ONTOGENETIC AND SITE-RELATED TRENDS IN THE DIET OF THE ATLANTIC SHARPNOSE SHARK *RHIZOPRIONODON TERRAENOVAE* FROM THE NORTHEAST GULF OF MEXICO

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ABSTRACT

Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson, 1836) diet is described from Crooked Island Sound, an embayment of the northeast Gulf of Mexico. Diet was assessed by life-stage and quantified using six indices: percent by number, percent by weight, frequency of occurrence, the index of relative importance (IRI), IRI expressed on a percent basis (%IRI), and %IRI based on prey category (%IRI$_{PC}$). Young-of-the-year (YOY) sharks (n = 56 examined, 37 non-empty stomachs) fed on a mix of teleosts (mostly clupeids, 44.6 %IRI$_{PC}$) and invertebrates (combined, 25.1 %IRI$_{PC}$), juveniles (n = 185 examined, 118 non-empty stomachs) on sciaenids (40.7 %IRI$_{PC}$) and clupeids (37.8 %IRI$_{PC}$), and mature sharks (n = 105 examined, 67 non-empty stomachs) on sciaenids (71.4 %IRI$_{PC}$). Differences in diet by site and ontogeny were tested by comparing the diet from Crooked Island Sound with previous published data from areas off St. Vincent Island in Apalachicola Bay, an adjacent estuary. Stomach contents were also used to expand on published prey size-predator size information. Spearman correlation analysis, Pianka's overlap values, null-model simulations, and simple correspondence analysis showed that life stage diet differed within and between sites. Three of four size-selectivity tests showed negative size selection. Absolute prey size and the range in absolute prey size increased with increasing shark size. Atlantic sharpnose shark diet was dominated by prey that were < 40% of shark length; however, 69% of prey items were 21%–40% of shark length while 26% were ≤ 20% of shark length. Variations in diet composition within and between the two sites are likely due to differences in shark size, overall habitat structure, and availability of potential prey species.

Sharks are hypothesized to be apex predators that structure marine communities through predation (Cortés, 1999). Despite this, there are few quantitative data on the diet of sharks. Quantitatively describing the diet and foraging ecology, habitat use, and predator-prey interactions of top predators in a community is a key step in ecosystem approaches to fisheries management; therefore, it is important that life-stage specific biological and ecological information be gathered to aid in the assessing and monitoring of shark populations and their prey.

The Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson, 1836) is the most abundant and exploited small coastal shark in U.S. Atlantic and Gulf of Mexico waters (Cortés, 2002). Atlantic sharpnose sharks are known to occur in a variety of coastal habitats in the Gulf of Mexico, some of which are proposed nursery areas (McCandless et al., 2002). In the northeast Gulf of Mexico, juvenile and mature Atlantic sharpnose sharks recruit to coastal waters beginning in April (Carlson and Brusher, 1999). Neonate sharks begin arriving in June (Carlson and Brusher, 1999; Carlson, 2002) and all life stages are present by late June and generally remain inshore until they emigrate offshore in the fall (Carlson and Brusher, 1999).

Few studies on the diet of Atlantic sharpnose shark have been completed. Barry (2002) and Hoffmayer and Parsons (2003) reported that Atlantic sharpnose sharks feed primarily on gulf menhaden *Brevoortia patronu*s (Goode, 1878) in coastal waters of Louisiana and Mississippi. Further, Hoffmayer and Parsons (2003) suggested an ontogenetic shift in diet from penaeid shrimp as juveniles to gulf menhaden when mature. Bethea et al. (2004) examined the diet of Atlantic sharpnose sharks from the Apalachicola Bay system in Florida and noted an ontogenetic shift in diet from crustaceans to teleosts. In the latter two studies, sciaenids were more important in the diet of sharks collected off Florida than those collected off Mississippi. These differences in diet may be due in part either to methodology and/or prey selection and availability by region. Bethea et al. (2004) also examined prey size selectivity and prey size-predator size relationships throughout all life history stages of Atlantic sharpnose shark; however, the study contained little diet information for juvenile sharks (40–75 cm fork length, FL). Information regarding predator selection and prey availability by habitat type is essential in determining which habitats provide a greater "nursery value" for a given species (Beck et al., 2001). The purpose of this study was to investigate and compare the foraging ecology of Atlantic sharpnose sharks from two hypothesized northeast Gulf of Mexico nursery areas with very different habitats. Here, we (1) describe and quantify the diet of each life stage within Crooked Island Sound, Florida; (2) compare the diet of life stages within Crooked Island Sound to previously published diet data from areas off St. Vincent Island, Florida (Bethea et al., 2004); (3) test for ontogenetic changes within Crooked Island Sound and compare those trends to trends observed at St. Vincent Island; and (4) expand on the prey size-predator size relationships for Atlantic sharpnose sharks presented in Bethea et al. (2004).

Methods

Sampling Areas.—Sharks were collected from fishery-independent surveys conducted in Crooked Island Sound, Florida (~30°N, 85°30′W), from April to October of 2002 and 2003 (Fig. 1). Crooked Island Sound is a semi-enclosed, relatively shallow barrier island system with one opening to the Gulf of Mexico. This area is characterized by seagrass beds, *Thalassia testudinum* (Banks and Solander ex König, 1805) and *Halodule wrightii* (Ascherson, 1868), and sand or mud flats (Collard, 1992; Carlson and Bethea, unpubl. data).

Previous research provided comparative data for sharks collected off St. Vincent Island, Florida (~29°40′N 85°10′W), in the Apalachicola Bay system from April to October of 2000 to 2002 (Bethea et al., 2004). In this area, there are no clear microhabitats (e.g., seagrass beds, sand flats, or tidal lagoons). Benthic habitat is generally uniform and characterized by a mix of clay, sand, and mud over a limestone bottom (Livingston, 1984).

Diet Composition.—*Collection of Sharks.*—A 186 m multi-panel, variable-stretch mesh gillnet was set randomly by depth strata and GPS location in depths ranging from 3 to 6 m. Most sets were made between 0700 and 1500 hrs CST. The net was anchored at both ends, allowed to soak for 0.75–1.0 hrs, and then retrieved and cleared of catch (following Carlson and Brusher, 1999). For each shark sampled, FL (mm), weight (kg), sex, and life stage were determined. The life stage of each shark was assessed and categorized as: (1) young-of-the-year (YOY; i.e., age 0+), characterized by either an open or healed but visible umbilical scar, (2) juvenile, defined as those not yet mature, or (3) mature. For males, mature sharks were those with well-developed testes, hardened claspers, and the ability to spread the rhipidion. Mature females were those with developed oocytes or the presence of pups (Parsons, 1983). In the field, sharks were placed in an ice-slurry for 1 hr before stomachs were extracted, placed
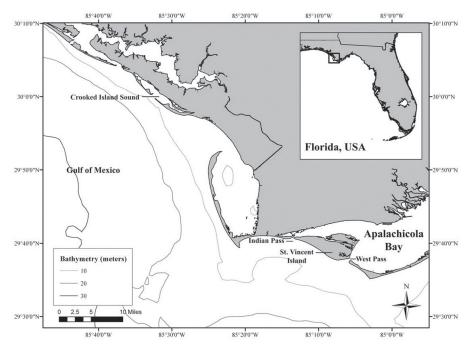
Figure 1. Map of sampling areas. Sharks were collected in Crooked Island Sound (latitude ~30°N 85°30′W), and on the Gulf of Mexico side of St. Vincent Island between Indian Pass and West Pass (~29°40′N, 85°10′W).

in labeled plastic bags, stored on ice, and frozen upon return to the laboratory. Occasionally, whole sharks were placed on ice and stomachs extracted in the laboratory.

Processing of Stomachs.—Stomachs were processed following Bethea et al. (2004). In general, stomachs were thawed, opened, and rinsed with water over a 595 μm sieve. Prey items found in the stomachs were identified to the lowest possible taxon, counted, and weighed. When possible for teleost prey items, FL or total length (TL) was measured directly. When partial teleost prey or whole but digested teleost prey were present and length could not be measured directly, the partial prey measurements of body depth (BD), caudal peduncle depth (CPD), snout to operculum length (SOL), and/or total otolith weight (TOW) were measured and predictive equations (detailed below) were used to estimate original FL or TL.

Analysis of Stomach Contents.—Diet was assessed by life-stage. Diets were quantified using three indices: percent by number (%N), percent by weight (%W), and percent by frequency of occurrence (%O). The index of relative importance (IRI; Pinkas et al., 1971) was also calculated as 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 among life-stages and sites, identifiable prey items were categorized into six major prey categories (PC) following Bethea et al. (2004): (1) family Clupeidae; (2) other pelagic teleosts; (3) family Sciaenidae; (4) other epibenthic teleosts; (5) crustaceans; and (6) other invertebrates. The index of relative importance on a percent basis was computed for the six major prey categories (%IRI$_{PC}$) and used in all analyses. Unidentifiable prey items were not used in any analyses.

Cumulative prey curves were constructed a posteriori for each life-stage to determine if an adequate number of stomachs had been collected to accurately describe diets (Ferry and Cailliet, 1996). When the curve reaches a stable asymptote, the number of stomachs analyzed is considered sufficient for describing dietary habits.

Ontogenetic and Site-Related Changes in Diet.—Because diet can be affected by changes in prey availability, dietary analysis was calculated using all diet data combined and the 2002 data only (the year that both locations were sampled simultaneously). To avoid low sample sizes of the 2002 collections, analysis was restricted to life-stages where at least three stomachs contained identifiable prey. All life-stages except YOY in Crooked Island Sound and juveniles at St. Vincent Island met this criterion, thus between site comparisons in 2002 were limited to mature sharks only. The %IRI of major prey category (%IRI$_{PC}$) was used in all comparisons. St. Vincent Island %IRI$_{PC}$ values are previously published in Bethea et al. (2004).

Three methods were used to test for changes in diet with ontogeny and site. First, differences were calculated using the Spearman rank correlation coefficient (r_s) following Fritz (1974) because the data violated assumptions of parametric tests. The null hypothesis for r_s was that the diets of the two groups being compared (e.g., YOY to juvenile in Crooked Island Sound) were not correlated ($r_s = 0$); therefore, if r_s was significant, the null hypothesis was rejected and the diets were considered similar. This method is preferred to overlap indices because it is not affected by the number of prey groupings that are chosen (Cortés, 1997).

Dietary overlap was calculated using Ecological Methodology v5.1 software (Krebs, 1999). All resources were assumed equally abundant and resource states were presented as %IRI$_{PC}$. Diet overlap values were obtained using Pianka's overlap index where resource state was prey category. Overlap index values range from 0 (no overlap) to 1.0 (complete overlap), and values ≥ 0.6 are considered "biologically significant" overlap (Pianka, 1976). The observed overlap values were then compared to a distribution of expected overlap values based on null-model simulations. The distribution of null-model data came from 1000 randomizations of the diet data (R3 randomization algorithm; Winemiller and Pianka, 1990). Simulations were performed using EcoSim v7.42 software (Gotelli and Entsminger, 2005). The observed value was considered statistically different from the null distribution if it was greater than or less than the simulated index 95% of the time (P < 0.05; Winemiller and Pianka, 1990). An observed value significantly less than the simulation index would suggest differences in diet or diet partitioning while an observed value significantly higher than the simulation index would suggest similarities in diet or the lack of competition for food resources.

Simple correspondence analysis was used to detect trends in diet relative to factors such as location (following Graham and Vrijenhoek, 1988) and ontogeny. In the contingency tables, life-stages were entered as rows and %IRI$_{PC}$ values as columns. A Chi-square test was used to verify that the rows and columns were independent.

Analysis of Potential Prey.—*Collection of Potential Prey.*—To determine size, number, and type of potential prey items in Crooked Island Sound, teleosts collected from the 186 m gillnet were placed on ice in the field, stored on ice at 4°C overnight, and examined the following day. A shorter (100 m) three-panel gill net with smaller variable stretch-mesh sizes (2.5–7.6 cm in intervals of 2.5 cm) was used to better sample potential prey size distributions (following Bethea et al., 2004). The 100 m gillnet was anchored at both ends, set in the same general location as the 186 m gillnet at least once a month from June to October in both years, allowed to soak for 2.0–5.0 hrs, retrieved, and cleared of catch as previously described. Because gillnets were inadequate in sampling epibenthic prey, a 6.7 m, semi-balloon otter trawl was used to sample prey sizes at least twice a month from June to October while gillnets were fishing. The trawl was towed parallel to the shore at 3.7 km/hr for 10 min at depths of approximately 3 m. Catch was cleared from the trawl and stored as previously described. Because of their condition from the trawl and the difficulty in recreating length, invertebrates were not used in any analyses.

Prey Size Analysis.—Potential prey items were measured (nearest mm) to obtain FL or TL, BD, CPD, and SOL, and weighed (nearest 0.1 g). Sagittal otoliths were removed and TOW measured. Predictive equations were constructed relating potential prey length (either FL or TL; both sites combined) with BD, CPD, SOL, and TOW using least-squares regression analysis (Zar, 1999). Equations used to reconstruct *Brevoortia* spp., gafftopsail catfish *Bagre marinus* (Mitchill, 1815), and star drum *Stellifer lanceolatus* (Holbrook, 1855) were taken

from Bethea et al. (2004). Equations used to reconstruct sand seatrout *Cynoscion arenarius* (Ginsburg, 1930) and Atlantic croaker *Micropogonias undulatus* (Linnaeus, 1766) were updated from Bethea et al. (2004). Predictive equations were generated for silver perch *Bairdiella chrysoura* (Lacepède, 1802), pinfish *Lagodon rhomboides* (Linnaeus, 1766), southern kingfish *Menticirrhus americanus* (Linnaeus, 1758), and Atlantic thread herring *Opisthonema oglinum* (Lesueur, 1818). These nine prey species made up most of the available prey and diets of Atlantic sharpnose sharks in Crooked Island Sound.

Size-selective feeding was examined by comparing sizes of potential fish prey to sizes of prey that were recovered from shark stomachs at that site. Because of low occurrence of measurable prey in the stomachs, length-frequency histograms were constructed for four of the nine major prey items taken from shark stomachs. Size selective feeding on *Brevoortia* spp., *C. arenarius*, *M. undulatus*, and *O. oglinum* was assessed for Atlantic sharpnose sharks in Crooked Island Sound. 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, an absolute prey size-predator size diagram was plotted for both areas combined. 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., 2000) were used to determine the upper and lower bounds (90th and 10th quantiles) of the relation between prey size and shark size. All teleost prey either found whole in stomachs or reconstructed using regression equations were used in these analyses. To examine the patterns of prey size use, a relative and cumulative frequency histogram of prey size-predator size ratios was created.

Results

Diet Composition.—*Analysis of Stomach Contents.*—A total of 346 Atlantic sharpnose sharks were examined for dietary analysis from collections made in Crooked Island Sound. Of those, 56 were YOY (250–520 mm FL; mean FL = 360.1 mm; 37 non-empty stomachs), 185 were juvenile (410–700 mm FL; mean FL = 542.2 mm; 118 non-empty stomachs), and 105 were mature (560–860 mm FL; mean FL = 737.7 mm; 67 non-empty stomachs).

Stomach contents of YOY Atlantic sharpnose shark included arthropods (decapod and isopod crustaceans), molluscs (squid, an unidentified gastropod, and one species of bivalve), one platyhelminth (Cestoda), and teleosts (representing seven families; Table 1A). Using diet data from all years combined (Fig. 2A), clupeids were the most important identifiable prey item in YOY diets from Crooked Island Sound (44.6% IRI_{PC}). Epibenthic teleosts other than sciaenids (mostly sparids and syngnathids) were the second most important identifiable prey item (18.1 %IRI_{PC}). Invertebrates other than crustaceans (12.8 %IRI_{PC}), crustaceans (12.3 %IRI_{PC}), and pelagic teleosts other than clupeids (10.9%IRI_{PC}) were also important in the diet. Sciaenids were of little dietary importance (1.4 %IRI_{PC}). Samples of YOY sharks in 2002 did not meet criterion for prey category analysis (Fig. 2B).

Juvenile Atlantic sharpnose shark stomachs contained angiosperms (*H. wrightii* and *T. testudinum*), annelids (Terebellidea), arthropods (decapod and isopod crustaceans), elasmobranchs (Dasyatidae), molluscs (squid), and teleosts (representing 12 families; Table 1B). Diet data from all years combined (Fig. 2A) indicated that sciaenids (mostly *Cynoscion* spp. and *M. undulatus*; 40.7 %IRI_{PC}) and clupeids (mostly *Brevoortia* spp. and *O. oglinum*; 37.8 %IRI_{PC}) dominated identifiable prey in juvenile diets from Crooked Island Sound. Other important identifiable prey items included crustaceans (mostly shrimp; 10.8 %IRI_{PC}) and epibenthic teleosts other than sciae-

Table 1. Stomach contents of (A) young-of-the-year (YOY; 250–520 mm FL; mean = 360.1 mm; N = 37 non-empty stomachs), (B) juvenile (410–700 mm FL; mean = 542.2 mm; N = 118 non-empty stomachs), and (C) mature (560–860 mm FL; mean = 737.7 mm; N = 67 non-empty stomachs) Atlantic sharpnose sharks from Crooked Island Sound, Florida, by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), and index of relative importance on a percent basis (%IRI).

Food Item	(A) YOY				(B) Juvenile				(C) Mature			
	%N	%W	%O	%IRI	%N	%W	%O	%IRI	%N	%W	%O	%IRI
Angiosperms												
Halodule wrightii					1.1	<0.1	1.3	0.1	1.8	<0.1	2.1	0.1
Thalassia testudinum					1.1	<0.1	1.7	0.1	2.7	0.1	1.0	0.1
Annelids												
Polychaeta					0.5	1.4	0.7	<0.1				
Terebellidae					0.5	0.2	0.7	<0.1				
Arthropods												
Crustacea					1.1	0.2	1.3	0.1	0.9	<0.1	1.0	<0.1
Decapoda												
Alpheidae												
Alpheus sp.					0.5	<0.1	0.7	<0.1				
Hippidae												
Emertia sp.					0.5	0.2	0.7	<0.1				
Penaeidae	1.4	0.2	1.9	0.1	0.5	0.3	0.7	<0.1				
Farfantepenaeus duorarum												
Farfantepenaeus sp.					0.5	<0.1	0.7	<0.1				
Unidentifiable decapod shrimp	1.4	0.6	1.9	0.1	4.7	0.5	6.0	1.3	1.8	0.2	2.1	0.1
Portunidae					0.5	<0.1	0.7	<0.1				
Arenaeus cribrarius	1.4	13.5	1.9	0.7								
Isopoda	1.4	0.1	1.9	0.1	1.6	0.4	1.3	0.1				
Echinoderms												
Ophiuroidea									0.9	<0.1	1.0	<0.1
Elasmobranchs												
Dasyatidae												
Dasyatis sp.					0.5	1.5	0.7	<0.1				

Table 1. Continued.

Food Item	(A) YOY %N	%W	%O	%IRI	(B) Juvenile %N	%W	%O	%IRI	(C) Mature %N	%W	%O	%IRI
Molluscs					0.5	0.1	0.7	<0.1				
Cephalopoda												
Teuthoidea												
Loliginidae	1.4	14.7	1.9	0.8	0.5	0.1	0.7	<0.1				
Loligo pealei					0.5	0.2	0.7	<0.1				
Bivalvia	1.4	<0.1	1.9	0.1	0.5	1.2	0.7	<0.1				
Gastropoda	1.4	<0.1	1.9	0.1								
Natacidae												
Sinum perspectivum	1.4	<0.1	1.9	0.1								
Platyhelminths												
Cestoda	1.4	<0.1	1.9	0.1								
Teleosts: epibenthic												
Ariidae	1.4	1.2	1.9	0.1	0.5	0.8	0.7	<0.1	0.9	0.1	1.0	<0.1
Bothidae					1.9	4.0	1.3	0.3				
Paralichthys albigutta									0.9	8.9	1.0	0.3
Cynoglossidae												
Symphurus sp.					0.5	0.1	0.7	<0.1				
Gerridae												
Eucinostomus sp.					0.5	0.3	0.7	<0.1				
Haemulidae												
Orthopristis chrysoptera					0.5	1.0	0.7	<0.1				
Ophichthidae												
Myrophis punctatus	1.4	0.2	1.9	0.1								
Sciaenidae					1.9	<0.1	1.3	0.1				
Bairdiella chrysoura					1.9	1.3	1.3	0.2	1.8	5.7	2.1	0.5
Cynoscion arenarius					1.9	7.4	2.0	0.7	4.6	3.2	4.2	1.0
Cynoscion nothus					0.9	0.4	0.7	<0.1				

Table 1. Continued.

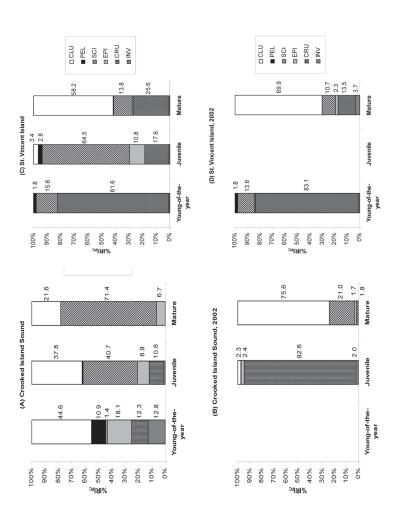| Food Item	(A) YOY				(B) Juvenile				(C) Mature			
	%N	%W	%O	%IRI	%N	%W	%O	%IRI	%N	%W	%O	%IRI
Cynoscion sp.					4.2	4.1	4.7	1.6	8.2	0.7	7.3	2.0
Leiostomus xanthurus					0.5	3.6	0.7	0.1	2.7	4.7	3.1	0.7
Menticirrhus americanus					0.5	0.3	0.7	<0.1				
Menticirrhus saxatilis					0.5	3.6	0.7	0.1				
Menticirrhus sp.					1.1	<0.1	1.3	0.1	1.8	8.8	2.0	0.7
Micropogonias undulatus	1.4	8.3	1.9	0.5	2.6	1.6	3.3	0.6	10.9	7.8	11.5	6.5
Stellifer lanceolatus					0.5	1.0	0.7	<0.1				
Sparidae					1.9	1.8	2.0	0.3	0.9	0.2	1.0	<0.1
Lagodon rhomboids	2.9	8.1	1.9	0.5	0.5	4.9	0.7	0.2	1.8	2.7	2.1	0.3
Syngnathidae	4.3	1.6	3.7	0.6	2.1	<0.1	0.7	<0.1	0.9	<0.1	1.0	0.2
Syodontidae												
Synodus foetens									2.7	3.1	1.0	0.2
Teleosts: pelagic												
Carangidae					0.5	0.3	0.7	<0.1				
Clupeidae	10.0	14.6	7.4	4.6	3.7	5.3	3.3	1.2	4.6	3.6	5.2	1.3
Brevoortia patronus					2.6	23.3	3.3	3.5	2.7	21.1	3.1	2.3
Brevoortia sp.					2.1	12.1	2.7	1.5	2.7	6.3	3.1	2.3
Harengula jaguana					1.1	2.2	0.7	0.1	0.9	1.0	1.0	<0.1
Opisthonema oglinum	4.3	10.8	5.6	2.1	4.2	4.0	1.3	0.4				
Engraulidae	4.3	2.1	3.7	0.7	0.5	0.2	0.7	<0.1				
Anchoa hepsetus					0.5	<0.1	0.7	<0.1				
Anchoa mitchilli	1.4	<0.1	1.9	<0.1								
Anchoa sp.	2.9	2.6	3.7	0.5	0.5	0.1	0.7	<0.1				
Teleosts: unidentifiable	51.4	20.7	48.2	88.3	44.2	8.7	40.7	86.9	42.7	21.7	42.7	83.1

Figure 2. Stomach contents of life stages of Atlantic sharpnose sharks based on the index of relative importance on a percent basis for the six major prey catego-ries (%IRI$_{PC}$) using stomachs with identifiable prey items > 3 in (A) Crooked Island Sound for all diet data combined (young-of-the-year (YOY), n = 37; juvenile, n = 118; mature, n = 67), (B) Crooked Island Sound for 2002 diet data only (juvenile, n = 39; mature, n = 15), (C) St. Vincent Island for all diet data combined (YOY, n = 127; juvenile, n = 15; mature, n = 42), and (D) St. Vincent Island for 2002 diet data only (YOY, n = 124; mature, n = 30). SVI data from Bethea et al. (2004). Missing life stages did not meet criterion for analysis. CLU = F. Clupeidae; PEL = other pelagic teleosts; SCI = F. Sciaenidae; EPI = other epibenthic teleosts; CRU = crustaceans; INV = other invertebrates. Prey categories <1.5%IRI$_{PC}$ are represented but not indicated with a value.

nids (mostly bothids, sparids, and syngnathids; 8.9 %IRI_{PC}). Invertebrates other than crustaceans and pelagic teleosts other than clupeids were of little dietary importance (< 2%IRI_{PC} collectively). Identifiable prey items in the diet of juveniles from the 2002 collections (stomachs with identifiable prey items > 3) were dominated by crustaceans (92.6%IRI_{PC}; Fig 2B). Epibenthic teleosts other than sciaenids, clupeids, and invertebrates other than crustaceans showed up in the diet in relatively small amounts (2.4%IRI_{PC}, 2.3%IRI_{PC}, 2.0%IRI_{PC}, respectively). Pelagic teleosts other than clupeids were not present.

Items found in mature Atlantic sharpnose shark stomachs included angiosperms (*T. testudinum*), arthropods (shrimp), echinoderms (Ophiuroidae), and teleosts (representing seven families; Table 1C). Sciaenids (mostly *M. undulatus*) dominated mature shark diets from Crooked Island Sound (71.4 %IRI_{PC}) using diet data from all years combined (Fig. 2A). Other important identifiable prey items included clupeids (mostly *Brevoortia* spp.; 21.56%IRI_{PC}) and epibenthic teleosts other than sciaenids (6.7%IRI_{PC}). Prey items of little importance included crustaceans and invertebrates other than crustaceans (<0.4%IRI_{PC} collectively). Pelagic teleosts other than clupeids were absent from mature shark stomachs. In 2002, clupeids were the most common identifiable prey category in the diet of mature sharks (75.6%IRI_{PC}; Fig. 2B) followed by sciaenids (21.0 %IRI_{PC}). Crustaceans and epibenthic teleosts other than sciaenids were of little importance in the diet (1.8 %IRI_{PC} and 1.7 %IRI_{PC}, respectively). Pelagic teleosts other than clupeids and invertebrates other than crustaceans were absent from the diet in 2002.

Cumulative Prey Curves.—Cumulative prey curves for YOY and juvenile Atlantic sharpnose sharks in Crooked Island Sound did not reach an asymptote (Fig. 3A,B), whereas the curve for mature Atlantic sharpnose sharks did (Fig. 3C). This indicates that the number of stomachs analyzed was sufficient to describe the diet for mature sharks only.

Ontogenetic and Site-Related Changes in Diet.—Spearman rank correlation coefficients indicated both ontogenetic shifts in prey types at Crooked Island Sound as well as geographic differences in diet for life-stages between Crooked Island Sound and St. Vincent Island, a neighboring site (Table 2, r_s values). Of 12 comparisons using all diet data combined, one indicated a significant similarity in diet (comparison of juvenile to mature sharks in Crooked Island Sound; r_s = 0.943, P = 0.005; Table 2A). Using only 2002 diet data (five possible combinations; Table 2B), only one indicated a significant similarity in diet (comparison of mature sharks at both locations; r_s = 0.841, P = 0.005).

Using Pianka's overlap index, half of the comparisons were higher than 0.6 when all diet data were combined (Table 2A, P_o values). Those included YOY sharks in Crooked Island Sound with both juveniles in Crooked Island Sound and mature sharks at St. Vincent Island (0.684 and 0.760, respectively) juvenile sharks in Crooked Island Sound with mature sharks at both locations (0.882 and 0.817, respectively) and juveniles at St. Vincent Island (0.782), and mature sharks in Crooked Island Sound with juveniles at St. Vincent Island (0.935). Two of five comparisons made using the 2002 diet data were considered "biologically significant." The comparisons of juvenile sharks in Crooked Island Sound to YOY sharks at St. Vincent Island and of mature sharks between both locations were above the arbitrary cutoff of 0.6 (0.987 and 0.978, respectively; Table 2B, P_o values).
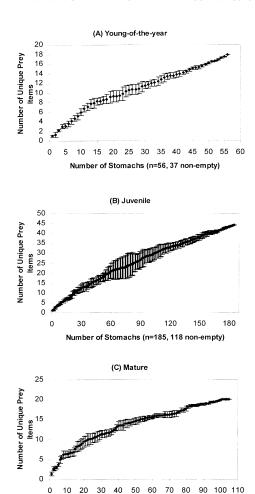
Figure 3. Randomized cumulative prey curves of Atlantic sharpnose shark (A) young-of-the-year (YOY) (n = 37), (B) juvenile (n = 118), (C) mature (n = 67) from Crooked Island Sound. Means are plotted ± SE.

Null-model simulations using all diet data combined showed low diet overlap. Of the 12 null-model simulations performed, only one was statistically different than expected. The comparison of juvenile to mature sharks at Crooked Island Sound was significantly higher than expected (0.395, P < 0.01). Simulations made using only 2002 diet data showed very low diet overlap (< 0.3) for all combinations (Table 2B, P_o* values). Only one comparison was statistically different than expected: the simulation comparing mature sharks in Crooked Island Sound to mature sharks at St. Vincent Island was significantly higher (0.287, P = 0.04).

Correspondence analysis accounted for 85.6% of the total variation among diets of maturity states at both locations using all diet data combined (Fig. 4A). Of this, axis 1 explained 46.4% and axis 2 explained 39.2%. For sharks collected at Crooked Island Sound, YOY grouped with invertebrates other than crustaceans and pelagic teleosts other than clupeids, juveniles with epibenthic teleosts other than sciaenids, and mature sharks with sciaenids. YOY sharks at St. Vincent Island grouped closely

Table 2. Spearman rank correlation coefficient (r_s), Pianka's overlap index (P_o), and Pianka's simulated overlap index based on 1000 randomizations of the diet data (P_o*) calculated from the %IRI$_{PC}$ (index of relative importance) of Atlantic sharpnose shark from two locations in the northeast Gulf of Mexico for (A) diet data from all years combined and (B) collections made in 2002 only. Life stages (YOY = young-of-the-year; JUV = juvenile; MAT = mature) in locations (CIS = Crooked Island Sound; SVI = St. Vincent Island) are compared (SVI data from Bethea et. al., 2004). Missing life stages in (B) did not meet criterion for analysis. Number of non-empty stomachs analyzed is in parentheses. Correlation coefficient (r_s) values in bold indicate significant diet similarity at α = 0.05. Overlap values (P_o) in bold indicate values over 0.6 or "biological significance" (Pianka, 1976). Simulated overlap values (P_o*) in bold indicate significance at α = 0.05.

Groups compared			r_s	P_o	P_o*
(A) All diet data					
CIS YOY (37)	/	CIS JUV (118)	−0.029	**0.684**	0.558
CIS YOY (37)	/	CIS MAT (67)	0.086	0.302	0.427
CIS YOY (37)	/	SVI YOY (127)	0.771	0.297	0.431
CIS YOY (37)	/	SVI JUV (15)	0.371	0.268	0.524
CIS YOY (37)	/	SVI MAT (42)	0.314	**0.760**	0.552
CIS JUV (118)	/	CIS MAT (67)	**0.943**	**0.882**	**0.395**
CIS JUV (118)	/	SVI YOY (127)	0.200	0.320	0.350
CIS JUV (118)	/	SVI JUV (15)	0.771	**0.782**	0.423
CIS JUV (118)	/	SVI MAT (42)	0.771	**0.817**	0.443
CIS MAT (67)	/	SVI YOY (127)	−0.086	0.183	0.263
CIS MAT (67)	/	SVI JUV (15)	0.421	**0.935**	0.333
CIS MAT (67)	/	SVI MAT (42)	0.600	0.462	0.341
(B) 2002 diet data					
CIS JUV (39)	/	CIS MAT (15)	0.319	0.049	0.223
CIS JUV (39)	/	SVI YOY (124)	−0.029	**0.987**	0.212
CIS JUV (39)	/	SVI MAT (30)	0.486	0.214	0.261
CIS MAT (15)	/	SVI YOY (124)	−0.116	0.068	0.261
CIS MAT (15)	/	SVI MAT (30)	**0.841**	**0.978**	**0.287**

with crustaceans, juveniles with sciaenids, and mature sharks with clupeids. The chi-square test for maturity state and prey category was significant (χ^2 = 493.3; P < 0.0001; df = 25), indicating dependence between life-stage and prey category. When using only 2002 diet data, correspondence analysis accounted for 99.0% of the total variation among diets of maturity states at both locations; axis 1 explained 93.2% and axis 2 explained 5.8% (Fig. 4B). For those collected from Crooked Island Sound, juveniles grouped closely with crustaceans and mature sharks grouped with sciaenids and clupeids. YOY sharks at St. Vincent Island also grouped closely with crustaceans and mature sharks also with sciaenids and clupeids. The chi-square test for maturity state and prey category was again significant (χ^2 = 305.2; P < 0.0001; df = 15), indicating dependence between life-stage and prey category.
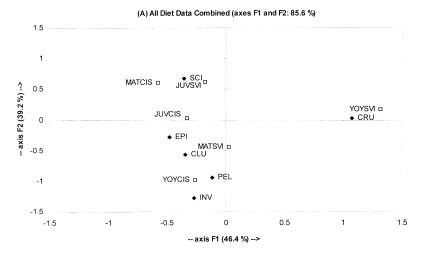
Analysis of Prey.—*Prey Diversity.*—In Crooked Island Sound, 3381 teleosts representing 45 species in 30 families were collected as potential prey in the gillnets and trawl. *Opisthonema oglinum*, *L. rhomboides*, and *Brevoortia* spp. made up ~67% of the catch in Crooked Island Sound (Table 3A). On the gulf-side of St. Vincent Island, 2519 teleosts representing 28 species in 12 families were collected as potential prey in the gillnets and trawl (Table 3B). Over 70% of the catch at St. Vincent Island was

Table 3. Numerically abundant prey species collected in (A) Crooked Island Sound, 2002–03, and (B) St. Vincent Island, 2000–02, using gillnets and trawl. N = total number caught. % = percentage of total catch.

(A) Crooked Island Sound

Species	Common Name	Small gillnet and trawl	
		N	%
Opisthonema oglinum	Atlantic thread herring	1,017	30.1
Lagodon rhomboides	Pinfish	747	22.1
Brevoortia spp.	Menhaden	494	14.6
Orthopristis chrysoptera	Pigfish	206	6.1
Arius felis	Hardhead catfish	200	5.9
Bagre marinus	Gafftopsail catfish	177	5.2
Harengula jaguana	Scaled sardine	135	4.0
Other	-	405	12.0

Species	Common Name	Large gillnet	
		N	%
Brevoortia spp.	Menhaden	500	50.1
Bagre marinus	Gafftopsail catfish	174	17.4
Arius felis	Hardhead catfish	164	16.4
Other	-	160	16.0

(B) St. Vincent Island

Species	Common Name	Small gillnet and trawl	
		N	%
Bagre marinus	Gafftopsail catfish	833	32.9
Brevoortia spp.	Menhaden	707	27.9
Chloroscombrus chrysurus	Atlantic bumper	274	10.8
Scomberomorus maculatus	Spanish mackerel	138	5.5
Anchoa spp.	Anchovies	123	4.9
Stellifer lanceolatus	Star drum	121	4.8
Arius felis	Hardhead catfish	57	2.3
Other	-	278	11.0

Species	Common Name	Large gillnet	
		N	%
Bagre marinus	Gafftopsail catfish	167	66.3
Scomberomorus maculatus	Spanish mackerel	30	11.9
Brevoortia spp.	Menhaden	22	8.7
Other	-	33	13.1

made up of *B. marinus*, *Brevoortia* spp., and Atlantic bumper *Chloroscombrus chrysurus* (Linnaeus, 1766) (Table 3B).

Potential teleost prey items in Crooked Island Sound ranged in size from 26 to 730 mm in length. Lookdown *Selene vomer* (Linnaeus, 1766) (26 mm FL), *Brevoortia* spp. (26 mm FL), and *Monacanthus* spp. (31 mm TL) were the smallest potential prey collected. The largest items collected were cobia *Rachycentron canadum* (Linnaeus, 1766) (730 mm FL), Spanish mackerel *Scomberomorus maculatus* (Mitchill, 1815) (650 mm FL), and bluefish *Pomatomus saltatrix* (Linnaeus, 1766) (540 mm FL). At St. Vincent Island, teleosts ranged in size from 28 to 1670 mm. The smallest were *S. lanceolatus* (28 mm TL), *S. vomer* (35 mm FL), and *Anchoa* spp. (39 mm FL). King
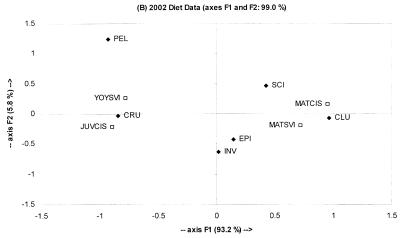
Figure 4. Plot of life stage and major prey category principal components for axis 1 and 2 of a correspondence analysis using the index of relative importance on a percent basis for the six major prey categories (%IRI$_{PC}$) for Atlantic sharpnose sharks. CIS = Crooked Island Sound; SVI = St. Vincent Island. SVI data from Bethea et al. (2004). YOY = young-of-the-year; JUV = juvenile; MAT = mature. CLU = F. Clupeidae; PEL = other pelagic teleosts; SCI = F. Sciaenidae; EPI = other epibenthic teleosts; CRU = crustaceans; INV = other invertebrates.

mackerel *S. cavalla* (Cuvier, 1829; 1670 mm FL), *S. maculatus* (635 mm FL), and *B. marinus* (600 mm FL) were the largest potential prey collected.

Predictive Equations.—Regressions relating external morphological measurements to length for major teleosts prey items found in the diet were all highly significant (P < 0.001), having r^2 values ranging from 0.83 to 0.98 (Table 4 and Bethea et al., 2004). 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.

Prey Size-Predator Size Relationships.—Length frequency distributions of *Brevoortia* spp., *C. arenarius*, *M. undulatus*, and *O. oglinum* found in stomachs were compared to the frequency distributions of lengths collected by all sampling gear for

Table 4. Least squares regression equations relating prey length to prey measurements for important teleost prey items in the diet of Atlantic sharpnose sharks in the northeastern Gulf of Mexico. FL = fork length (mm); TL = total length (mm). 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^2 values = coefficients of determination; N = number of fish measured. All regressions are highly significant (P < 0.001).

Prey species	Common name	Equation	Size range (mm TL)	Syx	r^2	N
Bairdiella chrysoura	Silver perch	TL = 3.81 (BD) + 4.14	63–190	0.05	0.84	30
		TL = 3.68 (SOL) + 10.83		0.07	0.87	30
		TL = 453.77 (TOW) + 88.07		0.06	0.89	30
Cynoscion arenarius	Sand seatrout	TL = 5.41 (BD) – 12.91	65–340	0.03	0.97	50
		TL = 3.60 (SOL) + 32.59		0.03	0.95	50
		TL = 356.65 (TOW) + 93.72	40–190	0.06	0.86	44
Lagodon rhomboides	Pinfish	FL = 2.75 (BD) + 1.11	42–180	0.03	0.94	86
Menticirrhus americanus	Southern kingfish	TL = 4.10 (BD) + 39.94	196–312	0.05	0.96	14
		TL = 977.29 (TOW) + 133.71		0.08	0.93	13
Micropogonias undulatus	Atlantic croaker	TL = 3.57 (BD) + 23.4	125–250	0.04	0.92	49
		TL = 2.73 (SOL) + 59.96		0.04	0.91	47
		TL = 277.14 (TOW) + 102.40		0.04	0.93	50
Opisthonema oglinum	Atlantic thread herring	FL = 3.08 BD + 10.26	75–215	0.01	0.94	480

both years in Crooked Island Sound (Fig. 5). Sharks showed negative size-selection for *Brevoortia* spp. (P = 0.0024), *C. arenarius* (P = 0.0016), and *M. undulatus* (P = 0.0238). Size-selection for *O. oglinum* was neutral (P = 0.1989).

Absolute prey sizes increased significantly with increasing FL for Atlantic sharpnose sharks (50th quantile, P < 0.001). In addition, both the maximum and minimum prey size consumed by Atlantic sharpnose increased significantly with increasing predator FL (90th quantile, P = 0.044; 10th quantile, P < 0.001; Fig. 6). Atlantic sharpnose sharks in Crooked Island Sound consumed prey that were small fractions of their length; ~98 % of all prey taken were < 40% of shark length. However, sharks more frequently consumed prey 21%–40% of shark length (relatively moderate-sized prey, 68.5% of all prey) than prey ≤ 20% of shark length (relatively small-sized prey, 25.5% of all prey; Fig. 7).

Discussion

Feeding Habits.—Diet of Atlantic sharpnose shark varied depending on where they were collected. In Crooked Island Sound, clupeids were important in the diet of all three life-stages. Additionally, YOY fed on invertebrates (mostly molluscs and arthropods) and epibenthic teleosts, juveniles fed on several different species of sciaenid, and mature sharks fed on mostly *Cynoscion* spp. and *M. undulatus*. In contrast, crustaceans (particularly shrimp) were important in the diet of all three life-stages at St. Vincent Island (Bethea et al., 2004). YOY also fed on *M. undulatus*, juveniles on silver seatrout *Cynoscion nothus* (Holbrook, 1855) and *S. lanceolatus*, while mature sharks supplemented their diet with *Brevoortia* spp. Geographic differences in diet have been documented in lemon shark *Negaprion brevirostris* (Poey, 1868) (Cortés and Gruber, 1990), sandbar shark *C. plumbeus* (Nardo, 1827) (Ellis, 2003), and starspotted smoothhound *Mustelus manazo* (Bleeker, 1854) (Yamaguchi and Taniuchi, 2000). Geographic differences in diet in the present study are most likely due to
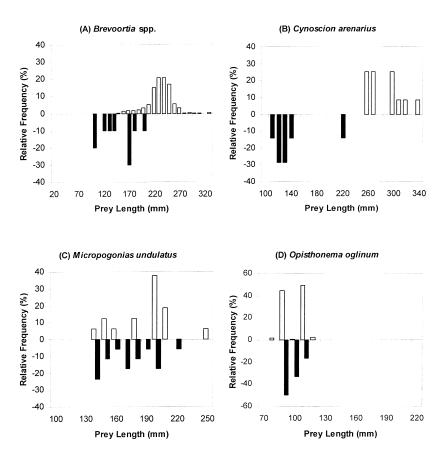
Figure 5. Size frequency distributions of teleost prey species found in Crooked Island Sound (positive y-axis) and in shark stomachs (negative y-axis). (A) *Brevoortia* spp. (positive n = 494, negative n = 10), (B) *Cynoscion arenarius* (positive n = 12, negative n = 7), (C) *Micropogonias undulatus* (positive n = 16, negative n = 17), and (D) *Opisthonema oglinum* (positive n = 1017, negative n = 6).

associations between life-stage, habitat, and prey availability. For example, potential prey species usually associated with seagrass beds; e.g., *L. rhomboides*, pigfish *Orthopristis chrysoptera* (Linnaeus 1766), were found in the diets and collected in relatively high numbers in Crooked Island Sound but not at St. Vincent Island. Likewise, schooling pelagic teleosts (e.g., *Anchoa* spp., *Brevoortia* spp.) and invertebrates associated with hard or muddy substrates (e.g., adult *Farfantepenaeus* spp.) were more commonly found in the diets and collected on the gulf side of St. Vincent Island (Bethea et al., 2004).

Ontogenetic diet shifts in prey type are common in sharks (see Wetherbee and Cortés, 2004 and references therein). In this study, YOY and juvenile sharks in Crooked Island Sound shifted from feeding on epibenthic teleosts and invertebrates to almost exclusively sciaenid teleosts when mature. YOY at St. Vincent Island shifted from a diet consisting almost exclusively of invertebrates to feeding on epibenthic teleosts as juveniles, and then to mostly pelagic teleosts when mature (Bethea et al., 2004). Ontogenetic diet shifts in prey type are most likely due to larger Atlantic sharpnose
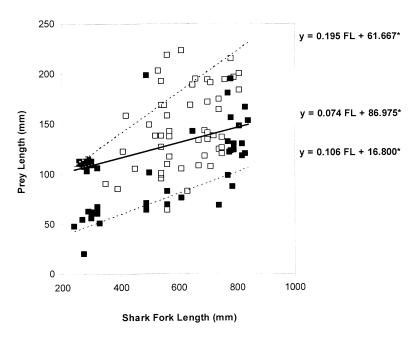
Figure 6. Prey size-predator size scatter diagram for Atlantic sharpnose shark (n = 108) in the northeastern Gulf of Mexico. Lines represent quantile regressions used to examine changes in prey size eaten with increasing shark size. (__) = median prey size (50th quantile). (…) = minimum and maximum prey sizes (10th and 90th quantiles). Each symbol is a single teleost prey eaten by a shark. Open squares are prey taken in Crooked Island Sound. Closed squares are prey taken at St. Vincent Island (Bethea et al., 2004). PL = prey length in millimeters, FL = shark fork length in millimeters. *Indicates significance at P < 0.05.

sharks being able to capture faster, more pelagic, or larger prey. Bethea et al. (2004) proposed an upper bound to the sizes of prey that Atlantic sharpnose sharks can take.

There are two main restrictions to diet analyses performed in this study. First, analyses were performed using identifiable prey only (%IRI$_{PC}$ values). Unfortunately, a majority of Atlantic sharpnose shark diet in Crooked Island Sound was unidentifiable teleost remains (YOY 88.3%IRI; juveniles 86.9%IRI; mature 83.1%IRI). The large discrepancy of unidentifiable teleosts in the diet between sharks collected in the current study and from St. Vincent Island may be related to prey diversity at each location; 45 different potential prey species were collected in gillnets and trawls at Crooked Island Sound as compared to 29 different species at St. Vincent Island. The time of day that samples were collected may also affect the outcome of identifiable items in the diet. Even though the majority of sampling at both locations occurred between 0700 and 1500 hrs CST, sharks at different locations may feed at different times of day. Atlantic sharpnose sharks in Crooked Island Sound could be captured at opposing times than they were feeding, thus showing more unidentifiable teleost remains in their diet and/or empty stomachs. Bethea et al. (2004) reported higher catches of Atlantic sharpnose sharks at night at St. Vincent Island, but only one overnight sampling trip was made to Crooked Island Sound with no clear increases in catch rates. Excluding a large portion of the diet from analysis may have had an effect on the diet comparisons drawn between sharks in Crooked Island Sound (the current
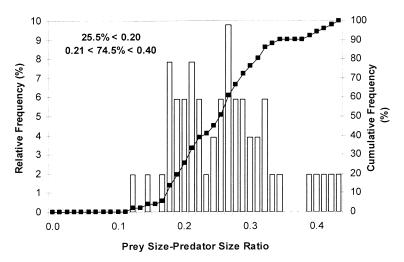
Figure 7. Relative frequency distributions of prey size-predator size ratios for Atlantic sharpnose sharks in Crooked Island Sound (n = 50). Open bars = relative frequencies at 1% intervals of prey size-predator size ratios. Filled squares = cumulative frequencies at 1% intervals.

study) and St. Vincent Island (Bethea et al., 2004); however, we assumed that unidentifiable prey made up the same proportions in the diet as identifiable prey. In the future, extensive sampling should be performed over the entire 24 hr cycle to insure that sharks with freshly eaten prey are collected; this would also aid in determining the diel feeding periodicity for the Atlantic sharpnose shark.

The second caveat to our diet analyses is the possible influence of temporal differences on the diet data. To address this, comparative diet analysis was performed using all diet data combined and diet data from collections made when sampling at both areas overlapped. Striking differences can be seen when comparing the overall diet data to the 2002 diet data for sharks in Crooked Island Sound; clupeids were almost absent from the diet of juveniles and the two most important prey categories in the diet of mature sharks (sciaenids and clupeids) were reversed. Analysis of the 2002 diet data was restricted to life-stages where at least three stomachs contained identifiable prey. As a result, YOY sharks were excluded and sample sizes were small for the other two life-stages (juveniles, n = 39 non-empty stomachs; mature, n = 15 non-empty stomachs). The differences in diet could also be due to the larger and possibly more dynamic prey base at Crooked Island Sound (mentioned above). A more diverse prey base may also explain why two out of three cumulative prey curves did not reach a stable asymptote even though more stomachs were analyzed from this location (n = 346, 222 non-empty stomachs compared to n = 300, 185 non-empty stomachs in Bethea et al., 2004). However, by pooling diet data over multiple years, a year effect (with differences in sample sizes) may confound site effects.

Prey Size-Selection.—Size-selective feeding has not been well studied for sharks. Bethea et al. (2004) performed size-selectivity tests for Atlantic sharpnose sharks at St. Vincent Island, finding negative size-selection for both *M. undulatus* and *S. lanceolatus*, but neutral size-section for *Brevoortia* spp. In this study, sharks in Crooked Island Sound exhibited clear negative size-selective feeding for two of their four main prey items; *Brevoortia* spp. and *M. undulatus*; negative size-selective feeding on *C. arenarius* was likely biased due to low sample size and the inability of the

gear to catch the prey sizes sharks consumed. The negative size-selection observed at both sites may be another indicator of the upper bound to sizes of prey that Atlantic sharpnose sharks can take.

While the absolute prey size consumed by Atlantic sharpnose sharks increased significantly with increasing shark size, the range of absolute prey increased only slightly. This pattern was also seen for Atlantic sharpnose sharks at St. Vincent Island (Bethea et al., 2004). Scharf et al. (2000) found that the range in absolute prey sizes increased dramatically with increasing predator size for 18 piscivores, including four elasmobranchs. Ontogenetic differences in median prey size eaten by Atlantic sharpnose sharks were probably due to increases in maximum and minimum prey size consumed.

Diet of Atlantic sharpnose sharks studied consisted of relatively intermediate prey (21%–40% of shark length). Scharf et al. (2000) found that over 75% of the elasmobranch diets examined consisted of prey that were < 20% of their length. The percentage of small-sized prey in the diet of Atlantic sharpnose sharks in Crooked Island Sound was considerably less than that of Atlantic sharpnose, blacktip, and finetooth sharks from St. Vincent Island (Bethea et al., 2004) and smooth dogfish *Mustelus canis* (Mitchill, 1815), spiny dogfish *Squalus acanthias* (Linneaus, 1758), and winter skate *Raja ocellata* (Mitchill, 1815) on the northeast U.S. continental shelf (Scharf et al., 2000). Frequency distributions of prey size-predator size ratios of Atlantic sharpnose sharks in Crooked Island Sound do not compare well with any teleost predators in general (Scharf et al., 2000).

Nursery Value.—Crooked Island Sound and the Apalachicola Bay system (e.g., St. Vincent Island) have been hypothesized to serve as nursery areas for Atlantic sharpnose sharks in the northeast Gulf of Mexico (Carlson, 2002). Quantitative examination of feeding ecology from different proposed nurseries is one way to begin to understand how juvenile sharks use nursery habitats and determine which habitat types have higher "nursery value" than others (sensu Beck et al., 2001). YOY Atlantic sharpnose sharks have very different diets depending on area, which could affect growth. Based on the metabolic rate of the similarly-sized blacknose shark *Carcharhinus acronotus* (Poey, 1860) (Carlson et al., 1999) and assuming 27% of consumed energy is lost as waste (Wetherbee and Cortés, 2004), a 0.9 kg YOY Atlantic sharpnose shark feeding on clupeids in Crooked Island Sound would have to eat 2.6% of its body weight per day just to maintain its weight. The same shark occupying the Apalachicola Bay system and feeding on a diet primarily of shrimp would have to eat 5.2% of its body weight per day to maintain its weight. Thus, sharks in the Apalachicola Bay system may require higher ration levels to fulfill energetic need. This could translate into less energy available for growth if consumption rates are not maintained. Although this is a simplified model of an energy budget, preliminary evidence suggests Crooked Island Sound provides a greater "nursery value" (Beck et al., 2001) than St. Vincent Island and the Apalachicola Bay system. Further studies on growth and survival of juvenile sharks are required to test this hypothesis.

assistance with the design of the project. The trawl was borrowed from B. Thompson in the Coastal Fisheries Institute at Louisiana State University. E.A. Dutton designed and wrote the program used to calculate cumulative prey curves. Opinions expressed herein are of the authors only. Reference to trade names does not imply endorsement by NOAA Fisheries.

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