rajidae	*Raja brachyura*		31		%IRI	56.83	0	0	41.73	1.44	0	0	0
	Rajidae	*R. clavata*		601		%IRI	7.30	0.69	9.51	78.89	3.53	0	0	0
	Rajidae	*R. montagui*		197		%IRI	10.15	0	4.29	73.60	11.96	0	0	0
	Rajidae	*R. naevus*		103		%IRI	45.09	0	5.21	44.50	5.20	0	0	0
	Scyliorhinidae	*Scyliorhinus canicula*		1206		%IRI	15.95	2.90	11.80	51.58	17.77	0	0	0
	Scyliorhinidae	*S. stellaris*		86		%IRI	14.98	27.14	2.82	53.04	0.40	0	0	1.62
	Squalidae	*Squalus acanthias*		837		%IRI	80.79	1.86	0.93	11.88	4.54	0	0	0
	Squatinidae	*Squatina squatina*		19		%IRI	93.75	2.08	0	4.17	0	0	0	0
Platell et al. (1998)	Urolophidae	*Trygonoptera mucosa*		146		%IRI	0	0	0.02	5.83	94.12	0	0.03	0
Subtrop/temperate	Urolophidae	*T. personata*		155		%IRI	0	0	0.01	55.25	44.74	0	0	0
	Urolophidae	*Urolophus lobatus*		192		%IRI	0.56	0	0	95.37	4.07	0	0	0
	Urolophidae	*U. paucimaculatus*		197		%IRI	0	0.02	0.04	93.04	6.90	0	0	0

Table 1.4. Diet compositions of elasmobranchs from comparative feeding ecology studies. CIO = central Indian, CP = central Pacific, MED = Mediterranean, NEP = northeast Pacific, NWA = northwest Atlantic, NWP = northwest Pacific, SEA = southeast Atlantic, SWIO = southwest Indian, SWP = southwest Pacific. Numbers (N) are presented as J = juvenile and A = adult. Habitat is presented as N = nearshore, E = estuary, and O = offshore. %IRI = index of relative importance on a percent basis, %N = percent number, %W = percent weight, %O = percent frequency of occurrence. See Table 1.1 for prey category definitions.

Study & Location	Family	Species	N (J)	N (A)	Habitat	Method	FISH	CEPH	MOL	CRUST	INV	VERT	PL	CHOND
Macpherson (1980)	Squalidae	*Dalatias licha*		31		%W	63.88	5.51	0	15.46	0	0	0	15.15
Trop/subtropical	Squalidae	*Etmopterus spinax*		353		%W	54.05	23.62	0	17.02	5.31	0	0	0
	Scyliorhinidae	*Galeus melastomus*		1559		%W	52.67	0	0	19.44	27.89	0	0	0
Snelson & Williams	Dasyatidae	*Dasyatis americana*		8		%N	40.00	0	0	60.00	0	0	0	0
(1981) Trop/subtropical	Carcharhinidae	*Negaprion brevirostris*		10		%N	78.60	0	0	14.30	0	0	0	7.10
Talent (1982)	Triakidae	*Mustelus californicus*		35		%IRI	0.19	0	0	99.81	0	0	0	0
Trop/subtropical	Triakidae	*M. californicus*	14			%IRI	0	0	0	100	0	0	0	0
	Triakidae	*M. henlei*		11		%IRI	5.92	0.26	0	93.82	0	0	0	0
	Triakidae	*M. henlei*	8			%IRI	0	0	0	100	0	0	0	0
	Myliobatidae	*Myliobatis californica*		101		%IRI	2.57	0	49.82	4.24	43.47	0	0	0
	Myliobatidae	*M. californica*	181			%IRI	0.10	0	98.87	0.76	0.27	0	0	0
	Rhinobatidae	*Rhinobatos productus*		72		%IRI	2.86	0	1.02	96.09	0.03	0	0	0
	Rhinobatidae	*R. productus*	6			%IRI	0.75	0	0	99.25	0	0	0	0
Mauchline	Squalidae	*Centroscymnus ceololepis*		18		%O	45.46	36.36	0	0	18.18	0	0	0
& Gordon (1983)	Squalidae	*C. crepidater*		23		%O	31.55	57.96	0	10.49	0	0	0	0
Subtrop/temperate	Squalidae	*Deania calcea*		65		%N	86.95	13.05	0	0	0	0	0	0
	Squalidae	*D. calcea*	49			%N	84.70	11.50	0	3.80	0	0	0	0
	Squalidae	*Etmopterus spinax*		39		%N	39.32	21.46	0	35.63	3.59	0	0	0
	Squalidae	*E. spinax*	107			%N	62.66	4.99	0	4.70	27.65	0	0	0
DeCrosta et al. (1984)	Carcharhinidae	*Carcharhinus amblyrhynchos*		95		%O	72.44	23.38	0	4.18	0	0	0	0
Trop/subtropical	Carcharhinidae	*C. galapagensis*		65		%O	61.07	38.93	0	0	0	0	0	0
	Carcharhinidae	*Galeocerdo cuvier*		35		%O	18.21	10.00	0	13.35	0	55.23	0	3.21
Stevens (1984)	Carcharhinidae	*Carcharhinus albimarginatus*		8		%O	83.33	16.67	0	0	0	0	0	0
Subtrop/temperate	Carcharhinidae	*C. falciformes*		7		%O	100	0	0	0	0	0	0	0
	Carcharhinidae	*C. melanopterus*		42		%O	46.88	3.15	6.24	12.48	9.39	0	21.86	0
	Carcharhinidae	*C. wheeleri*		8		%O	50.00	50.00	0	0	0	0	0	0
	Ginglymostomatidae	*Nebrius ferrugineus*		6		%O	29.99	29.99	10.02	0	0	0	0	0
	Carcharhinidae	*Negaprion acutidens*		24		%O	71.52	7.09	14.30	7.09	0	0	0	0
Baba et al. (1987)	Squalidae	*Centroscyllium ritteri*		72		%N	1.49	0.59	0.09	97.83	0	0	0	0
Trop/subtropical	Squalidae	*Etmopterus lucifer*		230		%N	12.36	82.40	0	5.12	0.12	0	0	0
	Squalidae	*E. unicolor*		84		%N	37.40	44.20	0	17.60	0.80	0	0	0

Table 1.4 (Cont'd). Diet compositions of elasmobranchs from comparative feeding ecology studies.

Study & Location	Family	Species	N (J)	N (A)	Habitat	Method	FISH	CEPH	MOL	CRUST	INV	VERT	PL	CHOND
Euzen (1987)	Hemiscyllidae	*Chiloscyllium griseum*		89		%N	30.30	2.30	7.80	33.50	26.10	0	0	0
Subtrop/temperate	Dasyatidae	*Dasyatis gerradi*		32		%N	0	0	0	98.70	1.30	0	0	0
	Dasyatidae	*D. zugei*		14		%N	0.50	0	94.30	4.90	0.30	0	0	0
	Dasyatidae	*Himantura uarnak*		15		%N	0.90	0	0	99.10	0	0	0	0
Cross (1988)	Scyliorhinidae	*Apristurus brunneus*		73		%IRI	9.90	2.29	2.52	85.29	0	0	0	0
Trop/subtropical	Scyliorhinidae	*Parmaturus xaniurus*		70		%IRI	6.73	0.12	0	93.15	0	0	0	0
Salini et al. (1990)	Carcharhinidae	*Carcharhinus amblyrhynchos*		30		%W	86.50	0	0.23	13.27	0	0	0	0
Subtrop/temperate	Carcharhinidae	*C. cautus*		20		%W	97.59	0	1.61	0.80	0	0	0	0
	Carcharhinidae	*C. dussumieri*		40		%W	64.86	0	0.30	33.83	0.60	0	0.41	0
	Carcharhinidae	*C. limbatus*		23		%W	96.30	0	0.50	3.20	0	0	0	0
	Dasyatidae	*Dasyatis sephen*		15		%W	12.53	0	87.47	0	0	0	0	0
	Carcharhinidae	*Negaprion acutidens*		32		%W	99.70	0	0	0.20	0	0	0.10	0
	Carcharhinidae	*Rhizoprionodon acutus*		130		%W	90.88	0	0	8.62	0.50	0	0	0
Smale (1991)	Carcharhinidae	*Carcharhinus brachyurus*		28		%IRI	46.60	44.70	0	0	0	0	0	8.70
Subtrop/temperate	Carcharhinidae	*C. brachyurus*	119			%IRI	23.70	76.10	0	0.02	0	0.04	0	0.07
	Carcharhinidae	*Carcharhinus obscurus*		7		%IRI	13.50	73.50	0	0	0	0	0	13.00
	Carcharhinidae	*C. obscurus*	67			%IRI	28.90	70.50	0	0.04	0	0	0	0.53
	Sphyrnidae	*Sphyrna zygaena*		5		%IRI	90.20	9.80	0	0	0	0	0	0.00
	Sphyrnidae	*S. zygaena*	144			%IRI	8.70	91.20	0	0	0	0	0	0.10
Stevens	Carcharhinidae	*Carcharhinus amblyrhynchoides*		186		%O	89.95	3.84	0	6.21	0	0	0	0
& McLoughlin	Carcharhinidae	*C. amboinensis*		31		%O	71.44	9.52	0	19.04	0	0	0	0
(1991)	Carcharhinidae	*C. brevipinna*		111		%O	89.90	8.12	0	2.08	0	0	0	0
Trop/subtropical	Carcharhinidae	*C. dussumieri*		526		%O	61.90	16.82	0	21.28	0	0	0	0
	Carcharhinidae	*C. macloti*		216		%O	94.50	4.40	0	1.10	0	0	0	0
	Carcharhinidae	*C. pluembeus*		181		%O	74.20	18.36	0.85	6.59	0	0	0	0
	Carcharhinidae	*Galeocerdo cuvier*		98		%O	39.01	9.77	1.63	9.77	0	38.92	0	0
	Hemigaleidae	*Hemigaleus microstoma*		446		%O	1.17	95.63	0.29	2.91	0	0	0	0
	Hemigaleidae	*Hemipristis elongatus*		111		%O	42.85	57.15	0	0	0	0	0	0
	Carcharhinidae	*Loxodon macrorhinus*		258		%O	48.76	12.01	0.64	38.59	0	0	0	0
	Carcharhinidae	*Rhizoprionodon acutus*		315		%O	75.36	15.27	0.97	8.40	0	0	0	0
	Carcharhinidae	*R. taylori*		68		%O	68.22	2.25	0	29.53	0	0	0	0
Yano (1991)	Squalidae	*Deania calcea*		61		%IRI	57.08	42.92	0	0	0	0	0	0
Subtrop/temperate	Squalidae	*D. profundorum*		15		%IRI	80.38	19.62	0	0	0	0	0	0

Table 1.4 (Cont'd). Diet compositions of elasmobranchs from comparative feeding ecology studies.

Study & Location	Family	Species	N (A)	Habitat	Method	FISH	CEPH	MOL	CRUST	INV	VERT	PL	CHOND
Ebert et al. (1992)	Squalidae	*Centrophorus squamosus*	21		%IRI	38.50	60.80	0	0.70	0	0	0	0
Subtrop/temperate	Squalidae	*Centroscyllium fabricii*	148		%IRI	20.70	1.70	0	77.60	0	0	0	0
	Squalidae	*Centroscymnus coelolepis*	93		%IRI	7.48	88.39	0.10	0.06	0	3.97	0	0
	Squalidae	*Deania calcea*	81		%IRI	96.46	3.50	0	0.04	0	0	0	0
	Squalidae	*D. profundorum*	78		%IRI	82.20	17.80	0	0	0	0	0	0
	Squalidae	*Etmopterus brachyurous*	81		%IRI	77.73	17.11	0	5.12	0.04	0	0	0
	Squalidae	*E. compagnoi*	26		%IRI	46.90	46.40	0	6.70	0	0	0	0
	Squalidae	*E. granulosus*	159		%IRI	18.30	60.10	0	21.60	0	0	0	0
	Squalidae	*Squalus acanthias*	176		%IRI	92.82	6.33	0	0.80	0.03	0	0	0
	Squalidae	*S. megalops*	88		%IRI	77.40	20.10	0	1.80	0.70	0	0	0
	Squalidae	*S. mitsukurii*	271		%IRI	77.23	22.74	0	0.03	0	0	0	0
Salini et al. (1992)	Carcharhinidae	*Carcharhinus amblyrhynchoides*	55	N	%W	99.00	0	0	1.00	0	0	0	0
Trop/subtropical	Carcharhinidae	*C. amblyrhynchos*	30	E	%W	86.50	0	0.23	13.27	0	0	0	0
	Carcharhinidae	*C. amblyrhynchos*	62	O	%W	64.30	0	11.60	24.10	0	0	0	0
	Carcharhinidae	*C. cautus*	20	E	%W	97.10	0	1.60	1.30	0	0	0	0
	Carcharhinidae	*C. cautus*	3	N	%W	95.98	0	4.02	0	0	0	0	0
	Carcharhinidae	*C. cautus*	21	O	%W	100	0	0	0	0	0	0	0
	Carcharhinidae	*C. dussumieri*	40	E	%W	65.52	0	0.03	34.18	0	0	0	0
	Carcharhinidae	*C. dussumieri*	1	N	%W	0	0	0	100	0	0	0	0
	Carcharhinidae	*C. dussumieri*	110	O	%W	53.37	0	7.34	39.29	0	0	0	0
	Carcharhinidae	*C. melanopterus*	6	O	%W	100	0	0	0	0	0	0	0
	Carcharhinidae	*C. sorrah*	3	E	%W	86.33	0	0	13.67	0	0	0	0
	Carcharhinidae	*C. sorrah*	16	O	%W	85.00	0	11.60	3.40	0	0	0	0
	Carcharhinidae	*C. tilstoni*	23	E	%W	96.40	0	0.50	3.10	0	0	0	0
	Carcharhinidae	*C. tilstoni*	16	N	%W	100	0	0	0	0	0	0	0
	Carcharhinidae	*C. tilstoni*	21	O	%W	100	0	0	0	0	0	0	0
	Hemigaleidae	*Hemigaleus microstoma*	16	O	%W	0	0	94.79	5.21	0	0	0	0
	Hemigaleidae	*Hemipristis elongatus*	3	O	%W	97.59	0	0	2.41	0	0	0	0
	Carcharhinidae	*Negaprion acutidens*	32	E	%W	99.80	0	0	0.20	0	0	0	0
	Carcharhinidae	*N. acutidens*	3	O	%W	0	0	100	0	0	0	0	0
	Carcharhinidae	*Rhizoprionodon acutus*	130	E	%W	91.34	0	0	8.66	0	0	0	0
	Carcharhinidae	*R. acutus*	77	N	%W	61.26	0	18.18	20.56	0	0	0	0
	Carcharhinidae	*R. acutus*	142	O	%W	79.18	0	7.51	13.31	0	0	0	0

Table 1.4 (Cont'd). Diet compositions of elasmobranchs from comparative feeding ecology studies.

Study & Location	Family	Species	N (A)	Habitat	Method	FISH	CEPH	MOL	CRUST	INV	VERT	PL	CHOND
Ebert et al. (1996)	Scyliorhinidae	*Apristurus microps*	88		%IRI	21.50	23.50	0	53.30	0.80	0	0	0.90
Subtrop/temperate	Scyliorhinidae	*A. saldanha*	11		%IRI	99.40	0.60	0	0	0	0	0	0
	Scyliorhinidae	*Galeus polli*	120		%IRI	94.70	1.80	0	3.50	0	0	0	0
	Scyliorhinidae	*Holohalaelurus regain*	383		%IRI	68.40	22.10	0	9.50	0	0	0	0
	Scyliorhinidae	*Scyliorhinus capensis*	140		%IRI	69.00	2.00	0	25.80	3.20	0	0	0
Gelsleichter et al. (1999)	Carcharhinidae	*Carcharhinus obscurus*	153		%IRI	85.42	0.06	0.03	3.22	0.10	0.05	0	11.12
Trop/subtropical	Triakidae	*Mustelus canis*	64		%IRI	3.27	0.10	8.18	87.76	0.69	0	0	0
	Odontaspididae	*Odontaspis taurus*	54		%IRI	64.98	0.07	0	0.02	0	0	0.02	34.91
	Carcharhinidae	*Rhizoprionodon terraenovae*	208		%IRI	64.00	1.27	0.09	34.52	0	0	0	0.12

Table 1.5. Symmetrical diet overlap matrix for species from McEachran et al. (1976). Diet compositions can be found in Table 1.3.

	R. erinacea	*R. clavata*	*R. radiata*
R. clavata	0.884	*	
R. radiata	0.889	0.989	*
R. sentra	0.836	0.725	0.796

Table 1.6. Symmetrical diet overlap matrices for species from Carrasson et al. (1992) on the (a) middle slope (984-2251 m) and (b) upper slope (371-667 m). J = juvenile, A = adult. Diet compositions can be found in Table 1.3.

(a)	*C. coelolepis (A)*	*C. coelolepis (J)*	*G. melastomus (J)*
C. coelolepis (J)	0.868	*	
Galeus melastomus (A)	0.681	0.814	*
G. melastomus (J)	0.526	0.612	0.940

(b)	*G. melastomus (A)*
G. melastomus (J)	0.833

Table 1.7. Symmetrical diet overlap matrix for species from Platell et al (1998). Diet compositions can be found in Table 1.3.

	T. mucosa	*T. personata*	*U. lobatus*
T. personata	0.768	*	
Urolophus lobatus	0.283	0.815	*
U. paucimaculatus	0.342	0.853	0.994

Table 1.8. Symmetrical diet overlap matrix for species from Ellis et al (1996). Diet compositions can be found in Table 1.3.

	M. asterias	*G. galeus*	*R. brachyura*	*R. clavata*	*R. montagui*	*R. naevus*	*S. canicula*	*S. stellaris*	*S. acanthias*
Galeorhinis galeus	0.078	*							
Raja brachyura	0.683	0.682	*						
R. clavata	0.922	0.236	0.747	*					
R. montagui	0.901	0.285	0.783	0.969	*				
R. naevus	0.709	0.624	0.961	0.846	0.878	*			
Scyliorhinus canicula	0.759	0.437	0.776	0.924	0.950	0.896	*		
S. stellaris	0.752	0.530	0.741	0.824	0.791	0.776	0.812	*	
Squalus acanthias	0.351	0.876	0.901	0.509	0.566	0.869	0.661	0.597	*
Squatina squatina	0.192	0.901	0.821	0.320	0.357	0.734	0.459	0.476	0.955

Table 1.9. Symmetrical diet overlap matrix for species from Macpherson (1980). Diet compositions can be found in Table 1.4.

	D. licha	*E. spinax*
Etmopterus spinax	0.851	*
Galeus melastomus	0.752	0.821

Table 1.10. Symmetrical diet overlap matrix for species from Snelson and Williams (1981). Diet compositions can be found in Table 1.4.

	D. americana
Negaprion brevirostris	0.839

Table 1.11. Symmetrical diet overlap matrix for species from Talent (1982). J = juvenile, A = adult. Diet compositions can be found in Table 1.4.

	M. californicus (A)	*M. californicus (J)*	*M. henlei (A)*	*M. henlei (J)*	*M. californica (A)*	*M. california (J)*	*R. productus (A)*
M. californicus (J)	0.999	*					
M. henlei (A)	0.974	0.968	*				
M. henlei (J)	0.999	1	0.968	*			
Myliobatis californica (A)	0.133	0.128	0.164	0.128	*		
M. california (J)	0.034	0.032	0.036	0.032	0.714	*	
Rhinobatos productus (A)	0.984	0.980	0.989	0.980	0.192	0.077	*
R. productus (J)	0.999	0.996	0.982	0.996	0.140	0.034	0.990

Table 1.12. Symmetrical diet overlap matrix for species from Mauchline and Gordon (1983). J = juvenile, A = adult. Diet compositions can be found in Table 1.4.

	C. ceololepis	*C. crepidater*	*D. calcea (A)*	*D. calcea (J)*	*E. spinax (A)*
C. crepidater	0.830	*			
Deania calcea (A)	0.820	0.740	*		
D. calcea (J)	0.798	0.775	0.981	*	
Etmopterus spinax (A)	0.768	0.864	0.730	0.803	*
E. spinax (J)	0.863	0.627	0.811	0.840	0.768

Table 1.13. Symmetrical diet overlap matrix for species from DeCrosta et al. (1984). Diet compositions can be found in Table 1.4.

	C. amblyrhynchos	*C. galapagensis*
C. galapagensis	0.961	*
Galeocerdo cuvier	0.544	0.487

Table 1.14. Symmetrical diet overlap matrix for species from Stevens (1984). Diet compositions can be found in Table 1.4.

	C. albimarginatus	*C. falciformes*	*C. melanopterus*	*C. wheeleri*	*N. ferrugineus*
C. falciformes	0.911	*			
C. melanopterus	0.676	0.664	*		
C. wheeleri	0.907	0.689	0.570	*	
Nebrius ferrugineus	0.762	0.506	0.539	0.928	*
Negaprion acutidens	0.875	0.840	0.802	0.748	0.727

Table 1.15. Symmetrical diet overlap matrix for species from Baba et al. (1987). Diet compositions can be found in Table 1.4.

	C. ritteri	*E. lucifer*
Etmopterus lucifer	0.206	*
E. unicolor	0.424	0.882

Table 1.16. Symmetrical diet overlap matrix for species from Euzen (1987). Diet compositions can be found in Table 1.4.

	C. griseum	*D. gerradi*	*D. zugei*
Dasyatis gerradi	0.578	*	
D. zugei	0.335	0.148	*
Himantura uarnak	0.570	0.989	0.149

Table 1.17. Symmetrical diet overlap matrix for species from Cross (1988). Diet compositions can be found in Table 1.4.

	A. brunneus
Parmaturus xaniurus	0.975

Table 1.18. Symmetrical diet overlap matrix for species from Salini (1990). Diet compositions can be found in Table 1.4.

	C. amblyrhynchos	*C. cautus*	*C. dussumieri*	*C. limbatus*	*D. sephen*	*N. acutidens*
C. cautus	0.945	*				
C. dussumieri	0.950	0.822	*			
C. limbatus	0.974	0.922	0.866	*		
Dasyatis sephen	0.283	0.340	0.262	0.303	*	
Negaprion acutidens	0.935	0.990	0.807	0.985	0.283	*
Rhizoprionodon acutus	0.992	0.961	0.923	0.985	0.275	0.958

Table 1.19. Symmetrical diet overlap matrix for species from Smale (1991). J = juvenile, A = adult. Diet compositions can be found in Table 1.4.

	C. brachyurus	*C. brachyurus*	*C. obscurus (A)*	*C. obscurus (J)*	*S. zygaena (A)*
Carcharhinus brachyurus	*				
C. brachyurus	0.901	*			
C. obscurus (A)	0.902	0.927	*		
C. obscurus (J)	0.932	0.996	0.927	*	
Sphyrna zygaena (A)	0.818	0.640	0.507	0.691	*
S. zygaena (J)	0.795	0.968	0.924	0.946	0.445

Table 1.20. Symmetrical diet overlap matrix for species from Stevens and McLoughlin (1991). Diet compositions can be found in Table 1.4.

	C. amblyrhynchoides	*C. amboinensis*	*C. brevipinna*	*C. dussumieri*	*C. macloti*	*C. pluembeus*	*G. cuvier*	*H. microstoma*	*H. elongates*	*L. macrorhinus*	*R. acutus*
C. amboinensis	0.959	*									
C. dussumieri	0.987	0.935	*								
C. brevipinna	0.918	0.990	0.904	*							
C. macloti	0.985	0.912	0.994	0.867	*						
C. pluembeus	0.953	0.963	0.967	0.962	0.938	*					
Galeocerdo cuvier	0.706	0.747	0.698	0.751	0.671	0.748	*				
Hemigaleus microstoma	0.204	0.336	0.275	0.448	0.193	0.453	0.328	*			
Hemipristis elongates	0.706	0.743	0.779	0.797	0.729	0.857	0.609	0.768	*		
Loxodon macrorhinus	0.842	0.956	0.805	0.970	0.768	0.885	0.728	0.392	0.687	*	
Rhizoprionodon acutus	0.963	0.975	0.968	0.969	0.941	0.998	0.753	0.416	0.827	0.902	*
R. taylori	0.928	0.974	0.874	0.949	0.863	0.886	0.708	0.191	0.603	0.954	0.910

Table 1.21. Symmetrical diet overlap matrix for species from Yano (1991). Diet compositions can be found in Table 1.4.

	D. profundorum
D. profundorum	0.954

Table 1.22. Symmetrical diet overlap matrix for species from Ebert et al. (1992). Diet compositions can be found in Table 1.4.

	C. squamosus	*C. fabricii*	*C. ceololepis*	*D. calcea*	*D. profundorum*	*E. brachyurous*	*E. compagnoi*	*E. granulosus*	*S. acanthias*	*S. megalops*
Centroscyllium fabricii	0.362	*								
Centroscymnus ceololepis	0.876	0.182	*							
Deania calcea	0.684	0.435	0.302	*						
D. profundorum	0.848	0.414	0.532	0.956	*					
Etmopterus brachyurous	0.842	0.544	0.521	0.938	0.972	*				
E. compagnoi	0.970	0.522	0.786	0.755	0.884	0.919	*			
E. granulosus	0.884	0.626	0.838	0.475	0.646	0.725	0.917	*		
Squalus acanthias	0.732	0.451	0.361	0.996	0.973	0.963	0.801	0.534	*	
S. megalops	0.869	0.470	0.560	0.939	0.986	0.993	0.920	0.708	0.963	*
S. mitsukurii	0.885	0.411	0.589	0.934	0.997	0.971	0.911	0.689	0.956	0.988

Table 1.23. Symmetrical diet overlap matrix for species from Salini et al. (1992) in (a) estuary, (b) nearshore, and (c) offshore habitats. Diet compositions can be found in Table 1.4.

(a) estuary	*C. amblyrhynchos*	*C. cautus*	*C. dussumieri*	*C. sorrah*	*C. tilstoni*	*N. acutidens*
C. cautus	0.951	*				
C. dussumieri	0.955	0.833	*			
C. sorrah	0.999	0.946	0.955	*		
C. tilstoni	0.973	0.995	0.869	0.970	*	
Negaprion acutidens	0.936	0.992	0.810	0.935	0.986	*
Rhizoprionodon acutus	0.995	0.969	0.924	0.995	0.987	0.961

(b) nearshore	*C. amblyrhynchoides*	*C. cautus*	*C. dussumieri*	*C. sorrah*
C. cautus	0.975	*		
C. dussumieri	0.040	0	*	
C. tilstoni	0.995	0.980	0	*
Rhizoprionodon acutus	0.798	0.834	0.397	0.772

Table 1.23 (Cont'd). Symmetrical diet overlap matrix for species from Salini et al. (1992) in the (a) estuary, (b) nearshore, and (c) offshore. Diet compositions can be found in Table 1.4.

(c) offshore	*C. amblyrhynchos*	*C. cautus*	*C. dussumieri*	*C. melanopterus*	*C. sorrah*	*C. tilstoni*	*H. microstoma*	*H. elongates*	*R. acutus*
C. cautus	0.793	*							
C. dussumieri	0.980	0.715	*						
C. melanopterus	0.793	1	0.715	*					
C. sorrah	0.926	0.921	0.842	0.921	*				
C. tilstoni	0.793	1	0.715	1	0.921	*			
Hemigaleus microstoma	0.363	0	0.306	0	0.306	0	*		
Hemipristis elongates	0.843	0.988	0.774	0.988	0.938	0.988	0.034	*	
Negaprion acutidens	0.269	0	0.193	0	0.269	0	0.973	0	*
Rhizoprionodon acutus	0.980	0.887	0.933	0.887	0.973	0.887	0.273	0.926	0.196

Table 1.24. Symmetrical diet overlap matrix for species from Ebert et al. (1996). Diet compositions can be found in Table 1.4.

	A. microps	*A. saldanha*	*G. polli*	*H. regain*
A. saldanha	0.431	*		
Galeus polli	0.546	0.980	*	
Holohalaelurus regain	0.781	0.838	0.901	*
Scyliorhinus capensis	0.787	0.832	0.900	0.885

Table 1.25. Symmetrical diet overlap matrix for species from Gelsleichter et al. (1999). Diet compositions can be found in Table 1.4.

	C. obscurus	*M. canis*	*O. taurus*
Mustelus canis	0.206	*	
Odontaspis taurus	0.927	0.097	*
Rhizoprionodon terraenovae	0.822	0.625	0.654

Figure 1.1. Variance plotted against numbers of unique species pairings used to get a mean.

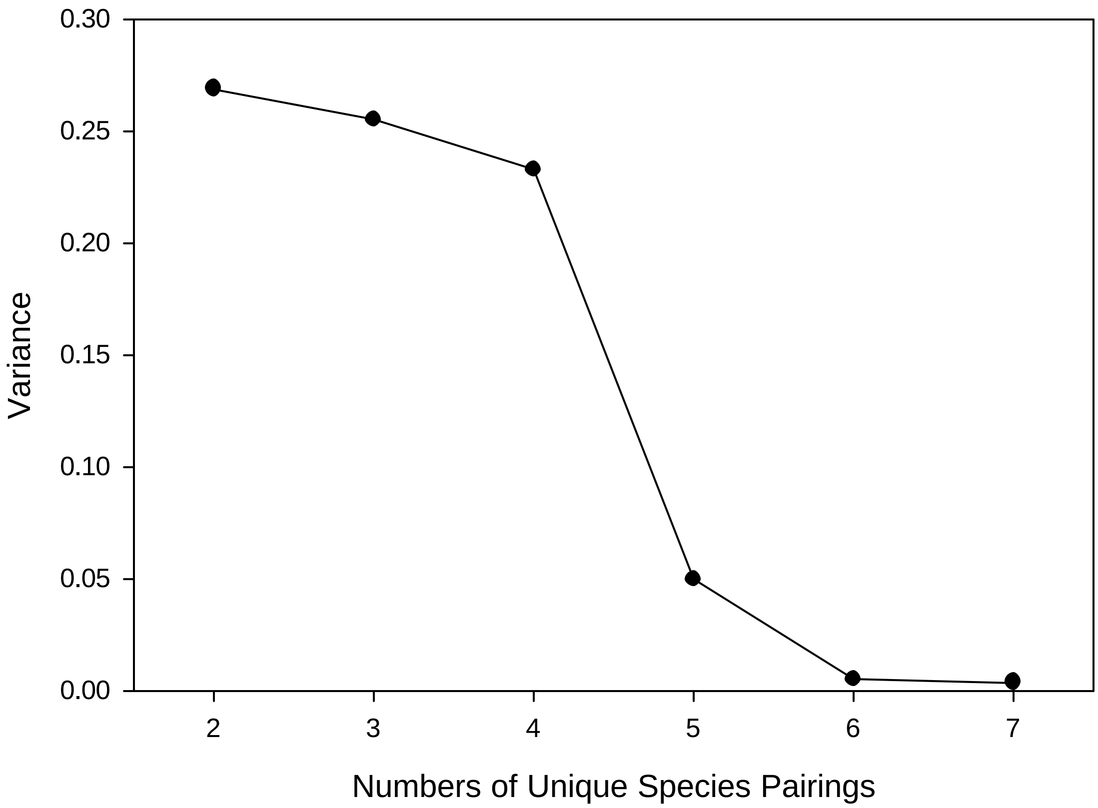


Figure 1.2. Mean (SE) family overlap values (MFOVs) among 5 families of elasmobranchs. CAR = Carcharhinidae (n = 139), RAJ = Rajidae (n = 12), SCY = Scyliorhinidae (n = 16), SQU = Squalidae (n = 76), TRI = Triakidae (n = 6).

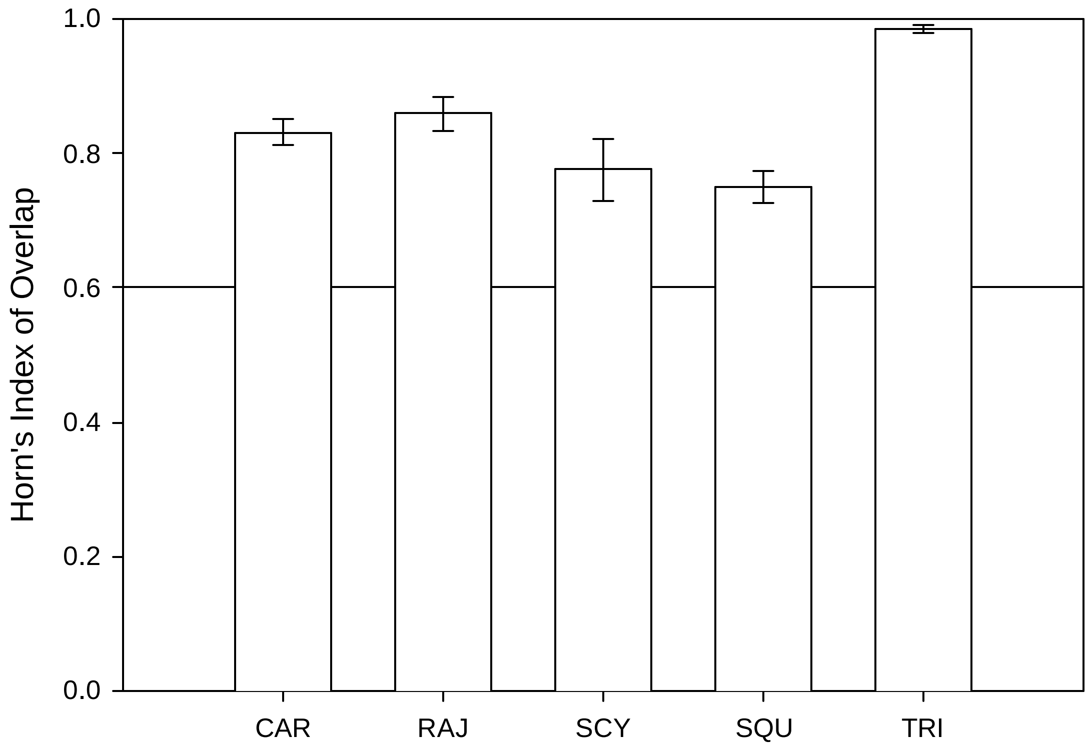


Figure 1.3. Mean (SE) diet overlap values for within family and between family comparisons for 5 families of elasmobranchs. (a) Carcharhinidae (n = 139 within, 59 between), (b) Rajidae (n = 12, 24), (c) Scyliorhinidae (n = 16, 25), (d) Squalidae (n = 76, 14), (e) Triakidae (n = 6, 28). Mann-Whitney U statistics and p-values are shown.

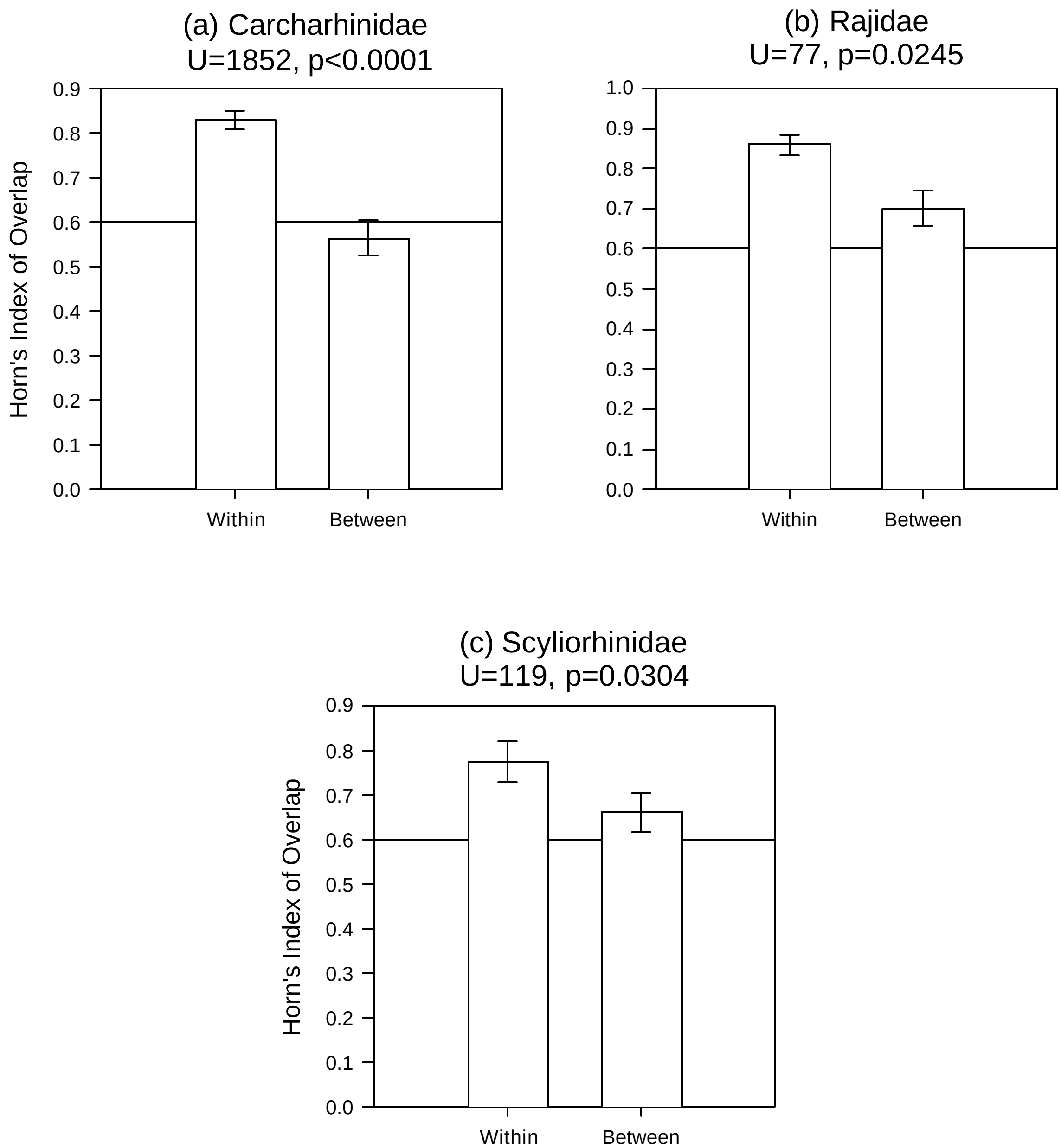


Figure 1.3 (Cont'd). Mean (SE) diet overlap values for within family and between family comparisons for 5 families of elasmobranchs.

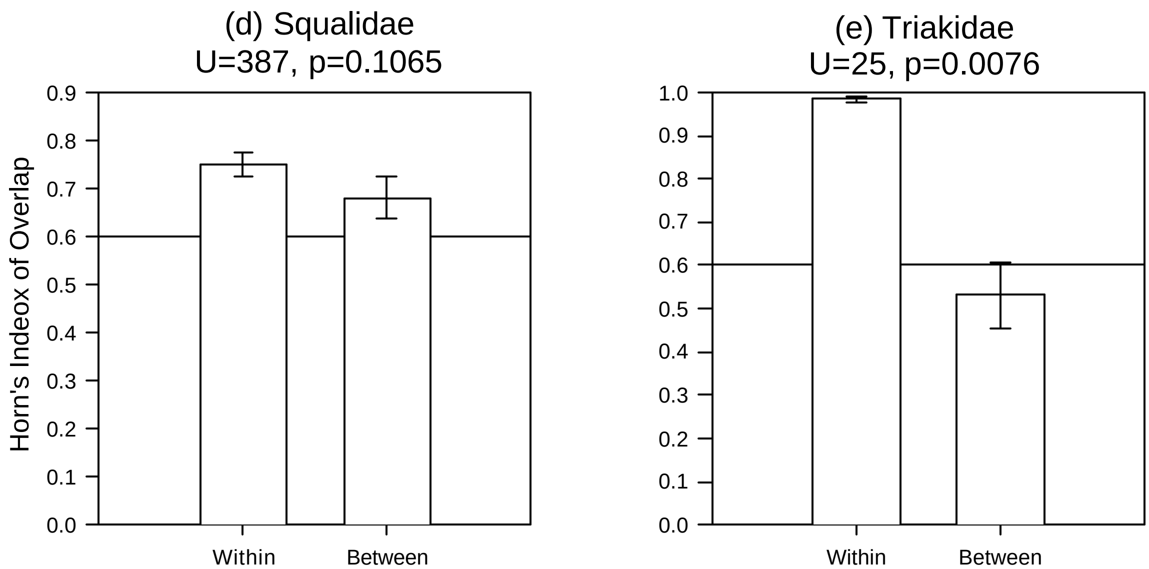
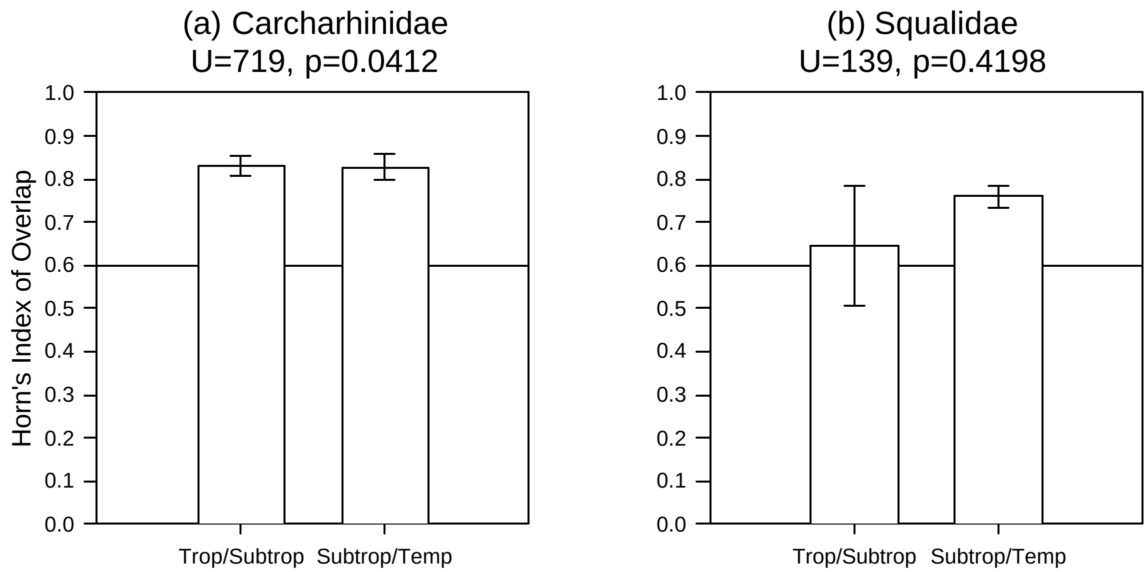


Figure 1.4. Mean (SE) regional family overlap values (MRFOVs) for 2 families of elasmobranchs. (a) Carcharhinidae (n = 122 Tropical/Subtropical, 7 Subtropical/Temperate) and Squalidae (n = 5, 71). Biogeographic regions are based on yearly average surface temperature of the area where the original study took place. Tropical/Subtropical = 15-20°C, Subtropical/Temperate < 15°C. Mann-Whitney U statistics and p-values are shown.



FORAGING ECOLOGY OF EARLY LIFE STAGES OF FOUR SHARK SPECIES (*RHIZOPRIONODON TERRAENOVAE, CARCHARHINUS LIMBATUS, CARCHARHINUS ISODON, AND CARCHARHINUS BREVIPINNA)* IN APALACHICOLA BAY, FLORIDA.

2.1 INTRODUCTION

Sharks are considered top predators and have an important role in marine ecosystems in relation to populations of fish and invertebrates at lower trophic levels (Cortés 1999; Stevens et al. 2000; Kitchell et al. 2002; Schindler et al. 2002). As such, their removal from coastal ecosystems could cause a trophic cascading effect within the remaining community, possibly altering the abundance of lower trophic, fishery-targeted species (Jennings and Kaiser 1998). Given this, it is important that fishery managers be supplied with accurate biological and ecological information to help them better assess and monitor populations of sharks and their prey.

In 1996 the U.S. Congress mandated the identification, conservation, and enhancement of Essential Fish Habitat (EFH) for all managed species. Congress defined EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity." Compared to teleosts, areas required for pupping, breeding, feeding, and growth to maturity for shark species is largely unknown (NMFS 1999a). Currently, only four U.S. institutions are conducting long-term shark monitoring and nursery habitat delineation programs (Virginia Institute of Marine Science, NMFS Panama City, Florida, NMFS Pascagoula, MS, and NMFS Narragansett, RI). Shark nurseries are defined as areas where gravid females give birth to young and where the young spend their first years of life. They have been documented in estuaries (Springer 1967, Snelson et al. 1984), bays (Hoese 1962, Gruber 1982, Carlson and Brusher 1999), and reef lagoons (Stevens 1984, Gruber et al. 1988). Heupel and Simpfendorfer (2002) examined juvenile blacktip shark habitat use with sonic tags in Terra Ceia Bay, Florida, and found mortality rates to be highest in the first few months of life. They concluded that protecting the nursery area during pupping season by enforcing timely fishery closures might help increase blacktip survival.

Since the 1980's, fishery landings of coastal shark species in the Gulf of Mexico have increased dramatically. For example, commercial landings of the blacktip shark (*Carcharhinus limbatus*) have increased by 2 orders of magnitude from 4 metric tons (t) in 1987 to 400 t in 2001. Gulf of Mexico inland recreational landings of cartilaginous fishes, a category that includes skates, rays, dogfish and other sharks, have increased from 17 t in 1981 to 144 t in 2001 (National Marine Fisheries Service Fisheries Statistics and Economics Division, 8 January 2003). There has also been an observed decline in the relative abundance of shark species in fishery-independent surveys. Carlson and Brusher (1999) noted a three-year declining trend in catch-per-unit-effort for juvenile Atlantic sharpnose (*Rhizoprionodon terraenovae*), finetooth (*Carcharhinus isodon*), and spinner sharks (*Carcharhinus brevipinna*) in coastal nursery areas of the northeast Gulf of Mexico.

The current Fishery Management Plan for sharks gives little consideration to ecosystem function likely because there is little quantitative species-specific data on trophic interactions and habitat requirements of sharks (NMFS 1999a). The Atlantic sharpnose and finetooth sharks are managed in the small coastal group as relatively small, fast-growing, and short-lived animals (NMFS 1993; NMFS 1999a). Biological and life history characteristics are well documented for the Atlantic sharpnose shark, but quantitative diet analysis is limited. Gelsleichter et al. (1999) examined the diet of adult Atlantic sharpnose sharks in the Mid-Atlantic Bight and Barry (2002) examined the diet of juvenile Atlantic sharpnose in the western Gulf of Mexico. No quantitative diet information for the finetooth shark has been published. The blacktip and spinner sharks are managed in the large coastal group as relatively large, slow-growing, and long-lived animals (NMFS 1993; NMFS 1999a). Very little quantitative diet data have been published for the blacktip shark. Dudley and Cliff (1993) examined adult blacktip shark stomachs taken from protective gillnets off the coast of Natal, South Africa, Barry (2002) examined juvenile blacktip shark stomachs taken from the western Gulf of Mexico, and Heupel and Hueter (2002) examined blacktip shark stomachs taken from the southeastern Gulf of Mexico. No quantitative diet information for the spinner shark has been published.

A total of 14 species of elasmobranchs (11 sharks, 3 rays) in the Apalachicola Bay system have been documented. Of those, blacktip, finetooth, Atlantic sharpnose, and spinner sharks are the most often encountered (J.K. Carlson, NMFS PC Laboratory, unpublished data; Table 2.1). Beginning in the spring, juvenile blacktip, finetooth, and spinner sharks recruit to the Apalachicola Bay system. In late May to early June, adults move into the bay system to give birth and mate. Young-of-the-year and juvenile Atlantic sharpnose, blacktip, finetooth, and spinner sharks are present in this area by the end of June and all species generally remain within this area until the fall when they move offshore (Carlson and Brusher 1999). Nursery areas provide substantial food resources in a low predation environment (Branstetter 1990; Simpfendorfer and Milward 1993); however, a proposed disadvantage of several species utilizing the same nursery area is the increased chance of competition among juveniles for food and habitat resources.

Teleosts piscivores are known to be size-selective predators, exhibiting selection for small-sized prey (Juanes and Conover 1995, Juanes 1994). It is unknown if shark species are size-selective. An understanding of the size-selective feeding behavior will be necessary to determine their prey requirements and any impacts these sharks may have on the size distribution of prey populations.

The purpose of this study was to investigate the foraging ecology of early life stages of Atlantic sharpnose, blacktip, finetooth, and spinner sharks in Apalachicola Bay, Florida, to determine if these juveniles compete for resources and to provide data that can be used to improve ecosystem-based fisheries management. Specifically, I wish to: 1) describe and quantify the diet of each shark species-life stage, 2) calculate diet overlap for shark species-life stage combinations to test hypotheses from Chapter One, 3) calculate habitat overlap for shark species-life stage combinations using fishery-independent catch data, and 4) examine prey size-predator size relationships for shark species. These four species of carcharhinid shark were chosen for this study based on historically high catch rates within the Apalachicola Bay system during summer months and similarities in morphology. It was hypothesized that these factors could lead to high resource overlap.

2.2 METHODS

2.2a Study Site

The Apalachicola Bay system is a river-influenced estuary and a documented shark nursery area (Carlson and Brusher 1999) in the northeastern Gulf of Mexico (Figure 2.2). Located well east of the influence of the Mississippi River, the Apalachicola Bay system is a highly productive region in an otherwise oligotrophic portion of the Gulf of Mexico. This system is one of the most productive bay systems in the state of Florida. Important resource species within the bay include blue crab, oysters, shrimp, croaker, black drum, flounder, menhaden, mullet, redfish, sea trout, sheepshead, tarpon, and several species of elasmobranchs (Livingston and Joyce 1977; Livingston 1983; J.K. Carlson, NMFS PC Laboratory, unpublished data).

2.2b Feeding Habits.

Collection of Samples. Sharks and potential prey items were taken from fishery-independent surveys conducted on the Gulf of Mexico side of St. Vincent Island, Florida, at the southwest end of the Apalachicola Bay system between Indian Pass and West Pass (Figure 2.2) from April through October of 1999-2002 (Table 2.2). Mid-column water temperature (^{o}C), dissolved oxygen (mg/l), and salinity (ppt) were measured with a YSI Model 85. The depth of the photic zone (cm) was determined using a secchi disk.

A 186 m (558 ft) multi-panel gillnet with variable stretch mesh sizes from 8.9 cm (3.5'') to 14.0 cm (5.5'') in intervals of 1.27 cm (0.5''), with an additional panel of 20.3 cm (8.0'') was used for sampling sharks and prey in the Apalachicola Bay system in both years. Each panel was approximately 31 m (101 ft) long and 3.3 m (10 ft) high. Except for the 20.3 cm mesh size panel, the panel webbing was clear monofilament, double knotted and double selvage. The webbing of the 20.3 cm mesh size panel was made of multifilament nylon; single knotted, and double selvage. The 186 m gill net was set at random stations. It was anchored at both ends, allowed to soak for 0.45-1.0 hours in depths ranging from 3-10 m, then retrieved and cleared of catch. There was little time for digestion before stomachs were extracted. For each shark sampled, precaudal, fork, total, and stretched total length (mm), weight (kg), sex, and life stage were determined. Fork length (FL; the distance from the tip of the snout to the fork in the tail) is a less subjective measurement than total length (TL; the distance from the tip of the snout to the tip of the tail in the relaxed position), and therefore was used in all analyses. The life stage of each shark species was assessed and categorized as: (1) young-of-the-year, characterized by either an open or healed but visible umbilical scar, (2) juvenile, characterized by a completely healed umbilical scar, or (3) adult. For males, adults were characterized as having well-developed testes and the ability to spread the rhipidion. Adult females were characterized as having oocytes greater than 20 mm in diameter or the presence of pups. Ultimately, no sharks greater than 1100 mm FL (~1200 mm TL) were included in this study. In the field, stomachs were extracted, placed in labeled plastic bags, stored on ice, and frozen upon returning to the laboratory. Occasionally, whole sharks were iced and stomachs extracted in the laboratory. Potential prey items were placed on ice in the field, stored on ice at 4^{o}C overnight, and examined the following day.

Preliminary analysis of stomach contents from spring and summer 2001 showed that sharks took considerably smaller prey than was collected in the 186 m gillnet. To better sample potential prey size distributions in the field, a 100 m (300 ft) multi-panel gill net with variable stretch-mesh sizes ranging from 2.5 cm (1.0”) to 7.6 cm (3.0”) in intervals of 2.5 cm (1.0”) was used in the Apalachicola Bay system during late-summer and fall 2001 and throughout 2002. The 2.5 cm mesh size panel was approximately 30 m (100 ft) long. The two 5.1 cm (2.0”) and the two 7.6 cm mesh size panels were all approximately 15 m (50 ft) long. Each panel was 3.3 m (10 ft) high. Except for the 2.5 cm mesh size panel, the panel webbing was clear monofilament, double knotted and double selvage. The webbing of the 2.5 cm mesh size panel was single knotted, double selvage multi- or monofilament nylon. The 100 m gillnet was anchored at both ends, set in the same general location as the 186 m gillnet, allowed to soak for 2.0-5.0 hours, and then retrieved. Sharks caught in the 100 m gillnet were cleared from the net and stored as previously described. After clearing sharks, the 100 m gillnet was stored on ice in a container below deck until returning to the laboratory where it was cleared of the remaining catch. Potential prey items were stored as previously stated and examined the following day.

Upon further investigation of stomach contents from 2001 and early-summer 2002, epibenthic prey were found to be important in the diets. Because gillnets were inadequate in sampling epibenthic prey, a 6.7 m (21 ft), semi-balloon otter trawl was used to sample benthic and epibenthic prey sizes in the field during late summer and fall 2002. The otter trawl had 1.9 cm (0.75”) mesh and 29 m (95 ft) separate bridles. Each door was 40x76x2 cm (16x30x0.78”) and 7.84 kg (17 lbs). The trawl was towed parallel to the shore at 2 knots for 10 minutes at depths of approximately 3 m. Catch was cleared from the trawl and potential prey were stored as previously described.

The Florida Marine Research Institute (FMRI) Fisheries-Independent Monitoring program provided additional prey size data for *Brevoortia spp.* and *Micropogonias undulatus* from western Apalachicola Bay for June, July, and August of 2001 (T. Tuckey, FMRI, personal communication 31 Oct 2002).

Laboratory Processing. Laboratory examinations were performed at the National Marine Fisheries Service Laboratory in Panama City, Florida, and at the North Carolina State University Center for Marine Sciences and Technology in Morehead City, North Carolina.

Stomachs were thawed for 1 hour, opened, and rinsed with water over a 595-micron (0.0234”) sieve. Prey items found in the stomachs were identified to the lowest possible taxon, counted, and weighed (to the nearest 0.0001 g). When possible for teleost prey items, fork (FL), total (TL), snout to operculum (SOL), and snout to vent lengths (SVL), body depth (BD), eye diameter (ED), and caudal peduncle depth (CPD) were measured (to the nearest mm). Otoliths founds in stomachs were weighed individually (to the nearest 0.0001 g) and stored dry in separate containers. All other prey items were stored in either 70% Alcohol or 10% Formalin. When partial teleost prey or whole but digested teleost prey were present, prey measurements (e.g., body depth) and predictive equations were used to estimate original fork or total length.

Potential prey items collected in the gillnets and trawl were separated, counted, weighed (to the nearest 0.0001 g), and measured (to the nearest mm). Precaudal (PCL), fork (FL), total (TL), snout to operculum (SOL), and snout to vent lengths (SVL), body depth (BD), eye diameter (ED), and caudal peduncle depth (CPD) were measured (to the nearest mm). Sagittal otoliths were removed and total (left plus right) otolith weight (TOW) measured (to the nearest 0.0001 g). Predictive equations were constructed relating fish measurements with eye diameter, body depth, caudal peduncle depth, snout to vent and snout to operculum lengths, and total otolith weight to prey fork (or total) length using least-squares regression analysis (Zar 1999). Equations were generated for gaftopsail catfish (*Bagre marinus*), gulf menhaden (*Brevoortia patronus*), sand seatrout (*Cynoscion arenarius*), Atlantic croaker (*Micropogonias undulatus*), and star drum (*Stellifer lanceolatus*). These five prey species made up a significant portion of available prey and diets of sharks in the Apalachicola Bay system.

Analysis of Stomach Contents. Shark diets were assessed by species and life stage: Atlantic sharpnose shark young-of-the-year, juvenile, and adult; blacktip shark young-of-the-year and juvenile; finetooth shark young-of-the-year and juvenile combined; spinner shark young-of-the-year and juvenile combined. Diets of finetooth and spinner shark life stages were combined due to low sample size and the relative consistency of diet with growth. In all analyses, finetooth and spinner shark life stages will be referred to as juvenile. Diets of each shark species-life stage were quantified using three indices: percent by number (%N), percent by weight (%W), and percent by frequency of occurrence (%O). Percent by number was calculated as the number of each prey type divided by the total number of prey items in the stomachs. Percent weight of a prey type was calculated as the total weight of each prey type divided by the total weight of prey items in the stomachs. Frequency of occurrence of a prey type was calculated as the number of stomachs containing the prey type divided by the total number of stomachs containing food. A fourth index, the index of relative importance

(IRI), was calculated as the sum of the percent weight and percent number multiplied by the frequency of occurrence for each prey type (IRI=%O(%N+%W); the IRI for each prey type was divided by the total IRI for all prey items to get the index of relative importance on a percent basis (%IRI; Cortés 1997).

To facilitate diet comparisons and standardize diet overlap analysis among the seven species-life stages, identifiable prey items were also categorized into six major prey categories (PC): (1) Family Clupeidae; (2) other pelagic teleosts; (3) Family Sciaenidae; (4) other epibenthic teleosts; (5) Crustaceans; (6) other invertebrates. The index of relative importance on a percent basis was also computed for the six major prey categories (%IRI^{PC}).

Cumulative prey curves were constructed *a posteriori* for all species-life stages to determine if an adequate number of stomachs had been collected to accurately describe diets (Ferry and Cailliet 1996). The order in which stomachs were analyzed was randomized ten times and the cumulative number of new prey items was counted for each randomization. The total number of stomachs analyzed was plotted against the mean number of new prey items that were found in the stomachs. If the curve reaches a stable asymptote, then the number of stomachs analyzed is considered sufficient in describing dietary habits.

During a one-hour soak, sharks could be attracted to and feed on items already caught in the gillnets. To test for net-feeding bias in the diet index estimates, identifiable prey taken from stomachs were classified as: (1) fresh or (2) digested. Fresh prey had no signs of digestion. Digested prey were considered anywhere from partially digested (e.g., starting to lose scales or fins) to well digested (e.g., several small pieces remaining). Percent occurrence of the six major prey categories (see above) was compared between fresh and digested categories for all shark species-life stages. If the percent occurrence of fresh prey items is similar to percent occurrence of digested prey items, then net-feeding is likely minimal and has little effect on diet index estimates (Buckel et al. 1999).

2.2c Dietary Overlap.

Dietary overlap was calculated using Ecological Methodology v5.1 software (Krebs 1999b). All resources were assumed equally abundant and resource states were presented as $\%IRI^{PC}$. Diet overlap matrices were constructed using Schoener's overlap index where resource state was prey category. Schoener's overlap index is calculated as:

$$P_{jk} = 1 - 0.5 \left(S \mid p_{ij} - p_{ik} \mid \right)$$

where,

P_{jk} = Percentage overlap between species *j* and species *k*

p_{ij} = Proportion resource *i* is of the total resources used by species *j*

p_{ik} = Proportion resource *i* is of the total resources used by species *k*

Overlap index values range from 0 (no overlap) to 1.0 (complete overlap), and values equal to or greater than 0.6 are considered "biologically significant" overlap (Pianka 1976).

Diet can be affected by changes in prey availability. Therefore, diet overlap was calculated by month (May-October) for 2001 and 2002. To avoid low sample sizes, overlap analysis was restricted to months when at least three stomachs contained identifiable prey for at least two of the seven species-life stages. Months that met the requirements in 2001 were July, August, and September. May, June, July, September, and October met requirements in 2002. Annual diet overlap for each shark species-life stage combination was obtained by averaging monthly estimates for 2001 and 2002. Overall diet overlap (2001 and 2002 diet data combined) for each shark species-life stage combination was obtained by averaging monthly diet estimates across years. For comparison, and ignoring the prey availability issues, estimates of diet overlap for each shark species-life stage combination were also calculated using all diet data combined (1999-2002).

In addition to using the arbitrary cutoff of 0.6, observed overlap values were compared to a distribution of expected overlap values based on a null model. The distribution of null model data came from 1000 randomizations of the 2001 and 2002 combined diet data (R3 randomization algorithm, Winemiller and Pianka 1990). Simulations were performed using EcoSim v7.41 software (Gotelli and Entsminger 2003). The observed value is considered statistically different from the null distribution if it is greater than or less than the simulated indices 95% of the time ($p<0.05$) (Winemiller and Pianka 1990). An observed value less than the simulation index would suggest interspecific competition and diet partitioning among shark species-life stage combinations. A value greater than the simulation index would suggest a lack of competition among shark species-life stage combinations or strong competition that has not yet led to resource partitioning.

2.2d Habitat Overlap.

Gillnet data from fishery independent surveys off St. Vincent Island, Florida, from April through October of 1996-2002 were used to assess habitat overlap of species-life stage combinations in the Apalachicola Bay system (J.K. Carlson, NMFS PC Laboratory, unpublished data). The survey design is described in Carlson and Brusher (1999). Bi-monthly to weekly sets were made at depths of 3-10 m using the 186 m multi-panel gillnet. In 2001 and 2002, the 100 m multi-panel gillnet was also used to supplement sample collection (See section 2.2a).

Habitat overlap was calculated on a daily basis using Schoener's overlap index where resource state was gillnet set (See section 2.2c). Analysis was restricted to dates between May and October of 1996-2002 when at least two gillnet sets (either the 186 m or 100 m gillnet or both) were made and at least two of the seven shark species-life stages were captured on the same day. The proportion of each species-life stage captured in a particular gillnet set was calculated as the number of a species-life stage captured on a particular day divided by the total number of that same species-life stage captured in all gillnet sets for that day. Seasonal habitat overlap was obtained for all species-life stage combinations by averaging daily estimates for a season for all years. Seasons were defined as: spring (May); summer (June, July, August); fall (September, October). Overall habitat overlap for all shark species-life stage combinations was obtained by averaging daily estimates across seasons and years.

Observed daily estimates of habitat overlap were compared to a distribution of expected overlap values based on a null model. Simulations were performed using EcoSim v7.21 software (Gotelli and Entsminger 2003). The observed overlap value was considered significantly different from the null distribution if the observed value was greater than or less than the simulated indices 95% of the time ($p<0.05$).

2.2e Prey Size Analysis.

Prey size analysis was restricted to Atlantic sharpnose, blacktip, and finetooth sharks collected June through October of 2001 and 2002. All teleost prey types found whole in stomachs and reconstructed using regression equations were used in this analysis.

Size-selective feeding was examined by comparing sizes of potential fish prey from the field to sizes of prey that were recovered from stomachs. Because of low occurrence of measurable prey in the stomachs, length-frequency histograms were constructed for only three of the five major prey items taken from shark stomachs. Size-selective feeding on *Brevoortia spp.* was assessed for Atlantic sharpnose, blacktip, and finetooth sharks. Size-selective feeding on *M. undulatus* and *S. lanceolatus* was assessed for Atlantic sharpnose and blacktip sharks. Prey length frequencies were not distributed normally and a median test was applied to compare the two prey length groups (Zar 1999).

To estimate changes in prey size with increasing shark size, absolute prey size-predator size diagrams were plotted for each shark. To determine if increases in the mean prey size (as determined by the 50th quantile) resulted from an increase in the maximum or minimum (or both) prey size taken, quantile regression techniques (Scharf et al. 1998) were used to determine the upper and lower bounds (90th and 10th quantiles) of the relation between prey size and shark size.

To examine the patterns of prey size use among sharks, relative and cumulative frequency histograms of prey size-predator size ratios and scatter diagrams of prey size-predator size ratios vs. predator size were created for each shark. Regression quantiles (90th and 10th) were generated to estimate the edges of the ratio scatter diagrams for each shark species. Here, trophic niche breadth was examined by determining the changes in the range of relative prey sizes with increase in predator size. This was assessed by visually examining if the 90th and 10th quantiles were parallel, converged, or diverged.

2.3 RESULTS

Mean (range) mid-water column temperature, salinity, dissolved oxygen, and depth of the photic zone readings from all sampling locations were: 27.7 ^{o}C (23.1-31.5 ^{o}C), 33.5 ppt (28.8-35.8 ppt), 5.0 mg/L (4.7-5.2 mg/L), 137 cm (50-450 cm) for 2001 and 28.4 ^{o}C (23.0-31.0 ^{o}C), 32.1 ppt (25.7-35.7 ppt), 5.4 mg/L (3.6-6.6 mg/L), 115 cm (40-290 cm) for 2002, respectively. These were relatively consistent with environmental readings seen historically at these sampling locations (J.K. Carlson, NMFS PC Laboratory, unpublished data).

2.3a Feeding Habits.

Atlantic sharpnose shark. A total of 300 Atlantic sharpnose sharks were examined for dietary analysis from collections made April through October of 1999-2002 (Table 2.3). Of these, 201 were young-of-the-year, 25 were juvenile, and 74 were adult (Figure 2.3a).

Of the 201 young-of-the-year Atlantic sharpnose shark stomachs examined, 127 contained prey items and 74 (36.82%) were empty. Items found in stomachs included teleosts (6 species representing 5 families), molluscs (cephalopod squid and 1 species of gastropod), arthropods (decapod crustaceans), angiosperms (*Halodule beaudettei*), and unidentifiable algae (Table 2.4). Crustaceans (mostly shrimp) dominated young-of-the-year diets (81.60%IRI^{PC}; Figure 2.4a). Sciaenids (mostly *Micropogonias undulatus*) were the second most important prey item (15.64%IRI^{PC}). Prey items of little importance included clupeids and other pelagic teleosts (~2%IRI^{PC} collectively), invertebrates other than crustaceans (mostly loliginid squid; ~1%IRI^{PC}), and epibenthic teleosts other than sciaenids (less than 0.1%IRI^{PC}).

Out of 25 juvenile Atlantic sharpnose shark stomachs, 15 contained prey and 10 (40%) were empty. Items found in stomachs included teleosts (6 species representing 6 families), molluscs (cephalopod squid), arthropods (shrimp and crab), angiosperms (*Halodule beaudettei*), and unidentifiable shell fragments (Table 2.5). Sciaenids (mostly *Cynoscion spp.*) dominated juvenile diets (64.45%IRI^{PC}; Figure 2.4b). Other important prey items included crustaceans (mostly shrimp; 17.57%IRI^{PC}) and epibenthic teleosts other than sciaenids (mostly *Bagre marinus*; 10.83%IRI^{PC}). Clupeids (mostly *Brevoortia spp.*; 3.42%IRI^{PC}) and other pelagic teleosts (2.79%IRI^{PC}) made up a small portion of juvenile diets. Invertebrates other than crustaceans were of little dietary importance (less than 1%IRI^{PC}).

Empty adult Atlantic sharpnose shark stomachs numbered 31 (42%) out of 74. Items found in stomachs included teleosts (7 species representing 6 families), molluscs (cephalopod squid), arthropods (2 species representing 3 orders), angiosperms (*Thallasia testudinum*), and unidentifiable shell fragments (Table 2.6). Clupeids (mostly *Brevoortia spp.*) dominated adult diets (58.15%IRI^{PC}; (Figure 2.4c). Other important prey items included crustaceans (mostly shrimp; 25.62%IRI^{PC}) and sciaenids (13.80%IRI^{PC}). Prey items of little importance included other pelagic and epibenthic teleosts (~1.2%IRI^{PC} collectively) and other invertebrates (~1%IRI^{PC}).

Blacktip shark. A total of 230 blacktip sharks were examined for dietary analysis from collections made April through October of 1999-2002 (Table 2.3). Of these, 75 were young-of-the-year and 155 were juvenile (Figure 2.3b).

Young-of-the-year blacktip sharks had the lowest percentage of empty stomachs. Out of 75 examined, 57 contained prey items and 18 (24%) were empty. Items found in stomachs included teleosts (7 species representing 6 families), arthropods (shrimp), and angiosperms (*Thallasia testudinum*) (Table 2.7). Sciaenids (mostly *Micropogonias undulatus*; 57.29%IRI^{PC}) and clupeids (mostly *Brevoortia spp.*; 41.80%IRI^{PC}) dominated young-of-the-year diets (Figure 2.5a). Prey items of little importance included other pelagic or other epibenthic teleosts (~0.9%IRI^{PC} collectively) and crustaceans (less than 0.1%IRI^{PC}). Invertebrates other than crustaceans were absent from young-of-the-year blacktip stomachs.

Out of 155 juvenile blacktip shark stomachs that were examined, 66 (43%) were empty. Items found in stomachs included teleosts (10 species representing 10 families), molluscs (3 orders), arthropods (shrimp), and angiosperms (*Halodule beaudettei*) (Table 2.8). Clupeids dominated juvenile diets (93.08%IRI^{PC}; Figure 2.5b). Sciaenids (mostly *Micropogonias undulatus*) were the second most important prey item (5.99%IRI^{PC}). Pelagic and epibenthic teleosts (~0.7% IRI^{PC} collectively) and crustaceans and other invertebrates (~0.2% IRI^{PC} collectively) were of little dietary importance.

Finetooth shark. A total of 109 juvenile finetooth sharks were examined for dietary analysis from collections made April through October of 1999-2002 (Table 2.3). Of these, 14 were young-of-the-year and 95 were juveniles (Figure 2.3c).

Over half of the juvenile finetooth shark stomachs examined were empty; 55 contained prey items and 54 (49%) were empty. Items found in stomachs included teleosts (5 species representing 6 families) and arthropods (shrimp). Clupeids (mostly *Brevoortia spp.*) dominated finetooth diets (97.29%IRI^{PC}; Table 2.9). Other pelagic teleosts were the second most important prey item (2.13%IRI^{PC}). Epibenthic teleosts other than sciaenids (less than 0.5%IRI^{PC}) and crustaceans (0.1%IRI^{PC}) were of little dietary importance. Sciaenids and invertebrates other than crustaceans were absent from finetooth stomachs.

Spinner shark. A total of 72 juvenile spinner sharks were examined for dietary analysis from collections made April through October of 1999-2002 (Table 2.3). Of these, 48 were young-of-the-year and 24 were juvenile (Figure 2.3d).

Half of the juvenile spinner shark stomachs examined were empty. Items found in stomachs included teleosts (3 species representing 4 families) and unidentifiable angiosperms (Table 2.10). Clupeids (mostly *Brevoortia spp.*) dominated spinner diets (99.10%IRI^{PC}). Prey items of little importance included other pelagic and epibenthic teleosts (less than 1%IRI^{PC} collectively). Sciaenids, crustaceans, and other invertebrates were absent from spinner stomachs.

Cumulative Prey Curves. Angiosperms and benthos were found in 11 stomachs collectively; 10 of those 11 stomachs contained other epibenthic prey items in high quantities. It has been suggested that the presence of angiosperms in shark stomachs is reflective of benthic feeding habits (Cortés and Gruber 1990; Cortés et al. 1996). For this reason, these items were considered incidental to prey capture and were not counted as unique prey items. All other identifiable prey items were counted as unique.

In general, all species-life stage cumulative prey curves showed either well-defined asymptotes or trends toward an asymptote (Figures 2.6-2.8). This indicates that sufficient stomachs were examined to describe diets for most of the species-life stages. The cumulative prey curves for juvenile Atlantic sharpnose, blacktip, and finetooth sharks show only a trend towards an asymptote (Figure 2.6b, 2.7b, 2.8a); more juvenile Atlantic sharpnose, blacktip, and finetooth shark stomachs may need to be examined to fully describe the diets of these species-life stages.

Net-feeding. There was some evidence of net feeding (Table 2.11). Sciaenids were found more frequently fresh than digested in four out of five species-life stages of Atlantic sharpnose and blacktip sharks (Table 2.11a and b). Adult Atlantic sharpnose sharks showed some evidence of net-feeding on clupeids (Table 2.11a). No other species-life stage showed a major difference between fresh and digested prey categories.

2.3b Diet Overlap.

Out of a total of 21 potential species-life stage combinations, mean annual diet overlap estimates were made for 9 combinations in 2001 and 15 combinations in 2002 (Table 2.12a and b). Mean annual diet overlap estimates were made for 19 species-life stage combinations from diet overlap estimates determined when months were combined over both years (Table 2.12c). Using diet overlap data collected at the monthly level, there was significantly higher diet overlap for species-life stage combinations that were within 100 mm average FL of each other than species life-stages that were greater or less than 100 mm average FL of each other (Mann-Whitney; U=94.5, p=0.0227).

To avoid redundancy, null-model diet overlap results will be presented starting with young-of-the-year Atlantic sharpnose sharks and moving from left to right in the overlap matrix (See Table 2.12). Each new paragraph will state results for independent null-model simulations. For example, simulations between young-of-the-year Atlantic sharpnose sharks and all other species-life stages will be presented in the young-of-the-year Atlantic sharpnose shark paragraph. Individual numbers within parentheses represent how many times an observed overlap value was compared to the null model for a particular combination.

For all comparisons, young-of-the-year Atlantic sharpnose sharks showed very low diet overlap (Schoener's overlap index <0.6; Table 2.12). Null-model simulations were performed for young-of-the-year Atlantic sharpnose sharks versus all other species-life stages. Out of 9 null-model simulations performed, 7 were lower than expected. One simulation was significantly lower than expected (versus young-of-the-year blacktip sharks; p=0.046). The other was not statistically different than expected.

Juvenile Atlantic sharpnose sharks showed low diet overlap (<0.6) for all comparisons except for comparisons when combined diet data (both years) was used to calculate diet overlap (Table 2.12). Null-model simulations were performed for juvenile Atlantic sharpnose sharks versus adult Atlantic sharpnose sharks (1 simulation), young-of-the-year (1) and juvenile blacktip sharks (1), and juvenile finetooth sharks. Half of the observed values from null-model simulations performed for juvenile Atlantic sharpnose sharks (2 out of 4) were lower than expected. None of the observed diet overlap values were significantly higher or lower than random.

Adult Atlantic sharpnose sharks showed very high diet overlap with young-of-the-year blacktip sharks and borderline diet overlap with other *Carcharhinus spp*. life stages (Table 2.12). All 10 observed diet overlap values for adult Atlantic sharpnose sharks versus young-of-the-year (3) and juvenile blacktip sharks (3), juvenile finetooth sharks (3), and juvenile spinner sharks (1) were higher than the null-model. Three observed diet overlap values were significantly higher than expected: 1 versus young-of-the-year blacktip sharks (p=0.026), 1 versus juvenile blacktip sharks (p=0.014), and 1 versus juvenile finetooth sharks (p=0.025). The remainder were not significantly different than random.

Young-of-the-year blacktip sharks had borderline diet overlap with other *Carcharhinus spp.* life stages (Table 2.12). Out of 14 null-model simulations performed for young-of-the-year blacktip sharks versus juvenile blacktip sharks (6), juvenile finetooth sharks (6), and juvenile spinner sharks (2), 12 observed values were higher than the null-model. Three observed diet overlap values were significantly higher: 2 versus juvenile blacktip sharks (p=0.033, p=0.029) and 1 versus juvenile finetooth sharks (p=0.034). The remainder were not significantly different than expected.

Juvenile blacktip, juvenile finetooth, and juvenile spinner sharks had very high diet overlap with each other (Table 2.12). All 8 observed diet overlap values for juvenile blacktip sharks versus juvenile finetooth sharks (6) and juvenile spinner sharks (2) were higher than expected. Two observed diet overlap values were significantly higher than expected: 1 versus juvenile finetooth sharks (p<0.001) and 1 versus juvenile spinner sharks (p=0.043). The remainder were not significantly different than random. Both observed diet overlap values for juvenile finetooth sharks versus juvenile spinner sharks were higher than expected, and 1 was significantly higher than random (p<0.001). The other was not significantly higher or lower than expected.

2.3c Habitat Overlap

Mean seasonal habitat overlap between all species-life stage combinations were calculated for nine dates in the spring, twenty-one dates in the summer, and ten dates in the fall (Table 2.13a, b, and c). The capture of different species-life stages in the same gillnet set on a given day was infrequent for nearly all combinations throughout all seasons in all years. Out of 40 dates that comparisons were made, high mean overlap (Schoener's overlap index equal to or greater than 0.6) occurred 6 times out of 63 combinations.

In the spring, 19 out of 21 mean habitat overlap values were biologically low (<0.6). The two mean habitat overlap values that were higher than 0.6 in the spring were young-of-the-year blacktip sharks versus juvenile spinner sharks and juvenile blacktip sharks versus juvenile finetooth sharks (1.00 and 0.612 respectively; Table 2.13a). Using spring data, a total of 17 independent null-model simulations were performed for young-of-the-year Atlantic sharpnose sharks, 15 for juvenile Atlantic sharpnose sharks, 20 for adult Atlantic sharpnose sharks, 7 for young-of-the-year blacktip sharks, 9 for juvenile blacktip sharks, and 2 for juvenile finetooth sharks. Of 70 observed habitat overlap values in the spring, 69 were not significantly different than the expected mean. A simulation performed for young-of-the-year versus adult Atlantic sharpnose sharks was significantly higher than random ($p<0.01$).

In the summer, 20 out of 21 mean habitat overlap values were biologically low (<0.6). Juvenile finetooth sharks versus juvenile spinner sharks was the only combination that showed biologically high overlap (0.797; Table 2.13b). Using summer data, 51 independent null-model simulations were performed for young-of-the-year Atlantic sharpnose sharks, 35 for juvenile Atlantic sharpnose sharks, 54 for adult Atlantic sharpnose sharks, 39 for young-of-the-year blacktip sharks, 23 for juvenile blacktip sharks, and 8 for juvenile finetooth sharks. Of the 210 observed habitat overlap values in the summer, 202 were not significant from the null-model. Of the 8 that were significant, 5 were higher and 3 were lower (all $p<0.001$).

In the fall, 18 out of 21 mean habitat overlap values were biologically low (<0.6; Table 2.13c). Juvenile spinner sharks showed biologically high mean habitat overlap with young-of-the-year blacktip sharks (0.676) and young-of-the-year Atlantic sharpnose sharks (0.900). Young-of-the-year Atlantic sharpnose sharks also showed high mean habitat overlap with juvenile Atlantic sharpnose sharks (0.834). Using fall data, 14 independent null-models were performed for young-of-the-year Atlantic sharpnose sharks, 14 for juvenile Atlantic sharpnose sharks, 9 for adult Atlantic sharpnose sharks, 15 for young-of-the-year blacktip sharks, 9 for juvenile blacktip sharks, and 6 for juvenile finetooth sharks. Of the 67 observed habitat overlap values in the fall, 61 were non-significant. Of the 6 that were significant, 3 were significantly higher and 3 were significantly lower (all $p<0.007$).

2.3d Prey Size Analysis

Predictive Equations. Over 2,500 fish representing 30 species in 12 families ranging in size from 28-650 mm total length were collected as potential prey (Table 2.14). Regressions relating external morphological measurements to total or fork length for five significant prey items were all highly significant ($p<0.0001$), having r^2 values ranging from 0.83 to 0.98 (Table 2.15). Regressions from measurements of total sagittal otolith weight were more variable than those using other measurements.

The use of predictive equations increased the size information available for prey items by an order of magnitude. Fork lengths of 29 *Brevoortia spp.* were estimated using the caudal peduncle depth regression equation, 21 using the body depth equation, and 1 using the snout to opercle equation. This increased the number of *Brevoortia spp.* with size information from 9 to 54. Total lengths of 42 *Micropogonias undulatus* were estimated using the total sagittal otolith weight regression equation, 2 using the caudal peduncle depth regression equation, and 1 using the body depth regression equation. The number of *M. undulatus* with size information increased from 2 to 45. Total lengths of 38 *Stellifer lanceolatus* were estimated using the total sagittal otolith weight regression equation and 1 using the body depth regression equation, increasing the number of *S. lanceolatus* with size information from 1 to 40. Fork lengths of 10 *Bagre marinus* (9 for Atlantic sharpnose, 1 for blacktip) and 5 *Cynoscion arenarius* (2 for Atlantic sharpnose, 3 for blacktip) were estimated using the total sagittal otolith weight regression equation. *Bagre marinus* and *C. arenarius* were not found whole in any stomachs.

Total sagittal otolith weight was most often used when recreating original length from partial remains for sciaenids. Digestion of otoliths can affect both the identification of prey species and reconstruction of original prey size (Jobling and Breiby 1986). Otoliths taken directly from stomachs were examined for digestion (e.g., smooth edges) and, if digestion damage was considered minimal, used to recreate length. Otoliths that showed signs of digestion were not used to reconstruct prey size. In addition, otoliths found in stomachs were never stored in alcohol or formalin.

Prey Size Selectivity. Length frequency distributions of *Brevoortia spp.*, *Micropogonias undulatus*, and *Stellifer lanceolatus* found in Atlantic sharpnose, blacktip, and finetooth shark stomachs were compared separately to the frequency distributions of lengths collected by the NMFS sampling gear and by the NMFS and FMRI sampling gear combined. Atlantic sharpnose (Figure 2.9a) and finetooth sharks (Figure 2.9c) trended towards negative size-selectivity for *Brevoortia spp*. using the NMFS length data, but the comparisons were non-significant (p=0.2250, p=0.3821); neutral size-selectivity for *Brevoortia spp.* was observed when all length data were combined (p=0.9721, p=0.6759). Blacktip sharks (Figure 2.9b) showed neutral size-selectivity for *Brevoortia spp*. using both the NMFS and the combined length data (p=0.8509, p=0.8462). The small *Brevoortia spp*. taken inside the bay by FMRI were rarely found in finetooth shark stomachs, and never found in Atlantic sharpnose or blacktip shark stomachs. Using the combined length data, size selectivity for *Micropogonias undulatus* by Atlantic sharpnose sharks was negative (Figure 2.10a; p<0.0001); for blacktip, it was neutral (Figure 2.10b; p=0.9675). *Micropogonias undulatus* data should be viewed with caution because predicted values of total length were obtained from extrapolating beyond the regression data range (Table 2.15). Atlantic sharpnose sharks showed marginally significant negative size selectivity for *S. lanceolatus* (Figure 2.11a; p=0.0571), but blacktip shark size-selection was positive (Figure 2.11b; p<0.0001).

Prey Size- Predator Size Relationships. Absolute prey sizes increased significantly with increasing fork length for Atlantic sharpnose and blacktip sharks (Figure 2.12). As predator fork length increased, both the maximum and minimum prey size consumed by Atlantic sharpnose increase significantly (Figure 2.12 a and Table 2.16). For blacktip sharks, the maximum prey size consumed showed significant increase with increasing shark fork length and the minimum prey size consumed showed only a marginal increase (Figure 2.12b and Table 2.16). The relation of prey size to finetooth shark fork length was not significant for any regression (Figure 2.12c). This was probably due to low sample size.

Atlantic sharpnose, blacktip, and finetooth sharks all consumed prey that were small fractions of their length (Figure 2.13). Over 60% of the diets of Atlantic sharpnose and finetooth sharks consisted of prey that were less than 20% of their length (Figure 2.12a,c). In contrast, blacktip sharks incorporated relatively larger prey in its diet; 58% of blacktip shark diet consisted of prey that was more than 20% of its length (Figure 2.13b). No shark diet consisted of relatively large prey; all prey were less than 36% of shark length. Relative prey size (prey size-predator size ratio plotted versus predator length) demonstrated a significant declining trend with increasing predator size for all three sharks (Figure 2.14). Atlantic sharpnose sharks showed a decrease in the range of relative prey sizes taken with increasing body size; however, blacktip sharks showed no significant change in range of relative prey sizes taken with increasing body size. This relationship was not examined for finetooth sharks due to low sample size.

2.4 DISCUSSION

This study represents the first attempt at quantifying the diets, diet overlap, and habitat use of early-life stages of several shark species. Twice as many stomachs were examined per species in this study than the average of previously published literature reported in Cortés (1999). For finetooth and spinner sharks, this represents the first quantitative information on foraging ecology. Additionally, the size-structured predator-prey data presented here are some of the first for these sharks and their teleost prey.

2.4a Feeding Habits

Atlantic sharpnose sharks are largely piscivorous; however, teleost prey types found in the stomachs of Atlantic sharpnose in Apalachicola Bay, FL, are somewhat different than teleost prey types found in the stomachs of Atlantic sharpnose sharks in the western Gulf of Mexico and the northwestern mid-Atlantic. Barry (2002) examined 54 young-of-the-year and juvenile Atlantic sharpnose sharks caught in gillnets in Terrebonne Bay, Louisiana. Of teleosts, he found *Brevoortia patronus* to be the most important prey item (43.09%IRI). Shrimp and squid were also important prey items (10.19%IRI and 2.55%IRI, respectively), but sciaenids were absent from the diets. When examining stomachs and calculating diet indices for Atlantic sharpnose sharks in Terrebonne Bay, Louisiana, stomachs that contained only eye lenses or otoliths were excluded. This may account for the reported absence of sciaenids. In this study, otoliths (both alone and with other prey items) were found in the stomachs of every life stage of Atlantic sharpnose shark. They were essential for identifying partial prey remains to family and species for arrids, clupeids, engraulids, lutjanids, and especially sciaenids. Gelsleichter et al. (1999) examined stomachs from 208 (mostly adult) Atlantic sharpnose captured on long-line in the Mid-Atlantic Bight and concluded that teleost prey (mostly paralichthyids) made up a significant portion of the diet (64%IRI), followed by crustaceans (mostly portunids; 34%IRI), molluscs (2%IRI), and elasmobranchs (0.1%IRI). Flatfishes were found to be an important prey item for Atlantic sharpnose in the western Gulf of Mexico (10.19%IRI; Barry 2002) and the Mid-Atlantic Bight (17.07%IRI; Gelsleichter et al. 1999), but were absent from the diet of all life-stages of Atlantic sharpnose collected in Apalachicola Bay, Florida. Compared to other epibenthic teleosts, few flatfish were collected as potential prey (Table 2.14).

Blacktip sharks in Apalachicola Bay, Florida, are also piscivorous. Heupel and Hueter (2002) examined 693 juvenile blacktip shark stomachs from Terra Ceia Bay, Florida. They found teleosts to be the most important prey item in the stomachs. Sparids (mostly *Lagodon rhomboides*; 28.7%IRI), clupeids (mostly *Opisthonema oglinum*; 22.7%IRI), sciaenids (mostly *Bairdiella chrysoura*; 13.2%IRI), and haemulids (mostly *Orthopristis chrysoptera*; 13.8%IRI) were the most important identifiable teleosts found in the diets. Barry (2002) examined 353 young-of-the-year and juvenile blacktip sharks caught in gillnets in coastal waters of Louisiana. He found teleosts to be the most important prey items (99.49%IRI). *Brevoortia patronus* (74.79%IRI) and sciaenids (mostly *Micropogonias undulatus*, 14.84%IRI) were the most common teleosts found in the diet. Dudley and

Cliff (1993) examined stomachs from 1290 (mostly adult) blacktip sharks caught in gillnets maintained by the Natal Shark Board (NSB) in South Africa. The diet of blacktip sharks collected from NSB nets consisted of 3 species of shark, 3 species of ray, 1 unidentifiable cetacean, 60 species of teleosts, and a few molluscs and crustaceans; teleosts (mostly clupeids, engraulids, and carangids) were the most important prey item followed by elasmobranchs (97.27% and 2.6%IRI, respectively; Dudley and Cliff 1993). In this study, *Brevoortia spp.* were the most common prey item for blacktip. Further evidence of this close relationship was found by the high occurrence of blacktip as bycatch in the Gulf of Mexico menhaden purse seine fishery (De Silva et al. 2001).

Quantitative diet information for the finetooth and spinner shark has not been published. Castro (1993) has published descriptive diet data for the finetooth shark in the northwest Atlantic off the coasts of South Carolina and Daytona Beach, FL. Of the 80 stomachs he examined, teleosts (*Brevoortia tyrannus*, *Leiostomus xanthurus*, *Scomberomorus maculatus*, and *Mugil sp.*) were most often found, followed by penaeid shrimp, and juvenile Atlantic sharpnose shark. Stevens and McLoughlin (1991) published a diet description for the spinner shark from the southwest Pacific Ocean, but did not quantify which families or species occurred in the diet; pelagic teleost fish occurred in the diets most often with cephalopods and crustaceans occurring less frequently.

Net-feeding most likely did not bias the diet indices. Sciaenids were found more frequently fresh than digested in the diets, but, in general, sciaenids were seldom collected in the gillnets (45 sciaenids collected from gillnet sets in 2000-2002). Although it appears net-feeding occurred, the influence on the diet indices was likely minimal because it was infrequent (64 fresh vs. 526 digested). Moreover, teleost species commonly collected in large numbers in the gillnets (e.g., Gaftopsail catfish, *Bagre marinus*, and Spanish mackerel, *Scomberomorus maculatus*) were seldom, if ever, seen in the diets.

Unlike teleosts that feed on plankton and invertebrates early in life and are exclusively piscivorous later in life (Popova 1978), Atlantic sharpnose, blacktip, finetooth, and spinner sharks found in Apalachicola Bay, Florida, are capable of feeding on fish from birth. Ontogenetic shifts in prey type were observed for Atlantic sharpnose and blacktip sharks. Atlantic sharpnose shifted from crustaceans and sciaenids to sciaenids and other epibenthic fish, and then to *Brevoortia spp*., sciaenids, and crustaceans. Blacktip sharks shifted from sciaenids and other epibenthic fish to almost exclusively *Brevoortia* species. Others have found changes in prey type with ontogeny in elasmobranchs. Cortés and Gruber (1990) examined stomachs of juvenile lemon sharks (*Negaprion brevirostris*) in the Bahamas and saw an ontogenetic shift from teleosts and portunid crabs (sharks <600 mm PCL) to a mix of teleosts, crustaceans, and molluscs (sharks 800-900 mm PCL), and then to elasmobranchs and lobsters (sharks >1400 mm PCL). In Hawaii, the tiger shark (*Galeocerdo cuvier*) was shown to shift from teleosts to items such as birds, sea turtles, marine mammals, and elasmobranchs as they grow (Lowe et al. 1996). Wetherbee et al. (1996) documented that the gray reef shark (*Carcharhinus galapagensis*) in Hawaii fed less on teleosts and more on elasmobranchs with increasing size. Yamaguchi and Taniuchi (2000) found that the diet of the starspotted-dogfish (*Mustelus manazo*) from Japan and Taiwan shifted from small invertebrates and crustaceans (sharks <600 mm TL) to larger crustaceans and small teleost fish (sharks >800 mm TL). The diet of the dusky shark (*Carcharhinus obscurus*) from western Australia showed a high occurrence of pelagic teleosts and cephalopods in small individuals with an increase in the occurrence of elasmobranchs in the larger individuals (Simpfendorfer et al. 2001). Ebert (2002) documented a change in diet with increasing size for the sevengill shark (*Notorhynchus cepedianus*), shifting from mostly teleosts (sharks <1200 mm TL) to chondrichthyan fishes and marine mammals (sharks >2200 mm TL). In this study, the diet shift may be attributed to larger Atlantic sharpnose and blacktip sharks being more capable of capturing faster, pelagic prey. However, there appears to be an upper limit to the types and sizes of prey that these sharks can take; relatively large bluefish (*Pomatomus saltatrix*), king and spanish mackerel (*Scomberomorus spp.*), carangids (Florida pompano, *Trachinotus carolinus*), and other elasmobranchs were collected in this system, but were never observed in the diets.

2.5b Dietary Overlap

Diet overlap between species of sharks has rarely been calculated. Although diet overlap was low for most species-life stage comparisons, diet overlap was generally higher for species-life stages that were similar in size (within 100 mm FL of each other). Significant diet overlap was observed between juvenile blacktip, finetooth, and spinner sharks. Adult Atlantic sharpnose sharks showed borderline significant overlap with these species-life stages as well. On average, these four species-life stages are very close in size (770.3 mm FL, 778.4 mm FL, 639.8 mm FL, and 775.5 mm FL respectively). Observed diet overlap was high between juvenile Atlantic sharpnose and young-of-the-year blacktip sharks when overlap was calculated using combined diet data (1999-2002). These two species-life stages are also close in average size (607.0 mm FL and 523.3 mm FL, respectively). Observed diet overlap was very low between young-of-the-year Atlantic sharpnose sharks and every other species-life stage. Young-of-the-year Atlantic sharpnose sharks are on average 300+ mm FL smaller than juvenile Atlantic sharpnose and young-of-the-year blacktip sharks and 500+ mm FL smaller than the other species-life stages. These findings are supported by the two comparative feeding ecology studies for elasmobranchs that examined diet by size. Ellis et al. (1996) examined the diets of 6 species of shark (from 4 families) and 4 species of rajid ray in the northeastern Atlantic. They found diet overlap to be higher between species of similar size and morphology. Platell et al. (1998) examined diet overlap between four Australian stingarees (Urolophidae) and concluded that highest dietary overlap occurred between similar size classes of species. Size-based diet overlap has also been observed in teleost fishes. Prout et al. (1990) observed high diet overlap between two species of perch (*Morone americana* and *Perca flavescens*) only when they were similar in size. Results from Chapter One provide evidence that, for most species of elasmobranchs, diet overlap will be higher for comparisons made between species that are closer in taxonomic relation and share foraging habitat. In addition to considerations from Chapter One, shark size should also be taken into account when developing hypotheses in elasmobranch resource partitioning studies.

2.4c Habitat Overlap

In general, low habitat overlap was observed between species-life stages. It is unknown how these results compare to other elasmobranch assemblages because no other studies were identified that examined habitat overlap between different species of sharks. Low habitat overlap values could result from sharks using separate habitats or using the same habitat at different times.

There are two main restrictions to the habitat overlap analysis performed in this study. First, the majority of sampling was done between 0800 and 1700h, causing habitat use at other times during the diel cycle to be missed. Three 24-hour sampling trips were attempted in 2002 (13 June, 18 July, and 7 August). Because of inclement weather, only one trip was successful in sampling throughout the entire diel cycle. On 13 June, blacktip and finetooth made up 74% of the target species catch during the day and Atlantic sharpnose made up 100% of the target species catch at night. Spinner sharks were not caught on this date. These results are preliminary and more nocturnal sampling needs to be done to confirm use of the same areas by different species at different times over the diel cycle. Lemon sharks (*Negaprion brevirostris*) in the Bahamas show an east-west movement pattern with sunrise and sunset (Gruber et al. 1988).

The second caveat to the habitat analysis is that the sampling was restricted to the gulf-side of St. Vincent Island, but sharks could also be using habitat inside Apalachicola Bay. The occurrence of angiosperms in shark stomachs may be an indication that these early life stages are moving into and out of the bay. Submerged vegetation is located on the bayside of St. George Island and at the mouth of the Apalachicola River (Protected Areas Geographic Information System project, 3 April 2003). The gulf-side of St. Vincent Island is generally uniform and characterized by muddy bottom and turbid water (J.K. Carlson, NMFS PC Laboratory, and D.M. Bethea, North Carolina State University, personal observation). Leopard sharks (*Triakis semifasciata*) in Tomales Bay, CA, have been shown to move toward the inner bay with the incoming tide and toward the outer bay with the outgoing tide, also showing greater movement at night compared to day (Ackerman et al. 2000).

The gulf-side of St. Vincent Island may be used for a brief period during certain early life stages. For example, the recruitment pulse of young-of-the-year Atlantic sharpnose sharks was captured by the gillnets in late-May 2002. Of the 201 young-of-the-year Atlantic sharpnose sharks collected for this study, 179 of those were collected in May 2002. Of those 179, 161 were collected in one particular gillnet set on 30 May 2002. The infrequent catch or absence of young-of-the-year Atlantic sharpnose sharks from all other gillnet sets made throughout the season could be an indication that this smaller species-life stage uses the gulf side of St. Vincent Island for a very short period of time, preferring the inner areas of the bay for protection from predators until reaching a larger size.

Like diet overlap, the degree of habitat overlap may also be dependent on size of the different species-life stages. Juvenile blacktip, finetooth, and spinner sharks in Apalachicola Bay had borderline habitat overlap across all months. Young-of-the-year Atlantic sharpnose sharks had borderline to low habitat overlap with all other species-life stages. Tiger sharks (*Galeocerdo cuvier*) have also been shown to segregate by size; juvenile tiger sharks are nocturnal, bottom-feeders and adults feed both at the surface during the day and at the bottom at night (Lowe et al. 1996).

2.4d Prey Size Analysis

Studies on teleost piscivores have shown that they select for small-sized prey (Juanes 1994; Juanes and Conover 1995; Buckel et al. 1999; Scharf et al. 2000). Size-selective feeding has not been well studied for shark species; no other study has examined elasmobranch size-selection on teleosts. Negative size-selection for Atlantic sharpnose feeding on *Micropogonias undulatus* was consistent with the only published size-selective feeding study in elasmobranchs. Cortés et al. (1996) found that bonnethead sharks (*Sphyrna tiburo*) in the southeast Gulf of Mexico preyed mainly upon relatively small-sized blue crab (*Callinectes sapidus*). Negative size selectivity was not found in the remaining nine comparisons. A major caveat to prey size analysis in the study was the inability to catch all available prey sizes due to size-selective gear bias. For future research, all three sampling methods (larger-meshed gillnet, smaller-meshed gillnet, and otter trawl) should be used throughout the study period. It would also be beneficial to accompany local commercial shrimp-trawl fishermen on fishing trips to enumerate and measure their bycatch.

While the absolute prey size consumed by Atlantic sharpnose and blacktip sharks increased significantly with increasing shark size, the range of absolute prey sizes taken did not. Scharf et al. (2000) found that the range in absolute prey sizes increased dramatically with increasing predator size for 18 of the piscivorous marine predators they examined, four of which were elasmobranchs. The minimum and maximum prey size data (90^{th} and 10^{th} quantiles) for Atlantic sharpnose and blacktip sharks showed some divergence, suggesting a slight increase in the range of prey sizes taken. Ontogenetic changes in median prey size eaten by Atlantic sharpnose and blacktip sharks were due to increases in maximum and minimum prey size consumed. At comparable sizes throughout their life stages, blacktip sharks are capable of taking larger prey than Atlantic sharpnose sharks. This could be an indication that blacktip shark gape size is larger than that of Atlantic sharpnose shark or that blacktip sharks are simply better at capturing larger, faster prey. Gape measurements were initially attempted in this study, but were not pursued due to difficulty and variability in measurement (i.e., live sharks were too active to safely measure and sacrificed sharks became rigid quickly).

Diets of elasmobranchs consist of relatively small prey. Scharf et al. (2000) found that over 75% of the elasmobranch diets examined consisted of prey that was less than 20% of their length. Frequency distributions of prey size-predator size ratios for Atlantic sharpnose and finetooth sharks compare well with ratio distributions for elasmobranchs in Scharf et al. (2000); however, prey size-predator size ratios for blacktip sharks do not. Blacktip sharks compare well with teleost predators from Scharf et al. (2000) that take considerable amounts of intermediate-sized prey while still feeding on small-sized prey (e.g., pollock, *Pollachius virens*, and windowpane, *Scopthalmus aquosus*).

Scharf et al. (2000) found that ontogenetic trophic niche breadth decreased for larger predators (>500 mm) and assumed that this was a result of the range of relative prey sizes available decreasing over time during the predator's ontogeny. Ontogenetic changes in the range of relative prey sizes taken may also represent changes in foraging habits of these sharks. Trophic niche breadth decreased as Atlantic sharpnose sharks increased in size; the lack of a decrease in trophic niche breadth in blacktip sharks may be due to the range of sizes sampled. While all life stages of Atlantic sharpnose shark were sampled, only juvenile life stages were sampled for blacktip sharks. To better assess changes in ontogenetic trophic niche breadth for blacktip sharks, stomachs from larger blacktip sharks need to be examined.

2.4e Conclusions

Are these sharks competing for available resources? Similar-sized species-life stages had high diet overlap. As a highly productive estuary, it could be that food resources are not limiting in the Apalachicola Bay system. If diet resources are limited, using different resource axes such as space or time could reduce interspecific interactions between sharks. Evidence for this is provided by the observed low habitat overlap. Coupled with the diet overlap results, consistently low habitat overlap suggests that juvenile sharks in Apalachicola Bay, Florida, compete for available habitat resources. More intensive monitoring, such as the use of telemetry and diel gillnet sampling (both inside and outside the bay), is needed to fully understand temporal and spatial habitat use patterns among these early life stages.

In addition to quantifying resource overlap within one nursery area, comparing growth rates of sharks among several nursery areas with different shark assemblages could be used to test for competition. A species-life stage with a relatively low growth rate in one nursery may be experiencing higher competition for available resources compared to that same species with a relatively higher growth rate in another nursery. When fed a diet of teleosts in the laboratory, young-of-the-year Atlantic sharpnose sharks grew almost three times as fast than when fed a diet of crustaceans (T. Lankford and N. Sanscrainte, University North Carolina Wilmington, personal communication 9 April 2003). Results are preliminary, but Atlantic sharpnose sharks in Crooked Island Sound, FL, have higher growth rates than Atlantic sharpnose sharks in Apalachicola Bay, FL;

additionally, blacktip, finetooth, and spinner sharks are found in relatively low numbers in Crooked Island Sound (J.K. Carlson, NMFS PC Laboratory, unpublished data). Stomach contents of Atlantic sharpnose from Crooked Island Sound need to be examined for differences in diet between the two areas. Young-of-the-year Atlantic sharpnose sharks in Crooked Island Sound may feed more on teleosts and less on crustaceans due to a decrease in competition for teleost resources (and/or decreased threat of predators) in that nursery area.

Sharks as a whole have been shown to occupy high trophic levels equivalent to those of marine mammals (Cortés 1999). Bioenergetic models for shark species are in the early stages of development, but the mass-specific consumption rates of blacknose (*Carcharhinus acronotus*) and bonnethead shark (*Sphyrna tiburo)* juveniles have been found to be higher when compared to adults (J.K. Carlson, NMFS PC Laboratory, unpublished data). Species-specific temperature- and size-based consumption rates are needed for juvenile sharks species to determine their predatory demand. If population biomass peaks in these early life stages as it does in some teleosts (Buckel et al. 1999), then predatory impact may peak as well, making these juvenile sharks important apex predators within this estuarine nursery area.

The development of Fisheries Ecosystem Plans, management plans that require the consideration of all biotic, abiotic, and human-related interactions with the target stock, have been recommended (NMFS 1999b); however, predator-prey relationships for the shark species-life stages in this study remain unknown (NMFS 1999a). The prey of Atlantic sharpnose, blacktip, finetooth, and spinner sharks that are also important resource species in this area include menhaden, Atlantic croaker, and shrimp. Quantifying the links among these sharks and the links between these sharks and resource species are critical for ecosystem modeling and a key step to a broader approach in fisheries management.

Table 2.1. Number of elasmobranchs by species caught in Apalachicola Bay, Florida, 1996-2000. Species are listed in descending order of total number caught over the five-year period. Data courtesy of SPAG NOAA NMFS Panama City, Florida.

Species	Common Name	1996	1997	1998	1999	2000	Total Caught
Carcharhinus limbatus	blacktip shark	113	201	98	51	24	482
Carcharhinus isodon	finetooth shark	169	260	9	22	7	467
Rhizoprionodon terraenovae	Atlantic sharpnose shark	66	149	64	52	6	337
Carcharhinus brevipinna	spinner shark	58	110	12	3	2	185
Sphyrna tiburo	bonnethead shark	69	17	33	28	4	151
Rhinoptera bonasus	cownose ray	16	7	19	29	41	112
Sphyrna lewini	scalloped hammerhead shark	6	44	1	34	24	109
Carcharhinus pluembeus	sandbar shark	8	20	24	1	2	55
Carcharhinus leucas	bull shark	5	8	0	2	1	16
Raja eglanteria	clearnose skate	0	0	0	6	0	6
Carcharhinus acronotus	blacknose shark	1	0	2	0	0	3
Dasyatis spp.	stingrays	0	0	0	2	0	2
Negaprion brevirostris	lemon shark	0	0	0	0	1	1
Carcharhinus obscurus	dusky shark	0	0	0	1	0	1

Table 2.2. Sampling dates and gear used to collect sharks and potential prey in Apalachicola Bay, Florida, during 2001 and 2002 field seasons. X indicates dates used.

Year	Month	Day	186 m gillnet	100 m gillnet	16 ft otter trawl
2001	May	11	X		
		18	X		
	June	19	X	X	
		29	X	X	
	July	23	X	X	
	August	14	X		
		30	X		
	September	17	X		
		19	X		
	October	16	X		
2002	April	22	X		
	May	9	X		
		23	X	X	
		30	X	X	
	June	4	X		
		13	X		
		14	X		
		29	X	X	
	July	1	X		
		18	X		
		23	X	X	X
		30	X	X	
	August	7	X		
	September	5	X	X	
	October	10	X	X	
		24	X		X

Table 2.3. Number of stomachs taken from sharks collected in Apalachicola Bay, Florida, April-October for (a) 1999, (b) 2000, (c) 2001, and (d) 2002. Tables (a)-(d) represent collections used to assess quantitative diet compositions. Tables (c) and (d) represent collections used to assess diet overlap and prey size analysis. ATSH = Atlantic sharpnose shark; BTIP = blacktip shark; FTTH = finetooth shark; SPIN = spinner shark.

(a) 1999	**April**	**May**	**June**	**July**	**August**	**September**	**October**	**Total**
ATSH young-of-the-year								
ATSH juvenile								
ATSH adult								
BTIP young-of-the-year						1		1
BTIP juvenile		1	2			7		10
FTTH juvenile	1					4		5
SPIN juvenile			1	1		6		8

(b) 2000	**April**	**May**	**June**	**July**	**August**	**September**	**October**	**Total**
ATSH young-of-the-year					1			1
ATSH juvenile				1	8			9
ATSH adult				6	2			8
BTIP young-of-the-year				1	1			2
BTIP juvenile			5	1	4			10
FTTH juvenile								
SPIN juvenile					3			3

(c) 2001	**April**	**May**	**June**	**July**	**August**	**September**	**October**	**Total**
ATSH young-of-the-year			1					1
ATSH juvenile						8	2	10
ATSH adult		2	4	2		5		13
BTIP young-of-the-year	3				8	10		21
BTIP juvenile			11	15	11	16		53
FTTH juvenile		1	2	24	2	4	2	35
SPIN juvenile		2			11	5	1	19

(d) 2002	**April**	**May**	**June**	**July**	**August**	**September**	**October**	**Total**
ATSH young-of-the-year		179	14	2	2	2		199
ATSH juvenile	1	1	1	1	2			6
ATSH adult		16	35	2				53
BTIP young-of-the-year		6	16	12	3	10	4	51
BTIP juvenile	2	16	29	21		8	6	82
FTTH juvenile		8	17	1	8	14	22	70
SPIN juvenile			17	12	8	5		42

Table 2.4. Diet composition of young-of-the-year Atlantic sharpnose sharks collected in Apalachicola Bay, Florida, May-October, 1999-2002. Diet composition by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), index of relative importance on a percent basis (%IRI), and index of relative importance on a percent basis for 6 major prey categories (%IRI^{PC}).

Prey Item	**%N**	**%W**	**%O**	**IRI**	**%IRI**	**%IRI^{PC}**
Pelagic Teleosts						1.77
F. Clupeidae						0.20
Brevoortia sp.	1.08	9.0110	1.57	15.89	0.35	
F. Engraulidae						
Anchoa mitchilli	4.32	4.5906	4.72	42.12	0.93	
Anchoa sp.	3.78	1.5226	4.72	25.07	0.55	
Epibenthic Teleosts						0.01
F. Arridae	1.62	3.5693	2.36	12.26	0.27	
Bagre marinus	1.62	3.5286	2.36	12.17	0.27	
F. Cynoglossidae	0.54	0.0007	0.79	0.43	0.01	
F. Sciaenidae	2.16	3.4480	3.15	17.67	0.39	15.64
Micropogonias undulatus	10.81	17.3854	12.60	355.23	7.82	
Cynoscion nothus	0.54	0.0111	0.79	0.43	0.01	
Cynoscion sp.	4.32	1.4216	4.72	27.15	0.60	
Stellifer lanceolatus	3.24	5.6239	3.15	27.93	0.61	
Unidentifiable Teleosts	8.65	1.9484	12.60	133.51	2.94	
Arthropods						
C. Crustacea	1.08	2.9303	1.57	6.32	0.14	81.60
O. Decapoda						
F. Peneaidae	12.43	5.8912	14.96	274.13	6.03	
Unidentifiable shrimp	34.59	36.8388	49.61	3543.55	77.97	
Molluscs						
C. Cephalopoda						
F. Loliginidae	5.41	2.1476	6.30	47.58	1.05	
C. Gastropoda						
Bittium sp.	0.54	0.0900	0.79	0.50	0.01	
Echinoderms						
Other Invertebrates						0.77
Angiosperms						
Halodule beaudettei	2.70	0.0397	0.79	2.16	0.05	
Benthos						
Unidentifiable Algae	0.54	0.0012	0.79	0.43	0.01	
Totals	185	144.4896	127	4544.50		
# Examined	201					
# Empty	74					
% Empty	36.82					
Average Fork Length (mm) (SE)	272.7 (1.02)					
Fork Length Range (mm)	235-330					
Average Weight (kg) (SE)	0.153 (0.004)					

Table 2.5. Diet composition of juvenile Atlantic sharpnose sharks collected from Apalachicola Bay, Florida, May-October, 1999-2002. Diet composition by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), index of relative importance on a percent basis (%IRI), and index of relative importance on a percent basis for 6 major prey categories (%IRI^{PC}).

Prey Item	**%N**	**%W**	**%O**	**IRI**	**%IRI**	**%IRI^{PC}**
Pelagic Teleosts						2.79
F. Carangidae						
Chloroscombrus chrysurus	1.49	6.0584	6.67	64.89	1.60	
F. Clupeidae	1.49	7.0600	6.67	57.02	1.41	3.42
Brevoortia sp.	2.99	12.1068	6.67	100.61	2.49	
F. Engraulidae						
Anchoa sp.	2.99	0.0095	13.33	39.93	0.99	
Epibenthic Teleosts						10.83
F. Arridae	1.49	0.9141	6.67	16.04	0.40	
Bagre marinus	5.97	7.4187	20.00	267.78	6.62	
F. Lutjanidae	2.99	0.6509	13.33	48.48	1.20	
F. Sciaenidae	2.99	0.0653	13.33	40.67	1.01	64.45
Cynoscion nothus	37.31	13.2358	20.00	1010.99	24.50	
Stellifer lanceolatus	11.94	31.5293	26.67	1159.19	28.66	
Unidentifiable Teleosts	5.97	1.9559	26.67	211.36	5.23	
Arthropods						
C. Crustacea						17.57
O. Decapoda						
F. Peneaidae	1.49	2.2445	6.67	24.91	0.62	
Unidentifiable shrimp	12.12	9.7741	40.00	868.58	21.48	
F. Portunidae	1.49	2.8975	6.67	29.27	0.72	
Molluscs						
C. Cephalopoda						
F. Loliginidae	4.48	1.8487	13.33	84.35	2.09	
Echinoderms						
Other Invertebrates						0.94
Angiosperms						
Halodule beaudettei	1.49	0.0136	6.67	10.04	0.25	
Benthos						
Shell fragment	1.49	0.0340	6.67	10.18	0.25	
Totals	66	73.5126	15	4044.48		
# Examined	25					
# Empty	10					
% Empty	40.00					
Average Fork Length (mm) (SE)	607.0 (10.1)					
Fork Length Range (mm)	490-700					
Average Weight (kg) (SE)	1.788 (0.091)					

Table 2.6. Diet composition of adult Atlantic sharpnose sharks collected from Apalachicola Bay, Florida, May-October, 1999-2002. Diet by percent number (%N), percent weight (%W), frequency of occurrence (%O), index of relative importance (IRI), index of relative percent importance on a percent basis (%IRI), and index of relative importance on a percent basis for 6 major prey categories ($\%IRI^{PC}$).

Prey Item	**%N**	**%W**	**%O**	**IRI**	**%IRI**	**$\%IRI^{PC}$**
Pelagic Teleosts						0.36
F. Carangidae	1.08	0.1168	2.33	2.77	0.07	
F. Clupeidae	2.15	0.2658	4.45	11.24	0.29	58.15
Brevoortia patronus	16.13	82.9474	27.91	2764.92	70.10	
Brevoortia sp.	3.23	0.5421	6.98	26.29	0.67	
F. Engraulidae						
Anchoa sp.	2.15	0.0469	4.65	10.22	0.26	
Epibenthic Teleosts						0.88
F. Arridae						
Bagre marinus	3.23	1.8817	6.98	35.63	0.90	
F. Ophichthidae	1.08	0.1755	2.33	2.91	0.07	
F. Sciaenidae	6.45	0.0848	6.98	45.60	1.16	13.80
Cynoscion arenarius	2.15	0.4548	6.98	18.18	0.46	
Cynoscion nothus	8.60	0.0148	2.33	20.04	0.51	
Cynoscion sp.	2.15	0.3890	4.65	11.81	0.30	
Menticirrhus littoralis	2.15	0.5196	4.65	12.42	0.31	
Micropogonias undulatus	4.30	0.3470	6.68	32.43	0.82	
Unidentifiable Teleosts	10.75	0.8874	23.26	270.70	6.86	
Arthropods						
C. Crustacea						
O. Decapoda	1.08	0.0006	2.33	2.50	0.06	25.62
F. Portunidae	3.23	0.9779	6.98	29.33	0.74	
Callinectes sapidus	1.08	0.8616	2.33	4.50	0.11	
Unidentifiable shrimp	13.98	6.5078	25.58	524.07	13.29	
O. Isopoda	1.08	0.0447	2.33	2.60	0.07	
O. Stomatopoda						
Squilla empusa	5.38	2.7769	6.98	56.88	1.44	
Molluscs						
C. Cephalopoda						
F. Loliginidae	5.38	0.1502	9.30	51.41	1.30	
Echinoderms						
C. Ophiuroidea	1.08	0.0015	2.33	2.50	0.06	
Other Invertebrates						1.18
Echinoderms						
Angiosperms						
Thallasia testudinum	1.08	0.0036	2.33	2.51	0.06	
Benthos						
Shell fragment	1.08	0.0014	2.33	2.50	0.06	
Totals	93	642.3377	43	3943.98		
# Examined	74					
# Empty	31					
Empty	41.89					
Average Fork Length (mm) (SE)	775.5 (5.4)					
Fork Length Range (mm)	670-865					
Average Weight (SE)	3.324 (0.063)					

Table 2.7. Diet composition of young-of-the-year blacktip sharks collected from Apalachicola Bay, Florida, May-October, 1999-2002. Diet by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), index of relative importance on a percent basis (%IRI), and index of relative importance on a percent basis for 6 major prey categories ($\%IRI^{PC}$).

Prey Item	**%N**	**%W**	**%O**	**IRI**	**%IRI**	**$\%IRI^{PC}$**
Pelagic Teleosts						0.70
F. Carangidae	1.32	0.0379	1.75	2.37	0.07	
F. Clupeidae	6.58	7.2669	8.77	121.45	3.52	41.80
Brevoortia patronus	14.47	33.1897	14.04	668.96	19.40	
Brevoortia sp.	7.89	7.6346	10.53	163.47	4.74	
F. Elopidae	1.32	0.8700	1.75	3.83	0.11	
Elops saurus	1.32	3.0922	1.75	7.73	0.22	
Epibenthic Teleosts						0.17
F. Arridae						
Bagre marinus	1.32	0.0016	1.75	2.31	0.07	
F. Sciaenidae	1.32	0.0495	1.75	2.40	0.07	57.29
Cynoscion sp.	2.63	3.5880	3.51	21.82	0.63	
Menticirrhus littoralis	1.32	0.1419	1.75	2.56	0.07	
Micropogonias undulatus	25.00	33.1679	28.07	1632.77	47.36	
Stellifer lanceolatus	9.21	5.2679	7.02	101.60	2.95	
F. Syngnathidae	1.32	0.0015	1.75	2.31	0.07	
Unidentifiable Teleosts	21.05	5.6341	26.32	702.28	20.37	
Arthropods						0.04
C. Crustacea						
O. Decapoda						
Unidentifiable shrimp	1.32	0.0318	1.75	2.36	0.07	
Molluscs						
Echinoderms						
Other Invertebrates						0.00
Angiosperms						
Thallasia testudinum	2.63	0.0248	3.51	9.32	0.27	
Benthos						
Totals	76	686.1765	57	3447.57		
# Examined	75					
# Empty	18					
% Empty	24.00					
Average Fork Length (mm) (SE)	523.3 (4.65)					
Fork Length Range (mm)	445-590					
Average Weight (kg) (SE)	1.75 (0.047)					

Table 2.8. Diet composition of juvenile blacktip sharks collected from Apalachicola Bay, Florida, May-October, 1999-2002. Diet by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), index of relative importance on a percent basis (%IRI), and index of relative importance on a percent basis for 6 major prey categories (%IRI^{PC}).

Prey Item	%N	%W	%O	IRI	%IRI	%IRI^{PC}
Pelagic Teleosts						0.22
F. Carangidae	0.63	0.0458	1.12	0.70	0.02	
F. Clupeidae	15.00	3.2802	21.35	390.25	9.05	93.08
Brevoortia patronus	25.63	67.5296	32.58	3035.37	70.36	
Brevoortia sp.	10.00	8.9289	13.48	255.22	5.92	
F. Elopidae						
Elops saurus	0.63	0.1799	1.12	0.90	0.02	
F. Engraulidae						
Anchoa sp.	1.88	0.0188	3.37	6.38	0.15	
Epibenthic Teleosts						0.49
F. Arridae						
Bagre marinus	0.63	0.0004	1.12	0.70	0.02	
F. Lutjanidae	0.63	0.0041	1.12	0.71	0.02	
F. Sciaenidae	0.63	0.0204	1.12	0.73	0.02	5.99
Cynoscion arenarius	1.88	4.0994	3.37	20.14	0.47	
Leiostomus xanthurus	0.63	3.9289	1.12	5.12	0.12	
Micropogonias undulatus	5.63	6.4897	8.99	108.90	2.52	
Stellifer lanceolatus	11.25	0.0631	1.12	12.71	0.29	
F. Sparidae						
Archosargus probatocephalus	0.63	2.6946	1.12	3.73	0.09	
F. Syngnathidae	0.63	0.0327	1.12	0.74	0.02	
Syngnathus sp.	0.63	0.1431	1.12	0.86	0.02	
F. Synodontidae	0.63	0.0041	1.12	0.71	0.02	
Unidentifiable Teleosts	18.13	0.5246	24.72	359.91	10.69	
Arthropods						
C. Crustacea						0.14
O. Decapoda						
F. Peneaidae						
Litopenaeus satiferus	0.63	1.2348	1.12	2.09	0.05	
Unidentifiable shrimp	1.25	0.7605	2.25	4.52	0.10	
Molluscs						
C. Cephalopoda						
F. Loliginidae	0.63	0.0004	1.12	0.70	0.02	
C. Gastropoda	0.63	0.0049	1.12	0.71	0.02	
C. Isopoda	0.63	0.0107	1.12	0.71	0.02	
Echinoderms						
Other Invertebrates						0.08
Angiosperms						
Halodule beaudettei	0.63	0.0003	1.12	0.70	0.02	
Benthos						
Totals	160	2445.6574	89	4314.36		
# Examined	155					
# Empty	66					
% Empty	42.58					
Average Fork Length (mm) (SE)	770.3 (7.45)					
Fork Length Range (mm)	620-1030					
Average Weight (kg) (SE)	5.36 (0.161)					

Table 2.9. Diet composition of juvenile finetooth sharks collected from Apalachicola Bay, Florida, May-October, 1999-2002. Diet by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), index of relative importance on a percent basis (%IRI), and index of relative importance for 6 major prey categories (%IRI^{PC}).

Prey Item	**%N**	**%W**	**%O**	**IRI**	**%IRI**	**%IRI^{PC}**
Pelagic Teleosts						2.13
F. Carangidae	3.95	0.2060	5.45	22.66	0.43	
Chloroscombrus chrysurus	1.32	0.2625	1.82	2.87	0.05	
F. Clupeidae	11.84	8.8215	16.36	338.13	6.37	97.29
Brevoortia patronus	38.16	74.6556	36.36	4102.31	77.31	
Brevoortia sp.	15.79	9.8404	18.18	466.00	8.78	
F. Elopidae						
Elops saurus	1.32	1.8295	1.82	5.72	0.11	
F. Engraulidae						
Anchoa sp.	5.26	0.0985	7.27	38.99	0.73	
Epibenthic Teleosts						0.49
F. Sciaenidae						0.00
F. Sparidae	1.32	0.5974	1.82	3.48	0.07	
F. Syngnathidae	2.63	0.2815	3.64	10.59	0.20	
Syngnathus sp.	1.32	1.3179	1.82	4.79	0.09	
Unidentifiable Teleosts	14.47	1.8288	20.00	326.05	6.14	
Arthropods						
C. Crustacea						0.10
O. Decapoda						
Unidentifiable shrimp	2.63	0.2603	3.64	10.52	0.20	
Molluscs						
Echinoderms						
Other Invertebrates						0.00
Angiosperms						
Benthos						
Totals	76	1421.1800	55	5306.58		
# Examined	109					
# Empty	54					
% Empty	49.54					
Average Fork Length (mm) (SE)	778.4 (14.82)					
Fork Length Range (mm)	388-1070					
Average Weight (kg) (SE)	5.20 (0.243)					

Table 2.10. Diet composition of juvenile spinner sharks collected from Apalachicola Bay, Florida, May-October, 1999-2002. Diet by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), and index of relative importance on a percent basis (%IRI), and index of relative importance on a percent basis for 6 major prey categories ($\%IRI^{PC}$).

Prey Item	**%N**	**%W**	**%O**	**IRI**	**%IRI**	**$\%IRI^{PC}$**
Pelagic Teleosts						0.54
F. Clupeidae	20.00	16.8260	16.67	613.77	16.25	99.10
Brevoortia patronus	17.78	67.0513	13.89	1178.18	31.18	
Brevoortia sp.	13.33	5.9920	11.11	214.73	5.68	
Harengula jaguana						
F. Engraulidae	2.22	0.0114	2.78	6.20	0.16	
Anchoa sp.	4.44	0.2012	2.78	12.90	0.34	
Epibenthic Teleosts						0.36
F. Arridae	2.22	0.0307	2.78	6.26	0.17	
F. Sciaenidae						0.00
F. Syngnathidae	2.22	0.0611	2.78	6.34	0.17	
Unidentifiable Teleosts	33.33	8.0026	41.67	1722.33	45.59	
Arthropods						
C. Crustacea						0.00
Molluscs						
Echinoderms						
Other Invertebrates						0.00
Angiosperms						
Unidentifiable angiosperms	2.22	0.0052	2.78	6.19	0.16	
Benthos						
Totals	45	879.8193	36	3778.12		
# Examined	72					
# Empty	36					
% Empty	50.00					
Average Fork Length (mm) (SE)	639.8 (15.4)					
Fork Length Range (mm)	460-960					
Average Weight (kg) (SE)	2.806 (0.221)					

Table 2.11. The total number of identifiable prey (*n*) found either fresh or digested in shark stomachs and the percentage contribution of the six major prey categories to Fresh and Digested categories. (a) Atlantic sharpnose, (b) blacktip, (c) finetooth and (d) spinner sharks. Fresh prey = no signs of digestion. Digested prey = partially digested (e.g. starting to lose scales or fins) to well digested (e.g. identifiable only by key morphological characteristics). ATSH = Atlantic sharpnose shark; BTIP = blacktip shark; FTTH = finetooth shark; SPIN = spinner shark. YOY = young-of-the-year; JUV = juvenile; MAT = adult.

(a)	**ATSH YOY**		**ATSH JUV**		**ATSH MAT**	
Prey Item	Fresh	Digested	Fresh	Digested	Fresh	Digested
n	12	151	1	58	21	60
Family Clupeidae		1.3		5.1	57.1	13.3
Other Pelagic Teleosts	25.0	7.9		5.1		5.0
Family Sciaenidae	58.4	21.9	100.0	55.9	4.8	38.3
Other Epibenthic Teleosts	8.3	4.0		11.9	4.8	6.8
Crustaceans		58.3		16.9	28.5	28.3
Other Invertebrates	8.3	6.6		5.1	4.8	8.3

(b)	**BTIP YOY**		**BTIP JUV**	
Prey Item	Fresh	Digested	Fresh	Digested
n	3	55	15	116
Family Clupeidae	33.3	83.6	66.8	84.5
Other Pelagic Teleosts		5.5		4.3
Family Sciaenidae	66.7	5.5	20.0	3.4
Other Epibenthic Teleosts		3.6	6.7	4.3
Crustaceans		1.8	6.7	2.6
Other Invertebrates				0.9

(c)	**FTTH**	
Prey Item	Fresh	Digested
n	10	55
Family Clupeidae	90.0	76.4
Other Pelagic Teleosts		16.4
Family Sciaenidae		
Other Epibenthic Teleosts	10.0	3.6
Crustaceans		
Other Invertebrates		3.6

(d)	**SPIN**	
Prey Item	Fresh	Digested
n	2	31
Family Clupeidae	100.0	83.9
Other Pelagic Teleosts		9.7
Family Sciaenidae		
Other Epibenthic Teleosts		6.4
Crustaceans		
Other Invertebrates		

Table 2.12. Mean (SE) symmetrical diet overlap matrices for shark species-life stage combinations collected in Apalachicola Bay, Florida, April-October 2001-2002. Diet overlap was calculated from (a) monthly estimates for 2001; (b) monthly estimates for 2002; (c) monthly estimates for 2001 and 2002 combined; and (d) combined diet data from 1999-2002. Entries in bold represent “biologically significant” (?0.6) overlap. Blank entries indicate the combination did not meet analysis inclusion criteria. ATSH = Atlantic sharpnose; BTIP = blacktip; FTTH = finetooth; SPIN = spinner. YOY = young of the year; JUV = juvenile; MAT = adult.

(a) 2001	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV		*				
ATSH MAT		0.486	*			
BTIP YOY		0.093	0.437	*		
BTIP JUV		0.017	0.039	0.598 (0.204)	*	
FTTH					**0.921**	*
SPIN				0.289	**0.790**	

(b) 2002	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV		*				
ATSH MAT	0.160 (0.080)		*			
BTIP YOY	0.030 (0.030)		**0.821 (0.122)**	*		
BTIP JUV	0.140 (0.140)		0.578 (0.015)	**0.614 (0.020)**	*	
FTTH	0.024 (0.016)		**0.726 (0.218)**	**0.679 (0.087)**	**0.832 (0.099)**	*
SPIN	0.000		0.508	0.547	**0.916**	**0.922**

(c) 2001, 2002	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV		*				
ATSH MAT	0.162 (0.078)	0.486	*			
BTIP YOY	0.031 (0.031)	0.269	**0.705 (0.135)**	*		
BTIP JUV	0.145 (0.145)	0.045	0.567 (0.102)	0.513 (0.118)	*	
FTTH	0.024 (0.016)	0	0.599 (0.179)	0.528 (0.129)	**0.911 (0.038)**	*
SPIN	0.000		0.508	0.418 (0.129)	**0.864 (0.074)**	**0.891 (0.101)**

(d) 1999-2002	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV	0.355	*				
ATSH MAT	0.408	0.370	*			
BTIP YOY	0.167	**0.616**	0.562	*		
BTIP JUV	0.066	0.103	**0.651**	0.482	*	
FTTH	0.015	0.061	0.591	0.427	**0.939**	*
SPIN	0.008	0.043	0.589	0.425	**0.937**	**0.982**

Table 2.13. Mean symmetrical habitat overlap values (SE) for species-life stage combinations collected in Apalachicola Bay, Florida, April-October 1996-2002. Entries are means pooled across all years within (a) Spring (May), (b) Summer (June, July, August), (c) Fall (September, October), and (d) across all months (May – October). Entries in bold represent "biologically significant" overlap. Zeros as entries represent seasons when the combination was captured, but not in the same gillnet set. Entries without a standard error value represent a single estimate. ATSH = Atlantic sharpnose; BTIP = blacktip; FTTH = finetooth; SPIN = spinner. YOY = young of the year; JUV = juvenile; MAT = adult.

(a) Spring	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV	0.286 (0.286)	*				
ATSH MAT	0.449 (0.094)	0.477 (0.205)	*			
BTIP YOY	0.072 (0.072)	0.500 (0.500)	0.347 (0.069)	*		
BTIP JUV	0.456 (0.158)	0.350 (0.117)	0.379 (0.138)	0.406 (0.094)	*	
FTTH	0.374 (0.207)	0.110 (0.110)	0.441 (0.171)	0.443 (0.224)	**0.612**	*
SPIN	0.00	0.567 (0.233)	0.445 (0.028)	**1.00**	0.575 (0.075)	0.350 (0.350)

(b) Summer	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV	0.320 (0.286)	*				
ATSH MAT	0.449 (0.107)	0.465 (0.134)	*			
BTIP YOY	0.549 (0.067)	0.375 (0.097)	0.419 (0.105)	*		
BTIP JUV	0.303 (0.084)	0.318 (0.126)	0.435 (0.082)	0.482 (0.079)	*	
FTTH	0.382 (0.083)	0.401 (0.127)	0.267 (0.075)	0.385 (0.081)	0.480 (0.085)	*
SPIN	0.475 (0.149)	0.455 (0.147)	0.547 (0.145)	0.532 (0.107)	0.595 (0.087)	**0.797 (0.083)**

(c) Fall	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV	**0.834 (0.167)**	*				
ATSH MAT	0.500 (0.500)	0.578 (0.174)	*			
BTIP YOY	0.409 (0.409)	0.167	0.143	*		
BTIP JUV	0.250 (0.250)	0.532	0.429	0.376 (0.069)	*	
FTTH	0.573 (0.145)	0.547 (0.069)	0.484 (0.065)	0.369 (0.138)	0.517 (0.158)	*
SPIN	**0.900 (0.100)**	0.507 (0.084)	0.472 (0.242)	**0.676 (0.182)**	0.285 (0.092)	0.550 (0.110)

(d) All Months	ATSH YOY	ATSH JUV	ATSH MAT	BTIP YOY	BTIP JUV	FTTH
ATSH JUV	0.426 (0.108)	*				
ATSH MAT	0.488 (0.083)	0.498 (0.089)	*			
BTIP YOY	0.412 (0.078)	0.379 (0.100)	0.390 (0.079)	*		
BTIP JUV	0.333 (0.090)	0.344 (0.091)	0.419 (0.066)	0.445 (0.052)	*	
FTTH	0.391 (0.071)	0.411 (0.077)	0.330 (0.059)	0.387 (0.064)	0.510 (0.070)	*
SPIN	0.512 (0.130)	0.500 (0.081)	0.509 (0.093)	**0.602 (0.089)**	0.518 (0.064)	**0.643 (0.076)**

Table 2.14. Teleost fish collected using all gear in Apalachicola Bay, Florida, April-October 1999-2002. Items are listed alphabetically according to family and scientific name. N = total number collected from all gear. * indicates items found in shark stomachs. ** indicates items found in shark stomachs but not collected in gear.

Family and Scientific Name	***Common Name***	***N***
Arridae		
Arius felis	Hardhead catfish	58
*Bagre marinus**	Gaftopsail catfish	834
Carangidae		
*Chloroscombrus chrysurus**	Atlantic bumper	275
Hemicaranx amblyrhynchus	Bluntnose jack	2
Oligoplites saurus	Leatherjacket	7
Selene setapinnis	Atlantic moonfish	18
Selene vomer	Lookdown	12
Trachinotus carolinus	Florida pompano	20
Clupeidae		
*Brevoortia spp.**	Gulf or Yellowfin menhaden	708
Opisthonema oglinum	Atlantic thread herring	6
*Harengula jaguana**	Scaled sardine	8
Cynoglossidae		
Symphurus plagiosa	Tonguefish	2
Elopidae		
*Elops saurus**	Ladyfish	39
Engraulidae		
*Anchoa spp.**	Striped or Bay anchovy	134
Pomatomidae		
Pomatomous saltatrix	Bluefish	10
Sciaenidae		
Bairdiella chrysoura	Silver perch	5
*Cynoscion arenarius**	Sand seatrout	48
*Cynoscion nothus**	Silver seatrout	5
*Leiostomus xanthurus**	Spot	2
Menticirrhus americanus	Southern kingfish	3
Menticirrhus littoralis	Gulf kingfish	3
*Micropogonias undulatus**	Atlantic croaker	44
*Stellifer lanceolatus**	Star drum	122
Scombridae		
Scomberomorus cavalla	King mackerel	3
Scomberomorus maculatus	Spanish mackerel	139
Solidae		
Trinectes maculatus	Hogchoker	10
Sparidae		
*Archosargus probatocephalus***	Sheepshead	0
Stromateidae		
Peprilus alepidotus	Harvestfish	38
Synodontidae		
Synodus foetens	Lizardfish	2

Table 2.15. Least squares regression equations relating prey length to prey measurements for five or the more significant teleost prey items in the diets of the four species-life stages. Prey items are listed in alphabetical order according to their family and scientific name. FL = fork length (mm); TL = total length (mm). Prey measurements were: BD = body depth (mm), CPD = caudal peduncle depth (mm), SOL = snout to operculum length (mm), and TOW = total otolith weight (g). Syx = standard error of regression coefficient; r-squared values = coefficients of determination; n = number of fish measured. All regressions are highly significant ($p < 0.0001$).

Prey Species	**Equation**	**Size Range**	**Syx**	**r-squared**	**n**
F. Arridae					
Bagre marinus	FL = 4.8690 (BD) + 26.5415	55-600 mm FL	0.0182	0.9528	144
(gaftopsail catfish)	FL = 14.9927 (CPD) – 16.7754		0.0181	0.9613	120
	FL = 3.7724 (SOL) + 33.9460		0.0098	0.9866	142
	FL = 68.3877 (TOW) + 171.9117		0.0303	0.8779	135
F. Clupeidae					
Brevoortia spp.	FL = 2.7060 (BD) + 20.3968	115-295 mm FL	0.0171	0.9587	144
(menhaden)	FL = 10.0422 (CPD) + 15.4794		0.0203	0.8968	252
	FL = 3.9450 (SOL) – 23.9203		0.0196	0.9444	146
F. Sciaenidae					
Cynoscion arenarius	TL = 5.5546 (BD) – 17.2871	65-340 mm TL	0.0279	0.9704	40
(sand seatrout)	TL = 14.6235 (CPD) – 19.1422		0.0360	0.9507	40
	TL = 3.6508 (SOL) + 30.9773		0.0347	0.9543	40
	TL = 343.1364 (TOW) + 94.1085		0.0666	0.8444	37
Micropogonias undulatus	TL = 3.1539 (BD) + 36.9735	125-185 mm TL	0.0450	0.9210	41
(Atlantic croaker)	TL = 12.7963 (CPD) + 3.8134		0.0680	0.8332	38
	TL = 3.1497 (SOL) + 46.5881		0.0468	0.9055	42
	TL = 260.7964 (TOW) + 104.8578		0.0520	0.8920	42
Stellifer lanceolatus	TL = 3.5547 (BD) + 9.5699	28-175 mm TL	0.0362	0.9463	43
(star drum)	TL = 11.9011 (CPD) – 2.6273		0.0518	0.9249	30
	TL = 3.8262 (SOL) + 23.9079		0.0721	0.8491	31
	TL = 748.9227 (TOW) + 54.7936		0.0541	0.8887	40

Table 2.16. Regression equations relating maximum, median, and minimum prey size to shark fork length for Atlantic sharpnose and blacktip sharks in Apalachicola Bay, Florida, April-October 2001-2002. PL = prey length in millimeters; FL = shark fork length in millimeters. The 90th and 10th quantiles were used to estimate the upper and lower bounds and the 50th quantile was used to estimate the median of each prey size-predator size scatter diagram.

Species	**90th quantile**	**50th quantile**	**10th quantile**	**n**
Atlantic sharpnose shark	PL=0.1412FL+49.3298 p=0.0014	PL=0.1088FL+38.0664 p<0.0001	PL=0.0969FL+11.4515 p=0.0019	57
Blacktip shark	PL=0.0877FL+123.9238 p=0.0308	PL=0.0678FL+98.6307 p=0.0067	PL=0.0288FL+87.0298 p=0.0610	85
Finetooth shark	PL=0.1134FL+85.4660 p=0.5092	PL=0.0149FL+124.9974 p=0.3117	PL=-0.08234FL+172.3953 p=0.4961	25

Figure 2.1. Average catch per unit effort (CPUE) by month of Atlantic sharpnose, blacktip, finetooth, and spinner sharks in Apalachicola Bay, Florida (1996-2000). (a) Apalachicola Bay, Florida, and (b) Crooked Island Sound, Florida. CPUE is defined as the number of sharks caught per hour per 186 m gillnet. Data courtesy of SPAG NOAA NMFS Panama City, Florida.

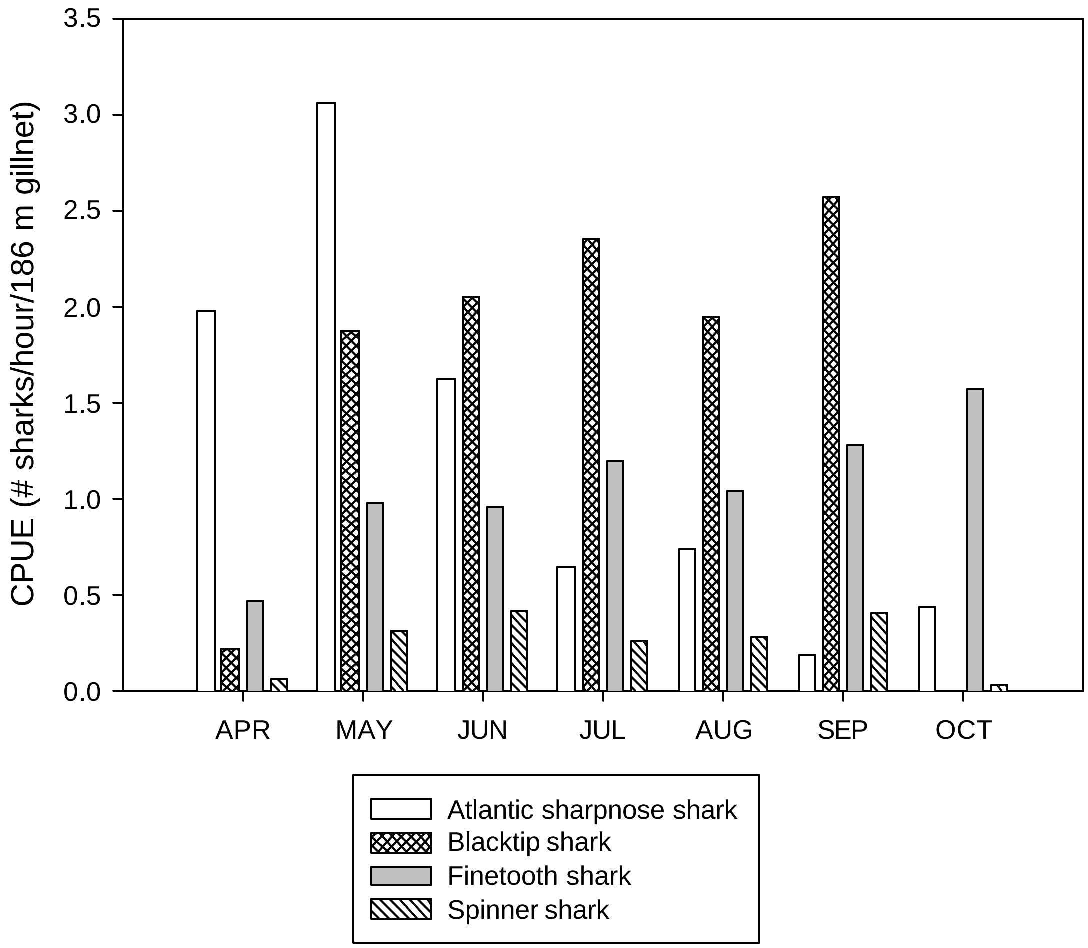


Figure 2.2. Map of Apalachicola Bay, Florida. Sharks and potential prey items were taken from fishery-independent surveys conducted by NMFS on the Gulf of Mexico side of St. Vincent Island, Florida, at the southwest end of the Apalachicola Bay system between Indian Pass and West Pass from April through October of 1999-2002. Map courtesy of Troy Tuckey, FMRI.

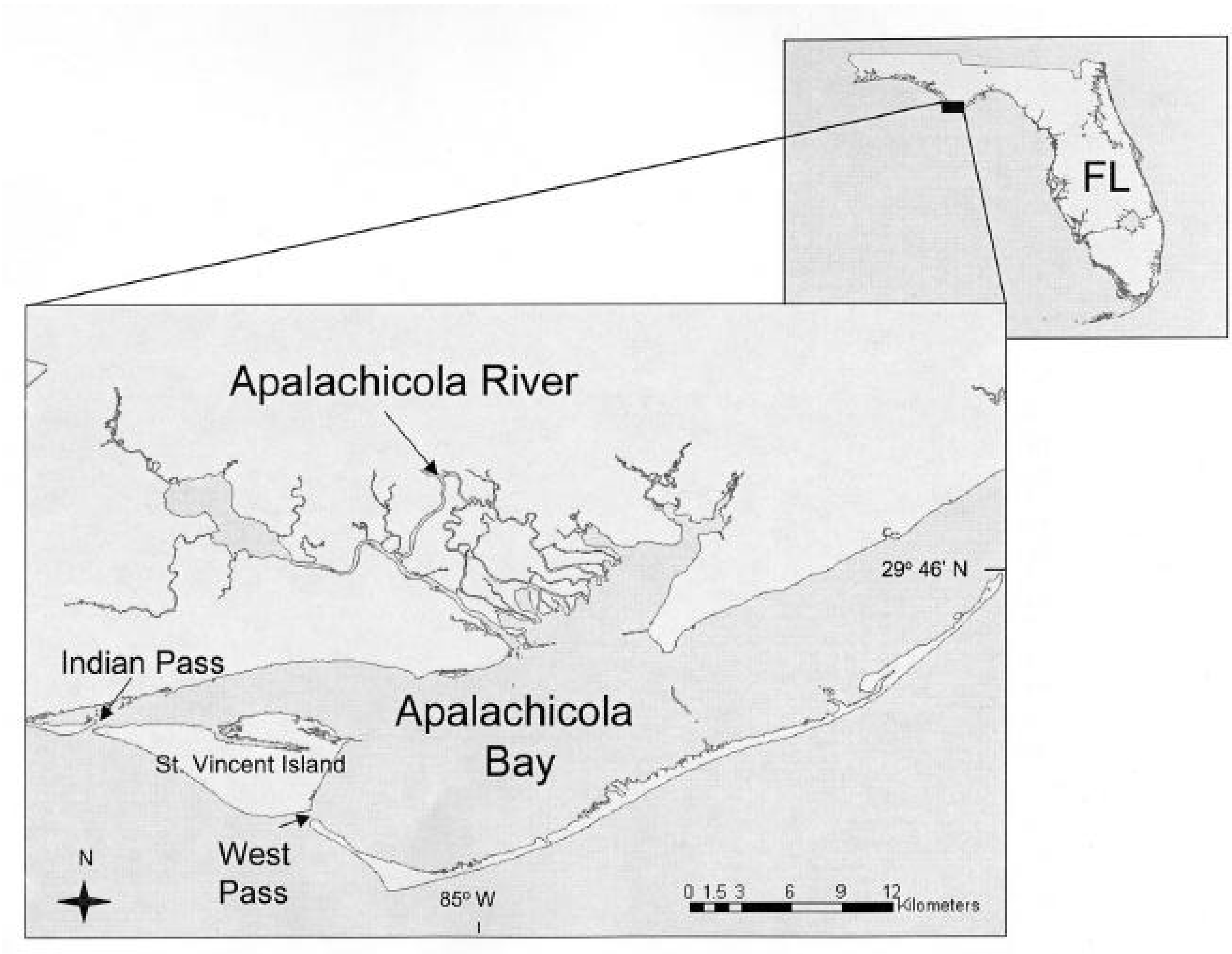


Figure 2.3. Relative frequency histograms of species-life stages examined from Apalachicola Bay, Florida, April-October 1999-2002. Open bars are young-of-the-year, cross-hatched bars are juveniles, and closed bars are adults. (a) Atlantic sharpnose shark (young-of-the-year=201, juvenile=25, adult=74), (b) blacktip shark (young-of-the-year=75, juvenile=155), (c) finetooth shark (young-of-the-year=14, juvenile=95), and (d) spinner shark (young-of-the-year=48, juvenile=24).

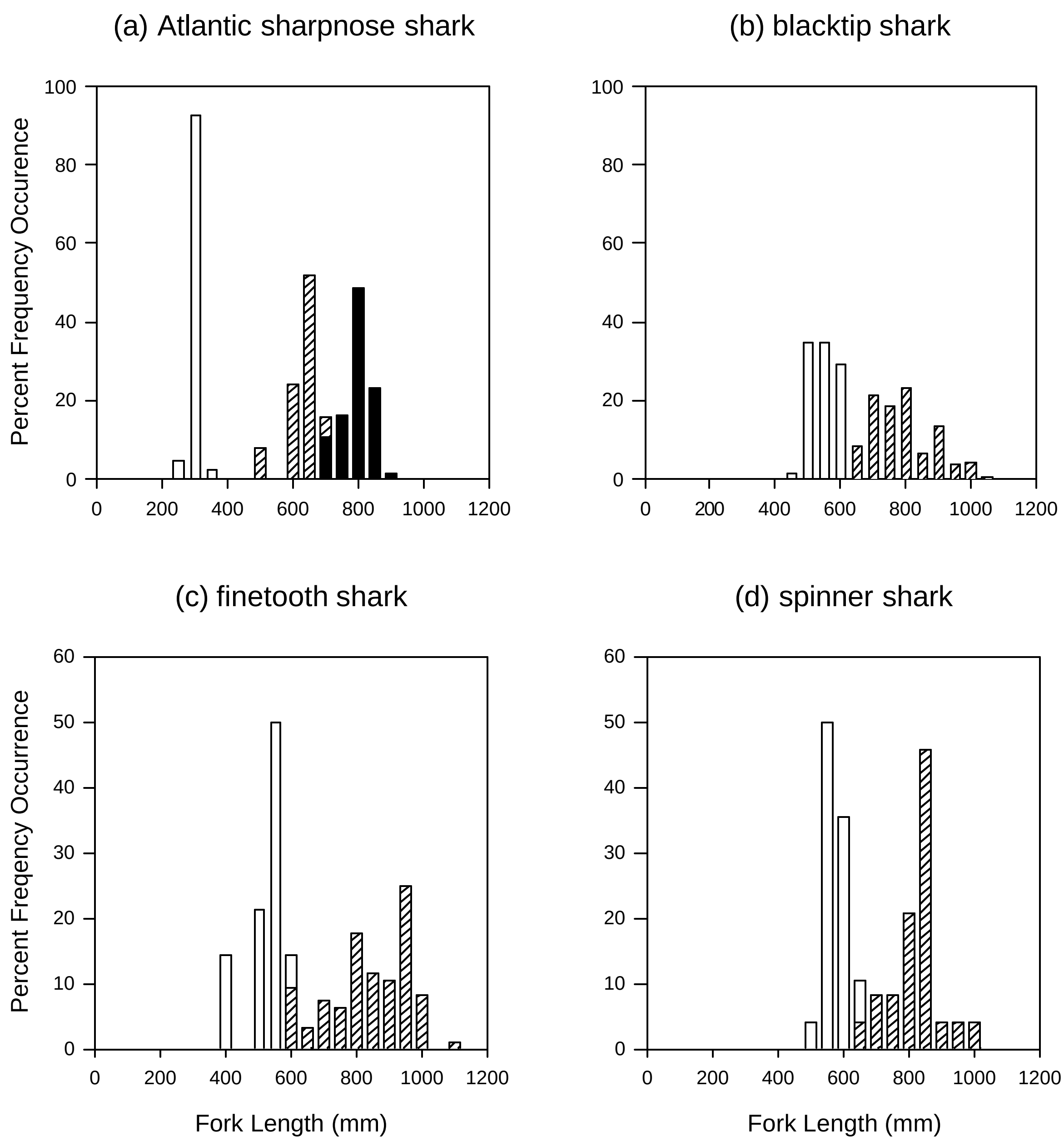


Figure 2.4. Diets of Atlantic sharpnose shark early life stages collected in Apalachicola Bay, Florida, April-October 1999-2002. (a) young-of-the-year, (b) juvenile, and (c) adult.

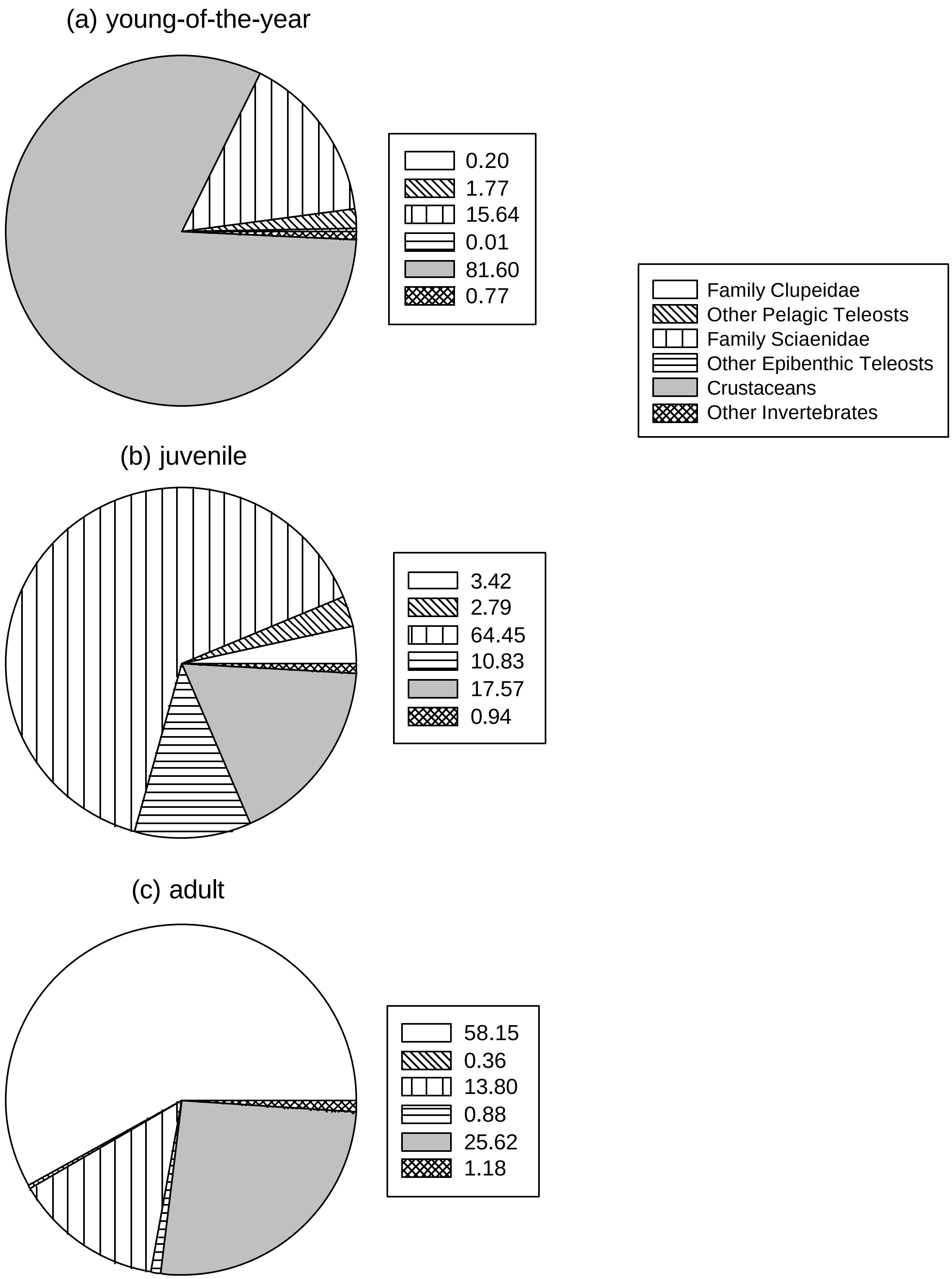


Figure 2.5. Diets of blacktip shark early life stages collected in Apalachicola Bay, Florida, April-October 1999-2002. (a) young-of-the-year, and (b) juvenile.

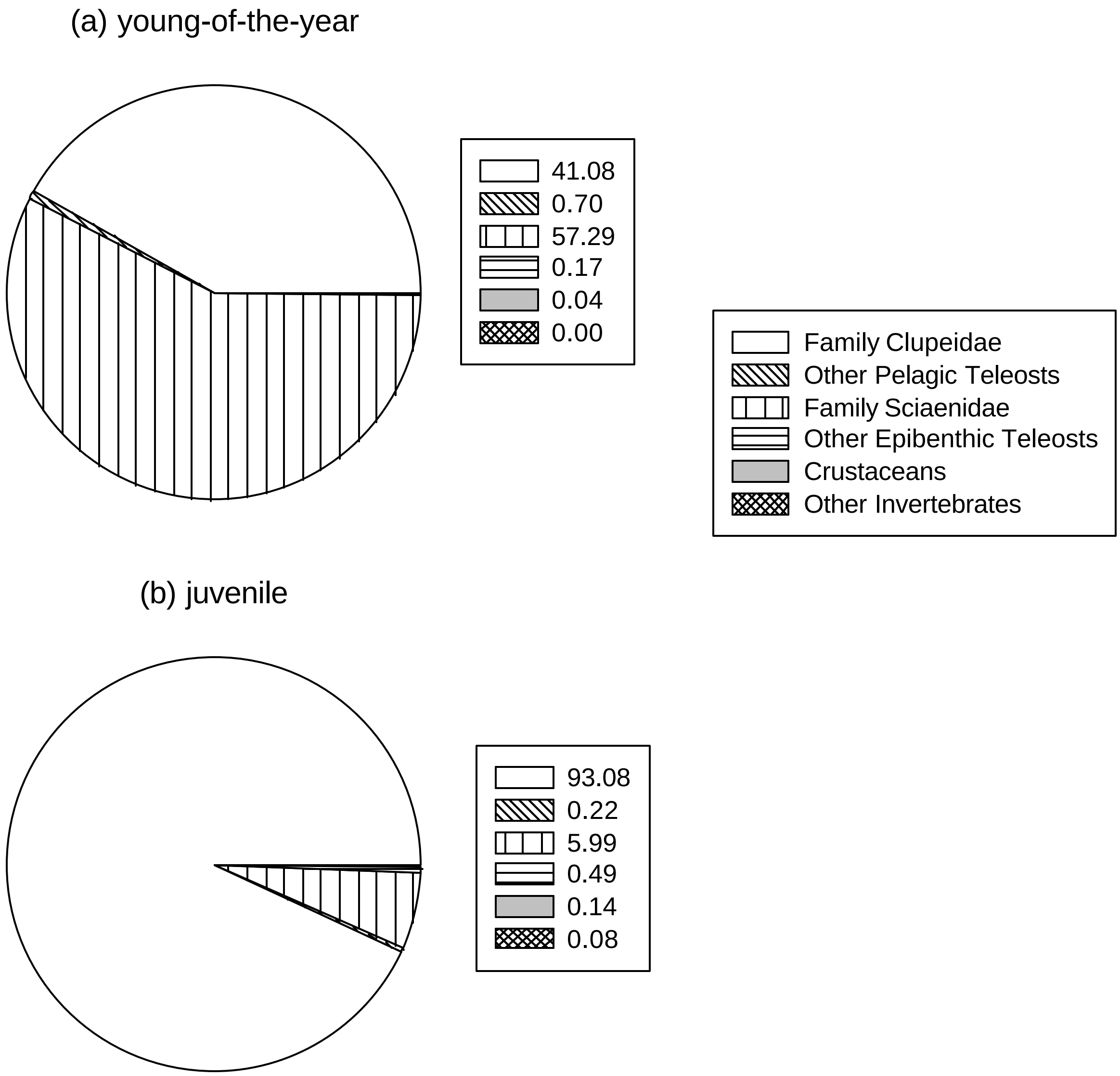


Figure 2.6. Randomized cumulative prey curves for Atlantic sharpnose sharks collected in Apalachicola Bay, Florida, April-October 1999-2002. (a) young-of-the-year (n=201), (b) juvenile (n=25), (c) adult (n=74). Means are plotted.

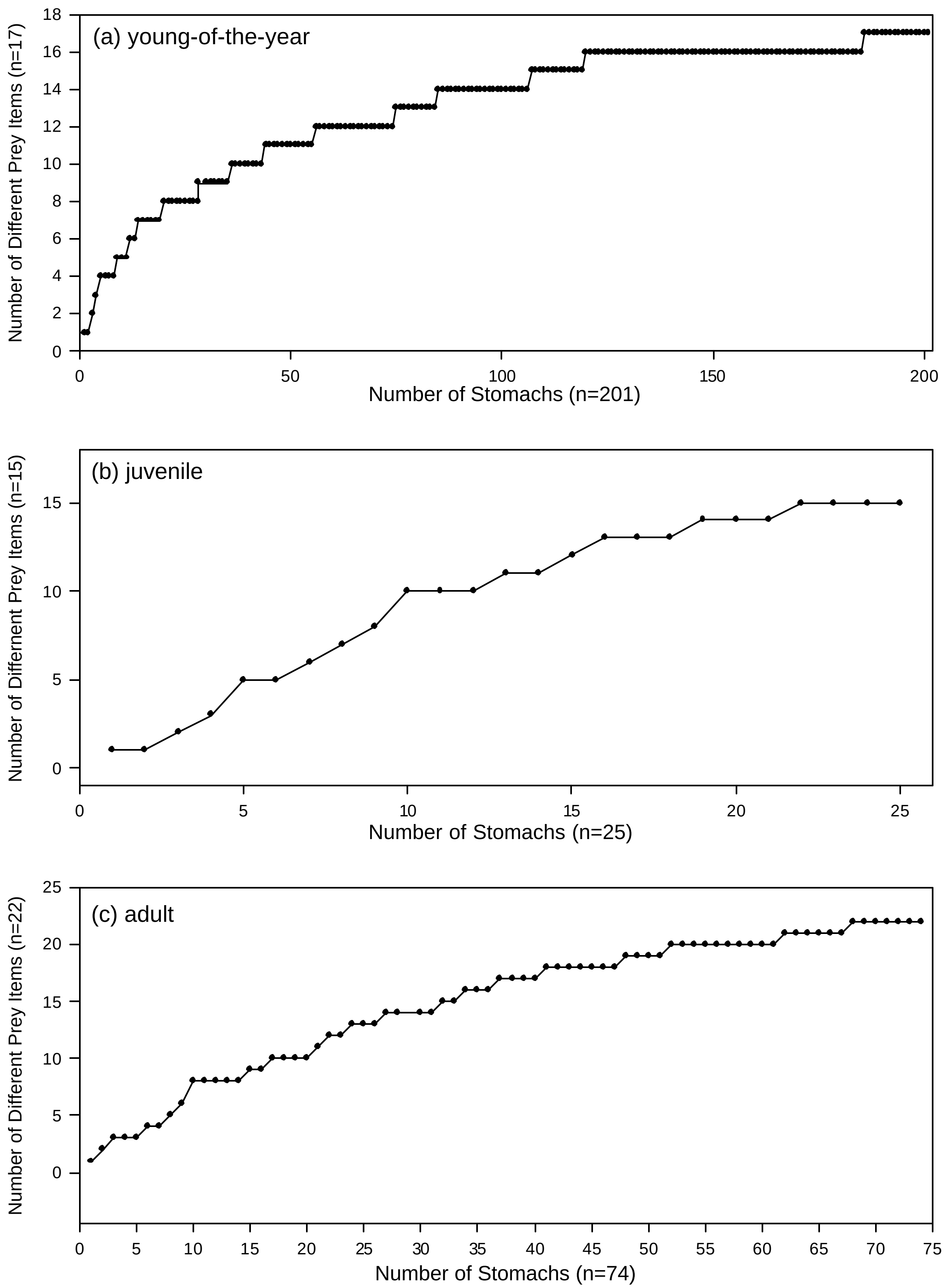


Figure 2.7. Randomized cumulative prey curves for blacktip sharks collected in Apalachicola Bay, Florida, April-October 1999-2002. (a) young-of-the-year (n=75) and (b) juvenile (n=155). Means are plotted.

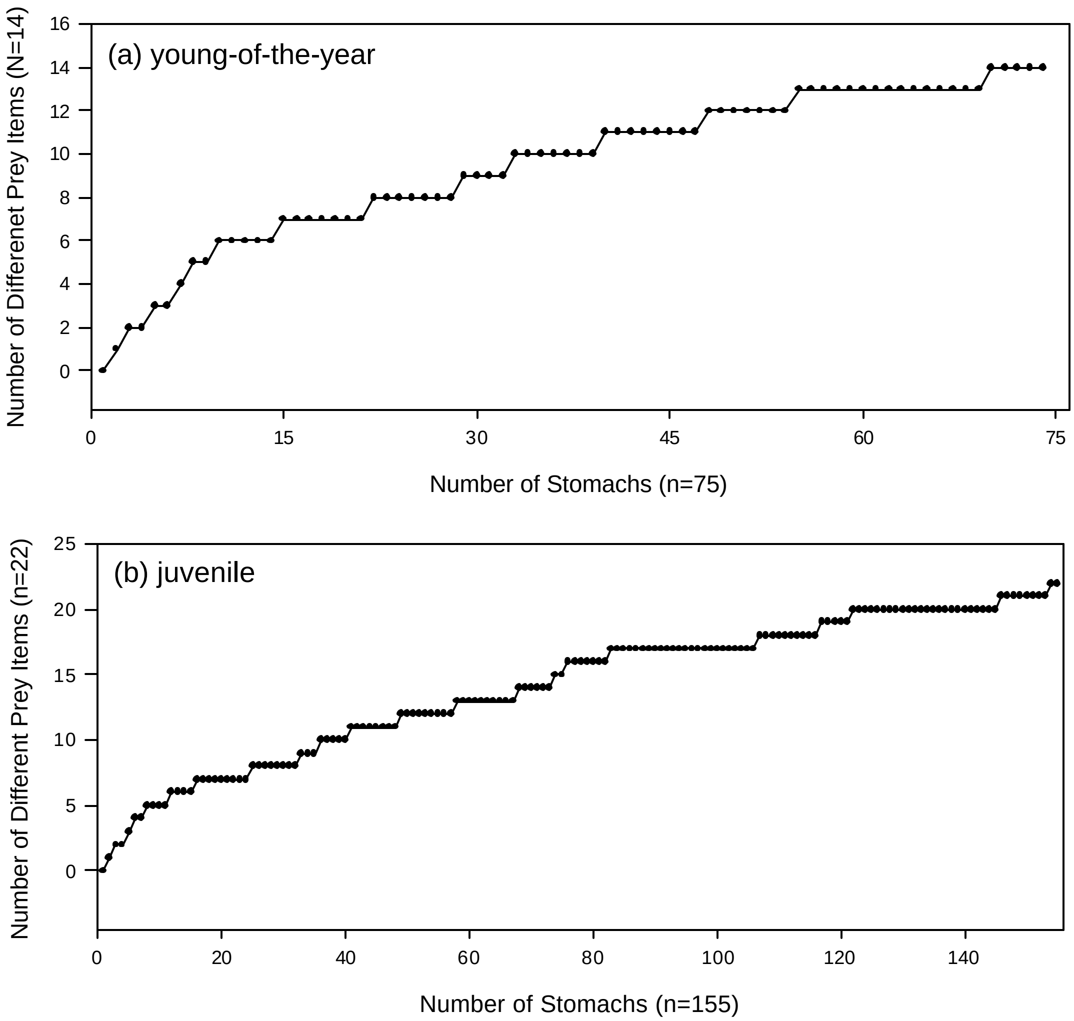


Figure 2.8. Randomized cumulative prey curves for finetooth and spinner sharks collected in Apalachicola Bay, Florida, April-October 1999-2002. (a) young-of-the-year and juvenile finetooth sharks (n=109) and (b) young-of-the-year and juvenile spinner sharks (n=72). Means are plotted.

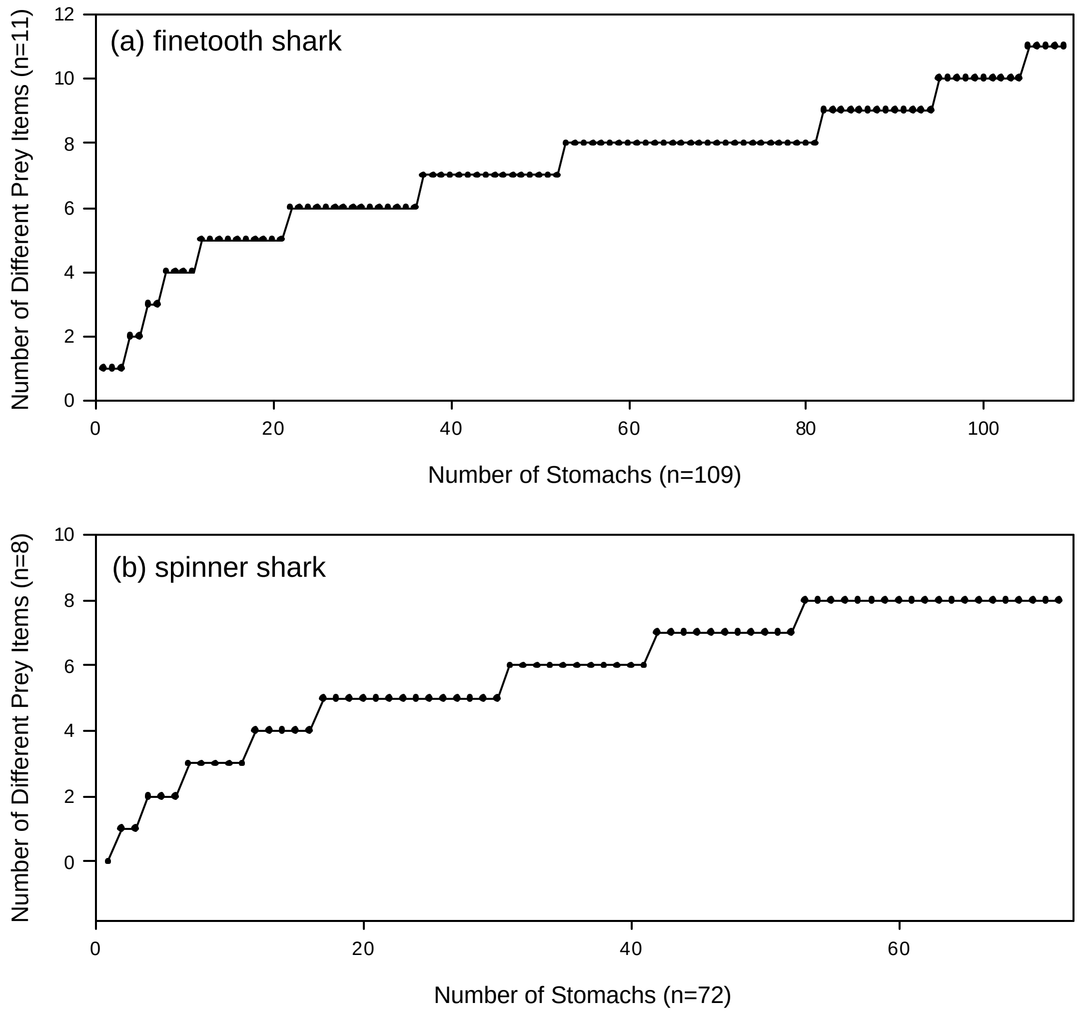


Figure 2.9. Relative size frequency distributions of *Brevoortia spp.* found in Apalachicola Bay, Florida May-October 2001-2002 (positive y-axis) and in stomachs (negative y-axis). (a) Atlantic sharpnose shark (n=10), (b) blacktip shark n=17), and (c) finetooth shark (n=17). Open positive bars = distribution data gathered from FMRI (n=145). Closed positive bars = distribution data gathered from NMFS (n=482).

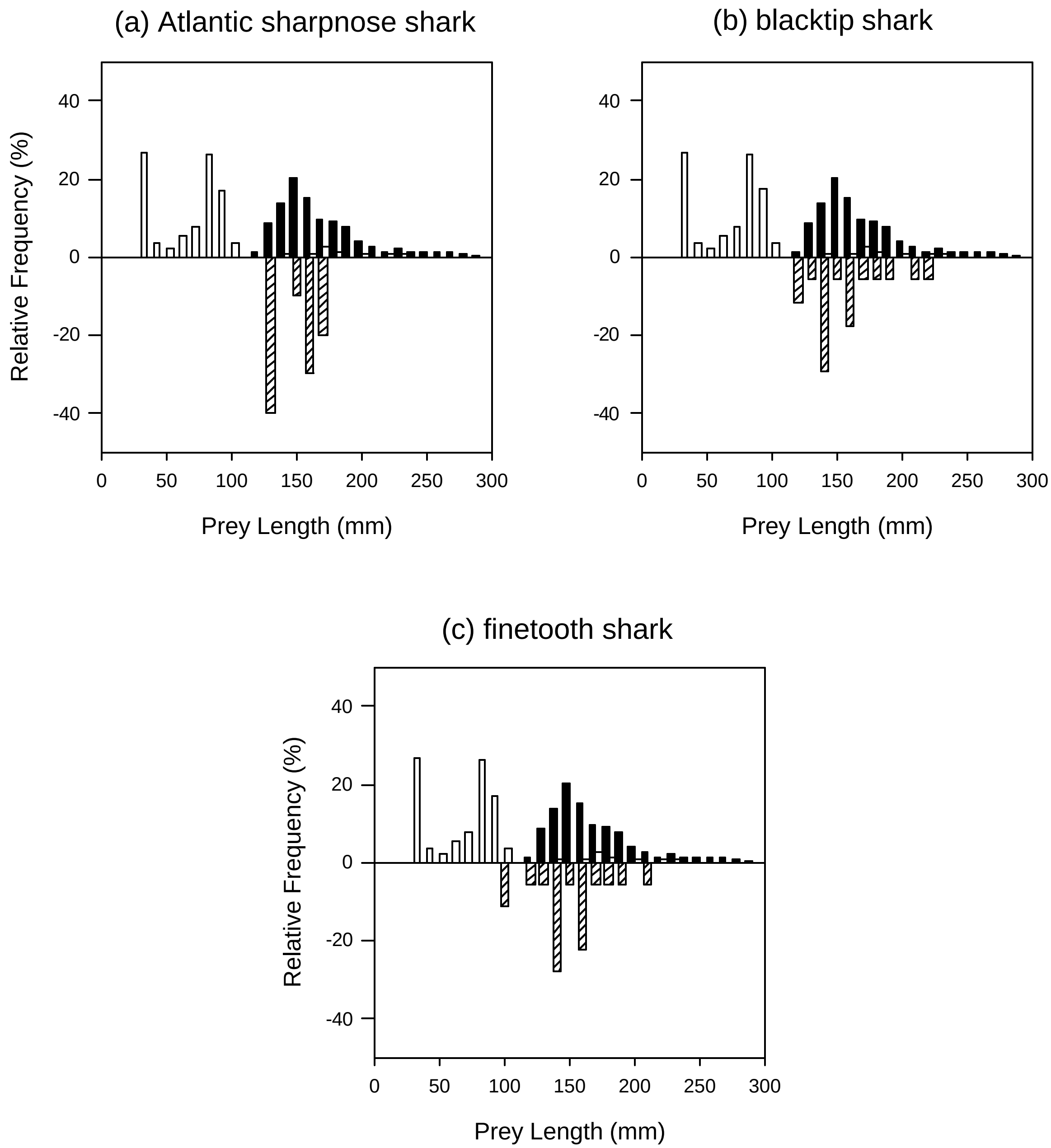


Figure 2.10. Relative size frequency distributions of *Micropogonias undulatus* found in Apalachicola Bay, Florida April-October 2001-2002 (positive y-axis) and in stomachs (negative y-axis). (a) Atlantic sharpnose shark (n=21) and (b) blacktip shark (n=22). Open positive bars = distribution data gathered from FMRI (n=314). Closed positive bars = distribution data gathered from NMFS (n=34).

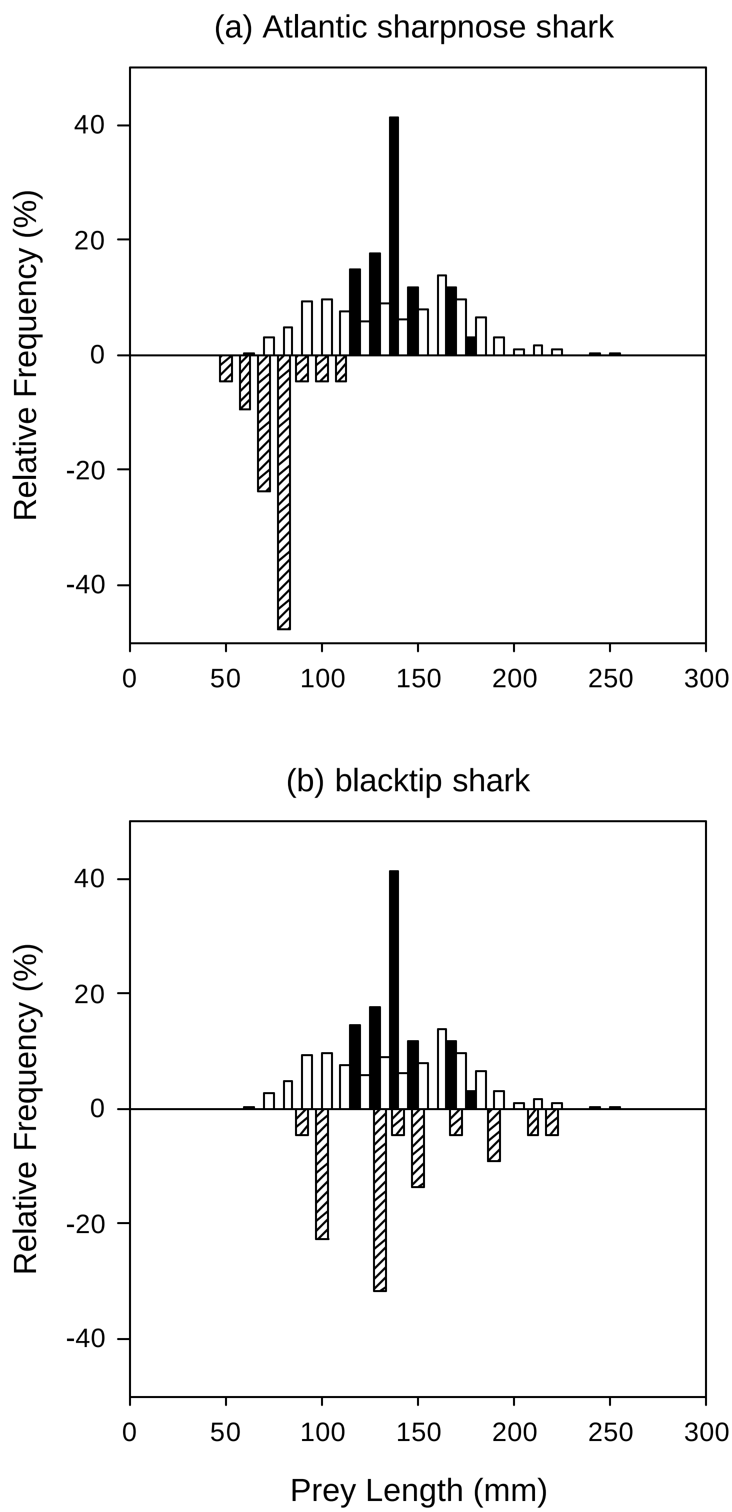


Figure 2.11. Relative size frequency distributions of *Stellifer lanceolatus* found in Apalachicola Bay, Florida April-October 2001-2002 (positive y-axis) and in stomachs (negative y-axis). (a) Atlantic sharpnose shark (n=13) and (b) blacktip shark (n=21). Closed positive bars = distribution data gathered from NMFS during fall and summer months (n=119).

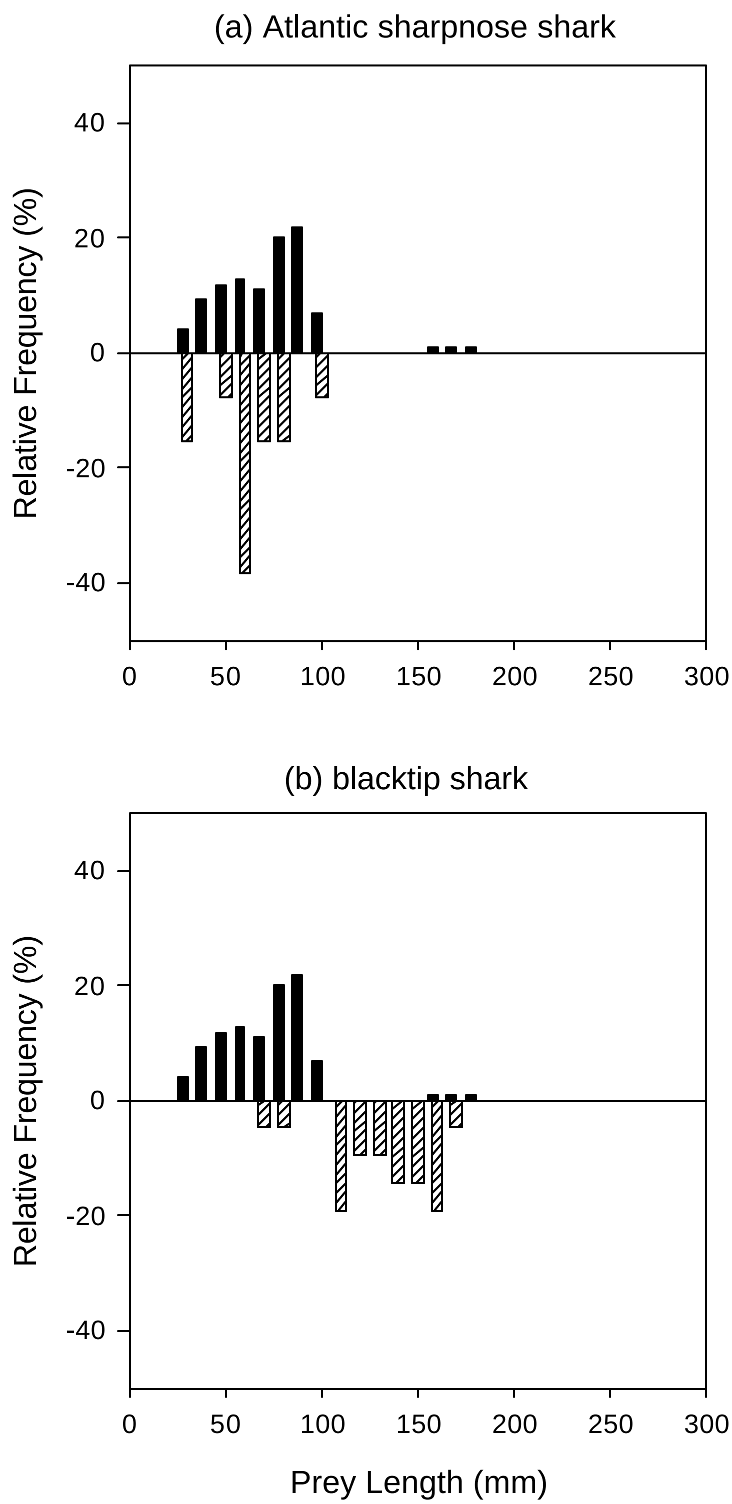


Figure 2.12. Prey size-predator size scatter diagrams for (a) Atlantic sharpnose, (b) blacktip, and (c) finetooth sharks in Apalachicola Bay, Florida. Each symbol is a single teleost prey eaten by a shark. Dark circle was omitted for analysis. Lines represent quantile regressions used to examine changes in prey size eaten with increasing shark size. Solid lines = median prey sizes. Dashed lines = minimum and maximum prey sizes. Regression equations are presented in Table 2.16.

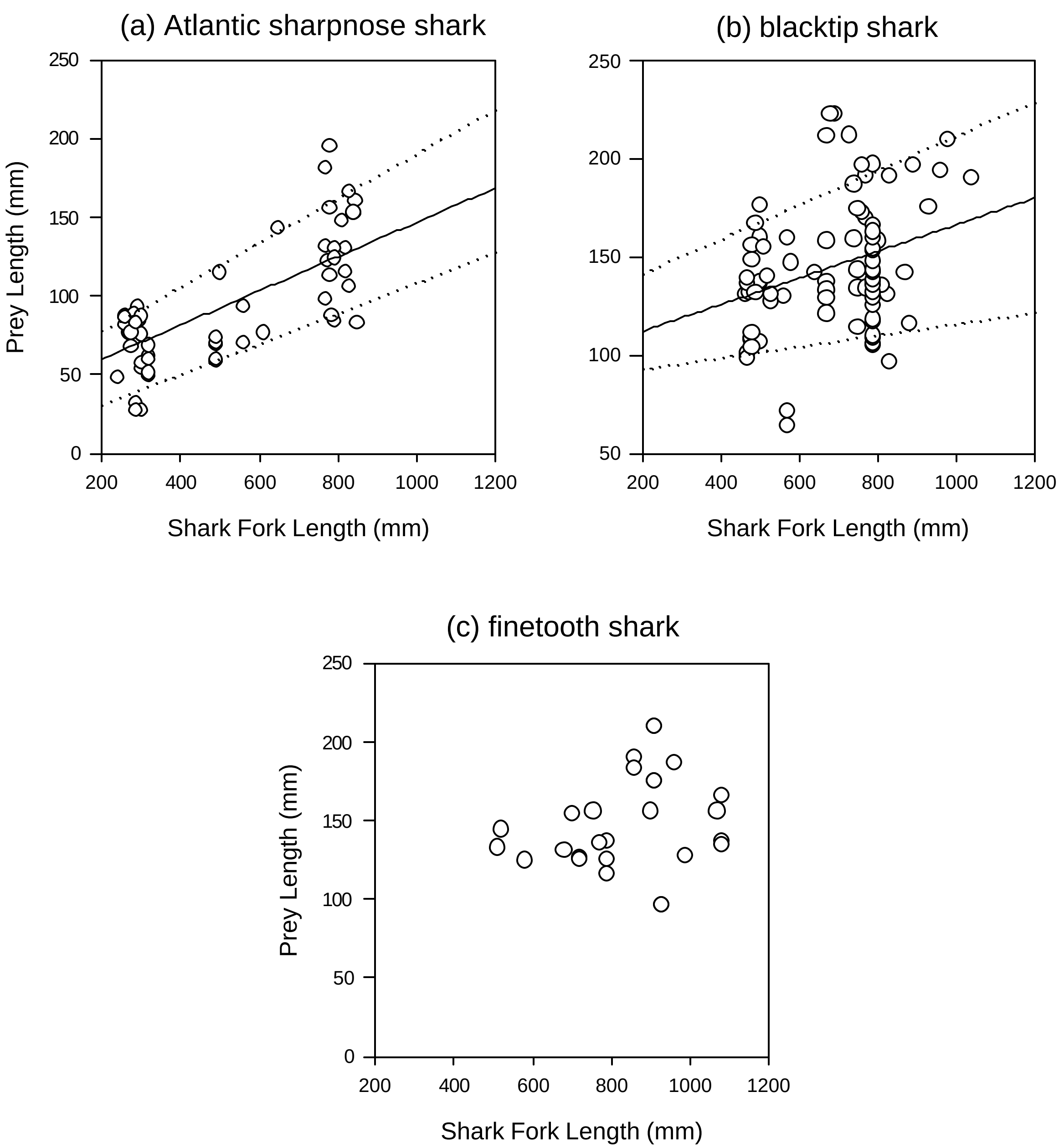


Figure 2.13. Distributions of prey size-predator size ratios for (a) Atlantic sharpnose, (b) blacktip, and (c) finetooth sharks in Apalachicola Bay, Florida. Open bars = relative frequencies at 0.1% intervals. Filled Circles = cumulative frequencies at 0.1% intervals.

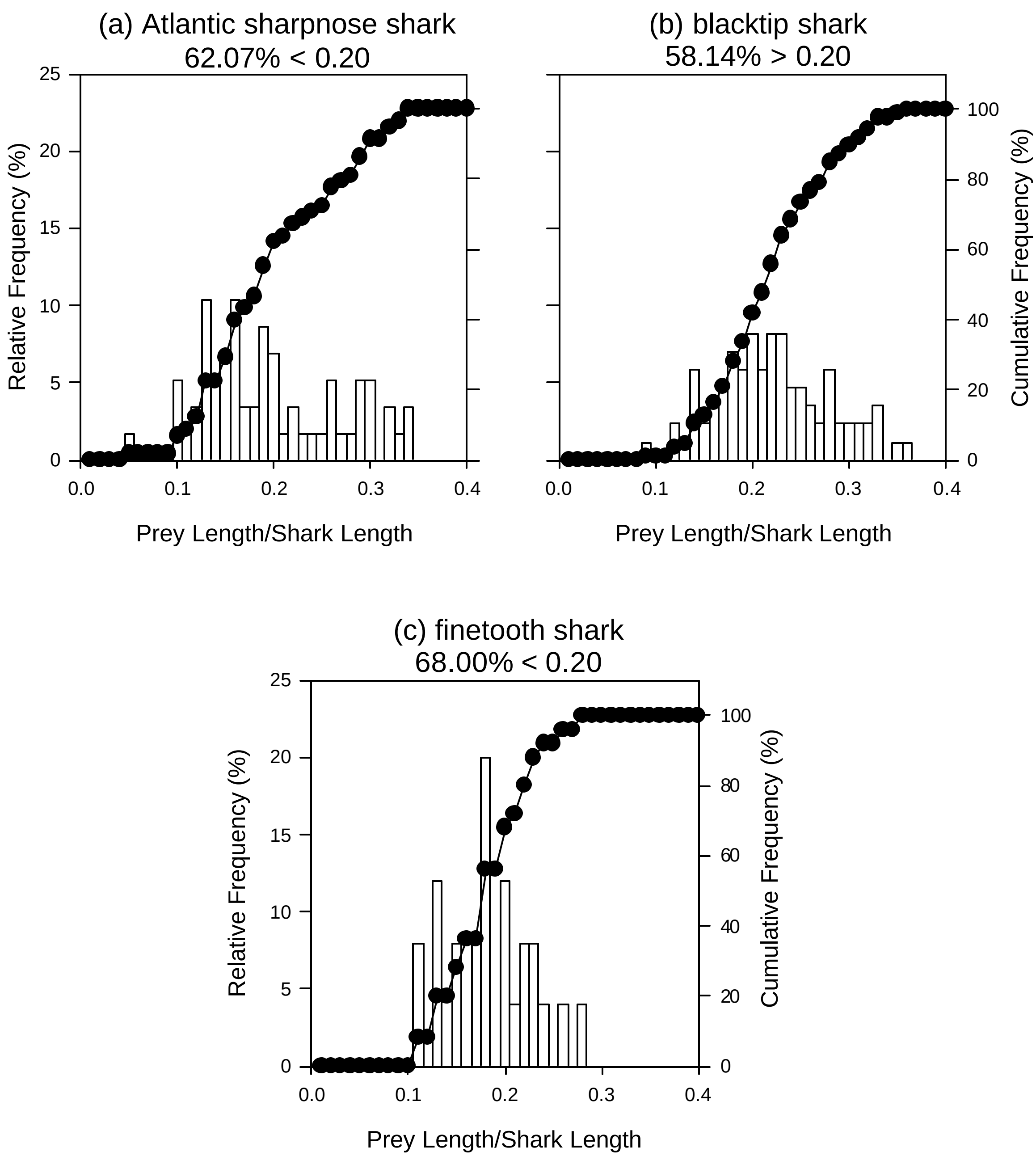
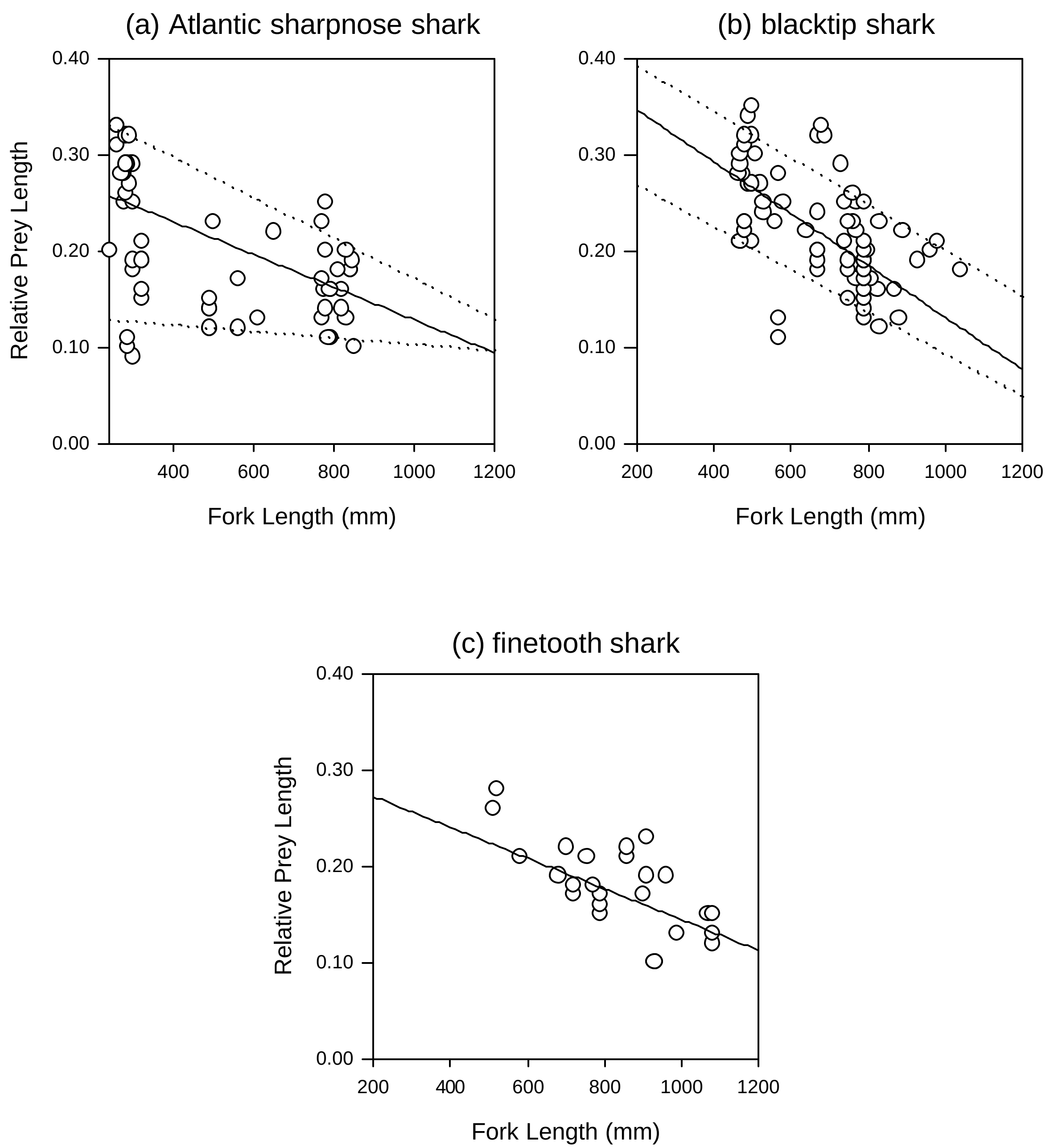


Figure 2.14. Scatter diagrams illustrating prey size-predator size ratio as a function of predator size for (a) Atlantic sharpnose, (b) blacktip, and (c) finetooth sharks in Apalachicola Bay, Florida. Each symbol represents the ratio of a single teleost prey eaten. Regression lines indicate change in the ranges of relative prey sizes eaten (trophic niche breadth) with increasing shark size.



LITERATURE CITED

Ackerman, J.T., M.C. Kondratieff, S.A. Matern, and J.J. Cech, Jr. (2000). Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environmental Biology of Fishes 58: 33-43.

Baba, O., Taniuchi, T., and Y. Nose (1987). Depth distribution and food habits of three species of small squaloid sharks off Choshi. Nippon Suisan Gakkaishi 53: 417-424.

Barry, K.P. (2002). Feeding habits of blacktip sharks, *Carcharhinus limbatus*, and Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, in Louisiana coastal waters. MSc. Thesis, Louisiana State University Baton Rouge, Louisiana: 80p.

Branstetter, S. (1990). Early life-history implications of selected carcharhinoid and lamniod sharks of the northwest Atlantic. NOAA Tech. Rep. NMFS 90: 17-28.

Buckel, J.A., M.J. Fogarty, and D.O. Conover (1999). Foraging habits of bluefish, *Pomatomus saltatrix*, on the U.S. east coast continental shelf. Fishery Bulletin 97: 758-775.

Carlson, J.K. and J.H. Brusher (1999). An index of abundance for coastal species of juvenile sharks from the northeast Gulf of Mexico. Marine Fisheries Review 61: 37-45.

Carrasson, M., Stefanescu, C., and J. E. Cartes (1992). Diets and bathymetric distributions of two bathyl sharks of the Catalan deep sea (western Mediterranean). Marine Ecology Progress Series 82: 21-30.

Castro, J.I. (1989). The biology of the golden hammerhead, *Sphyrna tudens*, off Trinidad. Environmental Biology of Fishes 24: 3-11.

Castro, J.I. (1993). The biology of the finetooth shark, *Carcharhinus isodon*. Environmental Biology of Fishes 36: 219-232.

Clarke, T.A. (1971). The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. Pacific Science 25: 133-144.

Cliff, G. (1995). Sharks caught in the protective gill nets off Kwazulu-Natal, South Africa. 8. The great hammerhead shark (*Sphyrna mokarran*) (Ruppell). South African Journal of Marine Science 15: 105-114.

Compagno, L.J.V. (1984). Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Species Catalogue, Vol. 4 Parts 1 and 2. 655 pp.

Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54: 726-738.

Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science 56: 707-717.

Cortés, E. and S. H. Gruber (1990). Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). Copeia 1: 204-218.

Cortés, E., Manire, C. A., and R. E. Hueter (1996). Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in southwest Florida. Bulletin of Marine Science 58: 353-367.

Cross, J.N. (1988). Aspects of the biology of two scyliorhind sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California. Fishery Bulletin 86: 691-702.

Crowder, L.B. (1990). Community ecology *In* Methods for Fish Biology. C.B. Schreck and P.B. Moyle (eds.). Bethesda, Maryland, American Fisheries Society: 609-632.

DeCrosta, M.A., Taylor, L.R., Jr., and J.D. Parrish (1984). Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. Pages 75-95 in Proceedings of the second symposium on resource investigations in the northwest Hawaiian Islands. Vol. 2, May 25-27, 1983. Univ. Hawaii Sea Grant MR-84-01.

De Silva, J.A., R.E. Condrey, and B.A. Thompson (2001). Profile of shark by catch in the U.S. Gulf of Mexico menhaden fishery. North American Journal of Fisheries Management 21: 111-124.

Dudley, S.F.J. and G. Cliff (1993). Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark Carcharhinus limbatus (Valenciennes). South African Journal of Marine Science 13:237-254.

Ebert, D.A., Compagno, L.J.V., and P.D. Cowley (1992). A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. South African Journal of Marine Science 12: 601-609.

Ebert, D.A., Cowley, P.D., and L.J.V. Compagno (1996). A preliminary investigation of the feeding ecology of catsharks (Scyliorhinidae) off the west coast of southern Africa. South African Journal of Marine Science 17: 233-240.

Ebert, D.A. (2002). Ontogenetic changes in the diet of the sevengill shark (*Notorhynchus cepedianus*). Marine and Freshwater Research 53: 517-523.

Ellis, J.R., M.G. Pawson, and S.E. Shackley (1996). The comparative feeding ecology of six species of sharks and four species of ray (Elasmobranchii) in the northeast Atlantic. Journal of the Marine Biological Association of the United Kingdom 76: 89-106.

Euzen, O (1987). Food habits and diet compositions of some fish of Kuwait. Kuwait Bulletin of Marine Science 9: 65-85.

Ferry, L.A. and G.M. Cailliet (1996). Sample size and data: Are we characterizing and comparing diet properly? p.71-80 *In* Feeding Ecology and Nutrition in Fish: Proceedings of the Symposium on the Feeding Ecology and Nutrition in Fish, International Congress on the Biology of Fishes, San Francisco, California. American Fisheries Society.

Gelsleichter, J., J.A. Musick, and S. Nichols (1999). Food habits of the smooth dogfish, *Mutelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, and the sand tiger shark, *Carcharias taurus*, from the northwest Atlantic Ocean. Environmental Biology of Fishes 54: 205-217.

Gotelli, N.J. and G.L. Entsminger (2003). EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Burlington, VT 05465. http://homepages.together.net/~gentsmin/ecosim.htm.

Gruber, S. H. (1982). Role of the lemon shark, *Negaprion brevirostris* (Poey), as a predator in the tropical marine environment: a multidisciplinary study. Florida Scientist 45: 46-75.

Gruber, S.H., D.R. Nelson, and J.F. Morrissey (1988). Patterns of activity and space utilization of lemon sharks, Negaprion brevirostris, in a shallow Bahamian lagoon. Bulletin of Marine Science 43: 61-76.

Helfman, G.S., B.B. Collette, and D. Facey (1999). The Diversity of Fishes. Malden, Massachusetts, Blackwell Science, Inc.: 179-196, 221-243.

Heupel, M.R. and R.E. Hueter (2002). Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Marine and Freshwater Research 53: 543-550.

Heupel, M.R. and C.A. Simpfendorfer (2002). Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Canadian Journal of Fishery and Aquatic Sciences 59: 624-632.

Hoese, H.D. (1962). Sharks and rays of Virginia's seaside bays. Chesapeake Science 3: 166-172.

Horn, H.S. (1966). Measurement of "overlap" in comparative ecological studies. The American Naturalist 100: 419-424.

Jennings, S. and M.J. Kaiser (1998). The effects of fishing on marine ecosystems. *In* Advances in Marine Biology. Academic Press, London. pp. 201-352

Juanes, F. (1994). What determines prey size selectivity is piscivorous fishes? *In* Theory and application in fish feeding ecology. D.J. Stouder, K.L. Fresh, and R.J. Feller (eds.). Belle W. Baruch Library in Marine Sciences, no.18, University of South Carolina Press, Columbia, SC. pp.79-100

Juanes, F. and D.O. Conover (1995). Size-structured piscivory: advection and linkage between predatory and prey recruitment in young-of-the-year bluefish. Marine Ecology Progress Series 128: 287-304.

Jobling, M. and A. Breiby (1986). The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71: 265-274.

Kitchell, J.F., T.E. Essington, C.H. Boggs, D.E. Schindler, and C.J. Walters (2002). The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. Ecosystems 5: 202-216.

Krebs, C.J. (1999a). Niche Measures and Resource Preferences *In* Ecological Methodology. E. Fogarty, V. McDougal and N. Murray (eds.). Menlo Park, California, Addison-Wesley Educational Publishers, Inc: 455-493.

Krebs, C.J. (1999b). Ecologic al Methodology Version 5.1. Department of Zoology, University of British Columbia. http://nhsbig.inhs.uiuc.edu/wes/krebs.html

Lalli, C.M. and T.R. Parsons (1997). The Abiotic Environment *In* Biological Oceanography, An Introduction. Woburn, MA, Reed Educational and Professional Publishing Ltd.: 21-24.

Livingston, R.J. 1983. Resource atlas of the Apalachicola estuary. Florida Sea Grant Publication. 64 pp.

Livingston, R.J. and E.A. Joyce, editors (1977). Proceedings of the conference on the Apalachicola drainage system, Gainesville, Florida. Florida Marine Research Publication No. 26.

Lowe, C. G., B. M. Wetherbee, et al. (1996). Ontogenetic dietary shift and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environmental Biology of Fishes 47: 203-211.

McEachran, J. D., D. F. Boesch, and J.A. Musick (1976). Food division within two sympatric species-pirs of skates (Pisces: Rajidae). Marine Biology 35: 301-317.

Macpherson, E. (1980). Régime alimentaire de *Galeus melastomus* (Rafinesque, 1810), *Etmopterus spinax* (L., 1758) et *Scymnorhinus licha* (Bonnaterre, 1788) en Méditerranee occidentale. Vie Milieu 30: 139-148.

Mauchline, J, and J.D.M. Gordon (1983) Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. Marine Biology 75: 269-278.

NMFS (1993). Fishery management plan for sharks of the Atlantic Ocean. Silver Springs, MD, U.S. Department of Commerce, Washington D.C. National Oceanic and Atmospheric Administration: 167p.

NMFS (1999a). Fishery management plan of the Atlantic tunas, swordfish and sharks. Silver Springs, MD, U.S. Department of Commerce, Washington D.C. National Oceanic and Atmospheric Administration: 321p.

NMFS (1999b). Ecosystem-based fishery management: A report to Congress by the Ecosystems Principles Advisory Panel. U.S. Department of Commerce, Washington D.C. National Oceanic and Atmospheric Administration: 53p.

National Marine Fisheries Service Narragansett, Rhode Island, Apex Predator Program. Last Updated 10 December 2002. Retrieved 24 February 2003. http://na.nefsc.noaa.gov/sharks/index.html

National Marine Fisheries Service Panama City, Florida, Shark Population Assessment Group. Last Updated 11 December 2002. Retrieved 24 February 2003. http://199.242.233.41/shark/shark_final_1.htm

National Marine Fisheries Service Pascagoula, Mississippi, Shark Team. Retrieved 24 February 2003. http://www.mslabs.noaa.gov/mslabs/resource/shark/shark.html

National Marine Fisheries Service Statistics and Economics Division. Last Updated 2 October 2002. Retrieved 8 January 2003. http://www.st.nmfs.gov/st1/

Parsons, G.R. (1987). Life history and bioenergetics of the bioenergetics of the bonnethead shark Sphyrna tiburo: a comparison of two populations. PhD. Dissertation, University of South Florida at St. Petersburg, Florida: 170p.

Pianka, E.R. (1976). Competition and niche theory *In* Theoretical ecology: principals and applications. R.M. May (ed.). Philadelphia, PA, W.D. Saunders: 114-141.

Platell, M.E., I.C. Potter, R.R. Clarke (1998). Resource partitioning by four species of elasmobranchs (Batoidae: Urolophidae) in coastal waters of temperate Australia. Marine Biology 131: 719-734.

Popova, O.A. (1978). The role of predaceous fish in ecosystems *In* Ecology of Freshwater Fish Production (Gerking, S.D., ed.), pp. 215-249. New York: John Wiley.

Protected Areas Geographic Information System project (PAGIS). Last updated 15 August 2000. Retrieved 3 April 2003. http://www.csc.noaa.gov/pagis/index.htm

Prout, M.W., E.L. Mills, and J.L. Forney (1990). Diet, growth, and potential competitive interactions between age-0 white perch and yellow perch in Oneida Lake, New York. Transactions of the American Fishery Society 119: 966-975.

Ross, S.T. (1986). Resource partitioning in fish assemblages: a review. Copeia 2: 352-388.

Salini, J.P., Blaber, S.J.M., and D.T. Brewer (1990). Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. Marine Biology 105: 363-374.

Salini, J.P., Blaber, S.J.M., and D.T. Brewer (1992). Diets of sharks from estuaries and adjacent waters of the north-eastern Gulf of Carpentaris, Australia. Australian Journal of Marine and Freshwater Research 43: 87-96.

Schindler, D.E., T.E. Essington, J.F. Kitchell, C. Boggs, and R. Hilborn (2002). Sharks and tunas: fisheries impacts on predators with contrasting life histories. Ecological Applications 12: 735-748.

Scharf, F.S., F. Juanes, and M. Sutherland (1998). Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. Ecology 79: 448-460.

Scharf, F.S., F. Juanes, and R.A. Roundtreee (2000). Predator-prey relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series 208: 229-248.

Schoener, T.W. (1974). Resource partitioning in ecological communities. Science 185: 27-39.

Simpfendorfer, C.A. and N.E. Milward (1993). Utilization of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environmental Biology of Fishes 37: 337-345.

Simpfendorfer, C.A., A. Goodreid, and R.B. McAuley (2001). Diet of three commercially important shark species from Western Australian waters. Marine and Freshwater Research 52: 975-985.

Smale, M.J. (1991). Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the eastern cape coast of South Africa. South African Journal of Marine Science 11: 31-42.

Smith, E.P. and T.M. Zaret (1982). Bias in estimating niche overlap. Ecology 63: 1248-1253.

Snelson, F.F. and S.E. Williams (1981). Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River lagoon system, Florida. Estuaries 4: 110-120.

Snelson, F.F., T.J. Mulligan, and S.E. Williams (1984). Food habits, occurrence and population structure of the bull shark, *Carcharhinus leucas*, in Florida coastal lagoons. Bulletin of Marine Science 34: 71-80.

Springer, S. (1967). Social organization of shark populations *In* Sharks, Skates and Rays. P.W. Gilbert, R.F. Mathewson and D.P. Rall (eds.). Baltimore, John Hopkins University Press. pp.149-174.

Stevens, J.D. (1984). Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. Proceedings of the Royal Society of London. Series B: Biological Sciences 222: 79-106.

Stevens, J. D., and K. J. McLoughlin (1991). Distribution, size, and sex composition, reproductive biology and diet of sharks from northern Australia. Australian Journal of Marine and Freshwater Research 40:129-146.

Stevens, J.D., R. Bonfil, N.K. Dulvy, and P.A. Walker (2000). The effects of fishing on sharks, rays, and chimeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science 57: 476-494.

Talent, L.G. (1982). Food habits of the gray smoothhound, *Mustelus californicus*, the brown smoothhound, *Mustelus henlei*, the shovelnose guitarfish, *Rhinobatos productus*, and the bay ray, *Myliobatis californica*, in Elkhorn Slouch, California. California Fish and Game 68: 224-234.

Virginia Institute of Marine Science Fisheries Ecosystem Monitoring and Assessment Project. Last Updated 17 December 20002. Retrieved 24 February 2003. http://www.fisheries.vims.edu/femap/index.html

Wetherbee, B.M., G.L. Crowe, and C.G. Lowe (1996). Biology of the Galapagos shark, *Carcharhinus galapagensis*, in Hawaii. Environmental Biology of Fishes 45: 299-310.

Winemiller, K.O. and E.R. Pianka (1990). Organization and natural assemblages of desert lizards and tropical fishes. Ecological Monographs 60: 27-55.

Wooton, R.J. (1998). Ecology of Teleost Fishes. Norwell, MA, Kluwer Academic Publishers: 27-63, 195-215.

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

Yano, K. 1991. Catch distribution, stomach contents, and size at maturity of two squaloid sharks, *Deania calcea* and *D. crepidalbus*, from the southeast Atlantic off Namibia. Bulletin of the Japanese Society of Fisheries Oceanography 55:189-196.

Zar, J.H. (1999). Biostatistical Analysis. Prentice-Hall, New Jersey. 4th Edition. p.223-226.